Hybridisation and Behavioural Variation: A Socio-Ecological Study of Hybrid Gibbons (*Hylobates agilis albibarbis x H. muelleri*) in Central Kalimantan, Indonesia

by

Samantha Bricknell

A thesis submitted for the degree of

Doctor of Philosophy

Department of Archaeology and Anthropology

AUSTRALIAN NATIONAL UNIVERSITY

April 1999

Except where otherwise indicated, the work presented in this thesis is entirely my own.

Samantha Bricknell

Samantha Bricknell
Department of Archaeology and Anthropology
Australian National University
20 April 1999

Abstract

The Barito Ulu watershed in Central Kalimantan is one of three known gibbon contact zones in South-East Asia and one of two sites where hybridisation between different species of gibbon has occurred, in this case between *Hylobates agilis albibarbis* and *H. muelleri.* Following previous studies on hybrid primates (e.g. baboons, macaques) which found evidence of behavioural differentation between hybrid forms and the parental species, an intensive 12 month socio-ecological study was conducted with hybrid gibbon groups residing in the vicinity of Muara Rekut in order to ascertain if hybridisation exerts any influence on gibbon social and/or ecological behaviour. Data on six primary behavioural parameters – activity pattern and budgeting, feeding ecology, home range use, patterns of territorial display and inter-group encounter behaviour, intra-group social relations and social composition, and song repertoire and singing behaviour – was collected and compared to the behaviour described for the parental species (*Hylobates agilis* and *H. muelleri*), other species of the lar group, and gibbons as a whole.

Albibarbis x *muelleri* hybrid gibbons demonstrated a basic socio-ecological repertoire similar to that described for both the parental species and other lar group gibbons but also displayed behavioural anomalies not yet, or only reported for one or two, gibbon populations. While some of these behavioural anomalies can be explained by referring to site-specific environmental and ecological factors, others, such as song structure, can not, and are proposed to be primary consequences of hybridisation. Some unusual traits (e.g. fruit choice), however, are difficult to unconditionally attribute to hybridisation and require comparative studies on parental populations living adjacent to the hybrid zone.

Potential secondary consequences of hybridisation are also investigated employing a hypothesis that alteration to the manifestation of one behaviour can, theoretically, induce changes in the manifestation of another. Examples of secondary consequences discussed include unusual social composition, pair bond stability, depression of territorial conflict, and improved feeding strategies. How these observed or proposed consequences affect the "success" of the *albibarbis* x *muelleri* hybrid population is examined in relation to various demographic indices such as reproductive potential. No uniformly positive or negative effect could, however, be discerned and, in turn, failed to explain the low reproductive rate exhibited by the hybrid population.

Table of Contents

List of Figures

List of Tables

Acknowledgments

The four and a half years I have spent researching and writing this thesis could not have been completed without the dedication, help, patience and support I have received from a great many people, both in the field and during the production phase of the thesis. To the following people, I extend my most sincere and heart-felt gratitude.

Fieldwork

To the Indonesian Institute of Sciences (LIPI) and the Department of Forestry for providing permission and research visas to conduct fieldwork in Indonesia.

To Rupert and Diana Ridgeway for their provision of logistical support while I was based at the Muara Rekut basecamp. Cheers also to Rupert, Diana and their daughter Rosie for creating memorable Christmas and New Years Eve's parties!

To the PBU workers - Surian, Nurdin, Kursani and Mulyadi - and their families - who were my neighbours and friends for my 12 months in the field. I especially thank my field guides, Kursani and Mulyadi, for their patience and dedication while assisting me in the collection of research data.

To Allan Williams who stayed for the long haul and who helped me with every aspect of fieldwork and camp life. I am indebted to you for your support, particularly during my illness and when the trials of living in a remote location became just a little too hard to bear. And thanks also for those great rice and cornbeef pies!

To fellow PBU researchers or visitors - Angela, Eric, Lazlo, Marija, Vera, Stuart, Tom, Frank and Jim - for the laughs, the tuak drinking,, and their much appreciated company . Thanks also to Lazlo for helping me with food species identifications and provision of vegetation plot databases and Stuart for allowing me to use his computer facilities when in Jakarta.

To the various people I met while travelling the Barito and Busang rivers or staying in Balikpapan and Banjarmasin. In particular I would like to thank Cendiana in Banjarmasin for assisting me in the collection and transport of supplies up to Muara Rekut (the bottle of Johnnie Walker was a nice surprise!), "Mr Hotel Muara Teweh" who allowed me to store said groceries at his hotel until river levels were conducive for hauling heavy *barang* up river, and Wahab for his humour and conversation while convalescing in Balikpapan.

To SOS Medika for efficiently organising my medi-vac from basecamp and the medical staff of the Women's Rumah Sakit in Balikpapan for looking after me so well during my stay there.

Pre- and post-fieldwork

To my supervisor, Dr Colin Groves, who inspired me as an undergraduate to work with primates and who has provided me with unsurpassed support and encouragement every step of the way.

To my adviser, Dr David Chivers, who allowed me to work with the hybrid gibbons at Barito Ulu and gave important advice on data interpretation.

To Dee Robbins for providing me with her data on Müller's gibbon.

To Drs Thomas Geissmann, Joe Marshall, Sompoad Srikosamatara and, in particular, Ulrich Reichard, for diligently responding to my questions on various aspects of gibbon social and singing behaviour.

To my colleagues Andrew Collis and Joanne Harding who read various chapters and offered good constructive criticism (even if I fought against it at the time!) over many cups of coffee at the salubrious Calypso Coffee Lounge.

To the administrative staff of the Department of Archaeology and Anthropology - Kathy Callen, Halim Gadji and Sue Fraser - for assisting me with desperately needed background tasks.

To Vance Merrill and Sophie Holloway who so very kindly gave me a job and a flexible work time-table when the scholarship ran out, providing me with the much needed money and time to complete the dissertation.

On a more personal level I would like to thank:

My friends, who provided me with the all-important time-out, allowing me to relax and forget every now and again about hybrid gibbons. Friends I would particularly like to salute include Lisa Stone, Melissa Wood, Rachel Clements, Liz Keith, Kathy Callen, Annie Evans, Sophie Holloway, Kevin May, Tim Denham, Tom Knight, Ben Evans, Joanne Harding and Andrew Collis. Two friends - Katie Willis and Kim McConkey - however, deserve special mention. Katie and Kim provided extraordinary encouragement of which I am deeply appreciative. Big cheers also to Kim for reading and passing comment on my work and sending me the Rekut data essential for the thesis.

And my family – My brother Stephen who diverted me from thesis stress with his unique sense of humour and for being the only person (I thank you!) for not asking me the eternal question "So, how's the thesis going?". And my parents, Brick and Janice Bricknell, who have been a constant and unfailing source of strength and love. Thanks must also be given to Dad who interpreted my garbled instructions to create the diagrams found in this thesis.

1

Introduction

1.1 Phylogeny and taxonomy of the Hylobatidae

1.1.1 An overview

Gibbons occupy the superfamily Hominoidea with the great apes (*Pongo, Gorilla* and *Pan*) and *Homo* but are separated into their own family, the Hylobatidae (Szalay and Delson, 1979), based on characteristics of social behaviour and locomotor (brachiation) specialisation, and the retention of certain primitive cranial and post-cranial characters (Groves, 1972; Andrews and Groves, 1976). According to Cronin et al. (1984) divergence from the hominoid line occurred approximately 13 - 15 million years BP with radiation into the existing lineages beginning around 4 - 5 million years ago. Goodman et al. (1998) place the date of divergence earlier, at around 18 million years ago.

Phylogenetic reconstructions based on chromosomal, morphological and behavioural traits (e.g. Groves, 1972; Creel and Preuschoft, 1976; 1984; Chivers, 1977a; van Tuinen and Ledbetter, 1983; Haimoff et al., 1984) have produced somewhat different interpretations of the phylogenetic relationship between gibbon taxa but a general trend was agreed upon. First to speciate were the siamang (subgenus *Symphalangus*, with a single species, *Hylobates syndactylus*) and the concolor group gibbons (*Nomascus*), followed by the hoolock (*H. hoolock)* and Kloss gibbon (*H. klossii*), and then the quite recent divergence of the lar group gibbons. Recent phylogenetic studies incorporating analysis of DNA sequences (Garza and Woodruff, 1992; Hayashi et al., 1995; Hall et al., 1996) have failed to find such a clear-cut sequence. Hall et al. (1996) have proposed that a polychotomous divergence best characterises the radiation of the Hylobatidae while Garza and Woodruff (1992) have suggested that the subgenera *Symphalangus*, *Nomascus* and *Hylobates* either radiated simultaneously or only did so over a short period of time. These three studies also question the previously held assumption that *klossii* radiated separately from the lar group. Each found *klossii* to be an "integral part" (Garza and Woodruff, 1992) of the lar group although there was disagreement as to which species *klossii* was more closely related to.

Since the first species, *Hylobates lar,* was described by Linnaeus in 1771, the classification of gibbons has undergone consistent modification, with taxonomists disputing the number of genera, subgenera and species. Hylobatids are now largely recognised as comprising one genus i.e. *Hylobates*, and divided into at least three subgenera – *Symphalangus, Nomascus* and *Hylobates.* In 1983, Prouty et al., using karyotypic data, proposed that the hoolock gibbon, which had held a somewhat tenuous position within *Hylobates,* be transferred to its own subgenus – *Bunopithecus* – a proposal supported by Groves (1984).

Symphalangus and *Bunopithecus* are monotypic, represented by the siamang (*H. (S). syndactylus*) and the hoolock gibbon (*H. (B). hoolock*) respectively. Siamang live in Sumatra and peninsular Malaysia (see Figure 1-1 for distribution of gibbon species) and some morphological differences exist between the two populations, primarily in the size of the body, molar cingula and M_3^3. This variation, however, is marginal according to Groves (1972; 1984) and the validity of geographic subspecies tenuous at best. The range of the hoolock gibbon covers Burma and parts of Bangladesh and Assam, extending from the Brahmaputra river in the west to the Salween river in the east (Groves, 1967). Two races – *H. hoolock hoolock* and *H.h.leuconedys* – have been recognised by Groves (1967) and confirmed by Marshall and Sugardjito (1986), distinguished by colouration of the genital tuft and back, degree of separation of the white (eye) brows, and skull morphology. The Chindwin river in Burma separates the two races with some evidence of interbreeding at the river's headwaters (Groves, 1967).

Figure 1-1 Distribution of gibbon species in Asia.

The remaining two subgenera – *Nomascus* and *Hylobates* – are composed of a number of forms whose classification remains problematic. The *Nomascus* gibbons were originally confined to one species (Groves, 1972) but Dao (1983), Ma and Wang (1986), Ma et al. (1988) and Groves and Wang (1990) have since separated them into three species – *H. (N). concolor, H. (N.) leucogenys* and *H. (N). gabriellae.* Differential morphology, in particular the shape of the baculum, and hair colour and thickness, was used by these authors to differentiate taxa. Subspecies have been described for both *H. concolor* and *H. gabriellae* (Groves and Wang, 1990; Groves, 1993).

An extensive array of shared and distinctive craniological, postcranial, external and karyological features (see Groves, 1984) defines the fourth sub-genus, *Hylobates*. Within the subgenus itself, a division based on primitive/derived characteristics separates the Kloss gibbon, restricted to the Mentawai Islands, from the remaining taxa (Groves, 1972; 1984), collectively and commonly referred to as the lar group gibbons. Hayashi et al. (1995) contend that *klossii* is more closely related to *lar* whereas both Garza and Woodruff (1992) and Hall et al. (1996) propose the *muelleri-pileatus* group as the sister clade.

Five differential lar group forms cover much of the Sunda shelf, consolidated into allopatric populations separated by wide river systems or straits. PPED (plasma protein electrophoretic distance) unit analysis has detected only a small degree of genetic divergence between these allopatric forms. This suggested to Cronin et al. (1984) that lar group gibbons either radiated quite recently (no later than 1.0 - 0.5 million years B.P.) or are not clearly separated but rather rated as semi- (or even sub-) species. Anatomically, the lar group are markedly similar with "considerable overlap" in cranial morphology (Creel and Preuschoft, 1976; 1984) and only "weak differences" in the postcranial skeleton (Groves, 1984). But distinct dental, external and behavioural differences do exist (Frisch, 1965; Marshall and Marshall, 1976; Chivers, 1977a; Groves, 1984; Haimoff et al., 1984; Marshall and Sugardjito, 1986), in particular the colouration and pattern of the pelage, and structure of male- and female-typical song phrases. Pelage and song are regularly employed tools in the discrimination of *agilis, lar, moloch, muelleri* and *pileatus*.

Disagreement as to which characteristics are appropriate for the elevation of taxa to specific status has continually frustrated any general consensus on the taxonomic position of the lar group gibbons. For example, Creel and Preuschoft (1976; 1984) insist that only cranial evidence is "adequate" and therefore recognise just the one species – *H. lar* – assigning the remaining four taxa (*agilis, moloch, muelleri* and *pileatus*) to the level of subspecies. In contrast, Haimoff et al. (1984), following Schultz (1933) and supported by Marshall and Marshall (1976) and Marshall and Sugardjito (1986), recognise five full species. Haimoff et al. (1984) warn against classification systems that are limited to anatomical data and promote the use of morphological and behavioural traits as well (for a list of these see Haimoff et al., 1984 p 629). Other scholars have accepted some pelage and song differences but omitted others, resulting in a classificatory compromise of two (Napier and Napier, 1967; Groves, 1972) and four species (Groves, 1984).

1.1.2 The status of the Bornean gibbons - one species or two?

Pertinent to this study is the taxonomic relationship existing between the two hylobatid forms found in Borneo. Occupying the greater part of the island is the endemic *Hylobates muelleri* or Müeller's gibbon. Its range, starting in the north-west, extends in a clock-wise direction around the island, terminating in the south-east (see Figure 1-2). Three races are recognised which intergrade into one another on their boundaries and are distinguished by overall colour and the presence or absence of black hands and feet (Marshall et al., 1984; Marshall and Sugardjito, 1986). In south-eastern Borneo is found *H.m.muelleri* which is mostly pale grey with a white brow and black colouration on the cap, venter, hands and toes. Further north, just above 2° degrees latitude and separated from *muelleri* by the Kerangan river (Medway, 1977), is *H.m.funereus*, also grey, with a black cap and venter and white brows, but tending not to have blacks hands or feet. Marshall and Sugardjito (1986), however, found no major differentiation in pelage colouration between *muelleri* and *funereus* races. Towards the west of the island resides *H.m.abbottii*, which is more uniformly mouse-grey or pale brown with occasional black colouration on the throat.

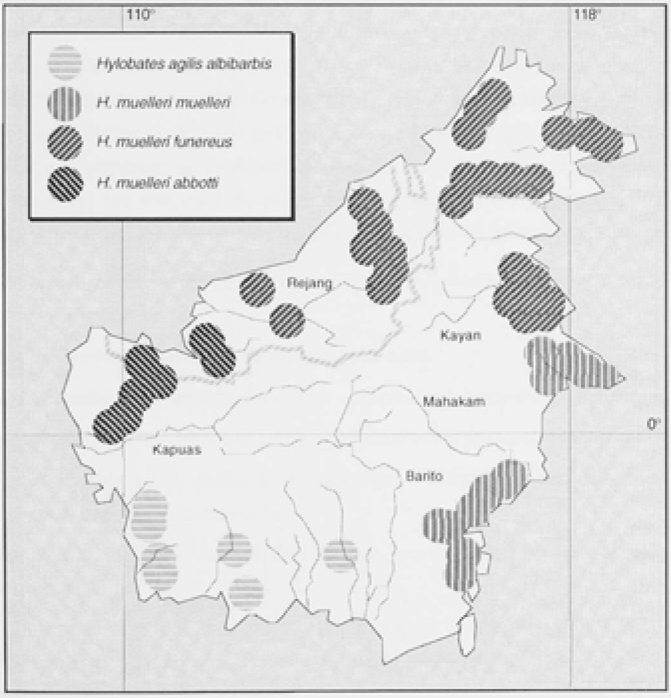


Figure 1-2 Distribution of *Hylobates agilis albibarbis* and subspecies of *H. muelleri* in Borneo. (Area shaded relates to site locations of museum specimens examined by Marshall and Sugardjito, 1986).

Replacing *muelleri* in south-western Borneo, specifically south of the Kapuas and west of the Barito rivers, is *H. agilis albibarbis*. *H.a.albibarbis* are a greyish brown colour with a golden buff rump and corona, dark brown cap and black-brown venter and inner limbs (Marshall et al, 1984; Marshall and Sugardjito, 1986). Males have white brows and white or cream cheek patches which are joined at the throat to resemble a beard. Females too have white brows, which are arched and separated, and occasionally patches of white hair on the cheeks. *H.a.albibarbis* produce a call, and in particular a great call, which is quite unlike that characteristic for *muelleri* but identical to the songs given by *agilis* in Sumatra and peninsular Malaysia (Marshall and Marshall, 1976; Marshall et al., 1984; Marshall and Sugardjito, 1986). Based on their vocal repertoire, the south-western population are considered a Bornean representative of *agilis* rather than a fourth racial form of *muelleri (*Marshall and Marshall; 1976; Medway, 1977; Chivers and Gittins, 1978; Marshall et al., 1984; Marshall and Sugardjito, 1986). *H. agilis* was one of the many colonisers which probably crossed into Borneo during the last Pleistocene glacial (Bodmer et al., 1991). The resident population are now distinct from their Sumatran and Malaysian conspecifics in various aspects of both coat colouration and pattern and have hence been assigned to the status of subspecies: *Hylobates agilis albibarbis*.

Groves (1971; 1984) has questioned this taxonomic placement, suggesting that the differences in pelage between *albibarbis* and *muelleri* are no greater than those observed between the three races of *muelleri*. Furthermore, *albibarbis* shares external characters with *muelleri* of which none can be "confused" with *agilis* (Groves, 1984). How then to classify an animal which is morphologically similar to *muelleri* but produces a call identical to *agilis*? Groves (1984) contends that it is inappropriate to allocate *albibarbis* to *agilis* on the strength of one character state (i.e. the song) but concedes the difficulties in evaluating the importance of call versus morphology when assigning taxonomic categories. A number of options were thus proposed:

1. that *albibarbis* is synonymous with *muelleri* – call structure can not be used to assign sub-specific status
2. that *albibarbis* and *muelleri* are distinct, with either:
    a. *albibarbis* a subspecies of *muelleri* – morphology is the critical taxonomic tool
    b. *albibarbis* a subspecies of *agilis* – call structure is the critical taxonomic tool
    c. *albibarbis* a full species in its own right – morphology and call structure are of equal importance in taxonomy
3. that *agilis, albibarbis* and *muelleri* are one species, either separate from *lar* or as a subspecies of *lar*

Groves (1984) prefers options 2c and 3, arguing that until calls can be shown to be of greater taxonomic significance compared to pelage colour, or *vice versa,* options 1, 2a and 2b remain weak at best.

The importance of pelage and song in species recognition has still not been resolved nor has the taxonomic status of *albibarbis* been verified. However, song play-back experiments in which gibbon pairs were exposed to the songs of con- and heterospecifics indicated that gibbons do use song to some extent to discriminate between like and unlike (Raemaekers and Raemaekers, 1985; Mitani, 1987a). Of particular significance are the results from Mitani's (1987a) experiment that found that male *albibarbis* in West Kalimantan tended to respond more aggressively to male solos performed by either local conspecifics and Sumatran *agilis* than those delivered by male Müller's gibbons. Thus in the absence of additional data directly relating to gibbon species recognition, and taking into account the results obtained from song play-back experiments, *albibarbis* will be considered as taxonomically distinct from *muelleri*, either as a full species or subspecies of *agilis*.

The existence and consequence of contact zones between two largely allopatric populations introduces a cogent method for the interpretation of problematic taxonomic groups. Of particular importance is the incidence of hybridisation. If little or no hybridisation is occurring at the point of contact, then it is probable that the contact groups represent distinct species. But if the two are intergrading, and hybrid forms comprise a unique and viable component of the population, then awarding full specific status to the hybridising taxa would contradict species definitions derived from the Biological Species Concept (Mayr, 1963; Paterson, 1985; Templeton, 1989; Mayr and Ashlock, 1991). A contact zone between *albibarbis* and *muelleri* was discovered by Marshall and Markaya in 1979 (Brockelman and Gittins, 1984; Marshall et al, 1984; Marshall and Sugardjito, 1986) with formal analysis of the extent of intergradation conducted by Robert Mather (1992). Before the extent and nature of the zone is described, and its bearing on the relationship between *albibarbis* and *muelleri*, theories on hybridisation and the maintenance of hybrid zones will be summarised.

1.2 Hybridisation

1.2.1 Hybrids and the formation of hybrid zones

1.2.1.1 Definitions of hybridisation

Hybridisation is effectively a process by which two normally distinct populations intergrade. While considerably more common in plants (Grant, 1963) or in animals (e.g. fish) which reproduce using an external form of fertilisation (Hubbs, 1955), it is not unknown in higher animals (see Gray, 1971). But what constitutes distinctive populations often depends on the interpretations of the theorist. In defining hybridisation as "the crossing of individuals belonging to two unlike natural populations that have secondarily come into contact", Mayr (1970) remained vague as to his interpretation of "unlike" but did indicate that hybridising populations had to have experienced isolation some time in the past. Stebbins (1959) suggested that hybridisation did not just occur between different species but could also be induced through the secondary contact of conspecific populations which had diverged in allopatry. He thus defined the process as the "crossing between individuals belonging in separate populations which have different adaptive norms". Harrison (1990; 1993) has criticised these, and other definitions, primarily because they incorporate a subjective determination as to what represents distinct and what does not. To remove this subjective component, hybridisation becomes the "interbreeding of individuals from two populations or groups of populations which are distinguishable on the basis of one or more heritable characters" (Harrison, 1990, modified from Woodruff, 1973). The use of an operational definition, such as that proposed by Harrison, introduces a means by which the study of hybridisation is simplified. It removes the need for a universal agreement on a single species concept, the assignment of populations to taxonomic groups, and a judgement on the fitness of hybrids and/or parental differences in terms of "adaptive norms" (Harrison, 1993).

Hybridisation arises from both primary and secondary episodes of intergradation. Primary contact hybridisation is represented by a "series of intermediate populations connect(ing) two subspecies" and responsive to environmental gradients (Mayr and Ashlock, 1991). These series of populations intergrade clinally with each population occupying an intermediate position in relation to adjacent populations. Secondary intergradation occurs when a previous barrier to gene flow is either broken down or neutralised, allowing the two populations to meet and inter-breed. Hybridisation resulting from secondary contact is often attributed to either habitat disruption or some form of environmental or geographical change. Largely due to human activity, and in particular the implementation of intensive agricultural practices, habitat disturbance acts to modify or destroy geographic or ecological barriers which have previously isolated populations (Stebbins, 1950; Mayr, 1963). Changes in range distribution, through contraction followed by re-expansion, may also precede hybrid events. Many of these are supposed to have occurred during the Pleistocene and post-Pleistocene periods, both in temperate areas (Hewitt, 1989; 1993) and tropical regions (Prance, 1982).

1.2.1.2 What is a hybrid and hybrid zone?

The terms hybrid and hybrid zone (see below) suffer from the same inconsistencies in definition as those plaguing the concept of hybridisation. A purist's interpretation would certainly regard only first generation (F_1) offspring, produced from *inter*-population crosses, as true hybrids (e.g. Anderson and Hubricht, 1938). The composition of most hybrid zones, however, rarely includes just F_1 individuals but rather a variable proportion of F_1 and backcross (F_2..F_x) forms (i.e. recombinant types). Harrison (1993) has proposed that a hybrid is better described as an individual of mixed ancestry. This interpretation allows both the recognition of first generation and back-crosses as legitimate members of the hybrid community and acknowledges that hybrids can be produced *within* and not just *between* populations.

The patterns of genotypic forms produced in the hybrid zone resemble geographic gradients or clines, leading to some interchangeability between the terms *hybrid zone* and *cline* in the literature (Barton and Hewitt, 1985). The extent and nature of the hybrid zone covers a range of clinal types, depending on the limits of definition and including:

- narrow or steep clines (Mayr, 1963; Key, 1981)
- multiple coincident clines (Bigelow, 1965; Short, 1969; Woodruff, 1973; Endler, 1977)
- chromosomal and climatic clines (e.g. Hewitt and Barton, 1980; Halliday et al., 1983)
- clines wider than the normal dispersal distance of the organism (e.g. Smith et al., 1983; Smith and Patton, 1984; Patton, 1993)

According to Barton and Hewitt (1985), this hotchpotch of definitions has led to "irretrievable" confusion with possible allocation of terms to contact areas which are neither clinal nor true hybrid zones. To counteract the confusion, they have proposed a simple, all encompassing definition for the hybrid zone; that is "a gradient or set of gradients in morphology or gene frequency, at one or more loci".

1.2.1.3 Origins of hybrid zones

The hybrid zone is thought to arise when two populations, which originally differentiated in allopatry, experience secondary contact (Mayr, 1942). In the absence of historical evidence, however, the origin of the zone and what influenced its formation is difficult to predict since primary and secondary intergradation produce identical patterns of variation (Endler, 1977). An alternative scenario postulates an *in situ* origin, responsive to spatially varying selection pressures or environmental gradients (Endler, 1977). Although Clarke (1966), Slatkin (1973) and Endler (1973; 1977) have developed models which show that geographic barriers are not an essential prerequisite to the formation of even very steep clines, most hybrid zones, at least in temperate areas, are postulated by more recent arguments to be probably the result of secondary contact (Hewitt, 1979; 1985; 1988; 1989; Hewitt and Barton, 1980; Barton and Hewitt, 1989). An analysis of 150 plus hybrid zones by Barton and Hewitt (1985) found that, despite the varying width of these zones, many exhibited multiple clines (i.e. clines for more than one character state). Primary and secondary contact between populations can create such "multiple coincident clines" and in any part of the population's range. However, the processes of range contraction and range expansion, which respectively reduce clines to multiple allelic differences between isolates and then introduces a new set of multiple coincident clines, still represents the most plausible explanation (Hewitt, 1988; 1989).

1.2.1.4 Maintenance of hybrid zones

The stability and hence maintenance of a cline is dependent on the forces of dispersal and selection. Barton and Hewitt (1985) have divided clines (in continuous habitats) into one of two classes, differentiated on the strength of selection and the dispersal effect. The stability of clines assigned to the first class, and referred to as "dispersal-independent cline", are maintained exclusively by selection; dispersal plays a negligible role and the resultant cline represents a smooth gradient in selection coefficients. The second class incorporates three models unified by a balance between the homogenising effect of dispersal and some cause of spatial heterogeneity. They are as follows:

1. *Neutral clines* – An original steep gradient decays with time to form an increasingly shallow cline (Mayr, 1963; Barton and Hewitt, 1985; Hewitt, 1988; 1989). The width of these clines is often quite large, up to 100 times wider than dispersal estimates, and are formed by two populations merging into one another. Homozygotes and heterozygotes share equal fitness.
2. *Waves of advance* – The "advance" of one or more advantageous alleles unique to one of the hybridising taxa eventually results in the saturation and possible extinction of the other hybridising population (Barton and Hewitt, 1985; Harrison, 1993).

3. *Dispersal/selection balance* – Clines are maintained by either environment differences (environmental transition clines) or selection against heterozygotes or recombinants (tension zones).

    - *Environmental transition clines* – These clines form along ecological transitions in the hybridising populations' range (Hewitt, 1985; 1988; 1989). The fitness of the homozygote varies depending on habitat type with alleles best suited to specific ecological conditions (Hewitt, 1988). A balance between gene flow and selection determines the width of the cline (Endler, 1977).

    - *Tension zones* – Barton and Hewitt (1985) have proposed that the great majority of hybrid zones are tension zones, maintained by a balance between hybrid selection and dispersal. In the tension zone proper, the heterozygote or hybrid is the inferior form, either because heterozygocity is disadvantageous at specific loci or because the fusion of two genomes produces a maladapted hybrid recombinant (Key, 1968). Zone stability is guaranteed by a balance between selection against the hybrid form, which introduces a decline in reproductive success, and gene flow, through mating and dispersal of better adapted homozygotes, which stabilises the zone. Spatial movement of the zone is also possible, induced by forces relating to individual fitness, population structure, and gene frequency effect (Barton and Hewitt, 1985).

1.2.2 Hybridisation amongst the primates

Although more common in captivity (Bernstein, 1966; Gray, 1971; Chiarelli, 1973; Bernstein and Gordon, 1980; Fox, 1984; Mootnick, 1984; Schilling, 1984a), primate hybridisation is not unknown in the wild. Cases of wild primate hybridisation reported in the literature are listed in Table 1-1. Most hybrid events have been reported within the Catarrhini where two normally allopatric populations have come into secondary contact through either the disruption to, or complete breakdown of, ecological barriers (Kummer et al., 1970; Struhsaker, 1970; Maples, 1972; Dunbar and Dunbar, 1974a; Shotake, 1981; Phillips-Conroy and Jolly, 1986; Samuels and Altmann, 1986; Ciani et al., 1989; Froehlich et al., 1991; Phillips-Conroy et al., 1991; Froehlich and Supriatna, 1996; Bynum et al., 1997; Jolly et al., 1997).

Probably the best studied primate hybrid zone occurs in the Awash Valley, Ethiopia between *Papio anubis* and *P. hamadryas*. The presence of a steep topographical and ecological gradient has largely separated the two baboon species, with *anubis* inhabiting the moist plateau savannas and forests above the Awash Falls and *hamadryas* establishing ranges in the drier thornscrubs and semi-desert regions below (Phillips-Conroy and Jolly, 1986). A contact zone, first described by Kummer and colleagues (Kummer and Kurt, 1963; Kummer, 1968; Kummer et al., 1970), found suspected hybrids living successfully within *hamadryas* groups occupying habitat at the foot of the falls. Subsequent studies have confirmed both the presence of the contact zone and the existence of hybrid forms (Nagel, 1971; 1973; Jolly and Brett, 1973; Kawai and Sugawara, 1976; Shotake et al. 1977; Sugawara, 1979; Phillips-Conroy and Jolly, 1981; Shotake, 1981) and revealed a consistent temporal change in both the nature and extent of the zone (Phillips-Conroy and Jolly, 1986). Over a period of eleven years, AH (*anubis*like)

Table 1-1 Hybrid and mixed species groups in wild living catarrhines.

Genus	Hybrid	Location	Source
Cercopithecus	*C. albogularis* x *C. mitis stuhlmanni*	Lake Manyara, Mto wa Mbu, Ngorongoro, Tanzania	1
	C. ascanius schmidti x *C. m. stuhlmanni*	Budongo Forest, Uganda	2
		Itwara Forest, Uganda	3
		Kibale Forest, West Uganda	4
	C.a.schmidti x *C. doggetti*	Gombe Stream National Park, Tanzania	5
	C. cephus x *C. erythrotis*	River Sanaga, Edea, and Lac Tisongo, Cameroun	6
	C. mona x *C. p. pogonias*	Idenau, Cameroun	6
	C.n.nictitans x *C. mona*	River Sanaga, Cameroun	6
Papio	*P. anubis* x *P. hamadryas*	Awash National Park, Ethiopia	7 to 22
	P. anubis x *P. cynocephalus*	Simba Springs and Ithumba Hill, Kenya	23
		Amboseli Basin, Amboseli National Park, Kenya	24, 25
Papio/ Theropithecus	*P. anubis* x *T. gelada*	Bole Valley, Amhara Plateau, Ethiopia	26
Macaca	*M. fascicularis* x *M. nemestrina*	Kuala Lumpur, Malaysia	27
		Kowloon Peninsula, Hong Kong	28
	M. nigra x *M. nigrescens*	Tambun, Mt Padang, North Sulawesi, Indonesia	29, 30, 31
	M. hecki x *M. nigrescens*	East of S. Bolango, North Sulawesi, Indonesia	30, 31
	M. tonkeana x *M. hecki*	Between Kebun Kopi and Toboli, Isthmus of Central Sulawesi, Indonesia	29, 30, 32, 33
	M. tonkeana x *M. maurus*	Maroangin, Tempe Depression, South Sulawesi, Indonesia	30, 34, 35, 36
	M. tonkeana x *M. ochreata*	Karaena River, Sulawesi, Indonesia	37
Trachypithecus/ Semnopithecus	*T. johnii* x *S. entellus*	Nilgiri Hills, India	38, 39, 40, 41
Hylobates	*H. lar* x *H. pileatus*	Takhong River, Khao Yai National Park, Thailand	42, 43, 44
	H. agilis x *H. lar*	Ulu Mudah, West Malaysia	45, 46
	H.a.albibarbis x *H. muelleri*	Barito Ulu, Central Kalimantan, Indonesia	47, 48, 49

1: Booth, 1968 2: Aldrich-Blake, 1968 3: J.F. Oates, personal communication to Struhsaker et al., 1988 4: Struhsaker et al., 1988 5: Clutton-Brock, 1972 6: Struhsaker, 1970 7: Kummer and Kurt, 1963 8: Kummer, 1968 9: Kummer et al., 1970 10: Nagel, 1971 11: Nagel, 1973 12: Jolly and Brett, 1973 13: Kawai and Sugawara, 1976 14: Shotake et al., 1977 15: Sugawara, 1979 16: Phillips-Conroy and Jolly, 1981 17: Shotake, 1981 18: Sugawara, 1982 19: Phillips-Conroy and Jolly, 1986 20: Sugawara, 1988 21: Phillips-Conroy and Jolly, 1991 22: Phillips-Conroy and Jolly, 1992 23: Maples, 1972 24: Altmann and Altmann, 1970 25: Samuels and Altmann, 1986 26: Dunbar and Dunbar, 1974a 27: Bernstein, 1966 28: Southwick and Southwick, 1983 29: Groves, 1980 30: Ciani et al., 1989 31: Watanabe and Matsumura, 1991 32: Watanabe et al. 1991a 33: Bynum et al., 1997 34: Supriatna et al., 1990 35: Supriatna, 1991 36: Froehlich and Supriatna, 1996 37: Watanabe et al, 1991b 38: Herzog and Hohmann, 1984 39: Hohmann et al, 1986 40: Hohmann, 1988 41: Hohmann, 1991 42: Marshall et al., 1972 43: Brockelman, 1978 44: Brockelman and Gittins, 1984 45: Gittins, 1978a 46: Gittins, 1979 47: Marshall et al., 1984 48: Marshall and Sugardjito, 1986 49: Bodmer et al., 1991 hybrids, HA (*hamadryas*like) hybrids and pure *hamadryas* individuals have appeared in increasingly greater numbers in above-Falls *anubis* troops. A migration has also occurred in the opposite direction with the presence of HA hybrids and pure *anubis* in groups which were originally composed solely of pure *hamadryas*. While the first hybrids observed in the Awash population were the product of matings between *anubis* and *hamadryas*, later hybrids are almost certainly the offspring of hybrids themselves (Phillips-Conroy and Jolly, 1986).

Mixed species groups and morphological variable forms have also been observed between species of guenon (Struhsaker, 1970); langur (Herzog and Hohmann, 1984; Hohmann et al., 1986; Hohmann, 1988: 1991); spider monkey (Froehlich et al., 1991); non-Sulawesi macaque (Bernstein, 1966; Southwick and Southwick, 1983) and other species of baboon (Maples, 1972; Dunbar and Dunbar, 1974a; Samuels and Altmann, 1986; Hayes et al., 1990; Jolly et al., 1997). The six endemic species of Sulawesi macaque are of particular note with evidence of marked gene flow and intergradation between distinctive forms forming communities of highly variable morphological types (Groves, 1980; Ciani et al., 1989; Supriatna et al., 1990; Watanabe and Matsumura, 1991; Watanabe et al., 1991a; 1991b; Froehlich and Supriatna, 1996; Bynum et al., 1997).

Disruption to the habitat remains a common precursor to many cases of primate hybridisation. For baboons, it has been the implementation of intensive agricultural practices that have driven populations away from their preferred habitat into areas normally used by related species. Allocation of land surrounding Nairobi and the Ulu escarpment for agriculture saw a subsequent rise in human population numbers, forcing *Papio anubis* to move to the Amboseli area basin and share ranges with local *P. cynocephalus* (Maples, 1972). Much the same occurred to *P. anubis* populations living in Ethiopia, in this case being evicted from the flat open ground on the Amhara plateau into the gorges area regularly used by *Theropithecus gelada* (Dunbar and Dunbar, 1974a). In Sulawesi, inter-specific barriers have been disrupted by logging, farming, and the building of amenities such as roads (Froehlich and Supriatna, 1996; Bynum et al., 1997).

Rather than human interference, Phillips-Conroy and Jolly (1986) have proposed an environmental explanation for the origin of the hybrid zone at the Awash Valley. Variable patterns of rainfall introduce periods of high and low productivity. For baboon populations living in normally floristically rich habitats, such as the above-Falls *anubis*, a marked decline in vegetational foodstuffs will induce higher rates of mortality compared to *hamadryas* populations living in less desirable areas. Although not as severely affected by the drought, *hamadryas* populations may also choose to migrate to areas which, although still poor, are better than the habitat in their normal range. It is at these times that *hamadryas* began penetrating the above-Falls *anubis* troops, leading to hybridisation between the two parental species. In years when weather conditions were ideal, the opposite scenario took place, with *anubis* and new hybrids expanding their range downstream, coming into contact and joining the resident *hamadryas* bands. Referring to East African weather patterns, Phillips-Conroy and Jolly (1986) were able to relate climatic variability to the location of the first contact point and the spread of the hybrid zone at the Awash Valley. From this they inferred that when the area experienced even weather patterns, the ecological boundary separating *anubis* and *hamadryas* would re-stabilise and sharpen, effectively reducing the extent of hybridisation.

The behavioural pathway through which individuals join troops of different species appears to rely, at least for baboons and macaques, on the process of male-transfer. Nagel (1973) had originally suggested that female abductions led to the formation of mixed species troops and subsequent hybridisation in the Awash Valley. The fact that Nagel never actually observed an abduction proper, just interactions between *anubis* females and *hamadryas* males, prompted Kawai and Sugawara (1976) to investigate an alternative explanation, the transfer of males. Male transfer is quite common for savanna baboons (Packer, 1975; 1979; Rhine et al., 1979) and not unusual for *hamadryas (*Sigg et al., 1982), suggesting to Phillips-Conroy and Jolly (1986) that male immigration is the more convincing, and the more likely, scenario. Immigration could certainly introduce the rapid changes observed in the composition of the hybrid zone population and, if bi-directional, explain the distribution of morphological variants. Subsequent observations of male hamadryas baboon migrating into *anubis* troops at the Awash Valley (Phillip-Conroy et al., 1992) support the hybridisation via immigration proposal.

Samuels and Altmann (1986) also adhere to a male group transfer theory, since individuals of different species in observed mixed *anubis* x *cynocephalus* groups were invariably male. For the hybridisation of Sulawesi macaques, the role of male immigration is inferred. Inter-group males show substantial tolerance to one another (Watanabe and Brotoisworo, 1982) and the absence of significant behavioural differences between species should allow successful social integration.

Not all primate hybrid events have occurred between allopatric populations, some have been between sympatric populations (Aldrich-Blake, 1968; Struhsaker, 1970; Clutton-Brock, 1972; Struhsaker et al., 1988). Guenons represent the hybridising taxa in all but one of these cases, producing hybrid offspring who remain within their mother's social group. Hybridisation between *Cercopithecus ascanius schmidti (*redtail monkeys) and *C. mitis stuhlmanni (*blue monkeys) has been observed at three locations in Uganda – the Budongo Forest (Aldrich-Blake, 1968), Itwara Forest (J.F. Oates, personal communication to Struhsaker et al., 1988) and the Kibale Forest (Struhsaker et al., 1988). At the latter site, three hybrids, two females and one male, were identified living amongst redtail monkeys. Other than some differences in food choice and inter-birth interval, their repertoire of social and ecological behaviours hardly deviated from that of the red-tails.

Low densities characterised the blue monkey population living in the hybrid area, restricting a male's ability to regularly mate with females. Further reducing his chances was the high male:female ratio. To compensate, male blue monkeys have looked for alternative partners i.e. red-tail females (Struhsaker et al., 1988). Observations of a blue male's six year attempt to copulate with redtail females indicated to Struhsaker et al. (1988) that a long term association, or indeed consortship itself, was not common and that unions occurred during brief, opportunistic encounters.

The fate of primate hybrid zones varies from case to case. In unusual situations such as that described for the guenons, hybrids remain a unique but small component of the population, outnumbered by pure parental species. But in zones where sexual and reproductive activity is less restricted, hybrids can predominate, with the formation of tension zones or even full introgression. The *anubis* x *hamadryas* hybrid zone at the Awash Valley probably represents a narrow tension zone since the width of the zone itself (at 25 km) is not significantly longer than the average dispersal range of the parental species (between 6.5 and 13.2 km) (Kummer, 1968; 1971; Kummer et al., 1970 but see Shotake, 1981). The steepness of clinal changes in morphology between varying Sulawesi macaque taxa are also suggestive of tension zones (Ciani et al., 1989; Bynum et al., 1997). Fuller introgression, however, does appear to have occurred between spider monkeys (Froehlich et al., 1991) and between *Macaca maurus* and *M. tonkeana*. The width of the hybrid zone between *maurus* and *tonkeana* measures at least 10 km at the western end of study area and at least 35 km at the eastern end (Supriatna et al., 1990; Supriatna, 1991; Froehlich and Supriatna, 1996). Average day ranges, however, are considerably shorter, pure *maurus* and *maurus* x *tonkeana* hybrids ranging no further than 1.5 km a day (Supriatna, 1991). Additional support for full introgression between *maurus* and *tonkeana* includes the absence of any significant ecological barrier at the zone of contact and the apparent fitness of the hybrids. Indeed, Froehlich and Supriatna (1996) have claimed that despite the physical differences between the two taxa, they in fact represent a single recognition species.

1.2.3 Hybridisation and the lar group gibbons

1.2.3.1 Location and description of contact zones

Different species of lar group gibbons are mostly isolated from one another by broad passages of water but at five distinct boundary areas within Southeast Asia, potential or actual specific contact has occurred (Brockelman and Gittins, 1984). Two of these sites – the Perak and Kelantan rivers in peninsular Malaysia and the area surrounding Lake Toba in Sumatra – demarcate part of the boundary which separates residential populations of *lar* and *agilis* but as yet no contact evidence has been discovered (Gittins, 1978a; Brockelman and Gittins, 1984). At the remaining three sites (see Figure 1-3), contact has not only been observed but so has the formation of mixed groups and, in at least two areas, the presence of hybrid forms.

1.2.3.1.1 Takhong river, Khao Yai National Park, Thailand

A small area of sympatry between *H. lar carpenteri* and *H. pileatus*, occurring at the headwaters of the Takhong River in the Khao Yai National Park, Thailand, was first described by Marshall et al. (1972). Since then, Warren Brockelman and colleagues have conducted extensive field research in the area, censusing groups and collecting pelage and song descriptions (Brockelman, 1978; Brockelman and Gittins, 1984). From the 210 groups detected living in the area, 61 groups were observed directly. Eighteen of these groups were found to contain either mixed pairs or hybrids. In addition, four trios were discovered, each composed of one male and two phenotypically different females. Hybrids differed from parental *pileatus* and *lar* in both characteristics of the pelage and song. Those individuals suspected to be hybrids because of their unusual colouration or facial hair patterns invariably produced calls that were intermediate in structure between those unique to the parental species. Furthermore, and with only one exception, gibbons ascribed to hybrid status because of their intermediate calls had a pelage somewhat different to that characteristic of *pileatus* and *lar*.

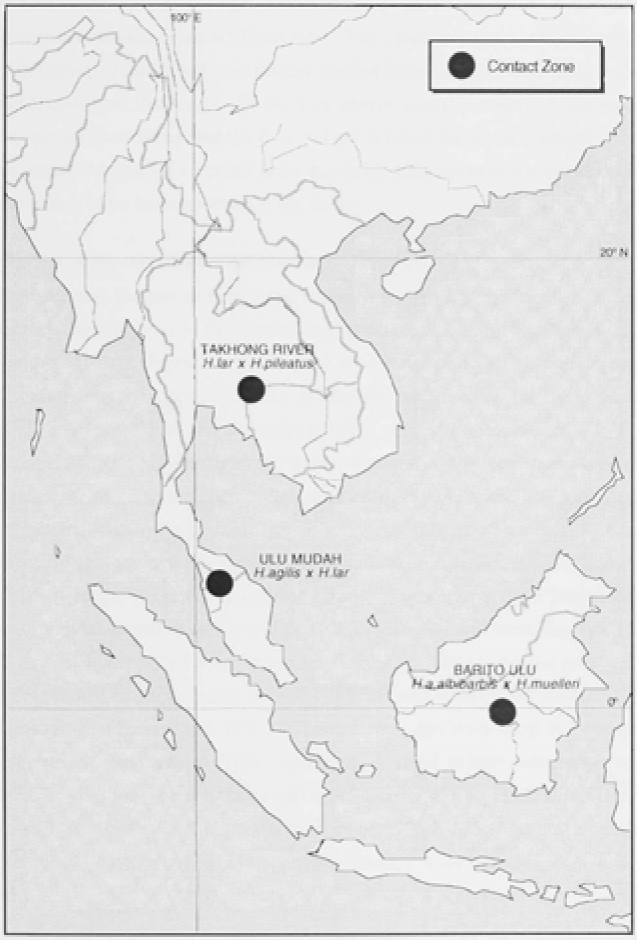


Figure 1-3 Location of gibbon contact zones.

The area of contact itself is quite narrow and characterised by a steep morphological gradient. Over a distance of 9 km, the frequency of pure forms changes from 90% *lar* to 90% *pileatus*. Within that 9 km, hybrids represent 6% of the population. Actual extension into pure species territory is limited too. Lar gibbons range no further than 4 km into the *pileatus* side of the zone and pileated gibbons are found only 5 km into the *lar* side (Brockelman and Gittins, 1984). Hybrids have dispersed somewhat further – 6 km into the *lar* area of occupation and 9-12 km into the *pileatus* domain.

1.2.3.1.2 Ulu Mudah, West Malaysia

In West Malaysia, the Mudah River, and its tributary the Teliang, delimit the boundary between *H.l.lar* in the north and *H. agilis* in the south. Within the Ulu Mudah Forest Reserve, through which these rivers run, Gittins (1978a; 1979) found populations of *lar* and *agilis* occupying forest lining opposite shores of an artificial lake. Two, possibly three, mixed groups were also discovered, resident pairs ascribed to different species based on coat colouration, face patterns, and male and female-specific songs. Of the two groups actually observed, the male of the pair was the alien species, indicating that the lake did not act as a barrier to interspecific contact. No hybrids were identified and little census work has been undertaken since insurgent behaviour in the area prevented Gittins from continuing his survey.[1]

1.2.3.1.3 Barito Ulu, Central Kalimantan, Borneo

The third contact zone, the one at which my research was conducted, occurs at the headwaters of the Barito and Kapuas rivers in the Indonesian province of Central Kalimantan, Borneo. The formidable width of these rivers has maintained separation between *H. muelleri* and *H. agilis albibarbis,* which line the opposite banks of the Barito River as far north as Muara Joloi (Marshall et al., 1984; Marshall and Sugardjito, 1986; personal observation): *H. muelleri* to the east of the Barito, and *H.a.albibarbis* to the west. Above the intersection at which the Joloi and Busang rivers merge to form the Barito, Marshall et al. (1984) noted a "sparse" population of hybrids, interspersed amongst a numerically stronger community of parental forms and located near a canopy bridge formed by large, interconnecting riparian trees. Song and pelage differences identified the presence of hybrids. Females gave great calls intermediate between the frequency modulated call of *agilis* and the trill of *muelleri* and were described by Marshall et al. (1984) as "reminiscent" of those given by *H. klossii*. Other unusual great calls and male phrases were attributed to backcrosses between hybrids and *muelleri* or *albibarbis* (Marshall et al., 1984; Marshall and Sugardjito, 1986). These songs also resembled, but remained distinct from, the structure of the parental-typic sequences. Hybrid pelage colouration was "suitably intermediate" too, with grey-brown backs and a yellowish-brown or buff rump contrasting with the dark brown/black venter and cap (Marshall et al., 1984; Marshall and Sugardjito, 1986). Facial pattern could be observed only for one individual, a male, whose brows were edged with a white band.

Reconnaissance work conducted by Bodmer et al. (1991) verified the existence of the hybrid zone. Hybrids were observed adjacent to the Joloi and Busang rivers and were also detected on the western bank of the Murung river, located to the east of the Busang. A two year study by Robert Mather (1992), which examined the location, size and composition of the Barito Ulu hybrid zone through the analysis of song structure, contributed considerable data and challenged Marshall and Sugardjito's (1986) assertion that the zone of contact was small and resembled that found at Khao Yai. Indeed, Mather estimated the hybrid zone to be at least 3,500 km^2, possibly covering an area as large as 10,000 km^2.

---

[1] Brockelman and Gittins (1984) have suggested that a 5-10 km zone at the headwaters of the Thepha river should represent another area of free mixing between *H.l.entelloides* and *H. agilis* but as yet nothing has been reported in the literature.

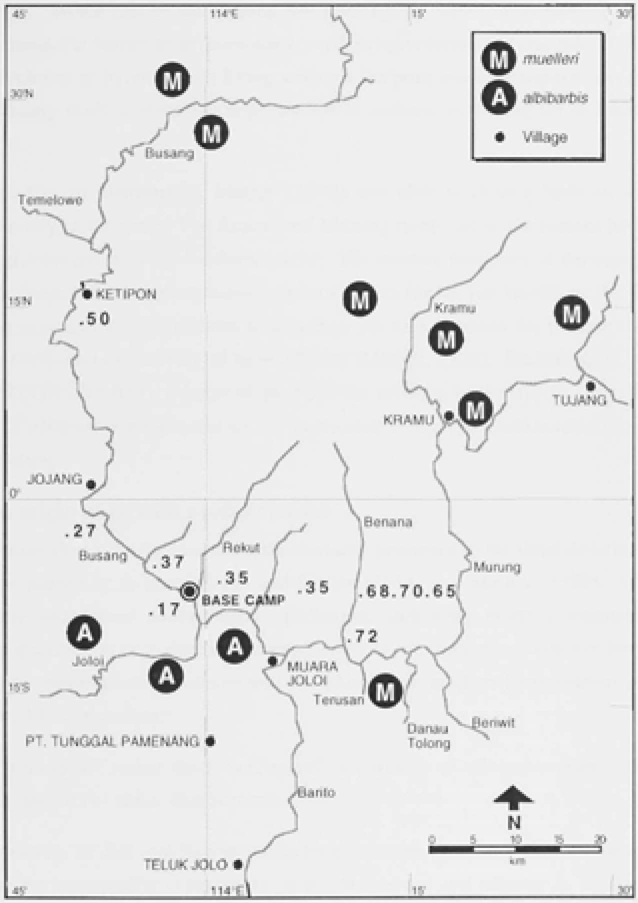


Figure 1-4 Distribution of hybrid gene frequencies (measured as p values) in selected survey sites in the Barito Ulu watershed. Each value represents the proportion of *albibarbis* and *muelleri* genes in the resident population where p=0 denotes pure *albibarbis* and p=1 denotes pure *muelleri*. (See Appendix I for method used to calculate p values). Figure modified from original map given in Mather (1992).

Figure 1-4 illustrates the distribution of hybrid gibbon gene frequencies (measured as p values – see Appendix I for calculation and description of p values) in the Barito Ulu watershed. Running at the latitude of the basecamp, the transition extends from an *agilis*-like genotype in the west to a *muelleri*-like genotype in the east. Small, intervening rivers such as the Rekut, Cahai and Pakang introduce little alteration to p values in the resident population. At points demarcated by the larger Busang, Benana and Murung rivers, however, p values change markedly, indicating that these three rivers function as significant barriers to gene flow (Mather, 1992). The centrally located Benana river effectively separates the hybrid population into two different gene pools. Gibbons residing between the Busang and Benana show a mean p value of 0.37 while gibbons found between the Benana and Murung have mean p values of 0.67

(Mather, 1992). To the east of the Benana, the Murung, by virtue of its size, proves to be an even more formidable barrier to gene exchange with hybrids located on one side of the river but little or no evidence of hybrid forms living amongst the pure *muelleri* population on the other. Along the Busang itself, a north-south gene cline is evident, extending for at least 70 km in length.

Using this pattern of distribution, Mather (1992) was able to delimit both an eastern and southern boundary to the zone. The Kramu and Murung rivers act as the eastern boundary and the Barito and Joloi rivers as the southern border. The western boundary of the zone, however, is yet to be defined, extending progressively westward the further one travels up the Busang. A population in excess of 35,000 gibbons now occupy the area between the Busang and Murung rivers and is composed exclusively of hybrid forms (Mather, 1992). Bodmer et al. (1991) and Mather (1992) failed to find evidence of pure species residing in the hybrid zone; the nearest populations of *albibarbis* are located to the south-west of the Joloi and *muelleri* to the south-east of the Murung.

1.2.3.2 The origin of gibbon contact zones

Secondary, rather than primary, contact is the probable precursor to the three described zones of intergradation according to Brockelman and Gittins (1984) and Mather (1992). In this case, populations re-established contact *after* speciation, following either a constriction then expansion of distribution or a shift in geographical range. Supportive evidence for secondary contact includes environmental, behavioural and phenotypic markers (Brockelman and Gittins, 1984; Mather, 1992) including:

- the "historical" rather than "ecological" separation of allopatric populations i.e. by rivers and straits rather than ecotones
- a similarity in diet and habitat preference between sympatric forms (which suggests complete interspecific competition; in the case of *lar* and *pileatus* in Thailand this has been confirmed)
- the absence of significant habitat differences between populations found both surrounding *and* removed from the contact zone

Alteration to the habitat, or expansion into areas where geographical barriers are impotent or absent, best explains the establishment of gibbon contact areas. At Ulu Mudah in West Malaysia, habitat destruction, one of the primary causes of hybridisation, has undoubtedly led to the formation of mixed *lar* x *agilis* groups since interspecifics live on the banks of an artificial lake located within logged forest. The *lar* x *pileatus* contact zone at the Takhong headwaters in Thailand may also be a result of habitat disturbance: marked deforestation occurring downstream from the zone could have pressured local populations, forcing both species to expand into and occupy the headwaters area (Mather, 1992).

At Barito Ulu, the situation is somewhat different. Forests have been left largely intact, the creation of *ladangs* (small agricultural plots produced through slash and burn cultivation) being the only form of human disturbance. So how, and where, did populations of *albibarbis* and

Figure 1-5 Proposed location of the original contact zone between *H.a.albibarbis* and *H. muelleri* and direction of spread of hybrid population. Figure modified from original map given in Mather (1992).

muelleri originally meet? The presence of large, overhanging dipterocarp trees on adjacent sides of the Busang river led Marshall et al. (1984) to propose that such trees acted as highways of interspecific migration. *H.a.albibarbis*, on the west bank of the Busang, were thus able to use these inter-connected pathways to cross over to the east or *muelleri* side of the river while *muelleri* were able to travel and meet *albibarbis* on the western side. Mather (1992) considers this scenario much too simplistic and not substantiated by p values calculated for hybrids living on opposite sides of the Busang. Examining the distribution of p values and the presence/absence of clines in the contact zone, Mather pinpointed a spot on the upper Busang, approximately 40 km from the main basecamp and near Ketipon, as the probable origin of the hybrid zone (see Figure 1-5). At this spot, the Busang is very narrow, a "small stream", and even less of a barrier to gene flow than the Rekut, Cahai and Pakang rivers. Mather (1992) has proposed that the hybridisation process, which probably began around 5000 to 10,000 years ago, originated at this point, enabling the populations of the two species to inter-breed and subsequently expand out into the adjacent, unoccupied areas surrounded by the Busang, Joloi, Barito and Murung rivers.

1.2.3.3 Stability and composition of gibbon hybrid zones

Brockelman and Marshall (1986) proposed that the degree of hybridisation which had occurred at the Takhong river and Barito Ulu contact zones was similar. According to Mather (1992), however, this claim was premature, especially considering the limited field research conducted at the latter site. Mather's own study at Barito Ulu did discover similarities between the two zones, such as the low reproductive rate demonstrated by hybrid groups (see Appendix II for tabulation of hybrid population demographics), but differences were particularly conspicuous:

1. ***Pair bond stability and group composition*** – Instability marked pair bonds in both mixed and hybrid groups at the Takhong headwaters, such that most groups dissolved within the period of study (W. Brockelman, personal communication to Haimoff et al., 1984). Trios were also present and, although polygamous social groupings are not unknown for pure species of gibbon (Srikosamatara and Brockelman, 1987; Hu et al., 1989; Choudhury, 1990; Ahsan, 1994; 1995; Bartlett and Brockelman, 1996; Brockelman, 1997; Sommer and Reichard, in prep), the proportion amongst the hybrid population was unusually common. Rigorous monitoring of pair combinations at Barito Ulu, however, has yet to be conducted but census data collected by Mather (1992) did contrast with group composition information from Khao Yai. In 35 groups scattered around the watershed, none were found to exhibit unusual social constructs (but see this study).
2. *The width of the zone* – It was mentioned previously that the width of the hybrid zone at the Takhong river headwaters is no greater than 9 km and characterised by a considerable and steep genotypic gradient. At Barito Ulu, the width of the zone is a lot greater, calculated as 50 km. Furthermore, the transition from a predominantly *agilis* to *muelleri* like genotype is mostly gradual and marked changes can be detected only at points where rivers have introduced some barrier to gene flow.
3. *The proportion of hybrids in the population* – While pure species predominate over hybrid forms at Takhong river (and Ulu Mudah), they are absent altogether in the hybrid zone at Barito Ulu. The estimated population of 35,000 gibbons occupying the area bordered by the Busang and Murung rivers is composed entirely of hybrids and back-crosses.

These extremes in both zone width and the proportional representation of hybrid to pure forms in the resident population reveal contrasting fates for each of the contact zones. The 9 km width of the zone at Khao Yai compared to the average range of dispersal for *lar* and *pileatus* gibbons (0.8 and 1.5 km respectively[2]) indicates the presence of a narrow tension zone which acts as a genetic sink. Selection against hybrids appears to be quite strong and the zone's existence

---

[2] These values represent average day range lengths for *lar* and *pileatus* respectively (Leighton, 1987).

seems to be sustained only by gene flow from parental populations (Mather, 1992). The situation at Ulu Mudah is also suggestive of strong selection against hybrid forms but because disruption to the zone is suspected (Groves, 1993), little more can be said about its fate.

In contrast, the hybrid population at Barito Ulu has been described as "demographically healthy" and "as viable as (that of) pure gibbons" (Mather, 1992). The absence of gene flow from parental populations and the sheer number of hybrids in the contact zone led Mather (1992) to designate the area a hybrid swarm (i.e. "a continuous series of hybrids that are morphologically distinct from one another" – Allaby, 1991).

1.2.3.4 Species concepts and the specific status of the hybridising taxa

According to the original biological species concept (Mayr, 1963), different species do not hybridise. This is because pre-mating isolation mechanisms, which may be in the form of ecological, temporal or ethological mating behaviour differences, prevent them from breeding with one another. Pre-mating mechanisms, however, are not always 100% effective, and selection against the hybridisation process might be implemented instead through pre-zygotic (mechanical isolation; gametic mortality or incompatibility) or post-zygotic (F1 or F2/backcross inviability or sterility; coevolutionary or cytomplasmic interactions) isolation (Dobzhansky, 1970; Templeton, 1989). Paterson (1985) has seriously questioned the isolation species concept, specifically because it is inconsistent with allopatric models of speciation and hence misleading about the process of speciation in general. Isolation may be a product of speciation but unlikely to be part of the process itself (Paterson, 1985; Templeton, 1989). An alternative model retains the concept of species-specific pre-mating behaviours but, instead of playing an isolational role which separates populations, these behaviours act to facilitate reproduction within each species. Paterson (1985) still views the species as a field for gene recombinants but a field delimited by a shared fertilisation system. Hence a species becomes "the most inclusive population of individual biparental organisms which share a common fertilisation system" with specific mate recognition systems or SMRS's guiding mate selection.

To accept Mayr's species definition of pre-mating isolation would mean that neither *lar, pileatus, muelleri* nor *agilis* could be considered true species. The evidence of post-zygotic isolation (i.e. reduced fitness of the hybrid offspring) suggests otherwise: that these taxa are indeed full species because the reproductive rate in hybrid offspring is significantly lower than that observed for the parental forms. In discussing the contrast in the nature and extent of the Takhong and Barito Ulu hybrid zones, Mather (1992) introduced two important questions – 1. how much hybridisation is permitted between two populations if they are to remain recognised species? and 2. how reduced does the fitness of the hybrid have to become before a fully operational post-zygotic isolation mechanism can be identified and a hybrid population classified as a full species?

To answer these questions, Mather (1992) focussed on hybrid population viability. As mentioned above, the hybrid population size at Takhong was not large, and was sustained by gene flow from the parental population. At Barito Ulu, parental gene flow was negligible, with the hybrid population maintaining itself successfully through hybrid-hybrid matings. Using the criterion of hybrid matings remaining fertile and producing viable offspring for at least three generations, Mather (1992) concluded that while *lar* and *pileatus* are likely to be representative of full species, *albibarbis* and *muelleri* are not.

Groves (1993) attempted to explain contrasting dynamics in the three hybrid zones through the concept of species mate recognition systems. He proposed that, for gibbons, discrimination between like and unlike incorporates both a visual (pelage) and auditory (song) component. It follows that if gibbons do indeed choose their mate relying on features such as coat colour or features of the song (e.g. structure; time of performance) then taxa which display similar physical and/or vocal features are likely to interbreed more readily than those who do not.

Examining the importance of pelage first, Groves found that at two contact points, one between subspecific forms of *H. lar* (*H.l.carpenteri* and *H.l.entelloides* – data from Carpenter, 1940 and Fooden, 1969) and the other between *H. lar* and *H. pileatus* at Khao Yai, like did tend to pair with physical like. Of the thirty seven *lar* groups described by Carpenter (1940) and Fooden (1969), thirty one were composed of individuals who had a similar coat colouring to their mate (i.e. dark x dark or pale x pale). At Khao Yai, nine of the twelve mixed species groups were also characterised by pairs with similar pelage colouration. Interestingly, in the two groups in which one of the mixed pairs was a pure pileated gibbon, their mate was the same colour. Pileated gibbons are sexually dichromatic with adult males having a black coat and adult females a buffy coloured coat with a black venter. According to Groves (1993), these results suggest that pelage colouration, as a species recognition signal, appears to be crucial only to the nonsexually dichromatic *lar* when it comes to mate choice.

Pelage colour of hybridising taxa at Ulu Mudah did not reveal any further significant trends and was represented by too small a sample size (n=2). With regard to *albibarbis* and *muelleri,* the absence of distinct pelage characters between the two species prevented any conclusive method for assessing assortative mating tendencies (Groves, 1993).

The female's great call has repeatedly been used as a key taxonomic tool when differentiating between gibbon, and particularly lar group, taxa. Mather (1992) has criticised this sole reliance on the great call, suggesting that duet interactions rather than "simple features of the great call alone" are crucial for specific mate recognition. Note type and sequencing, and participation of the mated pair in the introductory, organising and great call sequences, is much more similar in the duets of *agilis/albibarbis* and *muelleri* than it is for *lar* and *pileatus*. Hybrids between the former taxa should, therefore, suffer less interactive problems whilst duetting and, if successful duetting is related to reproductive success, a higher proportion of hybrid types should exist at Barito Ulu (Mather, 1992).

Great call variations have also been ignored by Groves (1993), referring instead to differential performance times of duets and especially male solos. Male *agilis* and *muelleri* commonly sing before or at dawn whereas *lar* and *pileatus* males delay their soloing until mid-morning (Gittins, 1979; 1984a; Srikosamatara and Brockelman, 1983; Mitani, 1984; 1987a; 1987b; 1988; Raemaekers et al., 1984; Dee Robbins, 1997 pers. comm.). With respect to duetting, *agilis, muelleri* and *pileatus* all duet just after dawn, while *lar* pairs wait until later in the morning to sing together (Gittins, 1979; 1984a; Srikosamatara and Brockelman, 1983; Mitani, 1984; 1985a; 1987b; 1988; Raemaekers et al., 1984; Robbins, 1997 pers. comm.). If timing of song delivery is important in species mate recognition, then the differences between *agilis* and *lar* (duets and solos) and *lar* and *pileatus* (delivery of the duet) compared to *agilis* and *muelleri* (no major differences) correlates nicely with the status of the respective hybrid zones. Results from play-back experiments in which *albibarbis* in West Kalimantan were exposed to the songs of conspecifics, Sumatran *agilis* and male *muelleri*, however, complicates the relationship (Mitani, 1987a). When played to *albibarbis* pairs, male *agilis* songs elicited expected responses (i.e. approaches and duetting) but the songs of male *muelleri* derived only subdued male responses (e.g. occasional approaches, no singing) and alarm calling from females. *H.a.albibarbis* appear to be able to recognise *muelleri* as a gibbon but not as a competitor and hence a conspecific (Mitani, 1987a). Play-back experiments where female *pileatus* calls were played to *lar* indicated a similar, if occasionally indecisive, ability to discriminate between like and unlike (Raemaekers and Raemaekers, 1985).

Groves (1993) dismisses, albeit carefully, these differential responses by promoting pelage and male song delivery time, instead, as important mate recognition characters. Marginal variation in pelage, coupled with inter-specific synchrony in the timing of male solos, may be strong enough to over-ride any effect song recognition has in the prevention of inter-breeding. For *lar* and *pileatus*, pelage is significantly different, potentially inhibiting parental types, and particularly *lar*, from hybridising on a consistent basis. For *agilis* and *lar,* who differ in both traits, inter-breeding would remain infrequent. Groves (1993) suspects that male song plays the pivotal role in mate recognition but its acceptance is dependent on comparing rates of hybridisation at the three sites. Unfortunately, the apparent disruption to the *agilis-lar* contact zone at Ulu Mudah will frustrate any future investigation.

1.3 The behavioural ecology of gibbons

The first field study of gibbons was conducted in 1937 by Coolidge, Schultz, Carpenter and Washburn (Coolidge, 1984) as part of the Asiatic Primate Expeditions. Since the publication of Carpenter's 1940 monograph "*A field study in Siam of the behaviour and social relations of the gibbon (Hylobates lar)*", and starting with Ellefson's 20 month study of *H. lar* in Malaysia, gibbons have received considerable research attention. The lar group represent the best studied hylobatids, each species the subject of at least one long term field study (*H. agilis* – Gittins, 1979; *H. lar* – Ellefson, 1968; 1974; Chivers, 1974; Raemaekers, 1977; *H. moloch* – Kappeler, 1984a; 1984b; *H. muelleri* – Leighton, unpubl; *H. pileatus* – Srikosamatara, 1980). Substantial field data have also been collected for the siamang (*H. syndactylus* – Chivers, 1974; Raemaekers, 1977) and Kloss gibbon (*H. klossii* – Tenaza, 1975; 1976; Tilson, 1981; Whitten, 1980) and the last decade or so has generated important information on hoolock gibbons (Alfred and Sati, 1990; 1991; Choudhury, 1990; 1991; Islam and Feeroz, 1992a; 1992b; Ahsan, 1994) and small, remnant populations of concolor gibbons (Haimoff et al., 1986; 1987; Yang et al., 1987; Bleisch and Chen, 1991; Lan, 1993; Sheeran, 1993). The opening up of Vietnam, Laos and Cambodia should see the initiation of research into the three remaining and poorly known species, *H. leucogenys*, *H. gabriellae* and *H. siki.*

Socially and ecologically, the gibbons appear to be a rather uniform group with the expression of basic behavioural parameters (e.g. diet composition, social structure) showing little variation both between species and differential sections of the conspecific population. However, as noted by Leighton (1987), the current catalogue of species-typical behaviours has largely been derived from the intensive study of just one or two groups over a period of time lasting no longer than one to two years. Field researchers such as Ryne Palombit, Ulrich Reichard and Volker Sommer have also argued this point. Recent work by these authors has shown that long-term research on a larger sample of study groups not only introduces important and previously unknown behavioural inter-population and inter-specific differences but seriously questions long-held theories of gibbon behaviour.

Gibbons are largely defined in relation to their diet, the production of songs, social structure and intra-group behaviour, and territoriality. Current knowledge and theories concerning these and other behavioural parameters are described in greater detail later in the text but to provide an introduction to the behaviour and ecology of gibbons, a review of these follows.

1.3.1 Diet

Gibbons are regularly classified as frugivores and for the most part they subsist on a diet including significant amounts of fruit (Chivers, 1984). While non-fig fruits are probably the preferred dietary item as they are nutritionally superior to other plant types (Leighton, 1993), figs are a notably consistent component of the diet. *Ficus* (fig) trees are commonly found in habitat used by gibbons and with their asynchronous fruiting cycles they represent a ready source of bountiful and easily digested food. At times of low fruit production, figs become especially important in the gibbon diet (*keystone mutualists* – Leighton and Leighton, 1983). They are also often relied upon as the first and last food source of the day, presumably as a means of compensating and preparing for the long overnight fast (Raemaekers, 1978a; 1979).

Differing combinations of supplementary foodstuffs define the diets of species such as the siamang (Chivers, 1974; Raemaekers, 1978a; 1979) but all gibbons take in at least small quantities of leaf, flower and invertebrate items. As monogastrenes, gibbons prefer not to consume mature foliage but use young leaf, flowers, leaf buds and shoots instead. Less likely to contain digestive-inhibitors (e.g. cellulose, secondary compounds), immature foliage also acts as a reservoir of much needed protein. Invertebrates are an additional source of protein and, for populations where leaf consumption is minimal, invertebrates comprise a significant proportion of the overall diet (e.g. Kloss gibbons – Whitten, 1982a).

1.3.2 Song

Probably *the* distinguishing feature of the gibbon is its song. Each species can be identified by a distinctive song structure and, with the exception of the hoolock gibbon, so can the sexes (Leighton, 1987). Typically performed in the early morning, gibbons may give calls individually (the solo) or with another (the duet). Solos are predominantly a male trait; the males of five species (*agilis, klossii, lar, muelleri* and *pileatus*) regularly perform individual songs, sometimes before sunrise and in chorus with neighbouring males (Chivers, 1974; Tenaza, 1976; Gittins, 1979; 1984a; Whitten, 1982b; 1984a; Srikosamatara and Brockelman, 1983; Mitani, 1984; 1987a; 1987b; 1988; Raemaekers et al., 1984; Geissmann, 1993). Both mated and unmated males solo, the latter presumably to attract a mate (Gittins and Raemaekers, 1980; Tilson, 1981).

Females are less likely to solo, reserving their singing performances to duets, although *klossii*, *moloch* and, to a lesser extent, *muelleri* females do often solo (Tenaza, 1976; Whitten, 1980; Kappeler, 1984b; Mitani, 1984). The female song is characterised by the great call – a sequence of notes which is species-specific and represents the climax point of the duet (Haimoff, 1984a). Males and females normally exchange notes and phrases during the rest of the duet, but at the initiation of the great call, the male falls silent and does not sing again until the female has completed her great call. Duets vary from species to species depending on participation of the sexes (Haimoff, 1984a). Those of *concolor, leucogenys* and *gabriellae* represent one extreme, with the great call being the female's only vocal contribution. Towards the other extreme are the duets of the siamang and hoolock gibbon, which are composed of equal vocal contributions from the sexes.

Why gibbons call is fundamentally related to defence of the mate and/or the physical territory (see a review in Chapter 8). Duetting has traditionally been considered a means by which the mated pair assert territorial exclusivity through a vocal inter-group spacing mechanism (Carpenter, 1940; Ellefson, 1968; Chivers, 1974; Marshall and Marshall, 1976; Tilson, 1979). Advertisement of the pair bond, or its maintenance, represent alternative, but not necessarily mutually exclusive, functions of regular duetting performances; gibbons sing either to strengthen their partnership, protect it from dissolution, or reduce the frequency, and hence, risk of territorial incursion (Chivers, 1974; Gittins, 1979; Brockelman, 1984; Raemaekers et al., 1984; Cowlishaw, 1992; 1996).

Differential functions are associated with the male and female song. Again, defence of territory is proposed but probably only applies to the song of the female (Cowlishaw, 1992; 1996). The resources the territory holds are, in effect, more important to the female gibbon since they are a strong determinant of her reproductive success. But the female gibbon may also sing with her mate, primarily to halt the unwanted advances of unattached females (Mitani, 1984; 1985a; Raemaekers and Raemaekers, 1985). Mate protection, and ultimately the maintenance of a monogamous social system, is likely to be the basis for the male song (Cowlishaw, 1992). Males exposed to recordings of songs invariably approach the source (Mitani, 1984; 1985a; 1985b; 1987a; 1987b; Raemaekers and Raemaekers, 1985) and they increase their frequency of singing in response to floater males (Cowlishaw, 1992). For the unmated male, soloing might aid his chances of acquiring a mate (Aldrich-Blake and Chivers, 1973; Ellefson, 1974; Tenaza, 1976; Kappeler, 1984b) or it might simply be a method by which to improve his song and/or locate mated pairs and the boundaries of their territory holdings (Mitani, 1988).

1.3.3 The social group – structure, monogamy and inter-individual relations

The family unit typifies the basic social structure of the gibbon – an adult pair joined by one to three offspring. An average group size of four is characteristic for most species (Leighton, 1987). Much larger groups have been observed for *H. concolor* (Delacour, 1933; Haimoff et al., 1986; 1987; Liu et al., 1989; Bleisch and Chen, 1991; Sheeran, 1993) but they are possibly a response to habitat fragmentation and the resultant loss of adequate dispersal areas for mature animals (Sheeran, 1993). Adult gibbons adhere to a monogamous social system according to Carpenter (1940). They form and maintain exclusive and life-long pair bond and represent the only breeding individuals in the social unit. Sexual interaction between the pair, however, is uncommon and occurs with any regularity only at distinct breeding periods (Chivers, 1974; Ellefson, 1974; Chivers and Raemaekers, 1980).

Birth intervals vary from individual to individual but young are produced on average every few years (Palombit, 1995). Offspring are tolerated by their parents until they reach sub-adulthood and/or sexual maturity where they experience the "period of peripheralisation" (Tilson, 1981). Increasing animosity, and at times outright aggression, from the adult pair, and particularly the same-sexed parent, forces the maturing gibbon to spatially and socially disassociate itself from the rest of the group. Eventually the subadult will leave the natal group to establish a territory and pair bond of its own (Chivers, 1974; Tilson, 1981; Leighton, 1987). Relations between other group members is remarkably congenial, especially for siamang family groups (Chivers, 1974; Gittins and Raemaekers, 1980; Fischer and Geissmann, 1990; Palombit, 1996) but overt social interactions remain uncommon; the social life of gibbons is rather appropriately referred to as "subdued" (Leighton, 1987).

Recent papers have shown that the relationship between monogamy and gibbons is not always a given. Palombit (1992; 1994a) discovered a "considerable turnover" in the composition of siamang and lar pair bonds at Ketambe, Sumatra, supporting observations by Chivers and Raemaekers (1980) who reported similar pair bond disruptions in groups of the same two species in Malaysia. While the death of a partner still accounted for the break down of some pair formations, intentional acts of desertion terminated others and, significantly, in a substantial number of cases. Rather than mating for life, some adult gibbons stayed with their partners for no longer than 17 to 24 months (Palombit, 1992; 1994a). Other gibbons have been found to investigate more temporary associations or consortships, primarily in the form of extra-pair copulations or EPCs (Palombit, 1994a; 1994b; Reichard, 1995). In this case, the rather extreme act of desertion has been replaced by occasional visits to neighbouring members of the opposite sex.

The existence of trios amongst some populations of gibbons suggests that new or additional partners are not always acquired outside the original group structure. Trios tend to occur amongst hybrid populations (Brockelman and Gittins, 1984; Marshall et al., 1984; this study) and in areas of habitat disturbance (Liu et al., 1989; Bleisch and Chen, 1991; Sheeran, 1993) but pure species trios residing in primary forest have been observed for *H. pileatus* (Srikosamatara and Brockelman, 1987), *H. hoolock* (Choudhury, 1990; Ahsan, 1995) and *H. lar* (Bartlett and Brockelman, 1996; Brockelman, 1997; Sommer and Reichard, in prep.). Most trios are polygynous but polyandry is not unknown and the presence of two infant carrying females in a *pileatus* trio (Srikosamatara and Brockelman, 1987) indicates that sexual interaction is not always restricted to the original pair.

1.3.4 Territory maintenance and intra-group contact

Within the larger home range, gibbons establish an area or territory which is routinely guarded against incursions from neighbouring groups of conspecifics. Advertisement of the territory holding and its defence is primarily achieved through the production of morning songs and physical contest on boundaries (Chivers, 1974; Gittins, 1979; 1980; Gittins and Raemaekers, 1980; Whitten, 1982c; Islam and Feeroz, 1992a; Ahsan, 1994). What the territory represents to the mated pair is still debated. Mitani's (1987a) and Raemaekers and Raemaekers' (1985) experiments, in which gibbons were exposed to the song of conspecifics, combined with Brockelman and Srikosamatara's (1984) analysis of sex-related roles in inter-group encounter behaviour, suggests that while the female is defending the *physical* territory, or more exactly the resources within it, the male is defending his mate.

Being a territorial animal, interactions between neighbouring groups are usually hostile and meetings on boundary areas often escalate into lengthy and aggressive clashes. The frequency of inter-group encounters varies from group to group and species to species, but common behavioural trends exist. Males regularly occupy the vanguard position and engage in boundary chases which might involve actual physical contact (e.g. striking, biting) with the opponent. Females normally retire to the background, advertising their hostility through song. But the role of males and females can inter-change and coincide. Adult female Kloss and Müeller's gibbon do lead or join their mates in chase-and-strike attacks (Tenaza, 1975; Mitani, 1985a) and males often contribute to the song of the female to produce a duet. During particularly aggressive encounters, members of both groups will spend considerable time in multiple chase formations where sex and age rarely dictates who attacks who.

Inter-group contact, however, is not always of an antagonistic nature. Reichard and Sommer (1997) observed lar gibbons making "friendly" approaches to members of neighbouring groups. EPCs have already been mentioned but adult males are also known to consort with immatures from other groups. The reaction of the infant and the relatives of the infant varied with each encounter but it is interesting to note that at times such approaches were received with little or no anxiety (Reichard and Sommer, 1997; Ulrich Reichard, 1998 pers. comm.).

1.4 Research Interest

1.4.1 Hybridisation and primate behaviour

The identification of primate hybrid zones has not always been followed by intensive studies on the social and ecological behaviour of the hybrid population, so there is a dearth of information on the influence, if any, hybridisation exerts on either or both of these behavioural parameters. Reports that do exist in the literature, while informative, represent quite different hybrid scenarios and are hence difficult to relate, both to each other and the situation at Barito Ulu. Nonetheless, before the aims of this research are stated a summary of these will be presented below.

Although hybrid baboon troops in the Awash Valley displayed many behavioural traits characteristic of the parental type they resembled morphologically, deviations to some social behaviours were evident and considered a result of gene flow from the second parental species (Nagel, 1973; Kawai and Sugawara, 1976; Sugawara, 1979; 1982; 1988). For example, the flow of *anubis* genes into the *hamadryas* population appears to have affected the "possessive" or herding behaviour of *hamadryas*-like males, knocking out key behavioural links (from *directing visual attention towards a female* to *giving neck-bites to a female*) in the principal behavioural pathway (Nagel, 1973; Sugawara, 1982). This differentiation in the herding ability of hybrid males has, in turn, altered the formation of sub-groups, with extremes in social unit composition. While some males have gained access to a large number of females, other males formed only very small one-male or pair-units or, in some cases, social bands containing no females at all. Gene flow in the opposite direction (i.e. *hamadryas* genes into the *anubis* population) has, in contrast, disrupted ties between females and between males, resulting in a constant change-over in subgroup composition and hence reduction in overall group integration. Sequential structures of male-specific behaviours have also been modified by hybridisation with their manifestation closely linked to the genetic make-up of the individual (see Sugawara, 1988). Olive and hamadryas baboons represent species which differ quite significantly in aspects of both their social and ecological behaviours, but what of hybridising primate taxa which are closer in their behavioural repertoire?

Field studies on Sulawesi macaques remain preliminary and research that has been completed suggest that they do not differ greatly in their behaviour (Dixson, 1977; Hadidian, 1980; Watanabe and Brotoisworo, 1982; Thierry, 1984; 1985; 1986; Baker and Estep, 1985; Petit and Thierry, 1992; 1994a; 1994b). A brief study of captive *M. ochreata* x *brunnescens* hybrids revealed the expression of a mosaic of agonistic, affiliative and sexual traits, specific to one or both of their parental types (Baker and Bynum, 1989). Guenons are also a relatively uniform group behaviourally but, in contrast to the hybrid macaques, both wild and captive hybrids exhibited no observable variation in social display (Struhsaker et al., 1988; Erhart et al., 1996). Instead, ecological responses were altered, specifically in their choice of food plants (Struhsaker et al., 1988). Hybrid *ascanius* x *mitis* guenons subsisted on diets comprised of food species used by both, one or neither of the parental species. These findings led Struhsaker et al. (1988) to argue that the successful integration of hybrids into redtail groups is evidence of behavioural plasticity between the parental species, indicating that social experience rather than genetic factors directs social affinities and displays. Behaviours which are probably under greater influence of genetic control include feeding ecology and mate choice.

1.4.2 Aims of the research

The Barito Ulu hybrid gibbon population represents a unique study group, by virtue of its size, the variability of resident genotypic forms and, ultimately, the apparent (reproductive) success of the population itself. Research by Mather (1992) focussed on estimating the nature and extent of the hybrid zone and describing (some of) the modifications exerted on song structure and singing behaviour. Since then, occasional studies have been conducted in an attempt to compile long-term information on hybrid gibbon behavioural ecology, but inconsistencies in measuring techniques and the brief nature of observation periods have provided only sporadic insight into the social and ecological behavioural repertoire of the hybrid gibbons.

This represents the first long-term behavioural study on *albibarbis* x *muelleri* hybrids and, in describing their behavioural ecology, I aim to answer the following questions:

1. Are there any observable changes to either the social or ecological behavioural repertoire of *albibarbis* x *muelleri* hybrid gibbons, compared to:
    a. the parental taxa *Hylobates agilis* and *H. muelleri*?
    b. the lar group?
    c. and gibbons in general?
2. Of the effects observed, which of these can be identified as being directly influenced by hybridisation?
3. Of those behaviours considered to have been modified by hybridisation, do they have any influence on the manifestation of other, closely related behavioural parameters?
4. Of those behaviours considered primary (2) or secondary (3) consequences of hybridisation, to what extent do they impinge on the reproductive success of the individual and the group displaying these behaviours and, by extrapolation, the population as a whole?
4. Of those behaviours not considered to have been unconditionally modified by hybridisation, have any been described for other gibbon populations and how do these relate to the recent work of Ryne Palombit, Ulrich Reichard and Volker Sommer which has challenged long held theories of gibbon ecological and social life?

2

The Study Site and Methods

2.1 The Study Site

2.1.1 Borneo

The island of Borneo represents the largest and most complete expanse of tropical rainforest within Indo-malaya (MacKinnon et al., 1996). Consistent patterns of rainfall and warm temperatures have produced an intensely rich floristic diversity including 10,000 to 15,000 species of flowering plants, 3000 species of trees (267 of which are dipterocarps), 2000 species of orchids and 1000 species of fern (Ashton, 1982; Whitmore, 1984; MacKinnon et al., 1996). Sharing both Asian and Australasian floristic elements, the forests of Borneo have in turn enabled a varied faunal distribution to flourish, including many endemic species (Inger, 1966; Smythies, 1981; Payne et al., 1985; Steubing, 1991; MacKinnon et al., 1996).

While soils are generally poor throughout Borneo, their composition is variable and has led to the establishment of eight primary forest formations – lowland and hill dipterocarp, mangrove, fresh water, peat swamp, ironwood (*ulin*), heath *(kerangas)*, and montane. The island exhibits substantial stratification of floral and faunal forms, and diversity is further increased by natural geographic barriers, to which the extensive river systems and the mountainous regions of the centre and the north greatly contribute. MacKinnon and MacKinnon (1986) have recognised nine basic biogeographical units for Borneo and the adjacent islands of the Natuna archipelago and Palawan which reflect the differences in endemism and diversity of plant and animal species found between these zones.

The fauna of Borneo is Asian in origin. At least 222 mammalian and 420 (resident) avian species have been identified (Smythies, 1981; Payne et al., 1985) and comparable or even greater variation is evident for reptiles, amphibians, fish, and invertebrates (Inger, 1966; Kottelat, 1982; Steubing, 1991; MacKinnon et al., 1996). Endemic species are common; of known species they range from 8.8% for birds to 37.8% for fish. Integrated with typically Bornean faunal forms are immigrant species from Sumatra which entered Borneo during the last Pleistocene glacial via a land bridge which connected West Kalimantan to the 'mainland' (Bodmer et al., 1991; MacKinnon et al. 1996). During the glacial these populations were restricted to the north-east and south-west of the island but subsequent improvements to the weather saw a steady expansion of both immigrants and endemics into other parts of the island (Bodmer et al., 1991). The impenetrable rivers and mountainous terrain of the centre, however, largely halted the two columns of migration, maintaining two basic (Bornean and Sumatran) faunal compositions in the north-east and south-west respectively. Animals who were able to penetrate geographical barriers established themselves successfully in their new habitats and in some cases hybridised with interspecific counterparts.

Humans arrived in Borneo at least 40,000 years ago (Harrisson and Harrisson, 1971; Harrisson, 1984; Bellwood, 1985). Multiple waves of migration have followed since, from the ancestors of the indigenous Dayaks to various groups of Malay, Filipino, Arab, Chinese and Indian settlers followed more recently by transmigrants from Java and other parts of Indonesia. Approximately 12.5 million people now live in Borneo (Buku Statistik, 1991 cited in MacKinnon et al., 1996), the majority of whom reside in the coastal and lowland areas. The poor drainage and swampy nature of the lowlands has restricted overland travel, generating a reliance on river transportation that continues today. For this reason, the interior remains largely unpopulated and mostly home to the indigenes of Borneo, the semi-nomadic Penan and largely sedentary Dayak who account for a quarter of the Bornean population. Representative of a diverse group of tribal peoples, the Penan and Dayak followed somewhat differential methods of subsistence. While the Penan exclusively used the forest for the supply of foods and trade materials, the Dayak established communities along the river's edge and constructed series of agricultural plots or *ladangs* for the bulk of food production (Langub, 1974; Ave and King, 1986; Hoffman, 1986; Sellato, 1989). Through the encouragement of the Indonesian and Malaysian governments, and the exploitation of forests for timber and mineral reserves, recent times have seen Penan and Dayak groups abandoning some aspects of their traditional lifestyle to establish more permanent settlements.

2.1.2 Barito Ulu and Muara Rekut

2.1.2.1 Project Barito Ulu and the establishment of the Rekut basecamp

In 1986, David Chivers and colleagues carried out reconnaissance work in the watershed of the upper Barito River, Central Kalimantan, Indonesia with the aim of establishing a research project (Project Barito Ulu) to investigate the role animal-plant interactions play in the regeneration of rain forest. Two years later, the first field study began and in the last ten years researchers primarily from Indonesia, the U.K., Australia and New Zealand have joined the Project to work on a wide range of zoological, botanical, geological and anthropological topics.

The main field site (Muara Rekut or *mouth of the Rekut*) is located on the Busang River and bordered on its eastern boundary by the Rekut river (see Figures 2-1 to 2-3). The Busang is a tributary of the second largest river in Borneo, the Barito, which runs 900 km from the town of Muara Joloi in the north of Central Kalimantan to the city of Banjarmasin (South Kalimantan) and on to the South Java Sea. The Barito is formed by the convergence of the Joloi and Murung rivers at a point approximately 14 km downstream from Muara Rekut and adjacent to the village of Muara Joloi. The Busang joins the river system 10 km up from this point of convergence where it drains into the Joloi river.

Figure 2-1 Borneo and location of study site.

Figure 2-2 Location of Muara Rekut field site in the Barito Ulu watershed.

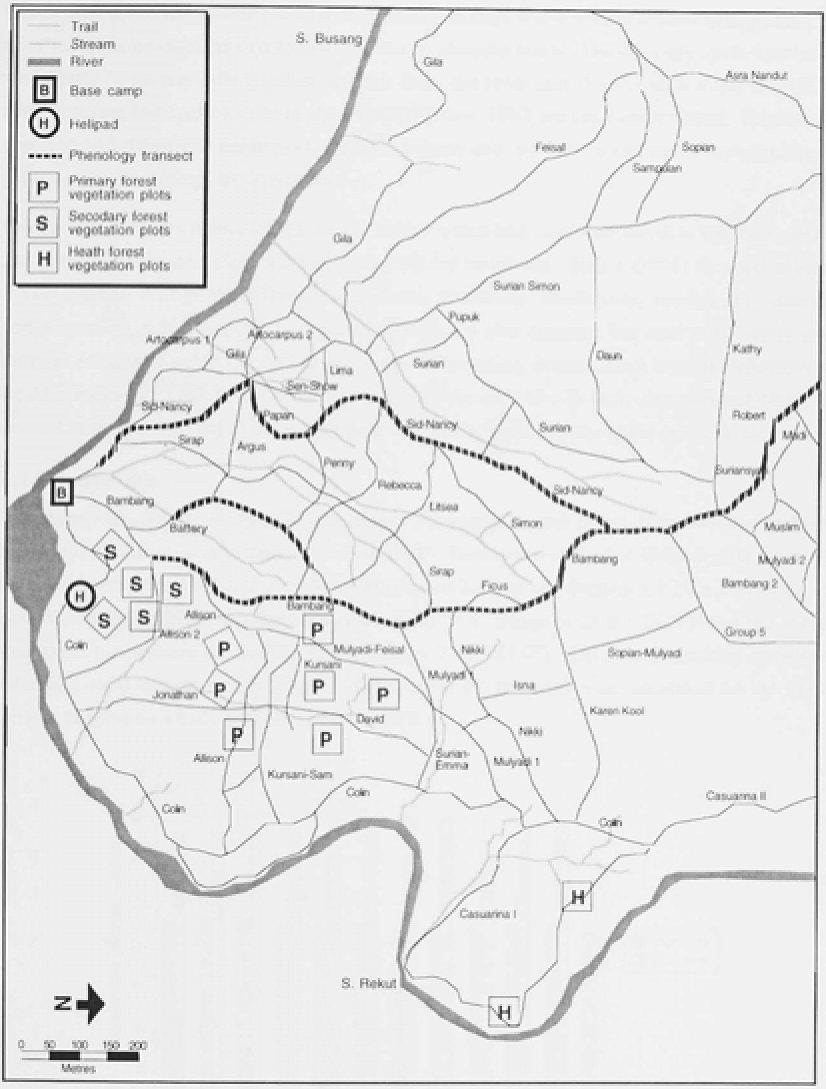


Figure 2-3 Muara Rekut field site – location of basecamp, trails, phenology transect, and primary, secondary and heath forest vegetation plots.

2.1.2.2 Geological, topographical and soil features

Located in the southern ranges of the Müller Mountains, one of the secondary mountain chains running through the centre of Borneo, the topography of Barito Ulu is typically rugged. Altitude ranges from 100 to 300 metres a.s.l., and slight inclines grade into hilly and sometimes mountainous terrain. Rocky banks and gorges line the river, the gorges so steep in places that access from the river is severely impeded. The rivers themselves are generally fast flowing and subservient to the fluctuating patterns of rainfall. On days when rainfall is particularly heavy, a river may rise as much as two to three metres in as many hours. During a dry spell, however, when little or no rain falls for four or more days, the river may drop to such a low level that river transport is disrupted or even abandoned (Mather, 1992; personal observation). Rapids are common and dangerous features of the inland rivers and, with the water as the main transport route, annual drownings are inevitable.

The rock formations characteristic of the Barito watershed were laid down in the Palaeocene and lower Miocene and show marked compositional variability. House (1991) detected at least 7 compounds within these rock formations, including sandstones, mudstones, quartz, conglomerates, schists, gneiss and granite. Soils are also complex but tend to be sandy and nutrient poor, and exhibit a yellow to orange colouration derived from iron and aluminium oxide constituents. While the concentration of nutrients is low in both, the marginal nitrogen content in podzols has led to the establishment of heath forest in parts of the research site.

2.1.2.3 Climate

The equatorial position of the field site creates a climate of warm to hot days, cool nights, high humidity, and a consistent delivery of rainfall. Temperatures varied little over the period between September 1995 and August 1996 (Figure 2-4 and see Section 2.2.2 for collection of climatic data). The mean minimum reached 22.5° C (range = 21.0 - 24.0°) and the mean maximum temperature reached 33.6° C (range = 27.0 - 37.0°). Likewise, humidity remained relatively even and extremely high. A mean of 94.1% humidity was calculated for the same period, ranging on a daily basis from 80 to 100%.

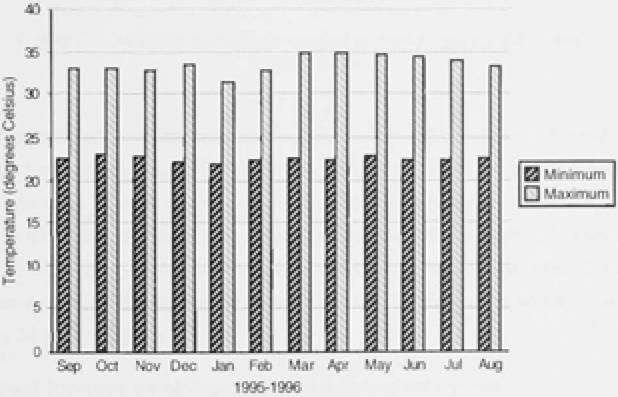


Figure 2-4 Monthly variation in mean maximum and minimum temperatures: September 1995 - August 1996.

While temperature stability excludes true seasons, or at least those found in more temperate environments, the pattern of rainfall in Borneo does introduce two recognisable climatic divisions – the wet and the dry. The dry spell at Rekut normally occurs between June and September followed by a four month period of intense rainfall starting in October and ending in

January (Rupert Ridgeway, 1995 pers. comm; Mather, 1992). Rainfall in Borneo, however, is not always so predictable nor does it follow a strictly annual cycle, as evidenced by the unusual fluctuating pattern occurring at Rekut during 1995 and 1996 (Figure 2-5). Rather than a concentration of wet and dry weather at set times of the year, one month of heavy rain was almost invariably followed by a month of reduced rainfall, in some instances the decline being quite considerable. The greatest levels of rain did fall at the expected time, despite two of the wet months (October and December 1995) having the lowest and second lowest readings, but it was the two dry seasons, covering the start and end of the observation period, which showed the greatest aberration. Instead of the normal reduction, rainfall actually increased to levels higher than that found for other months, even for some of those in the designated wet season. These unusual rainfall patterns led to some alteration in the forest's phenological activity and possibly disruptions to the feeding behaviour of its faunal inhabitants.

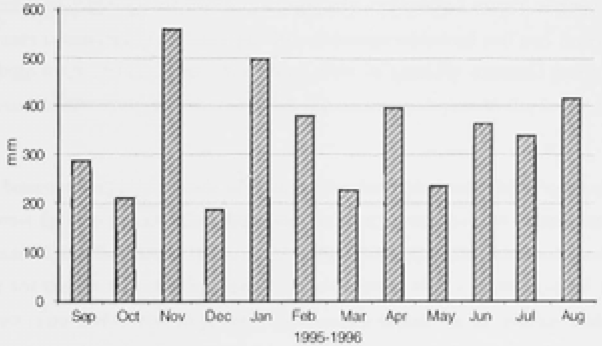


Figure 2-5 Monthly variation in rainfall at Rekut: September 1995 - August 1996.

Because of the unusually wet dry seasons[1], rainfall between September 1995 and August 1996 was especially high, calculated at 4119.3 mm and falling on 59.7% of days in the annual period. Sixteen straight days of rain at the end of August 1996 represented the longest period of consistent wet weather, while a 12 day period encompassing the last part of February 1996 and the first week of March 1996 saw no rain whatsoever. On average, wet days were more common than dry, rain activity occurring on 18.3 days in the month and as much as 99 mm falling over a 24 hour period.

2.1.2.4 Forest formations at Rekut and phenological cycles

The field site is comprised of three primary forest types and encompasses an area of 400 hectares. Predominant is the ubiquitous dipterocarp forest, so-called by the prevalence of trees from the family Dipterocarpaceae. Standing as high as 60 metres, but more commonly around 45 metres, the dipterocarps may represent as much as 10% of all resident trees (Ashton, 1982; MacKinnon et al., 1996). At Muara Rekut, this proportion is higher still (27.0%), indicating the

---

[1] The following dry season coincided with an El Niño induced drought which resulted in drastically reduced rainfall levels (Kim McConkey, 1997 pers. comm.).

importance of this plant family in the composition of central Bornean forests. Tree species diversity is greatest in primary dipterocarp forest at Muara Rekut with at least 47 representative families, 108 genera and 322 species (see Tables III-1 and III-4 in Appendix III for list of families and genera and list of species found in primary forest vegetation plots). Dipterocarpaceae is the predominant family in primary forest, followed by Euphorbiaceae, Anacardiaceae and Lauraceae. *Shorea* contributes greatly to the overall dominance of the dipterocarp family followed by *Dipterocarpus* and, to a much lesser extent, *Vatica* and *Hopea*. Other common trees in primary forest include *Swintonia glauca*, *Chisocheton* sp. and *Gonystylus* sp.

Climbing plants are another prevalent feature of the dipterocarp forest and includes fruit bearing vines wrapped around young tree forms, large woody climbers, strangling figs and clinging rattan. Epiphytic plants, such as ferns, colonise many of the tree branches. The forest floor itself is a mosaic of vegetational forms. A regularly replenished carpet of dead leaves, fallen fruit and flowers occasionally exposes patches of orange-coloured soil and is criss-crossed by the roots of both trees and climbers. Seedlings grow in spatially scattered patterns, tending to flourish in areas where sun penetrates through the emergent layers to the lower reaches of the forest.

Interspersed between larger stretches of dipterocarp forest is heath forest or *kerangas*. Heath forest is a forest formation extending from the Bornean coastline into inland areas of Borneo, normally founded on the coarsely textured soils (derived from siliceous parent material) inappropriate for the growth of other forest types (Brunig, 1974). The physical appearance of the heath forest is quite different to primary dipterocarp forest. Trees tend to be shorter, smaller and more densely packed together (Kartawinata, 1978; 1980; Whitmore, 1984; van Schaik and Mirmanto, 1985) and the overall hue of the foliage is closer to a reddish brown rather than the green-blue of the dipterocarp forest. Many of the plants of the heath forest have adapted to the quick drainage of the soils by producing pale, shiny and/or small leaves and dense tree crowns that aid in the restriction of water loss through transpirational cooling (Brunig, 1971). While individual species are still subject to desiccation (Peace and MacDonald, 1981), it is the features of the forest as a whole which act to reduce extensive water loss (MacKinnon et al., 1996).

Dipterocarp and heath forests share about a quarter of resident species. Dipterocarps still represent a significant proportion of the floral composition but in heath forest overall species diversity tends to be much lower (Brunig, 1974; Proctor et al., 1983). At Rekut, heath forest comprises 23 families, 57 genera and 111 species of plants (see Tables III-2 and III-5 in Appendix III for list of families and genera and list of species found in heath forest vegetation plots).

The third forest type found at Muara Rekut is an approximate 6.8 hectare belt of secondary forest surrounding the basecamp. A consequence of past agricultural activity, tracts of secondary forest range in age from around 20 to 50 years. Secondary forest is characterised by its composition of important tree species, in particular the prominence of the family Hypericaceae, but shares many minor tree species with other resident forest formations. Tree distribution displays an inconsistent array compared to that observed in primary forest. In areas where the forest has been regenerating for only 10 to 20 years, the canopy is lower and, in some places, discontinuous. The less dense nature of the canopy also allows more sunlight to diffuse through to the forest floor, enabling seedlings and other low-lying plants to flourish.

In secondary forest at Rekut 32 families, 71 genera and 137 species are resident (see Tables III-3 and III-6 in Appendix III for list of families and genera and list of species found in secondary forest vegetation plots). Euphorbiaceae and Hypericaceae, two plant families common to re-growth forests, overshadow the dipterocarp component. Their dominance is accounted for by the large number of secondary forest pioneers – *Macaranga, Glochidion* and *Cratoxylum* – which make up 42.3% of all species. *Pternandra* and *Dillenia* trees also grow in reasonable numbers as do species of the *Artocarpus* genus.

Plant part production in primary forest over the period September 1995 to August 1996 is illustrated in Figures 2-6 to 2-8. Despite the unusual rainfall pattern of the 1995-1996 season, peak production of young leaf, flower and fruit followed the same basic temporal pattern observed in previous years. A steady increase of young leaf growth reached a peak in December 1995, when 45.3% of all phenology trees underwent young leaf flushing, and declined again in January to exhibit a relatively constant production (around 15-20% of trees) to August 1996. Flowering occurred throughout the year too, but not as prominently. An average of 3.1% of trees produced flowers at any one time. Flowering activity peaked in December (5.2% of trees) and continued into January, followed by another peak in May. Plants often flower in response to water stress (Whitmore, 1984) and at Rekut this normally took place two months after a period of dry weather (Mather, 1992). An examination of rainfall patterns in the months preceding the two flowering peaks found a similar scenario – rainfall was either low (October), concentrated into just 12 days of the month (September) or there was an unusual and extended period of dry weather (March). Fruiting also occurred in two peaks, one to two months after the intense periods of flower production. Eight to ten percent of phenology trees bore fruit during this time.

2.1.2.5 Faunal composition

Since the late Pleistocene, when 'mainland' species crossed over from Sumatra into West Kalimantan, the expansion by endemic and immigrant fauna into and across central Borneo has been obstructed by the immense width of the Barito and Kapuas rivers. The high altitude of the headwaters, where the significant narrowing of rivers represents a less formidable barrier to river crossing, has further limited migration as some lowland species are simply unable to inhabit these areas (MacKinnon et al., 1996). Nonetheless, significant faunal diversity persists in this overlap zone and Barito Ulu is home to a wide range of species representative of Sumatran, Bornean and intermediate forms. Densities for major faunal groups (e.g. primates, ungulates), however, tend to be low compared to other parts of Southeast Asia, primarily because heavily leached soils that are characteristic to central Borneo retard major fruit production (Bodmer et al, 1991).

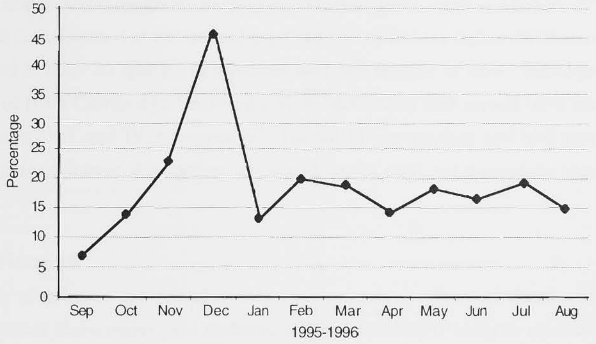


Figure 2-6 Monthly variation in the proportion of plot trees producing young leaf.

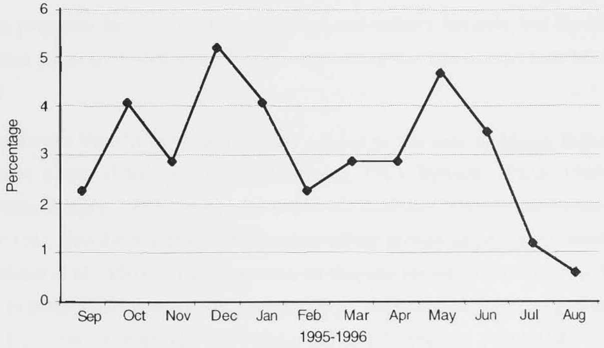


Figure 2-7 Monthly variation in the proportion of plot trees producing flower.

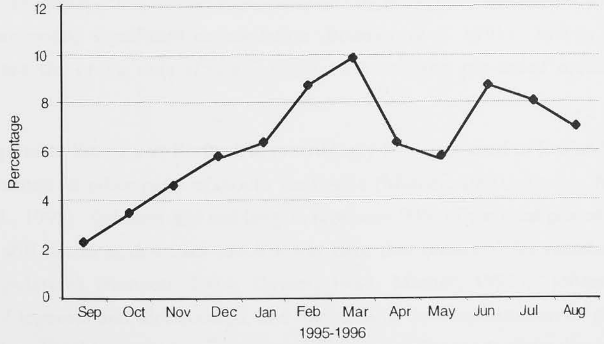


Figure 2-8 Monthly variation in the proportion of plot trees producing fruit (excluding fig).

Survey work conducted throughout Barito Ulu (Mather, 1990, cited in Mather, 1992; Bodmer et al., 1991) and concentrated at the immediate field site of Muara Rekut (Wilkinson et al., 1991) has recognised at least 80 species of mammal and 269 species of bird. Subsequent studies by undergraduates from Cambridge University, Kim McConkey and myself have added to this list (see Appendices IV.1 and IV.2 respectively for list of mammalian and bird species observed) and, in two cases, discovered a species of cat and one of otter not previously known to occur in the area.

2.1.2.5.1 Primates

Eight species of primate are found within the watershed. Four of these – the long tailed macaque (*Macaca fascicularis*), the endemic red leaf monkey (*Presbytis rubicunda*), slow loris (*Nycticebus coucang*) and western tarsier (*Tarsius bancanus*) – reside at the Rekut field site. While *M. fascicularis* largely ranged along river edges, the notoriously shy *P. rubicunda* remained inland, often splitting into foraging groups and occasionally coming down to the ground to search for insect larvae (personal observation). The slow loris and tarsier were less easy to detect, primarily because of their nocturnal and solitary lifestyle, but the latter have been observed within patches of secondary forest surrounding the basecamp (Kim McConkey, 1998 pers. comm.)

Proboscis monkeys (*Nasalis larvatus*) occupy habitat to the east of Muara Rekut. Originally considered to be a coastal living primate (Wolfheim, 1983; Bennett, 1986a; 1988; Bennett and Sebastian, 1988; Yeager, 1989), and restricted to the outlying swamp and mangrove forests, it was not until 1986 that the existence of inland dwelling groups of proboscis monkeys was first detected (Bodmer et al., 1991). Their location on riverine forests adjacent to the Murung River dramatically extended their known geographic range. My own sighting of proboscis monkeys in secondary forest on the Barito River (between Muara Teweh and Puruk Cahu – August 1995) suggests that this species is much more adaptable to inland forests than first thought.

The rare and little known white fronted langur (*Presbytis frontata)* is also found in the vicinity of the Murung River and, interestingly, in regions where the red leaf monkey is more or less absent. Intense interspecific competition, produced by ecological similarities, is probably the key factor preventing significant co-habitation (Bodmer, et al. 1991). Just as uncommon at Barito Ulu are the orang utan (*Pongo pygmaeus*) and the pig-tailed macaque (*Macaca nemestrina).*

The overall primate biomass at Barito Ulu is strikingly low compared to lowland or hill forest field sites located in other parts of South East Asia (Mather, 1990, cited in Mather, 1992; Bodmer et al., 1991). Gibbons and red langurs represent 90% of the total primate biomass but langurs are still found at densities much lower than that observed for mainland and other Bornean populations (Bennett, 1984; Davies, 1984; Mather, 1992). Differences in the proportion of legumes and dipterocarps, and variation in the concentration of plant chemical defences and availability of food species, probably accounts for much of the diversity in density measures. A reduced selection of fruit species at Barito Ulu has also been proposed as a primary factor leading to low densities of orang utan (Bodmer et al., 1991; Mather, 1992) as has the location of salt licks and the low level of salt in central Bornean plantstuffs (Payne et al., 1985; Caldecott, 1986, cited in Mather, 1992; Payne, 1988). Specific habitat requirements is another limiting factor, as evidenced by the tendency for local white-fronted langurs to inhabit forest where large tree and strangling fig density is high and *Eusideroxylon zwageri* trees are present (Mather, 1992).

2.1.2.5.2 Other mammals

Predominant ground dwelling mammals at Rekut included the bearded pig (*Sus barbatus*), the common (red) and Bornean yellow muntjac (*Muntiacus muntjak* and *M. atherodes)*, sambar deer (*Cervis unicolor*) and lesser and greater mouse-deer (*Tragulus javanicus* and *T. napu*). These species, excluding the bearded pig, were regularly encountered when walking forest trails but their exploitation by local hunters meant that the frequency of auditory detection (of vocalisations) far exceeded actual sightings. Pigs were more commonly spotted but all sightings occurred at basecamp when pigs made night-time raids on food crops. No pigs were observed in the forest but numerous nests were found. Other terrestrial animals included the sunbear, porcupine, pangolin, various mustelids (weasels, badgers and otters), cats, mongoose, rats, and some species of civet and squirrel. Two species not known to inhabit the headwaters of the Barito were also discovered during the 1995-1996 study season — the Oriental small-clawed otter (*Aonyx cinerea* – personal observation) and the Bay Cat (*Catopuma badia* – Allan Williams, 1995 pers. comm.)

Arboreal and semi-arboreal animals spotted during gibbon follows or around camp were predominantly bats (including various fruit, leaf-nosed and horseshoe bat species) and squirrels, but the colugo was also observed. Previous studies had found the large flying fox and six species of tree-shrew, but only a few were observed during the 1995-1996 research period.

2.1.2.5.3 Birds

Rekut abounded with an extensive array of birds. Within the forest, various species of hornbills, woodpeckers, bulbuls, bee-eaters, barbets, sunbirds, pigeons and babblers (amongst many others) were often observed, while eagles and other birds of prey remained a common sight soaring above the canopy. Down along the river's edge, and particularly in the early morning and late evening, kingfishers and fish-eagles ploughed the Busang river. Not all local species of kingfisher ate fish; some were also found catching insects in the trees bordering the basecamp. The great argus (*Argustanus argus*) is also resident at Rekut, and cleared areas used by the males as "dancing grounds" contrasted with the normal clutter of the forest floor.

2.1.2.5.4 Reptiles, amphibians and invertebrates

Monitor lizards, skinks and geckoes represented regular reptilian visitors to the basecamp but other legged reptiles were rarely seen either at camp or in the forest and remain unidentified. Five types of snake were also observed – king cobra, python, whip snake, pit viper and one unknown. Frogs remained visually undetected but night calls indicated a numerous presence.

Little research has been conducted on invertebrates at Rekut other than some work on moths, butterflies and dragonflies. Invertebrates dominated the forest in terms of sheer number and permeated every niche. At least sixteen broad morphological types were detected including beetles, stick insects, ticks, ants, termites, flies, mosquitoes, leeches, hornets, bees, midges, centipedes, millipedes, spiders (including the gibbon spider and bird eating spider), and scorpions.

2.1.2.6 Human activity at Barito Ulu

Compared to the Barito River, where villages regularly line the water's edge, the Barito Ulu watershed is largely uninhabited. Probably the greatest deterrence to large scale settlement is the problem associated with river transport. The rivers are notoriously difficult to negotiate and their use dependent on water levels, particularly if the mode of transportation is the slow moving *klotok*. The introduction of a river taxi service using long boats driven by 400 hp engines has substantially improved river transport, connecting the floating village of Teluk Jolo, the endpoint of the Barito speedboat system, with the upriver settlements of Muara Joloi, Muara Rekut and Parahau. Even so, the long boat service is not always reliable and can only be used when river levels are safe, leaving people stranded and unable to collect additional or essential stores during periods of low rainfall (personal observation).

While transmigrants and Javanese public service employees have moved to villages and towns further down the Barito river, the upper Barito and its tributaries are populated predominantly by the indigenous Dayak peoples. Many of the Barito Ulu Dayaks have converted to Islam but animist beliefs are still followed by some, and Christian missionaries, working from the provincial capital of Palangkaraya, make regular visits to the area (personal observation). The village of Muara Joloi is a symbol of the mélange of religious beliefs existing at Barito Ulu, divided into two sections dependent on faith. Muara Joloi I, with a population of just under 380 people, is Muslim while the 369 residents of Muara Joloi II observe an animist spirituality influenced to varying degrees by Christianity. Further up the Busang river, and past the basecamp, animism and/or Christianity replaces Islam. The latter is certainly not absent, however, and may be gathering a growing following, as evidenced by the transportation of an new *mesjid* dome up river in 1996 (personal observation).

On a day to day basis, differences in religious or spiritual affinity rarely disrupt community harmony but a sense of elitism does pervade the attitudes of the Dayaks who have adopted Islam. Quick to disassociate themselves from their Christian, and especially animist neighbours, they insist on both being known as Dayak Muslims and regarded as a separate cultural grouping (Kursani and Mulyadi, 1996 pers. comm.). Non-Muslims, in turn, are viewed as a somewhat backward component of the population, collectively and simply referred to as Dayak (personal observation). Religious partitioning also affects, and to an extent dictates, the occupational roles of local residents. Muslim Dayaks in Muara Joloi I and Teluk Jolo dominate, even control, commercial trade between the more remote areas in the watershed and the larger towns (Puruk Cahu and Muara Teweh) and cities (Banjarmasin) down south. Animist Dayaks, however, tend to rely on a lifestyle based on more traditional occupations such as the gathering of aloewood or *gaharu*, rattan, edible birdsnests or medicinal plants, fishing, and the hunting of forest animals. Hunting using dogs remains popular with the local animist population, the primary target being the bearded pig with some taking of deer (sambar deer, muntjac and mousedeer) and birds. The other activities, however, are becoming less and less viable. The introduction of electric fishing at the time of the study has already led to a vast reduction in fish numbers (Kim McConkey, 1997 pers. comm.). The trade in forest products is already extinct (Hall, 1993) or likely to be so in the very near future. Indeed, my own discussions with a group of *gaharu* collectors who passed through camp in May 1996 indicated that the money being paid was not worth the effort of collection. Expeditions were becoming increasingly longer as collectors needed to cover even greater distances to find new and productive sources of the sought after item.

Logging and mining industries, and to a lesser extent transportation, have given the men of Barito Ulu an alternative means of employment. Small scale logging is now illegal and instead work can be found with one of the four main logging companies, including Tunggal Pamenang, which has a large camp immediately north of Teluk Jolo. Activities range from felling of trees to the transportation of logs down river. In contrast, significant mining activity is restricted to the lower reaches of the Barito with local collection of gold or precious/semi-precious stones normally undertaken by family groups. Panning is still used to separate river sand from gold or stones but many families are now investing in engines that are secured on river rafts and used to draw up substantial quantities of sand for sifting (personal observation).

Food production, however, remains one of the more common forms of occupation. In the larger villages, small gardens are created but the growing of staples, such as rice, is reserved for the larger agricultural plots or *ladangs*. Created through slash-and-burn techniques and on land adjacent to the river and away from the village, *ladangs* are worked for one or two seasons by the one family before being left to regenerate. Rice forms the main harvest crop but cassava, corn, sugar cane, bananas, chillies, and additional indigenous food plants are also grown. The great majority of food grown in *ladangs* is used to supplement or comprise the majority of the diet of the tenant farmers. For some of the animist Dayaks it is also a primary source of income, in which produce is traded for money or coveted items such as coffee or sugar (personal observation).

2.2 Methods

2.2.1 Study site vegetation

2.2.1.1 Vegetational composition

Because the home range of the focus groups encompassed three different forest types (see Chapter 5), 50m x 50m plots in each were established for vegetational analysis (see Figure 2-3 for location of plots). A total of 14 plots were used – seven in primary forest (total area = 1.75 ha; 818 trees), five in secondary forest (total area = 1.25 ha; 701 trees) and two in heath forest (total area = 0.5 ha; 523 trees) – for a total of 2042 trees and an area representing 6.0% of the home range. Each plot tree had been tagged and given a four digit identity number. A database supplied by Dr Lazlo Nagy of Stirling University listed species identification for each plot tree as well as girth (measured in cm at breast height) and height (cm) measurements.

To estimate the distribution of plant families, genera and species in each forest formation and to compare these to the dietary choice of the hybrid gibbon, three commonly used measures were employed. Basal area was calculated in cm^2 and included only those trees whose girth was greater than 30cm. Tree species density was measured by dividing the number of individuals by the number of hectares, and relative density was calculated as the proportion of each species to the total number of species (Greig-Smith, 1964; Müeller-Dombois and Ellenberg, 1974).

2.2.1.2 Analysis of phenological cycles

Three of the plots used for the analysis of primary forest vegetational composition, and a phenology transect running through part of the home range of RBC1, were used for the collection of data on phenological activity, producing a sample of 443 and 172 trees respectively. Phenology trees in plots were monitored once a month, usually in the first week, by myself and/or Allan Williams. Transect trees were monitored three times a month by one of the workers as part of a long-term research project run by Dr John Proctor of Stirling University. To ensure comparability between the two phenological sources, only the recordings from the first of the tri-monthly transect monitors were combined with plot phenology data. Each tree, which had already been tagged and identified, was given a mark between 1 and 4 reflecting the degree of fruiting, flowering and young leaf flushing. A score of 1 meant no new or reproductive part growth, grading into a score of 4 which indicated maximum or complete coverage. When it came to measuring monthly variation in leaf, flower and fruit production, the 4 point scale was abandoned and plots tree were assigned either a 1 or a 0 depending on if they had produced that specific plant part or not.

2.2.2 Collection of climatic data

To assess the effect weather may exert on the use of basic behavioural activities (e.g. rest, feeding), conditions were recorded on each 10 minute scan. Eight categories, adapted from Davies (1984) and Stanford (1991), were defined and are given in Table 2-1. For statistical treatment, categories were reduced to three – sun, rain and cloud.

Table 2-1 Category of weather conditions recorded on each 10-minute scan.

Weather type category	Description of weather type
Sun 1	Full sun with clear skies
Sun 2	Mostly sunny, with 0-10% cloud cover
Sun 3	Mostly sunny, with 10-25% cloud cover
Cloud 1	Mostly cloudy, with cloud cover ranging from 30-50%
Cloud 2	Dark, overcast with up to 100% cloud cover
Rain 1	Light rain, skies may still be blue
Rain 2	Medium to heavy rain
Rain 3	Very heavy rain

Humidity levels, maximum and minimum temperatures were recorded once a day, around 1700 hours, using metric thermometers attached to one of the basecamp houses. Daily measures of rainfall were also collected at this time and were summed at the end of the month to give the total rainfall in mm.

2.2.3 Selection of study groups

Ten distinct gibbon groups were located within easy audible distance from Muara Rekut (see Figure 2-9). Three groups (RR1, RR2 and RR3) inhabit ranges to the south and east of the main forest reserve and across the Rekut river, while another two (BR1 and BR2) occupy habitat on the western bank of the Busang and directly adjacent to the basecamp. Within the forest spanning out from the basecamp, and protected by PBU, live another five groups – RBC1, RBC2, RBC3, RBC4 and RBC5.

Two, possibly three, unpaired males were also detected. A solitary male was observed in the upper regions of RBC2's home range and, two months later, travelling through the north-eastern boundary of RBC1's ranging area. It could not be confirmed that this male was the same individual but his acceptance of human observers on both occasions suggests that he was habituated. In 1991, Greenaway (unpubl.) and Lochowski (unpubl.) noted the presence of juvenile males in groups RBC1 and RBC3 and it is likely that the solitary males observed in the present study are one or both of these males (see Chapter 7). The second solitary male resided across the Busang river. This male, although never actually observed, was designated an unpaired male by virtue of his singing behaviour. A prolific singer, he called on almost every day of the observation period but on no occasion did he participate in a duet, his singing repertoire comprising just the solo.

The selection of focus groups depended on factors of habituation, ease of access to the home range, and ability to traverse the terrain. Starting in 1989, short-term studies had been conducted annually on the RBC gibbons, leading to the habituation of two groups and partial habituation of at least one other. It was decided that two of these groups – RBC1 and RBC2 – were the best study subjects since (a) their home ranges lay closest to basecamp and within an established network of forest trails, (b) they were fully habituated, and (c) previous research on these animals introduced a template on which I could base and compare my own data. Additional study groups were also selected from the RBC population. Attempts were made to locate BR and RR groups as they had as yet received no behavioural or ecological research attention. RR1 and RR2 were of particular interest since their ranges covered parts of heath forest (Surian, 1995 pers. comm. and personal observation). However, a combination of difficult terrain and the absence of habituation made sightings generally short-lived and the following of groups exceedingly difficult. RBC3 and RBC5 were therefore chosen as additional study groups.

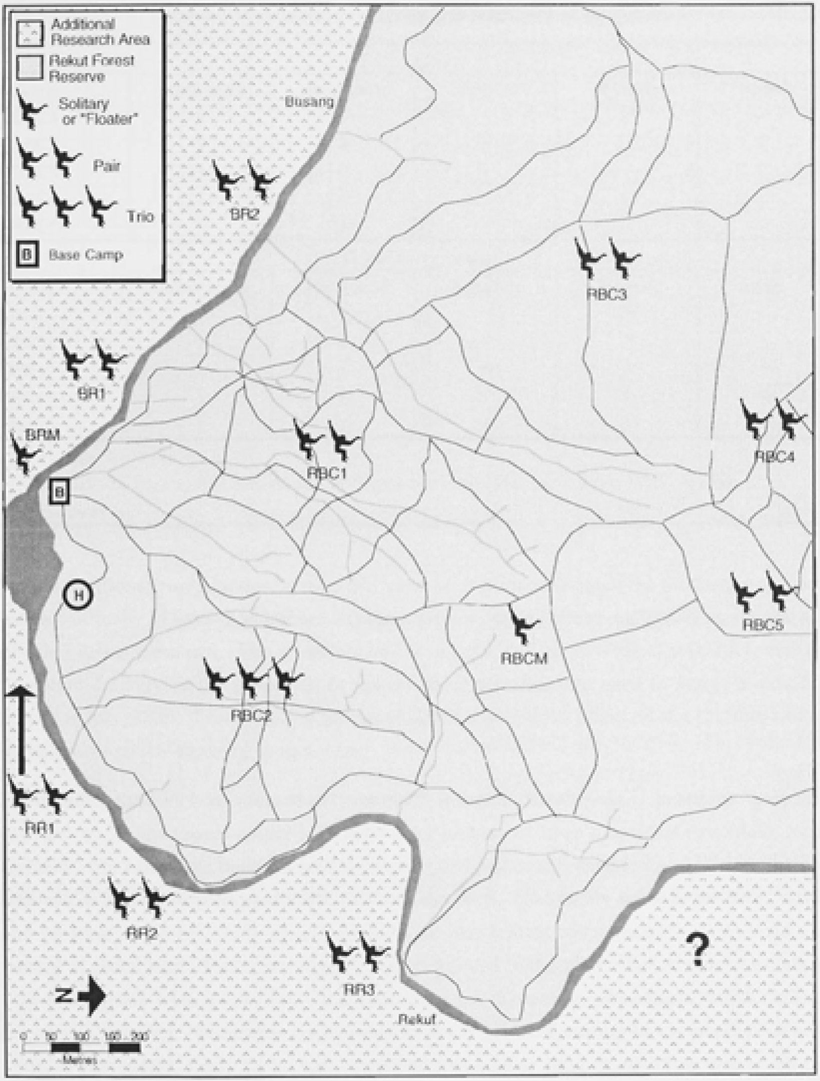


Figure 2-9 Location of groups and solitary individuals in research area.

2.2.4 Composition of groups and identification of individual gibbons

The composition of focus and other groups are shown in Table 2-2. Accurate identifications of group members could only be completed for RBC gibbons, giving a total of 5 adult males, 5 adult females, 1 subadult, two juveniles and two infants. Four of the five offspring were sexed – three females and one male.

Table 2-2 Composition of focus and additional study groups.

Focus groups

Group	Adult male	Adult female	Subadult	Juvenile	Infant
RBC1	1	1	-	1^F	-[1]
RBC2	1	1	1^F	-	1^F
RBC3	1	1	-	-	$1^?$
RBC4	1	1	-	1^M	-
RBC5	1	1	-	-	-

Additional groups

Group	Adult male	Adult female	Subadult	Juvenile	Infant
RR1	1	1	-	$1^{M?}$	-
RR2	1	1	*	*	*
RR3	1	1	*	*	*
BR1	1	1	1^F	*	*
BR2	1	1	*	*	*

^{F} = Female ^{M} = Male

[1] An infant was born to RBC1 in August or September 1996 (Kim McConkey, 1996 pers. comm.).

* Unknown

Within additional study groups, adult pairs could be confirmed through the production of duets but the difficulty in finding and observing these groups prevented data collection on age and sex of other group members. The co-production of a great call by two females in BR1, and the immature delivery of the great call by one of these females, was used to assign a subadult female to this group. Two chance sightings of RR1 identified the presence of a juvenile animal in the group, which appeared to be a male.

Physically, hybrid gibbons more closely resemble *H. agilis* than they do *H. muelleri*. Body hair is a dark chocolate brown colour with individual patterns of fawn to grey hair extending onto the back. For males, the lighter colour is concentrated just on the shoulders and shoulder blades whereas on females it is located lower down on the back. Underparts and legs are dark. Adult and subadult males are easily distinguished from their female counterparts by their build and pattern of facial hair. Males are slightly built compared to the pot-bellied females and, while both sexes retain white brows, only the males have the distinctive, white beard which outlines the cheeks and chin. Immatures are less easy to sex if genitalia can not be observed since both sexes display white, fluffy facial hair. Females start to lose their beards once they reach the early stages of sub-adulthood, the white hair eventually replaced by hair the same dark brown colour as that covering the rest of the body.

Four primary age classes were observed and defined in relation to body size, physical characteristics and distinctive behaviours (Table 2-3). Previous authors have recognised a fifth age-class – the adolescent (e.g. Carpenter, 1940; Ellefson, 1974; Tilson, 1979; Palombit, 1994a) or juvenile-II (Gittins, 1979) – which ranges from 4 to 6 years of age. The adolescent is described as a "medium sized animal (which) often travels and feeds alone" (Gittins, 1979) and the receiver of increasing aggression and spatial separation from its parents (Tilson, 1979). The juvenile female of RBC1 shared some behavioural traits with Gittens' (1979) juvenile-II, occasionally distancing herself from the other group members during bouts of travel and feeding. But her mother's response (i.e. contact calling) to these solitary forays and her small size indicated that she was still under the age of four. In the absence of an adolescent animal amongst the focus population, I have combined the juvenile/adolescent age classes.

Table 2-3 Description of age classes recognised for hybrid gibbons.

Age Class	Description
Infant	Between 0 and 2 years of age and of a very small size. Initially the infant is carried by its mother, probably for the first year of its life, but becomes increasingly independent of its mother between the ages of 1 and 2. Ingestion of solid food also starts at this stage but the infant still returns to its mother to suckle. Both sexes have white cheek and chin hair.
Juvenile/Adolescent	Ranges in age from 2 to 6 years. More or less complete independence from mother but still retains close contact and sleeps in the same night tree. Separation from the group elicits distress in the juvenile and searches and contact calls from the mother. Females begin to great call, if somewhat tentatively, with their mothers. Both sexes have white cheek and chin hair.
Subadult	Adult sized animal of six plus years. Males have developed the male-typical beard while females have lost the white cheek hair characteristic of younger forms. Great calling is more confidently given by females who regularly initiate or accompany their mother in the delivery of the great call sequence. Females also experience labial eversion which may make them more sexually attractive to their fathers.[4]
Adult	Physically no different from the subadult animal but have normally left the natal group and formed a pair-bond of its own. Adults duet regularly and defend the physical territory through aggressive inter-group encounters. Age is difficult to determine but previous authors (e.g. Carpenter, 1940; Ellefson, 1974; Gittins, 1979; Tilson, 1979; Palombit, 1995) consider adulthood to start at 6-8 years of age.

Identification of individual animals within habituated and semi-habituated groups was easily achieved since the type of group structure observed by gibbons results in a small number of group members and usually no more than one representative for each age/sex class. To distinguish the two females in RBC2 (if the adult female was not carrying the infant) or individuals from different groups if they were observed on their own and in an area of overlap, notes and diagrams on the physical appearance of each animal were recorded at the initial stages of the study. Three characteristics proved to be the best tools for recognising gibbons – the distribution and extent of fawn or grey coloured hair on the back and shoulders, the width of the brows and, for the males, the thickness of the cheek whiskers. Confirmation of a female's identity, particularly if she consistently remained out of view, came with the start of a song bout. Each female gave not only a distinct great call but demonstrated a unique delivery of notes in the introductory sequence.

2.2.5 Collection of behavioural data

The data presented in this work were collected over a twelve month period between September 1995 and August 1996. After initial follows, it was decided that RBC2 would become the

---

[4] The subadult age class is also the stage in life when a gibbon experiences intense aggression from its parents and eventual expulsion from the group (Tilson, 1981).

primary focus group and receive between 10 to 14 days of research attention a month. A third week would concentrate on following RBC1 and the rest of the month spent tracking other groups and collecting phenological data. Continual heavy rainfall (no singing and difficulty in observing animals), losing groups during consecutive day follows (resulting in having to re-start the month's primary data collection period), and illness (both my own and my field guides), however, frustrated strict adherence to this itinerary and some months (e.g. January 1996) saw a marked reduction in data collection. RBC2 were relatively easy to study but RBC1 did occasionally prove to be a difficult group to follow and we often lost them when negotiating the hilly, slippery and/or tangled terrain found at the top of their home range. Observation work with other groups was less successful, primarily due to their partial or unhabituated state. Some behavioural data, in particular on ranging behaviour, was collected for RBC3 and RBC5 but an attempt to observe one of the RR and/or BR gibbons was thwarted by the impenetrable and steep nature of their habitat and relied on chance observations

Previous research conducted at Rekut had led to the establishment of an extensive system of trail networks through the primary study site (see Figure 2-3). Additional trails were cut through parts of RBC2's home range through the course of the study in response to the identification of travelling pathways regularly used by this group. These trails were used to familiarise myself with the home ranges of the focus groups and to locate groups when they had been lost the previous day. The great majority of actual follows were conducted off-trail, using a *parang* (machete) to cut through lianas, rattan and other path-obstructing plants.

Both my field guides had significant experience at following primates, in particular Mulyadi who had assisted earlier field studies of gibbon, red leaf monkey, long-tailed macaque and proboscis monkey. Their knowledge of the general composition, location and ranging area of the habituated and semi-habituated groups enabled a relatively quick start to the collection of data. Discussions were made with all camp workers (Surian, Mulyadi, Kursani and Nurdin) to map out their sightings of RBC gibbon groups and construct a general outline of home range locations and boundaries. Pre-existing maps of the research area were then modified, drawn to a more appropriate scale, and divided into four key observation areas relating roughly to the ranging and overlap areas of RBC1, RBC2, RBC3 and RBC5 respectively.

Each month, a 5-day continuous follow was conducted with RBC2 and RBC1. If both follows had been completed within a 10 day period, an additional five observation days were spent with RBC2. The daily observation period usually started around 0510 - 0515 with the departure of the first gibbon from the night tree and terminated anytime between 1100 and 1600, depending on what time the group retired for the day. Variation in retirement times resulted in observation day lengths ranging from 5 to 10 hours.

A method of continuous scan sampling (Altmann, 1974) was employed to construct a behavioural profile of the activity period. At each 10 minute interval, the group was scanned, aided by Swarovski 10 x 40 binoculars, and their behavioural state recorded in a notebook. (Data checksheets had been prepared for field recordings but a notebook proved to be easier to carry and use). Previous research on (captive) gibbons (Bricknell, 1992 unpubl.) had condensed the extensive behavioural repertoire list prepared by Dolhinow (1978) to just nine behavioural states or activities – rest, travel, feed/forage, sing, play, groom, aggression, sexual interaction and display – and this ethogram was again used for this study (Table 2-4). Additional data collected during 10 minute scans included closest neighbour, inter-individual distance and height of individual. Behavioural events which involved multiple and complex displays and (normally) more than one participant – inter-group encounters and intra-group aggression, sexual and singing behaviour – required greater descriptive attention and were recorded as they occurred, regardless if they fell on a scan or not. The methods used to record these behaviours are outlined in greater detail in relevant chapters.

Table 2-4 Terms, codes and descriptions used to record and categorise gibbon behaviours.

Behavioural state	Description
Rest - R	Any behaviour in which the individual was predominantly stationary (sitting or lying down) and not engaged in any of the behaviours described below.
Travel - T	All locomotor behaviour (e.g brachiating, climbing, jumping, walking) except for that observed during feeding and/or foraging bouts or when a gibbon moves from one part of the tree to another during periods of respite.
Feed/Forage - F	Any behaviour involved in the selection, processing, ingestion and swallowing of food items.
Sing - V	The production of either a solo or duet or an alarm call variation of these.
Play - P	Any behaviour in which participation is voluntary and not associated with any apparent goal. Participants often display the "play-face".
Groom - Gmer - Groomer Gmee - Groomee	Visual and manual (i.e. with hands) inspection of body hair and removal of dirt particles or insects. Individuals may groom themselves (self-grooming) or another group member (allo-grooming).
Aggression interact - AIA - Aggressor AIV - Victim	Involving 2 or more animals and occurring in both intra- and inter-group encounters. Aggressive interactive behaviour includes both an aggressor and a victim. Aggressors are identified by their use of head-thrusts (with exposed canines) and their predominant role in chasing, striking, wrestling and biting. Victims are identified by submissive gestures (e.g. crouching) and disturbed vocalisations (e.g. *twoulwill, twitter* - see Chapter 8 for description).
Sexually interact - SI	Includes genital inspection (touching, licking), mounting and copulation.
Display - D	Usually observed during aggressive interactions, the displaying animal adopts postures or actions which include rapid brachiation, swinging, and grabbing of genitalia.

Mapping work concentrated on delineating the range pathway the group followed on each observation day. Location of the group was marked every 10 minutes on field maps and determined in relation to the position of trails, known off-trail landmarks, and the Rekut and Busang rivers. Direction of troop movement between scan points was aided by regularly consulting a Suunto compass. The position of food sources, night and singing trees, and the sites of intergroup encounters were added to field maps on occasion of use.

Whenever a gibbon started feeding, details were taken on the food type being eaten (young or mature leaf, leaf bud, fruit, fig, flower or flower bud, invertebrate), the physical appearance of the food type (e.g. colour, size, number of seeds), taste (of fruits), and taxonomic identity. Specimens of food items, and a leaf and piece of bark from the source, were bagged, labelled and taken back to camp for taxonomic verification, either by consulting Surian and/or comparing the food items with specimens stored in the herbarium. If the genus or species still could not be determined, specimens were dried and pressed (leaves, flowers) or stored in alcohol (fruits and figs) before being taken to the National Herbarium at Bogor.

At the end of each observation day, a meeting was held between myself and my field guide in which we went through my field notes to determine if I had missed any behavioural events. This was especially important on days when we had to separate in response to the focus group splitting into widely dispersed foraging units. Field notes and maps were then transferred to a clean checksheet and range map respectively and kept in a safe in another part of camp. On rest days, behavioural data was hand-tabulated and entered into a Macintosh Powerbook 180 lap-top computer, using both Excel spreadsheets and Microsoft Word documents to summarise daily and monthly data collections. These were backed up on two disks.

Overall, a total of 1460 hours were spent following the four focus groups (see Table 2-5). RBC2 was observed for 1028.5 hours giving an average of 85.7 monitoring hours a month. RBC1 received 286.1 hours of observation over 10 months (mean = 28.6 hours) and RBC3 and RBC5 monitored for brief periods at least every second month[5].

Table 2-5 Schedule of observation hours for focus groups: September 1995 - August 1996.

	Observation hours per group				
	RBC1	RBC2	RBC3	RBC5	Total
September 95	-	70.6	-	-	70.6
October 95	31.2	84.3	7.1	8.2	130.8
November 95	24.5	96.5	11.5	10.5	143.0
December 95	27.5	95.2	10.4	10.2	143.3
January 96	27.0	53.1	7.5	-	87.6
February 96	25.0	118.1	8.0	5.5	156.6
March 96	27.3	99.2	10.5	4.3	141.3
April 96	33.1	98.4	12.4	9.1	153.0
May 96	31.1	106.3	10.2	9.3	156.9
June 96	31.3	95.4	4.5	5.3	136.5
July 96	30.2	69.2	-	-	99.4
August 96	-	42.2	-	-	42.2
Total	1028.5	286.1	82.0	62.1	1460.1

2.2.6 Post-fieldwork analysis and presentation of data

On return to Australia, the data was transferred to Statview Version 4.0 for statistical analysis. Following methods used in previous primatological publications, non-parametric statistics (e.g. Mann Whitney, Kolmogorov-Smirnov) and Spearman rank correlations comprised the basic analytical tools. Extra indices and equations testing relationships between variables were drawn from various papers and are outlined in the relevant chapters. All statistical results are significant to $p < .05$ unless indicated otherwise.

Except where indicated, data to be presented in the forthcoming chapters are drawn from the 5-day behavioural profiles collected for RBC2 during each of the 12 observation months. To

---

[5] Difficulties in following RBC4 resulted in their removal from the observation schedule.

ensure RBC2 is representative of the hybrid gibbon population, however, data collected for RBC1, and to a lesser extent the other study groups, are also included, particularly in relation to activity budgets, diet, ranging patterns and singing behaviour.

Individuals from each group will be referred to using a three character code e.g. AF2. The first character identifies the age of the individual (e.g. A = adult), the second character its sex (e.g. F = female) and the third, the number of the group in which the individual is resident (e.g. 2 = RBC2). With regard to parental species, *agilis* is used to denote Malaysian, Sumatran *and* Bornean agile gibbons whereas *albibarbis* refers only to Bornean *agilis*.

3

Activity Budget and Patterns

3.1 Introduction

To ensure the physiological, reproductive and social fitness of both individual and group, an animal needs to successfully partition its day into a series of fundamental and essential maintenance activities or behaviours (Dunbar, 1988). For most vertebrate populations, the time interval (herein referred to as the activity period) into which these maintenance activities are distributed is restricted by the number of daylight hours. In most areas where primates are found, and particularly in equatorial zones in which the research area lies, a twelve hour period is available for the completion of these basic daily tasks. Some primate groups (e.g. langurs – Davies, 1984; Stanford, 1991) take advantage of this extended period, staying alert for most or all of the daylight hours. Other primates, such as gibbons, remain active for only part, terminating activities up to two or three hours before sunset (Gittins, 1979; Srikosamatara, 1984; Whitten, 1984b; Leighton, 1987). Potentially influencing the activity budget is a range of external (e.g. environmental and ecological) and internal (e.g. physiological) factors which create differential profiles for population and species groups. The interplay of these factors on the needs of different age and sex classes introduces further budgeting variation based at the individual level. Constructing an activity budget for the group, therefore, becomes the "sum of .... behavioural priorities" of each group member (Stanford, 1991) in relation to the ecological dynamics of the surroundings in which the group is placed.

Four key maintenance activities – travelling, feeding, resting and social behaviour – comprise the majority of an animal's activity period. Feeding and foraging behaviour clearly represent the more important of these, it being critical that an animal budgets its time appropriately so as to acquire its basic nutritional needs. How much of the day is spent engaged in feeding behaviours depends on a range of physiological and environmental factors, including body size, specific and individual metabolic requirements, and the nutritional quality of the diet and available food (Dunbar, 1988). Equally important is the allocation of time to the location and monitoring of food sources, identifying where important feeding sites are and ensuring maximal access to them.

Such food location activities can be achieved while the group travels around its home range but daily bouts of travel are important for other reasons. Travelling enables an individual or group to assess its home range for suitable sleeping and, if required, singing sites. For territorial species, daily coverage of the range also aids a primate group in their detection and eviction of invading conspecifics or food competitors. Influenced by parameters which may elicit differences both between and within species (see Dunbar, 1988), the time allocated to travelling, and especially feeding, probably governs the time spent in other, less important activities.

Periods of rest need to be taken at least once a day and not just for recuperative reasons. Remaining sedentary might be used by primates to engage in vigilance behaviour, aid in the digestion of food items such as mature leaves (e.g. colobine monkeys – Dunbar and Dunbar, 1974b; Stanford, 1991) or escape the heat of the day (Southwick et al., 1965; Hall, 1966; Aldrich-Blake, 1970). Nonetheless, resting generally represents a "source of uncommitted time" which can be siphoned off when another more pressing activity requires greater commitment (Dunbar, 1988). An example of this is demonstrated by tamarins who, when faced with periods of food shortages, reduce their time spent in resting behaviour so to allow more time for feeding and foraging (Terborgh, 1983).

If required, primates may also devote less time to social interactions. Conspecific primate populations which live in different habitat have been found to vary their use of intra-group social behaviours. For example, vervet monkeys and rhesus macaques living in fertile areas spend more time engaged in social activity, presumably because they experience less feeding pressure compared to groups in marginal areas (Lee, 1983; 1984; Seth and Seth, 1986). Primate species which are organised into highly structured groupings, where the upkeep of social affiliations demands regular attention, might be less inclined to reduce their social activity time. However, at times when it is imperative that an individual budgets its activity period in favour of another maintenance behaviour, social activities will have to be forgone. Pregnancy is one such time and female yellow baboons and geladas often withdraw socially from the group to increase their food intake (Altmann, 1980; Dunbar, 1983; Dunbar and Dunbar, 1988). Indeed, female geladas may increase their average daily feeding time by as much as 30%, sustaining this level of feeding after the birth and until the infant is weaned (Dunbar, 1983).

3.1.1 Outline of Chapter 3

The proportion of the day covered by a hybrid gibbon's activity period forms the first of the analytical sections (Section 3.4), suggesting possible environmental and ecological factors influencing monthly variation in the duration of the alert period. Presented in the following section (3.5) are the overall activity budget and the changes occurring in the use of maintenance behaviours between months, particularly in relation to food abundance and diet. Daily patterning of activities is described in Section 3.6, and in Section 3.7 individual differences are addressed. The influence weather has on the use or non-use of certain behaviours is investigated in Section 3.8, describing weather patterns at the field site and comparing these with maintenance activity changes.

Because social behaviour and singing receive considerable attention in later chapters, statistical analysis and discussion of results mostly concentrates on frequencies and socio-ecological determinants of resting, travelling and feeding behaviour.

3.2 Methods

3.2.1 Measurement of activity period length

The activity period was timed from when the first gibbon left the night tree to when the first gibbon entered the subsequent night tree (Chivers, et al., 1975; Gittins, 1979). Such a method may underestimate the actual time study animals were awake (by up to two hours) as the gibbons spend some time resting in their night trees before starting the day or going to sleep. However, gibbons were normally very quiet during these periods of rest, making it difficult, as Gittins (1979) also observed, to determine whether they were asleep or awake. The time at which the sun rose and set was measured each day to assess its effect, if any, on start and termination time of each activity period.

3.2.2 Construction of the individual and group activity budget

For the purposes of the activity budget, gibbon behaviour was reduced to five basic activities – the four key maintenance activities listed earlier plus singing. Definitions for these are as follows:

- *Rest* - Any behaviour in which the individual was predominantly stationary (sitting hanging, lying) and not engaged in any of the maintenance activities described below.
- *Travel* - All locomotor behaviour (e.g. brachiating, climbing, jumping, walking) except short bursts of movement during bouts of foraging or feeding.
- *Feed* - Both foraging and actual feeding behaviour, including the selection, processing and swallowing of food items.
- *Sing* - The production of either a solo, duet or an alarm call variation of these. Any other non-song vocalisations were normally associated with a social interaction, such as an aggressive encounter, or used to locate other group members, and hence allocated to the social category.
- *Social* - Any intra-group or inter-group social interaction between two or more individuals. Intra-group social behaviour includes grooming, playing, sexual contact and displays of aggression. Inter-group social interaction includes any associated behaviours (other than song performance) that occurs during an inter-group encounter, be it of an aggressive or affiliative nature.

The proportion of time each individual spent engaged in a maintenance activity was calculated from the corresponding number of 10 minute samples for that maintenance activity divided by the duration (in minutes) of the monthly and annual period. A group activity budget was then determined by combining individual data scores and dividing by the number of group members.

3.2.3 Constructing the activity pattern

A daily activity pattern was produced by calculating the proportional use of the different maintenance activities over the activity period. In actuality, data were disproportionately spread over the activity period, primarily because of the variation the hybrid gibbons displayed in the start and end times of their activity periods (see Section 3.4). As a result, mid-morning to early afternoon hours were represented by a substantially greater number of 10-minute observations. To counteract the potential bias produced by an unequal data spread, the total number of 10-minute observations was added for each hour and the proportion of each maintenance activity determined from these hourly totals.

3.2.4 The weather profile

To assess if a relation existed between weather and the use of maintenance activities, weather conditions were noted (using the scale given in Chapter 2) on each 10 minute observation scan. Very few observation days could be classified as either solely or predominantly sunny or rainy so to prevent any bias towards cloudy conditions, the number of scans, rather than the number of days, was employed as the unit of measurement. The proportion of each weather type was then calculated as the number of scans for cloud, sun or rain divided by the total number of weather records. Weather profiles were calculated for each of the 60 days and 5-day monthly samples, and the overall observation period.

3.3 A hybrid gibbon's day

The following describes a typical day in the life of the focus group RBC2:

In the hour leading up to dawn, an adult male across the Rekut or Busang river begins his solo. Neighbouring adult males respond, including the adult male of the focus group, to produce a chorus of up to 12 singers. As the sun rises, the males conclude their song and rest in the night tree. The group then remains quiet for up to half an hour, following which each individual leaves its sleeping position to urinate and defaecate. If the morning is wet or dark, the members of the group remain resting in their night trees for another thirty minutes. If little or no rain has fallen the previous night, the adult female may initiate a duet. The adult male leaves his night tree to join her, contributing his song immediately prior to the first great call. In turn, the subadult female enters the singing tree, albeit at a distance from the mated pair, and joins her mother in the great calling. Travel away from the singing tree occurs during the duet or immediately after the duet has concluded.

Gibbons start covering their home range around 06:30, travelling slowly and surveying the immediate area for territory invaders. If a heavily fruiting tree is close to the night tree, the group move directly to it, feeding for up to hour. Once satiated, another duet is delivered, often in response to a duet given by RBC1 or RR1, and is followed by a brief respite. After 0800, travelling increases and quickens as the group move around their home range in search of succulent feeding trees. The adult female refuses to carry the infant, enabling the infant to practice brachiating and climbing through the canopy. When the infant comes across a gap in the canopy too big to negotiate, she whimpers to attract the attention of her mother, who duly travels back to her and carries her across.

The group follows a similar path to that undertaken the day before, revisiting desirable food sources and checking the territory border where RBC1 and RBC5 have been known to cross over. If one of the neighbouring groups is found within their territory, the group will advance towards them. The adult female normally stays back, protecting her offspring and protesting the territory incursion by singing long and unstructured solos. A more active role is assumed by the adult male and subadult female, the former displaying to the invading male and both participating in bouts of chasing with the adult members of the other group. When the fight terminates, the group remain in the area for awhile, resting and surveying.

Alternate bouts of travelling and feeding continue until the early afternoon. During feeding stops, the subadult occasionally gets too close to the adult female and is punished by being chased out of the feeding tree and repeatedly struck. As the hottest part of the day is reached, the group begins to reduce its pace of travel. Bouts of resting become longer and more frequent and the adult and subadult members of the group use these rest periods to play with the infant or engage in grooming. Towards the end of the activity period, travelling is very slow, the gibbons spending much of their time foraging. Prolonged bouts of feeding occur only if a fruiting tree is discovered; this food source is often one which had been used earlier in the day.

A burst of speed signifies the end of the activity period as the group selects and enters its night trees. The adult female is the first to retire, carrying the infant and settling down on a branch. The infant plays for short time, watched by her mother, who eventually pulls the infant towards her to sleep cradled in her arms. The adult male and subadult female spend a little more time foraging, the former being the last to enter his night tree following a quick survey of the area.

3.4 The activity period

Hybrid gibbons had shorter activity periods compared to other gibbons, averaging 447.2 minutes or 7.5 hours per day (RBC1 and RBC2 combined and see Table 3-1). A remarkable feature of the activity period was its substantial variation in duration (see Figures 3-1 and 3-2), five hours separating the shortest day (300 minutes) from the longest (600 minutes). It was evident that activity periods started to increase in length towards the end of January 1996 (Figure 3-2) but monthly variation was not significant (H=18.46 d.f.=11 p>.05). Comparing months of lower (< 300mm) and higher (> 300mm) rainfall suggested that heavy rain had a slight, but insignificant, negative effect on activity period length (U=30 n_1=6 n_2=6 p>.05), gibbons tending to shorten their time spent active in wetter months (Section 3.8).

The proportion of fruit (figs and other fruit combined) in the diet had a stronger relationship with activity period duration (see Table 3-2). An increased fruit component in the diet provides gibbons with a greater amount of expendable energy, hence allowing them to stay active for a longer period of time. Monthly diets in which higher amounts of non-sugary foodstuffs (e.g. young leaves) are consumed may result in a reduction in the length of the activity period as individuals conserve what energy resources they have consumed for the long fast overnight. As hybrid gibbons spend an exceptional length of time in the night tree, it would be advantageous to the individual during times of lower fruit availability and/or consumption to spend less time in energy demanding activities (e.g. travelling around the home range) and hence retire earlier for the day. Activity period duration was inversely related to the level of consumption of young leaves, though this relationship was not significant.

Table 3-1 Activity period lengths for hybrid and pure species of gibbon.

Species	Study Site	Activity Period Length		Source
		Mean* (minutes)	Range	
H.a.albibarbis x H. muelleri	Barito Ulu, Central Kalimantan, Indonesia	447.5[1] 446.1[2]	300 - 600 302 - 540	This study
H. agilis	Sungai Dal, West Malaysia	550	390 - 660	Gittins, 1979; 1982
H. hoolock	Lawachara and Chunati Wildlife Sanctuary, Bangladesh	-	496 - 666	Islam and Feeroz, 1992a; 1992b
	Lawachara, West Bhanugach Forest Reserve, Bangladesh	543	-	Ahsan, 1994
H. klossii	Paitan, Siberut Island, Indonesia	637	554 - 694	Whitten, 1980; 1984b
H. lar	Kuala Lompat, West Malaysia	516	372 - 612	Raemaekers, 1979
	Kuala Lompat, West Malaysia	630 620	- -	MacKinnon and MacKinnon, 1978
	Ketambe, Sumatra, Indonesia	557 596	545 - 648 467 - 665	Palombit, 1997
H. moloch	Ujong Kulon, Java, Indonesia	600	-	Kappeler, 1981 cited in Chivers, 1984
H. muelleri	Kutai, East Kalimantan, Indonesia	486	324 - 576	Dee Robbins, 1996 pers. comm.
H. pileatus	Khao Soi Dao, Thailand	492	396 - 570	Srikosamatara, 1984
H. syndactylus	Kuala Lompat, West Malaysia	666 610	600 - 753 514 - 671	Chivers, 1974 *ibid.*
	Ketambe, Sumatra, Indonesia	618 570 620	390 - 714 423 - 685 377 - 742	Raemaekers, 1979 Palombit, 1997

* Single values for each reference = mean activity period lengths for > 1 study group; multiple values for each reference = the mean activity period length for individual groups (e.g. this study, Palombit, 1997).

[1] Activity period length for RBC2

[2] Activity period length for RBC1

Table 3-2 Rank correlation coefficient for activity period length and proportion of food type in the diet.

Dietary contribution	Correlation coefficient (n=12)	
	r_s	sig to
% of fruit in monthly diet	.650	≤.01
% of figs in monthly diet	.385	≥.05
% of young leaves in monthly diet	-.517	≥.05

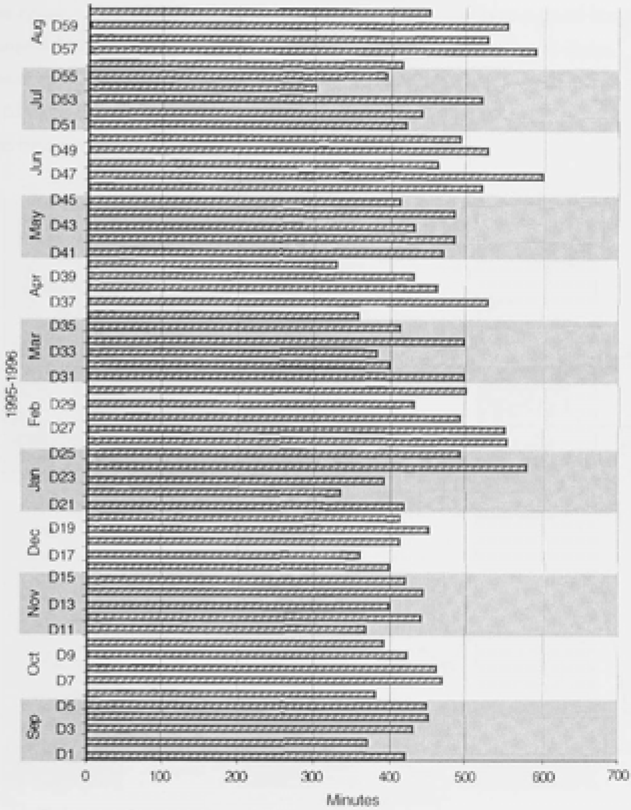


Figure 3-1 Variation in RBC2 activity period length over the 60 day sample.

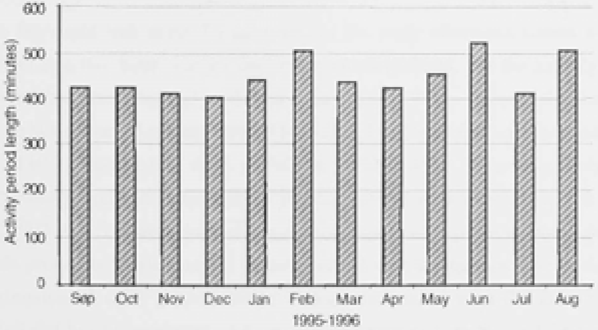


Figure 3-2 Monthly variation in RBC2's activity period length.

Gibbons left the night tree between 5 and 35 minutes after sunrise, later departures usually occurring in response to heavy rainfall or dark, heavy cloud cover (Figure 3-3). On occasion, RBC2 and RBC1 were not found in their night trees and RBC2 was once observed to leave as the sun was rising. This suggests that hybrid gibbons, like neighbouring red langurs and long tailed macaques, may sometimes begin their activities just prior to or at dawn. Variation in average monthly starting times was not significant (H=3.402) but mean daily rainfall each month did have an effect on the start of the activity period (r_s=.720 n=12 p<.02), high rainfall delaying the first movement of the day.

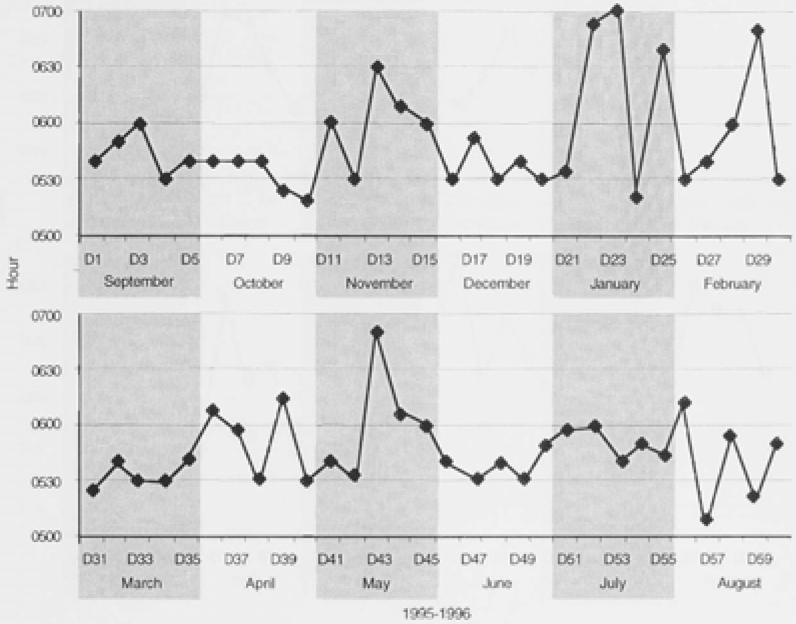


Figure 3-3 Variation in the time of RBC2's departure from the night tree.

Retirement to the night tree normally occurred in the early afternoon (mean = 1319 hours), approximately one to two hours earlier than other small gibbons, but the activity period ended anytime between late morning and mid afternoon (Figure 3-4). Indeed, the time that RBC2 entered their night tree varied substantially (H=33.063 d.f.=59 p<.005) and ranged from as early as 1050 and 1110 on succeeding days in July to 1530 in June. Previous studies conducted during the dry season indicated that hybrid gibbons retired in the middle of the day (Kursani and Mulyadi, 1995 pers. comm.), suggesting that late retirement times occurred in wet weather months. If this proved to be the case, it would contrast with the pattern observed at Sungai Dal where the extension of agile gibbon active periods coincided with the dry season (Gittins, 1979). Rainfall did have a moderate and positive correlation with the end time of the activity period (r_s=.545 n=12 p<.05) but retirement time appeared to depend on a combination of the amount of rain and the time it fell. Heavy rainfall overnight or particularly in the early morning delayed the gibbons' emergence from the night tree and hence necessitated a later retirement time so as to enable the group to locate enough food stuffs for provision of daily nutritional and energy requirements. If substantial rainfall occurred in the late morning, between 1030 and

1230, gibbons tended to rest in the sheltering tree, only continuing the activity period if few food sources had been visited prior to the downpour.

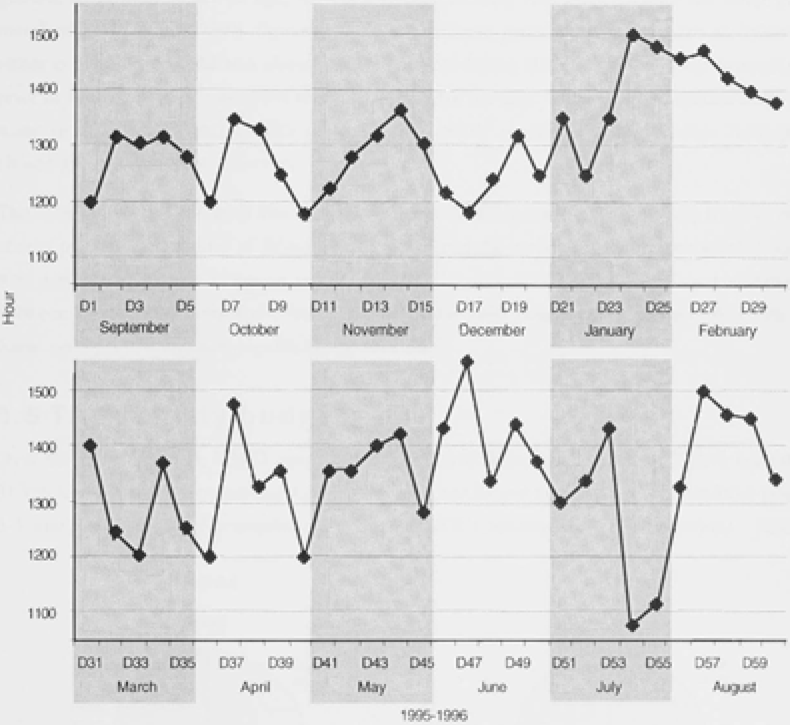


Figure 3-4 Variation in the time of RBC2's entry into the night tree.

One of the adults was the first individual to commence activities for the day, the subadult female only rarely venturing out of the night tree before her parents (Table 3-3). The adult male initiated significantly more departures from the night tree ($\chi2=38.7$ d.f.=2 $p<.01$), emerging first on 68.4% (n=41) of mornings. Forty percent of mornings on which the adult male was the first to become active were mornings in which the adult female sang the first duet of the day from the night tree. Adult male gibbons often approach their partner during the duet and, since the adults slept in different trees, this required the male to leave his tree to join the adult female in hers. On mornings in which no duetting occurs the adult male and female were equally likely to initiate night tree departures.

Table 3-3 Inter-individual variation in leading night tree departure and retirement.

	First to leave night tree		First to enter night tree	
	%	n	%	n
AM2	68.4	41	23.3	14
AF2	28.3	17	70.0	42
SF2	3.3	2	6.7	4

Activity periods were normally terminated first by the adult female ($\chi 2=38.8$ d.f.$=2$ $p<.01$) who selected her night tree some minutes before the subadult and the male retired. Occasionally, a gibbon, regardless of sex or age, stayed active up to forty-five minutes after the other group member(s) had entered their night trees. Late retirement generally resulted from an individual either continuing to feed at a choice food source or losing the rest of the group immediately prior to another gibbon's decision to end activities for the day. The separated gibbon then spent some time travelling and contact calling, occasionally stopping to feed, before finding the chosen site of retirement.

The location of the research site meant that time of sunrise and sunset varied little over the annual period, a maximum of fifteen minutes between the earliest and latest recorded times. It was predicted that this situation would prevent the detection of any significant association between sunrise and sunset and activity period start and end times, a prediction which was borne out by a low and non-significant correlation.

3.5 The activity budget

Over the annual period, RBC2 spent 25.5% of their activity period resting, 38.0% travelling, 31.1% feeding, 4.0% singing and 1.4% involved in social and range-defence behaviours (Figure 3-5 and see Figure 3-6 for monthly variation in RBC2's activity budget composition). RBC2's

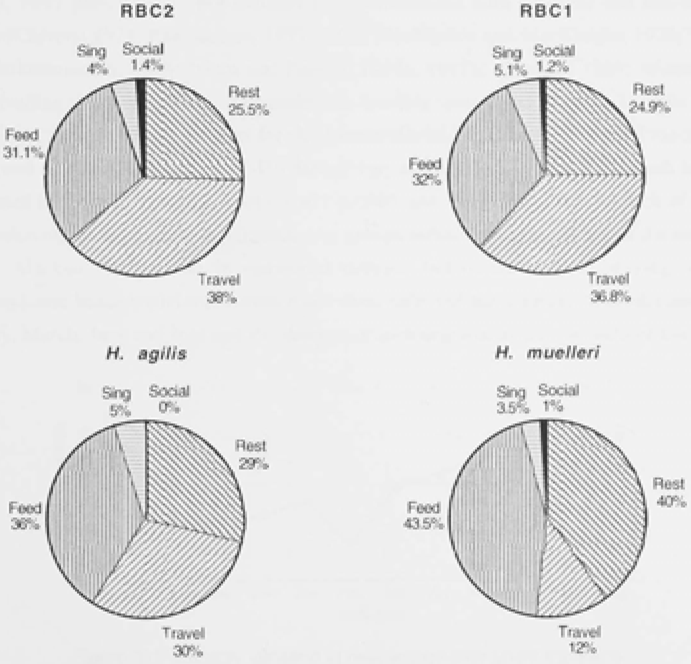


Figure 3-5 Activity budgets for hybrid groups RBC2 and RBC1 and parental species *Hylobates agilis* and *H. muelleri*. (Data for *agilis* from Gittins, 1979; data for *muelleri* from Dee Robbins, 1997 pers. comm.).

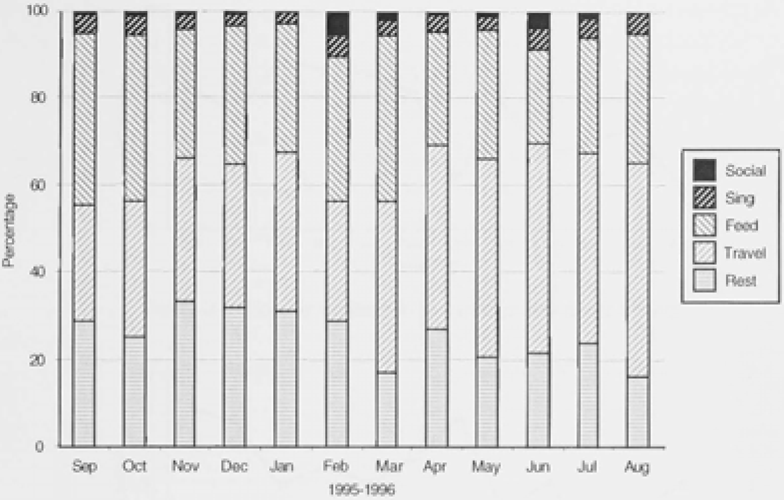


Figure 3-6 Monthly variation in RBC2's activity budget.

budget is comparable with that of RBC1 and the parent species (Gittins, 1979; 1982; Dee Robbins, 1997 pers. comm.) but exhibits some differences with other lar and non-lar group gibbons (Chivers; 1974; Raemaekers, 1977; 1979; MacKinnon and MacKinnon, 1978; Whitten, 1980; Srikosamatara, 1984; Islam and Feeroz, 1992a; 1992b; Sheeran, 1993; Ahsan, 1994). Both travelling and resting showed considerable monthly variation (Figures 3-7 – 3-8) but only a significant relationship was found for the former (H=26.13 d.f.=11 p<.005). Proportions of feeding and singing (Figures 3-9 – 3-10) did not vary as greatly from month to month but social and related behaviours did (H=36.44 d.f.=11 p<.001 and see Figure 3-11). Much of RBC2's social behaviour was directed at neighbouring groups rather than at members of the immediate group. Marked fluctuations in territorial defence behaviour (e.g. displaying, chasing, surveying), and hence social maintenance activities reflected the intensity of border conflicts in February, March, June and July and the absence of such disputes in other months of the year.

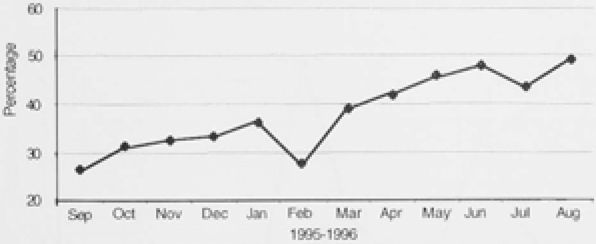


Figure 3-7 Monthly variation in percentage time spent travelling.

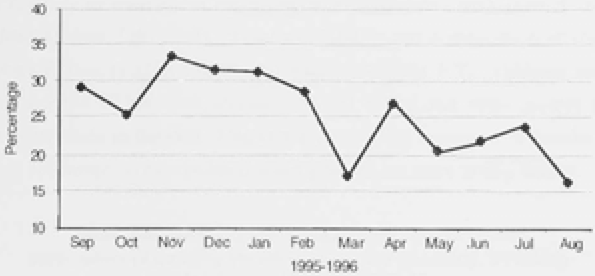


Figure 3-8 Monthly variation in percentage time spent resting.

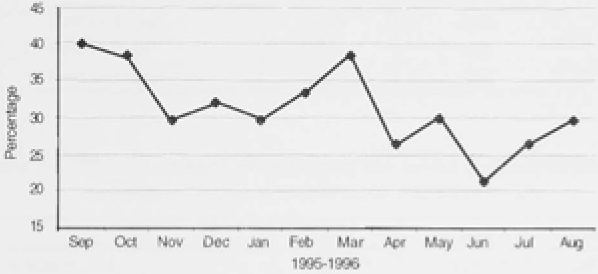


Figure 3-9 Monthly variation in percentage time spent feeding.

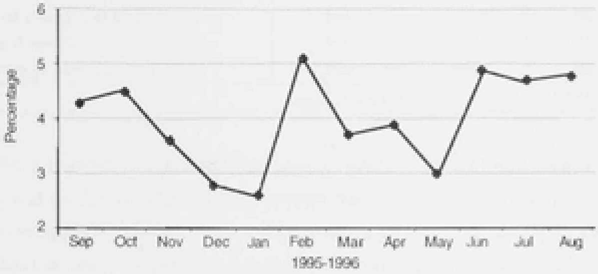


Figure 3-10 Monthly variation in percentage time spent singing.

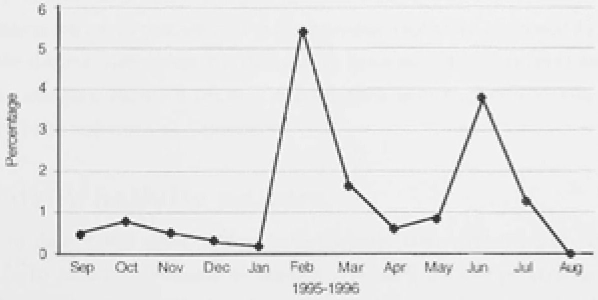


Figure 3-11 Monthly variation in percentage time spent in social behaviours.

Monthly fluctuations in time spent travelling were associated with inverse changes in both resting and feeding (see Table 3-4). Food availability and composition of the diet acted as primary ecological factors affecting these variations (Table 3-5). Gibbons spent more time resting during months of low fruit availability and eating and when greater proportions of young leaves were taken in the diet. Conversely, travelling increased in months of higher fruit availability and consumption but declined when gibbons ate more young leaves.

Table 3-4 Rank correlation coefficient for compared parameters of monthly variation in the use of resting, travelling and feeding maintenance activities.

Maintenance Activities	Correlation coefficient (n=12)	
	r_s	sig to
Rest vs Travel	-.699	≤.05
Rest vs Feed	.014	≥.05
Feed vs Travel	-.623	≤.05

Table 3-5 Effect of dietary, food availability and rainfall variables on monthly variation in the use of maintenance activities (n=12).

	Rest	Travel	Feed
% of fruit in diet	-.825**	.916***	.497
% of figs in diet	-.238	.028	.091
% of young leaves in diet	.783**	-.811**	.378
% of fruit availability	-.669*	.729*	-.414
% of young leaf availability	.161	.028	-.088
Total rainfall	.196	.161	-.557
Average daily rainfall	.280	-.007	-.424

significance level: * ≤.05 ** ≤.01 *** ≤.005

During months or seasons of bountiful fruit supply, gibbons are not only given the incentive to search longer and further for desired food species but, technically, are energetically able to do so due to the nutritional content of the primary dietary item. An ability to engage in more travelling behaviour may, in turn, induce gibbons to stay active for prolonged periods of time. Variation in daily travelling, however, did not correlate with activity period length and, instead, a relationship existed with daily changes in resting behaviour (r_s=-.629 n=60 p<.05). A contrasting interpretation to that offered in the previous section is suggested by these results; that is, it is the decline, rather than the increase, in quantities of fruit sources and dietary fruit items, and the energetic deficit it creates, which affects activity period lengths, necessitating gibbons to rest often and end their days earlier.

3.6 The daily activity pattern

The amount of time RBC2 spent resting varied significantly over the daily activity period (H=44.75 d.f.=10 p<.005). Patterns of feeding (H=34.99 d.f.=10 p<.005) and particularly singing (H=88.46 d.f.=10 p<.005) also showed marked temporal variation but bouts of travel and social behaviour were more evenly distributed. A comparison of the hourly patterning of different maintenance activities found just one significant correlation, resting behaviour declining when gibbons engaged in bouts of feeding (r_s=-.648 n=11 $p<.05$).

Hybrid gibbons rested predominantly in the early morning (Figure 3-12), immediately after leaving the night tree, and in the early afternoon the hour before the normal retiring time. Unlike other gibbons, resting did not peak in the middle of the day and normally occurred in short bursts after a substantial feed or between bouts of travelling. These brief respites may have served to allow lagging individuals to catch up with the rest of the group, to allow the leading gibbon time to decide on the direction of travel, or to permit another group member to direct troop movements. The scarcity of prolonged bouts of resting was quite striking, only two being observed to last longer than 12 minutes.

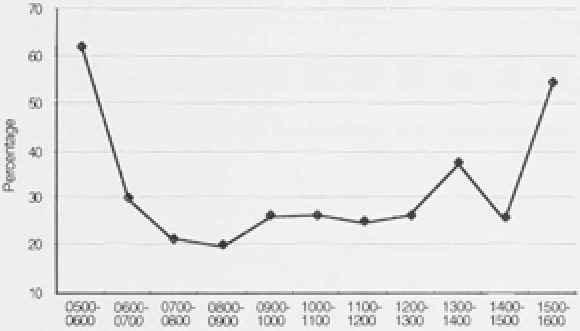


Figure 3-12 Temporal change in percentage time spent resting.

Travelling was minimal in the first two hours of the day, increasing in the mid-morning to form a minor peak between 0800-0900 and rising again after 1200 (Figure 3-13). A mid-morning upsurge in travelling may be a response to earlier peaks in singing and feeding, a result of the group deciding to patrol the territory after assessing the position of neighbouring groups and/or the group having gained the requisite energy following a sustained feeding bout. Gibbons again increased their travelling prior to retiring to the night trees, accounting for the peak after 1200. Bouts of almost continuous travelling, normally interspersed with brief feeding stops, started up to two hours before the end of the activity period and rates of travel became slower as the time of retirement became later. A five minute period prior to entry into the night tree was characterised by an increase in travel speed, a behaviour also observed for Kloss gibbons (Whitten, 1980).

Gibbons mostly feed in the early morning with rates of feeding showing little fluctuation over the rest of the activity period (Leighton, 1987). Hybrid gibbon feeding also peaks early in the morning but somewhat later than other species in relation to the start time of the activity period (Figure 3-14). Feeding may be delayed by a combination of factors – a peak of singing in the previous hour, the position of the night tree in relation to favoured food sources and/or a later start to the activity period. Nonetheless, gibbons probably access feeding sites, particularly those bearing fruits or figs, earlier in the day to obtain their fill before the source is depleted by other mammalian or avian competitors. Another minor peak in feeding occurs between 1100-1200 but no obvious rise in feeding occurs after mid-day. The absence of a pre-retirement peak of feeding may be a result of the exceptional variation in the end time of the activity period.

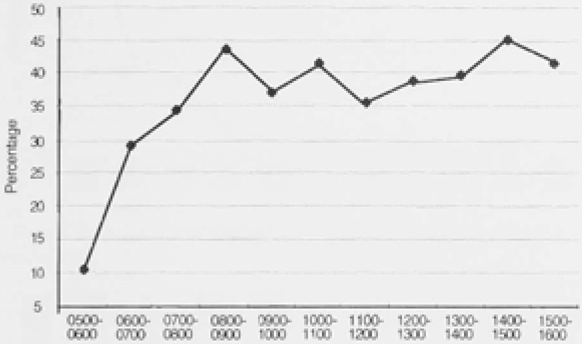


Figure 3-13 Temporal change in percentage time spent travelling.

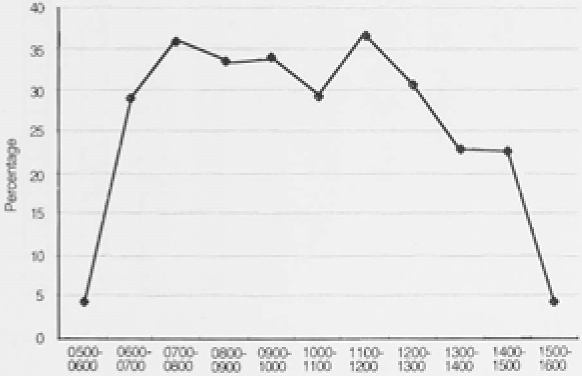


Figure 3-14 Temporal change in percentage time spent feeding.

Singing is largely an early morning behaviour, male songs dominating pre-activity period behaviour and female's performing their songs 1-2 hours later (Figure 3-15 and also see Chapter 8 for a more detailed discussion). Both intra- and inter-group social behaviour was spread out over the day with a possible concentration of grooming and play in the mid- to late morning (see Chapter 8 for temporal variation in the use of specific social behaviours). Overall temporal change in maintenance activity use is illustrated in Figure 3-16.

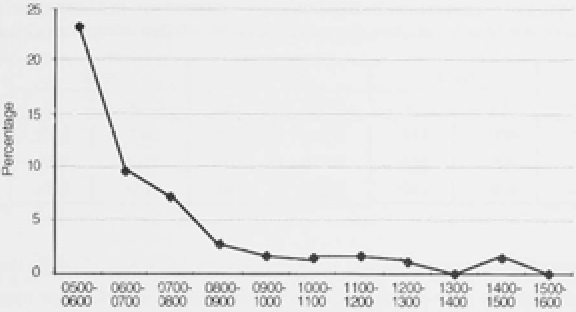


Figure 3-15 Temporal change in percentage time spent singing.

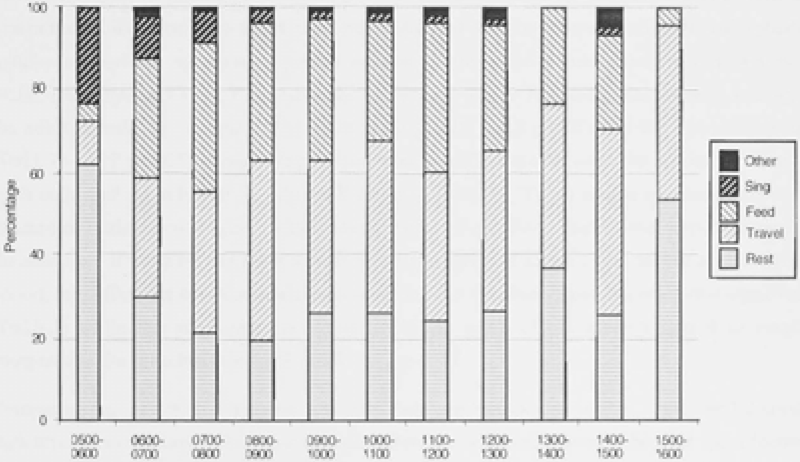


Figure 3-16 Temporal change in the use of maintenance behaviours.

3.7 Individual difference in activity patterns

It was evident from observations that the behaviour of the three mature members of RBC2 was highly synchronised. Resting, travelling, feeding and, to a lesser extent, social behaviours showed a high correlation between individuals (Table 3-6). Despite frequent production and participation in daily duets, vocalising behaviour was only moderately or weakly correlated. This inconsistency can at least be partially explained by the amount of male and female soloing. Male vocalising time increased in July and August 1996 due to the delivery of a greater number of morning solos which were of a considerable length. In contrast, the amount of female and male vocalising rose and fell respectively in February and June 1996 as a result of ongoing territorial disputes. The normal female response to a territory invasion was to sing, often on her own, and for lengthy periods of time. Although the male occasionally joined her song bout, he tended to play a more active role in territory defence (e.g. displaying to and chasing intruders) and therefore did not sing much during these observation periods.

Table 3-6 Rank correlation coefficients for parameters of maintenance activity use between RBC2 group members - social maintenance activities not included due to the small sample size.

n=12	Rest		Travel		Feed		Sing	
	r_s	sig to	r_s	sig to	r_s	sig to	r_s	sig to
AM2 vs AF2	.785	≤.02	.979	≤.004	.917	≤.006	.101	≥.05
AF2 vs SF2	.890	≤.01	.976	≤.004	.938	≤.004	.01	≥.05
AM2 vs SF2	.902	≤.01	.982	≤.004	.982	≤.004	.07	≥.05

Despite the group (RBC2) exhibiting similar variation in maintenance activities over the annual period, differences were obvious in the amount of time spent in each of these behaviours. The adult male rested less than the adult female ($T=13.5$ $n=12$ $p<.03$) and the subadult female ($T=2.5$ $n=12$ $p<.005$) but travelled more than the subadult female ($T=5$ $n=12$ $p<.005$) and fed more than the adult female ($T=10$ $n=12$ $p<.01$). Females rested for similar lengths of time but contrasted in the time they devoted to travelling and feeding, the adult female and subadult female respectively spending a greater amount of the activity period moving ($T=4.8$ $n=12$ $p<.005$) and feeding ($T=12.75$ $n=12$ $p<.025$). Singing was an important maintenance activity of the adult female, compared to the adult male ($T=16$ $n=12$ $p<.05$) and the subadult female ($T=11.75$ $n=12$ $p<.025$). Interestingly, there was no difference between the amount of time the adult male and the subadult female spent singing ($T=20.5$). These results are partly due to the absence of male dawn singing (which occurs before the defined start of the activity period) in the analysis. If the time the male spends soloing at dawn is added to the length of the activity period, the difference between adult male-adult female vocalising time becomes non-significant ($T=28.3$) while the adult male is found to devote more of his activity period to singing compared to the subadult female ($T=10.8$ $n=12$ $p<.02$).

Comparing the use of maintenance activities between individuals in RBC1 revealed a similar high level of synchrony. The most marked difference occurred between the time spent feeding, particularly between the adult male and adult female ($T=11.4$ $n=10$ $p<.01$), and is probably attributable to the adult female's pregnancy. Indeed, comparing the female's activity budget prior to and after becoming pregnant finds an increase in her feeding-time, particularly towards the latter stages of the pregnancy. Energy needs rise markedly during primate pregnancies, around 25% above normal levels during the latter stages (Abrams, 1968; Portman, 1970; Hanwell and Peaker, 1977). Females adapt to these nutritional demands by increasing their feeding time (e.g. baboons and geladas – Altmann, 1980; Dunbar and Dunbar, 1988; squirrel monkeys – Boinski, 1988) or altering their diet to include nutrients important for gestation or lactation (e.g. increase in plant and animal protein content in the diet of female guenons – Gautier-Hion, 1980). The adult female's daughter also fed more often than the adult male, primarily a result of her keeping in close contact with her mother and therefore engaging regularly in the same maintenance activity as her.

Over the daily activity period, the proportion of time spent resting and feeding had the strongest correlation (AM2: $r_s=-.857$ $n=12$ $p<.02$; SF2: $r_s=-.818$ $n=12$ $p<.02$), although the association was only moderate and not significant for the adult female ($r_s=-.557$ $n=12$ $p>.05$). Resting and travelling also showed a negative association but were not as closely correlated. Travelling and feeding had very little effect on each other. As for monthly activity budgets, daily patterns of behaviour were closely synchronised between group members.

3.8 The effect of weather on activity budget and patterns

Observation days consisted mostly of periods of sunny or cloudy conditions, rain accounting for only 6.5% of weather types (Figure 3-17). Monthly variation in the proportion of weather types was significant ($H=24.15$ d.f.$=11$ $p<.05$) but no obvious seasonality existed. The greatest amount of sunny weather occurred in May (68% of all observation minutes) while both cloud cover (62.3%) and rainfall (17.2%) reached maximum levels in February. Patterns of sunshine and cloud correlated inversely ($r_s=-.939$ $n=12$ $p<.002$) as it did for sun and rain ($r_s=-.518$ $n=12$ $p>.05$), although only the former relationship was significant.

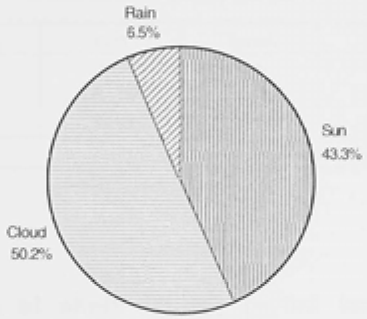


Figure 3-17 Proportion of weather type conditions: September 1995 - August 1996.

Activity budgets for each of the weather types are illustrated in Figure 3-18. Regardless of whether the day was predominantly sunny or cloudy, gibbons engaged in a similar use of maintenance activities. On rainy days, or during rainy periods, gibbons still spent the same amount of time in bouts of feeding but made more, lengthier rest stops (presumably taken to wait out the shower or storm), so reducing travel time through the home range. Both resting and travelling were significantly affected by the absence or presence of rainfall (Travel: $U=113.4$ $n_1=12$ $n_2=12$ $p<.02$; Rest: $U=99.02$ $n_1=12$ $n_2=12$ $p<.001$) but whether fluctuations in travel is a result of wet or dry conditions is difficult to determine.

An examination of the monthly variation in weather types showed no association with the corresponding use of maintenance activities but some relationship did exist in temporal patterning. Daily patterns of travel over the activity period had a significant and negative correlation with rain, occurring more regularly in sunny periods, although the correlation in this case was not significant (Table 3-7). Weather did not induce any changes in resting behaviour but had some effect on feeding, although this was apparent in some months – a negative correlation with cloud in February 1996 ($r_s=-.666$ $n=10$ $p<.05$) and positive correlations with sun in October ($r_s=.707$ $n=10$ $p<.03$) and December 1995 ($r_s=.911$ $n=10$ $p<.006$), and rain in May 1996 ($r_s=.688$ $n=10$ $p<.04$).

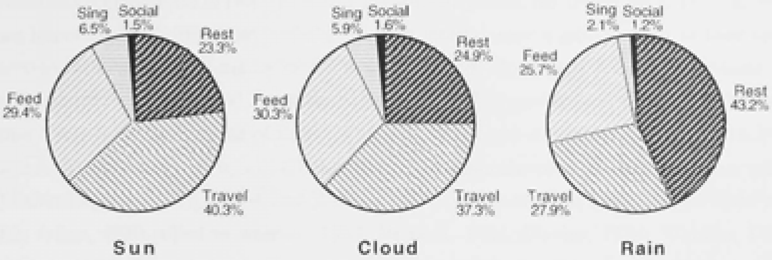


Figure 3-18 Proportional use of maintenance activities in different weather conditions.

Table 3-7 Effect of different weather conditions on daily patterns of maintenance activity use (n=10).

	Rest	Travel	Feed
Sun	-.055	.539	.006
Cloud	-.042	-.370	-.188
Rain	.365	-.973*	.195

significance level: * ≤.01

3.9 Discussion

3.9.1 Determinants of short activity period length

Despite occupying geographical areas where light is available for up to 12 hours a day, gibbons are rarely active for anything approaching that long. Hybrid gibbons, compared to other populations of gibbons, were particularly efficient, completing their daily routine of ecologically and socially important maintenance activities in an average of 7-8 hours. The critical factor determining the length of the hybrid gibbon activity period was the time of retirement to the night tree. On a monthly basis, a fruit rich habitat and diet and/or a series of days preceded by a night of heavy rain were recognised as basic factors which prolonged the length of the activity period. But on successive days, when fluctuations in activity period length were, in some months, quite marked, a more complex array of social (e.g. presence or absence of a late inter-group dispute), environmental (morning and afternoon rain) and ecological (e.g. exhaustion of an important food source) forces undoubtedly interacted to influence the group's decision on when to cease activities for the day. This marked variation in hybrid gibbon activity period length was not unusual in itself since most studied populations of gibbon demonstrate a similar variability in time spent alert. What was unexpected was the actual length of the activity period, between one to three hours shorter than other gibbon populations, and on some days no more than 5 hours long. Relatively short activity periods have also been found for *pileatus* and *muelleri* but little attention has been given to examining why these differences exist.

Of the tasks a gibbon has to perform during the activity period, the search for food is one of the more important. It is therefore probable that the relative ease a gibbon faces in food source detection influences the duration of the activity period. In fruit rich habitats gibbons may observe shorter activity periods since the acquisition of high energy foodstuffs can be achieved within a relatively short space of time. While the abundance of gibbon food trees (16.2% of plot trees[6]) and density of figs (6.0/ha) at Rekut is within the range detected at other gibbon field sites (Rijksen, 1978; Marsh and Wilson, 1981, cited in Mather, 1992; Davies and Payne, 1982; Johns, 1983, cited in Mather, 1992; Bennett, 1984; Davies, 1984; Whitten, 1984b; Leighton, 1987; Sugardjito, 1988; Yeager, 1989; Mather, unpubl. cited in Mather, 1992), overall fruiting activity is much lower (Bodmer et al., 1991; Kim McConkey, 1998 pers. comm.). In other words, hybrid gibbons at Rekut appear to have a relatively substantial range of food species to choose from but overall production and supply of preferred food items (i.e. fruits) is marginal. In such a habitat, it would be expected that gibbons need to spend more time active so as to ensure that what fruit is being produced is found by the resident groups. So why don't hybrid gibbons?

If the fruit produced at Rekut is of exceptional nutritional quality, then gibbons might not need to search that long for dietary fruit items. As long as a few preferred fruit sources can be detected and used each day, these should be enough to sustain the gibbon group and allow them to spend extended periods of time in the night tree. Unfortunately, this proposal can only remain hypothetical at this stage since no biochemical assays have been conducted on fruits collected at Barito Ulu and reports in the literature comparing food choice between different populations of langur (Waterman and Choo, 1981; Davies et al., 1988; Waterman et al., 1988) or orang utan (Sugardjito et al., 1987; Leighton, 1993; Leighton and Waterman, unpubl. cited in Leighton, 1993; Zens and Leighton, unpubl. cited in Leighton, 1993) have not investigated chemical property differences between fruits found at different locations.

An alternative explanation explores the effect of supply. Comparing mean activity period lengths for all species of gibbons (excluding *Nomascus)* with their average non-fig fruit intake did not reveal a significant relationship (r_s=-.332 n=15 p>.05) although the general trend was negative, indicating that when more fruit was consumed, gibbons retired to their night trees earlier. Fruit availability indices are not so widely reported in the literature but because most studied groups of gibbons were found to adjust their diet in relation to fluctuations in fruit production, it can be inferred, albeit cautiously, that gibbons also observe shorter activity period lengths when fruit is plentiful. This pattern was not found for hybrid gibbons who, in contrast, stayed active for longer periods of time when both fruit production and fruit consumption was high. The increase in an animal's expendable energy as a result of a high fruit intake was originally proposed to explain the relationship between fruit use and activity period length. The fact that daily variation in resting, rather than an energy demanding activity such as travelling, was correlated with activity period length suggested otherwise, i.e. hybrid gibbons respond to low periods of fruiting activity instead and reduced the time spent active so as to conserve

---

[6] This value does not include dipterocarps and *Swintonia glauca*. These plants were eaten by the hybrid gibbons but only rarely. Including these species, which are well represented in the plots, would increase the proportion of known hybrid gibbon foods to an overestimated 27.0% of all plot trees.

energy reserves. If this is true for hybrid gibbons, it might then follow that in an area of low fruit supply the best strategy is not to spend extended periods of time active but exploit what food sources can be detected quickly and retire relatively early to conserve energy.

3.9.2 Hybrid gibbon activity budgeting

The division of the activity period followed the basic gibbon pattern with some notable modification. Hybrid gibbons spent more than a third of their day travelling around the home range, and on some days as much as 60 to 70% of the day was devoted to movement. Compared to other gibbons, and particularly the parental *Hylobates muelleri*, this amount of travelling behaviour was exceptionally high. Of course, a comparison of activity budgets between study populations can be problematic since differential methodologies and definitions can be used from one study to the next (Stanford, 1991) and hence some caution must be employed before presenting specific or population differences. Nonetheless, hybrid gibbons did distinguish themselves with their almost continual movement over the activity period with few extended (> 5 minutes) periods of rest interrupting bouts of travel.

Dunbar (1988) has suggested that daily travel time is affected essentially by the size of the foraging group and the dispersion of food although, for baboons and geladas at least, there is little support for a relationship between travel and feeding time (Altmann, 1980; Dunbar and Sharman, 1983; Iwamoto and Dunbar, 1983; Dunbar and Dunbar, 1988). Such a relationship, however, was found to exist for hybrid gibbons but only food source distribution, rather than foraging group size, is likely to exert any influence on travelling behaviour. Gibbons may, therefore, need to devote more time to travel if food sources, and particularly important dietary items, are either low in abundance or distantly located to one another. However, at the field sites where both food abundance (the proportion of plot trees to be known gibbon foods) and gibbon activity budgets have been measured, no evidence of a consistent trend has been found ($p>.05$). Furthermore, hybrid gibbons still travelled more than species residing in habitats exhibiting comparable food tree density (e.g. *syndactylus* and *lar* at Kuala Lompat). The distribution or abundance of important food items, such as fruit and figs, rather than food sources in general may exert a greater influence on travel-time. Unfortunately, the poor representation of data relating to either inter-fruit source distance or abundance of fruit trees prevents appropriate investigation here but some information is available for fig densities. Figs exist at relatively low densities at Rekut but, again, field-site variation in abundance and proportional use of travelling behaviour produces an insignificant correlation ($p>0.5$). Furthermore, hybrid gibbons failed to respond to fluctuations in fig use with corresponding changes in daily travel use.

The activity budget, of course, is not a constant but a construct representative of a basic pattern. It is therefore important not just to look at the effects relatively fixed variables, such as food tree density, have on this basic pattern but also to investigate how factors which show temporal variation elicit responses. Two such influential variables found in this study were diet, in particular the contribution of non-fig fruit, and fruit production. Hybrid gibbon travel-time responded both to changes in non-fig fruit consumption and fruiting activity, groups travelling more often when fruit was abundant and comprised much of the diet.

A comparison of these variables with monthly or seasonal changes to the activity budget would be the preferred methodological procedure but relevant data is not always reproduced in the literature. An annual pattern for each variable is used instead. Overall fruiting activity is again insufficiently reported in the literature but figures on the proportion of non-fig fruit in the diet were available in most studies. The relationship between dietary fruit intake and time spent travelling was insignificant. But, in contrast with hybrid gibbons, the direction of the relationship was negative. Different study populations of orang utan also showed varied travel-time responses to changing fruit intake (MacKinnon, 1974; Rodman, 1977; Galdikas, 1988; Mitani, 1989), but Mitani (1989) explained this merely as a function of methodological problems. Undoubtedly, differential sampling techniques and the use of data from a small number of specific representatives hampers such comparative research (see Chivers, 1984) and may mask trends. But it is just as likely that a range of ecological and social variables which operate differently at the inter-population, or even the inter-group level, evoke these conflicting results.

An alternative approach, although simplistic, is that hybrid gibbons apportion so much of their activity budget to travelling because they occupy larger home ranges. A correlation between average travel-time and home range size for 12 populations of gibbon found a supportive, strong positive correlation (r_s=.831 n=12 $p<.05$). Being territory holders, it is imperative that gibbons monitor their territory on a regular basis and it follows that the larger the territory, the more time is required to do so.

The overall activity budget reflects an important compromise between group cohesion and the individual needs of its members. Variance in maintenance activity use by different age and sex groups was largely unremarkable for hybrid gibbons but inter-individual differences did exist. Of particular interest was variation in feeding time, both between the sexes and between females. In the absence of significant sexual dimorphism in body size, differential nutritional and energetic requirements (Post et al., 1980) probably represent the most critical determinants. A good example is the change in the activity budget of the adult female in RBC1. In December 1995 or January 1996, AF1 became pregnant and, over the next six to seven months, began to spend progressively longer periods of the activity period in foraging and feeding behaviours. These alterations to her activity budget contrasted not only with that of her mate's but also with her own budget prior to the pregnancy. Nutritional demands do not dissipate on the birth of the infant since lactation is just as energetically draining. Indeed, Altmann (1980), Dunbar (1983) and Dunbar and Dunbar (1988) observed that female yellow baboons and gelada continue to allocate enormous amounts of time to feeding only until the offspring show signs of independence. In RBC2, the adult female occasionally suckled her infant but actually fed significantly less often than her mate *and* the second non-reproductive female. A transition towards an activity budget with reduced levels of feeding time did not occur over the 12 observation period, indicating that the adult female was not responding to the growing social independence and intake of solid foods of her infant. But it must be remembered that the infant was already somewhat independent of its mother at the start of the field study and had probably reached the stage of weaning. With lactation a less important physiological constraint, time could be spent in other activities.

Why then did AF2 spend less time feeding compared to other mature animals? Feeding competition can introduce disparity in inter-individual activity budgets (Clutton-Brock, 1972; Post et al, 1980), deterring or preventing animals from feeding as often or as long as their group counterparts. But the adult female suffered no such discrimination, regularly choosing where the group was to feed and terminating her own feeding session independent of the behaviours of others. This argument is also made redundant when explaining differences between inter-group animals (e.g. AM1) since hybrid gibbon groups never fed together. In any case, a review of variation in inter-sexual maintenance activity found no obvious feeding-time bias towards either male or female gibbons, regardless of species. It might well be that the ecological and social requirements of the individual are just as important in determining activity patterns as are the equivalent needs of the basic age and sex groupings the individual represents.

4

Feeding Ecology

4.1 Introduction

The information derived from the study of an animal's feeding ecology is three-fold. Firstly, it facilitates an understanding of the relationship held between an animal and its immediate environment, recognising how the composition of the habitat and the phenological activity of resident flora affects the feeding behaviour of the individual and the group. Secondly, in defining the dietary characteristics of an animal and measuring the changes made to that diet over time, a framework is introduced from which aspects of the social and ecological behaviour of an animal can be interpreted. Thirdly, and with particular significance to this study, comparative research on the feeding behaviour of congenerics institutes a means by which ecological, physiological and genetic influences on feeding ecology can be proposed and assessed.

Gibbons routinely consume sizeable amounts of figs and other fruits but, like other frugivores, they supplement their diet with flowers, leaf matter and invertebrates (Chivers, 1974; 1975; 1977b; Gittins, 1979; 1982; Raemaekers, 1979; Tilson, 1979; Gittins and Raemaekers, 1980; Whitten, 1980; 1982a; 1984b; Kappeler, 1984b; Srikosamatara, 1984; Sugardjito, 1988; Islam and Feeroz, 1992a; 1992b; Lan, 1993; Sheeran, 1993; Ahsan, 1994). While comparable amounts of fruit, fig and flowers are taken by most species of gibbon, it is the use of other food types that reveals some inter-habitat and/or inter-specific differences. For example, young leaves are eaten significantly less often by *concolor* (Lan, 1993), *hoolock* (Islam and Feeroz, 1992a; 1992b), *klossii* (Whitten, 1982a) and *pileatus* (Srikosamatara, 1984) compared to other species of gibbon, and by *lar* and *syndactylus* at Ketambe (Palombit, 1997) compared to conspecific populations elsewhere (e.g. Kuala Lompat). Higher than normal levels of secondary compounds in the foliage found at Sirimuri could explain the avoidance of young leaves by Kloss gibbons (Whitten, 1982a), who compensate for the reduction in leaf protein by consuming larger proportions of animal (invertebrate) protein (a dietary adjustment also observed for pileated gibbons). Black gibbons at Mt Wuliang, in contrast, simply substituted young leaves with other leafy matter such as leaf shoots and buds (but see Sheeran, 1993). For hoolock gibbons at Lawachara, and lar gibbons and siamang at Ketambe, it was the availability of fruit which enabled a reduced dependence on young foliage, either in the form of consistent fruit and fig production (*hoolock* – Islam and Feeroz, 1992a) or the higher density of fig species in the habitat of island populations (*lar* and *syndactylus* – Palombit, 1997).

Compared to smaller gibbons, siamang show anomalies in their diet (Chivers, 1974; 1977b; Raemaekers, 1979; 1984; Gittins and Raemaekers, 1980), characterised by the higher proportion of leaves consumed. Unlike the dietary variations observed for *hoolock*, *klossii*, *concolor* and *pileatus*, the siamangs diet, according to Raemaekers (1984), is influenced primarily by physiological rather than ecological differences. It could be argued that the ecological constraints on two closely related sympatric primates could affect resource partitioning in such a way as to necessitate different diets or, in cases of major dietary overlap, the use of food items that are distinct in some morphological feature (eg. size – Lack, 1946; 1947). Studies of siamang sympatric with *lar* and *agilis* (Chivers, 1974; 1977b; Raemaekers, 1979; 1984; Gittins, 1979; Gittins and Raemaekers, 1980), however, reveal that such limitations do not shape the feeding habits of these species. The siamang's larger body size requires a greater expenditure of energy for travel so, to prevent excessive energy loss, siamang should range over shorter distances compared to the smaller bodied gibbons (Raemaekers, 1979). A reduced day range length, however, means that fewer fruit sources can be detected. The regular dietary use of a common and more evenly spread foodstuff than fruit obviates the problem of food access but leaves the animal with a potentially nutritionally poor diet. To cope with the low energy yield derived from their leafy diet, Raemaekers (1979) proposed that siamang metabolise food at a rate lower than that of other gibbon species.

Ecological and physiological constraints are routine interpretations of variation in the diet between different gibbon species, little attention has been given to the genetic component of food selection. Comparing food item use between species of gibbon, particularly those not sympatric with one another, *is* confounded by potential and real differences in the floristic composition of the environment which may disguise specific (read genetic) related food choice. The feeding ecology of hybrid animals, especially those living in the same habitat as parental species, represents an alternative template from which the genetic influences on dietary intake can be explored. One such example is the *Cercopithecus ascanius* x *mitis* hybrids of the Kibale forest, Uganda. These hybrids subsist on foodstuffs common to both redtail and blue monkeys but supplement the diet with food species used *only* by redtail monkeys or *only* by blue monkeys, or with species that rarely or don't feature in the diet of either cercopithecine (Struhsaker et al., 1988). Little contact was made between hybrids and blue monkeys during the course of Struhsaker et al.'s (1988) study, giving the hybrids little chance to learn or imitate the food selection behaviour of the blue monkeys. Instead, dietary peculiarities were attributed to the effects of hybridisation and a genetic component assigned to the process of food selection (Struhsaker et al., 1988).

4.1.1 Outline of Chapter 4

The feeding ecology of hybrid gibbons will be examined at three levels, assessing both the diet and the ecological factors influencing the annual, monthly and daily exploitation of food sources. Annual dietary composition will be examined in terms of the proportional use of, and selection for, food species (Section 4.4.1), food types (Section 4.4.2), and food items (Section 4.4.3) and through the identification of morphological characteristics gibbons appear to be selecting for when choosing foods (Section 4.4.2.1). Fruit selection will receive particular attention in the light of the role gibbons play in seed dispersal (Section 4.4.2.2.). Indices of dietetic diversity (Section 4.5.1) and changes in the consumption and importance of food items (Section 4.5.2) and types (Section 4.5.3) will be used to discuss monthly variation in the diet. In turn, dietary variation will be compared to phenological patterns to determine whether gibbon diets are affected by cycles in the availability of foodstuffs and the environmental conditions influencing plant part production. The third section will focus on the daily diet – the number of sources visited each hour and over the activity period (Section 4.6.1), the amount of revisitation to the same source or species, and the degree of overlap in diet between days comprising a 5-day follow. In Section 4.6.2 temporal patterning of food type choice is investigated, in particular the physiological and ecological reasons governing the use of different food types at different times of the day. The final section (4.7) discusses duration of feeding on food types.

4.2 Methods

4.2.1 Collection of feeding data

Feeding ecology data were collected using a combination of ten-minute scan sampling and continuous observation, the time spent feeding on a particular food source being selected as the unit of measurement. Previous ecological studies have employed the proportion of either feeding records (Clutton-Brock, 1972; Oates, 1977; 1988; Raemaekers, 1979; McKey et al., 1981; Marsh, 1981a; Newton, 1992; Islam and Feeroz, 1992b; Mturi, 1993) or the time spent feeding on each food item (Chivers, 1974; Clutton-Brock, 1975; Struhsaker, 1975; Gittins, 1979; Whitten, 1982a; Kool, 1993) to determine the contribution a plant taxon makes to a primate's diet. The accuracy of these methods has been questioned, however, due to their inconsistent relationship with the actual amount of food ingested (Hladik, 1977; Whitten, 1982a; Newton, 1992). Feeding records and feeding rates were strongly correlated in red colobus and black-and-white colobus diets (Oates, 1977; Marsh, 1981a) but little association was found in the case of hanuman langurs (Hladik, 1977) and Kloss gibbons (Whitten, 1982a). Occasional problems with both visibility and the collection of food items prevented consistent measurement of feeding rates and food weights, and thus length of feeding bouts was considered the more reliable indicator.

On each occasion when a gibbon commenced feeding from a new food source, or resumed feeding on the same source after a period of one hour (after Oates, 1977; Marsh, 1981a), the time was recorded (even if it did not start on a scan) and the duration of the feeding or foraging bout recorded with a stopwatch. Feeding durations were timed for each individual and the group average calculated by adding the times and dividing by the number of gibbons in the group. Only those sources actually observed being eaten at the time of a scan and during a 5-day sample will be discussed at length in the results although some mention will be made of non-sample foodstuffs.

4.2.2 Categories of food types

Thick foliage occasionally impeded the identification of plant parts but a clear view characterised the great majority of feeding observations. If visibility did prevent the detection of the food type, and it could be guaranteed that gibbons were the only animals feeding at the source, the surrounding forest floor was inspected for fresh half-eaten items or the feeding tree watched for discarded food falling from above. In all, a total of seven food types were taken by hybrid gibbons – figs, fruit, flowers and flower buds, young leaves, leaf buds and mature leaves. To remain consistent with previous studies on gibbon ecology (e.g. Chivers, 1974; 1984; Gittins, 1979; 1982; Gittins and Raemaekers, 1980; West, 1981; Whitten, 1982a; Kappeler, 1984b; Srikosamatara, 1984; Leighton, 1987; Islam and Feeroz, 1992a; 1992b; Sheeran, 1993; Ahsan, 1994), and to flag the importance of figs in the gibbon diet, figs were allocated to a food type category separate from non-fig fruits.

4.2.3 Identification of food sources

Each food source was located on a field map and tagged. Kursani, Mulyadi or myself initially attempted specific identification in the field. However, if the source could not be recognised, or if there was some uncertainty in the identification, a sample of the plant part, and a leaf and piece of bark from the source, was collected, stored in an air-tight plastic bag and taken back to camp. At camp, the sample was examined by either Surian or Dr Lazlo Nagy and compared with specimens held in the herbarium. Most plants were identified this way; if classification was still unresolved, the samples were dried, pressed and bagged and taken to the National Herbarium at Bogor.

4.2.4 Measurement of floristic composition and patterns of phenology

Measurement of phenology cycles and the distribution of tree species in the home range have already been discussed in Chapter 2. Phenological data were collected to determine whether changes in the monthly diet were responsive to variations in the forest's patterns of leaf flushing, fruiting and flowering. Vegetational analysis, in turn, was used to assess the degree of dietary selectivity.

4.2.5 A definition of feeding terms

Although there are only a few terms in the literature to describe primate food categories, they have consistently been used in different contexts by different authors. To alleviate confusion, definitions for each food category used in the following discussion are as follows:

- *Food source*: any vegetational (e.g., tree, climber) or animal matter a gibbon was observed to eat.
- *Food species*: the taxonomic classification of the food source.
- *Food type*: generally, the reproductive (figs, fruit or flowers) or leafy parts of a plant food source; interchangeable with plant type or plant phase. In some sections (e.g. Section 4.4.2), insects are also referred to as a food type.
- *Food item*: the food species and food type eaten (eg. *Eugenia ecostulata* fruit).

In the following text, food types may be designated with a two or three letter abbreviation. They are:

- *FIG* - figs
- *FR* - fruits other than figs
- *FL* - flowers
- *FLB* - flower buds
- *YL* - young leaves
- *LB* - leaf buds or shoots
- *INV* - invertebrates

4.3 Feeding techniques

Gibbons are fastidious feeders, inspecting their food carefully before consumption and discarding much of it after only one or two bites. Selection of leaves is particularly careful, as only the most tender of young leaves are acceptable to gibbons. Once an appropriate leaf is selected, it is plucked with the hand and eaten whole. Sometimes the leaf is stripped down the petiole and the two halves eaten separately. Leaf buds and flowers are removed using the thumb and forefinger and more than one may be picked before being taken to the mouth. With large flowers, such as those of the epiphyte *Loranthus*, the petals are peeled off one by one.

The manipulation of fruit depends on its size and the pliability of the pericarp. Small fruits (e.g. *Rhus nodosa*) and figs found in clusters are gathered in handfuls and tipped into the mouth. Rapid movement around the food tree is normally associated with the harvesting of these fruit forms, the feeding gibbon appearing to randomly collect fruit, with little attention being paid to the quality of the food about to be ingested. These fruits are similar in structure to the small fruits eaten by agile gibbons (Gittins, 1979; 1982): a thin, easily ruptured rind encased the pulp and the seeds were easily swallowed. The selection and processing of larger fruits takes slightly longer. Feeding on fruits with succulent pulps and pliant pericarps, such as *Artocarpus dadah* and *Garcinia parvifolia*, is characterised by intense scrutiny of the food before and after it is plucked from the branch. After visual examination, the fruit is tasted and, more often than not, dropped after only one bite; the ground surrounding the food source becomes littered with half eaten fruits. Analysis of discarded fruits indicates that seed consumption is sporadic. Fruits with thicker pericarps require some time investment in processing. Those with rubbery rinds (eg. *Nephelium*, *Dillenia*) are split open with the teeth and the pericarp peeled off with the fingers to reveal the seed and endocarp. Sometimes the index finger is used to scoop out the flesh. If the seeds were small enough, they are swallowed; usually, however, they are not, the gibbons sucking off the flesh and spitting out the rest. Woody pericarps (eg. *Lithocarpus*) are shaved and broken open by husking with the canines or, alternatively, weakened with a grinding action of the molars, the gibbon holding the fruit between its molars and continually biting down. Usually only the seed and some of the surrounding flesh is eaten, the less digestible parts of the fruit are discarded.

The consumption of insects follows either a deliberate search or an accidental discovery while travelling. Flying insects are caught in the hand as they fly past the gibbon, inspected and then eaten. Locations of termites, ants and larvae require a closer examination of the surrounding environment. Epiphytic ferns clinging to trunks are pared back, large fruits broken open, cups in branches perused, and bark ripped off boles and shaken. If the gibbon happens upon a termite or ant column, it watches the insects before feeding; the insects are usually collected by running the palm or back of the hand along the column, leaf or bark and transferred to the mouth by licking the hand. Otherwise, they are scooped up in the fingers.

Gittins (1979; 1982) defined two ways in which gibbons feed – feeding bouts and foraging – and these terms will also be used in describing hybrid gibbon feeding. Feeding bouts occur when groups come across a large or favoured food source. At least two members of the group enter the food tree and periods of feeding are lengthy, lasting on average between 10 and 25 minutes. During periods of travel, often between primary food sources and when travel speed is slow, gibbons independently visit, and spend short amounts of time in, smaller or less desirable food trees. Another group member may enter the same food source but rarely at the same time as the initial visitor. These sources are discovered by chance rather than sought for and are not re-visited unless the group uses the same pathway. This way of feeding is referred to as foraging.

Gibbons mainly assume a sitting posture when engaged in feeding bouts, extending an arm or leg to grab and remove the food item. If the item is just out of reach, they stand up. For more remotely placed items, on terminal branches or boles, a suspensory position is adopted, with the legs extended downward or tucked up against the chest. A hand or both feet are used to hold and/or collect the food. Gibbons remain stationary for most of the feeding bout, only moving to a new position when the food supply immediately surrounding them has been exhausted. While foraging, however, movement is more common, the gibbon climbing and brachiating, often rapidly, around the canopy and spending less time checking the condition of the food to be ingested.

4.4 The annual diet

4.4.1 Composition of the diet – food species

Over the 60 day sample, which encompassed the period September 1995 to August 1996, a total of 21063 minutes of feeding data were collected for RBC2. RBC2 mostly concentrated on plant phases found on trees (Table 4-1) but also visited climbers/lianas, and, to a lesser extent, stranglers, epiphytes and shrubs for dietary items. One hundred and fifty two recognised plant sources were used by RBC2 (Table 4-2), of which 134 were identified to at least family or generic level. RBC1 used 109 food sources during 3789 minutes of feeding activity (Table 4-2) and, like RBC2, also favoured trees, climbers/lianas and stranglers as primary sources of plant foods. Epiphytes and shrubs, however, received no observed feeding attention. Seventy-six species featured in the diets of both groups, representing 49.7% and 69.7% of RBC2 and RBC1's dietary sources respectively. Additional food species consumed by RBC2 and RBC1 are appended to the bottom of the table. The relatively small number of additional foods for

RBC2 reflects its dependence on similar food species during the month as substantial alterations to the diet were rare in the week(s) following the 5-day observation period.

From the 152 food sources which composed RBC2's diet, 44 families and 83 genera were recognised (see Tables 4-3 and 4-4). The highest ranked family was Moraceae which accounted for over a quarter (≈27.0%) of the diet. In comparison, the families Crypteroniaceae and Annonaceae, which were ranked second and third, contributed only 7.7% and 7.1% to the diet. The prominence of Moraceae in the group's diet was largely attributable to their use of *Ficus* and *Artocarpus*, the first and third most important food genera. *Ficus* was a particularly significant food taxon; a fifth of the total feeding time was spent on fig consumption. RBC2 fed from fifteen different species of fig, using at least one species in every month of the observation period. *Artocarpus* was also exploited throughout most of the year, mostly in December 1995, and April and June 1996, when *A. dadah* and *A. nitidus* trees were fruiting heavily. Seven of the ten most important food families – Crypteroniaceae, Gnetaceae, Guttiferae, Leguminosae, Bombaceae, Myrtaceae and Polygalaceae – were highly ranked largely through the use of one or two representative genera.

RBC2 exploited a minimum of 130 species although it is probable that the 22 unidentified plant sources also represent additional species. Fifty two percent (n=80) of food species were sources of fruit, 39.2% (n=60) of young leaves, 20.3% (n=31) of flowers and 5.9% (n=9) of leaf buds.

Table 4-1 Proportional feeding use of different plant life forms.

Group	Plant Life Form									
	Tree		Liana/Climber		Strangler		Epiphtye		Shrub	
	%	n	%	n	%	n	%	n	%	n
RBC2	65.4	100	29.4	45	3.9	6	0.7	1	0.7	1
RBC1	61.3	65	33.0	35	5.7	6	-	-	-	-

4.4.1.1 Important food species

The most important food provider during the year for RBC2 was *Crypteronia griffithii* which contributed 6.8% to the annual diet. Young leaves, fruit and flowers were all taken from this plant source. Surprisingly, this species' principal role in RBC2's diet was largely due to the consumption of its young leaves, particularly in September when *C. griffithii* was one of the few abundant food sources available in the home range. A deficiency in food, probably caused by an unusually high rainfall in the preceding months (see Section 4.5.1), necessitated the group to concentrate its feeding on just a few species. The presence of both a significant number of trees flushing (RBC2 visited 7 different trees in September) and the large amounts of young leaf in these trees made *C. griffithii* an especially attractive food source in a time of low edible or preferred food type production.

Table 4-2 Length of time and percentage of time spent feeding on each food species.

Family	Species	Life Form	RBC2			RBC1		
			Feeding time (mins)	Percentage of total feeding time	Rank	Feeding Time (mins)	Percentage of total feeding time	Rank
Actinidiaceae	*Saurauia* sp.	T	3	0.01	=150	14	0.37	=50
Anacardiaceae	*Gluta curtisii*	T	262	1.24	24	-	-	-
	G. rostrata	T	28	0.13	=106	-	-	-
	Mangifera pajang	T	43	0.20	=84	-	-	-
	Parishia maingayi	T	10	0.05	=132	-	-	-
	Pegia sarmentosa	L	9	0.04	=138	17	0.45	=45
	Rhus nodosa	C	797	3.78	4	-	-	-
	Swintonia glauca	T	32	0.15	=102	6	0.16	=74
	S. floribunda	T	-	-	-	24	0.63	36
Annonaceae	*Artabotrys costatus*	C	130	0.62	=45	-	-	-
	Desmos dunalii	C	31	0.15	=102	12	0.32	=56
	Ellipeia cuneifolia	C	171	0.81	37	18	0.48	=43
	Fissistigma manubriatum	C	383	1.82	=14	133	3.51	10
	Mezzettia havilandi	T	26	0.12	=113	-	-	-
	Oxymitra biglandulosa	C	60	0.28	=69	10	0.26	=58
	Polyalthia glauca	T	383	1.82	=14	36	0.95	=28
	P. sumatrana	T	9	0.04	=138	-	-	-
	Pyranidanthe prismatica	C	175	0.83	=35	21	0.55	=37
	Uvaria lobbiana	C	121	0.57	=47	-	-	-
Apocynaceae	*Willughbeia sp.*	C	174	0.83	=35	91	2.40	15
	Liana Oct 1	C	65	0.31	=66	15	0.40	49
Aquifoliaceae	*Ilex* sp.	C	287	1.36	22	-	-	-
Bombaceae	*Durio griffithii*	T	288	1.37	=20	-	-	-
	D. malaccensis	T	729	3.46	6	179	4.72	3
Burseraceae	*Canarium megalanthum*	T	16	0.08	=122	-	-	-
Convulvulaceae	*Erycibe maingayi*	C	11	0.05	=132	-	-	-
Crypteroniaceae	*Crypteronia griffithii*	T	1425	6.77	1	143	3.77	7
	C. paniculata	T	196	0.93	32	4	0.11	=81
Dilleniaceae	*Dillenia grandifolia*	T	162	0.77	39	28	0.74	=33
Dipterocarpaceae	*Dipterocarpus crinitus*	T	4	0.02	=144	-	-	-
	D. grandiflorus	T	-	-	-	2	0.05	=92
	Hopea griffithii	T	16	0.08	=122	-	-	-
	Shorea crassa	T	112	0.53	51	-	-	-
	S. kunstleri	T	23	0.11	=114	-	-	-
	S. parvifolia	T	5	0.02	=144	-	-	-
	Vatica rassak	T	1	0.01	=150	13	0.34	=54
	V. sumatrana	T	4	0.02	=144	1	0.03	=102
Ebenaceae	*Diospyros borneensis*	T	53	0.25	76	3	0.08	=87
	D. confertiflora	T	46	0.22	=79	-	-	-
	D. ferruginea	T	18	0.09	=119	14	0.37	=50
Ericaceae	*Rhododendron* sp.	T	61	0.29	68	-	-	-
Euphorbiaceae	*Aporusa lanata*	T	-	-	-	58	1.53	23
	Baccaurea sp.	T	49	0.23	78	16	0.42	48
	B. bracteata	T	248	1.12	26	2	0.05	=92
	Blumeodendron tokbrai	T	-	-	-	7	0.18	=72
	Glochidion borneensis	T	4	0.02	=144	-	-	-
	Phyllanthus emblica	T	27	0.13	=106	-	-	-
	Podadenia sp.	T	-	-	-	86	2.27	16
Fagaceae	*Lithocarpus pusillus*	T	46	0.22	=79	-	-	-
Flacourtiaceae	*Hydnocarpus woodii*	T	29	0.14	=105	3	0.08	=87
Gnetaceae	*Gnetum gnemon*	T	474	2.25	10	172	4.54	5
	G. gnemoides	C	-	0.03	=142	-	-	-
	G. latifolium	C	520	2.47	9	166	4.38	6
	G. neglectum	C	251	1.19	25	20	0.53	=39
Guttiferae	*Garcinia bancana*	T	24	0.11	=114	8	0.21	=68
	G. cornea	T	40	0.19	=90	2	0.05	=92
	G. cowa	T	90	0.43	58	-	-	-
	G. dulcis	T	166	0.79	38	64	1.69	21
	G. parvifolia	T	755	3.58	5	99	2.61	13
	G. sp A	T	70	0.33	65	1	0.03	=102
	G. sp B	T	51	0.24	77	5	0.13	=79
	G. sp C	T	-	-	-	2	0.05	=92
Hypericaceae	*Cratoxylum glaucum*	T	107	0.51	52	-	-	-

Table 4-2 (continued)

Family	Species	Life Form	RBC2			RBC1		
			Feeding time (mins)	Percentage of total feeding time	Rank	Feeding time (mins)	Percentage of total feeding time	Rank
Lauraceae	*Eusideroxylon zwageri*	T	45	0.21	=82	25	0.66	35
	Tree Jan 1	T	-	-	-	1	0.03	=102
	Tree July 1	T	40	0.19	=90	-	-	-
Leguminosae	*Acacia borneensis*	L	104	0.49	53	-	-	-
	Dialium indum	T	98	0.47	=55	32	0.84	31
	D. patens	T	466	2.21	11	3	0.08	=87
	Koompassia malaccensis	T	131	0.62	=45	-	-	-
	Parkia speciosa	T	217	1.03	=28	54	1.43	25
	Sindora coriacea	T	5	0.02	=144	-	-	-
	Liana Jan 1	L	21	0.10	=116	1	0.03	=102
Linaceae	*Indouchera* sp.	L	88	0.42	=59	-	-	-
Loganiaceae	*Fagrea ridleyi*	L	38	0.18	=96	7	0.18	=72
	Strychnos ignatii	L	42	0.20	=84	21	0.55	=37
Loranthaceae	*Loranthus* sp.	E	8	0.04	=138	3	0.08	=87
Melastomataceae	*Dissochaeta grasilis*	L	116	0.55	49	199	5.25	1
	D. sp A	L	18	0.09	=119	-	-	-
	Macrolene sp.	L	55	0.26	=74	1	0.03	=102
	Memecylon sp.	T	-	-	-	2	0.05	=92
	Pternandra rostrata	T	149	0.71	42	8	0.21	=68
Meliaceae	*Aglaia ganggo*	T	-	-	-	10	0.26	=58
	Sandoricum sp.	T	-	-	-	2	0.05	=92
	Walsura sp.	T	14	0.07	=126	-	-	-
Moraceae	*Artocarpus dadah*	T	697	3.31	7	8	0.21	=68
	A. elasticus	T	75	0.36	63	10	0.26	=58
	A. integer	T	16	0.08	=122	-	-	-
	A. kemando	T	100	0.47	=55	-	-	-
	A. nitidus	T	359	1.70	17	31	0.82	32
	A. sp A	T	42	0.20	=84	1	0.03	=102
	Ficus bracteata	S	121	0.57	=47	-	-	-
	F. callosa	T	10	0.05	=132	10	0.26	=58
	F. caulocarpa	S	89	0.42	=59	-	-	-
	F. chartaceae	T	114	0.54	50	-	-	-
	F. deltoidea	S	371	1.76	16	2	0.05	=92
	F. excavata	C	99	0.47	=55	-	-	-
	F. globosa	S	-	-	-	65	1.72	20
	F. obscura	S	153	0.73	41	-	-	-
	F. pellucido-punctata	S	225	1.07	27	10	0.26	=58
	F. sinuata	T	144	0.68	43	81	2.14	17
	F. stupenda	S	407	1.93	13	135	3.56	9
	F. subgelderi	S	1015	4.82	2	219	5.78	1
	F. sundaica	T	900	4.27	3	96	2.53	14
	F. subtecta	T	-	-	-	46	1.21	26
	F. vasculosa	T	42	0.20	=84	-	-	-
	F. villosa	C	464	2.20	12	-	-	-
	F. sp A	U	57	0.27	73	-	-	-
	F. sp B	S	-	-	-	9	0.24	=64
	Parartocarpus bracteatus	T	136	0.65	44	19	0.50	=41
	Prainea limpato	T	42	0.20	=84	14	0.37	=50
Myrisinaceae	*Embelia* sp.	L	40	0.19	=90	-	-	-
Myristicaceae	*Horsfieldia* sp.	T	-	-	-	6	0.16	=74
	Knema latifolia	T	10	0.05	=132	4	0.11	=81
	Myristica elliptica	T	58	0.28	=69	-	-	-
Myrtaceae	*Eugenia ecostulata*	T	534	2.54	8	142	3.75	8
	E. leucoxla	T	180	0.85	33	-	-	-
	E. papillosa	T	38	0.18	=96	-	-	-
	E. polyalthia	T	-	-	-	41	1.08	27
	E. sp A	T	13	0.06	=129	-	-	-
	E. sp B	T	102	0.48	54	4	0.11	=81
	E. sp C	T	-	-	-	36	0.95	=28
	Syzygium lineatum	T	32	0.15	=102	-	-	-
	Tristania grandifolia	T	10	0.05	-132	-	-	-
	Tristania whiteana	T	35	0.17	=98	-	-	-
Palmae	*Calamus pogonacanthus*	C	27	0.13	=106	-	-	-
Polygalaceae	*Xanthophyllum affine*	T	176	0.84	34	4	0.11	=81

Table 4-2 (continued)

Family	Species	Life Form	RBC2			RBC1		
			Feeding time (mins)	Percentage of total feeding time	Rank	Feeding time	Percentage of total feeding time	Rank
	X. griffithii	T	217	1.03	=28	-	-	-
	X. stipitatum	T	155	0.74	40	68	1.79	19
	X. sp A	T	28	0.13	=106	4	0.11	=81
Proteaceae	*Helicia* sp.	T	-	-	-	119	3.14	11
Rhamnaceae	*Zizyphus angustifolius*	T	12	0.06	=129	56	1.48	24
	Z. lenticellata	C	85	0.40	62	3	0.08	=87
Rosaceae	*Rubus elongatus*	L	22	0.10	=116	-	-	-
Rubiaceae	*Ixora* sp.	T	-	-	-	6	0.16	=74
	Psydrax sp.	T	47	0.22	=79	-	-	-
	Timonius sp.	T	40	0.19	=90	-	-	-
	Wenlandia sp.	T	42	0.20	=84	-	-	-
Sapindaceae	*Paranephelium xestophyllum*	T	346	1.64	18	117	3.09	12
	Pometia pinnata	T	41	0.19	=90	-	-	-
	Xerospermum noronhianum	T	33	0.16	=100	-	-	-
Ranunculae	*Clematis* sp.	L	45	0.21	=82	-	-	-
Rhamnaceae	*Ventilago* sp.	L	66	0.31	=66	-	-	-
Sapotaceae	*Palaquium eriocalyx*	T	12	0.06	=129	-	-	-
	Payena leerii	T	15	0.07	=126	-	-	-
Sterculiaceae	*Sterculia parvifolia*	T	-	-	-	14	0.37	=50
	Sterculiaceae sp 1	T	15	0.07	=126	6	0.16	=74
Theaceae	*Adinandra dumosa*	T	297	1.41	19	61	1.61	22
Thymelaceae	*Gonystylus affinis*	T	22	0.10	=116	-	-	-
	G. borneensis	T	11	0.05	=132	-	-	-
Tiliaceae	*Grewia blattifolia*	T	207	0.98	31	9	0.24	=64
	G. sp A	T	274	1.30	23	174	4.59	4
	Pentace excelsa	T	72	0.34	64	-	-	-
Ulmaceae	*Gironniera nervosa*	T	218	1.03	=28	-	-	-
Vitaceae	*Vitis* sp.	L	17	0.08	=122	17	0.45	=45
Unknown	Arau	C	289	1.37	=20	71	1.87	18
	Liana Oct 2	L	-	-	-	33	0.87	30
	Liana Oct 3	C	-	-	-	13	0.34	=54
	Tree Oct 4	T	-	-	-	2	0.05	=92
	Liana Nov 1	C	35	0.17	=98	1	0.03	=102
	Tree Dec 1	T	30	0.14	105	-	-	-
	Tree Dec 2	T	28	0.13	=106	-	-	-
	Tree Jan 2	T	9	0.04	=138	-	-	-
	Tree Jan 3	T	54	0.26	=74	-	-	-
	Tree Jan 4	T	-	-	-	3	0.08	=87
	Liana Jan 5	L	-	-	-	10	0.26	=58
	Liana Jan 4	L	28	0.13	=106	-	-	-
	Liana Feb 1	C	2	0.009	152	-	-	-
	Liana Feb 2	C	59	0.28	=69	19	0.50	=41
	Liana Feb 3	L	60	0.28	=69	12	0.32	=56
	Liana Feb 4	C	-	-	-	9	0.24	=64
	Tree Feb 5	T	-	-	-	2	0.05	=92
	Tree Mar 1	T	-	-	-	8	0.21	=68
	Liana Mar 2	L	-	-	-	6	0.16	=74
	Liana Mar 3	L	-	-	-	9	0.24	=64
	Liana Apr 1	C	6	0.03	=142	4	0.11	=81
	Liana Apr 2	L	39	0.19	=90	1	0.03	=102
	Liana Apr 3	L	-	-		5	0.13	=79
	Tree May 1	T	20	0.09	=119	-	-	-
	Liana May 2	C	5	0.02	=144	-	-	-
	Liana May 3	C	-	-	-	18	0.48	=43
	Tree May 4	T	-	-	-	20	0.53	=39
	Liana June 1	C	87	0.41	61	28	0.74	=33
	Liana June 2	L	-	-	-	17	0.45	=45
	Tree July 2	T	26	0.12	=112	-	-	-
	Liana July 3	L	33	0.16	=100	-	-	-
	Total Feeding Minutes =		21063			3789*		-

Key to Life Form: T = Tree; L = Liana; C = Climber; S = Strangler; E = Epiphyte
Additional identified food species: *Tabernaemontana* spp., *Parastemon urophyllus*, *Ficus* sp. C, *Pternandra* spp., *Cotylelobium lanceolatum*, *Albizia retusa*, *Litsea* spp.
* Only feeding data from RBC1 full-day follows was included to be compatible with RBC2 feeding data.

Table 4-3 Length of time and percentage of time RBC2 spent feeding on each family food source (includes only identified families).

Family	Feeding time (minutes)	Percentage of total feeding time	Rank
Actinidiaceae	3	0.01	44
Anacardiaceae	1181	5.61	6
Annonaceae	1489	7.07	3
Apocynaceae	239	1.13	17
Aquifoliaceae	287	1.36	16
Bombaceae	1017	4.83	8
Burseraceae	16	0.08	=38
Convulvulaceae	11	0.05	41
Crypteroniaceae	1621	7.70	2
Dilleniaceae	162	0.77	=20
Dipterocarpaceae	165	0.78	19
Ebanaceae	117	0.56	23
Ericaceae	61	0.20	31
Euphorbiaceae	328	1.56	14
Fagaceae	46	0.22	29
Flacourtiaceae	29	0.14	34
Gnetaceae	1252	5.94	4
Guttiferae	1196	5.68	5
Hypericaceae	107	0.51	24
Lauraceae	85	0.40	26
Leguminosae	1042	4.95	7
Linaceae	88	0.42	25
Loganiaceae	80	0.38	27
Loranthaceae	8	0.04	42
Melastomataceae	337	1.60	13
Meliaceae	14	0.07	40
Moraceae	5678	26.96	1
Myrisinaceae	40	0.19	32
Myristicaceae	68	0.32	28
Myrtaceae	944	4.48	9
Palmae	27	0.13	=35
Polygalaceae	576	2.73	10
Ranunculae	45	0.21	30
Rhamnaceae	163	0.77	=20
Rosaceae	22	0.10	37
Rubiaceae	129	0.61	22
Sapindaceae	420	1.99	12
Sapotaceae	27	0.13	=35
Sterculiaceae	5	0.02	43
Theaceae	297	1.41	15
Thymelaceae	33	0.16	33
Tiliaceae	553	2.63	11
Ulmaceae	218	1.03	18
Vitaceae	17	0.08	=38

Table 4-4 Length of time and percentage of time RBC2 spent feeding on each generic foodsource (includes only identified genera).

Family	Genus	Feeding time (minutes)	Percentage of total feeding time	Rank
Actinidiaceae	*Saurauia*	3	0.01	83
Anacardiaceae	*Gluta*	290	1.38	17
	Mangifera	43	0.20	=49
	Parishia	10	0.05	=72
	Rhus	797	3.78	7
	Pegia	9	0.04	=75
	Swintonia	5	0.02	=77
Annonaceae	*Artabotrys*	130	0.62	=30
	Desmos	31	0.15	=59
	Ellipeia	171	0.81	24
	Fissistigma	383	1.82	13
	Mezzettia	26	0.12	64
	Oxymitra	60	0.28	=41
	Polyalthia	392	1.86	12
	Pyranidanthe	175	0.83	=22
	Uvaria	121	0.57	32
Apocynaceae	*Willughbeia*	174	0.83	=22
Aquifoliaceae	*Ilex*	287	1.36	19
Bombaceae	*Durio*	729	3.46	8
Burseraceae	*Canarium*	16	0.08	=66
Convulvulaceae	*Erycibe*	11	0.05	=72
Crypteroniaceae	*Crypteronia*	1621	7.70	2
Dilleniaceae	*Dillenia*	162	0.77	25
Dipterocarpaceae	*Dipterocarpus*	4	0.02	=77
	Hopea	16	0.08	=66
	Shorea	140	0.66	27
	Vatica	5	0.02	=77
Ebanaceae	*Diospyros*	117	0.56	33
Ericaceae	*Rhododendron*	61	0.29	40
Euphorbiaceae	*Baccaurea*	297	1.41	=15
	Glochidion	4	0.02	=77
	Phyllanthus	27	0.13	=62
Fagaceae	*Lithocarpus*	46	0.22	=44
Flacourtiaceae	*Hydnocarpus*	29	0.14	61
Gnetaceae	*Gnetum*	1252	5.94	4
Guttiferae	*Garcinia*	1196	5.68	5
Hypericaceae	*Cratoxylum*	107	0.51	34
Lauraceae	*Eusideroxylon*	45	0.22	=44
Leguminosae	*Acacia*	104	0.49	35
	Dialium	564	2.68	10
	Koompassia	131	0.62	=30
	Parkia	217	1.03	=20
	Sindora	5	0.02	=77
Linaceae	*Indouchera*	88	0.42	37

Table 4-4 (continued)

Family	Genus	Feeding time (minutes)	Percentage of total feeding time	Rank
Loganiaceae	*Fagrea*	38	0.18	56
	Strychnos	42	0.20	=49
Loranthaceae	*Loranthus*	8	0.04	=75
Melastomataceae	*Dissochaeta*	134	0.64	29
	Macrolene	54	0.26	43
	Pternandra	149	0.71	26
Meliaceae	*Walsura*	14	0.07	=69
Moraceae	*Artocarpus*	1290	6.12	3
	Ficus	4211	19.99	1
	Parartocarpus	136	0.65	28
	Prainea	42	0.20	=49
Myrisinaceae	*Embelia*	40	0.19	=53
Myristicaceae	*Knema*	10	0.05	=72
	Myristica	58	0.28	=41
Myrtaceae	*Eugenia*	867	4.12	6
	Syzygium	32	0.15	=59
	Tristania	45	0.21	=47
Palmae	*Calamus*	27	0.13	=62
Polygalaceae	*Xanthophyllum*	576	2.73	9
Ranunculae	*Clematis*	45	0.21	=47
Rhamnaceae	*Ventilago*	66	0.31	39
	Zizyphus	97	0.46	36
Rosaceae	*Rubus*	22	0.10	65
Rubiaceae	*Psydrax*	47	0.22	=44
	Timonius	40	0.19	=53
	Wenlandia	42	0.20	=49
Sapindaceae	*Paranephelium*	346	1.64	14
	Pometia	41	0.19	=53
	Xerospermum	33	0.16	=57
Sapotaceae	*Palaquium*	12	0.06	71
	Payena	15	0.07	=69
Sterculiaceae	*Sterculiaceae*	5	0.02	=77
Theaceae	*Adinandra*	297	1.41	=15
Thymelaceae	*Gonystylus*	33	0.16	=57
Tiliaceae	*Grewia*	481	2.27	11
	Pentace	72	0.34	38
Ulmaceae	*Gironniera*	218	1.03	=20
Vitaceae	*Vitis*	17	0.08	=66
Unknown	*Arau*	289	1.37	18

Two fig species, *Ficus subgelderi* and *F. sundaica*, represented the second and third most important food species, accounting for 4.8% and 4.3% of feeding time respectively, and tending to be the preferred species of fig during months when more than one *Ficus* was fruiting. *F. subgelderi* was used in four of the 12 5-day samples but only made a significant contribution to the diet in two of those months. Interestingly, the heavy utilisation of *F. subgelderi* occurred in the same two months that *C. griffithii* featured prominently in the diet. Fruiting activity was retarded in September and October 1995 and only a limited number of plants, including a solitary but large *F. subgelderi* strangler, provided a plentiful and accessible supply of fruit.

RBC2 visited three *F. sundaica* trees in as many months, eating large amounts of this species of fig in February and August. In the former month, a *F. sundaica* stood at the site of a serious territorial confrontation between RBC2 and RBC1 (Section 6.4.3.1). Possibly influencing the seriousness of the dispute, the fig was occupied by the prevailing group which, in between fending off attacks, ate from the copious crop of fruit. Although RBC1 had the commanding position in the dispute, RBC2 did feed from the source (mainly after RBC1 had returned to their own territory) spending lengthy periods of time doing so.

Other high-ranking species also gained their importance in the overall diet by their use in just a few, and sometimes only one, month. Five of the remaining 10 most used food species were trees, three (*Garcinia parvifolia*, *Artocarpus dadah* and *Eugenia ecostulata*) of which provided fruit, one (*Durio malaccensis*) gave leaf matter and another (*Gnetum gnemon*) both young leaves and, predominantly, fruit. *Garcinia* and *Eugenia* are well represented in different forest types in Borneo, at least 50 species of the former being found in Sarawak and Brunei (Ashton, 1988) and "probably over 100" species of the latter in Kalimantan (Whitmore, 1989). Trees of these genera tend to be small to medium in height, *Garcinia* trees comprising much of the understorey of evergreen rainforest (Ashton, 1988). At least 9 and 14 species of these genera respectively have been recognised from plots in RBC2's home range and both focus groups selected fruit, flowers and young leaves from 8 and 7 of these respectively. The gibbons preference for *G. parvifolia* (3.6% – Rank 5) over other species of *Garcinia* was partially due to this species having two fruiting seasons during the observation period (and see Whitmore, 1984) but also to the structure of the fruit. Gibbons appeared to favour soft, pulpy fruits which had a slightly acidic taste and an orange-yellow-pink colouration (Section 4.2.2.1) and the fruits of *G. parvifolia* possessed all these characteristics. Other species were less easy to harvest (eg. *G. cornea* or *G. dulcis*), or were gathered from trees of smaller crop sizes or reduced fruiting activity.

Less important species of *Eugenia* (e.g. *E. leucoxla*) required little processing before consumption but it was the hard shelled, bitter tasting *E. ecostulata* (2.5% – Rank 8) on which gibbons spent the most time feeding. Not necessarily a preferred species, its prominence in the annual diet is possibly attributable to its significant contribution to the diets of September and October when, as previously stated, food production in the home range was low. This species, like *C. griffithii* and *F. subgelderi*, was one of the few sources available at the time. In contrast, *A. dadah* was undoubtedly a favoured food source. In December and April, two trees of this species fruited within the home range of RBC2 and received many visits. Both trees were around 25 m in height and laden with an abundant quantity of fruit, which was routinely visually scrutinised and tasted by the group before consumption.

Four species of *Gnetum* provided food for RBC2, in particular two species, *G. latifolium* and *G. gnemon*, which were ranked 9th (2.5%) and 10th (2.3%) in the diet. As previously mentioned, two plant types were taken from *G. gnemon*. A small tree with distinctive raised hoops encompassing the bole (Whitmore, 1984), it was distributed throughout the home range of RBC2. The group fed from sixteen individual trees, two of which RBC1 also visited (RBC1 exploiting an additional five in their territory), consuming some young leaf but predominantly eating the ellipsoid, orange-pink fruit. Easily harvested and requiring no preparation before ingestion, *G. gnemon* also showed marked fruiting activity in both number of trees and amount of fruit produced. Almost as widely dispersed, *G. latifolium* represented one of the two climber/liana species prominent in the diet. Gibbons concentrated on *G. latifolium*'s flowers or, to be precise, the yellow, spiky inflorescence, but young leaves were occasionally taken. The second climber was *Rhus nodosa* whose tiny, red-orange fruit made up almost half of the diet in May and accounted for 3.8% (Rank 4) of the annual diet.

4.4.1.2 Selection of food species

The specific composition of a primate diet subserves and is shaped by individual choice and the abundance of key food species. While a primate may prefer the fruits or young leaves of species A compared to those of species B, availability may be such that a primate is confined to consuming greater quantities of B. In effect, the "importance" of a food species in the overall diet is not necessarily a function of preference.

To detect food preference, selection ratios for each food species were calculated using a formula previously employed by McKey et al, 1981; Waterman and Choo, 1981; Oates, 1988, and Mturi, 1993. A species was considered selected for if SR > 1.0, not selected for if SR < 1.0 and consumed at a frequency equal to its abundance if SR = 1.0.

The formula:

$$\text{S.R.} = \frac{\text{\% of total feeding time accounted for by species } i}{\text{\% of total basal area accounted for by species } i}$$

Note: S.R. could only be calculated for tree species represented in plots.

RBC2 adopted a feeding regime of marked selectivity. Selection ratios for ten food species exceeded a value of 100; another eleven species were found to have SR's ranging from 30 to 82.7 (Table 4-5). Of the species representing the ten most selected sources, five were providers of fruit and three of young leaves and/or leaf buds. The remaining two species gave flowers or a combination of fruit and young leaves.

Table 4-5 Relative abundance of and selection for plant species used by RBC2.

Species	% Basal Area	Density	% Relative density	Selection ratio
Gluta curtisii	0.10	1.7	0.4	12.4
G. rostrata	0.02	0.6	0.1	6.2
Mangifera pajang	0.03	0.6	0.1	6.7
Parishia maingayi	0.12	1.7	0.4	0.4
Swintonia glauca	17.96	17.7	3.8	*
Polyalthia glauca	0.30	4.0	0.9	6.1
P. sumatrana	0.02	1.1	0.2	2.2
Willughbeia sp.	0.01	0.6	0.1	162.8
Durio griffithii	0.01	0.6	0.1	124.5
D. malaccensis	0.03	1.1	0.2	111.6
Canarium megalanthum	0.01	0.6	0.1	13.6
Crypteronia griffithii	0.03	1.1	0.2	233.5
Dillenia grandifolia	0.02	1.1	0.2	38.5
Dipterocarpus crinitus	0.42	2.9	0.6	0.1
Hopea griffithii	0.06	2.3	0.5	1.4
Shorea crassa	9.89	8.0	1.7	0.1
S. kunstleri	0.33	3.4	0.7	0.3
S. parvifolia	9.16	10.9	2.3	*
Vatica rassak	0.19	2.3	0.5	0.3
V. sumatrana	0.09	2.3	0.5	0.2
Diospyros borneensis	**	0.6	0.1	61.0
D. confertiflora	0.12	2.3	0.5	1.8
D. ferruginea	0.02	0.6	0.1	45.0
Baccaurea sp.	0.05	1.1	0.2	4.6
B. bracteata	0.02	1.1	0.2	56.0
Lithocarpus pusillus	0.06	1.1	0.2	4.0
Garcinia bancana	**	0.6	0.1	32.4
G. cornea	0.04	1.7	0.4	4.5
G. cowa	0.02	0.6	0.1	82.7
G. dulcis	0.05	1.7	0.4	15.8
G. parvifolia	0.02	1.1	0.2	179.0
Cratoxylum glaucum	0.02	0.6	0.1	30.0
Eusideroxylon zwageri	0.88	1.7	0.4	0.2
Dialium indum	0.91	2.9	0.6	0.5
D. patens	0.01	0.6	0.1	254.0
Koompassia malaccensis	1.40	3.4	0.7	0.4
Strychnos ignatti	0.01	-	-	27.4
Pternandra rostrata	0.06	1.7	0.4	12.5
Walsura sp.	0.03	1.1	0.2	2.4
Artocarpus dadah	0.04	1.1	0.2	78.8
A. elasticus	0.13	0.6	0.1	2.8
A. integer	0.02	0.6	0.1	4.0
A. kemando	0.04	0.6	0.1	12.1
A. nitidus	0.04	1.7	0.4	38.6
Artocarpus sp. A	0.02	1.1	0.2	9.0
Ficus stupenda	0.01	0.6	0.1	219.3
Prainea limpato	0.02	0.6	0.1	13.3

Table 4-5 (continued)

Species	% Basal Area	Density	% Relative density	Selection ratio
Knema latifolia	0.01	1.1	0.2	7.5
Myristica elliptica	0.03	1.1	0.2	10.4
Eugenia ecostulata	0.01	0.6	0.1	254.0
E. leucoxla	0.02	1.1	0.2	56.7
E. papillosa	0.06	0.6	0.1	3.2
Eugenia sp. A	0.03	1.1	0.2	2.1
Eugenia sp. B	**	0.6	0.1	160.0
Syzygium lineatum	0.01	0.6	0.1	24.2
Xanthophyllum affine	1.08	6.3	1.3	0.8
X. griffithii	0.02	0.6	0.1	49.1
X. stipitatum	0.09	1.1	0.2	8.6
Zizyphus angustifolius	**	0.6	0.1	15.4
Paranephelim xestophyllum	0.06	1.7	0.4	28.3
Pometia pinnata	0.22	1.7	0.4	0.9
Xerospermum noronhianum	0.07	1.1	0.2	2.2
Palaquium eriocalyx	0.01	0.6	0.1	6.7
Payena leeri	0.03	0.6	0.1	2.7
Gonystylus afinis	0.32	4.0	0.9	0.3
G. borneensis	1.09	8.0	1.7	0.1
Pentace excelsa	0.01	0.6	0.1	26.2
Gironniera nervosa	0.01	0.6	0.1	210.2

* Value < 0.01

** Value < 0.001

Note: Table includes only those plant species represented in the primary forest sample plots.

Overall, RBC2 chose 54 (78.3%) food species more than would be expected from their availability, suggesting that, while hybrid gibbons are dietetically restricted by the floristic composition of their home range, preference plays a substantial role in their selection of food species. To qualify this statement, correlations were run comparing selectivity and dietary ranks for all species, non-fig fruit and young leaf sources respectively. Relatively strong and positive relationships existed between the selection and consumption of food species for each category (Table 4-6). Again, these results indicate that RBC2 did not employ the "safer" of dietary strategies (i.e. relying on or concentrating their feeding on common plant forms) but invested their time in the search for and consumption of favoured food items.

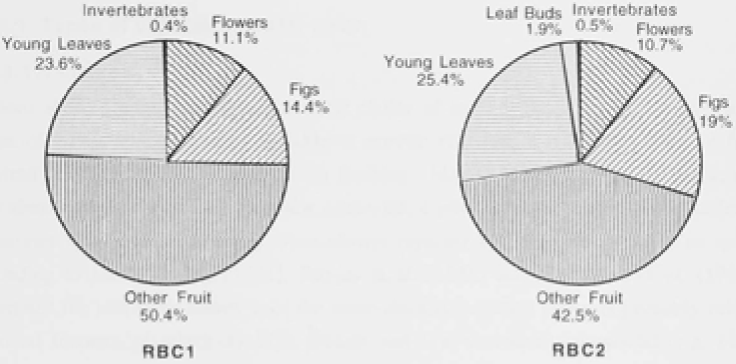
Table 4-6 Rank correlation coefficient for compared parameters of selection ratios for and actual consumption (total minutes spent feeding) of food species.

Selectivity vs dietary rank*	Correlation coefficient		
	r_s	n	sig to
Food species combined	.686	69	≤.0001
Fruit (excluding figs)	.698	26	≤.001
Young leaves	.672	38	≤.001

*Includes only those food species represented in vegetation plots

4.4.2 Contribution to the diet – food types

Hybrid gibbons relied on six of the seven food type categories defined in Section 4.2. Fruits other than figs comprised the largest proportion of RBC2's diet, 42.5% of RBC2's feeding time (see Figure 4-1 and Table 4-7.). Young leaves made up 25.4% of the diet, followed by figs which contributed 19.0%. Only mature flower forms were selected by RBC2, accounting for 10.7% of feeding (31 species), with only minimal amounts of time devoted to leaf bud and invertebrate consumption.



RBC1 **RBC2**

Figure 4-1 Food type composition of RBC1 and RBC2's diet.

Table 4-7 Number of sources consumed for each food type.

Food type	Number of sources used by each group	
	RBC2	RBC1
Fruit	67	46
Fig	13	9
Flower	31	16
Young leaf	60	38
Leaf buds/shoots	9	-
Insects	4	3

RBC1 showed a similar general trend in food type use. Non-fig fruit was the most important dietary component with a not insignificant contribution from young leaves and flowers. The primary difference between the diet of RBC1 and RBC2 was the consumption of fig. It was noted in the field that RBC1 appeared not to visit as many fig sources as RBC2 did, consuming non-fig fruit in much greater quantities. Fig densities were higher in RBC2's home range (7.7 figs/ha) compared to RBC1 (4.5 figs/ha) (McConkey, 1999), suggesting that the differential use of figs was related to abundance rather than indices of preference.

Compared to pure species of gibbon, RBC2 and RBC1 ate more flowers and less leaf matter. It is possible that flower consumption was a response to an increase in flower availability at Rekut during 1995-1996. Certainly, Gittins (1979) has remarked that the absence of "suitable" flowers at Sungai Dal during his study probably affected the reduced flower consumption observed for agile gibbons. Variation in sampling and observation schedules between studies might also lead to erroneous interpretations of interspecific feeding differences. Time spent recording feeding data for Kloss gibbons was relatively short, a factor which Whitten (1984b) proposes might account for the apparent dietary rejection of flowers by this species of gibbon. An alternative interpretation is that the focus hybrid gibbon groups simply liked eating flower. When a food source was flowering, RBC2 and RBC1 often spent long feeding bouts at the source. McConkey (1997, pers. comm.) observed a strong selection for flowers by these groups and, while my own results do not indicate as strong a preference (see Section 4.5.2.4), they did suggest that gibbons ate a lot of flower when they could.

4.4.2.1 Types of vegetable matter eaten

4.4.2.1.1 Leaves

Gibbons showed great consistency in their choice of leaf matter. Only the youngest, most tender of leaves appeared to be suitable as regular visitation and lengthy bouts of feeding occurred primarily at species undergoing flushing. Mature leaves were rarely eaten, despite their abundance in the forest. On a few occasions, a gibbon would inspect a mature leaf, and sometimes have a taste, but they were always rejected by being tossed aside or spat out. According to McKey et al. (1981), Davies et al. (1988) and Waterman et al. (1988) the preference for immature leaves over the more abundant mature forms is probably related to chemical features of relatively high protein and low secondary compound (e.g. phenols, tannins) and fibre content. Gibbons mostly chose soft, light green leaves but they also ate immature forms that were reddish-purple in colour (e.g. *Garcinia* spp.)

4.4.2.1.2 Flowers

In contrast to leaf selection, gibbons did not show preference for a particular form of floral morphology, instead consuming a diversity of edible flowers from the small, bud like forms of *Koompassia malaccensis*, the feathery spikes of *G. latifolium*, velvet petals of *Sindora coriaceae* and the fleshy, tri-coloured *Uvaria lobbiana*. Mature forms tended to be sought after, since only one instance of flower bud consumption was observed during the 5-day samples, but gibbons made numerous visits to flowering *G. latifolium* vines to eat the yellow, spiky inflorescences. Red, purple, green and multiple coloured flowers all contributed to the diet but it was mostly yellow and white flowers which gibbons fed on (Table 4-8).

Table 4-8 Flower colour choice.

Flower colour	Number of species		Consumption (minutes feeding time)	
	n	%	n	%
White	17	54.8	930	41.1
Yellow	7	22.6	980	43.3
Red	2	6.5	151	6.7
Green	2	6.5	52	2.3
Purple	1	3.2	20	0.9
Multicoloured	2	6.5	129	5.7
Total	31	100.0	2262	100.0

4.4.2.1.3 Fruit and figs

Not unexpectedly, dietary fruit items used by the focus groups showed considerable variation in morphological characteristics, such as the thickness, rigidity, and external features (e.g., pitting, spikes) of the pericarp, the type of pulp, number of seeds, colour of the rind and flesh, the presence or absence of dehiscence, and the parts of fruit eaten or ignored. My own sampling of known fruit sources revealed a range of tastes, from fibrous to bitter to sweet, with gibbons preferring fruits which tasted slightly sour or acidic. Following Raemaekers (1977) and Whitten (1982a), fruits selected by RBC2 are categorised below into 17 basic morphological types and divided into two main groups depending on the number of seeds. Group 1 fruits contain between 1 and 4 seeds, which make up a significant part of the fruit, while Group 2 fruits have many seeds (in the case of some fig species, more than 50 seeds), which occupy only a small part of the fruit (Table 4-9). Similarities exist between fruit categories described here and those summarised by Raemaekers and Whitten. A few, however, have not been mentioned in either of Raemaeker's or Whitten's papers and, indeed, some fruits eaten by RBC2 are listed by Whitten as fruits never consumed by Kloss gibbons, despite their availability in the home range.

Group 1: 1-4 seeds

A. A juicy pulp enclosed in either a rubbery, pitted or softly spiked pericarp. The teeth are normally employed to remove the pericarp, but occasionally fingers are used to peel back the rind, exposing the flesh and seed, which are both consumed; e.g. *Polyalthia glauca*, *Parartocarpus bracteatus*.

B. Small to medium fruits with a thin, easily removed pericarp and a juicy pulp. The seed is usually eaten with the flesh but is sometimes discarded; e.g. *Gnetum* spp, *Grewia blattifolia*.

C. Medium to large fruits with a fleshy mesocarp and woody endocarp. The seed is sometimes contained within a flattened stone; e.g. *Mangifera pajang*.

D. Mostly small fruits tending to have juicy, but in some species, a dry pulp surrounded by a very thin rind which is not removed before consumption; e.g. juicy pulp (*Syzygium lineatum*), dry pulp (*Eugenia leucoxla*).

E. A hard walled nut or samara, some with wing like sepals, and dry flesh. Processing of these fruits is substantial, gibbons having to use their teeth to bite and grind the rind to reveal the edible flesh and seed; e.g. *Pentace excelsa*, *Lithocarpus pusillus*.

F. Medium sized fruits with dry flesh and a rigid pericarp of medium thickness. All parts of the fruit are eaten but largely the rind and pulp is taken and the seed discarded; e.g. *Eugenia ecostulata*, *Eugenia* sp A.

G. Dehiscent fruits which split open, exposing a brightly coloured (red or orange) arillate seed or seeds. Seed and aril are consumed; e.g. *Knema latifolia*; *Myristica elliptica*. (Note: the arillate seed of *Paranephelium xestophyllum* is covered with a white, rather than red/yellow film).

H. Non-dehiscent fruits containing an arillate seed; e.g. *Xerospermum noronhianum*.

Group 2: > 4 seeds

A. Very small fruits with a very thin rind and eaten whole, often picked in handfuls
   i. Dry pulp - e.g. *Rhus nodosa*
   ii. Juicy pulp - e.g. *Pternandra rostrata*

B. Soft, juicy pulped fruits encased in a thin or pliable pericarp. All of the fruit is consumed (e.g. *Adinandra dumosa*) but sometimes only a few bites are taken before the fruit is discarded (e.g. velvet skinned *Artocarpus*, *Garcinia* spp.).

C. Fruits with a juicy pulp or seed jacket of a custard like consistency and a hard or rubbery rind which is removed to reveal the edible contents; e.g. *Baccaurea bracteata*.

D. Dark green ball covered in fleshy sepals and which splits open to reveal white flesh and many small, red seeds; e.g. *Dillenia grandifolia*.

E. Oval shaped capsule perched on a cup. Only the capsule, comprised of a thin pericarp and dry pulp, is eaten; e.g. *Crypteronia* spp.

F. Small, white, dehiscent capsule which splits into two parts; e.g. *Wenlandia* sp.

G. Extremely hard walled and large in size, these fruits provide a large amount of soft pulp for consumption but require a considerable degree of processing; e.g. *Hydnocarpus woodii*.

H. Long, leathery, twisted green pods which hang in small bunches. These dehiscent and fleshless fruits split open on maturity, gibbons consuming just the seeds; e.g. *Parkia speciosa*.

I. Inverted florescences (figs) with a fleshy receptacle forming the outer wall with the florets pointing inwards; e.g. *Ficus* spp. More species of small sized figs were taken but gibbons showed a preference for those of a medium size.

Table 4-9 Morphological category of fruit types and their proportional representation in the diet.

Fruit type	Number in diet	% no in diet	Time spent feeding	% time spent feeding
Group 1: 1-4 seeds				
A	10	12.5	712	5.5
B	17	21.3	1844	14.2
C	2	2.5	69	0.5
D	2	2.5	194	1.5
E	4	5.0	148	1.1
F	2	2.5	547	4.2
G	4	5.0	455	3.5
H	2	2.5	48	0.4
Group 2: > 4 seeds				
A	4	5.0	1133	8.7
B	13	16.3	2606	20.0
C	1	1.3	248	1.9
D	1	1.3	162	1.2
E	2	2.5	540	4.1
F	1	1.3	42	0.3
G	1	1.3	29	0.2
H	1	1.3	217	1.7
I	13	16.3	4026	30.9

4.4.2.2 Selection of fruit characteristics

In light of the role many animals and birds play in the regeneration of rainforest through the dispersal of seeds, theoretical and qualitative attention has been given to the types of fruit characteristics which plants may have evolved and display to attract efficient seed dispersers (Snow, 1971; van der Pijl, 1972; McKey, 1975; Howe and Estabrook, 1977; Janzen, 1980; Howe and Smallwood, 1982; Wheelwright and Orians, 1982; Janson, 1983; Knight and Siegfried, 1983; Gautier-Hion et al., 1985; Sourd and Gautier-Hion, 1986; Wilson and Whelan, 1990; Charles-Dominique, 1993; Julliot, 1996a; 1996b). Although previous research has largely concentrated on fruit choice by birds (Howe and Estabrook, 1977; Skutch, 1980; Stiles, 1980; Leighton and Leighton, 1983; Moermond and Denslow, 1983; Herrera, 1984; Levey et al., 1984; Wheelwright and Janson, 1985; Dowsett-Lemaire, 1988), some work has addressed, or includes data on, primate preferred fruits (Knight and Siegfried, 1983; Estrada and Coates-Estrada, 1984; 1986; Gautier-Hion et al., 1985; Janson et al., 1986; Sourd and Gautier-Hion, 1986; Kinzey and Norconk, 1990; Julliot and Sabatier, 1993; Leighton, 1993; Julliot, 1996a; 1996b). My own examination of fruit choice revealed some common trends but for rigorous statistical treatment the work of Kim McConkey (1999, unpubl.), who conducted an extensive study on hybrid gibbon fruit selection and seed dispersal at Rekut between 1996 and 1997, is a recommended reference.

4.4.2.2.1 Morphological features of consumed fruit

Four main morphological classifications were used to assess the physical characteristics of dietary fruits (physiognomical category (e.g., berry, drupe), colour, kind of pulp, and number of seeds) and results are presented in Table 4-10. Fruit consumed by the focus groups fell into six physiognomical types but only two forms were taken with any regularity – drupes followed by berries. A strong preference for fruits with juicy or watery pulps was evident with some partiality towards fruit forms containing only one or two seeds. Dietary fruit items exhibited a wide range of colours, eight primary groups (yellow, orange, red, purple, brown, green, black and white) in all. A single block of colour characterised the outer casing of most fruits used by hybrid gibbons but some were two-toned, either with a darker or lighter shade of the primary fruit colour (e.g., dark green spots on a lighter green background – Liana June 1 fruit) or with two distinct colours (purple spots on a white background – *Ficus caulocarpa*). No one single colour featured prominently in the fruit component of the diet but gibbons did favour brightly coloured fruits – orange, yellow, red and combined (59.1% of species, 61.1% of consumption). Interestingly, gibbons selected green fruits, only one of which was unripe, just as frequently as brightly coloured fruits and, indeed, slightly more often than those coloured yellow or red. This might be because green fruits were more commonly produced during the research period (Kim McConkey, 1998 pers. comm.)

When incorporating figs into the analysis, the importance of orange fruits in the diet rises, both in proportion of species (28.8%) and particularly in feeding time (40.0%), and the use of yellow fruits, in terms of time spent feeding, is greater than green fruits (19.0% compared to 14.9%). This result is attributable to the preference gibbons exhibited towards orange and yellow figs. Eight of the fifteen used species displayed a bright orange rind when ripe while two of the yellow species, *F. sundaica* and *F. villosa*, were principal items in the overall diet, ranked 2nd and 11th respectively. Of course, fruit characteristics are not necessarily independent of one another (Sourd and Gautier-Hion, 1986) – 89% of brightly coloured fruits eaten by guenons in Gabon had juicy pulps, arillate seeds, and were always coloured either orange or red. Drab outercasings tended to identify dry pulped fruits. The association between different morphological categories was not as strong for hybrid gibbon fruit but a definite trend existed. Two thirds of drupe species had orange or yellow exteriors and 45.5% of berries were coloured red or orange. Of the dehiscent fruit consumed, 75% possessed red, orange or yellow arils. Fruits composed of succulent pulp tended to be brightly coloured (67.9% – orange, red, yellow and purple combined) while dry and fleshless fruits were mostly (66.7%) green or brown.

Table 4-10 Selection for fruit morphological features.

Fruit morphologies	Number of fruit species	% of dietary fruit species		Time spent feeding	% consumption	
		-Fig	+Fig		- Fig	+Fig
Physiognomical category						
Berry	22	32.8	27.5	2664	29.6	20.5
Drupe	31	44.8	37.5	4635	51.5	35.6
Capsule	10	14.9	12.5	1327	14.8	10.1
Nut/Woody	3	4.5	3.8	147	1.6	1.1
Pod	1	1.5	1.3	217	2.4	1.7
Inverted infloresence	13	-	16.3	4026	-	30.9
Colour						
Red	11	14.9	13.8	1533	16.6	11.8
Orange	23	23.9	28.8	5214	32.1	40.0
Yellow	13	14.9	16.3	2479	12.4	19.0
Purple	4	6.0	5.0	1072	11.9	8.2
Green	16	22.4	20.0	1941	20.9	14.9
White	3	4.5	2.5	399	4.4	3.1
Brown	4	6.0	5.0	166	1.8	1.3
Black	2	3.0	2.5	35	0.4	0.3
Bicoloured	1	1.5	1.3	89	1.0	0.7
Unknown	3	4.5	3.8	92	1.0	0.7
Type of pulp						
Juicy	53	70.1	79.1	6136	68.2	47.1
Dry	11	25.4	16.4	2566	28.5	50.7
Fleshless	3	4.5	4.5	292	3.2	2.2
Number of seeds						
1 - 2	36	53.7	45.0	3911	43.5	30.0
3 - 5	12	17.9	15.0	2627	29.2	20.2
6 - 10	7	10.4	8.8	606	6.7	4.7
> 10	22	14.9	26.3	5741	19.1	44.1
Unknown	3	4.5	3.8	135	1.5	1.0

Certainly, hybrid gibbons do appear to use fruits which display particular morphological characteristics but are they actually selecting for them? One way to detect selection is to measure the influence fruit morphology has on the importance of a species in the annual diet and its index of selectivity. While gibbons may eat many fruits of a certain morphological type (e.g. orange pericarp), no statistical relation was found between physiognomical category, colour, seed number nor type of pulp and dietary or selectivity rank. Of course, fruit type choice is constrained by what specific morphological types are available at the time of selection and less desirable forms may be taken when preferred types are absent or found only in small quantities. For example, in a period of significant fruit depression occurring between the months of September and October 1995, RBC2 fed consistently on the fruit of *E. ecostulata*, a dry pulped berry enclosed in a green, hardened outer-casing and which represented the fourth most important non-fig fruit source. To account for the effect of availability, an improved method compares the fruits taken each month to the availability of different morphological types in the same time period (Leighton, 1993; Julliot, 1996b). However, the previously described uncertainties concerning the accuracy of phenological data seriously impede any reliable analysis on the availability of dietary items, potentially introducing bias either in favour or against the selection of fruit items. Additional problems relate to the specific composition of plot trees. A small, but relevant, number of fruit species (e.g. *G. blattifolia*) were not represented in the primary forest tree plots and of those that were present, not all showed synchronous fruiting activity with conspecifics in the rest of the range. For these reasons it has been considered inappropriate to conduct availability analysis here.

4.4.2.2.2 Preferred fruit types of other primate species and fruit selection syndromes

Other primate species choose fruit characteristics similar to those discussed above. Fleshy fruits (i.e., drupes and berries) are preferred to capsules, pods and nuts (Knight and Siegfried, 1983) as are fruits with succulent, juicy pulps (Rijksen, 1978; Gautier-Hion et al., 1985; Sourd and Gautier-Hion, 1986; Leighton, 1993; Ungar, 1995; Julliot, 1996a; 1996b). Colour is also an important attractant and although it may not play as fundamental a role in fruit choice as seems to be the case for some bird species (e.g., selection of purple-black and red fruits by turacos and hornbills – Gautier-Hion et al., 1985), it does appear to have an effect on fruit discrimination. Despite the regular use of green and/or brown fruits by collared titi's (Snodderly, 1979), spider monkeys (French Guyana – Sabatier, 1983 cited in Julliot, 1996b) and, to a lesser extent, red howler monkeys (Julliot, 1996a; 1996b), it is the brightly coloured fruits (yellow, orange and red) that are consistently taken by both New and Old World monkeys and the apes. Some primate species are particularly attracted to red and multicoloured fruits (*Miopithecus talapoin*, *Cercopithecus cephus*, *C. pogonias*, *C. nictitans*, *C. neglectus* and *Lophocebus albigena* – Gautier-Hion et al., 1985). Others prefer those coloured orange and yellow (Sourd and Gautier-Hion, 1986; *Alouatta seniculus* – Julliot, 1996a; 1996b; *Pongo pygmaeus* – Leighton, 1993); with an avoidance of red fruits in certain locales (Janson, 1983); or show little discrimination in their use of fruits of each colour (Terborgh, 1983).

The bilateral relationship existing between rainforest plants and the animals and birds which feed on their fruits has evolved to meet, and is sustained by, the needs of both participants. To ensure successful propagation, rainforest plants must attract an appropriate and efficient seed disperser. In turn, animals and birds consume fruit to provide a ready source of energy and other essential nutrients. Different groups of fruit eaters display variation in fruit preferences, relating to their abilities in detection (e.g. colour) and processing, nutritional requirements, and taste. Rainforest species may have responded to these preferences, such as selection for colour (Wilson and Whelan, 1990), by developing an enormous range of morphological types, designed to appeal to at least one class of frugivores.

Gautier-Hion et al. (1985), in their examination of fruit selection and resource partitioning in a rainforest community, identified distinct patterns or syndromes of fruit use by different birds and mammals (small rodents, large rodents, squirrels, ruminants and monkeys – see also Leighton and Leighton, 1983). These patterns suggested that plant species not only produce a fruit form suitable for at least one group of seed dispersers but one that guarantees regular visitation by the primary dispersal agent. In the rainforests of Gabon, primates serve species which yield dehiscent fruits with arrillate seeds or those characterised by bright colours and a fleshy body (Gautier-Hion et al., 1985). In South Africa, relatively large orange and yellow drupes or berries appeal to primates (Knight and Siegfried, 1983), while in French Guyana red howlers consistently return to species which produce an orange or yellow, middle to large sized fruit with an indehiscent pericarp and a few large seeds (Julliot, 1996b). Yellow to red fruits with inedible, indehiscent pericarps enclosing a watery pulp typify the preferred fruit type at Kutai (East Kalimantan, Indonesian Borneo) for long-tailed macaques, Müller's gibbons and orang utans (Leighton and Leighton, 1983; Leighton, 1993). And at Ketambe, Thomas' leaf monkey preferred the seeds of dry fleshed fruits in contrast to the succulent and acidic fruits chosen by *M. fascicularis, H. lar* and *P. pygmaeus* (Ungar, 1995). At Rekut, the "hybrid gibbon syndrome" of seed dispersal *appears* to rely on a steady production of sunset coloured fruits of a medium size, containing 1 or 2 seeds surrounded by a succulent, juicy pulp.

4.4.2.2.3 Nutritional, visual and taste selection for fruit

If gibbons, and other primates, are uniformly selecting fruits that display a particular set of characteristics, what is it about these characteristics they find so appealing? One possible attractant is the nutritional value of the fruit. Like the Rekut gibbons, moustached guenons (*Cercopithecus cephus)* and the orang utan regularly choose fruits with a succulent pulp or arillate seed (Sourd and Gautier-Hion, 1986; Leighton, 1993) and this suggests that similar nutritive qualities are sought by these primate species. Compared to dry or fleshy pulped fruits, those with juicy pulps contain a higher sugar content and are much less fibrous, allowing easy digestion and preventing difficulties in protein absorption (Sourd and Gautier-Hion, 1986). Primate-fruits, in Borneo at least, also contain a high fraction of digestible carbohydrate, a primary source of energy, with minimal quantities of chemical inhibitors (Leighton, 1993). Indeed, combined with patch size (crop size x pulp weight/fruit), digestible CHO content was one of the factors orang utans selected for, fruit species with high fractions consistently chosen over those with low concentrations (Leighton, 1993). An additional attribute of primate-fruits is the high content of water, essential, or at least beneficial, to a primate (e.g. hybrid gibbons) rarely observed to drink. Dehiscent fruits containing arillate seeds are also important in the guenon diet (19.7% of all fruit species), probably due to the rich protein and fatty acid composition of the aril (Sourd and Gautier-Hion, 1986). In comparison, gibbons rely less on such fruits (10.3% of species). This reduced dependence on arils could be a simple consequence of restricted availability[7], little fruiting activity during the time of the study, or a poor representation of species in the home range, denying the group consistent access.

---

[7] Kim McConkey (1998, pers. comm.) found that hybrid gibbons' avoidance of aril fruits was not related to reduced abundance.

Alternatively, hybrid gibbons are able to capture aril-specific nutrients from alternative, and possibly more abundant, fruit sources. A third explanation is introduced by the work of Zens and Leighton (unpubl., cited in Leighton, 1993) where the chemical terpene was found in many Bornean arillate fruits. If found in significant concentrations, terpene may act as a deterrent to feeding gibbons.

Selection is not always solely derived from requirement, being activated or shaped instead by physiological/neurological constraints or capabilities. An example of this is the preferential use of certain coloured fruits by different species of primate, which may be related to visual ability in identifying plant species or detecting fruits (Janson, 1983; Mollon et al, 1984; Bowmaker et al., 1987; Mollon, 1989; Jacobs et al., 1993; Jacobs, 1996; Osorio and Vorolyev, 1996). Prosimians and some platyrrhines are dichromats, possessing short and medium-long wavelength cone pigments that enable sensitivity to the blue, green and yellow spectral regions but not to the red (De Valois and Jacobs, 1968; Osorio and Vorolyev, 1996). Catarrhines, in contrast, are trichromats, and can detect the colour red due to a third, or longer wavelength, cone pigment which aids in red-green discrimination. It has been proposed that the development of trichromacy evolved with fruit colour (Polyak, 1957), improving a primate's ability to detect and determine the state of ripeness of a fruit source (Mollon, 1989) and thus potentially increase the number of items a frugivore can include in its diet. Tests comparing dichromatic and trichromatic vision certainly support the theory. Trichromatic animals are considerably better at distinguishing red from green, enhancing the detection of fruits against a blue-green background of leaves (Osorio and Vorolyev, 1996).

Taste and the ability to detect certain chemical substances is another physiological factor affecting fruit selection. Research conducted by Glaser and colleagues has detected phylogenetic differences in primate responses to natural and artificial sweeteners such as sucrose, alitame, aspartame and thaumatin (Glaser, 1993, 1994; Glaser et al., 1978; 1992; 1995). Current research has so far differentiated the strepsirrhines and playtrrhines from the catarrhines in relation to absence or possession of receptors for these chemicals. Further research examining taste differentiation within these broader taxonomic groups, particularly in conjunction with chemical analyses on known dietary fruits, might reveal further variation and help explain already observed inter-specific differences in fruit choice.

4.4.3 Contribution to the diet – food items

Gibbons normally fed on a single plant type from each of the food species (82.4% n=126), either because only one phase was temporally or spatially available to the group(s) during the observation period or, for reasons of nutrition or energetics, because other phases were not worth harvesting. The production of different food types was not always ignored, however, as the group sometimes used two (16.3% n=25) or three (1.3% n=2) plant phases from the same species.

A total of 179 food items comprised the diet of RBC2. Generally, the importance of food items was similar to the corresponding use of their specific counterpart, eight of the ten most used items having, with slight modification, equivalent ranks (see Appendix V – Table V.1). Figs were the main dietary food items, followed by five fruit sources and three young leaf sources. Most of the important food items represented the sole plant phase used from the parent species, the exceptions being *C. griffithii*, *G. gnemon* and *G. latifolium*. RBC2 ate young leaves, fruits, and, to a lesser extent, flowers from *C. griffithii*, while fruit (12) and young leaves (80) were taken from *G. gnemon*, and flowers (16) and fruit (40) from *G. latifolium*. The pattern of consumption of *C. griffithii* YL and FR resembled that of *R. nodosa* FR and *D. malaccensis* YL in that these items were used or made a significant proportion to the diet (> 30%) diet in only one of the 5-day follows.

4.5 Variation in the monthly diet

4.5.1 Dietetic diversity

Diet composition varied significantly, sometimes markedly, from month to month. An average of 57.9 food sources were used during each 5-day sample and ranged from just 26 in September to 95 in May (Table 4-11). The mean distance RBC2 travelled over the monthly observation period was strongly correlated with the number of food sources utilised during that month (r_s=.846 n=12 p=.005), the longer the day range length the greater the number of dietary components. The direction of the relationship between these two variables is not clear and it may be that gibbons feed from more food sources on days in which they travel further because the energy expenditure required for longer distance travelling necessitates more feeding visits. However, correlating variation in monthly proportions of food types with food source totals produces a similar result obtained with DRL (Table 4-12) – fruit has a positive effect on the number of sources used (r_s=.667 n=12 p=.03) while young leaves has a negative, although non-significant, one (r_s=-.594 n=12 p=.06). It has already been shown that gibbons range further in months when fruit availability and consumption is higher (Chapter 3). Longer daily travel routes, therefore, may instead be associated with the use of a larger variety of foods as gibbons not only increase the likelihood of locating new feeding trees but are also able to revisit previously used sources.

Table 4-11 Total number of food sources visited and dietetic diversity in the monthly diet.

Month	No of Food Sources Visited	Dietetic Diversity: Food Species	Dietetic Diversity: Food Items
September	26 (12)	1.835 (12)	1.877 (12)
October	37 (11)	2.399 (9)	2.497 (8)
November	46 (9.5)	3.069 (1)	3.069 (1)
December	53 (7.5)	2.570 (7)	2.606 (7)
January	56 (6)	2.810 (2)	2.855 (2)
February	46 (9.5)	2.219 (11)	2.409 (10)
March	65 (4)	2.634 (6)	2.798 (3)
April	80 (2)	2.642 (5)	2.686 (5)
May	95 (1)	2.458 (8)	2.458 (9)
June	53 (7.5)	2.255 (10)	2.255 (11)
July	64 (5)	2.772 (3)	2.772 (4)
August	74 (3)	2.649 (4)	2.649 (6)
Mean	57.9	2.526	2.576

Dietetic diversity can also be expressed by calculating the Shannon-Wiener diversity index H (Wilson and Bossert, 1971):

$$H_e = -\sum_{i=1}^{S} P_i \log_e P_i$$

in which *n* = the number of food species or items, P_i = the proportion of time spent feeding on the *i*th species, and $\log_e P_i$ = the natural logarithm of P_i. Higher values represent a more diverse diet, one in which less time was devoted to feeding on the most important food sources. Indices of diversity were calculated for both food species and food items for each month of the annual period (Table 4-11). The greatest diversity was found in the November diet, the least in September. As expected, dietetic diversity was strongly correlated with the proportion of time spent feeding on the top food items (Top 3 items: r_s=.867 n=12 p=.004). However, no relationship existed with monthly variation in proportion of food types consumed.

In most months, the top food item accounted for 20 to 30% of feeding time (dietary contribution of the top three food items for each month is given in Table 4-13). In November, when the most diverse diet was consumed, considerably less time was spent on the primary food item (*Ficus stupenda* FR – 9.1%), a similar trend being observed for the top three items. The even distribution of the gibbons' time between different food sources in November may have been related to crop size. Unlike other months, in which at least one or two sources were endowed with substantial amounts of the selected plant type, November crop sizes appeared to be smaller in all the trees and climbers visited. Gibbons, therefore, spent less time in each of these sources, perhaps as a means of preventing rapid exhaustion of the food supply. It was noticed that RBC2 foraged more often during this month, rarely stopping to engage in long-term bouts of feeding.

Table 4-12 Relationship between monthly variation in food type consumption and indices of dietary variation (n=12).

Food type	Number of sources	Dietetic diversity (Food Species)	Dietetic diversity (Food items)
Fruit	.667*	-.049	-.203
Fig	-.123	.224	.203
Flower	-.393	.119	.329
Young leaf	-.594	-.056	.028

significance level: * ≤.05

Reduced food supply also occurred in September but, in contrast to the situation in November, it was the number of food trees, rather than crop size, which acted as the limiting factor. Spells of dry weather or periods of water stress have been shown to induce young leaf flushing and flowering, respectively, in rainforest species (Medway, 1972; Whitmore, 1984). Thus the absence of a true dry season between June and August 1995, when rainfall levels were much higher than normal, may explain, at least in part, why few species produced young growth in the initial stages of the field study. However, it must be mentioned that such a simple relationship is not evident for all rainforest species or forest areas because other environmental factors are almost certainly involved (eg. amount of sunshine, number of successive cool nights

– Whitmore, 1984). Indeed, some plants may produce young growth in response to, or coinciding with, wetter times of the year (Medway, 1972; Fox, 1972 cited in MacKinnon et al., 1996). Whatever the reason for poor food production, gibbons visited only a few species in September, in particular *C. griffithii*, *F. subgelderi* and *E. ecostulata.* Extremely large crop sizes in *F. subgelderi* and *E. ecostulata* attracted the group to these sources while the heavy use of *C. griffithii* was mostly due to a significant number of trees flushing at this time.

Table 4-13 Contribution of the top three food items to the monthly diet.

Month	Top food item	2nd top food item	3rd top food item	Top 3 combined
September	30.7	24.7	9.2	64.6
October	23.8	17.4	12.0	53.3
November	9.1	8.8	8.2	26.1
December	24.2	13.0	13.0	50.1
January	23.4	7.6	10.6	41.6
February	22.2	18.8	17.3	58.3
March	23.0	9.0	8.7	32.0
April	19.1	17.0	6.4	42.4
May	45.9	10.4	5.8	62.0
June	23.5	20.5	13.8	58.8
July	29.2	8.5	6.9	44.6
August	21.4	13.2	7.5	42.1
Mean	24.6	14.1	10.0	48.0

Despite both the substantial number of sources fruiting and exploited in May, dietetic diversity was relatively low. Gibbons particularly favoured a species of climber (*R. nodosa*) in May, spending almost half of their feeding time (45.9%) eating its fruit, the second and third most important food items, *E. leucoxla* fruit and *Artocarpus kemando* fruit, accounting for markedly lower proportions of the diet. Feeding visits to *R. nodosa* were frequent, between two and eight on each day of the 5-day sample, to total 23 over the May observation period. Four factors clearly influenced the group's selection of *R. nodosa* as an important and regularly exploited food species – the number of climbers in fruit, crop size, location of food source, and harvesting time. RBC2 used thirteen different sources of *R. nodosa*, the largest number of sources from a single species used by the group both within a 5-day sample and in the 12 months of observation. Each climber produced substantial amounts of fruit, allowing numerous and lengthy bouts of feeding. Furthermore, frequent visits to climbers were facilitated by their location within the core ranging area and on primary foraging pathways. Gibbons did not have to travel far to access these food sources, their position on routes often used by the group meant that they were passed regularly. If the climbers had been more distantly located, the group may have been less inclined to visit them quite so often. Finally, the physical characteristics of the fruit added to their attraction, allowing effortless harvesting and consumption of many fruits in a short period of time. The fruit, which is described elsewhere, was very small in size, easily gathered and eaten and hence constituted a rich food source requiring little expenditure in time and energy in processing. Gibbons often went into a frenzy when using this source, grabbing handful after handful of fruit and constantly searching for new pockets of abundant growth.

4.5.2 Monthly variation in the use of food items

Because gibbons prefer those plant phases (flowers, young leaves and particularly fruit) which are produced intermittently and for short amounts of time, variation in the composition of monthly diet is affected by the availability of plant parts. Cycles of flowering, fruiting, and young leaf flushing are dependent on the species, the location of the tree, and changing temperature and rainfall conditions (Whitmore, 1984; MacKinnon et al., 1996). The production of reproductive parts occurs regularly in some species (flowers and fruits appearing at either annual or non-annual intervals) while, in others, cycling is unpredictable, seasons being potentially separated by an indeterminate number of years. Young leaves also typically flush at intervals but year round growth does occur in a number of species. Trees of the same species do not always produce plant parts at the same time and large crops may be found in different parts of the forest at different times of the year. Figs often fruit asynchronously and this was evident at Rekut, at least 22 different sources of 7 species of fig fruiting at least twice during the year. This phenomenon was also observed in *Gnetum*, *Adinandra* and *Artocarpus* and probably accounting for their recurrent use. Not all trees and lianas put out the one plant phase during the annual cycle, provision of different plant parts occurring simultaneously in separate trees (eg. *G. nervosa* FL and FR) or within a few weeks or months of one another (*C. griffithii* YL and FR; *D. malaccensis* LFB and YL; *G. latifolium* and *G. gnemon*).

For these reasons, no food item was used consistently over the annual period. Food species varied substantially, as was evidenced by a low monthly overlap in shared food species, which never exceeded 7%. The highest degree of overlap occurred between September and October in which 6.4% of food items were used in both diets, the lowest being between April and May when shared food items accounted for only 1.1% of the inter-monthly diet. Comparisons of diets separated by increasingly longer periods of time reveals even less similarity in composition.

Each of the monthly diets contained unique species but gibbons also repeatedly exploited many food sources, spending different amounts of time doing so in different months. Table 4-14 lists the twenty most important food items and shows the marked inter-monthly variation in their use. Food items never contributed to more than four monthly diets and six were used only once. Reused items tended to be eaten in adjacent months, accounting for a significant proportion (> 10%) of feeding time in one or sometimes two months, but much less in the diets of other months. Gibbons exhibited a more sporadic pattern of feeding on *A. dadah*, *G. gnemon*, *G. latifolium*, and three species of fig (*F. subgelderi*, *F. sundaica* and *F. stupenda*), a period of at least three months separating subsequent feeding visits.

Seven fig species featured consistently as an important food item, ranked 1st, 2nd and/or 3rd in the diets of nine of the observation months. Asynchronous fruiting activity, the wide range of *Ficus* species found in lowland evergreen rainforest, and a reliance on figs during times of low fruiting activity (i.e. keystone mutualism – Leighton and Leighton, 1983), contributed to their continuous use. Interestingly, in those months in which figs did not constitute part of the top 3, gibbons often fed on the fruits of the genus *Artocarpus*, which, like *Ficus*, is part of the family Moraceae. Other important food items changed from month to month except *C. griffithii* YL, *E. ecostulata* FR, *A. dadah* FR and *G. gnemon* FR which were used as prominently in the diet of a subsequent month. Possible reasons for this include limited food resources (*C. griffithii* and *E. ecostulata*), a second cycle of fruit production (*A. dadah*) and a four week period in which the species fruited (*G. gnemon*).

Table 4-14 Monthly contribution of top 20 food items to the monthly diet.

Food Item	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Ficus subgelderi FR	24.7	17.4	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8
Ficus sundaica FR	0.0	0.0	0.0	0.0	0.0	17.3	0.0	0.0	0.0	0.0	8.5	21.4
Crypteronia griffithii YL	30.7	3.5	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhus nodosa FR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	45.9	0.0	0.0	0.0
Garcinia parvifolia FR	0.0	0.0	0.0	0.0	0.0	18.8	0.0	1.3	0.2	0.0	0.0	4.0
Artocarpus dadah FR	0.0	0.0	0.0	24.2	0.0	0.0	0.8	19.1	0.0	0.0	0.0	0.0
Crypteronia griffithii FR	0.0	23.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.
Eugenia ecostulata FR	9.2	12.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Durio malaccensis YL	0.0	0.0	0.0	0.0	0.0	22.2	0.0	0.0	0.0	0.0	0.5	0.0
Dialium patens YL	8.2	0.0	0.0	0.0	0.0	4.7	3.6	0.0	0.0	0.0	0.0	6.0
Ficus villosa FR	0.0	0.0	0.0	0.0	0.0	0.0	23.0	0.0	0.0	0.0	0.0	0.0
Gnetum gnemon FR	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	1.5	0.0	6.9	13.2
Ficus stupenda FR	0.0	0.0	9.1	0.0	7.6	3.9	0.0	2.2	0.0	0.0	0.0	0.0
Polyalthia glauca FR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	20.5	1.8	0.0
Ficus deltoidea FR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.2	0.0
Gnetum latifolium FL	0.0	0.0	13.0	13.7	0.0	0.0	0.5	0.0	0.0	0.0	1.3	0.0
Paranephelium xestophyllum FR	0.0	0.0	0.0	0.0	23.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Artocarpus nitidus FR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.5	0.0	0.0
Adinandra dumosa FR	0.0	0.0	0.0	0.0	0.0	7.1	0.7	3.6	0.0	0.0	0.0	1.0
Ilex sp. YL	0.0	0.0	0.0	6.4	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0

4.5.3 Monthly variation in the selection and use of plant types

4.5.3.1 Variation in flower consumption

The proportion of time spent feeding on flowers was greatest during the first five months of the study, accounting for a fifth of the diet in October and averaging 16.2% of feeding time over this period (Figure 4-2). During the rest of the year, with the exception of March, flowers contributed considerably less to the diet. In March, the gibbons took advantage of, and fed extensively from, flowering *Crypteronia paniculata* trees. A slight rise also occurred in July when flowers from three different species were consumed. No flowers were eaten in August.

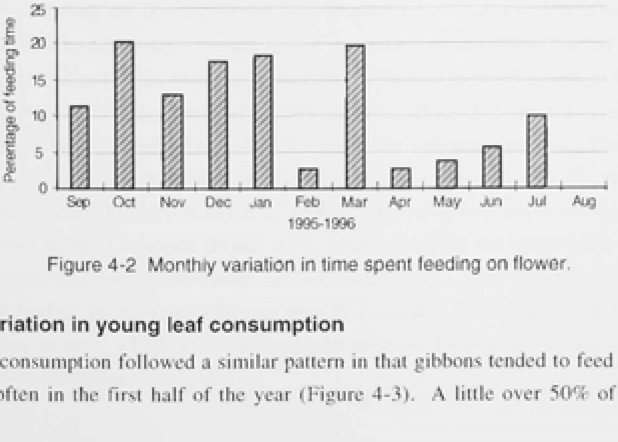


Figure 4-2 Monthly variation in time spent feeding on flower.

4.5.3.2 Variation in young leaf consumption

Young leaf consumption followed a similar pattern in that gibbons tended to feed on this food type more often in the first half of the year (Figure 4-3). A little over 50% of the group's feeding time in September was spent on young leaves and, between October and March, consumption fluctuated but never fell below 20% of the diet. Another rise in April preceded a three month period in which very little young leaf was taken. Few or no leaf buds were eaten in nine of the monthly diets, minor peaks occurring in November, February and April (Figure 4-4). These peaks coincided with similar increases in dietary proportions of young leaf and, in February and April, this plant type was taken solely from two different species of *Durio*.

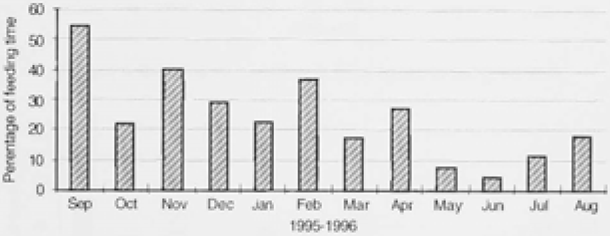


Figure 4-3 Monthly variation in time spent feeding on young leaf.

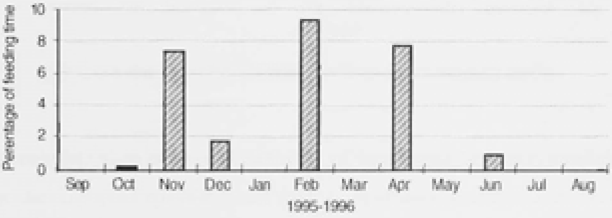


Figure 4-4 Monthly variation in time spent feeding on leaf bud.

4.5.3.3 Variation in fruit and fig consumption

Since gibbons are primarily frugivorous, a consistently high trend of fruit and fig eating would be expected, and was observed, for the great majority of monthly diets. In contrast to the monthly variation in the proportional use of young leaf and flower, gibbons spent more time feeding on fruit during the last half of the year (Figure 4-5). A depression of fruit eating in September was followed by a six month period in which fruit accounted for between 30 and 48% of the diet. After March, fruit consumption steadily rose to reach a peak in May, when a mammoth 84.1% of the diet consisted of fruit species. Declining again to around 40% of feeding time in July, a slight rise occurred during the following month. This pattern of variation had some relationship with the number of fruit sources used each month but the correlation was not significant (r_s=.537 n=12 p>.05). Fig eating was just as variable but did not show as distinct or fluid a pattern (Figure 4-6). Increases in fig use occurred in 3 peaks of 3 month duration (September-November, January-March and June-August) when gibbons concentrated feeding on three main fig species – *F. subgelderi, F. sundaica* and *F. villosa*. In the intervening months, which were characterised by lower proportions of figs in the diet (< 7%), none of these species were visited.

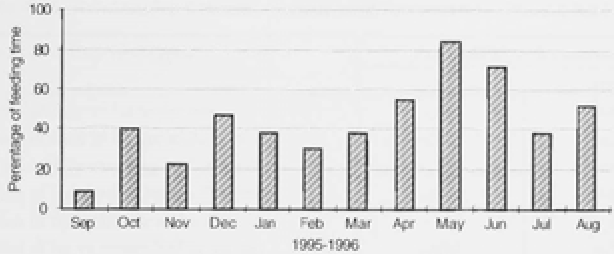


Figure 4-5 Monthly variation in time spent feeding on fruit.

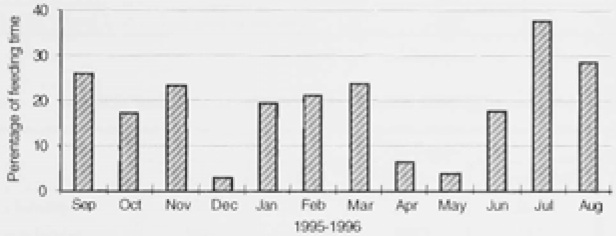


Figure 4-6 Monthly variation in time spent feeding on fig.

4.5.3.4 The relationship between patterns of food type use and availability

Variation in the use of a specific plant part is obviously associated with corresponding fluctuations in the use of another plant part but this relationship is not necessarily inclusive, and may be responsive to cycles in food availability. Consumption of flowers, young leaves, figs and leaf buds did not show any relationship to one another (Table 4-15) but monthly changes in the proportion of fruit showed a strong inverse correlation with the use of young leaves (r_s=-.720 n=12 p=.02) and a moderate, although not significant, correlation with figs (r_s=-.545 n=12 p>.05). Relationships between patterns of food type use, and the extent to which the plant part is exploited each month, can be influenced or dependent on the level of food production in the forest. A simple, but crude, measure of food availability incorporates data collected during the phenological study (Chapter 2) in which the percentage of sample trees flushing, fruiting or flowering was calculated for each month. Selectivity is determined by correlating the phenological index of each plant type with the corresponding proportion of young leaves, fruit/figs and flowers in the diet; significant correlations would be expected only if the use of a phytophase is consistently limited by its availability (Marsh, 1981a; Newton, 1992; Mturi, 1993). Feeding time and food availability were correlated positively for both flowers (r_s=.586 n=12 p=.05) and fruits (r_s=.674 n=12 p=.03) but little relationship was evident between the production and use of young leaves (Table 4-16).

Table 4-15 Relationship between monthly variation in use of different food types.

Proportion of dietary food types	Correlation coefficient (n=12)	
	r_s	sig to
Proportion of fruit vs fig in the diet	-.545	=.07
Proportion of fruit vs flower in the diet	-.343	=.26
Proportion of fruit vs young leaf in the diet	-.720	=.02
Proportion of fruit vs leaf bud in the diet	-.019	=.95
Proportion of fig vs flower in the diet	-.147	=.63
Proportion of fig vs young leaf in the diet	-.042	=.89
Proportion of fig vs leaf bud in the diet	-.433	=.15
Proportion of flower vs young leaf in the diet	.084	=.78
Proportion of flower vs leaf bud in the diet	-.145	=.63
Proportion of young leaf vs leaf bud in the diet	.429	=.15

Table 4-16 Monthly variation in relationship between food type use and availability.

	Food type				
	Fruit	Fig	Flower	Young leaf	Leaf bud
Fruit availability	.674*	-.220	-.538	.014	.019
Flower availability	.188	-.873**	.586*	-.185	.113
Young leaf availability	.308	-.084	.007	-.021	.418

significance level: * ≤0.05 ** ≤.01

It is apparent from these results that gibbons select for fruits and flowers but not young leaves. The inverse relationship between young leaf and fruit consumption can thus be interpreted as gibbons preferentially choosing fruit over young leaves whenever both are available in the forest, only increasing their feeding time on new leaf growth when fruiting activity is reduced. And what of the relationship between flowers and fruit? Subsequent feeding observations on the same study group discovered that gibbons responded particularly to peaks of flowering, their diet comprising considerable proportions of flowers during this time (Kim McConkey, 1997 pers. comm.). For two reasons, such behaviour does not appear to be as strongly evident from the author's year of observations. Firstly, the strength of the correlation between flower consumption and availability reached only a moderate level of association, indicating that while gibbons responded positively to flowering activity they did not do so on a completely consistent bais. Secondly, the use of flowers shared an inverse relationship with fruit availability level (rs=-.538 n=12 p=.05). Gibbons, therefore, consumed flowers when they were abundant but, if fruit was also available in large quantities, gibbons preferred to visit fruit sources instead.

Primates and other frugivorous animals (e.g. squirrels, hornbill) tend not to select for figs, primarily because they represent a nutritionally poor food source compared to other fruit species (Leighton and Leighton, 1983; Leighton, 1993). Containing little or no fat and only small amounts of digestible carbohydrate and protein, their attraction as a preferred food source is further limited by the considerable concentration of tannin and fiber (Leighton, 1993). In times of low fruit availability, however, figs act as keystone mutualists, providing a reservoir of easily harvested and abundant fruits which can be consumed in large and consistent quantities

(Leighton and Leighton, 1983; Leighton, 1993 but see Sugardjito et al., 1987). The normally large patch size associated with fruiting *Ficus* species add to their usefulness as a fruit substitute, counterbalancing the figs inferior nutritional quality. Hybrid gibbons exhibited an inverse relationship between fig and fruit consumption but one in which fruit availability did not play a contributory factors (r_s=-.220 n=12 p>.05). In month when little fruit production was occurring (e.g. September and October), figs made up a substantial proportion of the diet but at other low fruiting times (e.g. December), fig consumption was at its lowest. Thus, and although there is evidence for figs supplying an alternative energy source during times of low fruit supply, it is not totally convincing.

4.6 Characteristics of the daily diet

4.6.1 Number and cumulative use of daily sources

During the course of the day, gibbons range between feeding sites, revisiting previously used sources, discovering and spending considerable amounts of time at, preferential food supplies, and sampling other food species whilst travelling to the next feeding bout. As little as three, up to a maximum of sixteen, food sources were used each day, with a substantial range in the average number of daily food visits, from 5.2 in September to 19.0 in May (Table 4-17). Monthly variation was significant (H=20.02 d.f.=11 p<.05) and the daily number of food visits correlated strongly with the mean proportion of fruit in each days diet (r_s=.667 n=60 p=.03) and the day range length (r_s=.716 n=60 p<.0001). On average, 34.7% (Range: 12.5% - 54.2%) of food items used in the month comprised the daily diet. A similar proportion of food items (mean: 32.9% range: 25.9% - 52.9%) was taken on the first day of the 5-day sample followed by a mean of 26.4% on Day 2, 19.6% on Day 3, 14.4% on Day 4, and 6.7% on Day 5.

Table 4-17 Number of food sources used on a daily basis.

Month	Mean	Range
September	5.2	3 - 8
October	7.4	5 - 9
November	9.2	5 - 12
December	10.6	7 - 14
January	11.2	6 - 15
February	9.2	7 - 12
March	13.0	9 - 20
April	16.0	8 - 20
May	19.0	12 - 23
June	10.6	6 - 13
July	12.8	9 - 16
August	14.8	13 - 21
Annual period	11.6	3 - 23

Distinct food sources tended to be visited within the activity period but gibbons occasionally returned to the same source later in the day. Sources were normally used no more than twice a day with the exception of *A. dadah*, which received four visits on day one of the five-day sample in April. With few exceptions, food sources receiving more than one visit a day were those which featured prominently (i.e. top 3 items) in that month's diet. Food species were used more regularly during the activity period, RBC2 making return visits to as many as six different species in a single day in April and June. As was observed for food sources, gibbons normally fed from the same species twice a day but occasionally they frequently re-exploited a food species, such as in May and June when the group banqueted on fruit from five individual *R. nodosa* climbers and *G. gnemon* trees during one activity period. Three quarters (74.5% n=38) of the species to which gibbons made more than one daily feeding visit were producing fruit.

4.6.1.1 Important daily items

Important food items rarely changed between successive days of a 5-day sample and if the group did not feed from an important source one day, numerous or length visits were invariably made to it on the following day (see below). Around a third (mean = 34.2% range = 12.1% - 67.2%) of the day's feeding time was spent at the top food source and these were eaten on most, sometimes all, of the days comprising the five-day sample. Gibbons fed from the top ranked item on an average of 4.0 days (range 2-5) and ate the second and third ranked items on 3.0 (range 1-5) and 2.8 (range 1-5) days respectively.

4.6.1.2 Patterns of daily food type use

Patterns of food type use did not just change from month to month but also from one day to the next. Food types were not used every day, but on days in which they were selected, they sometimes contributed to as much as 100% of sample foodstuffs (Table 4-18). Not unexpectedly, fruit consumption made up a significant proportion of daily feeding time, accounting for an average of 43.5% of the diet on days when gibbons visited fruiting sources. When gibbons reduced their daily intake of fruit, they correspondingly increased the proportion of fig in the diet. On those days when fruit was eaten, figs made up an average of 26.8% of the daily feeding time. But when gibbons ate only minimal amounts of fruit, or excluded it altogether from the diet, they switched to figs, concentrating up to 42.3% of feeding activity on fig exploitation.

Table 4-18 Percentage of food types in the daily diet (mean and range) and the number of observations days on which they were consumed.

Food type	Proportion of daily diet		% of observation days
	Mean	Range	
Fruit	43.5	0 - 100.0	90.0
Fig	26.8	0 - 67.2	68.3
Flower	11.0	0 - 49.3	56.7
Young leaf	24.9	0 - 76.9	85.0
Leaf bud	1.7	0 - 40.0	20.0
Invertebrate	0.9	0 - 6.5	28.3

Young leaves contributed a similar proportion to the daily diet as figs (24.9%) but they were taken more regularly than figs and almost as frequently as fruit (85% of sample days). Visits to flowering sources occurred less often since only 34 of the 60 day observation period found gibbons feeding on flowers. When gibbons did include flowers in the diet, they spent, on average, a fifth of their feeding time consuming this plant type. Leaf buds and invertebrates did not contribute greatly to the annual diet and hence their use on a daily basis was intermittent at best.

4.6.1.3 Dietary overlap and foraging pathways

Not unexpectedly, and in contrast to the pattern of important food item use, hybrid gibbons did show some, and at times marked, alteration to dietary composition on successive days. The degree of dietary overlap was measured by summing the shared percentages of all food items consumed on the days compared (McKey and Waterman, 1982 modified from Struhsaker, 1975). As observed for black colobus monkeys (McKey and Waterman, 1982), time generally did not affect dietary overlap, the diets of most two-day combinations overlapping by an average of 34.7% but tending to be more alike in composition on days separated by one. Ranging patterns certainly influenced similarity in diet as the adoption of set pathways through the home range varied from month to month and similar routes were normally travelled on every second and sometimes third day, explaining the higher degree of dietary overlap between these days. This was particularly apparent in December, February and August when RBC2 used and alternated almost identical routes to visit important, and forage in less important, food species. Diet similarity and range behaviour are in turn responsive to changes in the availability, and rate of replenishment, of foods in the home range (Chivers, 1977b; Gittins, 1979). For example, species which produce large crops which ripen quickly (*A. dadah*), or which are used by many rainforest species (figs), will be visited almost every day while those which take longer to ripen (*D. eximia*), or which are not as attractive to food competitors, will receive less attention.

4.6.1.4 Inter-food source distance and visitation rates per hour

The feeding pathway a group chooses to follow, in terms of the time and distance taken to reach the next food source, can be examined by measuring the number of food trees visited per hour and how far the group travels to reach the next feeding site (Davies, 1984; Stanford, 1991). Between 0.40 (Day 5: September) and 3.22 (Day 5: May) sources were visited per hour, monthly averages given in Table 4-19. As for daily totals, fruit eating had a positive effect on the number of sources the group exploited each hour (r_s=.573 n=10 p=.05) and a strong association was evident with day range length (r_s=.755 n=60 p=.01). The distance between successive feeding sites, calculated by dividing the day range length with the number of sources visited (Davies, 1984; Stanford, 1991), ranged from 92.4 m in December to 170.8 m in June but variation was not significant (H=12.49 d.f.=11 p>.25). Proportion of plant types had no effect on how far the group ranged to visit successive food sources.

Table 4-19 Food source visitation rates.

Month	Mean number of food sources visited per hour	Range	Mean distance (in metres) between feeding sites
September	0.74	0.40 - 1.14	140.4
October	1.05	0.77 - 1.42	131.8
November	1.33	0.71 - 1.80	116.6
December	1.57	1.02 - 1.87	92.4
January	1.52	0.92 - 1.84	128.2
February	1.09	0.84 - 1.47	108.2
March	1.79	1.09 - 2.53	103.6
April	2.28	1.45 - 2.65	112.4
May	2.50	1.47 - 3.22	116.6
June	1.22	0.78 - 1.48	170.8
July	1.85	1.50 - 2.18	148.0
August	1.76	1.42 - 2.80	134.0
Annual period	1.55	0.40 - 3.22	125.3

4.6.2 Temporal patterning of food type choice

Different species of gibbon show variation in their temporal choice of food types but a general trend exists. Figs are taken in the early and late stages of the day and young leaves and flowers are eaten in the middle of the day (Chivers, 1977b; Raemaekers, 1977; 1978a; Gittins, 1982; Whitten, 1982a). Temporal changes in hybrid gibbon food type selection followed a similar pattern with some expected differentiation (Figure 4-7). While both figs and fruits were important food types in the first three hours of the morning and in the last hour of the day, gibbons preferred to visit figs before 0600 and after 1400. The time RBC2 devoted to fig feeding equalled or exceeded that of fruit consumption at these times. However, as the day progressed into the late morning and early afternoon, fig consumption declined steadily, only rising again after 1200, while fruit eating remained relatively constant, a slight peak occurring at 0900. Flowers contributed 10% or lower to the diet until a peak of feeding occurred in the middle of the day (1100-1300). No flowers were consumed after 1400. Gibbons also fed more on young leaves in the midday period, which extended between 1000 and 1300, than at any other time of the day. No young leaves were taken until after 0600, their consumption increasing towards 1000 and decreasing after 1300. Variation in leaf shoot and insect selection was not substantial, although gibbons appeared to prefer feeding on the former in the early morning.

Energetics and interspecific competition have been proposed to explain the consistent and marked use of figs in the first and last hour of the activity period by siamang and lar gibbons (Raemaekers, 1977; 1978a). Long overnight fasts are characteristic of many species; the average non-active period of RBC2 was 16.5 hours, an extremely long period of time to go without food. These fasts result in a major decrease in blood sugar levels and gibbons need to find an energy-rich and easily digestible food source quickly, preferably one rich in soluble sugars and requiring little harvest time (Raemaekers, 1977; 1978a). Such a source is the fig and its production in substantially sized crops makes it the ideal food type for the satisfaction of the whole group. Gibbons may also visit fig trees first to relieve competition with other frugivorous mammals and birds, and since gibbons prefer ripe figs, it is in their best interests to access the food source before it is depleted. Certainly, both explanations are applicable to hybrid gibbons. However, focus groups did not always leave the night tree, nor did they invariably start feeding before 0600, effectively leaving prized figs unprotected from exploitation by other frugivores. Moreover, the later start to the activity period did not see a high level of fig consumption carried over to the hour between 0600-0700, feeding time on *Ficus* declining instead.

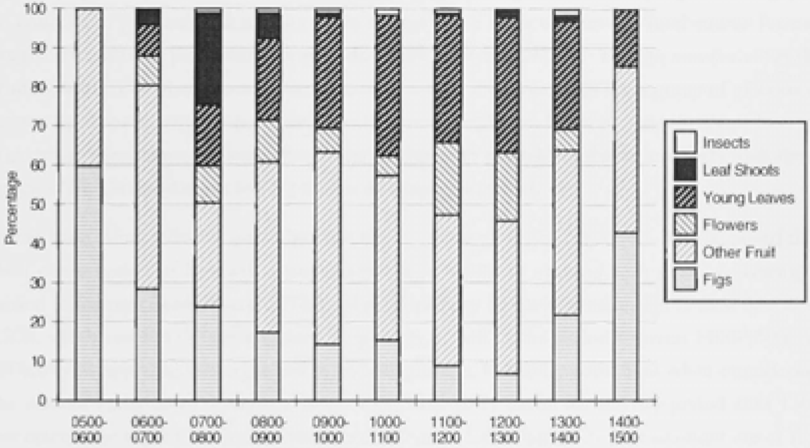


Figure 4-7 Temporal patterning of food type use.

To aid in explaining this drop in fig use, an examination was made of the start time of the activity period, the first food source visited and the time that feeding began. When gibbons commenced the first feeding bout of the day before 0600, the bout tended to occur at fig sources. If gibbons left the night tree before 0600 but did not start feeding until after the hour had passed, fruit sources, rather than figs, were more regularly visited first, and on mornings in which gibbons did not leave the night tree until after 0600, fig visitation was even less frequent. As previously stated, the consumption of fig was related to its availability and therefore it was interesting to find that the days on which gibbons fed both early and predominantly on figs coincided with months of greater fig abundance and use. In months where figs were not as widely available, gibbons relied mostly on other fruit species as the first source of the day. Not surprisingly, these species were those which featured prominently in at least one monthly diet (eg. *A. dadah*, *R. nodosa*, *G. parvifolia*). For an energy-depleted gibbon looking for an appropriate starter food, a source of known location, and one which is characterised by a large crop size and a fruit harvested easily or composed of a high sugar content, represented a perfect substitute for the fig.

The concentration on feeding on figs before 0600 in months of high fig consumption and the delay in feeding until after 0600 in times of lower fig exploitation may arise from the challenges of interspecific competition (or changes in the quality of the fig fruit over the day). Feeding competition with other primate species at Rekut appeared to be comparatively low, only a few observations being made of macaques or red leaf monkey converging on the same food tree as a group of gibbons. The dietary characteristics of red leaf monkeys (Davies, 1984), the long-tailed macaques tendency to range along river edges (personal observation) and the low group densities of both species in the Barito Ulu area (Bodmer et al., 1991) probably reduced their use of key gibbon food species. Tree shrews, sun bears and civets posed a greater threat to gibbon's food supply, although it was birds, in particular hornbills, and squirrels which represented the most serious competitor (McConkey, 1999). The morphological structure (bright colours, easy to collect and process) and fruiting cycle of figs make them a attractive food source for any frugivorous animal, particularly in periods of low fruit availability. Thus in months when the fruiting activity of plant species other than figs is low, it is imperative for a group of gibbons to access fig crops as early as possible so as to prevent depletion by other animals also reliant on figs during these times. When other desirable fruits are available, gibbons routinely visit those species first, the need to get to a fig source no longer so critical.

In the hour(s) immediately preceding the time gibbons enter the night tree, it is supposed that their consumption of figs will again increase as a means to contend with the long overnight period of fasting (Raemaekers, 1978a). Hybrid gibbons do include more figs in their diet after 1200, which reaches the same dietary proportion as fruit in the period between 1400-1500. A difficulty in applying this argument to hybrid gibbons, however, does arise when considering the marked variation in retirement time. RBC2 normally ended the activity period after 1300 but entered the night tree anytime between 1100 and 1530 (Chapter 3). A consistent use of figs would be expected over this time but such a pattern was not observed, gibbons showing little preferential use of figs before 1400, the lowest amount of fig eating actually occurring at 1200. Figs, therefore, may not be as essential, dietetically, for the gibbon in the pre-fast phase as they are the following morning. Alternatively, fruit, which comprises around 40% of feeding time in the hours after midday, may act as an appropriate dietetic substitute. Another interpretation suggests a possible masking effect of fruit consumption. Figs may be eaten in large amounts at the end of the activity period. But because the gibbons vary their retirement time from day to day, and month to month, and show little change in the amount of fruit eaten in the afternoon hours, increases in fig consumption are masked by the consistent and large quantities of fruit taken in the same time period. Each hour block between 1200 and 1500 was examined separately to determine if fig use did reach similar proportions to that of fruit but this was not found.

4.7 Duration of feeding

Discrete feeding sessions ranged considerably in duration, from just one minute (eg. *Vatica rassak* YL in November and *Glochidion* sp. FL in January) to over an hour (74 minutes – *F. subgelderi* in October). Gibbons spent less time feeding on sources while foraging, making brief visits (mean = 4.2 minutes) to food species encountered while travelling to the next major feeding site. When gibbons reached a large, important or previously visited food source, a feeding bout of longer duration (mean = 16.2 minutes) normally resulted, in which all or most members of the group participated.

Gibbons spent lengthy periods of time feeding on figs (mean = 21.8 minutes and see Table 4-20). Exceptionally long feeding bouts either took place in sources abundant with fruit or during months in which figs acted as keystone mutualists, gibbons often not leaving the fig source until almost an hour later. An average of 18.4 minutes was spent on flower species but some large, flowering climbers and trees received considerable attention during single bouts of feeding (eg. 68 minutes *Ellipeia cuneifolia* [November]; 66 minutes *Gluta curtisii* [September]; 57 minutes *Pyranidanthe prismatica* [January]). Indeed, during these bouts gibbons rarely ceased feeding for even short periods of respite, suggesting that flowers, possibly by nature of their rarity in the forest compared to other food types and their generally short lifespan, represented a highly prized food source. Fruit and young leaf eating occurred in shorter bouts, 14.1 and 15.6 minutes respectively. Approximately half an hour of fruit consumption characterised visits to *C. griffithii*, *E. ecostulata* and *G. nervosa* while slightly longer feeding visits were made to sources providing young leaf. Despite the predominance of *C. griffithii* YL's in RBC2's diet, it was the young leaves of *Dialium patens*, *Durio griffithii* and *D. malaccensis* on which the group spent significant amounts of time (average: 38.8, 32.0 and 29.0 minutes respectively) feeding.

Table 4-20 Mean feeding duration (in minutes) on each food type.

Food type	Mean duration of feeding	Range
Fruit	14.1	1.0 - 41.0
Fig	21.8	3.0 - 74.0
Flower	18.4	3.9 - 68.0
Young leaf	15.6	1.0 - 70.0
Leaf bud	16.6	1.0 - 66.0
Invertebrate	4.6	1.0 - 11.0

Feeding bout duration on each food type varied from month to month (Figure 4-8), significantly for flowers (H=21.68 d.f.=11 p<.025), figs (H=29.2 d.f.=11 p<.005) and fruit (H=42.0 d.f.=11 p<.001) but not for young leaves (H=9.96 d.f.=11 p>.05). Bouts of young leaf, and in particular, flower feeding increased in relation to rises in their monthly intake but little association was observed for fig and fruit variables (Table 4-21). However, the amount of fruit in each diet did affect the duration of feeding bouts on figs: the more fruit consumed each month, the less time spent at fig sources. A similar relationship was observed between length of visits to species producing young leaves and the quantity of fruit consumed.

Table 4-21 Relationship between the mean duration of feeding bouts and mean dietary proportion of each food type over the annual period (n=12).

Mean duration of food bout	Mean dietary proportion of each food type			
	Fruit	Fig	Flower	Young leaf
Fruit	-.308	-.210	.371	.266
Fig	-.699*	.462	.503	.273
Flower	-.476	-.119	.783**	.462
Young leaf	-.573*	.259	-.084	.685*

significance level: * ≤.05 ** ≤.01

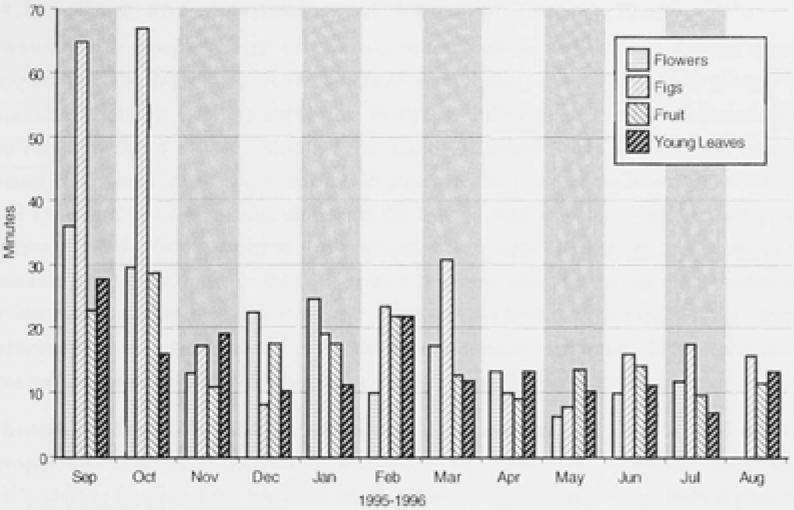


Figure 4-8 Monthly variation in mean duration of different food type feeding bouts.

4.8 Discussion

Diet is defined by a multiple of interactive forces, confining an animal to a basic yet flexible dietary specialisation. Gibbons, by virtue of their size and physiology, and the habitats they reside in, have adopted a rather uniform diet (see below) with only the siamang and the still little researched *Nomascus* gibbons exploiting a somewhat different feeding strategy. For the siamang, the variation in its diet compared to the smaller, and in particular lar group, gibbons has long been attributed to genetic differences between the two subgenera (Chivers and Raemaekers, 1980). A recent paper by Palombit (1997) reaffirms this contention. But between closely related species, such as the lar group, any dietary modifications are deemed instead to be a consequence of environmental differences. It is the quantity (availability of preferred food items) and quality (chemical and nutritional composition of plant forms) of potential food sources which act as the primary factor directing food choice.

H.a.albibarbis x muelleri hybrids conformed to the basic diet of the parental forms and other lar group gibbons but some dietary anomalies were observed. The consistency of these anomalies (in terms of actual food items consumed and dietary responses to plant part production) in the feeding habits of a hybrid animal does introduce some support for Struhsaker et al.'s (1988) proposal that food choice is under genetic control. Attempting to detect a specific or genetic component to food selection, however, requires the careful examination of both diet and food type availability of *agilis, muelleri* and hybrid gibbons, a task seriously confounded by the absence of populations co-existing at this study site. Nonetheless, initial discussion will be made here with the recommendation that further work on the feeding habits of hybrid gibbons be conducted south of the Rekut site where *albibarbis* and hybrids occupy adjacent residential areas.

4.8.1 Plant and morphological forms of gibbon food

Which dietary group a primate adheres to is immediately dependent on its size and digestive capability. Too big to subsist on insects or nectar, and lacking the gut morphology (e.g. sacculated stomach – Chivers and Hladik, 1980) that enables their more folivorous counterparts to regularly exploit foliage (Hladik, 1978; Kay and Davies, 1994), gibbons have adopted a mostly frugivorous diet, supplemented with other plant (e.g. leaves) or animal foodstuffs. For the hylobatid, this kind of diet represents the optimal feeding strategy and for two primary reasons. Firstly, fruit is found in sufficient quantity to supply the dietary bulk essential for a medium-sized animal and, in times when fruit is scarce, other food items can be substituted. Furthermore, gibbons, being monogastric primates, have high rates of food passage. Such an efficient form of nutrient-extraction is ideal for a fruit-based diet (Ungar, 1995), particularly if the species consumes high proportions of a fruit item (e.g. fig) low in nutritional quality.

Within each broad diet category, variation in the proportional selection of food types and morphological forms is a result of season-induced changes in the feeding habits of the individual or group and the differential diets observed by different species. Hybrid gibbon use of specific food types, such as fruits, figs and invertebrates, fell within the range demonstrated by other species of gibbon but young leaf and flower consumption were slightly lower and higher respectively. Other, and more marked, aberrations from the normal gibbon diet have been attributed either to differences in availability (e.g. *H. concolor* – Lan, 1993; *H. hoolock* – Islam and Feeroz, 1992a) or patterns of preference and/or deterrence induced by the chemical properties of plant stuffs (*H. klossii* – Whitten, 1982a; *H. lar* – Palombit, 1997). It is likely that these factors influenced hybrid gibbon food selection but a formal means of testing this remains wanting. Inconsistent reporting of phenological patterns, and the little work conducted on the chemical constituents of hylobatid food, prevents any accurate comparison between study sites on how food type availability and nutritional status relates to food type choice. Soil quality, however, provides a hint. The forests of Indonesian Borneo (Whitmore, 1984), and especially those of Central Kalimantan (MacKinnon et al., 1996), are founded on nutrient poor soils, much like those of the Mentawai Islands and Sumatra. Plants growing in such soils adapt by developing highly effective chemical defences, mostly in the form of secondary compounds, which probably act to deter Kloss gibbons, and maybe siamang and lar gibbons, from consuming sizeable quantities of leafy matter. It is conceivable, therefore, that hybrid gibbons refrain from excessive leaf consumption or, more importantly, concentrate the folivorous component of their diet on only on a few species (e.g. *C. griffithii*, *Dialium* spp., *Durio* spp. and *Xanthophyllum* spp.) because the low quality of soil at Rekut induces a high proportion of inedible forms of foliage.

Of the morphological forms selected by gibbons, general trends are easily recognised. Gibbons prefer immature or very young leaves, avoiding mature foliage if they can. Fruit sources tend to be ripe, succulent, brightly coloured (reds, oranges and yellows), and readily processed. Biochemical assays on similar food types taken by other primates suggest that the combination and level of chemical properties of plantstuffs does influence dietary decision (Oates, 1977; Milton, 1979; Oates et al., 1980; Waterman and Choo, 1981; Glander, 1982; Garber, 1984;

Waterman, 1984; Davies et al., 1988; Waterman et al., 1988; Ganzhorn, 1992; Garber, 1993; Kool, 1993; Leighton, 1993; Wrangham et al., 1993; Kar-Gupta and Kumar, 1994; Ungar, 1995 but see Janson et al., 1986; Marks et al., 1988; Rogers et al., 1990; Dasilva, 1992; Leighton, 1993; Barton and Whiten, 1994; Mowry et al., 1996; Heiduck, 1997). Primates tend to feed on items rich in essential or easily absorbed nutrients, avoiding those composed of compounds that either interfere with nutrient digestion or are potentially toxic to the consumer. If this finding can be extrapolated to gibbon feeding habits then young leaves and particularly ripe, succulent fruits represent the consummate food. Young leaves are easily digested (low fibre content), they are protein rich, and contain smaller concentrations of toxic compounds (Hladik, 1978; Davies et al., 1988; Waterman et al., 1988). With regard to gibbon fruit, ripe, succulent variants contain lower concentrations of tannin (Waterman, 1984), a compound that retards the activity of digestive enzymes, and are repositories of substantial quantities of simple sugars, locked within the fibrous pulp (Kay and Davies, 1994; Ungar, 1995).

The ability to manually process a food item is the next consideration that dictates what can be eaten and with what degree of difficulty. Gibbons are generally excluded from exploiting large fruits; they are cumbersome and hard to hold, especially for animals who rely on their hands for food processing and support (i.e. hanging, brachiation) whilst feeding (Ungar, 1995). Fruits with hard rinds are also best to avoid, again for reasons of manual dexterity or dental anatomy.

Hybrid gibbons, while observing the common hylobatid 'syndrome' of food type use, deviated somewhat in their choice of fruit forms. Undeniably, the favoured fruit was the sunset-coloured, pulpy drupe or berry but types of fruit avoided by other species despite their availability (e.g. *Lithocarpus* by Kloss gibbons – Whitten, 1982a) were eaten by the hybrids. Extremely large fruits, such as *H. woodii* and *P. bracteatus*, featured in the diet of RBC2 and RBC1. Both fruits have succulent pulps whose consumption would make a substantial meal, but it takes considerable effort to grasp such a big item while attempting to rupture the hard (*H. woodii)* or spiny (*P. bracteatus*) pericarp. Nonetheless, gibbons persisted with these species, returning to *P. bracteatus* sources in four of the observation months, although they would occasionally drop the fruit before all the pulp had been eaten.

Other fruits unique to the hybrid gibbon diet were the hard walled nuts, samaras or berries. Not all species of gibbon avoid these physiognomical types (e.g *Elaeocarpus* fruits consumed by *H. concolor* – Sheeran, 1993), and Gittins (1979; 1982) has made reference to agile gibbons needing to "husk" fruits before consumption, but overall, gibbons tend to shun such fruits as a regular or supplementary food item. To find the hybrid gibbons eating such fruits, not only enclosed in a shell difficult to penetrate but composed of dry or fleshless pulp, a foodstuff not easy to prepare or digest and possibly of poor nutritional value, was surprising. It must be stated that only a few of the fruits taken by hybrid gibbons resembled this morphological type and most contributed little to the diet, but two species, *Pentace excelsa* and *E. ecostulata*, were found to have high selection ratios and *E. ecostulata* was the eighth most important item in the annual diet. Of course, *E. ecostulata* was mostly eaten during a period when fruiting activity was quite low but it is still difficult to explain why such a fruit was used so excessively, particularly if preferred species, such as *K. latifolia* and *G. nervosa*, were fruiting at the same time.

4.8.2 Dietary responses to the habitat

The ephemeral dispersal of the frugivore's primary food source demands a diverse diet. In part it is catered for by the immense specific diversity found in the rainforest but it is also constantly subservient to the phenological changes of the residential flora. Hybrid gibbons used a wide range of food items and their diet changed constantly, responding to fluctuations in plant part production in much the same way pure species of gibbon do. During periods of substantial fruiting activity, gibbons banqueted on fruit items, and supplemented the diet with young leaves when intense utilisation of the preferred food source could not be maintained.

Peaks of flowering were also exploited by the hybrids but since no relationship existed between fruit and flower consumption, preference rather than dietary substitution (for fruit) appears to be a stronger factor directing usage. Because previous authors have made little comment on the importance of flowers in the gibbon diet or not always provided consistent information on the availability of food types, it is difficult to discriminate between real and perceived differences in feeding behaviour. The contribution flowers make to the hybrid gibbon annual diet, however, is the second highest found for current study populations and long feeding sessions were often dedicated to bountiful crops. Furthermore, a study subsequent to my own also found strong selection for flowers (Kim McConkey, 1999). Conclusive support is not yet available but there is at least suggestive data for the proposal that hybrid gibbons *select* for flowers while other species simply use them as a supplementary foodstuff.

In contrast, hybrid gibbons did not select strongly for figs nor did they regularly monitor their levels of fig consumption in relation to fruit use. The first of these conclusions is not so unusual; gibbons spend a great deal of time feeding on fig but nutritionally figs are inferior to other species of fruit and their attraction lies more with their reliable and voluminous fruit production and easy digestion. When the detection of non-fig fruit became more difficult, figs could be relied upon as a surrogate source of energy-giving sugars (Leighton and Leighton, 1993). In the fruit poor months of September and October 1995, fig eating reached particularly marked proportions. But in other observation months, including those when fruiting activity only marginally exceeded the phenological indices of September and October, and more species of fig were actually fruiting, fig eating showed no evidence of association with either fruit eating or abundance. To compensate for this reduced dependence on figs, hybrid gibbons have developed an alternative strategy to cope with fruit loss, incorporating other morphological forms or food types to "make up" the rest of the diet. One proposed strategy induces the gibbon to concentrate its feeding time on one coveted fruit item (e.g. *A. dadah*), to take advantage of less desirable but plentiful food sources, be they young leaves (*C. griffithii*) or non-succulent fruits (*E. ecostulata, C. griffithii* and *P. speciosa*), or to blend these strategic options, depending on, and responsive to, phenological activity and the gibbons' knowledge of food availability.

5

Ranging Behaviour

5.1 Introduction

5.1.1 Determinants of home range establishment and use

The way in which a primate group uses its habitat is governed, at least in part, by the distribution in time and space of essential resources (Clutton-Brock and Harvey, 1977; 1979; Dunbar, 1988). Temporal and spatial dispersal of resources combine to influence a group's ranging patterns on a daily, annual and life-time basis, determining the size of the area within which a group needs to live (i.e. the home range) and the day to day travel movements necessary for the acquisition, and in some cases protection, of these resources. This effect never remains static, though, as the inevitable fluctuations in resource availability compels groups to continually divert their ranging pathways, generating changing patterns of monthly, seasonal and annual habitat use.

Dietary requirements and specialisations, and particularly the supply of favoured foods, is probably the critical factor affecting ranging behaviour. Between dietary classes, ranging area is largely determined by the convenience of the primary food source. Frugivorous primates, compared to species subsisting on a more folivorous diet, tend to retain larger home ranges to accommodate the ephemeral and scattered distribution of fruit and to guard against the pressure of food competition (Clutton-Brock and Harvey, 1977; 1979; Dunbar, 1988). For those primates who have adopted a similar dietary strategy, it is habitat quality, or the dispersal and abundance of food, which can markedly affect home range size and use (Dunbar, 1988), and not just between different taxonomic groups. Populations of the same species who occupy distinct habitat types often show marked variation in the extent of their ranging, such as Hanuman langurs (Jay, 1963; Yoshiba, 1967; 1968; Newton, 1992).

Despite the undeniable effect food source dispersion has on ranging behaviour, it is too simplistic for a single factor to influence, or even control, a primate's decision on how large the home range should be, where to range and how far to travel (Terborgh, 1983; Barton et al., 1992). The shaping of the home range itself can also rely on the size, biomass and "metabolic weight" of the resident group, existing inter-specific competition, and population density (Milton and May, 1976; Clutton-Brock and Harvey, 1977; Waser, 1977; Harvey and Clutton-Brock, 1981; Dunbar, 1988; Barton et al., 1992). For example, large groups require large home ranges to support additional troop members, and groups who suffer from intense feeding competition need to occupy adequately sized ranging areas to alleviate the potential of food shortages and the costs associated with physical contest and nutritional deficiency. The local density of conspecifics further determines whether a group can afford to expand its range or if they have to make do with one smaller than average. Once the home range has been established, additional ecological factors direct the patterns of daily habitat exploitation. Those already identified include habitat structure (Kinzey and Gentry, 1979; Gautier-Hion et al., 1981; Whitten, 1982d), night tree position (Tenaza, 1975; Rasmussen, 1979; Whitten, 1982c), intragroup conflict (Isbell, 1983); intergroup encounters (Struhsaker, 1974; 1975; Rasmussen, 1979; Bennett, 1986b), distances travelled on previous days (Fossey and Harcourt, 1977) and the weather, in particular patterns of rainfall (Chivers, 1969; 1974; Raemaekers, 1980; Curtin, 1982; McKey and Waterman, 1982; Isbell, 1983; Barton et al., 1992) and temperature (Henzi et al., 1992).

5.1.2 Outline of Chapter 5

In this chapter, hybrid gibbon ranging behaviour will be examined at three levels – day range travel, size and differential use of the home range, and the temporal variation in ranging. Daily travel is assessed through the measurement of distances covered over the course of the activity period (DRL), the effect selected environmental correlates have on range distance (Section 5.3), and the rate of travel from hour to hour (Section 5.4). Day ranges are, in turn, transferred onto a single map to illustrate frequently used path routes and the extent of ranging, from which an estimation of home range size is calculated. The difference in area between the home ranges of hybrid and other populations of gibbon is discussed in Section 5.5. In Section 5.6, the differential use of the home range in relation to habitat quality and the distribution of food, sleep and night trees are investigated. Monthly variation and the ecological determinants of this variation comprise the last of the analytical sections (Section 5.7).

5.2 Methods

The methods used for determining ranging patterns are as follows:

5.2.1 Day range length and hourly rates of travel

Day range length (referred to as DRL from herein) was measured as the total distance in metres travelled during the activity period, that is, from the time the group left the sleeping site of the previous night to the time they entered the new night tree(s). The group's position was marked every 10 minutes on a field map. Group travel was usually cohesive but, on those days in which one or more members travelled slightly different pathways, the two-day range lengths were summed and the average calculated. Daily travel distances were measured with a mapping wheel using range maps prepared in the field.

5.2.2 Measurement of home range size

Range maps from each of the 60 day follows were scanned to produce a composite of travel routes over the observation period. A transparent overlay divided into 1cm x 1cm grids was placed over the composite map and the number of grid squares into which the gibbons ranged was counted. Each grid square represented a quadrat of 50m by 50m, the same scale employed in previous gibbon field studies (e.g. Chivers, 1974; Gittins, 1979). Quadrats of this size have the potential to expand the home range area to artificially large levels and thus it is preferable if smaller quadrats (25m x 25m) are used instead (see Whitten, 1982c), particularly in the detailed assessment of disproportionate home range use. In this case, however, accuracy needed to be evaluated against manageability of total quadrat number, especially in relation to statistical procedures, and since the larger scale had already produced 233 quadrats, it was decided that $^1/_4$ ha quadrats would be used. Home range size, in hectares, was calculated by multiplying the total number of quadrats entered by 0.250 (the area of the quadrat divided by the area of a hectare).

5.2.3 Measure of home range utilisation

The *use* of a quadrat was defined as the time spent in a particular quadrat divided by the total ranging time. Additional indices summed the number of visits to a quadrat or averaged the duration of occupation.

Habitat quality

I employed two methodological techniques outlined in papers by Newton (1992) and Harrison (1983a) to measure the effect of habitat quality. The first was Jacob's preference index:

$$P_i = \frac{[R_i - Q_i]}{[R_i + Q_i]}$$

R_i = % of occupancy records for habitat *i* or the % of total ranging time spent in habitat *i*

Q_i = % quadrats of habitat *i*

where a P_i value of +1 indicated complete selection, a P_i value of 0 indicated no preference and a P_i value of -1 indicated total avoidance (Jacob, 1974; Barnes et al., 1983; Newton, 1992).

Selection ratios modified by Harrison (1983a) represented alternative indices of spatial and temporal habitat selection. A selection ratio index was calculated for each month, then summed and divided by 12 to give an average value for the observation period.

Spatial selection:

$$\frac{\text{proportion of quadrats in a month's range made up by each habitat type}}{\text{proportion of the total range made up by the habitat type}}$$

Temporal selection:

$$\frac{\text{proportion of time spent in a habitat type}}{\text{proportion of the total range made up by the habitat type}}$$

Location of food, singing and night trees

Known food sources, singing and night trees were plotted onto maps of the home range and the number per quadrat added. Time spent feeding in each quadrat was also calculated as well as the number of occasions in which the group used a particular night or singing tree.

5.2.4 Evenness of home range use

To estimate how evenly the range was covered each month and over the annual period, quadrat use diversity was calculated using the Shannon Wiener index (see Methods in Chapter 4) where P_i became the proportion of time spent in the *n*th quadrat.

5.3 Day range length and environmental correlates

The distance RBC2 covered in a day's travel averaged 1436.4 metres (median = 1290 m) and ranged from 600 m to 3235 m (Figure 5-1). RBC1's day range length was slightly longer than RBC2, the group travelling a mean of 1516 metres a day. Figure 5-2 shows the distribution of day range lengths for both groups and Table 5-1 lists average DRLs for other populations of gibbon. While the day range length of RBC2 peaks at a distance of 1000-1200 m, RBC1 tends to range a further 100-200 m a day, 41.2% of all day journeys falling between 1200-1600 metres. This dissimilarity in day range length, however, is not significant (*W's*=831.6 n_1=24 n_2=60 p>.10).

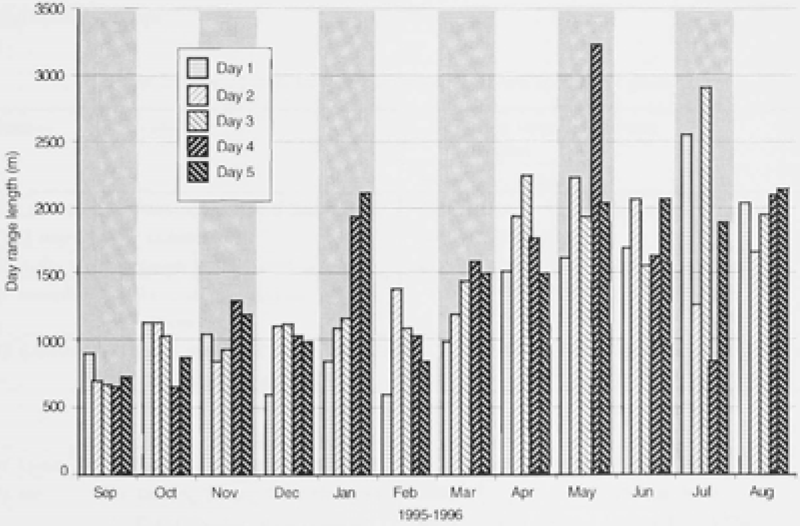


Figure 5-1 RBC2 day range lengths (n=60 days).

Previous studies have investigated the effect, if any, ecological factors have on primate ranging behaviour (reviewed in Section 5.1). The majority of these determined environmental correlates of variation in home range use rather than daily distance travelled and will be discussed later in the chapter. Of those studies in which DRL variation was considered, food availability and distribution appeared to have the strongest influence (Clutton-Brock, 1977; McKey, 1978 cited in Isbell, 1983; Rudran, 1978; Milton, 1980; Raemaekers, 1980; Marsh, 1981b; Isbell, 1983; Harrison, 1984; Barton et al, 1992; Henzi et al., 1992; Newton, 1992). An increase in feeding, and the abundance and diversity of dietary foodstuffs, saw an increase in the DRL of green monkeys (Harrison, 1984), forest Hanuman langurs (Newton, 1992); red colobus (Isbell, 1983); Tana River red colobus (Marsh, 1981b), howler monkeys (Milton, 1980), blue monkeys (Rudran, 1978), chacma baboons (Henzi et al., 1992), olive baboons (Barton et al., 1992), and siamang and lar gibbons (Raemaekers, 1980), although this relationship was only moderate for gibbons and partly affected by another environmental factor, rainfall.

DRLs of banded langurs and some populations of red colobus were not closely correlated with diet or food availability, these species tending to extend their day ranges in conjunction with a rise in the frequency of inter-group encounters (Struhsaker, 1974; 1975; Bennett, 1986b). This association may not be so inclusive and instead DRL may have been indirectly affected by exploitation of quality food sources. Although Struhsaker (1974) made no mention of sites of inter-group encounters, Bennett (1986b) observed that banded langur inter-group encounters usually occurred when neighbouring groups converged on a desirable but rare food source. Thus in times when preferred foods, normally fruits or flowers, were available, banded langurs travelled further to gain access to them and, in turn, increased the chance of encountering neighbouring groups.

Table 5-1 Day range lengths for hybrid and pure species of gibbon.

Species	Study Site	Day range length (metres)		Source
		Mean	Range	
H.a.albibarbis x H. muelleri	Barito Ulu, Central Kalimantan, Indonesia	1436[1] 1615[2]	600 - 3235 750 - 2320	This study
H. agilis	Sungai Dal, West Malaysia	1335	650 - 2200	Gittins, 1979; 1982
H. concolor	Wu Liang and Ai Lao, Yunnan, China	418*	90 - 750	Bleisch and Chen, 1991
H. hoolock	Lawachara and Chunati Wildlife Sanctuary, Bangladesh	-	600 - 1600	Islam and Feeroz, 1992a; 1992b
	Lawachara, West Bhanugach Forest Reserve, Bangladesh	1367	-	Ahsan, 1994
H. klossii	Paitan, Siberut Island, Indonesia	1514	885 - 2150	Whitten, 1982c; 1984b
H. lar	Tanjong Triang, West Malaysia	1600	-	Ellefson, 1974
	Kuala Lompat, West Malaysia	1490	450 - 2900	Raemaekers, 1979
H. moloch	Ujong Kulon, Java, Indonesia	1400	-	Kappeler, 1981 cited in Chivers, 1984
H. muelleri	Kutai, East Kalimantan, Indonesia	850	350 - 1890	Leighton, 1987
H. pileatus	Khao Soi Dao, Thailand	833	450 - 1350	Srikosamatara, 1984
H. syndactylus	Kuala Lompat, West Malaysia	800	485 - 1390	Chivers, 1974
		969	320 - 2860	*ibid*
		738	200 - 1700	Raemaekers, 1979
		933	150 - 1550	West, 1981

* Minimum day range length - estimated by calculating distance between singing locations on successive days.

[1] Day range length for RBC2

[2] Day range length for RBC1

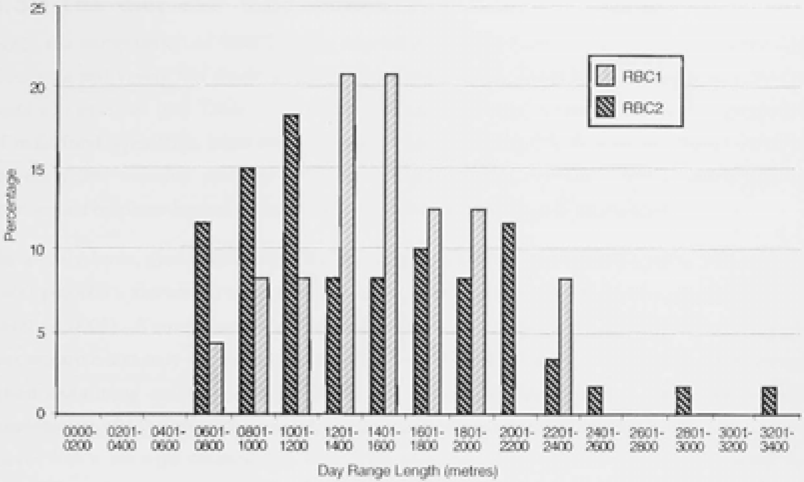


Figure 5-2 Distribution of day range lengths — RBC2 and RBC1.

In light of these results, I examined diet, food abundance, rainfall and intergroup conflicts for their role in determining DRL (see Table 5-2 for summary of results).

Table 5-2 Ecological and environmental correlates of day range length.

60 day sample (n=60)		
	r_s	sig to
Daily dietary proportion of fig	.023	=.86
Daily dietary proportion of fruit	.592	≤.0001
Daily dietary proportion of flower	-.187	=.15
Daily dietary proportion of young leaf	-.462	=.0004
Daily rainfall	-.238	=.06
Monthly average (n=12)		
	r_s	sig to
Daily dietary proportion of fig	.084	=.78
Daily dietary proportion of fruit	.683	=.02
Daily dietary proportion of flower	-.602	=.05
Daily dietary proportion of young leaf	-.704	=.02
Food species diversity	.249	=.41
Availability of fruit	.838	≤.01
Availability of flower	-.146	=.64
Availability of young leaf	.282	=.37
Average rainfall	-.277	=.36
Number of territorial encounters	.389	=.20

5.3.1 The diet and food availability

Since the composition of RBC2's diet was influenced, at least in part, by cycles of fruiting, flowering and young leaf flushing, both the utilisation and availability of food species and food parts was assessed (see Table 5-2). Utilisation was measured as the variation in the proportion of main food types (figs, other fruit, figs and other fruit combined, flowers and young leaves) in the daily and monthly diet and in terms of food species diversity. Food availability was represented by phenological changes in fruit, flower and young leaf production.

On a daily basis, fruit other than figs had a more substantial association with DRL (r_s=.592 n=60 p<.0001), showing a stronger correlation when combined with fig consumption (r_s=.649 n=60 p<.0001). Young leaves also had a significant correlation with DRL but the relationship was negative and only of moderate strength (r_s=-.462 n=60 p=.004). Correlations were stronger when examining monthly average DRL and food type exploitation. Again, the fig/fruit combination had the greatest association (r_s=.823 n=12 p=.006) but unlike the daily diet, young leaves had a stronger relationship with DRL (r_s=-.704 n=12 p=.02) than other non-fig fruit (r_s=.683 n=12 p=.02). Monthly dietary proportions of flowers exacted a similar strength association with DRL (r_s=-.602 n=12 p=.05) which was negative. Food species diversity had no effect.

Only the monthly availability in fruit exacted any significant influence on distances travelled per day, an increase in fruit associated with a rise in DRL (r_s=838 n=12 p<.01). Young leaf and flower availability held negative relationships with DRL but both were of poor correlational strength and insignificant.

These results indicate that hybrid gibbons travelled further when fruit was both prominent in the diet and abundant in the home range. But in months when young leaf and flower featured more prominently in the diet, gibbons covered shorter distances. Eating more fruit provides the gibbon with an increase in expendable energy, enabling it to devote more time to energy demanding activities, such as travelling, and hence greater home range coverage. Young leaves and flowers are, however, a nutritionally poor substitute for fruit and in times of decreased fruit consumption, it is in the best interests of the gibbon to limit time spent in energetic behaviours and restrict daily movement to reasonable distances. Differences in the distribution of key dietary food types should also affect range movements. Fruiting plants are generally more widely dispersed than young leaf sources, requiring the gibbon to travel further distances to access multiple sources. When more young leaf is in the diet, gibbons need not range as far as successive sources can be located over shorter distances.

5.3.2 Rainfall

Daily and monthly rainfall had the expected inverse relationship with DRL but neither of these correlates were significant (Table 5-2). An examination of the time and amount of rainfall, which had an effect on the length of the activity period, also did not appear to influence the distance travelled each day. Following Raemaekers (1980), the effect of successive days of wet (or dry) weather conditions on DRL was investigated (Table 5-3). On dry days, RBC2 was significantly more likely to range further in dry months than in wet months (W=80 n_1=9 n_2=20

$p<.05$) while in dry months, the group covered greater distances on dry days than on wet days ($W=108.6$ $n_1=10$ $n_2=20$ $p<.025$). RBC2, like siamang and lar gibbons, was also found to have longer wet day DRLs in dry months than dry day DRLs in wet months but this difference was not significant ($W=76$ $n_1=10$ $n_2=9$ $p>.05$). Raemaekers (1980) interpreted his results as indicative of the dampening effect rain has on DRL, particularly in a cumulative sense. Such an interpretation cannot be applied to RBC2's ranging behaviour as the results do not clarify whether it is the presence or the absence of rain that acts in part to determine the distance a group ranges each day.

Table 5-3 Day range lengths in wet and dry weather.

	Wet months	Dry months
Mean DRL (in metres) on wet days	1335.4	1401.6
Mean DRL (in metres) on dry days	1106.2	1813.0

5.3.3 Intergroup encounters

Encounters between RBC2 and its neighbours were infrequent and may explain the lack of correlation ($r_s=.389$ $n=12$ $p>.10$) between the number of territorial conflicts and length of the day journey. Some of these encounters took place in the vicinity of a highly favoured food source, such as a heavily fruiting fig tree, suggesting that incursions were occasionally the result of an invading group searching for, or attempting to exploit, said food sources. In the case of banded langurs and red colobus monkeys, home range overlap has been described respectively as "significant" (Bennett, 1986b) and "nearly complete" (Struhsaker, 1974) but this is not the case for hybrid gibbons. RBC2 shared only a minor portion of its home range with RBC1 and RBC5 and it is therefore possible that these groups rarely encountered one another as only a small proportion of quality food sources was shared.

5.4 Diurnal variation in hourly rates of travel

To determine varying use of the home range through the day, the distance covered during each hour of the activity period was calculated. Travel speeds ranged considerably - from 0 metres, when the group was engaged in an intensive bout of feeding or a rare prolonged period of rest, to 610 metres/hour (median = 320.0 m/hr). Hourly fluctuations in rates of travel were significant ($H=39.72$ d.f.$=11$ $p<.005$), this variation probably due to faster rates of travel at certain times of the day. As illustrated in Fig 5.3, the group travelled further during the first and last two hours of the activity period and travel rates remained static, with the exception of a slight peak at 0700-0800 hours, for the period in between. When comparing the travel rate for the peak hours with the rest of the activity period, the difference was significant ($U=8$ $n_1=3$ $n_2=7$ $p<.05$). Whitten (1982c) proposed that a rise in the travel speed by Kloss gibbons in the last two hours of the day was related to either the abandonment of other maintenance activities in the search for suitable night trees and/or the peripheral location of appropriate sleeping sites. Night trees were not distantly located in either RBC2's or RBC1's home ranges, suggesting instead that these groups increased their late activity period travel speeds in response to the need to quickly select a suitable night tree. Certainly it was observed in the field that travel increased in the time period immediately prior to settling down.

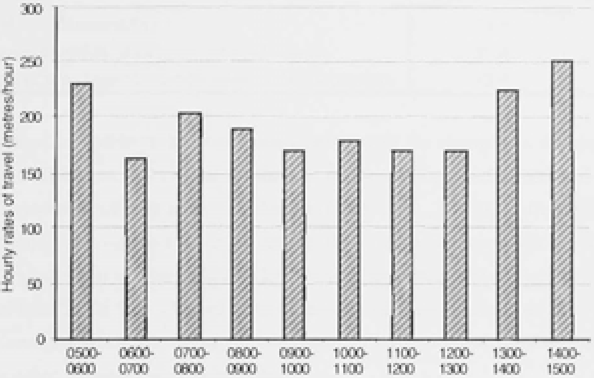


Figure 5-3 Temporal patterning of mean travel speeds (metres travelled/hour).

Faster travel speeds during the first hour of the morning are somewhat more difficult to interpret and complicated by the fact that the activity period did not always start before 0600 hours. For the purposes of this discussion, only days on which the activity period began between 0500-0600 will be examined (Table 5-4). Raemaekers (1980) considered it probable that gibbons covered greater distances in the first hour of the day in order to reach feeding trees as quickly as possible, either to occupy and exploit the food source before the arrival of competitors or to compensate for the overnight fast. The Rekut gibbons, however, often delayed feeding until 30 or more minutes after leaving the night tree (i.e. after 0600), but did not maintain a similar high rate of travel during this time period. On days on which the gibbons fed before 0600, the initial food source was always fruit and almost invariably a source which had been utilised previously, and often heavily, in the 5-day sample. If the desirability of a food source has any effect on travel speed, a higher rate of travel would be expected on post-0600 feeding mornings when a frequently visited food tree was utilised first. RBC2 did in fact travel significantly faster on such mornings, averaging 224.8 m/hr compared to a travel speed of 108.2 m/hr when the first feed stop of the day was at a new source (see Table 5-4). Direction of travel illustrated in ranging maps supports this finding; gibbons followed relatively straight and undeviating pathways when heading for a known food source but travelled more circuitous routes if the group had slept in a part of the home range where the location of potential food species was not known. Presumably on such mornings gibbons reduce their travel speed to compensate for the greater energy expenditure that may arise as a result of having to range further in search of a suitable starter food source. Either this or they travel more slowly to enable a thorough search of the area for new food sources.

Table 5-4 Variation in travel speed in relation to time of first feeding visit.

	Visited 1st food source < 0600	Visited 1st food source > 0600
Average travel speed (metres/hr)	224.8	108.2
Average distance travelled (metres) to 1st food source	88.0	124.0
Average length of time (min) before location of 1st food source	10.4	47.5

Hourly patterns of temperature had some association with the changes in distance travelled by green monkeys (Harrison, 1985) but neither temperature nor wind speed had any effect on travel speed in mountain living chacma baboons (Henzi et al., 1992). Unfortunately, measures of these variables are not available to assess their influence on hybrid gibbon ranging; accordingly, variation in consumption of key food items, maintenance activities and weather types are used (see Table 5-5). Travel rates seemed to increase somewhat with increases in fig consumption and time spent travelling but declined during periods of rainfall; but none of these nor any of the other variables were significant.

Table 5-5 Ecological, maintenance activity and weather correlates of day range length.

	Correlation coefficient (n=10)	
	r_s	sig to
Hourly variation in fig use	.600	=.09
Hourly variation in fruit use	-.133	=.71
Hourly variation in flower use	-.567	=.11
Hourly variation in young leaf use	-.233	=.51
Hourly variation in resting	-.317	=.37
Hourly variation in travelling	.650	=.07
Hourly variation in feeding	-.400	=.26
Hourly variation in sunshine	.067	=.86
Hourly variation in cloud cover	.100	=.78
Hourly variation in rainfall	-.561	=.10

5.5 Home range size and its determinants

A total of 233 quadrats were visited by RBC2 over the 60 day follow period, representing a home range size of 58.3 ha (Figure 5-4). Forty two of the $^1/_4$ quadrats lay on the perimeter of the home range and were either rarely used or contributed only part (< than half) of their area to the home range. If these are removed, the home range size is reduced to 48.0 ha and probably more accurately reflects the area RBC2 regularly utilises.

RBC1 resided in a similarly sized home range. Over 286 hours of observation time, the group entered 192 quadrats covering an area of 48.0 ha. Like RBC2, quadrats on the peripheries were visited sporadically. Measurement of home ranges for RBC3 and RBC5 was prevented due to inconsistent follows but estimates of partial range boundaries are given in Figure 5-4.

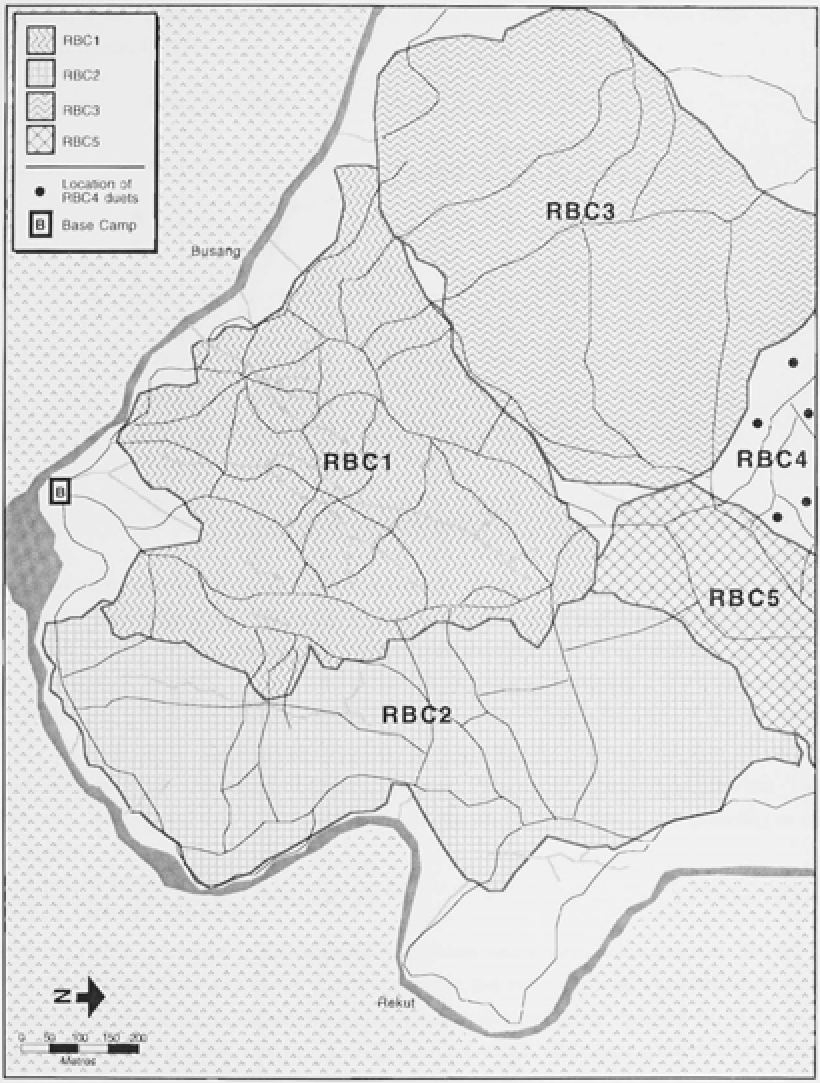


Figure 5-4 Home range boundaries of groups RBC1, RBC2, RBC3, and RBC5. (RBC4 were observed only rarely — the position of their ranging area in relation to neighbouring groups was estimated by estimating the location of song performances).

As the number of observation days increased, RBC2 correspondingly expanded its ranging into new parts of the home range. Figure 5-5 illustrates the cumulative use of previously unvisited quadrats over this period. A sharp rise occurring in the first three months tapered into a gradual incline over the following 9 months but did not produce an asymptote, indicating that the monthly 5-day sample was not adequate for establishment of the true home range size (see Clutton-Brock, 1975).

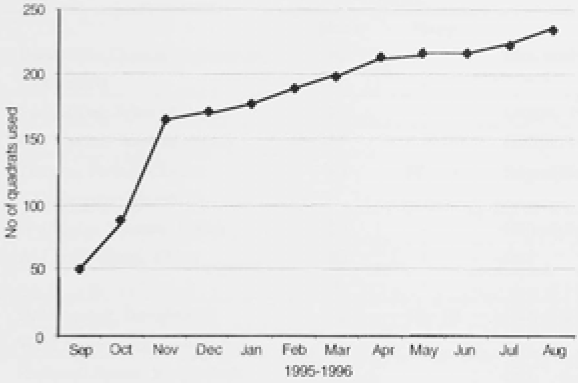


Figure 5-5 Cumulative use of home range quadrats over the 60 day sample period.

The home ranges of RBC2 and RBC1 are larger than most other populations of gibbon, excepting some populations of *lar* and *concolor* (Table 5-6). Population density (number of groups/km^2), type of diet, interspecific competition, predation and group size interact, and are, in turn, influenced by the quality of the habitat in determining how large a home range area an individual or group of primates requires or is limited to (Clutton-Brock and Harvey, 1977; 1979; Dunbar, 1988). The role these variables have in affecting gibbon home range size will be examined below in an attempt to explain the home range size of the hybrid gibbons. Diet, however, will be excluded (most species of gibbons have similar dietary components) as will predation.

5.5.1 Group density

Gittins (1979), investigating the relationship between home range size and group density for five populations of *lar* and *agilis*, found a negative but not significant correlation. My own extension of this analysis, incorporating home range size and group densities of all lar group gibbons, hoolock gibbons, siamang and *albibarbis* x *muelleri* hybrids, also found a negative correlation but the result was again not significant (r_s=-.303 n=13 p>.05). In contrast with other species of gibbon, siamang have a reasonably large proportion of leaves in the diet (Chivers, 1974; Raemaekers, 1979), which probably has some effect on its home range size. Folivorous primates tend to have smaller ranging areas due to a greater availability and less clumped nature of their primary food source (Clutton-Brock and Harvey, 1977; Dunbar, 1988 For these reasons, the siamang data were removed and a new correlation was run for the predominantly frugivorous gibbon species. The strength of the correlation was increased but only marginally so, and the relationship remains insignificant (r_s=-.442 n=12 p=.1).

Table 5-6 Home range size for pure species and hybrid gibbons.

Species	Study Site	Home range size (ha)		Source
		Mean	Range	
H.a.albibarbis x H. muelleri	Barito Ulu, Central Kalimantan, Indonesia	58[1] 48[2]	- -	This study
H. agilis	Sungai Dal, West Malaysia	29	-	Gittins, 1979; 1982
	Ulu Mudah, West Malaysia	25	-	Gittins, 1979
H.a.albibarbis	Tanjung Puting, Central Kalimantan, Indonesia	43	40 - 51	Sugardjito, 1988
H. concolor	Wu Liang, Yunnan, China	120	-	Bleisch and Chen, 1991
	Ai Lao, Yunnan, China	40 70	-	*ibid*
H. hoolock	Hollongapar, Bangladesh	22	18 - 30	Gittins and Tilson, 1984
	West Bhanugach, Bangladesh	18	-	*ibid*
	Rajkandi Forest, Bangladesh	23	-	*ibid*
	Lawachara and Chunati Wildlife Sanctuary, Bangladesh	35	-	Islam and Feeroz,1992a; 1992b
	Lawachara, West Bhanugach Forest Reserve, Bangladesh	51	26 - 86	Ahsan, 1994
H. klossii	Sirimuri, Siberut Island, Indonesia	7 11	5 - 8 7 - 12	Tenaza, 1975 Tilson, 1981
	Paitan, Siberut Island, Indonesia	(33)*	31 - 35	Whitten, 1982c
H. lar	Kuala Lompat, West Malaysia	27	16 - 32	Carpenter, 1940
		50	-	MacKinnon and MacKinnon, 1978
		57	50 - 57	Raemaekers, 1979
		54	50 - 58	Gittins and Raemaekers, 1980
	Tanjong Triang, West Malaysia	44	20 - 46	Ellefson, 1974
	Khao Yai, Thailand	16	-	Raemaekers et al. cited in Chivers, 1984
		24	21.5 - 26.5	Reichard and Sommer, 1997
H. moloch	Ujong Kulon, Java, Indonesia	17	12 - 22	Kappeler, 1984
H. muelleri	Kutai, East Kalimantan, Indonesia	(36)*	33 - 43	Leighton, 1987
H. pileatus	Khao Soi Dao, Thailand	36	-	Srikosamatara, 1984
H. syndactylus	Ulu Sempan, West Malaysia	18	15 - 25	Chivers, 1974
	Kuala Lompat, West Malaysia	34	-	*ibid*
		48	-	Gittins and Raemaekers, 1980

* Mean home range calculated by S.B. from data given in respective sources.

[1] Home range size for RBC2

[2] Home range size for RBC1

A simple comparison between hybrid gibbons and other gibbon populations experiencing either similar group densities or home range sizes also suggests a weak relationship between these two variables, at least for the subgenus *Hylobates*. Populations living at densities of approximately 3.0 groups/km^2 such as *muelleri* at Kutai (Leighton, 1987) and *klossii* at Siberut (Whitten, 1984b) had home ranges up to 27 ha smaller than the home ranges of the focus groups. In contrast, *lar* groups at Kuala Lompat and Tanjong Triang who, like hybrid gibbons, retain large home range sizes exceeding 50 ha (Ellefson, 1974; Gittins and Raemaekers, 1980) lived at considerably lower group densities.

5.5.2 Group size

Within or between closely related species groups (e.g. howler monkeys, colobus monkeys, langurs, baboons, macaques and geladas), the area of ranging may fluctuate with group size (Clutton-Brock and Harvey, 1977). Comparing home range and group size between different populations of the same species of gibbon, and between different specific groups, however, showed no association (r_s=.273 n=10 p>.10). The size of a gibbon group is largely restricted by its monogamous social structure; it is the number of offspring that determines the total number of members. Group size therefore probably exceeds no more than five individuals (two adults and three dependents) at any one time. Monogamy and its limitation on group size curtails the marked variation (i.e. number of adults) observed between some populations of primates (e.g. multi-male troops of *Semnopithecus entellus* [Jay, 1965; Ripley, 1967; Yoshiba, 1968; Hrdy, 1977; Laws and Vonder Haar Laws, 1984; Newton, 1992] and *Colobus badius* [Struhsaker, 1975; Gatinot, 1978]), and thus does not exert as strong as an effect on the area of a gibbon's home range.

5.5.3 Interspecific competition

In areas where one or more competitive species are absent or found at low densities, gibbons may not need to range as far to acquire adequate provision of favoured foodstuffs. For example, the absence of *Macaca fascicularis* in the Mentawai Islands has enabled Kloss gibbons at Sirimuri to maintain very small home ranges (MacKinnon, 1978 but see Whitten, 1982c). Frugivorous primates, such as long tailed macaques, are potentially serious food competitors for gibbons, particularly during seasons of low fruit availability, but it is the feeding habits of more closely related species (e.g. the siamang) which are liable to exert greater dietary pressure. At Krau Game reserve in West Malaysia, lar gibbons shared a greater proportion of dietary food items (48.5%) with another hylobatid, the siamang, than with either long-tailed macaques (32.5%) or the two species of leaf monkey, *Presbytis melalophos* (19.6%) and *Trachypithecus obscura* (2.02%). However, their dietary reliance on fruit (measured as proportion of diet) was closer to *M. fascicularis* than with the other three sympatric species of primate (MacKinnon and MacKinnon, 1980). A comparison of feeding behaviour of the primates at Ketambe in Sumatra (*P. thomasi*, *M. fascicularis*, *M. nemestrina*, *H. lar*, *H. syndactylus* and *P. pygmaeus*) also found greater use of similar food items between the hylobatid species but detected the potential for food competition to arise between gibbons and orang utans and, to a lesser extent, with long-tailed and pig-tailed macaques (Rijksen, 1978). At Rekut, gibbons shared their habitat with two other diurnal species of primate but only one of these, *M. fascicularis*, represented any formal threat to food supply; the diet of *P. rubicunda* is sufficiently different to prevent any major dietary overlap (Davies, 1984; Supriatna et al., 1986). Unfortunately, little work has been conducted on the feeding ecology of the macaques at Barito Ulu although chance sightings of macaques in the home ranges of RBC2 and RBC1 indicated that they exploited some of the same fruit species. However, macaques did tend to range along riverine rather than inland tracts of forest (personal observation) and were observed to enter secondary forest on a semi-regular basis (Kim McConkey, 1998 pers. comm.).

Long-tailed macaques live at substantially lower densities at Barito Ulu (1.4 individuals/sq km) than they do at Krau (39.0 individuals/sq km – MacKinnon and MacKinnon, 1980) or Ketambe (48.0 individuals/sq km – Rijksen, 1978). Combined with the research area's low overall primate biomass (120 kg/km^2), one of the lowest in South East Asia (Mather, 1992), it could be expected that the reduced foraging pressures on hybrid gibbons allow them to retain a smaller home range. Not so, as hybrid gibbon home ranges were not only of a similar size to those of *lar* at Krau but, as reported previously, were larger than most other species of gibbon. Of course, primates are not the only food competitors coexisting with gibbons in rainforest and indeed the adoption of different feeding strategies (e.g. opportunistic vs specialist), and the differential use of vertical and horizontal space, enable closely related animals to live in successful cohabitation (Rijksen, 1978). Birds, fruit-bats, squirrels, civets, and sun-bears all concentrate their diets on the favoured, but easily depleted, food item of the gibbon, namely fruit, and hence can exert feeding pressure on frugivorous primates. For example, Rijksen (1978) observed that hornbills and fruit-bats, particularly when foraging in large numbers, could decimate fruit sources often used by orang utans within days. According to Payne (1980) and Gautier-Hion et al. (1985), however, only a few species select fruit types or species similar, or the same, as items found in the primate diet (Chapter 4) and it is probably only in times of low fruit availability, when figs become an important dietary item (Leighton and Leighton, 1983 and Chapter 4), that primate and non-primate species compete excessively for food. Furthermore, those species which show some dietary overlap with gibbons create competition only if foraging regularly at the same canopy height (Payne, 1980).

Once again, detailed studies on the feeding habits of any of these animals are lacking for Barito Ulu but research undertaken recently by Kim McConkey on seed dispersal agents should provide valuable information on food competition existing at the field site. Preliminary results from her study indicate that it is squirrels, followed by hornbills, which represent the greatest threat to gibbon food supply (McConkey, 1999). My own observations suggest that other frugivores at Barito Ulu do not exert exceptional levels of feeding competition on gibbons, or certainly not to the extent that this factor alone necessitates a large home range size. However, if the density of food trees at the site is significantly lower than those at other areas where gibbon studies have been completed, it is then possible that interspecific competition can induce some effect.

5.5.4 Habitat quality

Probably the most important determinant of home range size is the quality of the habitat (Dunbar, 1988). Areas of low food tree productivity or density mean that groups of primates have to utilise larger home ranges compared to similar sized groups living in richer environments. Contrast in habitat quality has been used to explain the disparity in home range size between groups of macaques (Takasaki, 1981; Caldecott, 1986), vervets (Struhsaker, 1967; De Moor and Steffens, 1972), and chimpanzees (Suzuki, 1979) although a simple relation is not always evident (e.g. baboons – see Barton et al., 1992). Marsh (1981b), whilst discussing causes for the differences in red colobus ranging, has argued that differences in tree species diversity may play a role in home range size determination only in certain habitat types. In rainforests (e.g. Kibale), where diversity is particularly high and tree species are rare and widely dispersed, expansion of ranging is likely to introduce a group of primates to new, potential food sources. But, in forest types such as those at Mchelelo and Congolani in the Tana Forests, increasing the home range would probably be of little benefit as species/area curves suggest that only a negligible number of new species would be encountered (Marsh, 1981b).

Habitat quality can be measured in terms of annual rainfall (Rosenzweig, 1968; Coe et al., 1976; Barton et al., 1992), productivity of the habitat (Iwamoto, 1979) and availability of food trees (Struhsaker, 1974; Caldecott, 1986). Rainfall is not a particularly good index of gibbon habitat quality as most species are found in areas where rainfall is high and relatively even. Productivity and food tree availability, therefore, are more reliable indices of environmental richness. Because the former is difficult to estimate, the latter has become the preferred tool, although it is used more often to explain uneven use of the home range rather than its actual size (Chivers, 1974; Struhsaker, 1974; Gittins, 1979; Marsh, 1981b; McKey and Waterman, 1982; Whitten, 1982c; 1982d; Harrison, 1983a; Chapman, 1988; Barton et al., 1992; Henzi et al., 1992; Newton, 1992; Mturi, 1993). Food patch abundance at gibbon field sites has been measured in terms of number of figs/ha and the density of food trees (measured as the proportion of all plot trees). My own analysis found no relation between fig density and home range size ($p>.05$) but a strong and negative correlation existed with food tree density ($r_s=-.900$ $n=6$ $p<.05$).

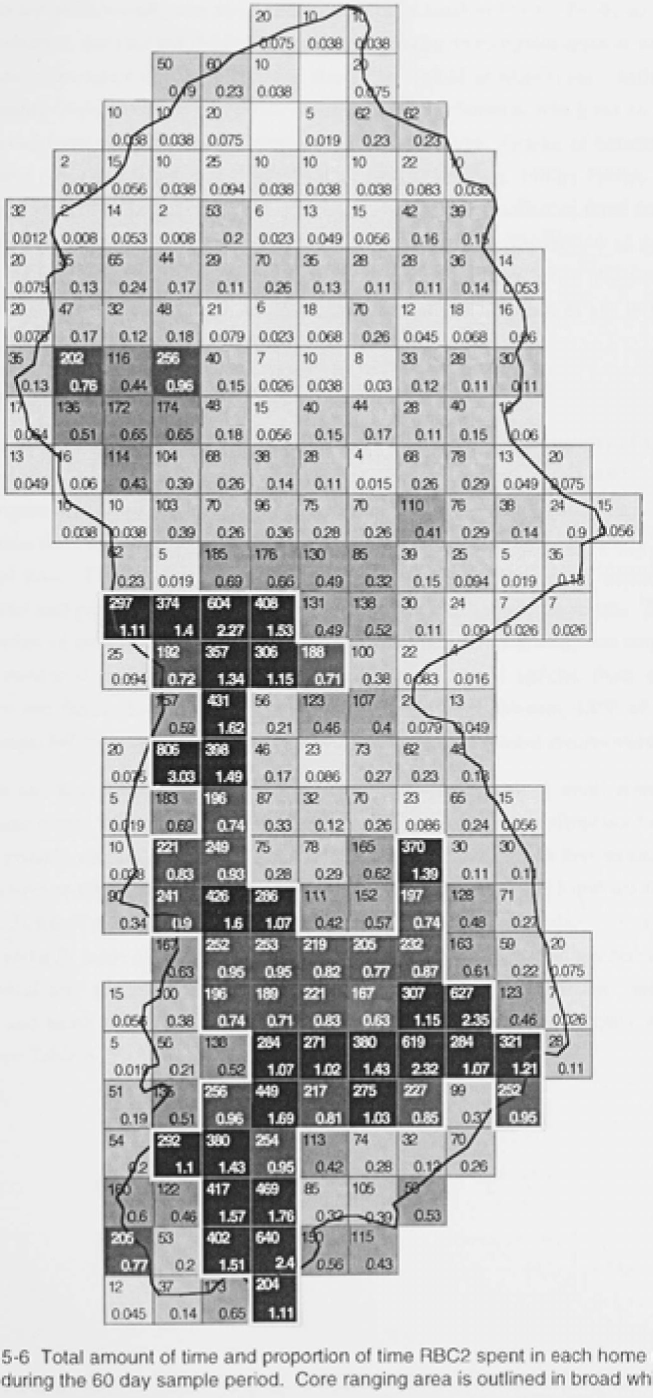
Although figs are an important component of the gibbon diet, it is not surprising that their distribution does not affect home range size. Gibbons do not necessarily prefer figs, usually relying on them during times of low fruit availability (Leighton and Leighton, 1983 and this study). Food tree proportion is somewhat more critical, particularly as the great majority of these are likely to be fruit sources. It has already been mentioned how fruit availability affects DRL and in the next section its role in the use of the home range will be discussed. If gibbons reside in a habitat that is low in either food species density or food production, the establishment of a larger home range is essential. It enables gibbons to cater for their selective dietary habits and ensures a wide(r) range of food items. While food tree density is comparable, if not higher, than that found at other research sites (see Table 5-9 for food tree density in primary forest), rates of food production are low (Kim McConkey, 1998 pers. comm.). It thus appears that diminished habitat quality, in terms of reduced food productions, is the crucial influential factor in the establishment and maintenance of sizeable home ranges at Rekut.

5.6 Differential use of the home range

Quadrat use frequency has been previously calculated as the number of visits to, or the time (total and mean duration) spent in, each quadrat. However, the number and mean duration of quadrat visits may be poor or even biased indicators of quadrat use frequency. To explain unevenness in home range utilisation, environmental factors such as food abundance or the presence of tree species suitable for sleeping or singing have been proposed as potential influences on ranging patterns (Chivers, 1974; Struhsaker, 1974; Gittins, 1979; Marsh, 1981b; McKey and Waterman, 1982; Whitten, 1982b; 1982c; Harrison, 1983a; Chapman, 1988; Barton et al., 1992; Henzi et al., 1992; Newton, 1992; Mturi, 1993). Thus, primates are effectively selecting quadrats for their provision of required or preferred environmental features. Totalling the number of visits to a quadrat does not necessarily denote its importance (as a visit may not always result in an extended stay) nor does it mean that the quadrat was entered for a specific purpose (e.g. the presence of a quality food source). Indeed, often visited quadrats may simply lie on the pathway between choice foraging sites or regularly used night trees (Harrison, 1983a). Mean duration times can potentially distort the detection of commonly used areas of the home range as rarely (i.e. once or twice) visited quadrats may have artificially high values not representative of their overall use. Such high values were calculated for some of the peripheral quadrats of RBC2's home range.

Quadrat usage can be estimated in three ways – total time spent in each quadrat, average time spent visiting a quadrat, and the total number of visits to each quadrat. The first method is the preferred tool but, before analysis could be started, it was important to detect whether these three indicators of quadrat usage were actually related. Correlation coefficients implied they were. The total time spent in each quadrat was significantly correlated with both the total number of entries (r_s=.888 n=233 p<.0001) and the average time spent visiting each quadrat (r_s=.676 n=233 p<.0001) but only a weak correlation was found between visit number and mean duration of visit (r_s=.305 n=233 p<.0001).

The distribution of time spent in each of the quadrats is illustrated in Figure 5-6. Thirty-five quadrats, representing 15.0% of the home range, accounted for approximately 50% of RBC2's time while 75.0% of occupancy records were concentrated in 32% (75 quadrats) of the home range. In contrast, just under half (47.9%) of the home range was utilised only 10 % of the time. A core area of 50 quadrats or 12.5 ha was located in the bottom half of the home range and accounted for 60.5% of all occupancy records. Rather than consisting of a compartment of quadrats utilised at an even intensity, RBC2's core area was composed of three sections of high intensity use connected by corridors of moderate intensity use. These corridors delineate pathways the group frequently employed to visit key sections of the core area and less favoured parts of the home range, but they also served as common foraging trails and thus have been included in the central ranging area.



					20 0.075	10 0.038	10 0.038					
			50 0.19	60 0.23	10 0.038		20 0.075					
		10 0.038	10 0.038	20 0.075		5 0.019	62 0.23	62 0.23				
	2 0.008	15 0.056	10 0.038	25 0.094	10 0.038	10 0.038	10 0.038	22 0.083	10 0.038			
32 0.012	2 0.008	14 0.053	2 0.008	53 0.2	6 0.023	13 0.049	15 0.056	42 0.16	39 0.15			
20 0.075	35 0.13	65 0.24	44 0.17	29 0.11	70 0.26	35 0.13	28 0.11	28 0.11	36 0.14	14 0.053		
20 0.075	47 0.17	32 0.12	48 0.18	21 0.079	6 0.023	18 0.068	70 0.26	12 0.045	18 0.068	16 0.06		
35 0.13	202 0.76	116 0.44	256 0.96	40 0.15	7 0.026	10 0.038	8 0.03	33 0.12	28 0.11	30 0.11		
17 0.064	136 0.51	172 0.65	174 0.65	48 0.18	15 0.056	40 0.15	44 0.17	28 0.11	40 0.15	16 0.06		
13 0.049	16 0.06	114 0.43	104 0.39	68 0.26	38 0.14	28 0.11	4 0.015	68 0.26	78 0.29	13 0.049	20 0.075	
	10 0.038	10 0.038	103 0.39	70 0.26	96 0.36	75 0.28	70 0.26	110 0.41	76 0.29	38 0.14	24 0.9	15 0.056
		62 0.23	5 0.019	185 0.69	176 0.66	130 0.49	85 0.32	39 0.15	25 0.094	5 0.019	36 0.14	
		297 1.11	374 1.4	604 2.27	408 1.53	131 0.49	138 0.52	30 0.11	24 0.09	7 0.026	7 0.026	
		25 0.094	192 0.72	357 1.34	306 1.15	188 0.71	100 0.38	22 0.083	4 0.016			
			157 0.59	431 1.62	56 0.21	123 0.46	107 0.4	21 0.079	13 0.049			
		20 0.075	806 3.03	398 1.49	46 0.17	23 0.086	73 0.27	62 0.23	48 0.18			
		5 0.019	183 0.69	196 0.74	87 0.33	32 0.12	70 0.26	23 0.086	65 0.24	15 0.056		
		10 0.038	221 0.83	249 0.93	75 0.28	78 0.29	165 0.62	370 1.39	30 0.11	30 0.11		
		90 0.34	241 0.9	426 1.6	286 1.07	111 0.42	152 0.57	197 0.74	128 0.48	71 0.27		
			167 0.63	252 0.95	253 0.95	219 0.82	205 0.77	232 0.87	163 0.61	59 0.22	20 0.075	
		15 0.056	100 0.38	196 0.74	189 0.71	221 0.83	167 0.63	307 1.15	627 2.35	123 0.46	7 0.026	
		5 0.019	56 0.21	138 0.52	284 1.07	271 1.02	380 1.43	619 2.32	284 1.07	321 1.21	28 0.11	
		51 0.19	136 0.51	256 0.96	449 1.69	217 0.81	275 1.03	227 0.85	99 0.37	252 0.95		
		54 0.2	292 1.1	380 1.43	254 0.95	113 0.42	74 0.28	32 0.12	70 0.26			
		160 0.6	122 0.46	417 1.57	469 1.76	85 0.32	105 0.39	58 0.53				
		205 0.77	53 0.2	402 1.51	640 2.4	150 0.56	115 0.43					
		12 0.045	37 0.14	173 0.65	204 1.11							

Figure 5-6 Total amount of time and proportion of time RBC2 spent in each home range quadrat during the 60 day sample period. Core ranging area is outlined in broad white line.

Gibbons do not differentially use their home range on a random basis. To do so would be counter-productive, denying the resident group both an ability to recognise areas of importance and a means of ascertaining which sections should be visited at what times. Influencing a group's ranging decisions are a composite of environmental features which act to attract or deter the group from regularly using various regions of the range. Grades of habitat type can direct primate range use (Caldecott, 1980; Marsh, 1981b; Whitten, 1982c; 1982d; Harrison, 1983a; Chapman, 1988; Barton et al., 1992; Newton, 1992) and the effect of three forest types on RBC2 ranging behaviour forms the first level of analysis. The distribution of appropriate food, night and singing trees are other known determinants (Gittins, 1979; Whitten, 1982c; Harrison, 1983a; Isbell, 1983; Chapman, 1988; Barton et al., 1992; Henzi et al., 1992 but see Struhsaker, 1974) and each will receive individual attention.

5.6.1 Influence of habitat type

A relatively consistent vegetational composition characterised the great majority of the habitat within which RBC2 has established its home range. Ninety one percent of RBC2's ranging area encompassed primary dipterocarp forest (Figure 5-7), consisting mostly of *Shorea* and *Dipterocarpus* trees interspersed with a wide variety of other tree species, including important gibbon food taxa. Two smaller areas of somewhat different vegetation lay adjacent to the primary forest and parts of these had also been incorporated into the home range. The south-western portion of the range, accounting for 2.9% of the total ranging area, was composed of secondary rainforest in which *Cratoxylum glaucum* and various species from the genus *Macaranga* and family Euphorbiaceae predominated. In the north-east, 6.0% of the range covered a larger belt of heath forest where mostly *Shorea* spp. and related species were found.

Despite the fact that secondary and heath forest accounted for only a small proportion of RBC2's home range, it was still worth investigating the effect, if any, differential forest types had on the group's ranging patterns. Habitat selection and avoidance was first measured using Jacob's preference index (Jacob, 1974; Barnes et al., 1983; Newton, 1992 and see formula in Section 5.2.3) where a P*i* value of +1 indicated complete selection, a P*i* value of 0 indicated no preference and a P*i* value of -1 indicated total avoidance (Newton, 1992 and see Section 5.2.3). Both temporal and spatial measures of habitat selection found that gibbons selected for secondary and heath forest less than expected and primary forest very slightly more than expected (see Table 5-7).

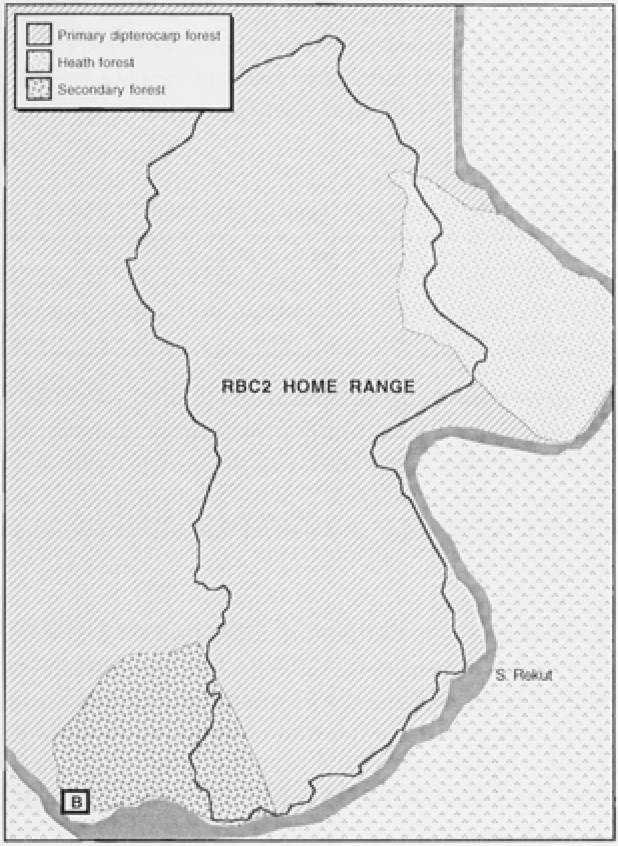


Figure 5-7 Distribution of primary, secondary and heath forest in and around RBC2's home range.

Table 5-7 Selection for forest types I (Jacob's preference index – Jacob, 1974).

Forest type	Jacob's preference index	
	Preference (No of entries)	Preference (Duration of total visits)
Primary forest	+ .006	+ .027
Secondary forest	- .089	- .107
Heath forest	- .365	- .579

P*i* = +1 = complete selection; 0 = no preference; -1 = total avoidance

To determine the accuracy of the first method, a second measure of habitat selection was derived from Harrison (1983a). Once again, spatial and temporal use of forest types were determined but this time for monthly range patterns to give an overall value (see Table 5-8 for overall results). Spatial selection ratios indicated that gibbons selected for primary forest over secondary and heath forest, especially the latter, and these ratios were significantly different (H=14.35 d.f.=2 p<.0001). However, indices for primary and secondary forest type selection did not differ that markedly and in some months the group did range more often than expected into both secondary and heath forest. A further confounding factor stemmed from results pertaining to temporal selection. In contrast to spatial use of the home range, gibbons did not select for primary forest, actually preferring to spend slightly longer periods of time in secondary forest.

Table 5-8 Selection for forest types II (Spatial and selection ratios – Harrison, 1983a).

	Spatial selection ratios	Temporal selection ratios
Primary forest	1.037	0.999
Secondary forest	0.963	1.068
Heath forest	0.456	0.860

These results indicate that while gibbons select for primary forest in relation to heath forest, only minor differences exist between their spatial and temporal use of primary and secondary forest types. Caldecott (1980) and Whitten (1982c; 1982d), investigating the effect different grades of habitat had on the ranging behaviour of *lar* and Kloss gibbons respectively, found that the primary influential factors were the structural indices of the resident trees and the distribution of food resources. In an attempt to explain why gibbons did not range into areas of high elevation, Caldecott (1980) determined that, with increasing altitude, forest structure at Gunung Benom in West Malaysia altered so that trees became more densely packed and on average had smaller girths and a shorter stature. Furthermore, floristic diversity also decreased with the increase in elevation, associated with a predicted decline in food productivity and availability. Whitten (1982c; 1982d) examined the forest within which Kloss gibbons were known to inhabit and found that although different grades of forest did not affect the overall use of the home range they did influence where specific maintenance activities (e.g. feeding, singing and travelling) occurred. For example, forest types composed of a larger proportion of tall trees correlated significantly with the density of female song trees while areas where a higher contribution of potential food sources existed induced gibbons to spend longer periods of time feeding there. To explain the apparent avoidance of heath forest but the absence of a marked difference in primary and secondary forest use, structural characteristics and food abundance in the three forest types is examined.

In terms of physical formation, heath forest represented a habitat potentially unsuitable for gibbon locomotion. Trees were densely packed together (a common feature of this forest type – Whitmore, 1984; MacKinnon et al., 1996) and presented an area with a less than ideal pattern of substrate spread for brachiatory locomotion. The structural components of secondary forest, however, also seem inappropriate for quick and effortless arboreal movement. Tree density was higher and basal area/ha lower, suggesting that a substantial proportion of resident trees in secondary forest were either smaller and/or more flimsy or that the canopy was discontinuous. A purely visual interpretation also distinguished inconsistent and scattered tree dispersion, particularly in the section lying outside the home range, with a preponderance of small trees and regular gaps in the canopy.

The availability and abundance of food species in each forest type at Rekut better correlates with the pattern of range use. In all taxonomic categories, primary forest tree composition was far greater than that found for either secondary or heath forest (Chapter 2), over double the number of species occurring in primary forest compared to minor habitat types. A reduction in floristic diversity could limit the number of potential food species available to a foraging animal and hence restrict visitation to food poor habitats. Comparing known dietary species and genera to their proportional representation in each of the forest types found poor food species representation in heath forest but did not detect any major differences between primary and secondary forest (Table 5-9). In fact, the density of food trees/ha in secondary forest was actually considerably larger (224 trees/ha) than it was in primary forest (126.9 trees/ha). *Pternandra*, *Artocarpus* and *Adinandra*, all relatively common food species in RBC2's diet and foods relied upon throughout the year (this study and McConkey, 1998 unpubl.), were well represented in secondary forest and the group could have chosen to range into this section to access these food sources. A more rigorous testing of the relationship between habitat type use and food source diversity selected the ten to forty most important food species in RBC2's diet and measured their contribution to each forest formation in terms of number of food trees/ha, % of overall basal area and food abundance. Each of these measures indicated that food species were more widely available in primary forest (Table 5-9), particularly in relation to heath forest.

Table 5-9 Vegetational characteristics of primary, secondary and heath forest formations in RBC2's home range.

Forest types	Proportion, density and percentage basal area for food trees				Top 10 known food species			Top 20 known food species		
	No of food trees	% of plot trees	Density (no/ha)	% of total BA	Density (no/ha)	Basal Area	% of total BA	Density (no/ha)	Basal Area	% of total BA
Primary forest	222	27.1	126.9	46.4	5.7	4.056	0.16	14.9	15.564	0.60
Secondary forest	280	39.9	224.0	71.5	1.6	1.053	0.01	12.8	22.989	0.29
Heath forest	71	13.6	100.0	4.2	0	0	0	2.0	0.013	0.01

Forest types	Top 30 known food species			Top 40 known food species			Food abundance (Total BA/size of plot area)			
	Density (no/ha)	Basal Area	% of total BA	Density (no/ha)	Basal Area	% of total BA	All food trees	Top 10	Top 20	Top 30
Primary forest	18.9	19.020	0.73	31.4	53.439	2.06	0.07	0.0003	0.0009	0.0011
Secondary forest	15.2	24.370	0.31	18.4	25.983	0.33	0.45	0.0001	0.0018	0.0019
Heath forest	8.0	0.393	0.18	10.0	0.411	0.19	<0.01	0	<0.0001	0.0001

Heath forest is further disadvantaged by low productivity and the excessive concentration of secondary compounds in some plant items (Whitmore, 1984; MacKinnon et al., 1996). To combat the low yield in plant item production induced by poor soils and the resultant decimation of these items by residential fauna, plants generate substantial levels of phenols, tannins and other compounds that are either toxic or unpalatable to most consumers. Being a frugivorous primate, gibbons lack the digestive ability to cope with more than finite levels of secondary compounds and much of the heath forest plant items would therefore be digestively unacceptable.

Food species distribution appears to be an important factor in forest formation use. RBC2 visited and spent more time in those forest types that were composed of a substantial number of preferred (primary forest) or supplementary (secondary forest) food plants. In contrast, heath forest offered little in food source diversity and thus gibbons only used the part of the range covering this forest type on an occasional basis. Structural characteristics of the forest substrates probably had some influence on ranging too, despite the inconsistent relationship with selection ratio values. Of course, if faced with less than optimal conditions, gibbons will occupy areas largely composed of heath or secondary forest. Hybrid groups across the Rekut river and east of the main research site inhabit ranges that incorporate significant tracts of heath forest (personal observation; Kim McConkey, 1998 pers. comm.). Between Teluk Jolo and Muara Joloi, agile gibbons have colonised forest only recently recovered from logging (personal observation; Rupert Ridgeway, 1995 pers. comm; Marija Dumancic, 1997 pers. comm.) and Müeller's gibbon are found in particularly poor regions of secondary forest surrounding Loksado in South Kalimantan (Allan Williams, 1998 pers. comm.).

5.6.2 Influence of the distribution of food sources

The previous section indicated that food source availability influenced RBC2's use of different habitat types, but did distribution within the home range affect overall ranging behaviour? Food sources were well spread out over the range but only 60.5% (n=141) of quadrats received feeding visits (Figure 5-8). Even so, the pattern of range use held a strong relationship with the location of food species (r_s=.724 n=233 p<.0001) as it did with the total length of time spent feeding in each quadrat (r_s=.876 n=233 p<.0001).

Fifty-six percent (n=258) of all food sources utilised by RBC2 were found in the core area and feeding visits and duration's tended to be concentrated there. Food source proportion may have simply been a consequence of the time the group spent in this section of the home range but a review of the diet and the position of known dietary items suggests otherwise. Many of the supplement (e.g. *Ficus* spp.) or favoured (e.g. *Artocarpus* spp.) foodstuffs consumed by RBC2 were located in the core area. The group therefore chose to remain in these parts on a regular basis to ensure the successful and consistent exploitation of the food species. Furthermore, the knowledge RBC2 acquired and demonstrated regarding the distribution of food sources would have been quite refined for the core area. If the group could rely on a few key species to complement the majority of the daily diet, the use of known and localised sources represented a ranging and feeding strategy more expedient than one in which a series of energetically and temporally redundant trips are made to distantly located feeding sites.

5.6.3 Influence of sleeping sites

Fifty-six sleeping sites were used by RBC2 over the 72 nights of the observation period. The location of these sleeping sites, and the proportion of sleeping occurrences in each quadrat, are shown in Figure 5-9. Only 46 quadrats (19.7% of all quadrats) were used for sleeping and the position of these sites in the home range showed a significant difference from an even distribution.

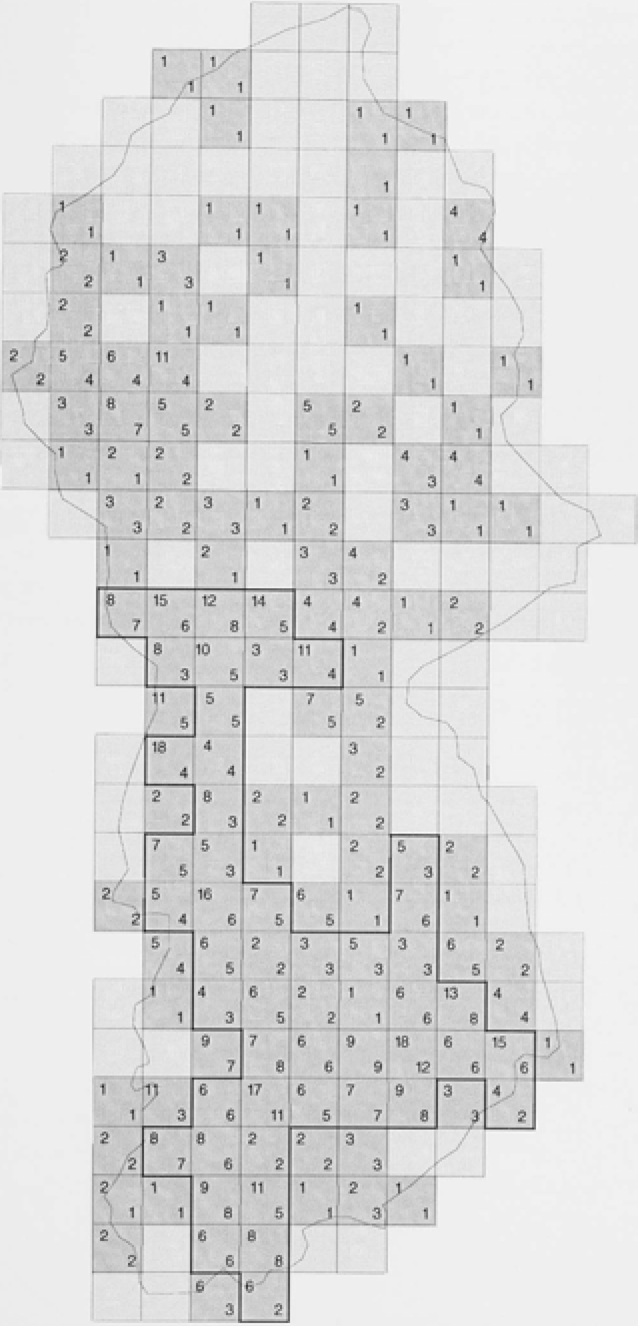


Figure 5-8 Number of visits to, and total number of, food sources located in each of RBC2's home range quadrats. (Number of visits given in top left hand corner of quadrat, number of sources given in bottom right hand corner of quadrat).

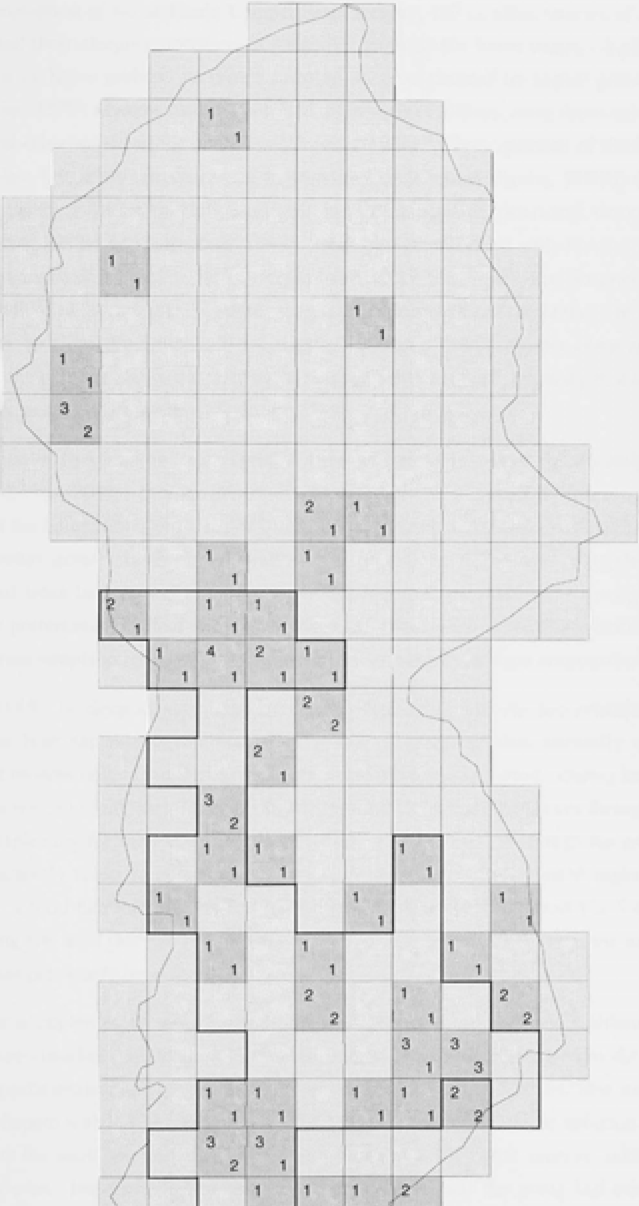


Figure 5-9 Number of visits to, and total number of, night trees located in each of RBC2's home range quadrats. (Number of visits given in top left hand corner of quadrat, number of sources given in bottom right hand corner of quadrat).

With the exception of *lar* at Kuala Lompat (Raemaekers, 1977), other species of gibbon also concentrated their sleeping positions in particular parts of the home range. Agile and some populations of Kloss gibbons preferred sleeping in areas situated on higher ground (Tenaza, 1975; Gittins, 1979) whereas siamang selected night trees in valleys, away from central areas of feeding and other maintenance activities (Chivers, 1974). Three quarters of hoolock gibbon sleeping sites lay on the periphery of the territory (Islam and Feeroz, 1992b) while Kloss gibbons at Paitan and pileated gibbons slept in trees distributed in, or around, the main ranging area (Whitten, 1982c; Srikosamatara, 1984). Both groups of hybrid gibbons showed a pattern similar to *pileatus* and *klossii*. Thirty sleeping sites (53.6% of total) were located within, and 56.9% (n=41) of nights spent in, the core area. Of those night trees outside the core area, 69.2% (n=18) were in close proximity to the boundary quadrats. RBC2 did not often spend nights away from the core area but when they did it was for only one night, returning to a sleeping site in the core area the following day.

Sleeping site location and quadrat visitation time was moderately but significantly correlated (r_s=.507 n=233 p<.0001). Despite this significant association, it is unlikely that sleeping sites in this part of the home range had a major influence on ranging behaviour. Although tree density was somewhat greater in the lower half of the range, the difference in height or foliage thickness of trees in core and non-core areas did not appear considerable enough to induce gibbons to preferentially select night trees there. Gibbons were more likely settling down in core area trees simply in response to spending the great majority of their ranging time there.

A third (30.4%) of sleeping sites were used more than once; one site accommodated retiring gibbons on four separate occasions. The re-use of sleeping sites normally occurred in subsequent months rather than during the same 5-day observation period. During months when a night tree was revisited, the group was following similar foraging pathways through the home range, re-exploiting the same choice fruit sources on a daily basis. Although the group did not normally actively select sleeping spots close to feeding sites, the revisited night trees were adjacent to a food tree the gibbons had been using consistently throughout the 5-day sample. The sleeping site used twice in June 1996 was also used in March when the same neighbouring food tree had previously been fruiting.

Individuals occupied night trees located within 5-20 metres of each other although, on one occasion, the subadult female slept more than one hundred metres away from the rest of her group. Approximately thirty minutes before retirement time, RBC2 became engaged in a territorial dispute with RBC1. Towards the final stages of the conflict, the subadult female lost contact with the adult pair and after briefly visiting a few known fruit sources, selected a night tree on her own. Interestingly, she returned to the sleeping site the group had used the night before, settling down in the tree her father had slept in. Sleeping trees tended to be from the Dipterocarpaceae (e.g. *Shorea*) or Leguminosae (e.g. *Koompassia*) and selected for their height and thick foliage, the latter often making it difficult for the observer to see the gibbons once they had entered the night tree. However, trees of less dense foliage were also chosen, usually by the male who, like hoolock males (Islam and Feeroz, 1992a), sometimes slept in leafless trees. Gibbons positioned themselves in the central part of the tree, lying on their back or sides on horizontal branches or propped up in a sitting posture between two V-shaped branches.

5.6.4 Influence of singing trees

RBC2 used substantially more singing trees, fifty-eight in all, compared to other species of gibbon. Kloss gibbons performed songs from only 30 trees (Whitten, 1982b) whereas moloch and hoolock gibbons utilised just fifteen each (Kappeler, 1984a; Islam and Feeroz, 1992a). Male dawn solos were always delivered from the night tree but the first duet of the day was often given away from the sleeping site as were all male and female morning solos. Thus, despite a significant correlation existing between singing and night tree location (r_s=.388 n=233 p<.0001), the association remained weak. RBC2's tendency to leave the night tree before delivering the morning song meant that the mated pair needed to select additional trees for duetting, accounting for their use of a greater number of singing trees compared to those groups which called predominantly from the sleeping site.

Singing, like sleeping and feeding, was concentrated in the core area, 69.0% (n=40) of singing trees and 73.6% (n=53) of song bouts being located in this part of the home range. The distribution of *moloch* singing trees was similar to that of hybrid gibbons but other species showed differing patterns. *Agilis* employed singing trees scattered throughout the home range (Gittins, 1979) while *hoolock* and *klossii* sang regularly on territorial boundaries (Tenaza, 1976; Whitten 1982b; Islam and Feeroz, 1992b). Thirty-nine percent of singing trees and over half of singing bouts (Figure 5-10) were situated close to the territory boundary with RBC1 and represented areas of previous (Kursani and Mulyadi, 1995 pers. comm.) and observed territorial incursions. Singing trees on the western side of the boundary and directly opposite RBC2's calling sites were often used by RBC1 to countersing with RBC2. Trees more centrally located and closer to the Rekut river, but not on the peripheries of the home range, acted as sites for calling bouts to and with RR1 and RR2. RBC2 sang and responded predominantly to RBC1 and RR1, suggesting that these groups were considered greater threats on territory maintenance than other surrounding groups. A significant correlation exists between singing tree position in the home range and variation in occupancy records (r_s=.515 n=233 p<.0001) and since hybrid gibbons call often (Chapter 8), the location of suitable singing trees probably exerts some influence on ranging behaviour and use of specific parts of the home range.

5.7 Monthly variation in home range use

RBC2 rarely covered more than 50% of the total ranging area over the 5-day sample and, on average, used just 38.7% of the home range (Table 5-10). Follow-up days subsequent to the main observation period did find the group directing travel into new regions, but in no month did they exhibit the routine circulation of the home range area characteristic of other gibbon species (Chivers, 1974; Gittins, 1979). Figures 5-11 and 5-12 illustrates the extension of monthly ranging.

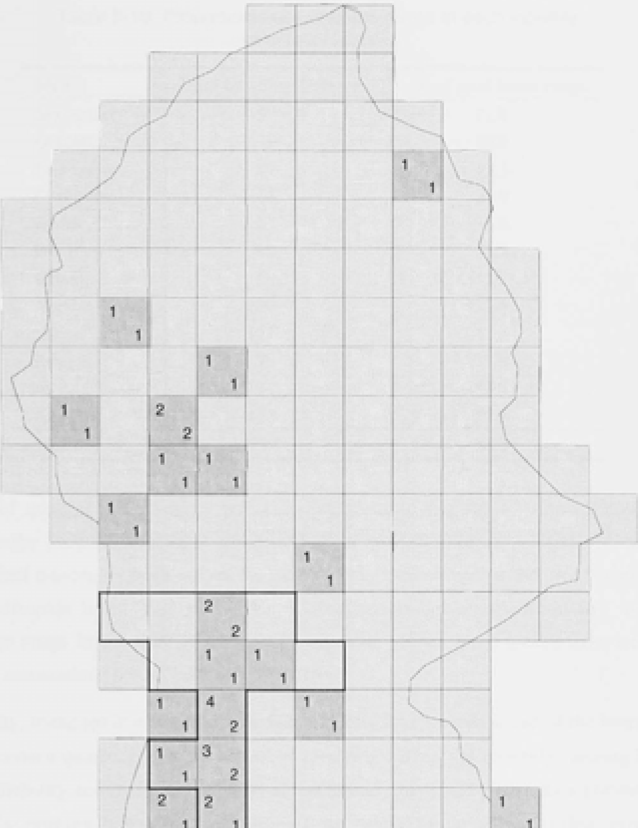


Figure 5-10 Number of visits to, and total number of, singing trees located in each of RBC2's home range quadrats. (Number of visits given in top left hand corner of quadrat, number of sources given in bottom right hand corner of quadrat).

Table 5-10 Proportional use of home range in each monthly observation period.

Month	Total no of quadrats used	% of total home range
September	52	22.2
October	70	29.9
November	99	42.3
December	63	26.9
January	83	35.5
February	66	28.2
March	99	42.3
April	120	51.3
May	111	47.4
June	78	33.3
July	124	53.0
August	123	52.6
Mean	90.7	38.7

An index of quadrat use diversity was calculated employing the Shannon-Weiner index H' where P_i = the proportion of time spent in the *n*th quadrat (Marsh, 1981b). Measures of the index reached reasonably high values for each month, indicating that the group visited areas on a disproportionate basis (Figure 5-13). A comparison between quadrat use diversity, the average day range length and the number of quadrats visited from month to month showed a significant association (W=.857 d.f.=11 p<.001).

Undoubtedly, some environmental factor induced RBC2 to vary their use of the home range and to favour certain quadrats or aggregation of quadrats within the monthly ranging area. Food source availability and dietary composition has already been advocated as a primary influence on RBC2's ranging behaviour and studies on home range use of other primates have demonstrated the strength of diet selection on a troop's movements (e.g. *Colobus* [cf. *badius*] *rufomitratus* – Marsh, 1981b). Its effect on patterns of monthly ranging will be assessed in two ways – the relationship it holds with the changing number of quadrats used each month and the proportion of time spent in the five, ten and fifteen most used quadrats.

The number of food sources consumed at sample times showed no correlation with range use diversity but if those sources eaten off-sample are included in the analysis, the correlation became significant (r_s=.641 n=12 p<.04). Certain dietary food types also correlated strongly, with an increase in quadrat number associated correspondingly with an increase in dietary fruit sources (r_s=.877 n=12 p<.004) and a decrease in young leaf consumption (r_s=-.715 n=12 p<.02).

Quadrats which received extended visits changed not only in location between 5-day samples but in their proportional importance to the total ranging time (Table 5-11). On average, 11.0% of visitation time occurred at the most frequently used quadrat and over half of the group's monthly activity time was spent in the top 15 quadrats. Correlations identical to those performed above produced conforming results (Table 5-12). Both the sample and total number of food sources used in the monthly diet did not hold a significant relationship with the total time spent in important ranging areas. The proportion of fruit in the diet did, however, but only

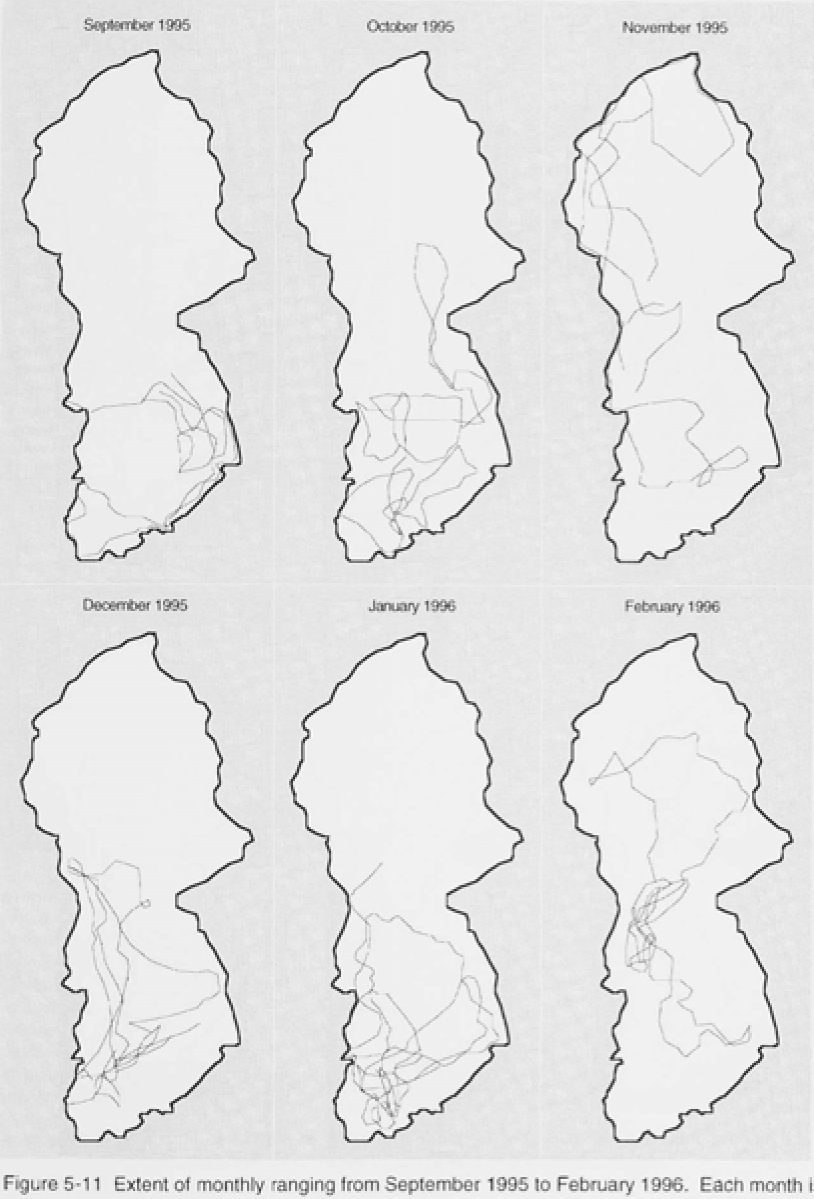


Figure 5-11 Extent of monthly ranging from September 1995 to February 1996. Each month is represented by an observation period of 5 continuous days.

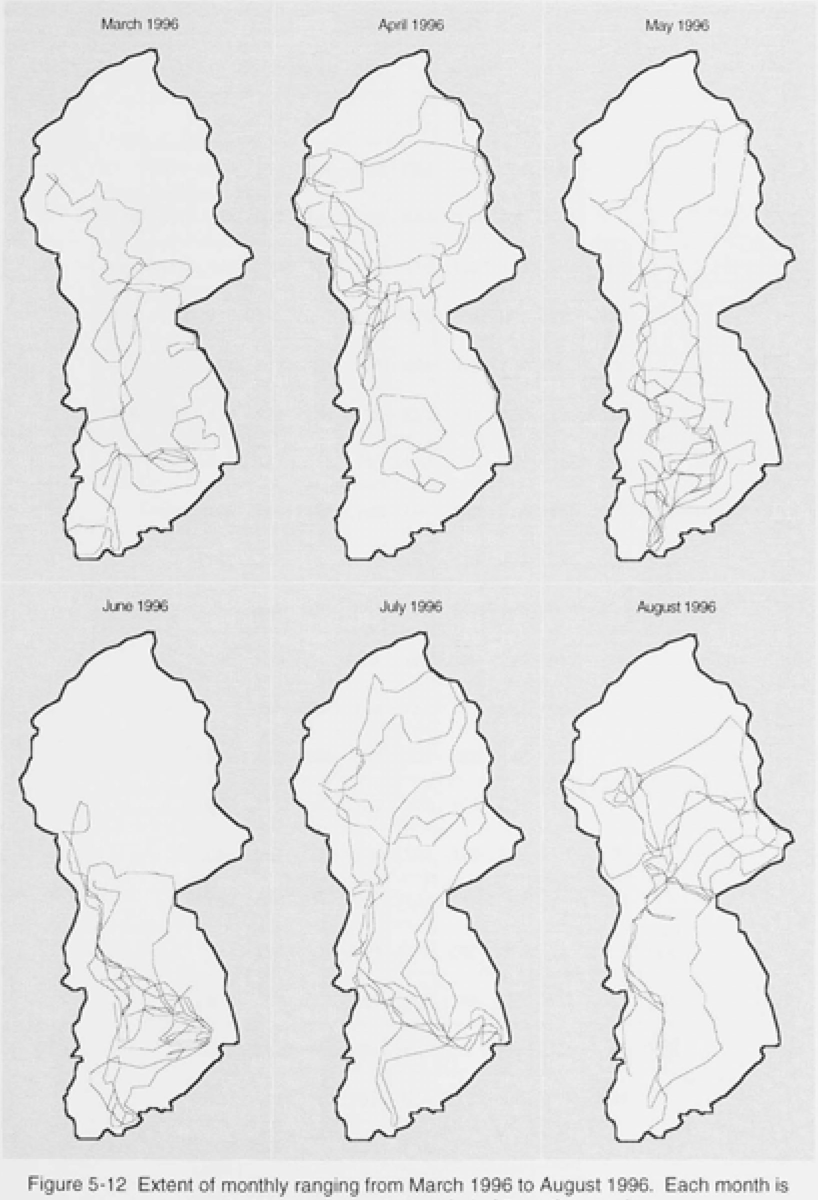


Figure 5-12 Extent of monthly ranging from March 1996 to August 1996. Each month is represented by an observation period of 5 continuous days.

					-.084	-.054	-.054					
			-.137	-.147	-.054		-.084					
		-.054	-.054	-.024		-.137	-.147	-.147				
	-.017	-.070	-.054	-.096	-.054	-.054	-.054	-.090	-.054			
-.110	-.017	-.068	-.017	-.140	-.038	-.064	-.070	-.127	-.123			
-.084	-.115	-.149	-.131	-.105	-.152	-.115	-.105	-.105	-.119	-.068		
-.061	-.150	-.110	-.134	-.087	-.038	-.079	-.152	-.060	-.079	-.073		
-.115	-.090	-.157	-.017	-.123	-.041	-.054	-.046	-.110	-.105	-.105		
-.076	-.149	-.122	-.122	-.134	-.070	-.123	-.131	-.105	-.123	-.073		
-.064	-.073	-.158	-.159	-.152	-.119	-.105	-.027	-.152	-.156	-.110	-.057	
	-.054	-.054	-.159	-.152	-.160	-.155	-.152	-.159	-.156	-.119	-.041	-.070
		-.147	-.033	-.111	-.119	-.152	-.158	-.123	-.096	-.033	-.115	
		.050	.204	.208	.282	-.152	-.148	-.105	-.094	-.041	-.041	
		-.096	-.103	.170	.069	-.106	-.160	-.090	-.017			
			-.135	.339	-.142	-.155	-.159	-.087	-.087			
		-.084	1.459	.258	-.131	-.092	-.153	-.146	-.134			
		-.033	-.111	-.097	-.159	-.110	-.152	-.091	-.149	-.070		
		-.054	-.067	-.029	-.155	-.156	-.129	.199	-.105	-.105		
		-.159	-.041	.326	.031	-.158	-.139	-.097	-.153	-.153		
			-.126	-.021	-.021	-.071	-.087	-.053	-.131	-.157	-.164	
		-.070	-.160	-.097	-.106	-.067	-.126	.070	.872	-.155	-.041	
		-.033	-.142	-.148	.031	.009	.222	.848	.031	.100	-.105	
		-.137	-.149	-.017	.385	-.074	.013	-.059	-.160	-.033		
		-.139	.455	.222	-.021	-.158	-.155	-.110	-.152			
		-.133	-.155	.307	.432	-.158	.620	-.123				
		-.087	-.140	.270	.912	-.141	-.158					
		-.061	-.119	-.122	-.100							

Figure 5-13 Diversity of quadrat use in RBC2's home range. Quadrat use diversity was calculated using the Shannon-Wiener index H'.

with the top 15 quadrats. These correlations, regardless of significance, were all negative. Young leaf consumption varied significantly with visitation time to the top 5, 10 and 15 quadrats but in all cases the relationship was positive.

Table 5-11 Proportion of ranging time spent in important quadrats.

	Proportion of ranging time spent in			
	Most frequently used quadrat	Top 5 used quadrat	Top 10 used quadrat	Top 15 used quadrat
September	10.2	40.8	62.6	77.3
October	8.1	32.5	48.2	59.1
November	6.1	19.3	33.6	46.3
December	10.4	42.6	61.6	71.6
January	15.7	36.1	50.4	60.7
February	24.7	48.9	63.0	72.8
March	10.4	25.3	37.7	47.8
April	7.3	22.2	33.0	41.6
May	10.2	27.0	42.8	54.2
June	5.7	22.1	38.3	50.8
July	10.8	25.0	38.9	49.7
August	12.0	30.1	41.6	50.2
Mean	11.0	31.0	46.0	56.8

RBC2 responded to periods of overall food or fruit abundance by covering larger parts of their home range. But when the availability or consumption of favoured foods declined and young leaves became a primary component of the diet, the group limited their ranging to a smaller area within which certain parts became the focus of occupation time. It has already been shown how changes in fruiting activity and the inclusion of fruit species in the diet correlate positively with activity period length, the proportion of the day spent travelling and DRL. The concordant association between these variables and those of quadrat use diversity (W=.812 d.f.=11 p<.001) implies that these variables are closely related and are, in turn, affected by a combination of food production and diet composition.

Table 5-12 Effect of monthly variation in number of food sources and dietary fruit and young leaf content on use of the home range (n=12).

	On-sample no of sources used		Total no of sources used		% of fruit in monthly diet		% of young leaf in monthly diet	
	rs	sig to	rs	sig to	rs	sig to	rs	sig to
Total no of quadrats used each month	.396	=.19	.640	≤.03	.877	≤.004	-.715	≤.02
Time spent in top 5 quadrats	-.272	=.37	-.308	=.31	-.578	=.06	.706	≤.02
Time spent in top 10 quadrats	-.406	=.18	-.483	=.11	-.575	=.06	.627	≤.04
Time spent in top 15 quadrats	-.406	=.18	-.497	=.10	-.598	=.05	.634	≤.04

5.8 Discussion – habitat quality, diet and patterns of ranging

Establishing a home range provides the resident with a comparatively fixed area of occupation in which the conduct of maintenance activities can be achieved with relative ease. Where and in what form the home range is secured depends on a myriad of social and environmental elements which interact further to influence the way the resident uses its domicile and to direct the variable patterns of movement responsive to different socio-ecological constraints. Day range length, home range size and differential use of the area of occupation are inter-related parameters of hybrid gibbon ranging behaviour. While demographics, inter- and intra-specific competition, and weather undoubtedly influence these, it is the quality of the habitat which induces the most consistent and obvious effect. The mechanics of the primary form of locomotion (i.e. brachiation) and the specifics of the diet (largely frugivorous and selective) are characteristics identified as key hylobatid requirements the habitat needs to cater for.

Ideally, an arboreal, brachiating animal requires a suitable representation of supports strong enough to hold the weight of an adult and a dispersion of substrates that allow the easy, but not cramped, negotiation of inter-tree distance. Secondary forest surrounding the home ranges of RBC2 (and RBC1) did not provide these essential features, or at least not in a consistent fashion, and thus gibbons based their ranging activities in areas structurally more appropriate. A selective diet concentrating on fruit, in turn, directed the gibbons to focus their range use on areas where tree species diversity was greatest and the proportion of potential food sources highest. Heath forest, while structurally adequate for a group of gibbons, provided a poor selection of items that were either known food sources or palatable to hylobatids. Therefore, it was mostly avoided.

Within the preferred habitat type, the location of trees suitable for singing and sleeping were both associated with ranging behaviour. However, it was the distribution of food trees, the availability of food items and the diet itself which influenced the group's selection of primary or core ranging areas and the changing patterns in range use. When the yield and dietary composition of ephemeral items such as fruit was high, gibbons extended the distances they travelled each day and visited a larger part of the home range. A decline in fruit productivity and the reliance on food types nutritionally less desirable but more evenly dispersed found gibbons restricting their movements to small sections of the range and covering shorter distances during the activity period.

The relationship between food availability and consumption and ranging remains unclear. One interpretation advocates the nutritional content, or more precisely, the energetic potential of the food type. Fruit is a better source of energy than young leaves and a gibbon correspondingly apportions its activity time to energetically demanding behaviours such as ranging (travelling) depending on dietary content. A diet composed mostly of fruit equips a gibbon with the energetic capacity to travel further distances. But when a poor fruit harvest leads to the substitution of fruit by young leaves, the best strategy is to conserve what energy can be gleaned from the inferior diet, limit the time engaged in energetically expensive activities, and restrict ranging to manageable distances.

Alternatively, the dispersal pattern of food types directs group movements. The importance of fruit in the diet of many rainforest animals, and its temporary and short-lived existence as an edible dietary item, requires a vigilant detection and exploitation strategy. The sporadic distribution of fruiting plants obligates gibbons to cover larger sections of the home range so they can locate, monitor and feed from key species. When significant amounts of young leaf are added to the diet, gibbons need not range quite as far since food supply is not as easily exhausted and the distribution is such that gibbons can detect and revisit sources within smaller bands of the home range. Of course, the nutritional qualities of the diet or the ease at which food items can be found are not necessarily mutually exclusive and undoubtedly the two merge to influence range utilisation.

If food and its availability are critical determinants of range use, then the quality of the home range itself (i.e. the proportion of potential food species and their productivity) should be the primary influence on the size of the ranging area. RBC2 and RBC1 had two of the largest ranges measured for study populations of gibbons, a response to the habitat's reduced capacity to provide an adequate variation in fruit sources. The limited number of dietary fruit items affects all resident frugivores, not just gibbons, inducing the potential for intense interspecific feeding competition if it does not exist already. I observed no overt competition but McConkey's (1999) research does suggest that some animals, in particular squirrels, could affect disruption to gibbon food supply, further necessitating the maintenance of a large home range.

6

Territorial Behaviour and Inter-Group Encounters

6.1 Introduction

6.1.1 Concepts of gibbon territoriality

Within the more flexible confines of the home range a primate group may establish an area of exclusive use which neighbouring conspecifics are prevented from entering. Inter-group competition over limited resources induces the formation of these areas or "territories" but their exclusivity depends on whether the benefits of extracting these resources outweighs the costs of active and regular defence (Brown, 1964). The economic defendability of a territory is related to the size of the ranging area (Dunbar, 1988). Any increase in the size of the ranging area normally corresponds with a rise in the number of potentially exploitable resources but also with a decrease in the ability to expel invading groups. It thus follows that the maintenance of a territory is likely to evolve if, and only if, an individual or group is able to locate range boundaries, and hence intruders, on a regular basis.

Using an index of defendability, which relates day range length to the overall home range size, Mitani and Rodman (1979) investigated the importance of "mobility" in the adoption of territoriality. Primate species lacking mobility about the range (i.e. those unable to frequently reach the peripheries of ranging areas in the course of their daily travels) never exhibited territorial behaviour while the majority of mobile species did. Some non-territorial species, however, were also found to be mobile, indicating that while mobility is necessary for territoriality it is does not inevitably lead to it.

Concepts of primate territoriality have extended from avian models in interpreting territorial defence as a means of ensuring access to food sources. However, to parallel the evolution of a behavioural mechanism between two such diverse groups of animals as primates and birds makes not only the erroneous assumption that both experience similar biological constraints, but also implies similar causes for the behavioural response (Ralls, 1977). Some primate species probably do defend territories to protect limited food supplies but alternatively, and in particular reference to monogamous primates, the critical resource worth defending, it has been argued, may in fact be the reproductive partner (Dunbar, 1988; van Schaik and Dunbar, 1990). The evidence Dunbar (1988) has presented in support of the mate defence theory incorporates five key behavioural observations which either negate the resource-defence theory (Points 1 - 3) or promotes the use of behaviours consistently displayed by territorial animals and proposed to protect the pair bond (Points 4 - 5). Dunbar (1988) argued that:

1. During times of critical food shortage, when the protection and securing of food resources is at its most imperative for group fitness, territorial behaviour actually disappears.
2. Competition between groups for food resources, even in non territorial primates, is never as intense as that existing within the group.
3. Some primate species who subsist on a largely folivorous diet still hold and defend territories despite the less patchy distribution and almost consistent availability of the primary dietary item.
4. Behaviours such as singing, which were initially proposed to aid in territorial defence, now appear to be a means by which a pair advertises their bonding status.
5. Primates exclusively direct their territorial behaviour at a same-sex intruder.

Like other territorial animals, gibbons retain an area within the home range which they exclude other gibbons from using. The defence of this territory is not excessively vigilant since gibbons show no evidence of patrolling behaviour or relentless visitation to peripheral areas (Chivers, 1974; Gittins, 1979; 1980; Whitten, 1982c; Islam and Feeroz, 1992a; 1992b). Gibbons, instead, demonstrate their territoriality through inter-group conflict and, primarily, the production of audible and frequently delivered songs. Experiments with play-back recordings (Mitani, 1984; 1985a; 1985b; 1987a; 1987b; Raemaekers et al., 1984; Raemaekers and Raemaekers, 1985) and field observations of inter-group encounters (Brockelman and Srikosamatara, 1984), however, now suggest that male and female gibbons sing to defend their "own personal space…for completely different reasons" (van Schaik and Dunbar, 1990).

The primary findings of both play-back experiments and field studies indicate that while the female song is related to defence of the physical territory and/or her partner (see Cowlishaw, 1992 and Chapter 8), the male sings to protect his mate from the unwanted advances of an intruding male. Contribution and intensity of aggression by the sexes at inter-group encounters uphold the differential motives for territorial behaviour (Carpenter, 1940; Ellefson, 1974; Chivers, 1975; Tenaza, 1975; Gittins, 1979; 1980; Brockelman and Srikosamatara, 1984; Islam and Feeroz, 1992a; Ahsan, 1994). Females participate to some extent in boundary disputes but compared to males their role is secondary and not as antagonistic (but see Tenaza, 1975 and Mitani, 1985b). Neighbouring groups are of minimal threat to a female gibbon as they are almost certainly territory holders and hence less likely to attempt procurement of her territory (the dear enemy effect – Getty, 1987). To the resident male, however, the presence of a male on the territory border constitutes a greater risk because, although actual loss of a mate to an intruding male is rare, extra-pair copulations and/or infanticide may result (Cowlishaw, 1992).

6.1.2 Outline of Chapter 6

To retain a format consistent with that of the previous chapter, the size and use of the territory proper receives initial attention. In Section 6.3.1 the degree of home range overlap is discussed followed by an estimation of the territory size for groups RBC1 and RBC2. A review of overlap and peripheral quadrat visitation is conducted in Section 6.3.2 to detect whether the focus group (RBC2) engaged in vigilant or only casual observance of its range boundaries.

The role of inter-group encounters in the preservation of integral range areas forms the second part of the chapter. Encounters are divided into three primary types – chance, ritual and intense – and are discussed in relation to duration, degree of aggression, and socio-ecological context (Sections 6.4 to 6.5).

The final section (Section 6.6) describes an aberration from "normal" encounter behaviour and addresses the context or motive influencing differential responses given by both residents and invaders during intense inter-group contact.

6.2 Methods

6.2.1 Home range overlap and size of the territory

Range paths of adjacent groups and the sites of inter-group encounters were plotted on to previously constructed home range maps. Territory borders were delineated by locating inter-group encounter on range maps and running a line along these points.

The area lying between the home range and territory boundaries of the resident group formed the overlap zone, the size of which was estimated by counting the number of constituent quadrats and converting to hectares using the method outlined in the previous chapter. In turn, the size of the territory was measured by summing the number of quadrats enclosed within the new border and calculating the area in hectares.

6.2.2 Description of inter-group encounters

To describe the inter-group encounter accurately and to ascertain the underlying socio-ecological context, continuous note taking, rather than 10 minute sample observations, constituted the method of data collection.

An inter-group encounter commenced when one or both participatory groups noticed the presence of another in the immediate area and reacted by either singing and/or approaching the other group. The time at which the encounter started was immediately noted, as was the identity of the disputing groups, the location of the encounter and any apparent antecedent to the dispute (e.g. a fruit source). Throughout the duration of the encounter, measured using a stopwatch, the individuals involved, the roles they played and the behaviours they adopted were methodically described, including any change to the behavioural response of a participant (e.g. the adult female retiring from a combative to a singing response). As it was impossible to observe all animals at once, particularly during multiple chase-and-strike attacks, field guides were enlisted to aid in the collection of encounter descriptions. While one of us wrote, the other two outlined the chain of events taking place.

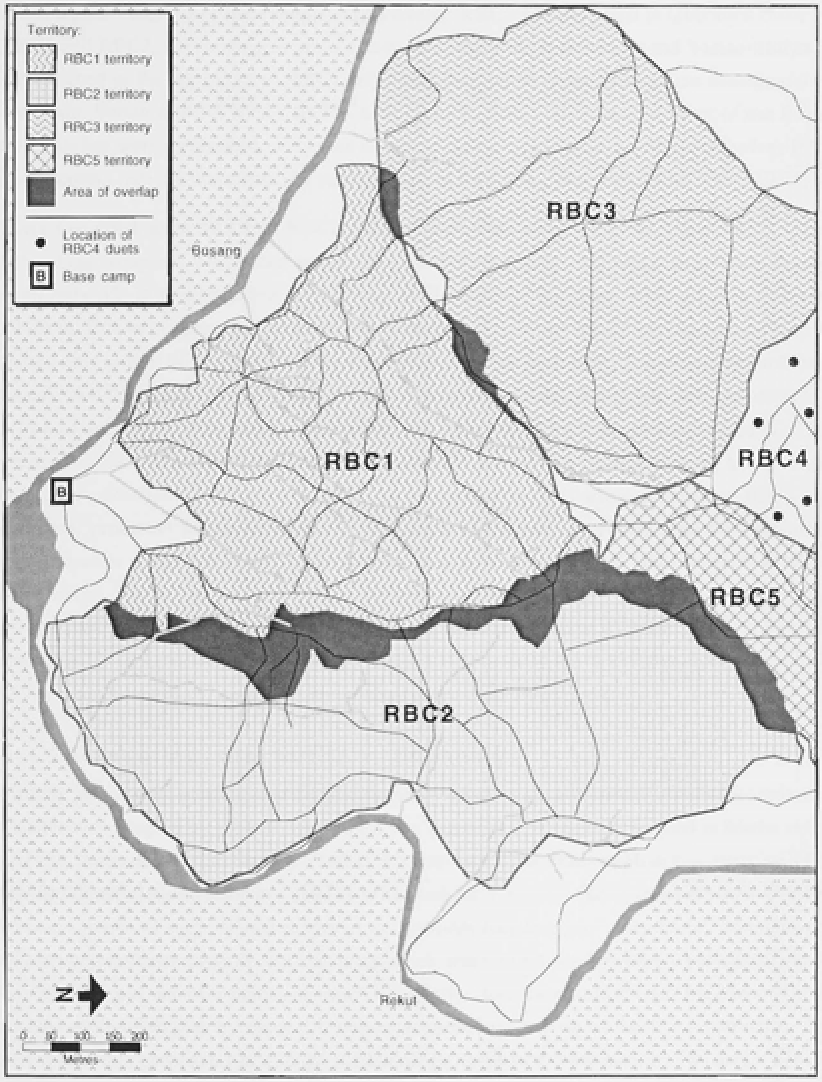


Figure 6-1 Territory boundaries of groups RBC1, RBC2, RBC3, and RBC5. Shaded areas represent areas of ranging overlap between neighbouring groups.

6.3 The territory

6.3.1 Home range overlap and size of territory

Home ranges of the four groups of gibbons residing in the Rekut research area are shown in Figure 6-1. The two focus groups, RBC2 and RBC1, were located in adjacent home ranges closest to camp, the Rekut and Busang rivers forming a natural barrier to the south-eastern and south-western regions of their ranges respectively. RBC5's home range neighboured those of RBC1 and RBC2, intersecting an area delineated by the trails Jl Bambang and Sopian-Mulyadi. RBC3 lived to the north-east of RBC1, adjoining their home range in a section encompassing the Daun, Surian and Sid-Nancy trails. A fifth group, RBC4, also inhabited part of the Rekut field site but were rarely seen. Previous sightings (Kursani, Mulyadi, Nurdin and Surian, 1995 pers. comm.) indicate they share the southern part of their home range with RBC3 and RBC5.

Forty-five quadrats or 19.3% of RBC2's home range was shared with RBC1 and RBC5. This proportion compares with other species of gibbon (Table 6-1). Home range overlap ranges from only 6% in neighbouring populations of H. moloch (Kappeler, 1981 cited in Chivers, 1984) to 38% in siamang (Chivers, 1974). Fourteen (31.1%) of RBC2 overlap quadrats were shared only with RBC5, thirty (66.7%) with RBC1, and one with both. It must be remembered, though, that the extent of home range overlap is only an estimate. RBC5 was not systematically followed and much of its ranging behaviour was determined from the location of calls. The group was also only semi-habituated, decreasing the probability of detection on home range boundaries (Reichard and Sommer, 1997)[8]. A more detailed study was conducted on RBC1 but continual problems following them for the length of the activity period possibly prevented determination of the full extent of its ranging and, potentially, use of other areas in RBC2's home range. Excluding the overlap zone from the total ranging area of RBC2 gives an area size of 47.25 ha. For RBC1, the area of exclusive use was calculated as 37.4 ha. These respective areas can be conceived as the "territory" (Burt, 1943) or even the "exclusive territory" (Jolly, 1972) as neighbouring groups were never observed to enter this region.

6.3.2 Monitoring the territory boundary

Calling, inter-group clashes, and limited home range overlap, are primary forms of territorial maintenance adopted by gibbons. However, the number of calling trees located in border areas and the frequency of inter-group clashes was neither remarkably high nor suggestive of a territorial population. Chivers (1974) remarked on a similar lack of calling and chasing between groups of siamang and proposed that gibbons may employ "more subtle" mechanisms of territory defence such as visiting peripheries more often, or for longer periods of time. Gibbons do not actively patrol territory boundaries like chimpanzees but may enter these regions more often than by chance to ensure territorial incursions are kept to a minimum. To investigate this proposal, I employed methodology developed previously by Harrison (1983b) and Chivers (1974).

---

[8] Reichard and Sommer (1997) have argued that accurate measurement of home range, overlap zone and territory size can only be achieved if all neighbouring groups are habituated. Unhabituated animals are less likely to be detected by human observers, leading to a respective over- and underestimation of focus and non-focus group territory size. Home range overlap between neighbouring, habituated groups of *H. lar* at Khao Yai was estimated at between 64.3% to 74.4% of a group's home range. This indicates that only a third of the home range can be considered an area of exclusive use (data from Neudenberger, 1993 cited in Sommer and Reichard, in prep).

Table 6-1 Territory size for pure and hybrid populations of gibbons.

Species	Study Site	Territory		Source
		Mean (ha)	% of home range	
H.a.albibarbis x H. muelleri	Barito Ulu, Central Kalimantan, Indonesia	47.31 37.42	81.6 76.0	This study
H. agilis	Sungai Dal, West Malaysia	22	76.0	Gittins, 1979, 1982
H. hoolock	Lawachara and Chunati Wildlife Sanctuary, Bangladesh	32	91.0	Islam and Feeroz, 1992a; 1992b
	Lawachara, West Bhanugach Forest Reserve, Bangladesh	29 73	70.7 84.9	Ahsan, 1994
H. klossii	Sirimuri, Siberut Island, Indonesia	2 - 3	-	Tilson, 1981
	Paitan, Siberut Island, Indonesia	21	64.0	Whitten, 1982c, 1984b
H. lar	Kuala Lompat, West Malaysia	11	75.0	Raemaekers, 1979
	Khao Yai, Thailand	15.8* 16.0 19.5	64.3 74.4 73.6	Reichard and Sommer, 1997; Sommer and Reichard, in prep.
H. moloch	Ujong Kulon, Java, Indonesia	16	94.0	Kappeler, 1981 cited in Chivers, 1984
H. muelleri	Kutai, East Kalimantan, Indonesia	38	88.0	Leighton, 1987
H. pileatus	Khao Soi Dao, Thailand	27	75.0	Srikosamatara, 1984
H. syndactylus	Kuala Lompat, West Malaysia	26	62.0	Chivers, 1974

* Mean territory size calculated by S.B. from data provided in relevant source.

[1] Territory size for RBC2

[2] Territory size for RBC1

In Harrison's (1983b) examination of territorial behaviour in green monkeys, the use of, and selection for, the *overlap zone* (i.e. the area utilised by more than one group) formed the index of territoriality. RBC2 made four hundred and sixteen visits to the overlap zone for a total of 5150 minutes, representing 19.5% and 19.3% respectively of overall spatial and temporal use (Table 6-2). A measure of whether overlap quadrats were actually used more often than expected was calculated by dividing both the proportion of visits and occupation time by the proportion of the home range the overlap quadrats contributed. Because the overlap zone accounted for 19.2% of RBC2's home range, spatial and temporal selection ratios for the overlap quadrats only reached 1.02 and 1.05, indicating that any selection for the overlap areas is marginal.

Table 6-2 Spatial and temporal selection for overlap zone (after Harrison, 1983b).

Spatial use and selection		Temporal use and selection	
Number of visits	416	Total duration of visits	5150
Use (%)	19.5	Use (%)	19.3
Selection ratio	1.02	Selection ratio	1.05

The frequency of visitation to peripheral areas compared to rates of entry into central quadrats constituted Chiver's (1974) measure of territoriality. Peripheral quadrats were defined as those lying on or adjacent to the ranging boundary and selected in reference to diagrams produced by Chivers (1974). To contrast the defence of the home range and the territory, allocation of quadrats to peripheral and central areas was done for both areas of occupation. Peripheral quadrats bordering the home range received slightly but significantly longer visits than central quadrats but gibbons did not range anywhere near as often into them (Table 6-3). In contrast, little difference was found between visitation time to central and peripheral areas of the territory and the variance between the proportion of central and peripheral quadrats visits was not as great as that found for the home.

Table 6-3 Use of central and peripheral areas of the home range and territory.

Ranging area	Central quadrats		Peripheral quadrats	
	Mean length of visit (minutes)	Proportion (%) of all quadrat visits	Mean length of visit (minutes)	Proportion (%) of all quadrat visits
Home range	11.8	65.9	13.6	34.1
Territory	11.7	54.1	12.6	45.9

Interestingly, RBC2 habitually visited quadrats that separated their ranging area from the home ranges of their neighbour groups but did not make as much effort to travel to peripheral areas adjacent to the Rekut river. RBC2 also significantly used the quadrats they shared with RBC1 much more than those they shared with RBC5. Of the total number of visits and time spent in overlap quadrats, 93.0% and 91.8% were in the RBC1 overlap zone, giving spatial and temporal selection ratios of 1.39 and 1.38 respectively.

Unequivocal support for an overtly *physical* form of territorial defence cannot be concluded from these results but there is some implication that RBC2 monitored the boundary to some extent. For example:

1. A considerable proportion of the overlap zone, particularly in the northern region of the home range, was not well represented by food species, but RBC2 still made relatively frequent visits to the area.
2. The group ranged into quadrats demarcating the territory border not only considerably more often than those lying on the perimeter of the home range but at an overall rate not that dissimilar to central quadrat visitation.
3. RBC2 tended to visit peripheral areas adjacent to the home ranges of neighbouring gibbons. Less time was spent travelling to peripheral quadrats on the southern and eastern side of the territory where the presence of the Rekut river prevented other gibbons from entering RBC2's territory. On the western and northern faces of the ranging area, RBC1 and RBC5 had established their own territories and if incursions were going to occur, this was the area they were going to take place.
4. RBC2 responded to the not insubstantial pressure RBC1 exerted on the integrity of their territory by spending more time in the overlap and peripheral areas that were at risk from RBC1 border crossings. Admittedly, a greater number of quadrats composed the RBC1 section of the overlap region but its close proximity to sections of the core area, and the markedly higher frequency of inter-group encounters with RBC1, were likely to be of greater influence in the direction of movements to this area.

6.4 Types of inter-group encounters and their associated behaviours

Disputes between neighbouring groups of gibbon are primarily stimulated by one or both groups seeing or hearing each other in the overlap zone or on the territory boundary (Gittins, 1979; 1980; Islam and Feeroz, 1992b; Reichard and Sommer, 1997) but the ensuing skirmish does not necessarily follow the same behavioural repertoire. Traditional theories of territorial behaviour imply that dispute location and prevailing ecological conditions influence confrontation strategies, animals appraising each situation to evoke an appropriate response. But if mate defence is a key factor in gibbon territoriality, if only for the adult male, the variation observed in defensive behaviours could instead reflect the risk a particular encounter represents in terms of cuckoldry or mate loss.

The intrinsic role singing plays in gibbon territorial defence has received considerable attention, particularly in the evaluation and attribution of defensive theories. In contrast, previous accounts of confrontations between conspecific groups of primates have been largely or only descriptive. With the exception of papers by Harrison (1983b) and Reichard and Sommer (1997), little attempt has been made to either categorise inter-group encounters or discuss the possible causes for the differences in associated behaviours or levels of aggression. More importantly, they have failed to extend the actualities of encounter behaviour away from a function restricted to the defence of the physical territory. To fill this gap in the current literature, inter-group encounters were categorised to examine the socio-ecological context of this form of territorial behaviour.

Harrison (1983b) classified green monkey inter-group encounters into four primary groups. Using this classification as a template, but modifying or eliminating categories to suit the context and behaviours associated with hybrid gibbon encounters, three distinct types of inter-group encounters could be recognised:

- Chance or "Call and Retreat"
- Ritual – Type I and II
- Intense

Each encounter type was differentiated primarily on the level of aggression and the participatory behaviours of group members but location and duration of the encounters also discriminated the three categories (see Figure 6-2 for location and type of encounter).

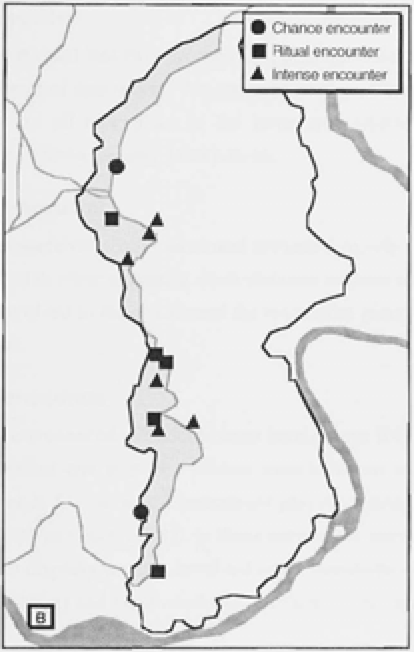


Figure 6-2 Location of chance, ritual and intense encounters between RBC2 and their neighbouring groups.

6.4.1 Chance or "call and retreat" encounter

I observed three chance encounters, one each between RBC2 and RBC5, RBC2 and RBC1 and RBC1 and RBC3. As was the case for green monkeys, these unexpected or "chance" meetings took place in locations one or both groups rarely visited. For example, the encounter between RBC2 and RBC5 occurred on the edges of a large clearing caused by multiple tree falls. Behaviour associated with this type of encounter included duetting, short periods of mutual observation (Reichard and Sommer's [1997] *sit-opposite*) and some approaching. A chance meeting between RBC2 and RBC5 is described below:

24 November 1995 – RBC2 and RBC5

0945: RBC2 are travelling NW and have just entered the overlap zone shared with RBC5. The group suddenly stops and the adult female begins calling. Approximately 40 m away is RBC5, whose adult female has also started to call.

0946: Adult males of both groups edge towards each other as each contribute to his mate's song.

0947: Female and offspring members of both groups turn around and move back in the direction they came from, continuing to call. The males watch and call to each other for another minute.

0948: Both adult males turn around and follow their respective groups.

6.4.2 Ritual encounter

Ritual encounters can be divided into two basic groups, distinguished largely on the duration of the encounter and the degree of aggression. No apparent or observable resource stimulated any of these confrontations but all took place in the same area where intense encounters had previously occurred i.e. on known territorial boundaries.

6.4.2.1 Type 1 ritual encounter

Type 1 ritual encounters were relatively short and consisted mostly of calling and watching. Both groups approached each other to quite a close distance and one or two chases were given. Only adult males were involved in the chases and the residential group gave the final pursuit as they expelled the intruders.

6.4.2.2 Type 2 ritual encounter

Type 2 ritual encounters commenced with duets from both groups followed by a rapid advance once they had caught sight of one another. Chases were common and usually only involved males although the subadult female was a prominent player in those taking place on the 18 March. Peculiar, or perhaps just coincidental, to these encounters were the *taunt* displays of the adult males. These *taunt* displays usually involved some manipulation (e.g. the breaking and shaking of surrounding foliage) and were conducted as close to the opposing male as possible. An example is given below:

8 May 1996 – RBC2 and RBC1

RBC2 and RBC1 have met in south-western section of the overlap area. Duetting started at 0555 but the groups did not meet until 0609. Between 0610 and 0630, RBC1 and RBC2 occupied adjacent trees approximately 10 metres apart. Only females called during this period, brachiating rapidly around their respective trees, while the males watched each other.

0630: The adult males begin a series of taunts and chases. First, AM1 brachiates up to the terminal branches of the tree he is in, reaches across to shake the branches of the adjacent tree, and then brachiates back. The observing male chases the aggressor.

0633: AM2 climbs to the edge of the tree and shakes the branches of the tree AM1 is watching from. He is chased back by the observing male.

0635: AM1 repeats the procedure but is not chased. Remaining on the peripheries, he leans over to shake the branches again. This time AM2 chases him back.

0638: AM2 repeats the branch shaking taunt and immediately retreats when the observing male rushes over to him.

After 10 to 15 minutes of *taunt* displays, one of the males initiates a series of chases, normally by trying to enter the tree the counter group is occupying. Unlike intense encounters (see below), the chaser never gets close enough to strike the fleeing male. Chase series lasted between 4 and 28 minutes and resulted in the repulsion of the invading group. Below is an account of the final stages of the ritual (II) encounter of 8 May 1996:

0640: AM1 attempts to enter RBC2's tree but is repelled by AM2 and SF2.

0644-0645: AM1 attempts to enter RBC2's tree again. RBC2 initially back away but eventually AM2 and SF2 chase him out. Behavioural sequence repeated again.

0646: AM1 succeeds in entering the peripheral part of RBC2's tree, threatening the resident group by exposing his canines and thrusting his head forward. AM2 and SF2, the former in the lead, immediately chase him out.

0649: Both groups' retreat from "confrontation" trees to a distance of 30 metres.

0650-0652: AM2 makes a final chase, RBC1 leave the area immediately. RBC2 leave two minutes later.

6.4.3 Intense encounter

Intense encounters between green monkeys were prompted by groups converging on an important food resource in the overlap zone (Harrison, 1983b), notably at times when other favoured foods were in short supply or unavailable. Six encounters between RBC2 and RBC1 showed similar patterning to Harrison's intense encounter since all skirmishes took place at fruiting sources but differed by virtue of one of the participant groups provoking the encounter by crossing over into the territory of the second group.

The preliminary stages of an intense encounter usually found one group already feeding in the food source when the other group arrived or both groups converging on the area at the same time. The reaction was immediate and extremely hostile as both groups moved swiftly towards each other to initiate a series of retaliatory chase-and-strike attacks (Reichard and Sommer's [1997] *chase and contact aggression*). Adult males were the main protagonists but the adult and subadult females also played an active role. Normally gibbons chased and attempted to strike same sex members of the opposing group but males were also observed to attack females and vice versa. This behaviour has also been observed in *H. lar* (Reichard and Sommer, 1997). Calling, mostly alarm solos or duets, accompanied the chases, and towards the end of the attack became the primary form of the adult female's defence as she withdrew, with her young offspring, from the main site of aggression. Characteristic of the intense encounter was the absence of calling from the invading group; only the resident group was observed to sing. Adult and subadult gibbons, particularly males, also engaged in display behaviour in between chases. Displaying during this part of the dispute mainly involved the use of foliage, gibbons stamping on, shaking and breaking off branches. Rapid brachiation and ricocheting was also common, as was defaecating.

Chase-and-strike attacks normally terminated with one of the groups moving into the food source. The other group responded by occupying adjacent trees and calling, displaying and attempting to evict the feeding group. Adult females always played a secondary role at this stage of the encounter, demonstrating their aggression through singing. Adult males, in particular the male not in the food source, rarely sang, spending most of the time observing or displaying. Brachiating slowly and with exaggerated over-arm movements, the adult male would position himself close to the opposing male, adopting a star shaped posture to reveal his genitalia. Gymnastic displays, incorporating swinging on one arm or by the feet, or repeatedly kicking his legs out in front of him, were common. Piloerection of hair on the shoulders and a facial gesture of exposed canines, arched "eyebrows" and a rapid head thrust were also used to intimidate as was grabbing the genitalia. Chasing between males did occur but not as frequently. Interestingly, the subadult female of RBC2 also engaged in chases and indeed, during February 5-9 and March 18 1996, played a more pro-active role than her father did![9] Subadult female lar gibbons are also known to chase males alone, in contrast with adult females who are usually accompanied by a male partner when involved in such behaviour (Reichard and Sommer, 1997). Intense encounters always ended with one of the groups leaving the area.

6.4.3.1 Intense encounters and territorial expansion

Five of the intense encounters occurred at a large *Ficus sundaica.* The *Ficus* was located close to RBC2's territorial boundary and within their core area and, during the five-day period in which four of the encounters took place, the tree was in full fruit. RBC2's reaction to RBC1 entering its core area to exploit this food source was considerably antagonistic but they were unable to deter the invading group. Indeed, it was not only RBC1 that mounted the more aggressive attack but they were the group that gained continual access to the *Ficus*, successfully repelling all attempts by RBC2 to evict them. Not one of the four encounters terminated with RBC2 driving RBC1 away. RBC2 either left the area, despite RBC1 still occupying and feeding from the *Ficus*, or RBC1 chose to retire of their own accord.

RBC1's control of the *Ficus* and the conflict was surprising, particularly as it was located in a heavily used and hence preferred part of RBC2's home range. So why was the resident group unable to mount a successful defence? Encounters between green monkeys resulting in the easy supplantation of one group by another usually occurred if the food resource being fought over was of importance to only one of the opposing groups (Harrison, 1983b). It could thus be argued that the *Ficus* was not as important a food source to RBC2 as it was to RBC1 and therefore not worth the extreme expenditures of time and energy required to defend it. An examination of feeding behaviour initially suggests that this is unlikely for two primary reasons. Firstly, in the week preceding the 5-day sample, RBC2 had made numerous visits to this particular fig, and at previous fruiting cycles, it had always received heavy exploitation (Kursani, 1996 pers. comm.). Secondly, the February encounters occurred during a period of peak fruit production when fruit was abundant in the home ranges of both RBC2 and RBC1. Figs are a nutritionally poor food item and unlikely to be worth fighting over if other, more nutritious fruits are available.

An examination of ranging maps developed from earlier short-term studies on the focus groups revealed that RBC1 had slowly expanded its territory into RBC2's home range. Field guides also indicated that in the period June-August 1995, immediately prior to this study, RBC1 had

---

[9] Lar pairs at Khao Yai also allowed their subadult offspring to play primary roles in range defence. Indeed, so much so that it appeared at times that the more readily a resident subadult engaged in territorial disputes, the less likely the resident pair would respond to the challenges of the neighbouring group (Ulrich Reichard, 1998 pers. comm.).

made numerous, aggressive incursions into areas normally used only by RBC2. The February 1996 conflict was a particularly serious confrontation and rather than being one in which gibbons contested to guarantee sole access to a food source it instead represented an attempt by RBC1 to annex part of RBC2's home range to its own. (Certainly, in the following week, RBC1 made regular visits to the site without being intercepted by RBC2 and on some of these gave duets from the *Ficus*.) The vigour of RBC1's prolonged attack may have intimidated RBC2 and, if territory expansion was RBC1's intention, RBC2 could have been, at least temporarily, cowed.

Subsequent encounters saw RBC2 adopting a more pro-active role. Of course, the great majority of encounters occurring after the February dispute were not related to the access of a desired resource and generally took place on accepted borders, and thus they always ended with the resident group supplanting the intruder. However, three disputes were just as hostile as those which took place in February but had the same outcome as the ritual encounters. What is more, RBC2 were the predominant aggressor, leading most of the chases and preventing RBC1 AM pushing further into the territory.

RBC2's display of authority, however, did not have a long-term effect. Observations on the focus groups between September 1996 and October 1997 found RBC1 regularly using the site of the February conflict (Kim McConkey, 1998 pers. comm.). In the period immediately following the end of my own study, RBC1 made cautious advances into the region but by 1997 the group moved confidently through what used to be a part of RBC2's territory. RBC2 also made visits to this area, suggesting that a new zone of home range overlap had been created.

6.4.4 Miscellaneous

One encounter, occurring on the 19 June 1996, could not be categorised. Although resembling a ritual encounter through the absence of a stimulatory resource and occurring in a location in which previous disputes had occurred, it consisted of behaviours, such as inter-sex chases, and a level of hostility characteristic of intense encounters. Indeed, the chase-and-strike attacks, and the commotion resulting, was so extreme that while escaping an RBC2 attack, the heavily pregnant adult female of RBC1 missed a hand-hold and fell 10 metres to the ground. Her fall temporarily extinguished the discord as members from both groups waited for her to recover from the fall and climb back to the middle canopy before resuming the conflict. The rest of the encounter was short-lived, a three-member drive from RBC2 forcing RBC1 out of the area.

6.5 Frequency, duration and context of inter-group encounters

Conflict frequency varies substantially between gibbon species. *H. lar* and *agilis* dispute territory boundaries every second day (Ellefson, 1974; Gittins, 1979) while *muelleri* met with neighbouring groups only once a month (Mitani, 1985b; Leighton, 1987). RBC2 was involved in a total of thirteen encounters (see Table 6-4). Nine of these occurred during the 60 day observation period, giving a rate of one encounter per 6.7 days or 0.15 encounters a day. Of the other four, one took place on a non-sample day and the remaining three whilst following RBC1.

Two additional territorial disputes involving RBC1 and RBC3 were also observed but none occurred between RBC1 and RBC5.

Inter-group encounters were distributed throughout most of the activity period, the earliest at 0555, the latest initiated at 1358. Although there was no concentration of encounters at particular times of the day, they were predominantly morning events, only one dispute occurring in the afternoon. No more than one dispute happened per day. Distribution through the observation period was more uneven. Except for a chance encounter in November 1995, RBC2 did not meet neighbouring groups until February 1996, five months after the start of the study. At least one encounter took place in each of the following months with the exception of August.

Table 6-4 Inter-group encounter type frequency, duration and context (all RBC groups).

	Encounter type		
	Call and Retreat	Ritual I and II	Intense
Number observed	3	6	6
Duration: mean	3.0	32.4	84.5
Duration: range	1 - 4	10 - 55	20 - 136
Location	Rarely used sections of the overlap zone	On or adjacent to established boundaries	Stimulated by one group crossing into the territory of another; takes place on or just within territory border.
Temporal distribution	No pattern	No pattern	No pattern
Context	Chance meeting	Preservation of territory boundaries	The securing of food resources; annexation or defence of territory; EPCs?; infanticide?
Associated behaviours	Duetting; mutual observation and some approaches.	Duetting; chases; mutual observation; and male displays.	Duetting and female alarm solos from the resident group only; mutual observation; chase-and-strike attacks (intra- and inter-sex); male displays; rapid brachiation; defaecating.

Examining environmental, dietary and phenological data does not provide any ecological explanation for the heightening of tension between RBC1 and RBC2. The absence of a true wet or dry season rules out a seasonal basis to encounter frequency; the aggregation of intense encounters in the first and third wettest 5-day sample periods is probably a coincidence. A particularly large fig tree in full fruit was probably an influential factor in the 4 day dispute between RBC2 and RBC1 in February 1996. However, comparing fruit consumption and production in the respective diet and home ranges of the neighbouring groups showed no overt differences that might have induced RBC1 to approach and enter RBC2's territory. Instead, encounter frequency possibly rose as a result of RBC1 regularly visiting the sites of previous intense encounters. Of the eight disputes occurring after February 1996, half were located at the site of the February conflict where possibly a new boundary division had been formed, one which RBC1 wanted to maintain. Moreover, an intense encounter on the 8th of June 1996 was followed the following month by a ritual meeting in the same region.

Of the fifteen encounters observed, RBC2 was involved in two chance encounters, five ritual encounters and six intense encounters, each category distinguished by duration. Chance encounters were very brief, lasting around 3 minutes. Ritual encounters were substantially longer, ranging from 10 to 55 minutes and averaging 34.5 minutes, while intense encounters were longer still, at a mean of 84.5 minutes (Table 6-4). On February the 5th and 6th 1996, intense encounters extended over more than 2 hours. Encounter length was determined by the seriousness of the dispute, which in turn was affected by its location and the ecological context surrounding it.

Chance encounters occurred in the overlap zone, primarily in marginal areas either rarely visited or composed of lower grade vegetation. These areas were of no particular value, in terms of resources, to either group and therefore did not demand costly bouts of fighting. Sites of chance encounters included an open section produced by multiple tree falls and a region of the home range which extended into secondary forest. Encounters close to or on established territory boundaries, and particularly those in the territory itself, however, would necessitate an escalation of aggression, and consequently dispute duration increases. Ritual encounters were located on territorial borders, often at sites of only recently established demarcations and adjacent to core ranging areas. Behaviour was thus hostile, both groups acting to preserve the boundary line and prevent the opposition crossing it. Countersinging, observed at all ritual encounters, complemented the displays and chases, advertising and establishing the territory proper. Intense encounters were more serious confrontations as these invariably resulted from one group (e.g. RBC1) crossing the border and entering the neighbouring group's (RBC2) territory. Prompting these territory incursions appeared to be the presence of a highly desirable food source as the resultant disputes were centred at trees heavy with fruit. (Aggressive displays between groups of green monkeys were also induced by rare and coveted food resources – Harrison, 1983b). The immediate outcome to such a dispute was the securing of the food resource by one of the groups but the long term could see the addition to, or partial loss of, the territory. It is therefore in the best interests of the invading, and particularly the resident, group to mount an affective attacking or defensive role. Prolonged and aggressive bouts of chasing and displaying, and singing on the part of the territory holder, were necessary responses for the protection and maintenance of the territory and the potential use of new and ecologically preferable areas.

6.6 An aberration from normal encounter behaviour

An intense encounter on the 8 June 1996 was distinguished by the unusual or previously unseen behaviour of both participatory groups. The adult male and subadult female of RBC2 were feeding in a fruiting *Parartocarpus bracteatus* tree, the adult female having just left with her infant for an adjacent tree. RBC1 are observed in the immediate area, heading directly towards RBC2. The following describes the subsequent events (note Tree A = tree where AF2 is located, Tree B = tree where AM2 and SF2 are located):

0935: RBC2 start calling on observing RBC1.

0940: AM2 and SF2 stop calling and resume feeding.

0941: Adult members of RBC1 are first seen by human observers, travelling directly towards Trees A and B. AM1 and AF1 enter Tree A, initially remaining on the peripheries. JF1 stops at a distance of 10-15 metres from the RBC2 occupied trees and stays there until RBC1 retreats.

0942-0943: Whilst AM2 and SF2 continue to feed, the adult members of RBC1 attempt to move closer to AF2 and I2. AM1 inches towards AF2 while AF1 moves around to the side of the tree, positioning herself between AF2 and the feeding members of RBC2.

0944: I2 breaks free from her mother's grasp and plays. AF1 edges closer to the infant and twice extends a hand towards I2. AF2 responds by grabbing the infant and continuing to call.

0945-0946: AM1 lunges at AF2. AF2 becomes distressed and starts brachiating around the central part of the tree, clasping the infant. Her solo changes structure to resemble an alarm call. AM1 and AF1 momentarily back off.

0947: AF1 moves closer towards the female. AF2 lunges at her and continues to brachiate around the tree, calling. AF1 lunges at AF2.

0948: AM1 lunges at AF2 again. AF2 responds with a lunge and then resumes calling and brachiating. Occasionally, she shakes the foliage.

0949: AF2 chases AF1.

0950: AM2 and SF2 finish feeding and chase RBC1 to 60 metres away.

1000-1016: Stand-off between RBC2 and RBC1 ensues, both groups silently observing each other. Occasionally the adult males displays to each other. Sixteen minutes later RBC1 retreats back into their territory.

Compared to previous intra-group clashes between RBC2 and RBC1, the peculiar circumstances of the June 8 encounter were defined by four principal variations to normal encounter behaviour, based on the uncharacteristic or previously unobserved behavioural actions of three of the encounter participants – AF1, AM1 and, in particular, AM2. They were:

1. The entry by AM1 and AF1 into a tree in which AF2 was resident, rather than negotiation of entry into the tree where their normal encounter combatants (e.g. AM2 and SF2) were feeding.
2. The absence of an immediate retaliatory response by AM2 and SF2. Neither individual attempted to head off RBC1's arrival at the feeding site, instead responding to the penetration of their territory with calling behaviour.
3. The pro-active role played by AF1 who had normally adopted a secondary position in encounter attacks.
4. The absence of "protection" behaviour from AM2, who despite being in an adjacent tree, only became involved in the confrontation some 7 minutes after RBC1 had first started their harassment of his mate (AF2).

In an attempt to interpret the events of the June 8 encounter, the behaviour of the mated pair of RBC1 and AM2 needs to be examined separately.

6.6.1 Why did AM1 and AF1 attack AF2?

Reichard (1998, pers comm.) has suggested that AF2 suffered an attack from RBC1 simply because she happened to be located in a tree which comprised part of a route taken by RBC1 in order to access the food source. On entering the tree they were unable to pass through it, finding it to be occupied and, therefore blocked, by AF2 and her infant. This might have been the case if RBC1 had entered the area from another direction or if AF2 had been quietly resting in Tree A. Instead, RBC1 approached the trees head-on, not at an angle which necessitated or invited passage through Tree A. Furthermore, it appears from their travel pathway that RBC1 made a deliberate, if only slight, detour to occupy Tree A. Of course, despite their initial direction of travel, RBC1 might have still chosen to take a somewhat deviating path to the fruit source. What isn't unclear, however, is why they entered Tree A, which they must have known to have been occupied (the female was singing there), when other adjacent trees were just as appropriate for use as access paths.

Strongly influencing RBC1's behaviour was almost certainly the fact that AF2 was unaccompanied. In previous encounters, AF2 had been able to maintain her distance from the combatants and, with the exception of two chase-and-strike events, never came into contact with either AM1 or AF1. On this occasion, her mate and daughter were close by but neither was positioned in between AF2 and RBC1 nor had they shown any assertive response to RBC1's territory intrusion. One possible scenario is that the adult pair of RBC1 chose to "mob" AF2. While it was not unknown for two gibbons to attack another gibbon (e.g. AM2 and SF2 were sometimes observed to chase AM1 together), what was unusual was the actual mobbing and encirclement of a lone individual. Motive for such mobbing behaviour might be viewed as being directed by an overall group response (Group action) or specifically driven by individual interest (Individual action).

6.6.1.1 Group action

Group action does not necessarily imply collaboration nor does it deny that sex-related interests are governing the behaviour of AM1 and AF1. However, in the following, the actions of AM1 and AF1 are interpreted as ultimately producing the same response effect by virtue of their reaction to the same stimulus.

RBC1 could have responded to a series of recent encounter defeats at the hands of RBC2 and/or the location of the current encounter by exhibiting a more cautious or somewhat modified plan of attack (i.e. confront AF2 rather than their normal combatants). Although it has been shown that these two groups alter their territorial response in relation to encounter context and location, marked behavioural variation within each encounter category was not observed. Of course, the number of inter-group fights which occurred during the study period was small but the consistent display of inter-group aggression by RBC1, and in particular that of the adult male, does not render a sudden dampening of aggressive behaviour likely. Furthermore, the absence of retaliatory behaviour from AM2 gave AM1 the perfect opportunity to launch a surprise attack on the feeding members of RBC2.

Another scenario suggests that RBC1 chose to harass AF2 in an attempt to attract the attention of AM2 and SF2 who would, in turn, stop feeding (to help AF2 and I2) and thus leave the feeding tree empty. If this was their plan, the fact that it did not achieve the desired result probably should have led them to take a more direct approach. Certainly, direct confrontation was a characteristic trait of AM1's territorial behaviour. Reichard (1998, pers. comm.) also questions this explanation through challenging the proposal of strategy. He argues that if gibbons are "clever" enough to develop such a strategy, then they are "clever" enough not to be fooled by it. Furthermore, if RBC1 really wanted to enter and feed from the food source, they would have at least attempted to do so. Past encounter outcomes supports this argument, since RBC1 repeatedly supplanted RBC2 from a fruit laden fig tree despite the location of the encounter.

6.6.1.2 Individual action

If no obvious group motive was behind RBC1's encounter response, then individual interests might have played a more prominent role in directing their behaviour.

6.6.1.2.1 Male interests

Recent papers describing extra-pair copulations between lar gibbons at Khao Yai (Reichard, 1995; Reichard and Sommer, 1997) and the absence of long-term bonding between some pairs of lar gibbons and siamang in Sumatra (Palombit, 1996) bring up the proposition that AM1 had more personal motives for harassing AF1, i.e. an attempt to open up extra-pair reproductive opportunities between himself and an extra-pair female. Previous encounters between AM1 and inter-group females had always been in the form of displays and/or chases. But during encounters with RBC2 any association he had with the females was almost invariably centred on the subadult female, who often engaged in primary or vanguard roles in territory defence and was therefore more likely to take part in physical clashes with AM1. In contrast, AF2's usual response to territory incursion was vocal and the only encounter contact she was observed to have with AM1 was during the chaotic inter- and intra-sex chases which sometimes initiated intense encounter events. Contact on these occasions was brief and consisted primarily of rapid chasing and physical assault on the fleeing gibbon. In all other encounters, AF2 remained in the background, AM2 and SF2 forming an effective barrier to any attempt AM1 might have made to gain access to AF2.

On June 8, however, AM1 found AF2 on her own, although not entirely isolated from her fellow group members. RBC1's approach to Trees A and B, however, did not generate the physical attack typically performed by either SF2 or, more importantly, AM2, which might have further encouraged AM1 to enter AF2's tree instead. Once in Tree A, AM1 was able to approach AF2, again with no response from AM2, and continue to do so for another seven minutes. While contact between AM1 and AF2 was conducted in a relatively short time frame, and under the watchful eye of AF1, it represented the first observed direct interaction between these two individuals. If hybrid gibbons do engage in extra-pair sex, then it is not unreasonable to suppose that the actions of AM1 were an attempt to open up a future reproductive relationship with AF2.

Of course, it is unlikely that the actions of AM1 were premeditated but it is indeed possible that he took advantage of the situation (i.e. the absence of reproach from AF2's mate) to attract AF2. His employment of a more aggressive stance, rather than the use of affiliative gestures, furthered his interests by introducing a double positive effect. Firstly, it allowed him to display his physical strength, and hence genetic "strength", to AF2 (but see Discussion). The fact that AM1 was able to continue this display without retaliatory response from AM2 improved his chances of impressing AF2 through promoting himself as a potential, and superior, breeding partner. Secondly, it acted as a behavioural means in which he could appease his own mate. Directing affiliative gestures towards one female when your own mate is watching is not in the best interests of the occasional polygynist. But acting aggressively towards another female would represent appropriate behaviour to his mate, indicating that he held little or no interest in the extra-pair female.

6.6.1.2.2 Female interests

Earlier encounters had seen some aggressive behaviour from AF1 but normally she played a role even more restrained than that of AF2, retiring to a considerable distance from the encounter site. On this occasion, when the primary aggressors showed little sign of expelling the intruders, she was able to display her hostility to AF2. Encouraging her hostile behaviour might have been an increase in feeding competition between the two females. If food resource distribution largely governs the dispersal of female gibbons, changing patterns in feeding competition (affected by factors such as the loss of territory holdings, reduced food availability and/or variation in group size through birth of infants or dispersal and death of other offspring) may affect the degree to which female gibbons participate in inter-group disputes. It has already been proposed that RBC1's incursions into RBC2's territory was a means to increase their ranging area. Whether this was in response to pressure from other neighbouring groups could not be discerned but differences in food availability between the two territories and the impending birth of a new group member might have induced AF1 to play a greater role in territory conflict.

6.6.1.2.3 Infanticide

Van Schaik and Dunbar (1990) proposed that one of the functions of observing a monogamous social system was the reduction or elimination of the incidence of infanticide. Indeed, infanticide is almost completely unknown for the (largely) monogamous gibbon with only one case so far documented (e.g. hoolock gibbons in the Garo Hills, NE India – Alfred and Sati, 1991). However, the absence of other reports of gibbon infanticide does not necessarily imply that it doesn't occur more often, particularly as such behaviour would be difficult to detect and therefore easily missed. Furthermore, some aspects of encounter behaviour recorded for *H. lar* at Khao Yai (Reichard and Sommer, 1997) are suggestive of the threat of kidnap or infanticide existing within gibbon society. Firstly, adult gibbons have been observed to make contact with immatures from other groups, and while contact behaviour described in Reichard and Sommer (1997) was always affiliative, it does not entirely refute the possibility that males (or females) with more antagonistic intentions would also attempt contact with inter-group immatures. Secondly, and as observed for the gibbons at Barito Ulu, males occasionally chase females. Inter-sex chases are not as common as same-sex chases but they have a greater chance of ending in "contact aggression" (Reichard and Sommer, 1997 and this study). Who the adult male is targeting when making these chases remains debatable but it may not always be the adult female. The fact that the adult female receives the brunt of the attack might be her way of protecting her offspring from the injurious, or indeed murderous, intentions of an adult male.

If either or both of these observations predict infanticidal behaviour, then the actions of one or both of the RBC1 adult pair could theoretically be interpreted as an intent to harm the infant of RBC2. But the function such behaviour would serve an adult extra-group gibbon is difficult to interpret when considering current hypotheses of primate infanticide (e.g. Sugiyama, 1965a; 1965b; 1966; 1984a; 1984b; Mohnot, 1971; Itani, 1972; 1982; Rudran, 1973; Hrdy, 1974; 1977; 1979; Parthasarathy and Rahaman, 1974; Curtin, 1977; Curtin and Dolhinow, 1978; 1979; Boggess, 1979; Ripley, 1980; Rijksen, 1981 and see reviews in Hrdy, 1979 and Sommer, 1987). This is primarily due to a focus on the patterns of infanticide occurring in large grouped, social primates such as Hanuman langurs but also because the great majority of infanticidal events takes place within the group, not between individuals from different groups.

For the adult male gibbon, the death of an extra-group female's infant could serve his interests if he engaged in, or planned to initiate, extra-pair copulations (e.g. *reproductive advantage hypothesis* – Hrdy, 1974; 1979). Losing an unweaned infant terminates the female's period of amenorrhoea, thus making her receptive to impregnation. However, if the male were to take advantage of the female's newly receptive state, he would need to make regular visits to the female, preferably before she started sexual activity with her own mate. This could prove very difficult for him, especially as opportunities for unharrassed consortship would be rare. But if he was a frequent visitor to the extra-group female, and she (eventually) accepted his advances, it might well be worth the effort if it meant the male could sire an infant with a female other than his mate.

For the adult female gibbon, resource competition (see Rudran, 1973) is a potential precursor to infanticidal behaviour. Infant killing during inter-group encounters, otherwise known as "xenophobic infanticide" (Southwick et al., 1974; Hrdy, 1979), has been observed for coyotes (Camenzind, 1978), Hanuman langurs (S. Ripley, personal communication to Hrdy, 1979) and rhesus macaques (Carpenter, 1942; D. Sade, personal communication to Hrdy, 1979). I have already proposed that the assaults conducted by RBC1 on RBC2's territory might have been a response to (an undetected) pressure on the integrity of their own territory. To counter that pressure, annexation of new territory is attempted and the extreme nature of an infanticidal event is one method of subduing the residents. However, the benefits gained from such behaviour are probably minimal, resulting in only some alleviation of pressure on shared resources (Hrdy, 1979). Furthermore, most incidences of xenophobic infanticide appear to be opportunistic rather than deliberate. It is therefore more likely that if the adult female of RBC1 had infanticidal intentions, they were derived at the scene of the encounter for reasons yet to be determined.

6.6.2 Why didn't AM2 respond immediately to RBC1?

Probably the most extraordinary behaviour observed during the encounter was that of AM2. This male had sometimes played a rather subdued role in territorial defence, particularly in comparison with the aggressive displays of AM1, but why on this occasion did he not only choose to ignore RBC1's territorial incursion but delay his response to the assault being waged on his mate? Four potential explanations are available. The first three address the absence of the secondary response while the fourth attempts to explain both primary and secondary response failures.

1. *The adult male resolved that it was the food source (e.g. P. bracteatus tree) which induced the dispute and, by occupying the tree, he and the subadult female would eventually discourage RBC1 from their territorial assault.* But if mate defence, rather than food resource defence, is the primary territorial concern of the male gibbon, it is extremely unlikely that an adult male gibbon would change his defensive strategy so that a fruit tree, which was located at two other known sites in the territory, was evaluated as a resource of more importance than his female partner.
2. *The instalment of the subadult female as a permanent member of the group could have led the adult male to reassess or realign his relationships with the two residential females. Consequently, he considered his association with the younger, subadult female to be stronger or of greater personal benefit (e.g. measured in terms of future reproductive opportunities) and to affirm or promote this change in partner alliance he chose to protect the younger female instead.* Once again, the argument is flawed and for two reasons. Firstly, it is true that the adult male devoted less social and associative time to his original mate (see Chapter 8) but this was not necessarily his decision nor did it ultimately disrupt the structure of the group. Indeed, the adult female maintained a dominant position over her daughter and, fifteen months after the completion of the study, the trio status of the group remained intact. Secondly, a female with an offspring, regardless of the relationship a male holds with another female, is important to the male (Ulrich Reichard, 1998 pers. comm.). Such a female has not only proved her reproductive capabilities but is currently caring for an infant which, presumably, has been fathered by this male.
3. *Following Point 2, the adult male could not protect both females and chose to defend the preferred female.* In all observed disputes prior and subsequent to this encounter, the adult male showed a consistently aggressive response. This aggression conferred an ability to both arrest contact between the invading male and the defending male's females and to evict his opponent. If he suffered from any latent difficulties in defending the two females, it remains unclear why he delayed or deferred participation on just one occasion. Also, as Reichard (1998 pers. comm.) points out, the second female was not under any immediate threat from the invading group. Thus AM2 was not required to protect SF2, giving him the opportunity to leave her at the food source in order to defend the adult female.

4. *The adult male did not immediately react because he simply did not gauge the gravity of the situation.* This initially seems unlikely in relation to both the primary and secondary response. Firstly, the residents had already demonstrated their animosity through the production of a duet. Secondly, RBC1 had displayed little evidence of being repelled by RBC2's singing, travelling further into the territory until coming into close visual, and then physical, association with RBC2. And thirdly, the behaviour of AM1's mate, and the actions of AM1 and AF1, could not have gone undetected nor could they have been interpreted as representative of a minor or irrelevant disturbance. However, in the absence of supportive evidence for Points 1 - 3, an inability to detect the seriousness of the encounter remains the best interpretation, although one which is difficult to prove (Ulrich Reichard, 1998 pers. comm.)

6.7 Discussion

6.7.1 Patterns of territory control and encounter context

The successful defence of the physical territory demands the preservation of the border, achieved in part through the routine inspection of boundaries. While demonstrating a more benign form of patrolling compared to other primates such as chimpanzees, gibbons do regularly visit peripheral areas of the territory. Chivers (1974) and Ahsan (1994) propose that this task is achieved when resident groups monitor the status of adjacent food sources. This may be so but the ranging patterns of RBC2 within their territory suggest that gibbons visit the border also to monitor the ranging behaviour of other groups, particularly those threatening the integrity of the territory. Despite the adequate supply of food species on the southern and eastern peripheries of their territory, RBC2 preferred to visit the north-western flanks where other groups had occupied neighbouring ranges. Within that region, RBC2 focussed their border checks even more narrowly, choosing to concentrate peripheral activities immediate to the ranging area of RBC1. This section of the border lay adjacent to part of RBC2's core area which could explain the high proportion of visits. However, it is just as likely that the numerous visits were a means by which RBC2 addressed the continual pressure RBC1 was mounting on border security.

Monitoring the border inevitably leads to groups meeting each other in boundary regions, the outcome representing a more overt form of territorial defence. Location of the encounter proved to be the primary discriminatory factor in the intensity of the encounter response. If groups met in areas of rare use, reaction was short-lived and unremarkable whereas those occurring at sites of previous encounters were characterised by aggressive displays and attempts by both groups to evict their opponent. Both chance and ritual encounters took place in the overlap zone but a comparison of habitat richness (denoted by the number of used food sources) found that ritual encounters were invariably associated with a better quality of habitat type.

A refined, and hence improved, assessment of territoriality examines the behavioural events surrounding an encounter of greater consequence i.e. incursion by one group into the territory of another. Six such encounters experienced by RBC2 could again represent resource-defence since all intense encounters appeared to have been initiated by contest over a fruit source.

Certainly, a favoured food species in full fruit is a prize worth winning and other species of gibbons are known to engage in disputes with conspecifics to obtain sole access to figs (Raemaekers, 1977; 1978b; Ahsan, 1994). But if other, more nutritious fruits are available in the home range at the time of the encounter, it is difficult to see why gibbons would invest considerable time in dispute over one food source. This is particularly pertinent to the February disputes where the four day conflict centred on a *Ficus*, a food source normally only of importance during periods of low fruit availability. Examining the ranging activities of the invading group (i.e. RBC1) prior and subsequent to the events in February eliminated some, if not all, of the uncertainty surrounding the incentive for the dispute. RBC1 had been slowly annexing parts of the shared overlap range, and then sections of RBC2's territory, to their own area of exclusive use. While this does not completely eliminate the immediate importance of the fig as a coveted food source, it is likely that the fig represented something different to the two groups. For the invading group, it served as a convenient pretext for the more serious intention of range acquisition, since securing the fig enabled the group to secure the surrounding area. For the resident group, the fig symbolised maintenance of the domicile, for its forfeiture meant not just loss of part of the territory but a section of the core area as well.

6.7.2 Differential motives for inter-group encounters

The appropriation of territory, its protection from non-residents, and the behavioural repertoire associated with counter-displays of challenge and resistance are propelled by the same objective – the security of sole access to essential resources. Theories of gibbon territoriality, and of the differential strategies adopted by males and females, have received almost consistent support from field studies. Indeed, many of the territorial events that occurred at Rekut followed a pattern not unlike that observed for other populations of gibbon. Not all did, however. While this was not unusual in itself, the extent of the behavioural deviation exhibited by particular individuals suggests that inter-group behaviour is not necessarily uniform or solely influenced by sex and age related interests but also the composition and stability of neighbouring groups and the differential circumstances characterising each encounter. Another consideration as yet unaddressed in the literature is the motive or interests driving the behaviour of gibbons who actually cross the territory border. Although some elements of gibbon territoriality are still germane to such interactions (e.g. it is still in the best interests of the invading male to act aggressively so as to protect his mate) their actions, in effect, are not defensive *per se*. Appropriation, rather than defensive strategies, might be the influential factor in their behavioural response.

Already defined incentives for observed encounter behaviours might be modified if some aspect of the encounter context is altered. Confrontations between hybrid groups within the territory of one of the combatants usually found adult male and female gibbons playing roles conforming to basic sex-related behavioural norms. But these encounters were considerably more aggressive than those occurring on pre-existing borders or in overlap zones, with males engaged often in chase-and-strike attacks and displays, and females more likely to play a physically active, and not just a vocal, role. For the residents of the territory, this behaviour is not so unusual. An alien group has entered an area established for the exclusive use of the territory holders and their presence is a serious threat to sole ownership. For the invaders, some elements of defensive behaviour (e.g. mate defence) are still important but it is the confiscation or appropriation of their opponent's territory, and what that represents to each individual, which represents the ultimate goal. Incorporating previously un-held area into their own home range, even if it only forms a new section of the overlap zone, provides the adult pair and their offspring with an increased choice in food and other (e.g. appropriate singing trees) resources. Expanding the range in which both groups, or individuals from those groups, can meet without serious retaliation from a neighbouring group also increases the opportunities for gibbons to pursue affiliative interactions or even extra-pair copulations.

On the occasion when the encounter event is altered even further so that the actions of just one individual deviates from the norm, other participants might react to this by modifying their own behavioural response. And it is then that other interests, again appropriative rather than defensive, which might direct previously unobserved interactive behaviour. For the final part of the discussion, the events of the June 8 intense encounter between RBC2 and RBC1 will be used as a template to examine this proposal, focussing on two contrasting outcomes of unusual encounter behaviour – EPCs and enforcement of the pair bond.

6.7.2.1 Inter-group contact and the potential for EPCs

Adult male gibbons do not appear to single out counter-females for prolonged antagonistic treatment, reserving such behaviour for neighbouring males. Therefore, focussing attention on a neighbouring female, when the traditional combatant is nearby, suggests that an adult male has approached the female for a reason. One potential outcome from initiating and maintaining contact with a neighbouring female is extra-pair copulation. No evidence of EPC activity was detected during the study period but AM1 was observed on three occasions travelling *unaccompanied* and *within* RBC2's territory, suggesting that he was not merely making an impudent trip across the border but had motive driving his expedition. Detecting instability in a neighbouring group, cued either by its unusual social structure or the coquettish behaviour of a resident female, is encouragement enough for an alien male interested in seeking EPCs. The trio status of RBC2 (see Chapter 7) could represent such an influential factor. A group in which two females are resident could loosen, if not completely unravel, the bond established between the original pair or frustrate the newly mature female in her ability to develop an exclusive relationship with the male. Either situation is certainly consummate for a female to seek another, if only temporary, consortship.

An attempt to establish an extra pair relationship, however, predicts affiliative gestures on behalf of the soliciting male, not the antagonistic display performed by AM1. Approaches made by male lar gibbons to neighbouring females were consistently amiable, although female responses to these approaches were often unsure and sometimes frightened (Reichard and Sommer, 1997; Ulrich Reichard, 1998 pers. comm.). Choosing to confront a female rather than one's normal combatants could still represent a male gibbon's attempt to make contact with an extra-group female but the continual presence of his mate thwarts any chance of employing friendly approaches. Hence, an aggressive stance is taken. There is, of course, the possibility, however slight, that a male gibbon actually uses aggressive displays to attract a female. Maybe in the past he has obtained EPCs with extra-group females through initial, but at least anticipated, unfriendly gestures (Andrew Collis, 1998 pers. comm.). Certainly, other male primates (e.g. orang utans) use their greater physical strength to coerce, harass or intimidate females into having sex with them (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995) but in gibbons the absence of sexual dimorphism in body size or other physical dimensions (e.g. length of canines) makes it unlikely a male gibbon can force sexual relations with a female.

Alternatively, exhibiting hostilities enables a male to demonstrate his physical fitness, improving his ability to impress a female, particularly if the female's mate has failed to protect her. If this is indeed the male's strategy, he would have to ensure that his behaviour did not put the female at risk of injury or so frighten her that she will not consider extra-pair relations in the future. A more effective way of demonstrating his superiority, however, is to challenge the female's mate (Ulrich Reichard, 1998 pers. comm.). In the case of AM1, this does seem to have been the better option as he had shown in the past to be a strong and victorious combatant. Continuing to inflict encounter losses on the female's mate could lead to the female evaluating her mate as somewhat inferior and subsequently attempting consortship with another male.

6.7.2.2 Enforced monogamy

An alternative scenario proposes that a male acts aggressively towards an extra-group female because changing ecological factors necessitate sustained antagonistic relationship toward extra-group gibbons, regardless of sex. It has been suggested by Reichard (1998 pers. comm.) that for gibbons "at the brink where food limitations are at a crossroad between monogamous and polygynous grouping", ecologically induced changes such as increases in feeding competition have the potential to "shift... the system towards male and female enforced monogamous groupings". It has already been proposed that RBC1 were suffering some form of habitat contraction or degradation, creating the need to expand their home range into new areas (i.e. RBC2's territory). Faced with the potential or actual decline in resources, maintenance of the pair bond is an essential. Defending a territory with a mate is considerably easier and a resident pair are less likely to suffer continual boundary assaults. For the adult male, therefore, any "selfish" interests, such as EPC investigation, are to be abandoned in pursuit of pair bond security. An extra-pair female represents such a threat, and therefore to demonstrate loyalty to his mate and, indeed, reduce the chances of her abandoning him for another male, it is best to attack the neighbouring female.

An adult female threatened by feeding competition, or in close contact with an individual who could potentially destabilise her pair bond (i.e. an extra pair female), should also show aggressive behaviour to the source of that competition or destabilisation i.e a neighbouring female. The fact that adult females do not readily engage in confrontational behaviours is therefore not necessarily due to a defensive strategy of less importance than those proposed for male gibbons but because other factors preclude their participation. One such factor could be the protection of offspring. For example, AF1 had a juvenile daughter who, although independent, was quite small and therefore still vulnerable to attack. Furthermore, AF1 was pregnant at the time RBC1-RBC2 encounters were observed. To shield her daughter and to safeguard her pregnancy, AF1 regularly chose to remain on the perimeter of encounter conflict.

In the situation when normal extra-group aggressors do not play their usual defence role, thereby reducing the harm that can be inflicted on a female's offspring, a female has the opportunity to exert hostilities on the expected conflict partner – another female gibbon. The fact that AF1 positioned herself between AF2 and the feeding members of RBC2 certainly suggests that neither AM1 or SF2 concerned her. This scenario does not diminish the trauma a neighbouring, and threatened, female could affect on the attacking female but with her mate also harassing the extra-group female, she might consider herself in less danger.

7

Social Organisation and Intra-Group Social Behaviour

7.1 Introduction

Gibbons predominantly live in small family groups comprised of an adult pair and an average of 2 offspring (Carpenter, 1940; Chivers, 1974; Ellefson, 1974; Tenaza, 1975; Gittins, 1979; Chivers and Raemaekers, 1980; Gittins and Raemaekers, 1980; Tilson, 1981; Whitten, 1984b; Islam and Feeroz, 1992a; 1992b; Ahsan, 1994). Relations in the group are generally relaxed and tolerant, and adults are proposed to observe a monogamous social system, based on the maintenance of a stable, mate-for-life pair bond (Carpenter, 1940; Gittins and Raemaekers, 1980; Brockelman and Srikosamatara, 1984; Leighton, 1987). Co-dominance is considered to characterise the relationship between the mated pair (Carpenter, 1940) but incidents of domination by a pair member over his or her partner have been recorded for *lar* (Ellefson, 1974), *pileatus* (Srikosamatara, 1980) and *muelleri* (Leighton, 1987). In three of these cases, the assertive animal maintained its dominance throughout the course of the study. In the fourth group, a relatively ambivalent dominance relationship existed until it transformed into one which favoured the adult female, the re-direction in dominance coinciding with the latter stages of the adult female's pregnancy (Ellefson, 1974). These observations suggest that, rather than being a fixed rule, dominance relations are instead peculiar to each pair grouping and susceptible to physiological or ecological changes.

Gibbons are not especially gregarious animals and Gittins (1979) has observed that the infrequency of overt social contact between group members makes it difficult to detect the true nature of social relations operating in the family unit. Concentrating on defined gibbon social behaviours also ignores the concept that gibbons employ more subtle cues to direct group activities and relationships (Gittins, 1979). Gibbons may actually rely on social perception, rather than traditionally defined acts of social solicitation (e.g. grooming), to gauge and interact successfully and harmoniously with other group members.

Possibly the only overt display of intra-group social behaviour surrounds the emigration of the subadult. Offspring continue to reside in the natal group until they reach an age when they are either perceived by a parent to represent an ecological or sexual threat or decide themselves to find a mate and establish a territory of their own (Chivers, 1974; Tilson, 1981; Leighton, 1987). The former scenario, referred to as the process of separation or peripheralisation (Tilson, 1981), may last as long as two years and see a gradual increase in parental⇒offspring directed aggression, mostly from a same-sexed parent. Subadult animals respond to the tension by distancing themselves from the core of the group. Eventually they leave, often occupying an area within their own parent's territory or adjacent to it (Tilson, 1981; Leighton, 1987).

Three commonly held precepts of gibbon social organisation – the dispersal of mature offspring, pair bond stability and the adoption of a monogamous social system – have recently been countered, or at least questioned, by either the results of long-term research or demographic data collected on species only recently subject to long term field research (i.e. the concolor group).

The first of these precepts holds that on sexual maturation subadult offspring are peripheralised from the natal group. In *H. lar* groups at Khao Yai, however, adult:subadult relations do not necessarily follow this pattern; there are three documented cases of subadult males maintaining residency in their natal groups several years after sexual maturation (Suwanvecho and Brockelman, 1997; 1998). Compared to other offspring, the status of the subadult males was somewhat lower but overall group relations remained congenial. Suwanvecho and Brockelman (1997; 1998) have suggested that long-term stays by subadult gibbons are tolerated by the adult pair by virtue of the services the subadult can provide, such as guardianship of younger offspring and contribution to territorial defence.

The second precept deals with the stability of the pair bond. The evolution of a stable pair relationship, that dissolves only on the death of one or both partners, is proposed to have been influenced by a) the "inflexibility" of gibbon behaviour (Kinzey, 1987), b) the need to preserve "life-long" pair bonds for the successful rearing of slowly maturing offspring (Gittins and Raemaekers, 1980) and/or c) a means by which the risk of infanticide is reduced (van Schaik and Dunbar, 1990). Some studies describe a "remarkable degree of stability" (Palombit, 1994a) in gibbon pair bonds (e.g. *H.a.albibarbis* at Gunung Palung Nature Reserve, West Kalimantan) but long-term projects at Kuala Lompat, Ketambe, and Khao Yai have found that in populations of *H. lar* and *H. syndactylus* adult pair composition can not only undergo "considerable turnover" but may be induced by the deliberate choice of one individual to leave his or her mate (Palombit, 1992; 1994a). Over a period of ten years at Kuala Lompat, male or female desertion terminated at least five pair bonds (Chivers and Raemaekers, 1980). At Ketambe only one of the five original pairs remained together by the end of the six year study, and eight of the eleven pairs followed over the same period dissolved, five by an intentional act of desertion (Palombit, 1992; 1994a). And at Khao Yai, a third of 65 groups censused by Brockelman and colleagues included offspring aged less than two years apart (Brockelman, unpubl. cited in Brockelman et al., 1998). According to Sommer and Reichard (in prep.), this suggests that the mated pairs in these groups are not long-term associations but a result of more recent pair formations. Temporary disruptions to gibbon pair bonds, in the form of extra-pair copulations (EPCs), have also been observed for gibbons. For example, at Ketambe a female siamang copulated at least once with three different neighbouring males (Palombit, 1994a; 1994b), while at Khao Yai, extra-pair sexual activity was observed between a female *lar* and mated males of two adjacent groups (Reichard, 1995). Indeed, the number of EPCs at Khao Yai represented 12% of all observed copulatory bouts.

The third and final precept concerns the social unit itself and the typical group structure of a monogamous primate. Again, the inflexibility of gibbon behaviour has been employed in the past to explain the gibbon's strict adherence to the pair bonded, family unit but gibbon group composition data reported in the last ten years suggest that gibbons are actually more flexible, socially and ecologically, than first thought (Sheeran, 1993). Census work on *H. concolor* by

Xu et al. (1983 cited in Haimoff et al., 1986) and Haimoff et al. (1986; 1987) supported a much earlier observation by Delacour (1933) that this species resides in larger than normal groups (average size: 7.0) and actually observe a polygynous social system. Recent studies on the same *concolor* population have also reported both large group size and an excess of adult sized members, but more cautious interpretation has been made on the type of social system adopted (Bleisch and Chen, 1991; Sheeran, 1993). According to Bleisch and Chen (1991), the participation of multiple female singers in a "duet" does not necessarily imply a harem since the extra females might in actual fact be the subadult daughters of the mated female. In turn, Sheeran (1993) has stated that black gibbons are "probably monogamous". However, she concedes that the environmental disruptions at Mt Wuliang, combined with the apparent sex imbalance (males > females) in the groups surveyed, may lead to "some atypical family formations".

Strange social groups are, however, also found in areas where less obvious or little environmental disturbance has occurred. Hybrid and mixed species trios have been found in hybrid zones on the upper side of the Takhong river in Thailand (Marshall et al., 1984) and at Barito Ulu (this study) while pure species trios have been observed for *pileatus* (Srikosamatara and Brockelman, 1987), *hoolock* (Choudhury, 1990; Ahsan, 1994; 1995) and *lar* (Bartlett and Brockelman, 1996; Brockelman, 1997; Sommer and Reichard, in prep.). While most trio formations are polygynous, polyandrous associations are not unknown, having been documented for one group of hoolock gibbons (Choudhury, 1990) and three lar groups (Bartlett and Brockelman, 1996; Brockelman, 1997; Sommer and Reichard, in prep). Both familial pathways (e.g. *pileatus* – Srikosamatara and Brockelman, 1987; *hoolock* – Ahsan 1994; 1995) and immigration events (e.g. *lar* – Bartlett and Brockelman, 1996; Sommer and Reichard, in prep.) have led to the formation of polygamous groups.

7.1.1 Outline of Chapter 7

Three primary categories of hybrid gibbon social behaviour were recognised and each will be treated separately. After group composition is briefly described (Section 7.3), discussion will focus on associative behaviours or the strength of relationships existing in the hybrid gibbon group. Group cohesion (Section 7.4) introduces an investigation into group relations by measuring the degree to which individuals co-ordinate their activities with one another and identifying the ecological and social factors modifying associative activity use. Estimations of spatial proximity, how they are affected by maintenance activities, and individual direction of activities (Section 7.5) provide further insight into group and inter-individual harmony.

The final category looks at the social behaviours themselves – affiliative interactions (Section 7.6) such as grooming, sexual behaviour, and play, and agonistic encounters or intra-group aggression (Section 7.7). Each behavioural type will be examined in terms of frequency, participation of group members, and the context surrounding them.

7.2 Methods

The detection of social interactions between members of a gibbon group is frustrated by factors of small group size, the elevated position they occupy in the canopy, and the rapidity and often silent nature of the performance (Brockelman, 1984 and personal observation). The general finding that gibbons infrequently engage in intra-group social contact further impedes the recording of social behaviours, as the chance of actually observing such behaviours is effectively reduced. For these reasons, and in contrast to studies on other primates, a detailed social behavioural repertoire could not be relied upon and hence basic indices of social affiliation (e.g. grooming, play) or discord (e.g. aggression) were employed.

Data on social behaviours were derived from both the monthly 5-day sample periods and additional full-day follows in an attempt to accurately depict the social relations existing in focus groups RBC2 and RBC1. Furthermore, and because intra-group social activity was so rare in both groups, observations of actual behaviours (e.g. grooming) not collected at ten-minute intervals will also be included in the subsequent analysis and discussion. The collection of data for the three primary categories outlined in the Aims are as follows:

7.2.1 Associative behaviours

- *Group cohesion* – For each month, and over the annual period, the number of scans in which all group members, pair groupings (e.g. adult male-adult female only) or no group members were engaged in the same maintenance activity was calculated and divided by the total to give a proportional score. The potential for discord whilst feeding, and its influence on group relations, prompted an examination of who feeds with whom and, in turn, similar associative calculations were made on feeding bouts where at least two group members participated.

- *Inter-individual distance* – The position of each individual relative to another group member was assessed by estimating inter-individual distances in metres. A focal animal was chosen for each hour block, and distances between that individual and other visible group members measured every 10 minutes. When assessing the effect of maintenance activity on IID, only scans in which all members of the group were engaged in the same behaviour were used in statistical analysis.

7.2.2 Indices of social rank

- *Direction of group movements* – Whenever a maintenance activity was started or terminated, the individual instigating that change was identified. Only those activity changes in which all group members participated were included in the statistical analysis.

7.2.3 Affiliative and agonistic social behaviours

The documenting of these behaviours included both a quantitative assessment – initiation time and duration of encounter, frequency of activity – and a qualitative component, in which the individuals involved and the sequence of events were described. Four primary activities were recognised — grooming, play, sexual behaviour and aggressive interactions.

7.3 A brief look at focus group composition and pair bond stability

The focus groups RBC2 and RBC1 were both composed of an adult pair and their offspring (for composition of other groups see Table 2-4 in Chapter 2). RBC2 consisted of four individuals – an adult male, adult female, subadult female and infant (possibly female) – while RBC1 was composed of three members – adult male, adult female and juvenile female. Two to four weeks after the study was completed, RBC1 gained a new member with the birth of an infant.

During the initial stages of the study it was predicted that the subadult female of RBC2 was about to undergo, if she was not already experiencing, the period of peripheralisation subadult gibbons endure prior to their emigration from the natal group. This prediction was originally prompted by her size and estimated age (6-7 years but see Section 7.8.2.1) but supported later by the apparently closer relation she shared with her father compared to the one she held with her mother (see Tilson, 1981). This prediction was not borne out; the subadult's position in the group in August 1996 remained identical to that observed 12 months earlier[10]. Compared to the estimated age of female dispersal for other species of gibbon (Carpenter, 1940; Chivers and Gittins, 1978; Gittins and Raemaekers, 1980 but see Ellefson, 1974; Geissmann, 1991; Palombit, 1995), and considering that females often take longer to leave the family group (Tilson, 1981), this subadult may have been too young for the peripheralisation process or was simply not ready to go. However, the social dynamics operating between the three mature members of this group (to be discussed later) suggest instead that the subadult has become entrenched in family life, resulting in the formation of a trio. For the remainder of this chapter, the social structure of RBC2 will therefore be considered as that of a polygynous trio.

Any comment on the stability of hybrid gibbon pair formations is severely hampered by the inconsistent pattern of census work conducted at Rekut. Between 1988 and 1991, survey work by Mather (1992), Kool (personal communication to Mather, 1992), Greenaway (1991) and Lochowski (1991) found no apparent change in group stability. Between 1991 and 1995, information became less reliable, primarily because gibbons were located just once a year, each time by a new set of observers unable to relate current group membership to that of the previous year. Therefore, while I could monitor changes in the age and sex composition of a group, I had no way of monitoring the identity of each individual and prove that members of the adult pair were the same from year to year.

7.4 Group cohesion

An assessment of the proportion of time a hybrid gibbon spent in behavioural synchrony with at least another group member found a high degree of integration. Of the 10 minute scans in which every gibbon could be observed, RBC2 and RBC1 displayed a level of cohesion on par

---

[10] SF2 maintained her residency in RBC2 between September 1996 and October 1997 (Kim McConkey 1997 pers. comm.).

with the "harmonious" siamang (Chivers, 1974; 1976; Gittins and Raemaekers, 1980), all group members involved in the same activity 76.8% and 74.0% of the time respectively (Table 7-1). Equivalent data have not been reported for either *agilis* or *muelleri* but activity in *lar* was much less cohesive. Measured as the percentage of overall scans in which the whole group could be observed, *lar* group members were visible only 57.0% of the time, compared to the 96.0% of scans recorded for siamang (Raemaekers, 1979; Gittins and Raemaekers, 1980).

Table 7-1 Group cohesion in RBC2 and RBC1.

RBC2									
All in same activity		AM2 and AF2 in same activity		AM2 and SF2 in same activity		AF2 and SF2 in same activity		All in different activities	
%	n	%	n	%	n	%	n	%	n
76.8	1968	5.2	134	8.2	211	8.0	204	1.8	45
RBC1									
All in same activity		AM1 and AF1 in same activity		AM1 and JF1 in same activity		AF1 and JF1 in same activity		All in different activities	
%	n	%	n	%	n	%	n	%	n
74.0	694	6.0	56	7.4	69	11.7	110	1.0	9

n = number of ten-minute scans

A further 21.4% of scans saw RBC2 members undertake activities with just one other gibbon. The subadult female synchronised her behaviour with either the adult male or adult female more often than the two adults did with each other (Table 7-1). Chi square tests revealed that behavioural synchrony between the subadult female and either one of the adult pair was significantly more common when compared to the observed rate of behavioural synchrony between the adult pair (see Table 7-2). However, the subadult female did not show any significant tendency to spend more time in behavioural synchrony with one or the other adult.

Table 7-2 Observed and expected rates of behavioural synchrony between different pairs.

RBC2							
Pair	Expected n	Observed n	Pair	Expected n	Observed n	χ^2	sig to
AM2-AF2	169	134	AM2-SF2	169	204	14.5	≤.001
AF2-AM2	172.5	134	AF2-SF2	172.5	211	17.2	≤.001
SF2-AM2	207.5	204	SF2-AF2	207.5	211	0.1	≥.050
RBC1							
Pair	Expected n	Observed n	Pair	Expected n	Observed n	χ^2	sig to
AM1-AF1	62.5	56	AM1-JF1	62.5	69	1.4	≥.050
AF1-AM1	83.0	56	AF1-JF1	83.0	110	17.6	≤.001
JF1-AM1	89.5	69	JF1-AF1	89.5	110	9.4	≤.005

n= number of ten-minute scans

The most common pair association in RBC1 was between the adult female and the juvenile female but as was the case for RBC2, the adult male also spent more time involved in the same maintenance activity with his daughter than with his mate (Table 7-1). While significant differences existed between who the adult female and juvenile female were more likely to be in behavioural synchrony with, no such differences was found for the adult male (see Table 7-2).

Food sources, particularly those characterised by a prized food item (e.g. fruit, meat), are sites where group hierarchy is displayed (e.g. *Cercopithecus aethiops* – Wrangham, 1981; Wrangham and Waterman, 1981; Whitten, 1983; Fairbanks and McGuire, 1984). More easily demonstrated in larger groups, and confounded by the apparent co-dominance of the adult pair, the arrival and resultant behaviour at a food site may not shed any obvious light on the relations between members of a gibbon group. However, in light of the results presented above, association at feeding sites was also examined. During the 732 RBC2 feeding bouts, in which the behaviour of all individuals could be determined, 54.2% saw all members feeding in the same tree (Table 7-3). Of those bouts in which only two gibbons accessed the food source, the adult male fed more often with the subadult female than with the adult female but, unlike maintenance activity synchrony, this difference did not reach significance (Table 7-4). The adult female fed just as often with her male partner as with her daughter. These findings do not suggest any preferential feeding pair formations and indeed, gibbons were more likely to feed on their own than with another group member.

Table 7-3 Feeding cohesion in RBC2 and RBC1.

RBC2									
All in same food source		AM2 and AF2 in same food source		AM2 and SF2 in same food source		AF2 and SF2 in same food source		All in different food source	
%	n	%	n	%	n	%	n	%	n
54.2	394	4.3	31	6.3	46	4.4	32	31.4	228
RBC1									
All in same food source		AM1 and AF1 in same food source		AM1 and JF1 in same food source		AF1 and JF1 in same food source		All in different food source	
%	n	%	n	%	n	%	n	%	n
57.9	147	2.8	7	3.1	8	9.8	25	26.4	67

n = number of feeding bouts in which the activity of all individuals could be observed

Table 7-4 Observed and expected rates of feeding synchrony between different pairs.

RBC2							
Pair	Expected n	Observed n	Pair	Expected n	Observed n	χ^2	sig to
AM2-AF2	38.5	31	AM2-SF2	38.5	46	2.9	≥.050
AF2-AM2	31.5	31	AF2-SF2	31.5	32	*	≥.010
SF2-AM2	39	46	SF2-AF2	39	32	2.5	≥.050
RBC1							
Pair	Expected n	Observed n	Pair	Expected n	Observed n	χ^2	sig to
AM1-AF1	7.5	7	AM1-JF1	7.5	8	0.1	≥.010
AF1-AM1	16	7	AF1-JF1	16	25	10.1	≤.001
JF1-AM1	16.5	8	JF1-AF1	16.5	25	8.8	≤.005

n = number of feeding bouts * value < 0.1

RBC1 also tended to feed together as a group or individually (Table 7-3). Individual feeding bouts were regularly undertaken by the adult female who often left the group to forage and feed on her own. When feeding in pairs, the adult and juvenile female combination represented the more popular association, accounting for 9.8% of all feeding bouts.

No distinct patterning characterised any of the RBC2 maintenance activity associations, and monthly variation in the frequency of one association grouping did not correlate with changes in another (Table 7-5). Aggressive behaviour directed at the subadult female by the adult female (Section 7.7) predicted some reduction in use of the same feeding tree, especially during bouts when the adult male was occupied in another endeavour, but the prediction was not realised. Dietary changes and food type availability also bore little effect on feeding pair formation (Tables 7-6 and 7-7) but some of the trends were interesting. During months when there was either a greater concentration of flower in the diet or a greater proportion of trees flowering in the home range, the adult male fed less often with the adult female. He also reduced feeding associations with the subadult female when flower content in the diet had risen but not to the same extent as that shown with his partner. In contrast, increases in dietary fruit and fruit availability saw the adult male and female feeding together more often, at the expense of feeding bouts with the subadult female.

Table 7-5 Relationship between monthly variation in RBC2 pair associations (n=12).

Pair associations	r_s	sig to
AM2 and AF2 vs AM2 and SF2	-.280	=.35
AM2 and AF2 vs AF2 and SF2	.347	=.25
AM2 and SF2 vs AF2 and SF2	.042	=.89

Table 7-6 Effect of monthly variation in diet on RBC2 feeding associations (n=12).

% diet food type	Feeding pair association					
	AM2 and AF2		AM2 and SF2		AF2 and SF2	
	r_s	sig to	r_s	sig to	r_s	sig to
% diet fruit	.284	=.35	-.270	=.37	-.118	=.71
% diet fig	.329	=.27	.273	=.36	-.100	=.75
% diet flower	-.417	=.17	-.409	=.18	.201	=.84
% diet young leaves	-.480	=.11	-.158	=.60	-.209	=.51

Table 7-7 Effect of monthly variation in food availability on RBC2 feeding associations (n=12).

Food availability	Feeding pair association					
	AM2 and AF2		AM2 and SF2		AF2 and SF2	
	r_s	sig to	r_s	sig to	r_s	sig to
% fruit sources	.473	=.10	.369	=.29	-.404	=.18
% flower sources	-.451	=.13	-.161	=.59	-.350	=.25
% young leaf sources	-.196	=.50	-.004	=.99	.098	=.75

7.5 Spatial relations

7.5.1 Inter-individual distance

To aid in the understanding of the social relationships existing between group members, field biologists have employed various measures of spatial patterning, including inter-individual distance. This measure, by focussing on the average distance individual animals retain in relation to each other, assesses and categorises the strength or lack thereof of the relationships found between different age and sex classes. If one animal is more closely aligned to another, or shares a congenial and/or co-dominant affiliation with them, it would be expected that these animals maintain or accept a closer distance association than if the pair had a relationship governed by tension or indifference. For example, mother-infant combinations are regularly found close together whereas juveniles or subadults receiving hostilities from a same-sexed parent would vigilantly keep their distance (Chivers, 1974; Gittins, 1979; Tilson, 1981).

The closest pair association in RBC2 was, not surprisingly, between the adult female and her infant (Table 7-8). On average, the two spent their time less than 5 metres apart. Mature animals rarely accepted or initiated close proximal positions to one another (Tables 7-8 and 7-9), corresponding with the typical asocial nature of gibbons and partly explained by the infrequency of behaviours requiring contact (e.g. grooming and sex – see Sections 7.6.1 and 7.6.2). Despite their low level of association, a common trend was observed and consistent with the findings outlined in the previous section – both females preferred to maintain closer distances to the adult male than to each other. This difference was significant for both the adult female ($\chi 2=4.12$ d.f.=1 $p<.05$) and the subadult female ($\chi 2=3.98$ d.f.=1 $p<.05$). Adult pairs from the two focus groups exhibited similar average distances to each other.

Table 7-8 Inter-individual distances (in metres) between RBC2 group members.

Pair combination	Mean	Median	Range
AM2 and AF2	7.2	6.0	1 - 54
AM2 and SF2	6.7	5.0	1 - 48
AM2 and I2	7.8	5.0	1 - 54
AF2 and SF2	8.9	7.0	1 - 56
AF2 and I2	0.6	1.0	1 - 6
SF2 and I2	9.0	8.0	1 - 54

Table 7-9 Inter-individual (in metres) between RBC1 group members.

Pair combination	Mean	Median	Range
AM1 and AF1	8.1	6.0	1 - 57
AM1 and JF1	9.2	8.0	1 - 60
AF1 and JF1	4.3	3.0	1 - 34

Inter-individual distance for each pair association showed some, but not a significant, monthly variation. Nonetheless, social and ecological parameters were tested against this variation to assess their influence, if any, on spatial patterning. The rarity of overt displays of social interactions (i.e. grooming, sex and aggression) constrains formal analysis and, indeed, the absence of a consistent pattern in any of these behaviours resulted in only weak and non-significant correlations with inter-individual distance. No month(s) saw a concentration of social activity but in the periods encompassing December-January and February-May, when AF⇒SAF directed aggression reached a peak of sorts (Section 7.8), distances between the two females tended to be somewhat larger, and significantly so when compared to the other months of the study ($U=14.3$ $n_1=4$ $n_2=8$ $p<.05$). Of course, concluding that a firm relationship between sociality and spatial proximity does not operate in hybrid gibbon groups ignores the possibility that more subtle social mechanisms are employed to govern spacing associations.

Changes in the diet and food availability exerted little effect on inter-individual distance, although in those months with both a high dietary fruit content and a large proportion of trees producing fruits, individuals did space out over larger distances. It was noticed during these times that the group regularly dispersed into solo foraging expeditions, the abundance of fruit inviting gibbons to investigate all that was available and hence inducing them to spend more time at further distances from each other. Weather and spacing were not well correlated. RBC2 did observe behaviour similar to siamang (Chivers, 1974), preferring to keep closer together on cloudy and rainy days than on days which were predominantly sunny, but the association did not reach significance.

The strength of the relationship between two animals can also be determined by calculating the percentage of time the pair spend in "close proximity". Definitions of close proximity vary from study to study (e.g. Altmann (1980) and Stanford (1991)) but, to be consistent with other gibbon research, Palombit's (1996) criterion of a 1 meter separation with no displays of allogrooming or sexual behaviour will be used here. Palombit (1996) found a very low incidence of close proximal spacing between *lar* gibbon mated pairs and this was also evident for all pair groupings in hybrid gibbons. With the exception of the mother-infant association, no pair combination spent more than 2% of spatial observations less than 1 meter apart. Consistent with findings reported earlier, the mated pair of RBC2 initiated close proximity more often with each other than the pair in RBC1 did, and the two females in the former group preferred the adult male to be their close neighbour. Altmann (1980) has proposed that a pair of animals can not be considered "spatially associated" if they spend less than 5% of their time in close proximity. Even if Altmann or Stanford's criterion of proximity (2 meter separation) is employed here, percentage of scans still remains very low. This suggests that the strength of the pair bond in hybrid gibbons is relatively low, or at least in relation to the larger siamang where adult pair association exceeds the 5% cut-off (Palombit, 1996).

7.5.2 Spacing and maintenance activities

The type of maintenance activity the group were involved in influenced the degree of spatial patterning. Gibbons allowed other group members to maintain relatively close proximity to them during some activities but preferred to distance themselves during others. Excluding social interactions such as grooming, gibbons initiated and sustained the closest contact during singing and feeding bouts, extending inter-individual distance when involved in resting, travelling and, especially, foraging.

Gibbon groups almost always occupied the same singing tree, separated by no more than 5-10 metres. Gibbons rarely encroached on these distances, probably for two reasons. Firstly, the delivery of the great call was invariably associated with an energetic display of gymnastics and to ensure animals did not collide with one another, adequate spacing requirements had to be maintained. Secondly, the substrate from which gibbons regularly performed their song (i.e. the terminal branches of the singing tree) were probably too weak to support more than one animal. On occasion, however, the adult male and adult female sang only 2-3 metres away from each other, usually immediately after the great call embrace.

Close spatial relations were also exhibited during bouts of feeding. Like agile gibbons at Sungai Dal (Gittins, 1979), the average distance between feeding animals was 5 - 10 metres, but sometimes individuals would feed almost side-by-side, their solitude preserved simply by keeping their backs to one another. Gittins (1979) stated that in a feeding context, agile gibbons are "very tolerant of intrusion of individual space" and this seems to be a more appropriate interpretation of the feeding spatial patterns observed for RBC2 and RBC1. Of course, when tensions did arise between group members, this tolerance broke down and gibbons would feed at much larger distances (> 10 metres) from each other.

Resting periods were so brief that gibbons rarely came together to enjoy this less strenuous activity, evidently preferring to sit alone. Indeed, as soon as the leading individual stopped to rest, other troop members would often stop too and, if the group was travelling or foraging, this often meant resting gibbons were separated by over 10 - 15 metres. During longer periods of rest, inter-individual distances tended to be smaller since group members either chose to settle next to each other or were able to reduce the distance between them and a neighbouring animal as the bout progressed

Travelling, and in particular foraging, found gibbons maintaining greater distances to one another. When moving through the home range, the group travelled in single file, individuals generally separated from each other by no more than 20 metres. During foraging expeditions, gibbons consistently kept further apart. Inter-individual distances averaged 10 - 20 metres as they did for travelling but, in contrast, group members spent similar amounts of time separated by even larger distances, sometimes as much as 60 metres between the leading gibbon and those trailing behind.

7.5.3 Direction of activities

Identifying the individual who initiates and terminates maintenance activities can indicate who directs group behaviour and help in assessing dominance relations in the gibbon adult pair. Neither sex commanded travel leadership nor the decision to rest, and although duetting was invariably started by the adult female, a territorial function rather than a assertion of position explains this sex imbalance (Tables 7-10 and 7-11).

Table 7-10 Inter-individual variation in the initiation of maintenance activities.

	RBC2					
	AM2		AF2		SF2	
	%	n	%	n	%	n
Rest	27.1	32	42.4	50	30.5	36
Travel	35.2	92	38.9	102	25.9	68
Sing (duet)	0.0	-	100.0	83	0.0	-
Feed	31.0	36	58.6	68	10.3	12
	RBC1					
	AM1		AF1		JF1	
	%	n	%	n	%	n
Rest	44.4	28	52.4	33	3.2	2
Travel	49.2	58	42.4	50	8.5	10
Sing (duet)	0.0	-	100.0	36	0.0	-
Feed	42.9	21	51.0	25	6.1	3

n = number of bouts (includes only those bouts in which all individuals participated in the same activity)

Behaviour at food sources proved to be a stronger indicator. The mature members of RBC2 did not equally control feeding visit initiation or its duration. Of the 116 feeding bouts in which all gibbons participated and the first feeder was detected, the adult female initiated just over half of them, significantly more often than the subadult female (χ^2=39.2 d.f.=1 p<.01) and the adult male (χ^2=9.8 d.f.=1 p<.01). The group also showed an unequal distribution in who terminated feeding visits (χ^2=7.16 d.f.=2 p<.05), and, once again, it was the adult female who determined when the bout ended. In contrast, the adult female of RBC1 entered feeding trees only slightly more often than her male partner who, in turn, left the food source first on 61% of group feeding visits.

Table 7-11 Inter-individual variation in the termination of maintenance activities.

	RBC2					
	AM2		AF2		SF2	
	%	n	%	n	%	n
Rest	34.1	44	37.2	48	28.7	37
Travel	32.8	76	40.9	95	26.3	61
Feed	30.7	59	42.2	81	27.1	52
	RBC1					
	AM1		AF1		JF1	
	%	n	%	n	%	n
Rest	57.3	55	41.7	40	1.0	1
Travel	43.3	26	48.3	29	8.3	5
Feed	61.0	50	30.5	25	8.5	7

n = number of bouts (includes only those bouts in which all individuals participated in the same activity)

7.6 Affiliative intra-group behaviour

7.6.1 Grooming

Gibbons devote more of their time to social grooming than any other intra-group social behaviour (Chivers, 1974; Ellefson, 1974) but considerably less frequently compared to the more social primates where bouts of grooming may aid in the formation of alliances or coalitions and/or cement bonds between both kin and unrelated animals (Goosen, 1987; Walters and Seyfarth, 1987; Dunbar, 1988). Grooming accounts for no more than 5% of the gibbon activity budget with some species engaged in grooming bouts only once every few days (*agilis* – Gittins, 1979; *muelleri* – Leighton, 1987). Hybrid gibbons showed a similar lack of interest in regular grooming sessions. Grooming behaviour in RBC2 and RBC1 was observed on just 21 (35%) and 12 (26.1%) of observation days respectively. Indeed, grooming was so infrequent it could not be attributed a score in the overall activity budget.

Normally only one or two discrete bouts of grooming occurred a day but during two unusually long resting periods up to four sessions took place. Grooming sequences were quite short, lasting on average 3.4 minutes. Bouts lasted a little longer, ranging from 2 to 14 minutes and averaging 6.7 minutes, but are shorter than those recorded for *lar* (Ellefson, 1974) and siamang (Chivers, 1974). Bouts of social grooming between members of RBC2 were spread relatively evenly throughout the activity period, the earliest bout recorded at 0700, and the latest after 1400 (Figure 7-1). In contrast, RBC1 gibbons only ever groomed each other after mid-day, these bouts coinciding with an increase in resting prior to night tree selection and retirement. Grooming usually took place during the brief rest stops characteristic of these groups but sometimes a gibbon initiated a session immediately after a feeding visit. When visibility permitted, post-retirement grooming between the adult female and her young(er) offspring was also observed in the night tree.

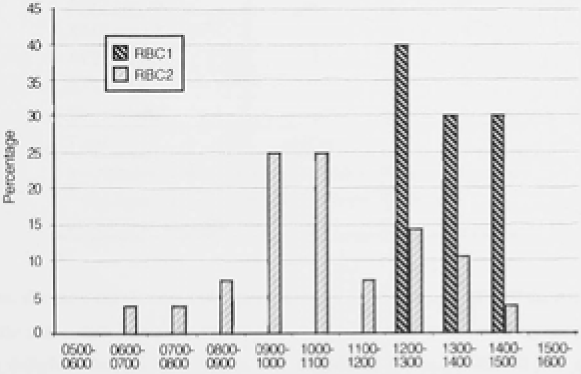


Figure 7-1 Temporal patterning of grooming behaviour.

Chivers (1974) noted that grooming, at least during the activity period, normally involved mature animals, with immature animals receiving attention once the group had concluded their activities for the day. Temporal patterning of grooming partnerships in RBC2 displayed a similar trend but one which may have been influenced by their sleeping arrangements. Not sharing night trees meant that the mature members of RBC2 could engage in such behaviour only during the day and hence they did.

Eighty six percent of RBC2 activity period grooming involved mature animals only (Table 7-12). Siamang and *lar* grooming pairs also centred around combinations of mature group members (Chivers, 1974; Ellefson, 1974) although in the *agilis* group studied by Gittins (1979) it was the adult male and juvenile male who regularly groomed together. Gittins (1979) suggested that these two individuals groomed often to reduce the tension developing between them. Despite the occasionally strained relationship between the adult female and her subadult daughter, only two bouts of grooming occurred between them. Instead, the subadult chose to enter grooming sessions with her father, accounting for 46.4% of all pair groupings. The adult male was also the preferred grooming partner of the adult female; the two engaged in 32.1% of all bouts. In all incidences, the subadult initiated grooming.

The infant in RBC2 participated in just four bouts of grooming outside the night tree. Two of these bouts were with her mother and one each with the adult male and subadult female. The low incidence of daily grooming between mother and infant does not necessarily mean that the two rarely groomed since it is my impression that the two probably did groom frequently but only in the solitude of the night tree.

Table 7-12 Frequency of grooming partnerships in RBC2.

Grooming partners	%	n
AM2 and AF2	32.1	9
AM2 and SF2	46.4	13
AM2 and I2	3.6	1
AF2 and SF2	7.1	2
AF2 and I2	7.1*	2
SF2 and I2	3.6	1
Total	100.0	28

n = number of bouts which occurred in the activity period

* this figure does not include grooming bouts that occurred in the night tree (n = 23)

RBC1 gibbons divided their time relatively equally to different pair groupings (Table 7-13). The adult male and adult female groomed each other slightly more frequently than they did their juvenile daughter but this difference was not significant. In fact, as the year progressed, the juvenile's participation in grooming bouts with her parents increased but she still spent a reasonable proportion of her grooming time with her mother in the night tree.

Table 7-13 Frequency of grooming partnerships in RBC1.

Grooming partners	%	n
AM1 and AF1	46.7	7
AM1 and JF1	20.0	3
AF1 and JF1	33.3*	5
Total	100.0	15

n = number of bouts which occurred in the activity period

* this figure does not include grooming bouts that occurred in the night tree (n = 11)

7.6.2 Sexual and reproductive behaviour

With the exception of reports by Chivers and Raemaekers (1980), Mitani (1990) and Palombit (1995), longitudinal data on the reproductive behaviour of gibbons still remains scarce and reveals no obvious trends. A further limitation is the actual infrequency of sexual activity in a gibbon's life, a field study of up to two years possibly finding little or no sexual behaviour (Leighton, 1987). As a result, sightings of sexual behaviour remained rare in this study too.

7.6.2.1 Sexual receptivity

Female gibbons display some physical change to genitalia during menstruation/ovulation although not to the same extent or as distinct as those characteristic of other primate species (e.g. the reddening and swelling of sexual glands around the perineum of female baboons and macaques – Rowell, 1972; Dixson, 1977). In wild *lar*, Carpenter (1941) observed changes in the colour and turgidity of female genitalia, and in captive *lar* and *hoolock* females, variation in the colour, eversion and turgidity of the urethral eminence, labia minora and vaginal wall coincided with different stages of the menstrual cycle (Matthews, 1946; Berkson and Chiacumpa, 1969; Breznock et al., 1977; Kawakami and Kollias, 1984; Dahl and Nadler, 1989; 1992; Nadler and Dahl, 1992 cited in Palombit, 1995). Female siamang also showed changes to external genitalia, primarily in the colour of the vulva which alternated between black, white and red (Chivers, 1974). All three mature females showed cyclical patterns of labial swelling which followed the proposed 28-30 day menstrual cycle. Eversion appeared to be maximal at times coinciding with sexual behaviour but clear sightings of female genitalia only occurred during a session of genital inspection involving AM2 and SF2 and a period of sexual activity between the adult pair of RBC1.

7.6.2.2 Sexual behaviour

While Gittins (1979) and Sheeran (1993) saw no signs of sexual activity, other field studies have detected a distinct breeding period in which sexual activity rises markedly over an interval of up to five months (Chivers, 1974; Ellefson, 1974; Chivers and Raemaekers, 1980). Sporadic bouts of sexual behaviour may occur (e.g. hoolock gibbons at Lawachara – Islam and Feeroz, 1992a) but consistent displays take place only once every few years (Ellefson, 1974). Very few incidences of sex occurred within RBC2 (Table 7-14) – two completed copulations between the adult male and adult female (19 October and 1 July) and three attempted copulations, one with the adult female (18 October) and two with the subadult female (7 February and 17 May). In contrast, and representing a breeding period proper, the mated pair of RBC1 concentrated all but one of their copulatory bouts in a short two week period, encompassing the last week of December and first days of January.[11] In eight days, two attempted and five completed copulations were observed, giving a rate of 0.88 bouts per day. A birth in August 1998, approximately seven to eight months after this peak of sexual activity and corresponding with average gestation time for gibbons (Carpenter, 1940; Chivers, 1974), indicates that conception occurred during this breeding period.

Table 7-14 Frequency of sexual behaviour.

Pair combination	Attempted copulation		Copulation with introgression	
	%	n	%	n
AM2 and AF2	33.3	1	66.7	2
AM2 and SF2	100.0	2	-	-
AM1 and AF1	28.6	2	71.4	5
Total	41.7	5	58.3	7

All possible and completed copulations were dorso-ventral and resembled sexual positioning described for other hylobatids (Carpenter, 1940; Chivers, 1974; Ellefson, 1974; Leighton, 1987). On no occasion did females solicit males; hybrid males, like their *syndactylus*, *klossii* and *muelleri* counterparts (Chivers, 1974; Tilson, 1981; Leighton, 1987) initiated all copulatory bouts. A male solicited a female by thrusting against her back or side and, if the female was interested, she dropped into a crouching position and raised her pelvis. Copulation lasted 2-3 minutes on average in which the male gave an average of 41 thrusts a minute. During some bouts, the male temporarily stopped thrusting to change his position or to allow his partner to change hers. No vocalisations, such as the *whine-squeals* given by *lar* (Ellefson, 1974), were heard but the height at which all copulations took place may have prevented their detection. When the male had finished, the female immediately got up and moved to a distance approximately three to five metres away from her mate. The two remained sitting quietly until one or the other initiated another maintenance activity.

One incidence of genital inspection occurred in April between the adult male and subadult female of RBC2. While grooming his reclining daughter, the adult male proceeded to visually and then physically inspect her external genitalia, lowering his head to sniff this region and using his fingers to touch her. The subadult remained passive throughout the examination and, surprisingly, so did the adult female who continued to feed despite being only 10 metres away and aware of her mate's activities. No apparent or observed sexual behaviour occurred between father and daughter in the following days.

With the exception of the previously described genital inspection and one copulatory bout between the adult male and female of RBC1, all bouts of sexual behaviour occurred before midday. RBC2 tended to engage in sexual displays in the early morning; three of the four

---

[11] A 5-day sample with RBC2 between the 15-20 December and the rain-related difficulties associated with finding RBC1 in January prevented observation in the weeks preceding and following this time.

copulations, completed or otherwise, took place between 0600-0800. RBC1 sexual behaviour peaked later in the morning, between 1000-1200. Normally coinciding with periods of rest, the RBC1 mated pair once engaged in a copulatory bout directly after a feeding visit.

7.6.2.3 Pregnancy and inter-birth intervals

In April, three to four months after the probable conception, the abdomen of RBC1 adult female was noticeably enlarged. Palombit (1995) has reported that abdominal distension occurs slightly later in pregnancy, approximately 150 - 160 days (i.e. 5 months) after conception, with full distension immediately prior to parturition (190 - 220 days). As indicated in the previous section, the pregnancy was carried to full-term, despite the adult female's fall during an intergroup encounter with RBC2. Unfortunately, neither the birth nor the new infant was seen, occurring only a matter of weeks after the field study had been completed.

7.6.3 Play

Not unexpectedly, play behaviour was common for the young members of RBC2 (IF2) and RBC1 (JF1) but only an occasional past-time for the mature individuals (Table 7-15). Although scan sample data were not collected for the infant, regular notes taken on its social behaviour showed that she devoted a good proportion of her non-travelling and feeding time to exploration or play, usually when the rest of the group were resting or settled in the night tree. Solitary games dominated most of her recreation time, centring either around the manipulation of some material found in the home range or a display of gymnastics. In the former (referred to as *object play* – Walters, 1987), the infant extracted plantstuffs (e.g. twigs) or caught invertebrates which she threw, caught, bit and chewed on before discarding them for another play tool or activity. Energetic bouts of play (*solitary locomotor play* – Walters, 1987) involved considerable agility and flexibility as the infant performed routines incorporating hanging (by arms or legs), swinging, and jumping and crashing into the foliage below.

Table 7-15 Frequency of individual play.

RBC2	%	n
AM2	1.6	2
AF2	0.0	0
SF2	0.0	0
I2	98.4	126
RBC1	%	n
AM1	0.0	0
AF1	0.0	0
JF1	100.0	25

Bouts of social play occurred less frequently, twenty one encounters involving the infant of RBC2 and eight with the juvenile female of RBC1 (Table 7-16). In both groups it was the father who commonly initiated play with them or responded to their entreaties, the adult male-immature female combination accounting respectively for 50.0% (n=11) and 75.0% (n=6) of RBC2 and RBC1 pair associations in play. Adult males normally played with their young during the activity period, either when the group had stopped for a period of rest or while his mate continued to feed in a food patch he had recently left. The adult females also played with the infant and juvenile during the day but it is my impression that most play interaction between mother and daughter, particularly in RBC2, occurred once they had settled in the night tree.

Table 7-16 Frequency of social play pair combinations.

RBC2	%	n
AM2 and AF2	0.0	0
AM2 and SF2	0.0	0
AM2 and I2	50.0	11
AF2 and SF2	4.5	1
AF2 and I2	31.8	7
SF2 and I2	13.6	3
RBC1	**%**	**n**
AM1 and AF1	0.0	0
AM1 and JF1	75.0	6
AF1 and JF1	25.0	2

The subadult female did not play as often with her sister as her parents did, possibly because the adult female did not always approve of any form of close interaction between the two. During the three bouts in which the sisters did play, the adult female did not make any attempts to interrupt the game nor did she intently observe the proceedings. However, on another occasion (reported in Section 7.8) she responded quite aggressively to the subadult accepting the infant's invitation to play.

Although adults normally played with the infant, they also engaged in bouts of play on their own or with each other. Twice the adult male of RBC2 was observed in object play, removing plant material or squirrel fur from abandoned birds nests to be used in a game of throw-and-catch or to be trailed behind while brachiating. Leap-frog featured in a short play session between the adult and subadult females, the latter hurdling the former three times before being caught and tussled with. Grappling between the adult male and adult female also occurred once during a play session with the infant.

Despite the evident enjoyment gibbons received from play, it was a rare behaviour and accounted for less than 1% of both RBC2's and RBC1's activity budget. An absence of regular play has also been reported for lar and agile gibbons (Gittins, 1979; Gittins and Raemaekers, 1980) but occurs at a slightly higher, although still very low, rate in siamang (Chivers, 1974; Gittins and Raemaekers, 1980). Solitary or social play did not occur at any particular time of the day, possibly because of the absence of a true resting period. However, social play did take place more often in the late morning and early afternoon, only two bouts (one for each of the focus groups) occurring before 0900.

7.7 Aggressive intra-group behaviour

The mostly peaceful and tolerant relationship displayed between members of a gibbon group largely precludes regular or particularly violent displays of aggression. Agonistic interactions are not common and when they do occur, bouts are usually short-lived and rarely disrupt the harmony existing within the group (Chivers, 1974). Signs of tension are mostly conspicuous at feeding sites where normally co-dominant or amicable individuals may engage in, or accept, hostile behaviour but it is the onset of certain behaviours (e.g a period of sexual activity) or the maturation of offspring which magnifies intra-group aggression (Chivers, 1974; Tilson, 1979; 1981; Gittins and Raemaekers, 1980; Leighton, 1987).

Aggression did not feature commonly in RBC2 nor RBC1 intra-group social behaviour, just 20 and 2 bouts respectively occurring between group members. The suppressed intra-group friction within RBC1 compared to RBC2 is not necessarily related to a disparity in observation days but more likely reflects the differing social dynamics existing in these two groups. Although juveniles do suffer some victimisation from their parents (Chivers, 1974; Ellefson, 1974; Gittins, 1979; Gittins and Raemaekers, 1980; Leighton, 1987; Fischer and Geissmann, 1990), they do not represent an overt threat, be it sexual (i.e. to their same sexed parent) or ecological (e.g. food supply), to their parents. Thus juveniles are mostly immune to serious or continual harassment. The little aggression directed at the juvenile female of RBC1 by either of her parents was therefore not unexpected and the tolerant, if not indifferent, relationship between the adult pair neutralised any potential disquietude. In contrast, the social composition of RBC2 augurs some degree of hostility. The presence of not only a sexually mature daughter, but one who appears to be firmly entrenched in the group and engaged in harmonious alliance with her father, is illustrative of a situation conducive to the stimulation of discord, or exacerbation of already existing tensions, between the two females. Because of the unique social composition of RBC2 and their greater rate of intra-group hostilities, discussion of aggression will focus on observations derived from this group.

Of the twenty aggressive interactions, the adult male took part in only four (Tables 7-17 and 7-18). The adult male played the role of aggressor in three of these encounters, directing his displeasure on every occasion at the subadult female. Two of these incidents were elicited when the subadult got too close to him while feeding (see Table 7-19 for aggressive bout context). During the fourth encounter, he was the victim of an attack by the adult female after entering a tree she was feeding in.

Table 7-17 Frequency of aggressive interactions.

Group	Total no of aggressive interactions	No of aggressive interactions / day
RBC2	20	0.24
RBC1	2	0.05

Table 7-18 Participation and role played in RBC2 aggressive interactions.

	No of bouts	% of bouts	No of bouts: aggressor	No of bouts: victim
AM2	4	20.0	3	1
AF2	18	90.0	18	0
SF2	19	95.0	0	19

Aggressor > Victim	No of bouts	% of bouts aggressor involved	% of all bouts
AM2 > AF2	0	0.0	0.0
AM2 > SF2	3	75.0	15.0
AF2 > AM2	1	5.9	5.0
AF2 > SF2	17	94.4	85.0
SF2 > AM2	0	0.0	0.0
SF2 > AF2	0	0.0	0.0

Table 7-19 Context for aggressive interactions between mature members of RBC2.

Stimulus	%	n
Invasion of space - feeding	40.0	8
Invasion of space - other	20.0	4
Too close to infant	5.0	1
Unknown	30.0	6

The remaining sixteen displays of aggression involved the adult female and her daughter in which the former was the aggressor every time. Although the context for five of these aggressive interactions could not be discerned, the majority arose from the subadult maintaining too close a proximity to the adult female. Such invasions of individual space and the resultant attack, occurred either during bouts of resting or feeding, the latter of which always centred around a fruit source and concluded with a displacement. An example is given below. (Note that in this incident the adult male joined his partner in attacking the subadult female. This was unusual behaviour as he normally ignored such bouts of harassment).

3 April 1996 – 0920

> RBC2 have just started feeding in a fruiting *Baccaurea* tree. SF2 runs along a branch towards her feeding mother who immediately turns around and chases her back along the branch. When she catches up with her, they start grappling, eventually dropping down to suspend from the branch in a *hang-wrestle*. After a short period (approx. 50 seconds) of struggling, SF2 falls to a lower branch, either from a push or in an attempt to escape her mother. The adult male, who has spent this time feeding in another part of the tree, brachiates over to AF2 and then joins her in chasing the SF2 out of the tree. SF2 flees to a neighbouring tree, emitting the bird-squeal vocalisations, and does not return to the food source until both parents have become engrossed in fruit selection and consumption.

In all but two of the AF2-SF2 aggressive encounters, the subadult exhibited only submissive or appeasement gestures, enduring the chase and the associated blows to the body, and responding to attacks with fear vocalisations (bird squeals, *twoulwills* or screams – see Sections 8.3.2 and 8.3.3), crouch postures and escape from the site of the attack. If she returned to the tree, she did so with some caution, occupying a position at a respectful distance from her mother and only after a period of time presumably long enough to guarantee a lessening of tension. Two encounters saw SF2 stand up to AF2 to a certain extent although both ended with a deferential display by the younger gibbon.

21 March 1996 – 0640

> RBC2 are feeding in a *Ficus villosa* tree. SF2 is feeding in between her mother and infant sister. SF2 moves slightly towards AF2 who responds by moving over to SF2 and pulling the hair on her arms. SF2 refuses to move and fends off her mother by raising and flailing her arms. AF2 backs off momentarily but then runs along the branch to SF2, screaming while slapping at her. She then chases SF2 but in contrast to previous chases, SF2 stops on the edges of the tree, turns around and stares at AF2, with a slight lowering of the head. They both stare at each other for a few seconds, followed by a forward head thrust by AF2. AF2 then returns back to the tree to feed. Two minutes later SF2 also resumes feeding but at some distance from her mother.

Resting intervals often saw the infant leave her mother to seek out other group members. As previously mentioned, the adult female allowed her infant contact with both the adult male and the subadult female but took exception on one occasion to the subadult nursing the infant. As for the previously described incident, the subadult female was not initially intimidated by her mother.

11 May 1996 – 0850

> AF2 and I2 are resting together. SF2 joins them, sitting approximately a metre away. Not able to induce her mother to play with her, I2 runs over to SF2 who picks her up and holds her in a typical nursing position. Unaware of I2's absence, AF2 remains resting but on turning around, and seeing where her younger daughter has got to, she threatens SF2 with a forward head thrust, exposing her canines. SF2 does not release I2. AF2 then gets up and walks over to SF2, standing over and staring at her. SF2 holds on to I2 for another 10 seconds before letting her go and leaving the tree.

Sixty percent (n=12) of the aggressive interactions between the adult and subadult females occurred in just 4 months, little or no conflict existing, or observed, for the rest of the year (Figure 7-2). Previous reports on the peripheralisation of subadults described a steady increase in antagonistic behaviour directed at the subadult (Chivers, 1974; Gittins and Raemaekers, 1980), sometimes erupting into a period of concerted and relentless attacks (Tilson, 1981). Peaking of aggression in RBC2 did not follow this trend, the subadult receiving most threats in months 4 (December), 5 (January), 8 (April) and 9 (May) of the study period. The fluctuating pattern of RBC2 intra-group aggression may, instead, reflect a corresponding variation in specific social and environmental factors which can, at least theoretically, provoke or smooth tensions between mother and daughter.

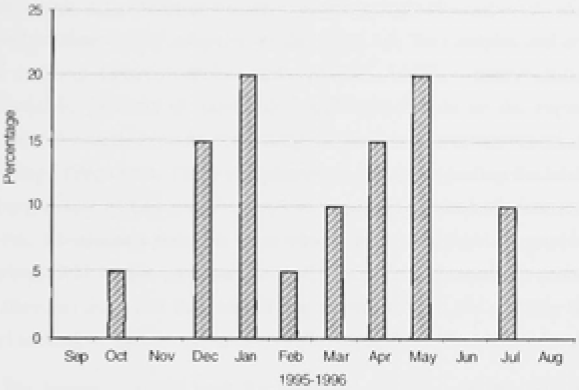


Figure 7-2 Monthly variation in the frequency of RBC2 aggressive encounters.

An examination of the effect of social factors on monthly levels of AF-SF aggression incorporated a comparison with spatial and activity associations and the frequency of grooming and sexual behaviour. Aggressive encounters did not correlate with either category of pair associations ($p>.05$) and apparently was not dependent on whether the subadult spent more time with her mother or father. Similar statistical analysis using rates of grooming and sexual activity was inappropriate due to the small sample size of affiliative behaviours and hence only trends can be explained. Grooming is considered to be a social tool in which bonds are established and maintained and hence may aid in the reduction of group antagonism (but see Oki and Maeda, 1973; Fischer and Geissmann, 1990). In captive lar gibbons and siamang, agonistic encounters did show a significant and negative correlation with both the number of grooming bouts/hour and grooming duration/animal/hour (Fischer and Geissmann, 1990) but little relation was obvious between these variables in RBC2.

Some evidence, however, was found for an association between the increase in female-female tension and the adult male exhibiting sexual interest in his daughter, if only for the period encompassing March - May 1996. During, or just prior to this time, the subadult endured nine attacks from the adult female but also received sexual advances from the adult male, mostly in the form of inspection of her genitalia (once) and two attempted copulations. The adult female may have been alarmed at the attention the adult male was showing towards the subadult female and responded by asserting her position as the senior female in the group.

7.8 Discussion

7.8.1 Hybridity and gibbon social behaviours

Before assigning similarities or variations in social organisation observed between different groupings of animals to functions of taxonomy or social-ecology, recognition must be made of the process through which these behaviours are governed. While some behaviours are controlled by *phylogenetic adaptation* (Kummer, 1971) or "the product of the behavioural programs with which individuals of that species are genetically endowed" (Sugawara, 1988) others are greatly influenced by *adaptive modification* i.e., the complex and differential social relationships existing between individuals (Hinde, 1975). Successfully detecting or "abstracting specific patterns of inter-individual interactions or the repertory of innate behaviour of the individual from the very complex social relationships among the members of free ranging group" (Sugawara, 1988) complicates any study regarding the intrinsic nature of a species social organisation. Comparative work incorporating genetically intermediary or hybrid groups, however, introduces a template from which the development of certain behaviours can be tested. Various field studies on populations of *P. anubis, P. hamadryas* and hybrid groups in the Awash Valley has done just that, identifying a genetic basis for sleeping site choice, male aggression and herding technique (Kummer, 1968; Nagel, 1973; Kawai and Sugawara, 1976).

Investigating the genetic or social basis for hylobatid social repertoire and structure is not so easily achieved for three primary reasons. Firstly, striking differences in the social organisation of species such as *P. anubis* and *P. hamadryas* are largely absent from any cross-species comparison within *Hylobates*. Secondly, gibbon social display is rarely as demonstrative or as frequent as that of highly social primates such as baboons and probably relies on cues the human observer is yet to discern. Thirdly, the most common method used to measure social conformity or nonconformity (the frequency of a specific behaviour or behavioural routine [e.g. grooming]) is a clumsy and potentially unreliable indicator of both phylogenetic preference and species similarity. Sugawara (1988) has argued that the *use* of a behaviour is not under the exclusive control of the genes but is influenced just as strongly by the social environment within which the group finds itself, the status each individual holds, and the social context under which the behaviour is performed. Furthermore, the sequence of behaviours preceding, comprising and following the social interaction are just as important to the analysis of social behaviour as the actual display itself. With these analytical and behavioural limitations in place, discussion on the social behaviour of the hybrid gibbon compared to that of the parental *agilis* and *muelleri* becomes somewhat restricted. The fact that gibbon intra-group social interactions are both so rare and easy to miss leaves only the basic and simplistic measures of frequency and variation to calibrate any specific differences or effects of hybridity.

Indices of social relations presented in this chapter found no evidence for disruption to the harmony or success of the gibbon family unit and in fact both focus groups showed a level of behavioural synchrony greater than that observed for *agilis*, *muelleri* and other lar group gibbons. Although reliant on the security that the group provides, and despite maintaining relatively close association during some activities, individuals in RBC2 and RBC1 still demonstrated the independent attitude characteristic of the smaller gibbons. Group members rarely came together for bouts of rest and, in turn, grooming interactions, or simple bodily contact, tended to be uncommon. Furthermore, consistent displays of sexual interest coincided exclusively with the breeding period and infrequent bouts of aggression introduced only minor and short-lived discord into the group. Whether gibbons in general do not need consistent social assurance or instruction, or if the composition of the group exempts group members from engaging in overt social contact, remains a topic for debate but it seemed quite evident that extreme tolerance, rather than indifference, governed the relationships between members of hybrid groups.

7.8.2 Variation in gibbon social organisation

Hybridisation and its changes to the social repertoire alters both the method through which an animal signals its social status or intent and the way it interprets or responds to the actions of another. To what extent social, or indeed ecological, behaviour is modified can in turn generate varying degrees of transformation to the social structure itself. Again, research on hybrid baboon populations presents the most complete examination of hybridity and group composition (Sugawara, 1982; 1988; Phillips-Conroy and Jolly, 1986; 1991) and demonstrates how unique social structures arise from differential parental forms. For a genus like *Hylobates*, where interspecific social organisation is proposed to observe the same, rather strict family unit composition, variation in social structuring would appear to be given less scope. However, if behaviour is so affected that gibbons do not demonstrate the *normal* patterns of social recognition and protocol, social grouping might be somewhat modified.

Previous work conducted at Barito Ulu found no evidence of mixed trios or "strange social groups" (Bodmer et al., 1991; Mather, 1992). My own census of groups surrounding the primary research area also indicated, with one exception, that hybrid gibbons observed the traditional family social system. But census techniques employed by both Mather and myself were either too limited or not sophisticated enough to accurately identify the true social situation of most study groups (see Chapter 9 for further discussion) and hence unusual social groupings may have gone undetected.

The social behaviour described for RBC2 does suggest that this group represented a polygynous trio. Unequivocal demonstration of polygyny in RBC2 required both females to carry infants at the time of the study, or to show evidence (e.g. pendulous nipples) of having produced offspring in the past, but reproductive behaviour could be confirmed only for the older, adult female. While a strict interpretation of polygyny serves to confirm that a gibbon group *has* adopted a polygynous social structure, the absence of supportive criteria does not invalidate its existence. It may be that females will only tolerate bigamy if only one female breeds with the male (Brockelman and Srikosamatara, 1984). Social interactions between mature group provide beneficial insight into the dynamics of the group and serve just as credibly as markers of social structure.

7.8.2.1 The identity of the subadult female

Before evidence is presented supporting the proposal that RBC2 is a trio formed via a familial pathway, it must be determined unconditionally that the second female is indeed the daughter of the mated pair and has reached sexual maturity.[12] Greenaway (1991) and Lochowski (1991) report that in 1991 RBC2 was composed of an adult pair, a subadult female and an infant. In

---

[12] The absence of a consistent naming system for groups surrounding the basecamp introduced considerable confusion to this process, making it difficult to relate census data from one report to the next. Greenaway (1991, unpubl.) and Lochowski (1991, unpubl.), however, included home range maps in their report which allowed the identification of relevant groups.

the year preceding my study (i.e. 1994-1995) RBC2 also comprised four individuals – an adult pair, a subadult female and a "large, probably subadult" male (Kursani, 1995 pers. comm.). The latter observation contradicts both traditional concepts of gibbon social group organisation and mean inter-birth spacing. To explain this observation, and at the same time identify the second female in RBC2, four scenarios are proposed (note the second male observed in 1994 is referred to as SM2).

1. *SF2 and SM2 are, respectively, the subadult female and infant observed by Greenaway and Lochowski in 1990-1991.*

   This scenario insists that SF2 was, in fact, approximately 9-13 years of age and therefore an adult at the time of the 1995-1996 study. SF2 was certainly adult sized and it is not inconceivable that she was older than first reported. The absence of pendulous nipples indicated that SF2 had not begun her "reproductive career" but this was not necessarily a sign of not having reached sexual maturity. For some female gibbons, the interval between menarche and reproduction can be as long as four years (Palombit, 1995). Furthermore, it has been suggested that females living in a polygynous group might be more tolerant of one another if only one female breeds with the resident male.

2. *The original subadult female left the group between 1991 - 1994 and either SF2 or SM2 is the infant observed in 1991.* It follows that:

   a. *SM2 is the infant born to the RBC2 adult pair and SF2 immigrated from elsewhere.*

   As a rule, territory holding, pair-bonded females do not respond agreeably to alien females attempting border crossings or interactions with their mates. Aggressive behaviours demarcate these female-female relationships and no social or ecological reason can be presented in this case to explain why an adult female would accept another female, and an unrelated one at that, into her group.

   b. *SF2 is the infant born to the adult pair and SM2 immigrated from elsewhere.*

   The argument given above also applies to male gibbons although an incidence of polyandry via immigration has been reported for *lar* (see Bartlett and Brockelman, 1996). In 1991, neighbouring groups RBC1 and RBC3 had resident juvenile males who would have reached subadulthood between 1991-1994. One of these males may have transferred temporarily into RBC2 but why he would have done so, and why RBC2 would let him, remains unclear.

   c. *SM2 and SF2 are, in fact, brother and sister, the younger sibling born sometime after March 1991.*

   Patterns of hylobatid reproductive behaviour initially renders this explanation unlikely. For a start, it would be unusual for a wild female gibbon to produce two offspring within 12 to 24 months of one another, despite the variability in inter-birth interval reported for gibbons (Hill, 1967; Chivers and Raemaekers, 1980; Mitani, 1990; Palombit, 1995). Of course, if the adult female had given birth to infants fathered by different males, it might

> then be possible for two closely aged and related offspring to reside in the one group (see Sommer and Reichard, in prep.). In the absence of direct observation of EPCs and information on pair bond dynamics in the RBC groups, this theory cannot be substantiated. However, a lone, habituated male was spotted feeding in the northern section of RBC2's home range in January 1996.[13] The fact that the male remained unperturbed, even when we stood directly under the small tree he was feeding in, suggested that he had originally been a member of on of the habituated groups.

Although none of the options can be verified with the available data, it is still my contention that the second female in RBC2 is the daughter of the resident pair. Although polygynous associations in the Khao Yai hybrid zone have presumably been formed by the immigration of a new female into the group (Brockelman and Gittins, 1984), patterns of female-female distribution and the general intolerance female gibbons show to other, strange female gibbons suggest that females are more willing to accept a polygynous social setting with a related female.

7.8.2.2 The social position of the adult and subadult females

The relationship shared by the adult and subadult female was one moderated by social distance and disrupted on occasion by tension and antagonism. Such a relationship is not so unusual for gibbons; even the mated pair demonstrates a bond devoid of continual and overt social solicitation; but interactive display between the two females implied that they expected (adult female) or complied with (subadult female) an association of conditional tolerance. Consequently, the adult male represented a preferable social partner to the two females. Both females spent a greater proportion of their time in behavioural synchrony with the male than they did with each other, and spatial distancing indicated that relationships were more harmonious, or at least more compatible, between the sexes. Incidences of affiliative and aggressive behaviour maintained the status of pair relationships. Grooming never became more than an occasional social activity but females repeatedly chose the male as their grooming partner. Furthermore, when group members interacted aggressively, it always involved, with the exception of one incident, a displeased adult female harassing the subadult, provoked by spatial incursions or improper behaviour (e.g. cradling the infant) from the latter individual.

Same-sex parents are normally the first to shun the subadult and they are invariably the aggressor who inflicts the most extreme forms of harassment (Chivers, 1974; Tilson, 1981; Leighton, 1987). The subadult female's age and her apparent sexual maturity (labial eversions and sexual interest from her father) are incentive enough for an adult female to initiate a regimen of isolation, and the basic nature of the female-female relationship existing in RBC2 accords with previous descriptions of peripheralisation. But examining the patterns of, and responses to, social interactions within RBC2 reveals some substantial inconsistency. All accounts of subadult eviction stress the temporal intensification of parent⇒offspring directed aggression, and the repeated assaults the subadult endures from a parent if their other parent shows any sign of sexual interest in them. A process of increasing antipathy was conspicuously

---

[13] A lone male was again observed in this area in 1997 (Kim McConkey, 1998 pers. comm.).

absent from the relationship between the adult and subadult females and their association was akin to one of restrained tolerance, punctuated by occasional discord. The females did maintain respectful distances but spacing intervals were not marked nor did they increase as the study progressed. Feeding visits represented situations in which incursions on space would not be accepted by the older female but other than a few incidences of tension, she regularly allowed her daughter to feed at the same source and in close association. In turn, aggressive encounters tended to be sporadic events and showed little or no relation to known precursors, only some evidence was found to link bouts of aggression (in March, April and May) to incidences of sexual activity between father and daughter. These sexual interactions sometimes took place in full view of the adult female but she never once responded and in fact appeared to be rather disinterested by the whole proceedings. Certainly a strange reaction, and one in complete contrast to the behaviour of adult female who considers her daughter a threat to the stability of the pair bond!

7.8.2.3 Familial trio formation in RBC2 - socio-demographic delays to subadult dispersal

If the trio RBC2 was formed via a familial pathway, what factors led to the subadult female being able to retain her position in the natal group? Ecological disturbance is arguably a primary factor in the disruption of both dispersal patterns and social unit norms (see Liu et al., 1989; Sheeran, 1993) but neither habitat degradation nor human predation is marked in the main research area. A lack of potential mates, possibly influenced by a low birth rate in the hybrid population, may discourage subadults from leaving their natal group. The problems of establishing a territory on one's own, and the associated pressure of having to solely evade resident groups, can be just as burdensome as daily subjection to parental harassment. Certainly, the subadult female of RBC2 was faced with a dearth of potential suitors, just two unattached males living within the research area. Pairing with the first of these males, or even just meeting him, proved to be an impossibility for the subadult female since this male lived across the Busang river and at a point where the absence of an interconnecting pathway removed any chance of a river crossing. The range location of the second male, on the other hand, introduced many opportunities for mate solicitation and acquisition. Interestingly, neither the subadult female nor the unattached male appeared to take advantage of this opportunity. Actual or attempted meetings between the two were never observed, delivery of solo s remained uncommon and not once they did they respond to the song of the other.

Nowhere to go, due to the high density of conspecifics and/or tightly restricted territory holdings, can also impede a subadults ability to disperse. At the time of the study, RBC2's territory was being squeezed by RBC1, conceivably induced by the pressure RBC1 itself was experiencing from neighbouring groups. Rekut gibbons appeared not to live at problematic densities and therefore some other (undetected) factor (e.g. uneven resource distribution) may have compelled groups to extend or tighten borders. Restrictions in ranging space do not augur well for an individual hoping to establish a territory of its own and again it might prove to be less of an ordeal to stay within the group than to range in an area owned by others.

If difficulties in mate acquisition and territory procurement are able to dissuade a subadult from leaving its natal group, can they also persuade a mated pair to halt, at least temporarily, their peripheralisation behaviour? When the integrity of the ranging area is being threatened, unnecessary losses of territory holdings should be guarded against. Expelling a mature offspring runs the real risk of conceding a part of the territory to this individual, so allowing a subadult to stay for the short-term constitutes the preferable option to the mated pair (but see Emlen and Oring, 1977; Vehrencamp, 1983). Sharing resources with another, rather than giving them up entirely, exacts far less injury to the status and health of the group. In contrast, it is doubtful that an adult pair would be sympathetic to their offspring's unsuccessful attempts at mate solicitation. With time, an unattached subadult becomes an increasingly greater sexual threat to its same-sexed parent, and eventually the tension between the two results in one or the other having to leave. Better for the adult to expel the subadult as soon as possible.

In contrast, delaying the eviction of a subadult might in fact benefit the adult pair (Suwanvecho and Brockelman, 1997; 1998), if only for the short-term. The presence of another mature individual in the group provides the infant or juvenile with an additional playmate. For the mother, the subadult may also represent a de-facto guardian, enabling the adult female to spend more time away from her younger offspring in pursuit of other important maintenance activities (e.g. the location and consumption of food). Aiding the defence of the territory is another role the subadult might play (Suwanvecho and Brockelman, 1997; 1998). It has already been mentioned that if a subadult *lar* proves him or herself to be a committed encounter participant, adult gibbons will often downgrade their role in territory defence to let their offspring occupy the vanguard position (Ulrich Reichard, 1998 pers. comm.). With regard to RBC2, it was obvious that the subadult did not engage readily in babysitting duties. Nor was she encouraged to do so by the adult female (e.g. 11 May 1996 intra-group aggression). She did, however, participate vigorously in inter-group encounters. Her motives may not have necessarily been altruistic but her assistance was consistent and effective. Such behaviour could thus influence the adult pair to accept an extended period of residency for the subadult female.

7.8.2.4 Trio formation: The recognition of like versus unlike

An alternative theory considers the strength of inherent, rather than external, influences on the formation of "unusual" social groupings. One such innate effect concerns the ability gibbons display in the recognition of songs that are structurally different to their own. The song (e.g. structure, time of delivery) has already been proposed as one of the primary mate recognition systems employed by gibbons (Marshall et al., 1984; Marshall and Sugardjito, 1986; Groves, 1993) and a means by which animals protect the pair bond. If gibbons do exhibit trouble in recognising the identity of hetero-specifics, and more importantly those of the same sex, it follows that song recognition might then be a primary factor which influences under what circumstances polyandrous and polygynous associations form (Colin Groves, 1998 pers. comm.).

An examination of the specific identity of same-sex members in described cases of gibbon polygamy[14] reveals an interesting distinction between polyandrous and polygynous associations. In all polyandrous groups so far reported *(H. lar* and *H. hoolock)*, resident males were the same species. In polygynous associations, however, only two of the ten trios described consisted of same-species females and, in the case of one of these trios (i.e. the *H. hoolock* trio described by Ahsan, 1994; 1995), group formation was the result of unusual circumstances. For the remaining eight polygynous trios, group composition and location was found to be remarkably consistent. All were observed at gibbon contact zones and female membership consisted of individuals of differential specific or hybrid identity. Furthermore, not one trio described from any of the three known contact zones was characterised by a polyandrous association. Although the current sample is small, these findings prompts the question – why do trio-living males associate only with males of the same species when trio-living females tend to live with hybrid females or those of another species.?

Experiments recording behavioural response to the song of a conspecific compared to that of another species have been conducted for *H. agilis albibarbis* (Mitani, 1987a) and *H. lar* (Raemaekers and Raemaekers, 1985). In both experiments, groups responded to the song of a different species (*muelleri* and *pileatus* respectively), but not to the same extent as when exposed to the song of their own species (see Table 7-20 for summary of results). Both Mitani (1987a) and Raemaekers and Raemaekers (1985) have argued that these results are indicative of the gibbon's ability to use song as a means of discriminating between like and un-like. But whether gibbons can actually identify the call of another species as that of a gibbon, or can actually and correctly sex the caller, has been questioned by Mitani (1987a) and Raemaekers and Raemaekers (1985) and might explain the muted behavioural response gibbons give to the calls of another species.

Table 7-20 Differential responses to the call of a same-sex conspecific and heterospecific. (Table compiled from data given in Raemaekers and Raemaekers, 1985 and Mitani, 1987a).

	Male song						Female song			
	Conspecific (*albibarbis*)		Conspecific (*agilis* - Sumatra)		Heterospecific (*muelleri*)		Conspecific (*lar*)		Heterospecific (*pileatus*)	
	%	n	%	n	%	n	%	n	%	n
Male approach	100.0	9	100.0	9	55.7	5	75.0	6[1]	62.5	5[1]
Female approach	22.2	2	22.2	2	11.1	1	87.5	7	0.0	0
Male solo	11.1	1	0.0	0	0.0	0	*	*	*	*
Female solo	11.1	1	11.1	1	0.0	0	*	*	*	*
Duet	11.1	1	0.0	0	55.6	5	100.0	8	12.5	1
Male alarm call	66.7	6	33.3	3	33.3	3	*	*	*	*
Female alarm call	33.3	3	22.2	2	77.8	7	*	*	*	*

Male song: n = number of play-back experiments (Mitani, 1987a)

Female song: n = number of target groups (Raemaekers and Raemaekers, 1985)

[1] includes approaches made by adult pair together

---

[14] *H. concolor* trios were not included in this examination due to their location in forests altered by marked deforestation or other forms of habitat disturbance.

Unfortunately, comparing the results of these two studies is hampered by the fact that only male *muelleri* songs were played to *agilis* while only female *pileatus* songs were played to *lar*. Nonetheless, examining the behaviours given by male *agilis* and female *lar* when exposed to the call of a member of a different species, but of the same sex, suggests some differential degree in recognition. Male *albibarbis* did not show any marked tendency to react more strongly to the male songs of specific counterparts. When exposed to the male solo of either another *albibarbis* or Sumatran *agilis*, the male approached the source on every occasion, rarely soloed and sometimes gave an alarm call. When exposed to the solo of a male Müeller's gibbon, approaches were also regularly made and singing responses were mostly in the form of an alarm call. Alarm call responses were slightly more frequent when local *agilis* calls were played but, interestingly, the same rate of response was given when exposed to Sumatran *agilis* and *muelleri* songs. The frequency of male solo responses showed much less differentiation. In contrast, female *lar* showed considerable polarity in their responses to female *lar* and *pileatus* calls. When exposed to the great call of another *lar* gibbon, the female invariably initiated the duet, approached the source of the call, and led these approaches, either on her own or accompanied by her mate. When a female *pileatus* call was played, the *lar* female still approached the source but only on five of the eight playbacks and never as the leader. Of further significance was the absence of a female singing response, either in the form of a duet or a solo.

The behaviours displayed by male (*albibarbis*) gibbons in response to calls given by other gibbons, of the same and different species, and of the same sex, does not readily explain the relationship between song recognition and willingness to live in a polygamous social organisation. However, the results obtained from the Raemaekers and Raemaekers (1985) study indicate that such a relationship might exist for female gibbons. The *lar* female's failure to consistently and aggressively respond to the song of a *pileatus* female suggested to Raemaekers and Raemaekers (1985) that females of different species show greater tolerance to one another and thus may be more accepting of residency in a polygamous social unit.

And what of hybrid gibbons? In a population where hybridisation and cycles of backcrossing have produced animals of varying genetic composition, alterations to how one animal perceives another may play a more substantial role in the modification of behavioural norms than external forces such as threats on territory maintenance. If a defining behavioural trait, characteristic to one individual, is so affected that its performance in another animal only partially resembles the trait's original manifestation, it is then quite conceivable that the first animal will not correctly identify the status of the second. The great calls performed by the adult and subadult females of RBC2 did not vary as significantly as those of the mixed trio females but the delivery of the climactic notes, the most important feature of the great call, were easily distinguishable between the two (see Chapter 9 for description). The fact that the adult female routinely reserved the majority of her singing responses to females who gave great calls identical to her own suggests that the adult female did not or could not *recognise* the subadult's great call, and therefore the subadult herself, as representative of a sexual threat. Implementing a concerted program of eviction was therefore not necessary. As long as the younger female observed her subordinant position in the group, refraining from destabilising the pair bond or interrupting resource acquisition, the female did not feel the need to terminate her daughter's residency and accepted the new social grouping.

8

Song Structure, Song Repertoire and Patterns of Singing Behaviour

8.1 Introduction

8.1.1 Gibbon songs and song function

8.1.1.1 Gibbon song types

Gibbons are characterised by their production of complex and elaborate songs. These songs are species-specific and are delivered by one or both members of the mated pair and occasionally their subadult offspring (Marshall and Marshall, 1976; Haimoff, 1984a; Marshall and Sugardjito, 1986). Duets are the most common type of song bout and range from the male-dominated duets of *H. concolor*, *H. leucogenys* and *H. gabriellae* and the female-dominated duets of *H. klossii* to those in which contribution by both sexes is more or less equal, e.g. *H. syndactylus* and *H. hoolock* (Chivers, 1974; Tenaza, 1975; 1976; Gittins, 1979; 1984a; 1984b; Whitten, 1980; 1982b; 1984a; Deputte, 1982; Gittins and Tilson, 1984; Goustard, 1984; Haimoff, 1984a; 1984b; 1984c; 1985; Mitani, 1984; 1985a; 1987b; Raemaekers et al., 1984; Schilling, 1984b; Geissmann, 1993). Uncertainty, however, still surrounds the duetting behaviour of *H. moloch*. Studies of wild living moloch gibbons has revealed no evidence of duetting (Kappeler, 1984a) and, indeed, singing by mated males was never observed. However, a song bout recorded by Marshall and Marshall may exhibit communal singing in the organising sequence (Geissmann, 1993) and some captive groups of *H. moloch* have been heard to duet (Haimoff, 1983; 1976 recording by Marshall and Marshall in Cowlishaw, 1992; Geissmann, 1993). Duetting probably does occur in *H. moloch* but only occasionally and only in some groups.

Gibbons also give solo song bouts which are frequently performed by both mated and unmated male agile, Kloss, lar, Müller's, pileated and perhaps moloch gibbons (Chivers, 1974; Tenaza, 1976; Gittins, 1979; 1984a; 1984b; Whitten, 1982b; 1984a; Kappeler, 1984a; Haimoff, 1984a; 1984b; 1985; Mitani, 1984; 1987a; 1987b; 1988; Raemaekers et al., 1984; Mitani and Marler, 1989; Geissmann, 1993). Female soloing is unknown for most species of gibbon, and is observed regularly only in Kloss and moloch gibbons (Tenaza, 1976; Whitten, 1980; Kappeler, 1984a), occasionally in Müller's gibbons (Mitani, 1984) and sometimes in hoolock gibbons (Ahsan, 1994). Females from species not known to solo may do so in response to some crisis, for example, the death of their partner (Caldecott and Haimoff, 1983).

8.1.1.2 Function of the duet

The function of gibbon singing has been reviewed extensively in the literature (Carpenter; 1940; Ellefson, 1968; 1974; Aldrich-Blake and Chivers, 1973; Brockelman et al., 1974; Chivers, 1974; 1976; Chivers et al., 1975; Tenaza, 1976; Gittins, 1978b; Wickler, 1980;

Whitten, 1982b; Brockelman, 1984; Haimoff, 1984a; Mitani, 1984; Haimoff and Gittins, 1985; Raemaekers and Raemaekers, 1985; Cowlishaw, 1992; 1996) and proposed to relate to either territorial or mate defence. Traditionally, the duet is considered to aid territorial exclusivity through mediation of intergroup spacing (Carpenter, 1940; Ellefson, 1968; 1974; Brockelman et al., 1974; Chivers, 1974; 1976; Marshall and Marshall, 1976; Tenaza, 1976; Gittins, 1978b; Whitten, 1982b; Brockelman and Srikosamatara, 1984; Mitani, 1984; 1985a). Playback experiments conducted by Mitani (1985a; 1985b; 1987a) and Raemaekers and Raemaekers (1985) found that the majority of target groups responded to the playing of a duet by orienting to and approaching the source of the song and performing their own duet once the recording had finished. The location of the playback in relation to the target group's territory also had a significant effect on response behaviour. More vigorous responses were displayed for centre playbacks compared to songs played on the boundary and outside the target group's territory. According to Mitani (1988), these results indicate that gibbons use song bout location to determine appropriate territorial responses.

Alternatively, duetting may serve intra-group social dynamics, through the maintenance of visual and/or audible contact between a singing mated pair, synchronisation of reproductive behaviour, group orientation and cohesion, and/or formation and preservation of the pair bond (Chivers, 1974; 1976; Wickler, 1980; Brockelman, 1984; Haimoff, 1984a; Mitani, 1984; Raemaekers et al., 1984). Raemaekers et al. (1984) argue that, for lar gibbons at least, singing does not play a significant role in either the maintenance of contact between duetting adult pairs or the synchronisation of sexual behaviour. Chivers (1974), however, has reported a strong association between sexual behaviour and calling in siamang.

Intense duetting often accompanies the initial period of pairbonding (Brockelman and Srikosamatara, 1984; Geissmann, 1986; 1993) and, if one of the pair does not reject the other, duetting frequency continues to increase with the gradual development of a synchronised singing routine (Maples et al., 1989). Once the bond has been established, the duet itself continues to solidify the relationship. As evidence for this theory, Raemaekers et al. (1984) point to the pair-specific patterns of lar gibbons while Brockelman and Srikosamatara (1984) and Geissmann (1986) refer to the increase in singing behaviour observed between newly paired pileated gibbons and siamang respectively. This increase in duetting, according to Brockelman and Srikosamatara (1984), is due to selective pressures which favour shortening the time necessary to learn a duet which, in turn, reduces the chance of mate competition. Brockelman (1984) has also suggested that the duet, or rather its features of repetitiveness, stereotypy and intensity, is selected for because of the pleasurable stimulation the pair derives from its performance. The duet, rather than sex, is the proximate mechanism which prevents mate desertion and, hence, strengthens the pair bond (Raemaekers et al., 1984).

Rather than pair bond maintenance, duetting might be responsible instead for pair bond advertisement (Cowlishaw, 1992). Duetting as a medium through which the existence of a pairbond is advertised incorporates alternate mate defence hypotheses proposed by Gittins (1979) and van Schaik and Dunbar (1990). Mated gibbons choose to sing with their partners in order to prevent the approach of another same-sexed individual, who could potentially be attracted to their mate if he/she sang on their own. The benefits gained from regular duetting performances serves to stabilise the bond. For the female, it reduces the chance of desertion by her male partner and for the male gibbon, it decreases both the risk of infanticide and opportunities for his mate to engage in EPCs.

8.1.1.3 Sex-specific song function

Patterns of singing behaviour exhibited by male and female gibbons is thought by Cowlishaw (1992; 1996) to reflect differential, sex-related motives for calling. For the male gibbon, mate attraction or defence is probably the primary function of song performance. Bachelor males call longer and more often than mated males (Raemaekers et al., 1984; Mitani, 1988) and since they do not hold territories, it is presumed they sing to advertise for a mate (Aldrich-Blake and Chivers, 1973; Ellefson 1974; Tenaza, 1976; Kappeler, 1984a). Females are, however, less likely to be attracted to a male without a territory and Mitani (1988) has suggested that, instead, unmated males sing a) to improve their songs and b) to assess potential territory acquisition through the location of mated pairs in the immediate area. Mated males do not need to advertise for a mate, practice their songs or establish a territory, but they do have to contend with other males who may entice their female partner into extra-pair copulations and, in extreme cases, desertion. Mated males therefore sing to ward off unmated males (Cowlishaw, 1992). Supportive evidence for a mate defence function includes an increase in approach responses made by males when exposed to male solos (Mitani, 1984; 1987a; Raemaekers and Raemaekers, 1985) and a positive correlation between frequency of singing and number of unattached males surrounding the male's territory (Cowlishaw, 1992; 1996).

Preservation of the territory, and the resources it holds, is of utmost importance to the female gibbon and singing represents one method in which territory ownership can be declared. Female gibbons consistently sing from territory boundaries, deliver solos and initiate duets during encounters, and respond to increases in territorial threat with an increase in singing behaviour (Ellefson, 1974; Tenaza, 1976; Cowlishaw, 1992). However, females also display intensely aggressive responses to the songs of unaccompanied females (Mitani, 1984; Raemaekers and Raemaekers, 1985), which are marked in comparison to the responses given to duets. This behaviour implies that an element of mate defence also defines the singing behaviour of female gibbons.

8.1.2 The songs of hybrid gibbons

First-generation (F1) hybrid and F2 backcross gibbons produce songs that not only incorporate vocal characteristics typical of or unique to the parental species but are structured in such a way to suggest there is at least some genetic basis to song format (Marler and Tenaza, 1977; Brockelman and Schilling, 1984; Geissmann, 1984; 1993; Marshall et al., 1984; Tenaza, 1985; Marshall and Sugardjito, 1986). For example, four captive hybrid females, who had a *H. lar* mother, gave great call notes that in terms of speed, shape and type of climax were more representative of their father's species than of their mother's (Geissmann, 1993). Hybrid songs may be highly variable in certain aspects of their structure (e.g. the duration, number of notes and number of accelerations in the great call) but are generally stable and retain a hybrid specific repertoire and organisation (Geissmann, 1993). Indeed, both wild and captive females who have lived in partial or total acoustic isolation from other hybrid females, and therefore could not have learnt their song, still deliver similar or identical great calls to their hybrid counterparts (Brockelman and Schilling, 1984; Marshall et al., 1984; Marshall and Sugardjito, 1986; Geissmann, 1993).

Hybridity primarily affects the song of the male gibbon through the modification of the male-specific phrases or codas, in the notes employed, and the way they are combined. For example, if a male has either a *muelleri* or *pileatus* parent, he will always produce trills in his songs (Geissmann, 1993). In contrast, and in other hybrid combinations, songs are recognised because they lack notes characteristic to one of the parental species (e.g. *pileatus* x *lar* male hybrids do not use quaver or other complex *hoots* – Geissmann, 1993). Some hybrid males also produce figures not known or described for pure species, such as the exhalation-inhalation-exhalation sequences given regularly by *pileatus* x *lar* males and occasionally by *pileatus* x *moloch* males (Geissmann, 1993).

In the song of the female gibbon, it is the climactic great call which is altered by hybridity. Structurally, these great calls occupy a position intermediate between the sequences given by females of the two parental species, most noticeably in the rate of note emission and the type of climax. Lar group female hybrids, who have one parent typified by a *frequency-modulated* great call climax (e.g. *agilis* or *lar*) and the other by an *acceleration-type* climax (e.g. *muelleri* or *pileatus*), always produce a great call that is composed of notes of increasing frequency and an acceleration-type climax (Geissmann, 1984; 1993; Tenaza, 1985; Marshall and Sugardjito, 1986). General structure and note speed is not affected by specific parentage (Geissmann, 1993) although it appears that it may introduce some alteration to note shape. For example, a sonagram of a *muelleri* (paternal sp.) x *agilis* (maternal sp.) hybrid great call illustrated in Geissmann's 1993 dissertation shows greater similarity in climactic note shape to those of pure *muelleri* than a correspondent sonagram for *agilis* (paternal sp.) x *muelleri* (maternal sp.) hybrids did.

A backcross produces a great call closer in structure to the species with which it shares a greater proportion of its genetic makeup. Female *muelleri*-backcrosses retain the acceleration-type climax but deliver a great call that more closely resembles the trill or bubble characteristic of Müller's gibbons, albeit with a slower delivery of notes (Marshall and Sugardjito, 1986). In contrast, female *agilis*-backcrosses lose the acceleration-type climax, producing a frequency-modulated climax instead, which incorporates a greater number of climactic notes (Marshall and Sugardjito, 1986).

8.1.3 Outline of Chapter 8

Mather (1992) conducted an extensive study of the calls of gibbons in the Barito Ulu area, incorporating the area bordered by the Busang and Murung rivers. Concentrating on the acoustic features of the great call, the most species-specific and least variable of duet sequences, Mather found a range of great call variants given by hybrid females, distinguished by their rate of emission of climax notes and, using this variable, calculated hybridity values for each of the recorded females. But he made little discussion on either sequence structure or note presentation in duets and solos. Some descriptive analysis has been completed by Geissmann (1993) on the songs of captive *H. muelleri* x *H. agilis* hybrids and by Marshall and Sugardjito (1986) on hybrids and backcrosses at the research area (see Sections 8.4 and 8.5), but detail remains lacking.

To supplement previous studies on hybrid gibbon calls, and to document the range of song types existing in the hybrid zone, a classification is outlined in Sections 8.3 to 8.5. The notes produced by hybrids and backcrosses are listed in Section 8.3 as are the figures and phrases characteristic to solos and duets. Additional non-calling vocalisations are also described. Sections 8.4 and 8.5 concentrate on the duet. Three primary duet types – normal, disturbed and female-female – are described in these sections but it is the structure of the normal duet which receives the most descriptive attention, in particular the great call, which showed some spectacular variation between neighbouring groups. Solos, both male and female, are presented in Section 8.6.

Sections 8.7 and 8.8 respectively examine the lengths of different song types, the frequency at which they are produced, and the time at which they are delivered. In turn, stimuli and environmental/ecological conditions are proposed and discussed in Sections 8.9 and 8.10 in relation to their importance in eliciting or deterring singing behaviour.

8.2 Methods

In the absence of appropriate recording equipment, songs given by gibbons at Barito Ulu were documented instead with detailed field notes, relying on a previously attained familiarity with gibbon calls and reference to key articles on the singing behaviour of *H. agilis*, *H. muelleri* and hybrid forms. An initial three week period was spent listening each day to the dawn and morning songs of all audible groups to provide an introduction to, and understanding of, the basic structure, in terms of notes and sequences, of gibbons songs in that area.

Six primary categories of singing data, outlined below, were collected on the songs of all audible groups at Barito Ulu but the most reliable information came from the study of focus groups RBC2 and RBC1.

- *Type of song* – e.g. normal duet, disturbed duet or male/female solo.
- *Duration of song bout* – The start time of the song bout was recorded by referring to a wristwatch and the length of the song bout measured using a stopwatch.
- *Participants* – Vocal contributors were identified for each song bout and the time they began and ended their singing contribution noted.
- *Structure of the song* – Each sequence was timed, the number of great calls counted, and the use and combination of notes classified as accurately as possible. Particular attention was paid to the structure of the great call as it was essential in determining the hybridity status of the calling female. Duets followed the same basic sequence and note

use pattern and were therefore relatively easy to describe but the variability and complexity of male phrases prevented concise descriptions of male solos.

- *Context for singing* – Probable or possible causes (e.g. another group singing, inter-group conflict) eliciting the song bout.

Additional information collected included:

- environmental (e.g. rainfall) and ecological (e.g. fruiting activity) conditions potentially affecting a gibbon's decision to sing.
- other vocal behaviour i.e. figures and noises made by gibbons in non-singing contexts.

Unlike previous chapters, data presented in this chapter are taken from both the 5-day sample plus additional full-day follows. Singing behaviour on field days in which the groups could not be found until later in the morning, or were lost during the activity period, was discarded to prevent the potential of bias.

8.3 The vocal repertoire

8.3.1 Notes

Hybrid gibbon song bouts are composed of four classes of notes which are also given in song bouts of the parent species[15] (Gittins, 1979; Haimoff, 1984a; 1984b; 1985; Mitani, 1985). These notes may be delivered singly or coupled to produce figures and phrases.

Wa

The *wa* note is the most commonly produced note and is delivered by both sexes. Used in every type of song bout and every sequence, it is a short note which is uninflected and rises steeply. During territorial conflicts, female songs are punctuated by sharp and highly pitched *was* which intensify and then lessen as the conflict winds down. Duets by RBC1 and RBC2 were easily distinguished by the delivery of *wa* notes in the introductory sequence. AF1 always started duets with sharp, ringing *was* whereas AF2 produced softer *was* which never seemed to reach the same resonance. *Was* are also produced by *agilis* (Gittins' [1979] *whoop*), *lar* (Raemaekers et al., 1984 and corresponds to Carpenter's [1940] Type II vocalisation and Ellefson's [1974] *hoot*), *hoolock* (Haimoff, 1984a), *pileatus* (Haimoff, 1984a), and *moloch* (Kappeler, 1984a), and are similar to the *whoops* of *H. klossii* (Whitten, 1980).

Oo

Normally a short note, the monotonal *oo* is delivered at a low, even pitch and given by either sex in both duets and solos. *Oos* are introduced by the male into the introductory sequence of the duet and occasionally given in the organising sequence. These notes are not exclusive to song bouts and are often used as a contact or location call when animals become separated. Contact calls may be given by more than one gibbon and increase in delivery when separated

---

[15] The *agilis*-specific *waow* note (Haimoff, 198b), normally delivered in male solos, were never heard in RBC1 or RBC2 song bouts.

individuals become closer. *Oos* are also given when gibbons, particularly the adult males, are feeding in high quality food sources, such as fruiting trees or climbers. Agile gibbons have also been observed to use *oos* when feeding, presumably to maintain inter-individual spacing (Gittins, 1979; 1984a). All lar group gibbons and the hoolock gibbon produce *oo* or *oo*-similar notes in duets, solos and/or contact calls.

Oo-wa

This note is produced by combining an *oo* with a *wa*. *Oo-wa* notes are infectious and exchanged between the female and male in the organising sequence of the duet. The pre-climactic notes of the great call are also composed of *oo-wa* notes.

8.3.2 Figures

Wa-aa

A rarely given figure in duets but quite common in solos, the *wa-aa* (Gittins' (1979) *whoo-aa*) was specific to the adult male. During frenetic bouts of singing, the male repeated the *aa* part of the note to produce a rapid *wa-aa-aa-aa*. *Wa-aa* notes are sometimes given in couplets as observed by Marshall and Sugardjito (1986).

Twoulwill

Reminiscent of the distinctive ululating call, the *twoulwill*, given by Islamic women, this figure is comprised of a single *oo* note followed by a series of rapidly delivered *wa* notes. The figure had a vibratory effect and was high in pitch and volume. Only females are heard to deliver the *twoulwill*, possibly because of its similarity to the climactic notes of the great call. The *twoulwill* probably functions as an alarm or disturbed call. On one occasion, the two resident females of RBC2 *twoulwill*ed after being surprised, possibly frightened, by the adult male when he crashed through the tree they were feeding in while in another situation the subadult female gave the figure during a dispute with her mother. *Twoulwills* are given in inter-group encounter contexts too. A confrontation on a territorial boundary between RBC1 and RBC2 was initiated by a *twoulwill* from AF2, which was answered with a *twoulwill* from AF1.

8.3.3 Noises

Noises are indicators of an animal's distress or alarm and are normally given by the offspring in response to a parent's inattention or aggression. If an adult gibbon uttered a noise, it was always given by a female and during intra-group confrontations.

Twitter

Probably the most unexpected and unusual of the hybrid gibbon vocalisations, the twitter is a noise unique to the subadult female. Very similar to the twitter of a bird, it is a rare call and heard only during intra-group disputes and in response to parental attack.

Squeal

Primarily heard during intra-group conflict, the squeal is emitted by the subadult female when being chased or struck by one of her parents. In boundary disputes, adult females are also heard to squeal when attacked or chased by a member of the opposing group. Squeals are produced by *agilis* (Gittins, 1979), *syndactylus* (Chivers, 1974) and *lar* (Ellefson's [1974] *screech*, Baldwin and Teleki's [1976] *shrill squeal*; Bricknell, 1992 unpubl.).

Whimper-Squeal

The infant of RBC2 usually gave the whimper-squeal. Whimper-squealing became particularly intense and incessant when the infant had to negotiate transit from one substrate to the next. In the earlier stages of the study, the mother answered the squeals by returning to the infant and carrying it across. The whimper-squeal corresponds to the *cry* of *agilis* (Gittins, 1979), *fretting cry* of *lar* (Ellefson, 1974), *prolonged squeal* of *klossii* (Marler and Tenaza, 1977) and *bleating* of *syndactylus* (Chivers, 1976).

8.3.4 Phrases

Phrases are specific to the sexes and characterised by the great-call, the coda and those delivered in the male solo. The great call sequence is relatively inflexible in structure and is given only by the female with the exception of the male siamang, hoolock and pileated gibbon which make some contribution to the overall sequence (Chivers, 1974; Haimoff, 1984a). Codas are normally delivered towards the end of, or directly after, the great call and are specific to male gibbons, observed in agile, lar, pileated and concolor group gibbons (Haimoff, 1984a). The *oo-wa* and *wa* exchange often heard after *muelleri* female great calls has been classified as a coda by Marler and Tenaza (1977) and Marshall and Sugardjito (1986) but Haimoff (1984a), Leighton (personal communication to Haimoff, 1984b) and Marshall and Marshall (1976) disagree since these exchanges are not uniform in structure like other codas and involve vocal participation from both sexes. Although similar exchanges were heard post-great call in the duets of RBC1 and RBC2, Haimoff's interpretation of codas will be respected here. The structure of the great call sequence and the highly variable coda is described in the next section.

8.4 The duet

With the exception of the concolor gibbons, the duet is composed of three sequences – the introductory sequence, the organising sequence and the great call sequence (Haimoff, 1984a). The introductory sequence is produced at the beginning of the song bout. It is easily differentiated from the other sequences and is produced only once. Alternation between the organising and great call sequences comprises the rest of the song bout. Highly variable in structure, the organising sequence enables the mated pair to organise and coordinate both their vocal and non-vocal behaviour in the lead-up to the great call sequence (Haimoff, 1984a). The third of the sequences, the great call, is the least variable of the duet and species-specific. Normal duets accounted for 83.1% and 92.1% respectively of RBC2 and RBC1 duets (see Table 8-1).

Table 8-1 Duet variants and frequency of performance.

	Duet variants					
	Normal duets		Disturbed duets		Female-female duets	
	RBC2	RBC1	RBC2	RBC1	RBC2	RBC1
%	83.1	92.1	6.0	7.9	10.8	-
Total (n)	69	35	5	3	9	-

Previous analysis of hybrid gibbon duets indicates that hybridity affects minor structural change to the introductory and organising sequences but introduces significant modification to the great call sequence (Geissmann, 1984; 1993; Haimoff, 1984a; Tenaza, 1985; Marshall and Sugardjito, 1986; Mather, 1992). The duets of hybrid groups both immediately and more distantly located to the main research area correspondingly showed only secondary differences in the structure of the introductory and organising sequences and hence descriptions are based on two sources, the focus groups RBC2 and RBC1. Considerably more variation was heard in the form of the great call between groups and these will be examined in more detail (for a summary of hybrid gibbon duet structure see Table 8-2).

Table 8-2 Description, duration and sex/age related participation in hybrid gibbon duets

Sequence	Description	Duration of sequence[1] (sec)			Participation			
		Mean	Range	n	Adult male	Adult female	Sub-adult	Juvenile
Introductory sequence	Soft, short *was* introduced the duet, followed by loud, sometimes reverberating *wa* notes which became longer in their delivery. *Oo* notes are introduced after the first series of *was* exchanges between the adult pair. No formalised phrases are given.	217.0	23 - 600	121	●	●	❍	❍
Organising sequence	The organising sequence preceding the first great call is simplistic, composed primarily of *wa* notes but with a few, sporadic *oo-wa* exchanges. Subsequent organising sequences are more complex and mostly comprised of lengthy *oo-wa* exchanges interspersed with periods of silence and *wa* and *oo* delivery. Pre-great call notes are represented by rapid and breathy *wa* notes.	87.4	28 - 518	920	●	●	✪	✪
Great call sequence: *agilis* -backcross	One to two long monotonal *was* rise in pitch to produce two or three climactic notes that decline again for the delivery of the sequence's terminal notes.	11.9	9 - 15	168	❍	●	✪	✪
Great call sequence: hybrid	Long *oo* notes develop into rapidly delivered *oo-wa* notes followed by an accelerated series of *wa* notes to form the climax.	11.3	7 - 13	802	❍	●	✪	✪
Great call sequence: *muelleri*-backcross	Two slowly delivered *oo-wa* notes precede an increasingly rapid series of *oo-was* that shorten into *wa* notes and the characteristic climactic trill.	10.8	8 - 12	978	❍	●	✪	✪

[1] Sequence durations were not measured from the same number of duets.

● Always contributes to sequence ✪ Sometimes contributes to sequence ❍ Never contributes to sequence

8.4.1 Introductory sequence

All RBC2 duets were initiated by the adult female (see Section 8.9 for context) and announced by the delivery of 3-5 very soft and short *wa* notes. In contrast, RBC1 adult female introduced the duet with only 1-2 soft *was* followed immediately with very loud, reverberating *was*. As the females brachiated or climbed to a prominent position in the singing tree, these notes intensified and steadily became louder and longer. The onset of singing by the adult female normally stimulated the adult male to discontinue the activity he was engaged in and move towards his partner. After 1-2 minutes, he joined the female in giving *was* and introduced *oo* notes to the sequence. Little or no structure was evident in the introductory sequence, appearing to consist of randomly performed *wa* and *oo* notes, and both animals remained stationary in a sitting position. The subadult female (RBC2) occasionally joined in the introductory sequence but usually only the adults participated. Introductory sequences could be exceptionally short (23 seconds) or quite long (600 seconds or 10 minutes) but averaged 3.6 minutes (217 seconds).

8.4.2 Organising sequence

The organising sequence, delivered prior to the first great call and between subsequent great calls, was distinguishable from the introductory sequence by the inclusion of *oo-wa* notes and a greater synchrony in note delivery. The first organising sequence was distinct from the others in its more simplistic structure, composed mostly of *wa* notes but with an occasional *oo-wa*. As the organising sequence proceeded towards the delivery of the first great call, the adult male and adult female started to produce shorter *wa* notes which ultimately synchronised. Once this synchrony had been achieved, the female gave very short, rapid and breathy *wa* notes. This series of notes are referred to as the "pre-great-call" notes and announced the start of the great call (Haimoff, 1985). Vocal participation by the male halted as the first of the pre-great call notes were given and presumably the function of these notes is to silence the male. Organising sequences after the first great call were more complex in structure. Following the great call, the gibbons rested in silence for a period ranging from 2-34 seconds before resuming their singing. *Wa* and *oo* notes opened the sequence which progressively intensified to develop into *oo-wa* notes. A distinguishing feature of the organising sequence is the *oo-wa* exchange between the adult male and adult female. Due to their position within the dense canopy, it was difficult to determine which sex initiated the exchange but, in Müller's and agile gibbons, it is the male who begins the exchange (Haimoff, 1984b; Haimoff, 1985). Between 3 and 34 *oo-wa* exchanges occurred in the sequence, interspersed with periods of silence and delivery of sporadic *was* and *oos*. On occasion, the sequence prior to and after the final great call saw a reduction or complete absence of *oo-wa* exchanges. Indeed, if the duet did not terminate on the great call the participants tended to finish the song bout with *was*.

Organising sequences were shorter than introductory sequences, averaging 87 seconds (1.45 minutes) in duration and ranging from 28 seconds (0.47 minutes) to 518 seconds (8.62 minutes). Gibbons normally delivered the organising sequence in a stationary position, either sitting or hanging. Slow climbing and brachiation, however, does occur, presumably to transfer to different vocalising posts and hence increase the listening range of the duet. On rare occasions, the group travelled when performing the organising sequence, usually in order to meet an invading group.

8.4.3 Great call sequence

Specifically unique both in form and structure, the great call sequence is the principal component of the duet (Haimoff, 1984a) and, despite the individuality present in some of its features (Tenaza, 1976; Haimoff, 1983; Haimoff and Gittins, 1985; Haimoff and Tilson, 1985), it remains the least variable of the duet sections. Female gibbons at Barito Ulu gave a range of great call types that exhibited either a *muelleri*-like or *agilis*-like sequence of note delivery. In the absence of recordings, the true extent of great call variation cannot be described but three primary sequence types – hybrid, *muelleri*-backcross and *agilis*-backcross – were easily identified.

8.4.3.1 Hybrid great calls

Two females, the subadult of RBC2 and the adult female of RR3, produced hybrid great calls similar in structure to those described by Marshall and Sugardjito (1986) and Geissmann (1993). The juvenile female of RBC1 also produced a great call resembling an immature version of the hybrid form. Introduced by a set of long *oo* notes and followed by rapidly delivered *oo-wa* notes, the sequence climaxed with a series of accelerating, but not trilling, *wa* notes. As observed by Marshall and Sugardjito (1986), the pre-climactic (*oo-wa*) and climactic section of the great call was accompanied by a "spectacular" rise in pitch.

8.4.3.2 *Muelleri*-backcross great calls

Both focus adult females (RBC1 and RBC2) and the adult females of RBC4 and RR1 gave *muelleri*-like great calls. Very similar, in both structure and the use of notes, to the great call of hybrid females, it differs from the latter in the female's ability to generate climactic notes at an intensely rapid rate. The sequence starts with two relatively slowly delivered *oo-wa* notes. These notes continue to be given but at a more rapid rate which respectively shortens and lengthens the duration of the *oo* and *wa* component. As the female reaches the climactic part of the great call, *wa* notes are produced extremely quickly to form a bubble or trill which never quite reaches the same speed of note delivery observed in the trill of a Müeller's gibbon. Occasionally, the great call sequence ended with a series of breathy wa notes (*wa-hh wa-hh wa-hh*) which sounded as if the female was out of breath and only audible if standing directly under the calling female. A period of silence followed the end of all great calls except once when the adult female of RBC1 delivered two short, sharp *was*.

8.4.3.3 *Agilis*-backcross great calls

Five females, from groups RBC3, BR1, BR2, and RR2, occupied areas from which *agilis*-backcross great calls were heard. After the pre-great call notes, the female delivered one or two long monotonal *wa* notes which rose in pitch to form a series of two or three climactic notes to descend again into the terminal notes. As observed by Marshall and Sugardjito (1986), most females did not show a decline in the pitch during the production of the monotonal *was* nor did they limit themselves to just one or two climactic notes. One or both of the BR females did, however, drop pitch on the second monotonal note.

The great call of the adult female in RBC5 was quite unusual and incorporated aspects of both *muelleri* and *agilis* great calls. The initial, or build-up, notes resembled the *ooloo-wa* series characteristic of hybrids and *muelleri*-backcrosses but did not progress into the accelerating climax expected. Instead, there was a sudden decline in note speed as the female produced a soaring climax which differed from other *agilis*-backcrosses with an additional climactic note. Such individual-specific calls are rare but not unknown for gibbons and may occur in the songs of both males and females (Thomas Geissmann, 1998 pers. comm.).

8.4.3.4 Characteristics of great call variants

8.4.3.4.1 Duration and frequency of great call sequences

Great call sequences ranged from approximately 8.4 to 14.8 seconds in duration, similar to duration lengths measured from sonagrams given in Mather (1992). The great calls of *muelleri*-backcross females tended to be somewhat shorter (mean = 10.8 seconds) than those of hybrids (mean = 11.3 seconds), which in turn were shorter than the great calls of *agilis*-backcrosses (mean = 11.9 seconds), but this difference was not significant (p>.05). Comparing the number of sequence notes, and the timing of the climax between great call types, however, could not be conducted due to the absence of sonagrams. Graphs produced in papers by Marshall and Sugardjito (1986) and Mather (1992) suggest that climax notes are reached earlier in the *muelleri*-backcross and hybrid great calls. Certainly, this seemed to be the case on the unusual occasion when females producing different great call types sang the sequence in synchrony.

The group RBC2 presents not only an ideal model in which the delivery of alternate forms of great calls can be compared with some accuracy but also one where discussion can be made on the duetting behaviour of a mother and daughter living in a trio. Of the 591 great calls given in 83 duets, 96.4% were initiated by the adult female. The immediacy of the daughter's response varied but the delivery of her first *oo* note normally coincided with either the end of the female's first, or the start of her second, *oo* note. During the delivery of the rest of the great call, the subadult's song, or specifically the rate of note emission, lagged somewhat behind that of her mother's, the latter reaching the climactic phase before the former. Although notes couldn't be counted, it was apparent that the climax of the adult female was composed of significantly more notes, producing, at a rough estimate, two or three notes to the subadult's one. Timing of the end of the great call varied from duet to duet. At the beginning of the study, the subadult female often finished her great call a few notes before her mother but towards the end of the study she terminated her call either in synchrony with her mother or just after.

The slower delivery of the subadult female's great call is not necessarily a result of her age. Immature female gibbons may produce shorter sequences (Geissmann, 1993 and as observed for the juvenile female of RBC1) but subadults produce great calls that are similar in length and identical in structure to their mother's (Joe Marshall, 1997 pers. comm.). While early sequence termination is likely to be a factor of the subadult's age, her actual rate of note emission is almost certainly influenced by her hybridity status.

An average of 7.2 and 6.6 great calls per duet were given respectively by the adult and subadult females (Table 8-3). The two females usually participated in the great call sequence together, singing concurrently in 84.8% of great calls. The females also performed great calls on their own and for most of the study these came mostly from the adult female. Of the 90 solo great calls, just over three quarters were sung by the older female. However, towards the end of the study, the subadult female attempted more great calling on her own and occasionally delivered the first great call of the duet.

The adult female of RBC1 gave, on average, an additional two great calls per duet compared to her contemporary in RBC2. Accompanied by her juvenile daughter on 65.2% of these, the significant difference in great calls between the focus groups is probably attributable to a similar difference in duration of the duet (see Section 8.6). Number of great calls and duet length were significantly correlated for both RBC2 (r_s=.678 n=83 p<.0001) and particularly RBC1 (r_s=.854 n=36 p<.0001).

Table 8-3 Characteristics of great calling by RBC2 and RBC1 females.

Group and individuals	Number of great calls	Great calls per duet		Proportion of solo great calls		Number of aborted great calls	
		Mean	Range	%	n	%	n
RBC2 (total)	591						
AF2	570	7.2	1 - 18	76.7	69	0.5	3
SF2	522	6.6	0 - 16	23.3	21	1.3	7
RBC1 (total)	348						
AF1	348	9.7	1 - 21	100.0	121	2.0	7
JF1	227	6.3	0 - 10	-	0	4.8	11

% of great calls performed together - AF2 and SF2: 84.8% n = 501

% of great calls performed together - AF1 and JF1: 65.2% n = 227

8.4.3.4.2 Aborted great calls

Stalling or aborting the great call can advertise inherent problems in the interaction between a singing mated pair (Haimoff, 1984a) and if more common in hybrid or backcross female songs it could indicate that hybrid pair groupings are less stable (Mather, 1992). The proportion of aborted great calls by all audible females at Barito Ulu (i.e. any great call terminated before the climax is reached), however, was relatively low. Some females were never heard to interrupt their great calls while others did so only seldomly. Of the 573 great calls AF2 gave, only three were aborted (Table 8-3). Relatively successful great calling can also be attributed to AF1 who terminated just 7 (2.0%) of her 348 great calls. Further discussion of other song bouts features proposed by Mather to be potentially indicative of the sub-optimality of the hybrid duet is presented in this chapter's discussion.

8.4.3.4.3 Behavioural responses to the great call

Possibly silenced by the female's pre-great call notes, and as observed for *H. muelleri* (Haimoff, 1985) and *H. agilis* (Haimoff, 1984b), males made no vocal contribution to the great call proper. Instead, adult males responded more energetically, brachiating and jumping around the singing tree with the occasional shaking and breaking of branches. Adult females and, to a lesser extent, her offspring accompanied the adult male in this explosive behaviour. If the adult male was separated from the female at the initial stages of the great call, he moved quickly over to her before she delivered the climax and sometimes the two embraced each other during or immediately after the climactic phase.

8.5 Other duets

8.5.1 Disturbed duets

Disturbed duets were distinguished by their altered and apparently structureless sequences and resembled those of wild and captive siamang in their common features of continuous note delivery, lack of rhythm and participation of all or most group members (Chivers, 1974; Raemaekers et al., 1984; Bricknell, 1992 unpubl.). *Wa* notes predominated in disturbed duets, sometimes being the only note used. Featured less frequently were *oos* and even less often, or sometimes not at all, *oo-was* and *oo-wa* exchanges. The general arrangement of notes and phrases and the specific participation of individuals, evident in normal duets, were also lacking.

RBC2 and RBC1 gave five and three disturbed duets respectively, which represented 6.0% and 7.9% of all duets. Two types of disturbed songs were recognised and differed in the use of great calls and the context in which they were given. The first type (I) is classified as an alarm call proper and given in response to hunters and their dogs using forest trails below and an alarm call by a giant squirrel. In the case of RBC1 alarm duets, no obvious stimulus was determined. Neither adult nor subadult females great called in these alarm songs and there was no obvious shift from the introductory sequence into the organising sequence, suggesting the song bout is composed of randomly given notes rather than distinct sequences. All members of the group, except the infant, participated in the alarm duet, delivering continuous *was* and *oos* which rarely synchronised. Adults never initiated *oo-wa* exchanges.

Some structure is evident in the second type of disturbed duet (II). Elicited by an agonistic encounter between the adult and subadult females, conflict duets eventually developed into normal duets. Females gave urgent and highly pitched *was*, interspersed by *oos* and the occasional contribution from the adult male. Unlike the alarm duet type I, great calling did occur, the first of which was delivered earlier in the song than in most normal duets. *Oo-was* were introduced after the first great call but not exchanged until the third or fourth organising sequence. These exchanges signified the normalising of the duet.

8.5.2 Female-female duets

An unusual trait of singing behaviour displayed by RBC2 was the performance of nine duets (10.8% of duets; 7.0% of all song bouts) which received no vocal contribution from the adult male. Instead, the adult female duetted with the subadult female, producing a song similar to the normal duet. The adult female began these female-female duets and sang the introduction on her own, joined by her daughter in the organising sequences and the great call. Despite the absence of the male song, the subadult did not attempt to produce male-characteristic phrases or codas but did exchange *oo-was*, although less frequently, with her mother in the organising sequence.

The function of female-female duets, or the reason why they occurred, is not clear. No particular context elicited these song bouts nor did the male appear to be pre-occupied with more pressing or demanding activities when the adult female began the duet. Indeed, he often sat observing the females or fed as they gave the introductory and organising sequences and only occasionally gave an acrobatic display during the great call sequence.

8.6 Solos

8.6.1 Male solos

A complete classification of phrases delivered in male solos is impractical due to the range produced both between and within songs. Without sonagrams, description of variants is made even more difficult. Although the songs of all males at Barito Ulu were listened to and descriptions attempted, only the solos of the adult males of focus groups RBC2 and RBC1 will be presented here since they received the most attention.

Müller's and agile males start solos with a medley of *wa* and *oo* notes, also observed for AM1 and AM2. A few soft *wa* notes were followed by longer *oo* notes and then a series of *wa* and *oo* note combinations which increased in volume and intensity. As observed for *muelleri* males (Haimoff, 1985), long pauses separated the introductory phases. Between 1-3 minutes later, phrases became noticeably longer in length with use of more notes and an increase in complexity. Males introduced *oo-was* and *wa-aas* at this stage of the solo, developing phrases which varied in their arrangement of these notes and the occasional use of singular *was* and *oos*. Eventually, the bi-phasic *wa-aas* (Marshall and Sugardjito, 1986; Geissmann, 1993) were incorporated into phrases, two or three given with *was* and some *oos*. Trills did not feature in either male's solos and the emission of quaver notes was absent or not recognised. Description and recordings provided in Marshall and Sugardjito (1986) suggest that both AM1 and AM2 were *agilis*-backcrosses.

At the initial stages, and when more than one male was soloing, songs of neighbouring males often overlapped. However, as phrases intensified in complexity and lengthened in duration, a neighbouring male often stopped to listen to the song of their countersinging partner, responding once the latter had completed his phrase. When more than two resident males engaged in bout of chorusing, listening pauses were less common.

8.6.2 Female solos

Female gibbons at Barito Ulu soloed less often than their male counterparts (Section 8.7 and see Table 8-4), preferring to make their vocal contribution to the duet. Individually variable, some females were never heard to solo while others sang on their own at least once or twice a month. Both females in RBC2 produced solos of two types, the adult female on nine occasions and the subadult twice.

Table 8-4 Proportion of male and female soloing in RBC2 and RBC1.

	RBC2			RBC1	
	AM2	AF2	SF2	AM1	AF1
%	76.1	19.6	4.3	91.3	8.7
Total (n)	35	9	2	21	2

In populations of Müller's gibbons where females do solo, the song does not differ from that given in the duet (Mitani, 1984). Although not identical, some (Type I) solos of the hybrid adult female did share many features with the duet song i.e. three distinct sequences composed mainly of *wa* notes interspersed with *oos* and *oo-was*. Differences existed in the use of *oo-wa* notes and number of great calls, both produced at a lower rate or sometimes not at all. Only 44.4% (n=4) of AF2 Type I solos involved great calling, three of which were directed at RBC1 hovering on the edge of the territory boundary.

The other five AF2 solos (Type II) started with a similar introduction of soft *was* which developed into a series of *wa* syllables. An organising sequence of *wa* and *oo* notes followed but instead of proceeding to the great call, the female continued to sing variable phrases comprised of the three primary song notes. Each phrase consisted of three to five notes and in especially long solos, these phrases became more complex as the song progressed. Four of the Type II solos coincided with bouts of countersinging with the adult female of RR1. Long pauses interrupted bouts of singing from soloing females, presumably so they could listen to the song of the responding female.

8.7 Frequency and duration of song bouts

Hybrid gibbons were prolific vocalisers, most groups calling on three out of four observation days. RBC2 gave a mean of 1.54 song bouts per day, an average greater than that recorded for most other populations of gibbon (Ellefson, 1968; 1974; Chivers, 1974; Tenaza, 1975; 1976; Raemaekers, 1977; Rijksen, 1978; Tilson, 1979; Srikosamatara, 1980; Whitten, 1980; 1982b; Gittins and Tilson, 1984; Kappeler, 1984a; Islam and Feeroz, 1992a; 1994b; Lan, 1993; Ahsan, 1994 and see Table 8-5). Two daily bouts of calling were usual for this group but on rare occasions they performed as many as five songs during the activity period. The delivery of additional songs was often, but not always, a consequence of some type of disturbance, usually a territorial dispute. RBC1 gave an average of 1.61 song bouts a day but were equally likely to sing once or twice a day.

Table 8-5 Frequency and duration of hybrid and pure species songs.

Species	Study Site	Duet			Male solo			Female solo			Source
		Ave no of bouts/day	Duration (mean)	Duration (range)	Ave no of bouts/day	Duration (mean)	Duration (range)	Ave no of bouts/day	Duration (mean)	Duration (range)	
H.a.albibarbis x H. muelleri	Barito Ulu, Central Kalimantan, Indonesia	0.99	15.7	3.0 - 73.0	0.51	27.0	4.0 - 65.0	0.07	22.1	6.0 - 60.0	1
H.a.albibarbis	Gunung Palung, West Kalimantan, Indonesia	0.93	-	-	0.77	44.6	33.0 - 56.1	•	•	•	2, 3, 4
H. agilis	Sungai Dal, West Malaysia	1.45	17.0[1] 11.0[2]	1.0 - 133.0 1.0 - 76.0	0.35	26.0	3.0 - 91.0	•	•	•	5, 6, 7, 8
	Ulu Mudah, West Malaysia	1.90	-	-	-	-	-	•	•	•	5
H. concolor	Wuliang and Ai Lao, Yunnan, China	-	10.0	5.0 - 29.0	•	•	•	•	•	•	9
		≅ 1	12.9	-	-	> 12.9	-	•	•	•	10
		0.59	11.4[3]	1.8 - 26.8	•	•	•	•	•	•	11
H. hoolock	Hollongapar, Assam	0.97	14.4	4.0 - 32.0	•	•	•	•	•	•	12, 13
	West Bhanugach, Bangladesh	0.60	20.0	3.0 - 37.0	•	•	•	•	•	•	*ibid*
	Lawachara and Chunati Wildlife Sanctuary, Bangladesh	≅ 1	-	7.0 - 28.0	•	•	•	•	•	•	14, 15
	Lawachara, West Bhanugach Forest Reserve, Bangladesh	0.67	14.4	1.0 - 44.0	•	•	•	2.7[4]	8.5	1.0 - 46.0	16
	Chunati Wildlife Sanctuary, Bangladesh	0.30	22.1	5.0 - 42.0	•	•	•	-	-	-	*ibid*
H. klossii	Paitan, Siberut Island, Indonesia	0.23*	20.0	-	0.59	44.0	3.0 - 108.0	*	*	*	17, 18
	Sirimuri, Siberut Island, Indonesia	0.22*	19.4	-	0.40	26.5	6.0 - 88.0	*	*	*	19, 20
H. lar	Khao Yai, Thailand	1.30	11.7	9.4 - 15.3[5]	0.20[6] 1.0[7]	23.6 44.6	- -	0.1	0.9	-	21
	Kuala Lompat, West Malaysia	0.73	16.0	2.0 - 68.0	0.17	26.5	-	•	•	•	22
	Sungai Tekam, West Malaysia	0.54	7.3	-	-	-	-	•	•	•	23, 24
	Tanjong Triang, West Malaysia	0.85	13.0	-	-	-	-	•	•	•	25

Table 8-5 (continued)

Species	Study Site	Duet			Male solo			Female solo			Source
		Ave no of bouts/day	Duration (mean)	Duration (range)	Ave no of bouts/day	Duration (mean)	Duration (range)	Ave no of bouts/day	Duration (mean)	Duration (range)	
H. lar	Ulu Gombak, West Malaysia	1.34	14.8	-	-	-	-	•	•	•	22
	Ulu Sempan, West Malaysia	0.58	26.2	-	0.38	30.8	-	•	•	•	22
	Ketambe, Sumatra, Indonesia	0.42	16.0	-	-	-	-	•	•	•	26
H. moloch	Ujong Kulon, Java, Indonesia	•	•	•	•[8]	•	•	1.3	9.3	1.0 - 87.0	27
H. muelleri	Kutai, East Kalimantan, Indonesia	0.66[7] 1.68	18.6 15.6	-	0.14	20.0[9]	≥ 60.0	-	7.5	-	28, 29, 30
H. pileatus	Khao Soi Dao, Thailand	0.60	14.6	-	•	•	•	•	•	•	31, 32
H. syndactylus	Kuala Lompat, West Malaysia	0.33	14.6	-	•	•	•	•	•	•	22
	Ulu Gombak, West Malaysia	0.26	14.8	-	•	•	•	•	•	•	22
	Ulu Sempan, West Malaysia	0.23	17.6	-	•	•	•	•	•	•	22
	Ketambe, Sumatra, Indonesia	0.27	17.0	-	•	•	•	•	•	•	26

- Information not available in literature

• Specific song bout not given by species

* Male Kloss gibbons often do not sing with their female partners.

[1] Mean duration for group DG1 dawn duets.

[2] Mean calculated by S.B. from morning duet durations measured by Gittins (1979) for 5 *agilis* groups.

[3] Mean calculated by S.B. from mean duet durations measured by Sheeran (1993) for four *concolor* groups

[4] Mean solo duration for one female hoolock gibbon.

[5] Mean calculated by S.B from mean duet durations measured by Raemaekers et al. (1984) for 7 *lar* groups.

[6] Solo durations for adult males.

[7] Solo durations for subadult males.

[8] Kappeler never heard male moloch gibbons sing but captive individuals have been observed to call occasionally.

[9] Average calculated by S.B. from mean solo durations measured by Mitani (1988) for 8 *muelleri* males.

1: This study 2: Mitani, 1987a 3: Mitani, 1988 4: Mitani, 1990 5: Gittins, 1979 6: Gittins, 1984a 7: Gittins, 1984b 8: Haimoff, 1984a 9: Haimoff et al. 1987 10: Lan, 1993 11: Sheeran, 1993 12: Tilson, 1979 13: Gittins and Tilson, 1984 14: Islam and Feeroz, 1992a 15: Islam and Feeroz, 1992b 16: Ahsan, 1994 17: Whitten, 1982b 18: Whitten, 1982b 19: Tenaza, 1975 20: Tenaza, 1976 21: Raemaekers et al., 1984 22: Chivers, 1974 23: Johns, 1983 cited in Cowlishaw, 1992 24: Johns, 1984 cited in Cowlishaw, 1992 25: Ellefson, 1974 26: Rijksen, 1978 27: Kappeler, 1984a 28: Mitani, 1984 29: Mitani, 1985a 30: Mitani, 1988 31: Srikosamatara and Brockelman, 1983 32: Brockelman and Srikosamatara, 1984

Duetting occurred regularly, at least once a day, and accounted for 64.3% and 62.3% of RBC2 and RBC1 song bouts respectively (Table 8-6). On singing days, an average of 1.30 and 1.27 duets were performed by RBC2 and RBC1. Gibbons soloed less often but adult males still gave solos every second day. Adult males in the Rekut areas appeared to solo at similar rates with the exception of BR1 male who was particularly prolific, calling on any morning when it wasn't raining and often on rainy days too. Females engaged less in soloing behaviour and, indeed, only 4 adult females (in groups RBC1, RBC2, RR1 and RR2) were heard to sing alone. Since females did not always great call when soloing, it is possible that solos of more distantly located females could not be detected or were missed. However, in other gibbon species in which the duet is the principal song bout type, female soloing appears to be an individual phenomenon. For example, in Müller's gibbons, female soloing has been observed, albeit rarely, by Marshall and Marshall (1976) and Mitani (1984) but not by Haimoff (1985), Marshall and Sugardjito (1986), Geissmann (1993) or Robbins (1996, pers. comm.). Hybrids did not solo habitually, the mean number of solos per day ranging from just 0.03 to 0.11. RBC2 and RR1 females soloed more often than RBC1 and RR2 females, occasionally participating in bouts of countersinging with each other.

Table 8-6 Proportional delivery of duets and solos by RBC2 and RBC1.

Type of song	RBC2		RBC1	
	%	n	%	n
Duet	64.3	83	62.3	38
Male solo	27.1	35	34.4	21
Female solo	8.5	11	3.3	2

The duration of RBC2 duets were similar to those of other lar group gibbons and averaged 15.6 minutes (see Tables 8-5 and 8-7). Eighty five percent of RBC2 duets continued for less than 20 minutes, half of these between 11 and 20 minutes in duration (Figure 8-1). RBC1 duetted for significantly longer periods of time ($z=-2.71$ $n_1=83$ $n_2=38$ $p<.025$) but surrounding groups performed duets of similar length to RBC2. Duet lengths of RBC2 did vary between months (Figure 8-2) but not significantly ($H=10$ d.f.=11 $p>.25$).

Table 8-7 Duration of duets of resident groups (only includes normal duets).

Group	Mean duration	Range	n
RBC1	20.6	7.0 - 59.0	35
RBC2	15.6	5.0 - 73.0	69
RBC3	14.8	5.0 - 62.0	21
RBC4	15.2	3.0 - 46.0	16
RBC5	13.4	3.0 - 37.0	18
RR1	17.1	6.0 - 71.0	30
RR2	14.6	6.0 - 48.0	25
RR3	14.4	5.0 - 26.0	7
BR1	16.5	7.0 - 54.0	28
BR2	15.1	6.0 - 33.0	25

RBC2 gibbons, regardless of sex, called longer when producing a song bout on their own (Table 8-8) but only significantly so for AM2 ($z=-2.88$ $n_1=83$ $n_2=35$ $p<.025$ and see Figure 8-3). Little difference was found between the duration of AM2 solos compared to those given by AF2 and SF2 and despite a marked range in AM2's average monthly solo length (Figure 8-4), the variation was not significant.

Table 8-8 Duration of RBC2 and RBC1 solos.

Duration	RBC2			RBC1	
	AM2	AF2	SF2	AM1	AF1
Mean (minutes)	22.3	18.1	24.5	31.7	10.5
Range	5.0 - 56.0	6.0 - 60.0	14.0 - 35.0	8.0 - 50.0	6.0 - 15.0
n	35	9	2	21	2

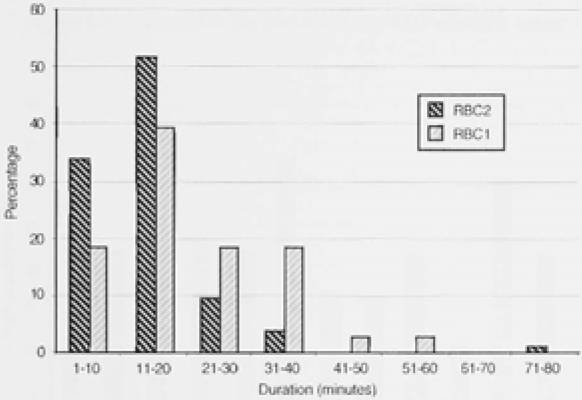


Figure 8-1 Variation in RBC2 and RBC1 duet length.

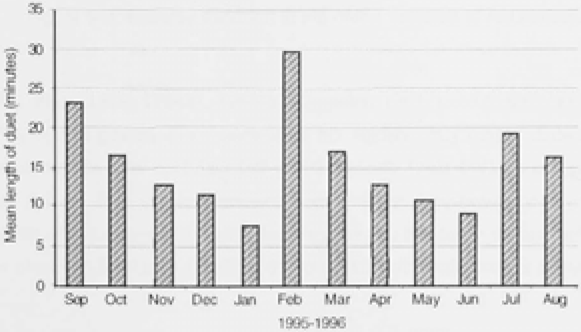


Figure 8-2 Monthly variation in the mean duration of RBC2 duets.

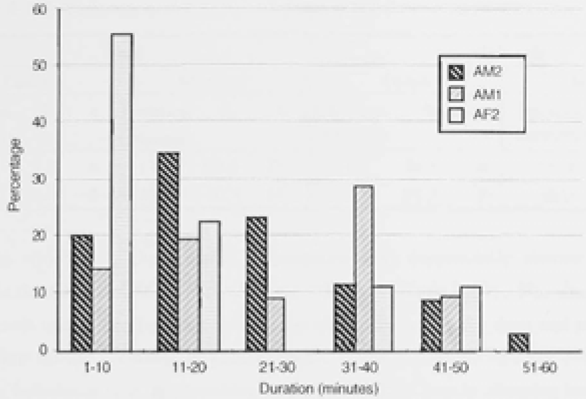


Figure 8-3 Variation in the duration AM2, AM1 and AF2 solos.

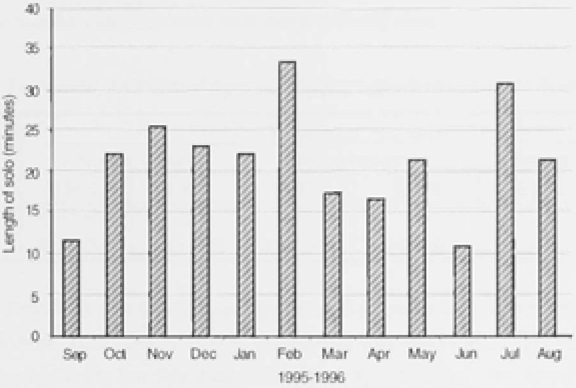


Figure 8-4 Monthly variation in the mean duration of AM2 solos.

Unlike *agilis* (Gittins, 1979; 1984a), *moloch* (Kappeler, 1984a) and some populations of *klossii* (Tenaza, 1976), hybrid gibbon dawn duets were not significantly longer in duration than those sung in the morning ($z=-1.48$ $n_1=12$ $n_2=109$ $p>.05$ and see Table 8-9). A comparison of RBC2 duet durations for the first six performance hours of the day, however, found a significant difference ($H=28.60$ d.f.=5 $p<.005$), with duets tending to be longer if sung before 0600. This trend was not observed by RBC1 ($H=5.14$ d.f.=5 $p>.05$) who sang longer duets between 0700-0800.

Males soloed at dawn more often than they did in the morning; 74.3% of RBC2 adult male's solos and 95.2% of RBC1 adult male solos were sung before 0530 (Table 8-9). Dawn solos were shorter than morning solos but not significantly so ($z=0.97$ $p>.05$). Male Kloss gibbons at Paitan also had similar length dawn and morning solos (Whitten, 1984a) but other populations called longer if soloing before sunrise (Tenaza, 1976).

Table 8-9 Frequency and duration of dawn and morning duets and male solos.

	Duet						Male solo					
	Dawn			Morning			Dawn			Morning		
	Duration (minutes)	%	n	Duration (minutes)	%	n	Duration (minutes)	%	n	Duration (minutes)	%	n
RBC2	21.0	7.2	6	13.8	92.8	77	21.3	74.3	26	25.0	25.7	9
RBC1	31.6	13.2	5	20.2	86.8	33	32.5	95.2	20	16.0	4.8	1

Those duets in which only the females participated were consistently shorter than those in which the male duetted ($z=4.46$ $n_1=9$ $n_2=74$ $p< 0.001$ – see Table 8-10). The absence of a male contributor meant one of the females had to play the male role in the duet and in all cases this was the subadult female. Unable to produce male-specific phrases and not displaying male-typical singing behaviour (e.g. approaching female at start of duet or clasping her at the climax of the great call) meant that the adult female did not receive the vocal and behavioural cues she normally obtained when duetting. It is proposed that the loss of these cues prevented the adult female from continuing with the duet and, on each occasion in which the male did not contribute, she was the individual who terminated the song bout.

Table 8-10 Duration of normal, disturbed and female-female duets.

	Duration of duet variants					
	Normal duets		Disturbed duets		Female-Female duets	
	RBC2	RBC1	RBC2	RBC1	RBC2	RBC1
Mean duration	15.6	20.6	9.6	7.3	5.7	-
Range	5.0 - 73.0	7.0 - 59.0	4.0 - 20.0	5.0 - 9.0	3.0 - 12.0	-

It was noted in the field that RBC2 duets delivered in response to boundary conflicts tended to be longer than those stimulated by calls of neighbouring groups (Table 8-11). On average, they lasted 5.4 minutes longer but this difference was not significant. An examination was also made of lengths of duets directed at different groups, particularly those which persistently received vocal attention from RBC2 or included females producing similar (ie. *muelleri*-like) great calls. Despite RBC2 making regular vocal contact with some groups and often ignoring others, they did not call longer to the former groups nor did they differentiate in their response to duets characterised by *muelleri*-like and *agilis*-like great calls.

Table 8-11 Duration of RBC2 duets elicited by different stimuli.

	Stimulus					
	Territorial behaviour		Neighbouring groups call		Type of great call	
	Other group calling from home range	Other group located in or near territory	Common-response groups	Occasional-response groups	*Muelleri*-like great call	*Agilis*-like great call
Duration	13.3	18.7	14.3	12.0	14.1	12.2
n	36	13	35	11	61	29

8.8 Distribution of song bouts through the day

RBC2 called throughout the activity period but concentrated their calling behaviour to a three hour period in the early morning. Combining duets and solos, a peak of calling occurred approximately an hour after dawn (i.e. between 0600 - 0700) and 78.3% of all song bouts were produced between 0400 and 0800. Mather (1992) found a similar distribution of calling at Barito Ulu, the consistent delivery of songs over the first four hours of the morning an outcome of the variety of intermediate forms resident in the area.

Duet singing by RBC2 peaked in the hour after dawn with 79.5% (n=66) of all duets delivered between 0500 and 0800 (Figure 8-5). Dawn duets were rare and only one was delivered before sunrise. Other duets given from the night tree started around 10 minutes after dawn and on mornings when heavy rain fell or the light in the forest was particularly poor, calling could be delayed by as much as 48 minutes after dawn. Most duets, however, were morning song bouts and the first duet of the day normally occurred between 0600 and 0800, once the group had left the night tree and finished the first or second feeding bout of the day. RBC1 showed a similar pattern of duetting, performing 76.4% of their duets before 0800 and rarely duetting before 0530 (Figure 8-5).

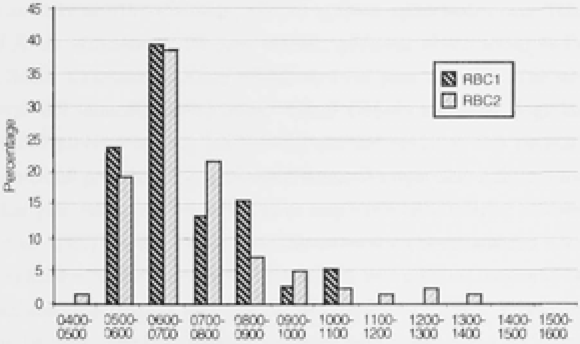


Figure 8-5 Daily distribution of duets performed by RBC2 and RBC1.

Male solos were prevalent (e.g. AM2) or predominant (e.g. AM1) between 0400 - 0530, and only the adult male called before dawn (Figure 8-6). Surrounding males also mostly soloed between 0400 and 0530. Counter-singing and chorusing was a common feature of male pre-dawn solos. RBC2 male counter-sang only with adult males of RBC5 and, in particular, RBC1 and RR1 but sang with other males during bouts of chorusing.

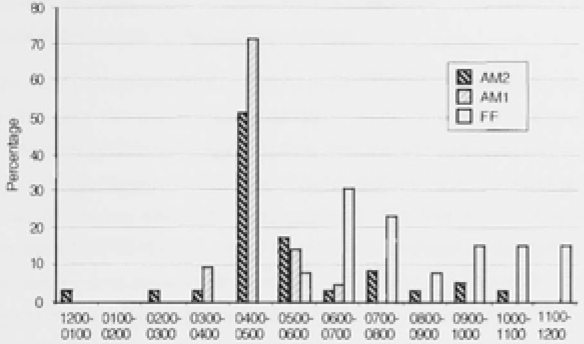


Figure 8-6 Daily distribution of solos performed by AM1, AM2 and FF (AF2/AF1/SF2 combined).

On one occasion, the adult male of RBC2 and males from neighbouring groups started calling at 2400 hours and continued to call intermittently throughout the night, sometimes on their own but occasionally in bouts of counter-singing or chorusing. Male Kloss gibbons have also been known to solo as early as 0100 (Whitten, 1982b) as have *agilis* males near Teluk Jolo (Rupert Ridgeway and Allan Williams, 1996 pers. comm.; personal observation) and *muelleri* in the Loksado area, South Kalimantan (Allan Williams, 1998 pers. comm.). The stimulus for such early calling was not immediately obvious. Local Dayaks and their dogs hunting for pigs sometimes induced gibbons to sing but hunting did not occur on this particular night. The presence of a potential predator (e.g. a clouded leopard) might also induce a male or males to start singing. Lar gibbons have been observed to sing when encountering a "dangerous animal" (Raemaekers et al. 1985) but these calls were disturbed song bouts and did not stimulate other groups or individuals to sing. Although it is possible that gibbons may sing in response to a predator, it is unlikely that singing would be sustained for 4 to 5 hours. Furthermore, females at Rekut tended to be the primary contributor to alarm call responses but no female was heard to participate in the singing. It is more likely that the particularly bright moon that night had some affect on the early calling behaviour. In September 1989, clear nights and full moons induced gibbons at Barito Ulu to duet before 0430 (Mather, 1992) and Gittins (1979) has also noticed that on brighter than normal mornings, when the moon had set late, *agilis* males began their solos earlier.

Soloing after dawn accounted for almost half of all solos delivered by RBC2 and, unlike pre-dawn singing, was not dominated by solos of the adult male (Figure 8-6). Indeed, the level of male solo singing decreases markedly once the sun has risen. Surrounding males also showed a considerable decline in solo singing after dawn, particularly RBC1 adult male who was only heard to solo once in the morning. Male gibbons may contribute less time to morning singing since they need to assess "the benefits of singing after dawn ... against the costs of not feeding, discovering new food sources, or patrolling ... the home range" (Whitten, 1982a). Behaviour typical at dawn (e.g, sleeping, some intra-group social behaviour) can occur at any time during the day and hence is not critical to the pre-dawn period.

If male gibbons sing predominantly at dawn in order to leave more time in the day for other important activities (e.g. the search and consumption of food), then why don't female gibbons do the same? Assuming that territorial defence, and the protection of key resources, is the primary function of the female song, regular song performance is essential, regardless of whether the time of singing interrupts other pursuits. The female's tendency to sing in the morning, rather than later in the day, is, in turn, probably related to the differential acoustics operating in the rainforest at different times of the day. Waser and Waser (1977) have proposed that sound projection and call detection is optimal in the early morning period.

8.9 Context for singing

8.9.1 Normal and disturbed duets

The commencement of a song bout by a neighbouring group often induces gibbons to start singing and this was the primary circumstance stimulating RBC2 and RBC1 duets (Table 8-12). Gibbons may respond to the song of any audible group but the focus groups tended to sing when close neighbours duetted. The duets of RBC1 and, in particular, RR1 were most commonly responded to by RBC2, the latter accounting for a fifth of all duets, while RBC1 answered RBC2, RBC3 and BR2 duets equally. RR1's importance in eliciting RBC2 duets was surprising considering the location of RR1's home range. The Rekut river separates the home ranges of the two groups and there are no obvious points (such as the presence of touching trees) along the river where either group could cross over and enter the other's territory. The absence of stimulation by the duets of RBC5, a group whose home range merges with that of RBC2, makes this observation even more remarkable. It is interesting to note that the great calls of RR1 and RBC1 are similar to those of RBC2 (the female produces a *muelleri* backcross great call) while those of RBC5, and other groups which elicited less response, produced soaring *agilis*-like great calls. It is possible that RBC2 identify groups producing *muelleri*-like great calls, regardless of their location, as providing more of a threat, be it territorial or mate-loss related, than those producing a dissimilar great call. This call response behaviour, however, was not evident for RBC1. Duets were stimulated almost equally by groups who shared a territorial boundary and those across the Busang river. Further, there was no proclivity to sing to groups whose females gave *muelleri*-like great calls as the adult females of BR1, BR2 and RBC3 all gave *agilis*-backcross great calls.

A wider examination of call response behaviour (Table 8-13) finds that (female) hybrid gibbons do display a significant tendency to respond to those songs given by females who produce a similar great call (χ^2=4.31 d.f.=1 p≤0.05). This is particularly interesting when considering the non-uniform pattern of great call variants in the immediate research area, resulting in female gibbons having at least one neighbour who produces a dissimilar great call. Females still call to neighbours who produce a different great call but frequently reserve their singing response to females, in adjacent territories or in more distant locations, who deliver the same great call variant.

Table 8-12 Context for RBC2 and RBC1 duetting (includes all duet variants).

Stimuli	RBC2		RBC1	
	%	n	%	n
No apparent stimuli	30.1	25	39.5	15
Other groups call*	43.4	36	47.4	18
Call by RBC1	14.5	12	*	*
Call by RBC2	*	*	10.5	4
Call by RBC3	-	-	10.5	4
Call by RR1	16.9	14	-	-
Call by RR2	6.0	5	2.6	1
Call by BR1	3.6	3	10.5	4
Call by BR2	-	-	10.5	4
Gibbon chorus	2.4	2	2.6	1
Territorial dispute	15.7	13	13.2	5
Encounter with RBC1	14.5	12	*	*
Encounter with RBC2	*	*	7.9	3
Encounter with RBC3	**	**	2.6	1
Encounter with RBC5	1.2	1	-	-
Miscellaneous	10.8	9	2.6	1
Intra-group aggression	2.4	2	-	-
After copulation	1.2	1	-	-
From fruit source	2.4	2	2.6	1
Red langurs in food source	1.2	1	-	-
Hunters and dogs on trails	1.2	1	-	-
Alarm call of giant squirrel	1.2	1	-	-

* RBC5 and RR3 omitted from table since their calls were not observed to stimulate RBC2 or RBC1 duets.

** Home ranges do not overlap.

Table 8-13 Differential song response rates given to similar and dissimilar great call variants.

Song response combinations	Number of songs eliciting song response*	Frequency of songs eliciting song response	
		Total songs	Song response combination
Same	85	58.6	-
agilis-backcross ⇒*agilis*-backcross	33	22.8	38.9
muelleri-backcross ⇒*muelleri*-backcross	49	33.8	57.6
hybrid ⇒ hybrid	3	2.1	3.5
Different	60	41.3	-
agilis-backcross ⇒ *muelleri*-backcross	23	15.9	38.3
muelleri-backcross ⇒ *agilis*-backcross	28	19.3	46.7
agilis-backcross ⇒ hybrid	2	1.4	3.3
hybrid ⇒ *agilis*-backcross	0	0	0.0
muelleri-backcross ⇒ hybrid	5	3.4	8.3
hybrid ⇒ *muelleri*-backcross	2	1.4	0.0

* total number of *agilis*-backcross songs = 107

* total number of *muelleri*-backcross songs = 134

* total number of hybrid songs = 25

Tenaza (1976) observed that Kloss gibbons frequently sang together, or chorused, as male and female songs were rarely given without another same-sex member of a surrounding group responding (but see Whitten, 1980). Hybrid gibbons often accompanied other groups in bouts of duetting but not as frequently as Kloss gibbons. Around 70% of RBC2 and RBC1 duets involved chorusing, either by responding to, or being accompanied by, another group or groups, and were occasionally stimulated by bouts of multiple group singing. Chorusing tended to commence within immediate neighbouring groups and spread gradually to those more distantly located.

Territorial disputes accounted for 15.7% of RBC2 duets, all but one of these confrontations occurring with RBC1. Observations of territorial fights between RBC2 and a neighbouring group suggested that the group whose territory has been trespassed were more likely to be the singing group. Indeed, on all occasions in which RBC1 invaded RBC2's territory (i.e. an intense encounter), only the latter group was observed to sing. RBC1 remained silent and during the one intense encounter in which they did sing, only the female contributed, producing a disturbed solo which contained no great calls. RBC1 also duetted in response to territorial conflict, once when RBC3 entered their territory and on three occasions when they met RBC2 on the territory boundary (ritual encounter). During a two week border dispute with RBC2 in February 1996, RBC1 crossed the boundary undetected and duetted from a heavily fruiting *Ficus sundaica* tree. This tree had been the site of intense fighting and displacement between RBC2 and RBC1 the previous week and thus this duet could be interpreted as a declaration of range acquisition.

A series of miscellaneous stimuli were also observed. Feeding in heavily fruiting trees and a copulatory bout between the adult male and the adult female immediately preceded the delivery of a duet. Periods of high food abundance (*klossii*, *lar* and *syndactylus*), the presence of a desirable food source in lean times (*moloch*) and mating (*syndactylus*) may increase the frequency of singing (Chivers et al., 1975; Tenaza, 1976; Chivers and Raemaekers, 1980; Whitten, 1982b; Kappeler, 1984a). It is therefore conceivable that a bout of singing may be directly elicited by copulation or the discovery of a valued food resource. Another duet, given during an encounter with a troop of red langurs in a potential food source, could also have been related to the discovery and defence of a feeding tree. Feeding interactions between hybrid gibbons and other primates or hornbills were also reported by Mather (1992) but Mitani (1985a) has suggested that such singing displays are merely a response to the presence of another primate species rather than defence *per se* of the food tree.

8.9.2 Solos

Although duets may be delivered in response to a number of varied stimuli, solos tended to occur for no apparent reason or when a neighbouring, same-sex gibbon was soloing (Table 8-14). Indeed, 71.4% of all AM2 solos were initiated when a neighbouring male or males began soloing. Both the adult male and the adult female of RBC2 favoured soloing in response to performances by same-sex members of RBC1 and RR1. The male also sang twice with males from BR1 and BR2. Song bouts of four close neighbouring males accounted for 66.7% of RBC1 male solos and no discrimination in counter-singing partner was observed. Territorial trespass by RBC3 and RBC2 stimulated the solos of RBC1 adult female who was never heard to countersing with other females.

Table 8-14 Context for RBC2 and RBC1 soloing.

	RBC2						RBC1			
	AM2		AF2		SF2		AM1		AF1	
	%	n	%	n	%	n	%	n	%	n
No apparent stimuli	22.9	8	33.3	3	100.0	2	33.3	7	-	-
Other groups call*	71.4	25	44.4	4	-	-	66.7	14	-	-
Call by RBC1	20.0	7	11.1	1	-	-	•	•	•	•
Call by RBC2	•	•	•	•	•	•	19.0	4	-	-
Call by RBC3	-	-	-	-	-	-	14.3	3	-	-
Call by RBC5	5.7	2	-	-	-	-	-	-	-	-
Call by RR1	28.6	10	33.3	3	-	-	-	-	-	-
Call by BR1	5.7	2	-	-	-	-	19.0	4	-	-
Call by BR2	-	-	-	-	-	-	4.8	1	-	-
Gibbon chorus	11.4	4	-	-	-	-	4.8	1	-	-
Territorial dispute	-	-	22.2	2	-	-	-	-	100.0	2
Encounter with RBC1	-	-	22.2	2	-	-	•	•	•	•
Encounter with RBC2	•	•	•	•	•	•	-	-	50.0	1
Encounter with RBC3	**	**	**	**	**	**	-	-	50.0	1
Miscellaneous	5.7	2	-	-	-	-	-		-	-
From fruit source	5.7	2	-	-	-	-	-		-	-

* RR3 omitted from table since their calls were not observed to stimulate RBC2 or RBC1 solos.

** Home ranges do not overlap

8.10 Environmental influences on singing

Gibbons prefer not to sing in inclement weather, delaying their song or not performing at all after nights of heavy rainfall or during rain showers (Chivers, 1974; Gittins, 1979; Whitten, 1982b). While rainfall at Rekut did not significantly affect the length of duets or solos, the total amount of singing (in minutes) or the average number of male solos, it did affect the mean number of duets given over the 5-day observation period (Table 8-15) and whether gibbons actually sang or not. On those days in which RBC2 and/or RBC1 were heard to sing, approximately fifty percent were characterised by an absence of rainfall (Table 8-16). Furthermore, over three quarters of singing days occurred on days when rainfall was 5mm or less.

Table 8-15 Effect of rainfall on the frequency and duration of duets and solos.

	Total rainfall - month (n=12)		Total rainfall - 5-day sample (n=12)	
	r_s	sig to	r_s	sig to
Mean number of duets	.057	=.85	-.618	=.04
Mean number of male solos	.071	=.82	.346	=.25
Total duration singing	.350	=.25	-.182	=.55
Total duration duetting	.011	=.97	-.137	=.65
Total duration soloing	.217	=.47	.091	=.77

Table 8-16 Rainfall levels and frequency of singing on singing days.

	RBC2		RBC1	
	% of singing days	n	% of singing days	n
No rain	45.3	29	51.7	15
1 - 5 mm	23.4	15	34.5	10
6 - 10 mm	15.6	10	3.4	1
11 - 20 mm	7.8	5	3.4	1
> 20 mm	7.8	5	6.9	2

Comparing the frequency of singing performances over the observation period also shows a tendency to abstain from calling during wet weather (Table 8-17). Males sang solos on 64.7% of dry days but only on 28% of wet days. As noticed by Whitten (1982b), male hybrid gibbons also delivered dawn songs less frequently if heavy rain had fallen the previous night. Solos were never heard on mornings if more than 3 mm of rain fell during the night. Of course, a night of little or no rainfall did not always mean that the male would sing and indeed he did not on 35.3% of such mornings. Duetting was not as greatly influenced by rainfall. If substantial amounts of rain (e.g. > 15 mm) fell the previous night, no duetting occurred but lesser downpours did not always deter the production of these songs, normally having a delaying effect instead. Of the mornings characterised by an absence of rain, RBC2 duetted on 29 (85.3%) and remained silent on five.

Table 8-17 Frequency of soloing and duetting on dry and wet days.

	Dry days				Wet days			
	No of days sang		No of days did not sing		No of days sang		No of days did not sing	
	%	n	%	n	%	n	%	n
Male solo	64.7	22	35.3	12	28.0	14	72.0	36
Duet	85.3	29	14.7	5	64.0	32	36.0	18

If the function of the female song is defence of the territory, months in which the resident group are undergoing consistent territory incursion could be associated with an increase in singing. The infrequent level of intragroup conflict prevents any former statistical analysis but some discussion can be made on general trends. The level of RBC2 singing rose markedly during a period in February in which conflict between the group and RBC1 occurred regularly over a two week period. In the 5-day session in which RBC2 was under observation the total number of minutes spent singing (duetting and combined) and the average number of song bouts was the highest for all 12 month 5-day follows. In May and June, however, when incursions occurred on two days each, results were less convincing. Although the total length duetting and total length singing were relatively high for the respective months, RBC2 did not sing as frequently as they did in February and, surprisingly, the average number of song bouts for these months were ranked 10th and 11th. Constant pressure from the invading group, as seen in February, rather than occasional or short-lived dashes across the territory border, is seemingly the cue for an increase in singing behaviour. Gibbons not only call for long periods when engaged in bouts of antagonism but spend more time duetting the following morning.

Defence of the territory proper extends to defence of key resources within it and hence gibbons may alter their rate of singing behaviour in response to patterns of food abundance and/or food type consumption. Interestingly, there was little association between the frequency of singing and duration of songs with fruit consumption or fruit availability. Increases in fruit in the diet did find a rise in the length of the duet but not on a significant level (Table 8-18). The proportion of figs in the diet correlated positively with the average number of solos given per month and the mean duration of duets. When gibbons sang from, or close by, fruit sources, they invariably were heavily fruiting fig trees. Although the focus groups did not select for figs, preferentially taking other fruit forms when they were available, figs did represent a useful food sources in times of low food availability and for this reason are worth protecting. Gibbons also increased the average number of male solos and the length of the duet in months when flower was abundant in the home range. This is an interesting result considering the already described dietary preference for flowers during peak periods of flowering activity (Chapter 4).

Table 8-18 Effect of diet and food availability on singing.

	Diet				Food availability		
	% FR	% Fig	% FL	% YL	% FR	% FL	% YL
Ave no of duets	-.184	.290	.240	-.244	.016	-.080	-.368
Ave no of solos	.081	.631*	.190	-.194	-.152	.791**	-.080
Ave length of duet	.532	.585*	.067	.522	.079	.687*	.074
Ave length of male solo	.018	.056	-.137	-.095	-.005	-.032	-.606*
Total duration singing	.056	.231	.448	-.217	.253	.569	.189
Total duration ductting	.182	-.336	.123	-.424	.033	-.598*	.074
Total duration soloing	.273	-.375	.084	-.273	.032	.582*	-.228

Significance level: * $p \leq .05$ ** $p \leq .01$

8.11 Discussion

8.11.1 Hybridity and singing interactions of the mated pair

In most aspects of their singing behaviour, hybrid gibbons differed very little from other populations of gibbon. Song duration, performance time, song bout stimulation, and potential environmental influences followed the same basic pattern observed for *agilis* and *muelleri* as did the songs themselves, in terms of notes used, sequence organisation and participation. More unusual singing traits are assigned to the effects of hybridity. The semi-regular performance of a female-female duet by RBC2 is certainly related to the trio status of this group and the bizarre *twoulwills* and twitters of the focus group females probably also a consequence of hybridisation. While these singing peculiarities have little or no greater effect on the hybrid individual, group or population, other traits, such as great call variation and frequency of female soloing, can. Mather (1992) has suggested that the range of gibbon hybrid types at Barito Ulu, and the continual and inevitable pairing of individuals representative of different hybridity states, could impair the singing relationship between the mated pair in such a way as to reduce their reproductive potential. An inability to recognise or adapt to the song of their mate diminishes the signalling power, and hence function, of the duet, affecting a decline in fitness induced either by the rigours of relentless, physical territory defence or, worse, the loss by desertion of a mate.

A successfully transmitted duet depends fundamentally on a mated pair's ability to coordinate and integrate their songs. In a population, such as the one found at Rekut, where individuals of varying hybridity status produce a distinct array of song forms, duet arrangement may not be quite so easy to achieve and lead to the delivery of song bouts that are sub-optimal in their structure and, invariably, function. If the duet's effectiveness, either as a means of advertising the territory/pair bond or as a facilitator of pair bond maintenance, is diminished, instability could be promoted and eventually result in the reduction of reproductive fitness (Mather, 1992).

Certain aspects of singing behaviour could serve as potential indicators of duetting complications but if one was to accept those features proposed by Mather (1992), it would appear that evidence for interactive difficulties in hybrid gibbon duetting is contradictory at best. Hybrid gibbons tend to sing more often than most other lar group gibbons and this could be related to the delivery of a less than successful duet. However, if major interactive problems do occur between a hybrid mated pair, duets should only continue for short periods of time, one or other of the pair choosing to terminate the song bout early rather than continue with a structurally inferior version. Hybrid gibbons do not produce short duets, instead delivering duets similar in length to those of *agilis* or *muelleri*, if not slightly longer.

If the pair cannot exchange the correct vocal cues, then song organisation or performance of key sequences, such as the great call, will suffer. The overall structure of the hybrid duet, in terms of organisation sequence and note use, did not differ greatly from the duets performed by *agilis* or *muelleri,* but the critical feature of the song, the great call, did undergo some transformation. Mather (1992) has suggested that hybrid or backcross great calls are defective signals compared to the great calls of *agilis* or *muelleri* since the climactic notes peculiar to these species are not quite achieved in the hybrid forms. This may be so but the actual delivery of the great call is possibly a better indicator of successful organisation between the mated pair (i.e. adult female receives the correct pre-great call cues from the adult male) and the singing capabilities of the adult female (i.e. an ability to reach and complete the climactic note sequence). Most characteristics of hybrid female great calling behaviour are indicative of competent delivery – great calls were always preceded by the appropriate introductory notes and exchanges, female gibbons rarely aborted their great calls, and the climactic note series did not drift from the common format. But the measure of great call delivery per minute proved to be contradictory. Mather (1992) reported that females in the Rekut research area gave a rate of great calls intermediate (0.71) between that of *agilis* (0.66) and *muelleri* (0.85), but the present study found a much lower rate, RBC2 and RBC1 females respectively averaging 0.54 and 0.49 great calls/minute.

Moloch and Kloss female gibbons solo regularly, primarily because their male partners rarely or only sometimes participate in community bouts of singing. In contrast, hybrid females can elicit singing performances from their mates and so why some females choose to sing alone is open to interpretation. Again, interactive duetting problems could induce a female to sing on her own or prevent a male in joining his mate in the duet (Mather, 1992). Certainly, the Type I solos produced by Rekut females may have arisen from temporary or permanent communication problems between the mated pair since the song resembled the basic structure of the duet (i.e. included great calls). However, five primary points outlined below suggest instead that soloing is a behavioural quirk peculiar to certain female members of the hybrid population and not a consequence of inherent duetting difficulties.

1. Three of the five Type I solos performed by AF2 were given during territorial encounters with RBC1. If the function of the female song is to declare ownership of territory, it would not be unusual for the female to contribute to such an incident by singing alone, particularly if her mate is playing a more pro-active defensive role.
2. Female solos did not always follow the typical duet format (Type II solos), particularly in the composition of phrases. The delivery of sequences in a form not familiar to the adult male or different from what he expects is not necessarily a technical fault of the female but a decision to sing a variant of her own song and to sing alone. The fact that females almost always sing Type II solos in chorus with a neighbouring female supports the interpretation that there has been a deliberate modification to the female song, allowing them to project their message without interruption from the adult male.
3. Younger females (e.g. subadult of RBC2) produced solos. Although the subadult participated in duets with her parents, and did so quite successfully, she never sang a duet with her father and therefore could not have perceived a potentially incompatible duetting relationship.
4. Only some of the females at Rekut soloed. It is possible that only a few females experienced duetting difficulties with their mate but it is more likely that soloing was an individually distributed behavioural phenomenon, a hypothesis supported by reports of the presence and absence of soloing behaviour in different populations of *muelleri*.

8.11.2 Great call variants and their recognition

The ability to recognise all the great call variants in one's surroundings is to the female gibbon's advantage as it a) enables her to successfully identify and locate her neighbours and therefore b) appropriately defend her territory or mate against potentially destabilising individuals. If unable to do so, partner desertion, polygynous associations, and regular shifts in boundary location might characterise the population's social dynamics. In the previous chapter, a review of song playback experiments conducted by Raemaekers and Raemaekers (1985) suggested that female *lar* can identify the songs of female *pileatus* as those of a gibbon but retain some difficulty in determining the sex of the caller. The fact that polygynous trios are much more frequent in hybrid zones further implies that an inherent problem exists in female inter-specific song recognition. But in areas where a population is constantly exposed to more than one song type, familiarity could be obtained and result in a uniform display response that is independent of the song variant produced by either the response giver or receiver.

At Rekut, where a variety of great call types are performed, female gibbons do show some tendency to direct their singing responses to females who produce similar great calls, although this trend is very much dependent on the individual. For example, the adult female of RBC2 sings consistently with, or in response to, females who also give *muelleri*-backcross great calls. This is especially significant when comparing the singing attention directed to the adult females of RR1 (*muelleri*-backcross) and RBC5 (*agilis*-backcross), the former of which receives considerably more of AF2's vocal responses despite occupying a home range that is separated from RBC2's home range by a river. In contrast, it is location, rather than great call type, which appears to determine which groups some females (e.g. the adult female of RBC1) sing to and with.

Song discrimination in gibbons, however, is still little understood, thus plaguing any decisive discussion on song response patterns occurring at Barito Ulu. While some play-back experiments with both wild (Raemaekers and Raemaekers, 1985) and captive gibbons (Maples et al., 1989) display a differentiation between the response rates given to the calls of con- and inter-specifics, other experiments (e.g. Mitani, 1987a; 1987b) fail to find as marked a distinction. Furthermore, gibbons do not always show an ability to distinguish between familiar (e.g. their own and their neighbours) and unfamiliar songs (more distantly located gibbons) given by individuals within their own species (Mitani, 1985b). It is indeed possible that both methodological technique and disparities in experimental procedure used by different researchers has produced unexpected, inconsistent or incorrectly interpreted patterns of song recognition (Mitani, 1985b; Ulrich Reichard, 1998 pers. comm.). On the other hand, socio-ecological factors such as group density and frequency of inter-group contact might play as prominent, if not a more influential role in the gibbons' "ability" to discriminate between like and un-like (Mitani, 1985b). Until considerable data is collected on general trends in both male and female song recognition, and, more specifically, on song response patterns and associated behaviours amongst hybrids, the process of song discrimination can only remain speculative. Nonetheless, there does exist a tendency for female *albibarbis* x *muelleri* hybrids to call to females producing a similar great call and this effect on the status of the hybrid population is investigated in the final chapter.

9

Discussion

9.1 Summary of findings – primary consequences of hybridisation

Comparing the behavioural repertoire of a hybrid animal to that of the parental species, and distinguishing those behaviours which are either unique to the hybrid population or demonstrate a modified version of the behaviour's original manifestation(s), suggests there has been some form of hybridising effect. To unconditionally attribute behavioural modification to hybridisation, however, insists that that behaviour be under significant genetic control and only marginally or less potently affected by the animal's immediate ecological or social environment. Previous recognition of hybridisation-influenced behaviours in other populations of hybrid primate was achieved either because

1. the behaviour in question was absent in one of, or markedly different in its presentation between, parental species or because
2. hybrid primates living in pure species groups exhibited behaviours either not observed in, or were a variation or composition of responses displayed by, parental species.

These criteria are somewhat more difficult to apply to the *albibarbis* x *muelleri* hybrid population since a general behavioural uniformity characterises the lar group gibbons and the absence of pure *albibarbis* or *muelleri* in the research area prevents any direct comparison between pure and hybrid populations. Nonetheless, and despite *albibarbis x muelleri* hybrid gibbons displaying relative conformity to the basic behavioural patterns observed for agile and Müller's gibbons, unique behavioural traits and responses are used by the hybrids. Hybrid gibbon behaviours found to contrast with those reported for other gibbon populations include differential activity, feeding, ranging and social interaction strategies, and modifications to song structure and repertoire. While some of these behaviours can be explained with reference to influential environmental, ecological and/or social factors, others fail to comply with known gibbon responses and therefore represent potential behavioural indices of hybridity.

9.1.1 Singing behaviour

The great majority of modified behaviours described for other hybrid primates have been those used in communicative and social contexts and it is the key distinguishing feature of the gibbon, its song, which has been the most obvious recipient of the hybridisation effect. While individual song variation is not unknown for gibbons (e.g. Haimoff and Gittins, 1985; Haimoff and Tilson, 1985; Thomas Geissmann, 1998 pers. comm.), the marked alteration to specific sections of the hybrid gibbon song (e.g. the female great call) indicates a strong genetic basis to gibbon song structure. Female hybrid gibbons at Barito Ulu produce great calls that are intermediate to (e.g. hybrid), or a distinct variation of (e.g. *agilis*-backcross and *muelleri*-

backcross), those given by pure *agilis/albibarbis* and *muelleri*. The climax of the great call is particularly distinct, especially in the speed of note delivery, inclusion or exclusion of climax notes, and/or the sound of the song notes being produced. The effect of hybridisation on the songs of male hybrid gibbons is less obvious but the absence or only occasional use of trills and quaver notes is a conspicuous example of song modification. Noises used to communicate the state of the individual, such as the *twoulwill* and the *twitter* which are given in both aggressive or submissive contexts, are another outcome of hybridisation influenced changes to vocal responses.

Alteration to the structure of the primary male and female song might then induce changes to the frequency and duration of the song performance, particularly in song variants such as the duet where the two sexes need to successfully coordinate their respective vocal contributions. Because both organisation, note use and note exchange differs very little between *agilis* and *muelleri*, and between the parental species and hybrid gibbons, potential difficulties between the duetting pair are not as extreme as those produced for other hybrid combinations (e.g. *lar* and *pileatus* – see Mather, 1992). However, the structural changes made to the principal component of the duet, the great call, has the very real effect of disrupting singing coordination. This is particularly enhanced in a population where the parental species deliver quite different great calls, producing a much wider range of great call variants. The intermediate duration of *albibarbis* x *muelleri* duets, the uniform behavioural response male gibbons give to the great call, the absence of a conspicuous rate of aborted great calls, and the use of appropriate vocal responses prior to, and after, the great call, however, testifies to a relative ease in both singing coordination and competent song delivery. Only two factors are suggestive of some inherent singing difficulties — the tendency for (some) female hybrids to solo and the lower rate of great call production. In my opinion, and in contrast to Mather (1992), the fact that hybrid females soloed is not a particularly strong indicator of either individual or pair singing problems. My reasons for this are four-fold — (1) females only solo intermittently, (2) solos are often performed during territorial incursions, (3) young females also solo, and (4) the format of the solo differs quite considerably from that of the female's duet contribution. Furthermore, soloing in female Müller's gibbons follows the same pattern as observed for the hybrid population — only some females call and only on an occasional basis. Rate of great call production is a stronger indication of the competency of song delivery but the low rate calculated for this study contrasts so greatly with that estimated by Mather (1992) that no definite conclusions can be drawn.

9.1.2 Social behaviour

Traditional measures of social contact between gibbon group members (e.g. grooming) was generally restrained and rather infrequent but not significantly so when compared to some other populations of gibbon (e.g. agile gibbons at Sungai Dal – Gittins, 1979). Failure to find a distinct difference between hybrid and pure species in the frequency of their social interactions is probably not so surprising. Sugawara (1988) has already claimed that the social environment plays as important a role as the genes do in the control and use of a specific behaviour. Besides, hybridisation is more likely to exert a more direct or obvious effect on the *presentation* of the behaviour rather than the *frequency* of performance. While this is relatively easy to detect for primate species that engage regularly in lengthy and/or elaborate social displays (e.g. baboons), the often silent, brief and "subdued" nature of intra-group gibbon social contact presents difficulties when analysing variation in gibbon behavioural expression. It is my contention that social cueing between gibbons is a much more subtle exercise compared to other primate species and might reflect a general pattern for animals which associate in small social groups. So far, only the elementary social behaviours (e.g. play, groom, sex) have received any considerable attention from field researchers with the occasional description (e.g. facial and other expressions described by Baldwin and Teleki, 1976) of associated, and potentially more legitimate, indicators of social intent and response. Until a more thorough catalogue of gibbon social expression is compiled, a real understanding of the social relations existing between gibbon group members and how hybridisation affects it remains difficult to assess.

9.1.3 Feeding ecology

Food choice by hybrid gibbons exhibits some deviation from the typical gibbon diet. Like other populations of gibbons, hybrids regularly choose pulpy drupes and berries as their consummate food source, consuming large quantities of non-fig fruit when it is abundant. Less desirable fruits also feature in the diet and, while this is not unusual in itself, the morphological complexities (i.e. in terms of easy manipulation) and questionable nutritional value of these fruit species contrasts the hybrid fruit diet with that of other lar group gibbons. Flower consumption is also prominent in the hybrid gibbon diet; McConkey (1999) and this study has corroborated that hybrid gibbons not only selected for flowers but spent extensive feeding bouts at flowering sources. Other populations of gibbon also eat flower but not to the same extent as hybrid gibbons.

Explanations of necessity and positive selection can be applied to these feeding aberrations if phenological data suggest that gibbons eat inferior fruits and mature flowers in response to poor fruiting cycles and abundant flower production respectively. McConkey (1998, pers. comm.) has suggested that the actual supply of fruit (as opposed to the number of food trees) at Rekut is lower than that found at other research sites in South East Asia, forcing resident gibbons to occasionally choose undesirable fruit sources. This may be so but even when appropriate fruits are abundant in the home range, and such fruits contribute over 60% to the daily or monthly diet, inferior fruits are still consumed. Furthermore, some receive regular feeding visits throughout the year (e.g. *Parartocarpus bracteatus*), are taken in large quantities when more appropriate fruits are available (e.g. *Eugenia ecostulata*), or are highly selected for (e.g. *Pentace excelsa*).

Significant flower consumption is also not necessarily an absolute response to phenological patterns. Hybrid gibbons do modify their flower consumption in relation to fluctuations in flower production. But flowering activity at Rekut during the 1995-1996 field season was no higher than that recorded for previous or successive years. This implies that it is not a glut of available flower that induces hybrid gibbons to exploit a relatively high flower intake but an inherent preference for flower. Additional forms of evidence support this proposition. Firstly, flowers do not share any significant relationship, either positive or negative, with other food type consumption, suggesting that flower is not used as a replacement or purely supplementary food source. Secondly, fig use actually drops markedly when more flower is available in the home range. Hybrid gibbons do not select for fig as strongly as other populations of gibbon do but nutritionally a fig represents a source of greater worth than a flower. Nonetheless, when flower is available, fig is avoided. A third form of indirect evidence finds a positive relationship between frequency of singing and an abundance of flower in the home range. Rather than devoting more time to singing performances when fruit activity is high, hybrid gibbons actually produce longer songs more often when flower is available. The true function of the male and female gibbon song is still unresolved but if there is a territorial (read resource protection) basis to singing, it is interesting to note that it is a peak of flowering which is associated with increases in singing performance.

While it is possible that the feeding strategies described above are effects of hybridisation, the absence of pure *albibarbis* and *muelleri* groups in the immediate research area prevents any unqualified conclusions on the importance of dietary deviations. The potential and probable ecological differences existing between the field site and other parts of Borneo and western Malaysia also prevents any stringent comparison with the diet of other populations of *agilis* and *muelleri*. Furthermore, it is difficult to ascertain whether food or morphological type choice is under strong genetic control since the only reference to a genetic basis to food selection (hybrid guenons – Struhsaker et al., 1988) is derived from variations of food *species* use. However, the food choices made by hybrid gibbons are sufficiently different to propose that feeding is influenced somewhat by the genetic composition of the feeder. Indeed, previous researchers have employed the greater consumption of leaf by siamang and the concolor group gibbons as indices of specific, and hence gene-influenced, variation.

The type of diet exploited by the hybrid gibbon, with its preference for flower and willingness to use a broad range of fruit morphologies, provides the consumer with an improved series of differential feeding strategies. A more flexible dietary regime, in turn, not only allows hybrid gibbons to select the appropriate combination of food sources in relation to current (and future) conditions of food production but also engenders a more adaptable approach to differing ecological conditions.

Food species variation at Muara Rekut is comparable with that of other South East Asian research sites but actual food production is though to be low, possibly because of the poor condition of the local soils (Kim McConkey, 1998 pers. comm.). Selecting food items normally shunned by one or both parental species (e.g. hard walled, fleshless fruits), and not relying as heavily on traditional supplement foods (e.g. figs), provides the hybrid with the very real ability of coping adequately with periods of food depression. Feeding strategies can also be modified on a consistent basis. When a favoured foodstuff is widely available in the home range, it comprises a substantial proportion of the diet. But at times when over-exploitation might lead to shortages in the immediate future, topping up the diet with a less than ideal but reasonably nutritious food item reduces the risk of there being no appropriate food stuffs for consumption.

The taking of unusual plant products may also explain why hybrid gibbons occasionally use and, in some cases, actually occupy environment not conducive to gibbon feeding requirements.

The home ranges of RBC2 (and RBC1) incorporated areas of secondary forest, and gibbons residing across the Rekut river occupied areas consisting of significant tracts of heath forest. It was shown that the number of known gibbon food species in secondary forest at Rekut was quite high, undoubtedly an influential factor in RBC2's frequency of use. But a propensity to accept a wider array of food types, in particular differential fruit morphologies, could also induce them into such areas, allowing them to increase their dietary content by consuming foods not normally or not so widely available in primary forest. The same argument applies for heath forest. Compared to primary forest, plant (and food) species variation is very low in heath forest and little in the way of gibbon-specific foods is available. Nonetheless, hybrid gibbons will occasionally range into heath forest and, in regions where even larger areas of heath forest dissect sections of primary forest, hybrid gibbons still establish home ranges. Flexibility in dietary selection again aids the ability to occupy such poor habitat . Hybrid gibbons rely on primary forest for favoured foods but can also utilise heath forest, and the food products it produces, to supplement the diet.

9.1.4 Activity budgets and home range use

Activity budgeting and home range use are two behavioural parameters difficult to quantify with hybridisation since both are controlled by an extensive array of variables. Extracting these variables, and identifying what effect hybridisation has had on the way a hybrid gibbon budgets its day and how it uses its home range, again requires the presence of at least one or both parental species resident in the hybrid area. Some distinct deviations from the general pattern followed by other gibbons were detected but each of these can be explained satisfactorily referring to physiological or ecological factors.

9.2 Secondary consequences of hybridisation

The intricate network of relationships encompassing the social and ecological behaviours of an animal suggests that changes to the manifestation of one behaviour could, theoretically, induce changes to the manifestation of other, related behaviours. One previously documented example describes the range of social congregations observed in *anubis* x *hamadryas* baboon troops, thought to have arisen from the differential ability hybrid baboon males display in their herding technique (Kummer, 1968; Nagel, 1973; Kawai and Sugawara, 1976; Sugawara, 1982; 1988). Other, albeit brief, studies have failed to find any secondary consequences of hybridisation, such as the hybrid macaques and cercopithecines who reside in relatively stable, harmonious groups despite the myriad of social expressions given by group members (Struhsaker et al., 1988; Baker and Bynum 1989; Erhart et al., 1996). In this section, those behavioural parameters considered to be primary derivatives of hybridisation will be examined for their observed and potential effect on other aspects of gibbon social and ecological behaviour. Until further research is completed, the discussion can only remain speculative but introduces a number of relational hypotheses.

9.2.1 Song variation and social composition

One of the potential secondary outcomes of gibbon hybridisation is the influence song variation has on group composition. Deviations from the traditional family unit are not unknown for pure species gibbons but do tend to occur more frequently in contact areas, where song variation is considerably greater. The ubiquitous polygamous social construct observed in hybrid areas is the polygynous trio, comprised of an adult male and two females of differing hybridity or specific status. Interestingly, playback experiments conducted by Raemaekers and Raemaekers (1985) and Mitani (1987a) found evidence for sex differences in song recognition that can be used to explain the predominance of polygyny in hybrid zones. While male gibbons display similarly aggressive responses to the male songs of both con- and hetero-specifics, females exhibit only significant aggression when exposed to the songs of females from the same species. This suggests that female gibbons have difficulty in recognising the same-sex song of another gibbon species as representative of a sexual threat. If this is the case, then in areas where individuals produce dissimilar great calls, female gibbons might be more inclined, ecological conditions permitting, to accept a polygynous social setting.

In the immediate research area at Rekut, where three basic great call variations are given by female hybrids, one polygynous trio – RBC2 – was identified. The females resident in the group, considered to be mother and daughter, gave different great calls — AF2 delivered a *muelleri*-backcross great call and SF2 performed a hybrid type great call. Mather (1992) determined that the rate of climax note emission is the key factor distinguishing the hybridity status of the female caller. Since the primary difference detected between the great calls of AF2 and SF2 was the speed of the climax delivery, it is possible that it is this feature which hybrid (and other) female gibbons use to identify the caller. And if females, such as AF2, do indeed have an inherent problem in recognising modified or unusual great calls, alterations to climax delivery could be enough to prevent accurate or competent identification processes and hence appropriate behavioural responses (e.g. marked female-female aggression).

Of course, the fact that this and Mather's (1992) study failed to detect other polygynous groups in the study population is a strong challenge to the song-recognition hypothesis. However, in my opinion, the supposed absence of marked polygyny in the *albibarbis* x *muelleri* gibbon population is more likely a consequence of the method of census data collection used by Mather and myself. Mather (1992) relied mostly on a brief (1 hour or less) identification process to describe the social composition of hybrid groups. Considering that all but a few of the census groups were unhabituated, this time frame is much too short to get more than a perception of group composition and existing inter-group social relations. In this study, only a small sample population were studied, of which just half were observed for a period of time essential for confirmation of group composition. The rest were censused using song data. Although some information on the number of mature or maturing individuals in a group can be derived from short-term or auditory census techniques, the social position of the individual can not. To obtain a clearer picture of social structure in the hybrid population, a wide-scale survey is necessary where social organisation for each group is determined using a combination of visual and auditory identification techniques.

9.2.2 Song variation and inter-group relations

Mather (1992) suggested that the modifications made to the gibbon song as a result of hybridisation transforms the hybrid song into a somewhat "inferior signal" compared to the calls given by the parental species. Depending on the function of the male and female song, these changes could loosen the pair bond relationship and/or curtail effective resource or mate defence; the latter because the pair is less committed to such defensive strategies or because neighbouring groups perceive the pair bond as weak and hence subject the pair to relentless territorial transgressions. An inability to communicate stable territory ownership and management and/or long term commitment to the pair bond could induce (compared to pure species populations) increased disruptions to boundary locations, eviction from territories, and frequent bouts of inter-group conflict. None of these are evident for the immediate study population. Since Greenaway and Lochowski's field studies in 1990-1991, parts of RBC2 and RBC3's home range have been annexed by RBC1 but, otherwise, range boundaries for these and groups RBC4 and RBC5 have undergone relatively little transformation. More pertinently, low monthly and annual rates of inter-group conflict also reflected effective territory defence. The infrequency of border contact between the focus groups RBC1 and RBC2 and their neighbours was undoubtedly affected by the reduced chance of observing interactions involving unhabituated groups (see Reichard and Sommer, 1997). But the habituated groups RBC1 and RBC2 also spent little of the annual research period engaged in border clashes, a finding supported by earlier studies (e.g. Greenaway, 1991; Lochowski, 1991; Emma-Jane Stokes, 1999 pers. comm.).

The concept of song variation and recognition also introduces potential differential territorial responses. The adult female of RBC2 responded more often to females who delivered *muelleri*-backcross great calls than to females who gave either hybrid or *agilis*-backcross great calls. This was particularly conspicuous when comparing the rate of response to the adult females of RR1 and RBC5. The former (AFR1), who produced *muelleri*-backcross great calls, received considerable vocal attention despite living across the Rekut river. The second female (AF5), whose great call was an unusual variant of the *agilis*-backcross, occupied a home range bordering AF2's but received little or no response from AF2. It must be said that AF5 did not call as much as AFR1, possibly because she had difficulties with song production, and this might explain the discrepancy between call responses. However, when AF5 did call, AF2 was never heard to answer her song with one of her own. In contrast, the adult female of RBC1, who also produced a *muelleri*-backcross great call, did not show a similar response trend to AF2 and sang equally as often to her *agilis*-backcross neighbours (e.g. the females of BR1, BR2, RBC3) as she did to AF2. However, data given in Table 8-13 in Chapter 8 indicates that a general and significant relationship does exist between response rate and similarity of the great call variant.

If females consistently direct their vocal replies to females producing great calls similar to their own, then other displays of territorial defence, such as physical inter-group aggression, might also occur more frequently between these individuals and their social groups. As a result, disproportionate incidences of border conflict would occur depending on the type of great call given by neighbouring females. This hypothesis is initially supported by the frequency of differential inter-group conflicts observed in this study but Greenaway (1991, unpubl.) and Lochowski (1991, unpubl.) described quite a different scenario. RBC1 clashed four times with RBC2 over a three month period but engaged in border disputes with the unhabituated RBC3 on seven occasions. RBC2 were never observed to encounter RBC5. While these results fail to support the above hypothesis, they do show an interesting consistency with singing-response trends observed for the adult females of RBC1 and RBC2. In this study, where RBC2 received the greater proportion of observation time, the focus group was found to clash more often with the group (i.e. RBC1) they directed most of their duets to. In Greenaway's (1991) and Lochowski's (1991) studies, where the three study groups (RBC1, RBC2 and RBC3) received relatively equal periods of field research time, RBC1 showed some tendency to clash more often with RBC3. On the whole, however, RBC1 engaged in inter-group confrontations at a rate similar to the proportion of specific-group directed song responses.

9.2.3 Pair bond stability and extra-pair relations

Another social consequence potentially arising from hybridisation is a lessening of the strength of the pair bond. Again, structural modification to the song and the resultant difficulties a pair might experience in producing a competent duet could lead to early terminations of the pair relationship. Indeed, hybrid *lar* x *pileatus* gibbons are characterised by a higher than normal (i.e. compared to sympatric pure *lar* and *pileatus)* frequency of pair bond dissolution which Mather (1992) has suggested is related to the problems the pair experiences in duet co-ordination. For the *albibarbis* x *muelleri* population, however, Mather (1992) and I have both argued that hybrid pairs do not appear to suffer from any conspicuous disruption to interactive singing capabilities (see above). The average number of bouts (duets and solos combined) and proportion of time devoted to singing per day does tend to be greater for the *albibarbis* x *muelleri* hybrid compared to parental species. But the rate of singing for each song type, although higher than that observed for *muelleri* at Kutai, is comparable to *agilis* at Sungai Dal.

Alteration to, or the loss of fundamental elements of, social exchange can also have a negative effect on the relationship between the mated pair. The rather subtle forms of social interaction employed by the gibbon, and its presentation so high up in the canopy, does, however, encumber any detailed description on inter-individual sociality. An alternative, albeit less sophisticated, method is to refer to the frequency of social display which finds that hybrid pairs do not engage regularly in intra-group social behaviours. This result is not so unusual since most gibbons, pure or hybrid, are not especially gregarious. Besides, measures of spatial proximity and inter-individual distance portray the hybrid group as a particularly cohesive social unit. Such strong cohesiveness might suggest that *albibarbis* x *muelleri* hybrids are less likely to terminate their present relationship in search of a more appropriate (singing or social) partner. To confirm that hybrid gibbons do regularly change partners, routine collection of census data such as that described in Palombit (1992) is imperative. Despite the regularity of brief field studies occurring at Rekut in the five year period leading up to my study, no formal identification or monitoring process has been conducted with the basecamp gibbons (see Section 9.4).

Of course, pair bond stability is not just susceptible to internal forces but is also prone to the effects of external factors, such as the solicitation behaviour of the philandering neighbour. Temporary consortship and partner desertion has been described for lar gibbons and siamang (Palombit, 1992; 1994a; 1994b: Reichard, 1995; Sommer and Reichard, in press) and in some cases was induced simply by the zealous appeals of an extra-group individual rather than the effects of an unusual or unsuitable internal social environment. Therefore, observing EPCs and other related behaviours in hybrid gibbons could be viewed simply as additional evidence for recent claims of variable gibbon sociality. On the other hand, this kind of behaviour could reflect the influence hybridisation exerts on other behavioural parameters such as social composition. For example, males who live in "normal" pair-bonded groups might perceive surrounding polygynous groups as either "unstable" or "impotent". It follows that if one of these adult males wanted to seek brief relations with neighbouring females, he might improve his chances of obtaining EPCs by focussing his solicitations on females who reside in groups that are socially distinct from his own. Furthermore, females in polygnous groups and who therefore share their mate with another female, might also be more inclined to engage in extra-group consortship and accept these attempts at solicitation.

No actual affiliative or sexual contact was observed between the females of the polygynous RBC2 with neighbouring males but the behaviour of AM1 is suggestive of contact attempts. On three separate occasions, AM1 was observed to cross into RBC2's territory and travel within the border area on his own. The failure to detect either AF1 or JF1 implied that AM1 had deliberately left the group to cross the border region. What AM1's intentions were can only be subject to speculation, but it seems unlikely he would attempt territorial claims without the backing of his mate. The search for contact opportunities is a likelier explanation for a gibbon to engage in solitary travel through the territory of another group.

AM1 also displayed somewhat unusual behaviour in territorial encounters which might again represent contact behaviour. For example, a good proportion of his time during inter-group encounters was spent approaching and chasing SF2 rather than AM2. This was undoubtedly related to the prominent role SF2 played in border conflict but such interactions also provided AM1 with the chance to assess both the strength of the relationship between the mature animals in RBC2 and the sexual willingness of SF2. AM1's attack on AF2 described in Chapter 7 is another potential example of a contact attempt. While the aggressive response displayed by AM1 appears on the surface to be counter-productive and less effective than the employment of affiliative behaviours, it could be argued that such a strategy actually served two, equally beneficial purposes i.e. it enabled the male to initiate relations with the extra-group female without arousing the suspicions of his mate.

9.3 Behavioural variation and success of the hybrid population

Mather's (1992) analysis of the demographic structure of the *albibarbis* x *muelleri* hybrid zone found a "demographically healthy" population, able to replicate itself without needing to rely on gene flow from neighbouring parental species. However, he also found that hybrid gibbon group sizes, predicted on the basis of fig abundance, tended to be smaller than other gibbon populations and calculated the mean group size at Muara Rekut as 2.8 (n=25). Mean group size of hybrid groups during the 1995-1996 field season was also low, an average of 3.0 individuals per group (n=7). These values are at the extreme end of mean group sizes calculated for different populations (range: 3.0 (*albibarbis* at Tanjung Puting [Sugardjito, 1988]) – 4.6 (*albibarbis* at Gunung Palung [Mitani, 1990]) and considerably less than the average calculated for each species.

Mather (1992) proposed that low birth rates, rather than high mortality and dispersal rates, is the key demographic factor influencing the maintenance of small group sizes in the hybrid zone. My own, albeit limited assessment, of birth rate amongst the five RBC adult females did not discover as low a birth rate. Between the five and a half year period spanning February 1991 and August 1996, *at least* five infants were born to the adult females, giving the number of births/female/year as 0.18. Not a particularly high value but not so different to that calculated for pure *albibarbis* at Tanjung Putting (0.16 – Sugardjito, 1988). Mean inter-birth interval covering the same period – estimated at 5.5 years – was also not as long as the 7.9 years calculated by Mather (1992) but is generally longer than that documented for pure species of gibbon.

The effect of behavioural variation on reproductive success received some attention from Mather (1992) who attempted to relate low reproductive rates with duet coordination. Because hybrid gibbons sing longer and more often than pure species, and because hybrid females deliver more solos than their parental counterparts (but see above), Mather (1992) suggested that the additional time and energy hybrid females use for frequent singing performances reduces the amount of energy available for reproductive purposes. Although I found no evidence for increased singing time in the hybrid population, I followed Mather's (1992) recommendation and compared the activity budgets of hybrid gibbons with those of pure *agilis* and *muelleri*. No differences occur between hybrids and either *agilis* or *muelleri* in the mean time spent singing each day. Hybrid and agile gibbons devote 5% of their day to singing while Müller's gibbons contribute a comparable 4% of their activity budget to song performance.

So what influence, if any, do the behaviours identified as definitely or potentially affected by hybridisation exert on the reproductive success of the hybrid population? The following examines some of the behavioural changes outlined in the preceding sections and considers their importance, be it positive or negative, or direct or indirect, on the fecundity of the hybrid female gibbon.

9.3.1 Unusual social composition

At Khao Yai, the reproductive rate of hybrid and mixed species groups is significantly lower than that for pure *lar* and *pileatus* (Warren Brockelman, personal communication to Robert Mather, 1992). Fifty four percent of pure species groups have infants whereas only 30% of hybrid groups contain young. While there is no indication as to how many of the hybrid and mixed groups have young offspring, the fact that a reasonable proportion of the contact population is composed of polygynous trios suggests that low birth rate is at least partially related to unusual group formation. Furthermore, the regular dissolution of polygynous associations observed at Khao Yai can only retard reproductive potential. An inability to maintain bonds with the reproductive partner not only causes stress to the female but reduces suitable reproductive conditions and opportunity (see Section 9.3.2).

It is proposed that a female living in a polygynous association may suffer a reduced reproductive rate either because her overall health (measured in terms of access to important food resources) or her opportunity to engage in sexual interactions with the resident male is comprised by the presence of another, sexually mature female. For example, and regardless of the quality or wealth of food source distribution in the home range, a female residing in a trio is still having to share, and hence lose, more of her potential diet to another female, and any offspring this second female may produce, than she would if she were living in a monogamous social unit. While this may not affect the immediate feeding concerns of the female, it could have an accumulative, detrimental effect on her general, and thus reproductive, health.

With regard to reproductive opportunity, little is still known about how sexual relations operate in a polygynous gibbon group. In the polygynous *pileatus* group described by Srikosamatara and Brockelman (1987), both resident females had young, while in the *hoolock* trio reported by Ahsan (1994, 1995), the adult male copulated with both his female partners. This implies that sexual exclusion is not a definitive requirement of trio stability, further supported by my own observations of sexual behaviour occurring between the adult male of RBC2 and the adult and sub-adult females. However, none of these cases necessarily preclude that a differential rate of sexual participation was occurring in the respective groups. While Ahsan (1995) did not describe the frequency of copulatory participation for each of the females in the *hoolock* trio, only one gave birth during his field study. Furthermore, in RBC2, the dominant adult female engaged in more sexual activity with the adult male and was the only female to have produced young. The sub-adult females sexual interaction with the adult male consisted mostly of genital touching with only one possible incidence of mounting and copulation.

Sexual, and hence reproductive, opportunity for trio living females might vary from group to group, explaining the differing breeding situations described above. In groups where females are tolerant of one another's sexual interaction with the adult male, reproductive rates won't be as greatly affected. But in trios where one female is limited in her sexual behaviour, her chances of falling pregnant are considerably diminished. How this relates to her reproductive situation if she had not become a member of a trio further affects measures of overall rates of reproduction. Little research has been conducted on either typical or polygamous group formation in gibbons, providing little data on the respective ease of, and precursors to, formation of each of the social units. While unusual events, such as the death of both parents (e.g. hoolock gibbons – Ahsan, 1995), undoubtedly lead to some cases of gibbon polygyny, it can also be supposed that females choose to live in polygynous associations because a dearth of potential mates prevents establishment of exclusive pair bonds. If this is a common precursor to polygyny, then the reproductive rate of a female can only be improved if she becomes an adult male's second mate. For example, her living conditions might be better (i.e. there is a greater supply of food sources and group support for territory defence) and her chances of copulation and conception increased. But if relations between the two residents are largely antagonistic and/or the female is precluded from sexual activity with the adult male, then her birth rate becomes effectively nil.

9.3.2 Pair bond stability and social cohesion

Pair bond stability, along with food supply and paternal infant care, are considered the primary influential factors in gibbon reproductive potential (Brockelman et al., 1974; Kleiman, 1977; Gittins and Raemaekers, 1980; Barlow, 1988). So far, a scarcity of gibbon reproductive data prevents any real attempt to define the strength and nature of the relationship existing between fecundity and permanency of the pair bond. Preliminary data from Palombit's (1995) study on reproduction in lar gibbons and siamang suggests that a positive relationship exists since females involved in long-term pair bonds give birth to more young. Furthermore, pair changes sometimes lead to the loss of offspring, through either pregnancy termination or infant abandonment.

Pair bond instability is yet to be confirmed for the *albibarbis* x *muelleri* hybrids and evidence for potential antecedents to instability is contradictory. If it does exist, constant change to pair combinations can only lead to disruptions in reproduction. New pairs do not establish social and song familiarity with one another readily and, until that familiarity is achieved, the ability to conceive remains low. The constant change in partners requires a continual investment in the acquisition of pair bond harmony, potentially causing stress to the female. Infant survival represents another casualty of pair bond instability. As mentioned above, miscarriages and abandonment's do occur during or immediately after transfer and, although infanticide remains a real risk.

9.3.3 Reduced incidence of territorial disputes

Hybrid gibbons do not participate in border conflicts that often, which might be a consequence of song-based differential responses to neighbouring groups. Not having to engage in continual, rigorous defence of the territory, however, can only be beneficial to the hybrid female. Firstly, spending less time in physical territory maintenance (i.e. inter-group clashes) allows the female to engage in reproduction-positive pursuits such as feeding and the search for nutritious foodstuffs. Secondly, less conflict means less stress. And thirdly, the absence of dramatic changes to territory border location prevents the female having to constantly adapt her ranging habits and hence food acquisition skills. Retaining a ranging area of known size enables the female to successfully use her territory, as she knows where to find food sources and when.

9.3.4 Improved feeding strategies

The proposed flexible feeding strategies of hybrid gibbons is another factor that would have a positive, rather than a negative, effect on reproductive potential. It improves adaptability and allows gibbons to cope dietetically with food poor habitat or periods of low food resource availability. The ability to alter the diet ensures the female is supplied with an adequate diet, if not in quality then at least in quantity. Overall health is therefore maintained, in turn sustaining reproductive potential.

Overall, a net positive or negative effect on reproductive rate is difficult to discern. This is partly because many of the behavioural anomalies discussed are still suppositional but also because vital information on correlates of gibbon reproductive success remains limited. It is indeed feasible that the lower rate of reproduction in the hybrid population is greatly affected by external factors, such as the "limited production" habitat they are found in, than any behavioural variation unique to, or exaggerated in, the *albibarbis* x *muelleri* hybrid. Nonetheless, the estimated 35,000 strong hybrid population living in the Barito Ulu watershed, and the absence of any major deviations from gibbon typical behaviour, testifies to the establishment of a successful, breeding population that has not been severely or negatively affected by hybridisation induced behavioural variation.

9.4 Directions for future research

The data compiled here represent the first long-term, continuous study on the behaviour of hybrid gibbons. While important information concerning the ecological and social dynamics of the *albibarbis* x *muelleri* hybrid gibbon was collected, and real and potential effects of hybridisation on behaviour discerned, further research is needed to establish the true range of variation in the behavioural repertoire of the *albibarbis* x *muelleri* hybrid and how that variation impinges on the individual, group and population as a whole. Suggested future research includes:

1. Concurrent field studies on *albibarbis* and *muelleri* populations living in areas bordering the hybrid zone. Assuming that ecological conditions are comparable between the three (i.e. *albibarbis, muelleri* and hybrid) field sites, research on parental populations will provide a more appropriate, and more direct, method of comparison between pure and hybrid behavioural profiles.
2. An expansion of Mather's (1992) research on female song variants. Since song structure is the most obvious consequence of hybridisation, more detailed description on the range of female song variants produced by the hybrid population is important for
    a. further analysis on the inheritance of song and
    b. to investigate whether individual variability is more pronounced in hybrid gibbons, particularly within specific great call type (e.g. *muelleri*-backcross) groups.
3. Following (2), an investigation of the range of song variants given by male hybrid gibbons. Because of the complexity of the male solo, and the yet to be determined mechanics of male song inheritance, the singing behaviour of male hybrids was largely neglected in this and Mather's (1992) study. A compilation, and subsequent sonagram analysis, of male songs produced in the hybrid zone again provides information on the genetic basis of gibbon song and individual variability in the hybrid zone but also determines whether males can be, like females, assigned to specific hybrid classes and therefore recognised in terms of their song structure.

4. Following (2) and (3), a study of the frequency of song response rates given between gibbons which give "similar" songs to those who give slightly different or dissimilar songs. An interesting extension to this research is to habituate and focus research on a groups of gibbons whose ranges are not dissected by rivers, and correlate the frequency of response rates with the rate of inter-group aggressive (and affiliative) contact.
5. An additional, long-term census focussing on the social composition of hybrid groups in order to ascertain whether
    a. unusual social groups do occur more often in hybrid zones and if they are largely, or solely, polygynous and
    b. if they occur to a greater, comparable or lesser extent than observed in the *lar* x *pileatus* hybrid zone.
6. A second field project concentrating on behavioural differences between the hybrid and pure species population at Khao Yai. The differential success of the Khao Yai and Barito Ulu hybrid populations is still not understood and comparative research may highlight whether it is hybridisation-modified behaviours, or contrast in habitat, which influences population size.

9.5 Final Conclusions

1. *H.a.albibarbis* x *muelleri* hybrid gibbons demonstrate a behavioural repertoire generally similar to the parental species and other lar group gibbons. Behavioural anomalies, however, are observed, some of which are proposed as probable or possible consequences of hybridisation.
2. The most direct consequence of hybridisation on the behaviour of the hybrid gibbon is the modification made to song structure and other vocalisations. Other behaviours definitely influenced by hybridisation are more difficult to detect and require a comparison with neighbouring parental populations for confirmation of hybrid uniqueness.
2. Direct consequences of hybridisation are proposed to influence other aspects of the hybrid gibbon behaviour. For example, the marked variation observed in the female's great call and the range of song types produced in the hybrid may lead to increased incidences of polygyny and reduced territory maintenance pressure. Another example relates to food type choice and an improved adaptability to food poor seasons and habitat.
3. Actual and proposed primary and secondary consequences of hybridity do not exact any net negative effect to explain the low reproductive rate of the hybrid population.

Appendices

Appendix I

Measurement of Hybrid Indices (p values)

The distribution of hybrid types in the Barito Ulu watershed was calculated by Mather (1992) using species-distinct female song variables. Because some features of the great call are thought to be inherited (Brockelman and Schilling, 1984; Geissmann, 1984; 1993; Tenaza, 1985; Marshall and Sugardjito, 1986), Mather selected 29 quantitative great call characteristics and measured their range of overlap between the great calls of *agilis* and *muelleri*. Six of the acoustic characteristics — total number of notes, number of climax notes, rate of note emission, rate of climax note emission, duration of the mid-climax note, and the climax inter-note interval — were found to display a range of values quite different between the two species. Using these six variables, Mather (1992) then compared their range of overlap for songs given by a sample of 78 hybrid females located in the Barito Ulu hybrid zone. Two variables in the hybrid great call — rate of climax note emission (cn/sec) and mid-climax note duration (mcnd) — did not fall within the range of the parental types, suggesting that they were under strong genetic control. Mather (1992) therefore proposed that these two variables could be used not only to "positively discriminate" between the great calls of agile, Müller's and hybrid gibbons but denote the hybridity status of (female) gibbons in the hybrid zone.

A hybrid index or p value was developed by Mather (1992) using values of cn/sec to reflect the proportion of *agilis* and *muelleri* genes in each hybrid individual. To calculate the p value for any hybrid gibbon, the following equation was employed:

$$p = \frac{\log(\text{cn/sec.}[H]) - \log(\text{cn/sec.}[A])}{\log(\text{cn/sec.}[M] - \log(\text{cn/sec.}[A])}$$

where A = the mean cn/sec value for pure agile gibbons living south of the Joloi River; M = the mean cn/sec value for pure Müller's gibbons located south of the Barito River, and H = the cn/sec value for the hybrid individual. P values range from 0 (indicating a pure agile gibbon) to 1 (indicating a pure Müller's gibbon).

To calculate the proportion of agile and Müller's gibbon genes in a population located in any part of the hybrid zone, Mather (1992) added the sum of all individual p values for females from that sample population and divided the total by the number of females in the sample:

$$p_s = \frac{\sum p_i}{N}$$

where p_i equals the p value for each female in the sample population; N equals the number of females in the sample population; and p_s equals the overall p value for that sample population.

Population p values were measured for six survey sites that followed a west-east transect running from the Muara Rekut basecamp, located on the eastern bank of the Busang, to the west bank of the Murung River. (Additional data were collected from sites on the west bank of the

Busang, along an approximate north-south transect; south of the Barito, and east of the Murung, again following an approximate north-south transect – see Table I-1 below).

Table I-1 Mean and range of p values for hybrid population in the Barito Ulu watershed.

Sample population	p value	Range	N
Site 1	0.37	0.13 - 0.80	28
Site 2	0.35	0.17 - 0.63	8
Site 4	0.35	0.13 - 0.63	11
Site 7	0.68	0.14 - 0.80	14
Site 8	0.70	0.27 - 0.86	15
Site 9	0.65	0.21 - 0.80	19

See Figure 1-4 for location of survey sites

Appendix II
Hybrid gibbon demographics

Table II-1 shows the calculated demographic variables.

Table II-1 Demographic variables for the hybrid gibbon population at Muara Rekut.

Demographic variables	This study[1]	Mather (1992)[2]
Mean group size	3.0	2.8
Age class composition		
% Adults	66.7	71.4
% Subadults/Juveniles	22.2	18.6
% Infants	11.1	10.0
Mean birth rate (number of births/female/year)	0.18[3]	0.13
Mean inter-birth interval	5.5[3]	7.9
Mean mortality rate (number of deaths/group/year)	0.0	0.043
Life expectancy[a]	23.0	21.0
Population growth[b]	0.05	0.037
Population doubling time (in years)	13.9	19.0

[1] Data pertain to the period 1995-1996 unless indicated otherwise

[2] Data pertain to the period 1988-1990

[3] Data pertain to the period 1991 to 1996

Life expectancy, population growth and population doubling time were calculated using the following formulas from Caughley (1977):

- Life expectancy (assuming population growth is insignificant and birth rate is constant):

$$L = \frac{2n-j}{2j}$$

where j = the number of infants aged between 0-1 years of age and n = number of individuals in the population.

- Exponential rate of population growth:

$$r = \frac{ln N_t - ln N_o}{t}$$

where ln = the natural logarithm, Nt = population size at time t, No = population size at time 0, and t = is the time elapsed in years.

- Population doubling time:

$$\frac{0.6931}{r}$$

where r = the exponential rate of population growth.

Appendix III
Vegetation Profiles

Tables III-1 to III-6 lists the tree family, genera and species identified in vegatation plots located in primary, heath and secondary forest. Basal area, proportion of basal area, density, and relative density are calculated for each family, genus and species (see Chapter 2 for definitions of vegetation measures). Plot sites are illustrated in Chapter 2, Figure 2-3.

Table III-1 Basal area, density and relative density of identified tree families and genera in primary forest vegetation plots (Area = 1.75 ha).

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Anacardiaceae	1359.636	3.81	32.5	6.97	*Buchanania*	0.570	*	1.1	0.24
					Gluta	17.676	0.09	4.6	0.98
					Koordersiodendron	0.889	*	1.1	0.24
					Mangifera	7.350	0.04	2.3	0.49
					Parishia	3.026	0.01	1.7	0.37
					Swintonia	603.716	2.89	19.4	4.16
Annonaceae	96.612	0.27	13.7	2.93	*Cyathocalyx*	0.861	*	1.7	0.37
					Polyalthia	23.931	0.11	6.3	1.34
Apocynaceae	6.826	0.02	1.7	0.37	*Dyera*	3.563	0.02	0.6	0.12
					Tabernaemontana	0.132	*	0.6	0.12
					Willughbeia	0.131	*	0.6	0.12
Bignoniaceae	0.116	*	0.6	0.12	*Oroxylum*	0.116	*	0.6	0.12
Bombaceae	8.159	0.02	4.0	0.86	*Bombax*	0.432	*	1.1	0.24
					Durio	4.834	0.02	2.9	0.61
Burseraceae	157.632	0.44	14.3	3.06	*Canarium*	4.133	0.02	2.3	0.49
					Dacryodes	86.228	0.41	11.4	2.44
					Burseraceae 1	1.528	0.01	0.6	0.12
Celastraceae	1.140	*	1.7	0.37	*Kokoona*	1.140	*	1.7	0.12
Crypteroniaceae	0.753	*	1.1	0.24	*Crypteronia*	0.753	*	1.1	0.24
Dilleniaceae	1.718	0.05	1.1	0.37	*Dillenia*	1.718	0.01	1.7	0.37
Dipterocarpaceae	31497.661	88.22	126.3	27.01	*Dipterocarpus*	1071.668	5.13	18.9	4.03
					Hopea	43.381	0.21	6.9	1.47
					Shorea	15937.301	76.30	86.9	18.58
					Vatica	133.100	0.64	13.1	2.81
					Dipterocarpaceae 1	0.139	*	0.6	0.12
Ebananceae	146.144	0.41	15.4	3.30	*Diospyros*	146.144	0.70	15.4	3.30

Table III-1 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Elaeocarpus	0.268	0.01	0.6	0.12	*Elaeocarpus*	0.268	0.01	0.6	0.12
Ericaceae	1.732	0.01	0.6	0.12	*Rhododendron*	1.732	0.01	0.6	0.12
Euphorbiaceae	782.828	2.11	40.0	8.56	*Aporusa*	0.966	0.01	1.7	0.37
					Baccaurea	3.249	0.02	2.3	0.49
					Bridelia	0.873	*	1.1	0.24
					Chaetocarpus	9.976	0.046	3.4	0.73
					Croton	5.391	0.03	4.0	0.85
					Drypetes	0.736	*	1.1	0.24
					Elasteriospermum	1.375	0.01	1.7	0.37
					Macaranga	1.753	0.01	2.3	0.49
					Mallotus	2.156	0.01	2.9	0.61
					Neoscortechinia	0.451	*	0.6	0.12
Fagaceae	91.982	0.26	6.9	1.47	*Castanopsis*	2.124	0.01	0.6	0.12
					Lithocarpus	47.405	0.23	5.1	1.10
Flacourtiaceae	19.431	0.05	4.6	0.98	*Hydnocarpus*	19.431	0.09	4.6	0.98
Guttiferae	106.194	0.30	8.6	1.83	*Callophyllum*	4.881	0.03	1.7	0.37
					Garcinia	21.009	0.10	6.9	1.47
					Mesua	12.335	0.06	2.9	0.61
Hypericaceae	0.044	*	0.6	0.12	*Cratoxylum*	0.437	*	0.6	0.12
Lauraceae	493.705	1.38	18.3	3.91	*Cinnamomum*	0.233	*	0.6	0.12
					Cryptocarya	3.221	0.02	1.7	0.37
					Dehaasia	14.862	0.07	3.4	0.73
					Endiandra	2.270	0.01	1.1	0.24
					Eusideroxylon	22.809	0.11	1.7	0.37
Lecythidiaceae	3.262	0.01	2.3	0.49	*Barringtonia*	3.262	0.02	2.3	0.49
Leguminosae	714.560	2.00	17.7	3.79	*Dialium*	118.939	0.57	9.1	1.96

Table III-1 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
					Koompassia	100.110	0.48	6.3	1.34
					Pithecellobium	2.297	0.01	0.6	0.12
					Sindora	18.528	0.09	1.7	0.37
Linaceae	0.229	*	0.6	0.12	*Ctenolophon*	0.229	*	0.6	0.12
Loganiaceae	0.189	*	0.6	0.12	*Strychnos*	0.189	*	0.6	0.12
Magnoliaceae	0.135	*	1.1	0.24	*Talauma*	0.135	0.01	1.1	0.24
Melastomataceae	5.023	0.01	3.4	0.73	*Pternandra*	1.470	0.01	1.7	0.37
					Memecylon	1.059	0.01	1.7	0.37
Meliaceae	220.59	0.62	17.7	3.79	*Aglaia*	9.117	0.04	2.9	0.61
					Chisocheton	55.576	0.27	9.7	2.08
					Dysoxylum	6.326	0.03	2.9	0.61
					Sandoricum	0.488	*	0.6	0.12
					Walsura	1.356	0.01	1.7	0.37
Moraceae	140.039	0.39	12.6	2.69	*Artocarpus*	115.066	0.55	11.4	2.44
					Ficus	0.228	*	0.6	0.12
					Prainea	0.396	*	0.6	0.12
Myristicaceae	265.471	0.74	18.3	3.91	*Gymnacranthera*	22.446	0.11	4.6	0.98
					Horsfieldia	8.470	0.04	3.4	0.73
					Knema	2.156	0.01	1.7	0.37
					Myristica	7.173	0.03	4.0	0.86
Myrtaceae	324.133	0.91	17.1	3.67	*Eugenia*	309.839	1.48	16.6	3.55
					Syzygium	0.161	*	0.6	0.12
Olaceae	2.971	0.01	2.3	0.49	*Ochanostachys*	2.971	*	2.3	0.49
Palmaceae	0.238	*	0.6	0.12	*Oncospermum*	0.138	*	0.6	0.12
Polygalaceae	98.011	0.27	9.7	2.08	*Xanthophyllum*	98.011	0.47	9.7	2.08
Rhamnaceae	0.102	*	0.6	0.12	*Zizyphus*	0.102	*	0.6	0.12

Table III-1 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Rhizophoraceae	0.0919	*	0.6	0.12	*Pellacalyx*	0.092	*	0.6	0.12
Rosaceae	7.354	0.02	2.3	0.49	*Parastemon*	5.879	0.03	1.7	0.37
					Prunus	0.082	*	0.6	0.12
Rubiaceae	11.473	0.03	4.0	0.86	*Nauclea*	2.668	0.01	1.1	0.24
					Porterandia	0.622	*	1.1	0.24
					Wendlandia	0.129	*	0.6	0.12
Rutaceae	1.338	*	1.7	0.37	*Euodia*	1.338	0.01	1.7	0.37
Sapindaceae	61.181	0.17	8.6	1.87	*Lepisanthes*	0.091	*	0.6	0.12
					Mischocarpus	0.506	*	1.1	0.12
					Nephelium	7.680	0.04	3.4	0.73
					Pometia	5.764	0.03	1.7	0.37
					Xerospermum	1.812	0.01	1.1	0.24
					Sapindaceae 1	0.084	*	0.6	0.12
Sapotaceae	285.592	0.80	16.6	3.55	*Ganua*	47.124	0.23	8.0	1.71
					Madhuca	16.217	0.08	2.9	0.61
					Palaquium	12.882	0.06	3.4	0.73
					Payena	0.669	*	0.6	0.12
					Planchonella	0.255	*	0.6	0.12
Sterculiaceae	40.489	0.11	6.9	1.47	*Heritiera*	4.158	0.02	1.1	0.24
					Scaphium	1.851	0.01	1.1	0.24
					Sterculia	0.982	0.01	1.7	0.37
Symplocaceae	0.937	*	1.1	0.24	*Symplocos*	0.937	0.01	1.1	0.24
Theaceae	0.517	*	1.1	0.24	*Adinandra*	0.517	*	1.1	0.24
Thymelaceae	96.107	0.27	14.3	3.06	*Gonystylus*	96.107	0.46	14.3	3.06
Tiliaceae	5.569	0.03	2.3	0.49	*Microcos*	0.085	*	0.6	0.12
					Pentace	4.279	0.02	1.7	0.37

Table III-1 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Ulmaceae	0.126	*	0.6	0.12	*Gironniera*	0.126	*	0.6	0.12
Verbenanceae	39.191	0.11	5.7	1.22	*Teijsmanniodendron*	1.014	0.01	0.6	0.12
					Vitex	27.600	0.13	5.7	1.22
Violaceae	1.095	*	0.6		*Rinorea*	1.095	0.01	0.1	0.12
Unidentified	-	-	-	-	Unidentified	1477.368	7.07	47.4	10.15

[1] Includes identified genera and forms discriminated to genus level

* Values < 0.01

Total number of identified trees in plots = 735

Total number of unidentified trees in plots = 83

Table III-2 Basal area, density and relative density of identified tree families and genera in heath forest vegetation plots (Area = 0.5 ha).

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Anacardiaceae	1.957	0.17	76	7.27	*Buchanania*	0.105	0.02	2	0.19
					Campnosperma	0.097	0.02	2	0.19
					Gluta	5.774	1.12	32	3.06
					Koordersiodendron	0.012	*	2	0.19
					Melanochyla	0.020	*	2	0.19
					Parishia	0.097	0.02	6	0.57
					Semecarpus	0.019	*	2	0.19
					Swintonia	3.260	0.63	20	1.91
					Anacardiaceae 1	0.032	0.01	2	0.19
					Anacardiaceae 2	0.023	*	2	0.19
					Anacardiaceae 3	0.099	0.02	2	0.19
					Anacardiaceae 4	0.022	*	2	0.19
Annonaceae	0.707	0.06	16	1.53	*Cyathocalyx*	0.050	0.01	4	0.38
					Polyalthia	0.013	*	2	0.19
					Annonaceae 1	0.093	0.02	6	0.57
					Annonaceae 2	0.040	0.01	4	0.38
Burseraceae	0.542	0.05	2	0.19	*Dacryodes*	0.542	0.11	2	0.19
Casuarinaceae	0.692	0.06	12	1.15	*Casuarina*	0.692	0.13	12	1.15
Celastraceae	23.434	2.02	48	4.49	*Bhesa*	1.672	0.32	18	1.72
					Lophopetalum	12.586	2.44	30	2.87
Dipterocarpaceae	942.769	81.45	374	35.76	*Cotylelobium*	2.210	0.43	20	1.91
					Dipterocarpus	1.721	0.33	14	1.34
					Hopea	89.045	17.25	118	11.28
					Shorea	310.126	60.09	210	20.08
					Vatica	0.473	0.09	12	1.15
Ebanceae	0.245	0.02	8	0.76	*Diospyros*	0.245	0.05	8	0.76

Table III-2 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Euphorbiaceae	1.957	0.17	14	1.34	*Baccaurea*	0.380	0.07	8	0.76
					Macaranga	0.613	0.12	6	0.57
Fagaceae	0.684	0.06	14	1.31	*Castanopsis*	0.192	0.04	8	0.76
					Lithocarpus	0.152	0.03	6	0.57
Guttiferae	54.507	4.71	126	12.05	*Callophyllum*	0.469	0.09	12	1.15
					Garcinia	16.308	3.16	80	7.65
					Mesua	5.356	1.04	28	2.68
					Guttiferae 1	0.018	*	2	0.19
					Guttiferae 2	0.045	0.01	4	0.38
Icaniaceae	0.916	0.08	16	1.53	*Stemonurus*	0.734	0.14	14	1.34
					Icaniaceae 1	0.010	*	2	0.19
Lauraceae	1.737	0.15	40	3.82	*Alseodaphne*	0.090	0.02	6	0.57
					Dehaasia	0.019	*	2	0.19
					Lauraceae 1	0.565	0.11	8	0.76
					Lauraceae 2	0.016	*	2	0.19
Leguminosae	6.875	0.59	52	4.97	*Archidendron*	0.025	*	2	0.19
					Dialium	3.921	0.76	44	4.21
					Sindora	0.234	0.05	6	0.57
Melastomataceae	1.100	0.09	14	1.34	*Memecylon*	0.116	0.02	6	0.57
					Pternandra	0.501	0.10	8	0.76
Meliaceae	2.542	0.22	16	1.53	*Sandoricum*	2.542	0.49	16	1.53
Myristicaceae	0.011	*	2	0.19	*Horsfieldia*	0.011	*	2	0.19
Myrtaceae	103.860	9.00	142	13.58	*Eugenia*	28.056	5.44	68	6.50
					Tristania	19.031	3.69	74	7.07
Sapindaceae	1.108	0.10	16	1.53	*Lepisanthes*	0.903	0.17	14	1.34
					Xerospermum	0.010	*	2	0.19

Table III-2 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
Sapotaceae	7.860	0.68	38	3.63	*Madhuca*	1.057	0.20	16	1.53
					Palaquium	1.871	0.36	16	1.53
					Sapotaceae 1	0.019	*	2	0.19
					Sapotaceae 2	0.017	*	2	0.19
					Sapotaceae 3	0.019	*	2	0.19
Sterculiaceae	0.009	*	2	0.19	Sterculiaceae 1	0.009	*	2	0.19
Symplocaceae	0.031	*	2	0.19	*Symplocos*	0.031	*	2	0.19
Theaceae	0.162	0.01	6	0.57	Theaceae 1	0.162	0.03	6	0.57
Thymelaceae	3.530	0.31	26	2.49	*Gonystylus*	3.530	0.68	26	2.49

[1] Includes identified genera and forms discriminated to genus level

* Values < 0.01

Total number of identified trees in plots = 523

Table III-3 Basal area, density and relative density of identified tree families and genera1 in secondary forest vegetation plots (Area = 1.25 ha).

Family	Basal Area	% of B.A.	Density	Relative Density	Genus[1]	Basal Area	% of B.A.	Density	Relative Density
Actinidiaceae	7.007	0.04	4.8	0.86	*Saurauia*	7.007	0.04	4.8	0.92
Anacardiaceae	43.334	0.24	8.8	1.57	*Campnosperma*	2.430	0.02	2.4	0.46
					Gluta	0.113	*	0.8	0.15
					Mangifera	7.078	0.056	3.2	0.61
					Semecarpus	0.081	*	0.8	0.15
					Swintonia	3.036	0.03	1.6	0.31
Annonaceae	37.915	0.21	9.6	1.71	*Cyathocalyx*	5.175	0.04	3.2	0.61
					Mezzettia	0.101	*	0.8	0.15
					Polyalthia	0.158	*	0.8	0.15
					Pseudocarpus	1.046	0.01	1.6	0.31
					Pseuduvaria	0.482	*	0.8	0.15
Bombaceae	4.112	0.02	1.6	0.29	*Durio*	4.111	0.03	1.6	0.31
Burseraceae	1.122	0.01	2.4	0.43	*Canarium*	0.091	*	0.8	0.15
					Dacryodes	0.574	0.01	1.6	0.31
Dilleniaceae	313.220	1.75	36.8	6.56	*Dillenia*	313.217	2.58	36.8	7.07
Dipterocarpaceae	553.546	3.10	24.8	4.42	*Cotylelobium*	0.128	*	0.8	0.15
					Dipterocarpus	7.083	0.06	1.6	0.31
					Shorea	379.304	3.12	20.0	3.84
					Vatica	1.068	0.01	2.4	0.46
Ebanaceae	3.179	0.02	3.2	0.57	*Diospyros*	3.179	0.03	3.2	0.61
Euphorbiaceae	10572.509	59.20	188.8	33.67	*Baccaurea*	2.246	0.02	3.2	0.61
					Croton	0.084	*	0.8	0.15
					Endospermum	0.103	*	0.8	0.15
					Glochidion	1257.454	10.36	81.6	15.67
					Macaranga	3877.093	31.93	98.4	18.89
Fagaceae	3.176	0.02	3.2	0.57	*Castanopsis*	0.671	0.01	1.6	0.31

Table III-3 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
					Lithocarpus	0.928	0.01	1.6	0.31
Flacourtiaceae	37.578	0.21	5.6	1.00	Flacourtiaceae 1	37.580	0.31	2.4	1.08
Guttiferae	1.295	0.01	2.4	0.43	*Garcinia*	1.295	0.01	2.4	0.46
Hypericaceae	4662.070	26.10	57.6	10.27	*Cratoxylum*	4662.070	38.40	57.6	11.06
Lauraceae	166.157	0.93	20.8	3.71	*Cryptocarya*	5.055	0.04	3.2	0.61
					Dehaasia	0.079	*	0.8	0.15
					Endiandra	3.500	0.03	3.2	0.61
					Litsea	21.270	0.18	8.8	1.69
Lecythidaceae	0.108	*	0.8	0.14	*Barringtonia*	0.108	*	0.8	0.15
Leguminosae	4.464	0.03	4.0	0.57	*Archidendron*	0.498	*	1.6	0.31
					Cassia	0.486	*	0.8	0.15
					Koompassia	0.504	*	1.6	0.31
Magnoliaceae	0.106	*	0.8	0.14	*Talauma*	0.106	*	0.8	0.15
Melastomataceae	437.324	2.45	48.0	8.56	*Pternandra*	437.324	3.60	48.0	9.22
Meliaceae	0.460	*	1.6	0.29	*Chisocheton*	0.133	*	0.8	0.31
					Walsura	0.098	*	0.8	0.31
Moraceae	264.202	1.48	28.8	5.14	*Artocarpus*	134.083	1.10	20.8	3.99
					Ficus	18.497	0.15	7.2	1.38
					Moraceae 1	0.140	*	0.8	0.15
Myristicaceae	9.915	0.06	4.8	0.75	*Gymnacranthera*	0.085	*	0.8	0.15
					Horsfieldia	8.164	0.07	4.0	0.77
Myrtaceae	161.033	0.90	13.6	2.43	*Eugenia*	15.588	0.13	8.0	1.54
					Tristania	76.418	0.63	5.6	1.08
Rubiaceae	235.796	1.32	24.0	4.28	*Anthocephalus*	0.694	0.01	0.8	0.15
					Nauclea	6.877	0.06	6.4	1.23
					Porterandia	2.372	0.02	2.4	0.46

Table III-3 (continued)

Family	Basal Area	% of B.A.	Density	Relative Density	Genus	Basal Area	% of B.A.	Density	Relative Density
					Timonius	31.989	0.260	5.6	1.08
					Wendlandia	14.482	0.120	6.4	1.23
Sapindaceae	11.533	0.07	4.0	0.71	*Mischocarpus*	0.181	0.002	0.8	0.15
					Nephelium	0.561	0.005	1.6	0.31
					Pometia	4.936	0.041	1.6	0.31
Sapotaceae	4.972	0.03	2.4	0.43	*Ganua*	1.148	0.010	0.8	0.15
					Payena	0.770	0.006	0.8	0.15
					Sapotaceae 1	0.079	*	0.8	0.15
Sterculiaceae	4.029	0.02	4.0	0.71	Sterculiaceae 1	2.898	0.024	3.2	0.61
					Sterculiaceae 2	0.093	*	0.8	0.15
Symplocaceae	0.092	*	0.8	0.14	*Symplocos*	0.092	*	0.8	0.15
Theaceae	14.964	0.08	5.6	1.00	*Adinandra*	12.541	*	4.8	0.92
					Ternstroemia	0.107	*	0.8	0.15
Thymelaceae	0.390	*	0.8	0.14	*Gonystylus*	0.390	0.002	0.8	0.15
Tiliaceae	0.226	*	0.8	0.14	*Pentace*	0.226	0.001	0.8	0.15
Ulmaceae	0.092	*	0.8	0.14	*Gironniera*	0.092	*	0.8	0.15
Verbenaceae	36.510	0.20	13.6	2.43	*Callicarpa*	0.414	0.003	1.6	0.31
					Geunsia	15.594	0.130	8.8	1.69
					Vitex	0.139	0.001	3.2	0.61

[1] Includes only identified genera and plant forms discriminated to the genus level

Value < 0.01

Total number of identified trees in plot = 668

Total number of unidentified trees in plot = 33

Table III-4 Basal area, density and relative density of identified tree species in primary forest vegetation plots (Area = 1.75 ha).

Family	Species	Basal Area	% of BA	Density	Relative Density
Anacardiaceae	*Buchanania* sp.	0.570	0.02	1.1	0.24
	Gluta curtissi	2.596	0.10	1.7	0.37
	G. rostrata	0.542	0.02	0.6	0.12
	G. torquata	0.168	0.01	0.6	0.12
	G. velutina	0.160	0.01	0.6	0.12
	G. wallichii	1.097	0.04	1.1	0.24
	Koordersiodendron pinnatum	0.889	0.03	1.1	0.24
	Mangifera pajang	0.768	0.03	0.6	0.12
	M. sp 1	3.369	0.13	1.7	0.37
	Parishia maingayi	3.026	0.12	1.7	0.37
	Swintonia glauca	464.916	17.96	17.7	3.79
	S. spillea	1.081	0.04	0.6	0.12
	S. sp 1	0.626	0.02	0.6	0.12
	S. sp 2	1.387	0.05	0.6	0.12
	Anacardiaceae 1	0.840	*	1.1	0.24
	Anacardiaceae 2	0.091	*	0.6	0.12
	Anacardiaceae 3	0.533	0.02	0.6	0.12
Annonaceae	*Cyathocalyx* sp.	0.861	0.03	1.7	0.37
	Polyalthia glauca	7.887	0.30	4.0	0.85
	P. laterifolia	1.956	0.08	1.1	0.24
	P. sumatrana	0.469	0.02	1.1	0.24
	Annonaceae 1	1.553	0.06	1.7	0.37
	Annonaceae 2	0.127	0.01	0.6	0.12
	Annonaceae 3	0.085	*	0.6	0.12
	Annonaceae 4	0.107	*	0.6	0.12
	Annonaceae 5	1.261	0.05	1.1	0.24
	Annonaceae 6	0.096	*	0.6	0.12
	Annonaceae 7	0.126	0.01	0.6	0.12
Apocynceae	*Dyera costulata*	3.563	0.14	0.6	0.12
	Tabernaemontana sp.	0.132	0.01	0.6	0.12
	Willughbeia coricoea	0.131	0.01	0.6	0.12
Bignoniaceae	*Oroxylum* sp.	0.116	0.01	0.6	0.12
Bombaceae	*Bombax ceiba*	0.432	0.02	1.1	0.24
	Durio griffithii	0.288	0.01	0.6	0.12
	D. lanceolatus	0.105	*	0.6	0.12
	D. malaccensis	0.798	0.03	1.1	0.24
	D. sp 1	0.198	0.01	0.6	0.12
Burseraceae	*Canarium megalanthum*	0.153	0.01	0.6	0.12
	C. sp 1	2.694	0.01	1.7	0.37
	Dacryodes rostrata	24.569	0.95	5.7	1.22
	D. rugosa	0.109	*	0.6	0.12
	D. sp 1	4.290	0.17	2.9	0.62
	D. sp 2	1.396	0.05	1.1	0.24
	D. sp 4	0.557	0.02	1.1	0.24
	Burseraceae 1	1.528	0.06	0.6	0.12

Table III-4 (continued)

Family	Species	Basal Area**	% of BA	Density	Relative Density
Celastraceae	*Kokoona* sp.	1.14	0.04	1.7	0.37
Crypteroniaceae	*Crypteronia griffithii*	0.753	0.03	1.1	0.24
Dilleniaceae	*Dillenia grandifolia*	0.509	0.02	1.1	0.24
	D. sp 1	0.357	0.01	0.6	0.12
Dipterocarpaceae	*Dipterocarpus costulatus*	0.317	0.01	0.6	0.12
	D. crinitus	10.793	0.42	2.9	0.62
	D. eurynchus	6.789	0.26	2.3	0.49
	D. grandiflorus	14.407	0.56	1.1	0.24
	D. kerrii	117.609	4.54	4.6	0.98
	D. lowii	20.181	0.78	1.1	0.24
	D. oblongifolius	0.110	*	0.6	0.12
	D. sublamellatus	3.846	0.15	1.7	0.37
	D. sp 1	0.921	0.04	1.7	0.37
	D. sp 2	10.515	0.41	1.1	0.24
	D. sp 3	0.136	0.01	0.6	0.12
	D. sp 5	0.082	*	0.6	0.12
	Hopea dryobalanoides	6.743	0.26	0.6	0.12
	H. griffithii	1.455	0.06	2.3	0.49
	H. mengerawan	4.297	0.17	3.4	0.73
	H. nervosa	0.505	0.02	0.6	0.12
	Shorea amplexicaulis	33.163	1.28	3.4	0.73
	S. atrinervosa	27.646	1.07	2.3	0.49
	S. beccariana	68.515	2.65	6.9	1.47
	S. bentongensis	1.358	0.05	0.6	0.12
	S. crassa	256.197	9.89	8.0	1.65
	S. fallax	1.344	0.05	1.7	0.37
	S. gibbosa	0.771	0.03	1.1	0.24
	S. kunstleri	8.605	0.33	3.4	0.73
	S. leprosula	190.033	7.34	10.3	2.20
	S. macroptera	299.843	11.58	5.7	1.22
	S. multiflora	0.447	0.02	1.1	0.24
	S. parvifolia	237.186	9.16	10.9	2.32
	S. pauciflora	1.039	0.04	0.6	0.12
	S. pinanga	19.494	0.75	4.6	0.98
	S. pubistyla	15.122	0.58	1.1	0.24
	S. ovalis	0.861	0.03	0.6	0.12
	S. smithiana	3.547	0.14	1.7	0.37
	S. stenoptera	0.163	0.01	0.6	0.12
	S. xanthophylla	2.965	0.11	1.1	0.24
	S. sp 1	0.718	0.03	0.6	0.12
	S. sp 2	30.552	1.18	8.0	1.65
	S. sp 3	19.105	0.74	3.4	0.73
	S. sp 4	1.511	0.06	1.7	0.37
	S. sp 5	11.732	0.45	1.1	0.24
	S. sp 6	1.537	0.06	1.1	0.24
	S. sp 7	0.088	0.03	0.6	0.12
	S. sp 8	13.286	0.51	2.3	0.49
	S. sp 9	0.321	0.01	0.6	0.12

Table III-4 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	S. sp 10	0.121	0.01	0.6	0.12
	S. sp 11	2.110	0.08	0.6	0.12
	S. sp 12	0.183	0.01	0.6	0.12
	Vatica brunigii	0.559	0.02	0.6	0.12
	V. micrantha	1.770	0.07	1.7	0.37
	V. oblongifolia	0.424	0.02	1.1	0.24
	V. rassak	4.913	0.19	2.3	0.49
	V. sumatrana	2.193	0.09	2.3	0.49
	V. sp 1	5.841	0.23	2.3	0.49
	V. sp 3	0.087	*	0.6	0.12
	V. sp 4	0.088	*	0.6	0.12
	V. sp 5	1.815	0.07	1.1	0.24
	V. sp 7	0.570	0.02	0.6	0.12
	Dipterocarpaceae 1	0.139	0.01	0.6	0.12
Ebanaceae	*Diospyros borneensis*	0.106	*	0.6	0.12
	D. confertiflora	3.151	0.12	2.3	0.49
	D. ferruginea	0.523	0.02	0.6	0.12
	D. venosa	0.529	0.02	0.6	0.12
	D. sp 1	3.404	0.13	2.9	0.61
	D. sp 3	1.803	0.07	1.7	0.37
	D. sp 4	0.451	0.02	1.1	0.24
	D. sp 5	4.293	0.17	2.3	0.49
	D. sp 7	0.139	0.01	0.6	0.12
	D. sp 8	0.144	0.01	0.6	0.12
	D. sp 9	0.594	0.02	1.1	0.24
	D. sp 10	1.175	0.05	1.1	0.24
Elaeocarpaceae	*Elaeocarpus griffithii*	0.268	0.01	0.6	0.12
Ericaceae	*Rhododendron* sp.	1.732	0.07	0.6	0.12
Euphorbiaceae	*Aporusa elmeri*	0.095	*	0.6	0.12
	A. sp 1	0.456	0.02	1.1	0.24
	Baccaurea bracteata	0.387	0.02	1.1	0.24
	B. sp 1	1.393	0.05	1.1	0.24
	Bridelia sp.	0.873	0.03	1.1	0.24
	Chaetocarpus pubescens	4.893	0.19	2.3	0.49
	C. sp 1	0.336	0.01	0.6	0.12
	C. sp 2	0.135	0.01	0.6	0.12
	Croton sp.	5.391	0.21	4.0	0.85
	Drypetes pendula	0.736	0.03	1.1	0.24
	Elateriospermum tapos	1.375	0.05	1.7	0.37
	Macaranga confertiflora	0.139	0.01	0.6	0.12
	M. conifera	0.067	*	0.6	0.12
	M. hypoleuca	0.478	0.02	1.1	0.24
	Mallotus echinanthus	0.820	0.03	1.7	0.37
	M. sp 1	0.077	*	0.6	0.12
	M. sp 2	0.081	*	0.6	0.12
	Neoscortechinia kingii	0.451	0.02	0.6	0.12
	Euphorbiaceae 1	1.287	0.05	1.7	0.37
	Euphorbiaceae 2	3.819	0.15	3.4	0.73

Table III-4 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	Euphorbiaceae 4	1.289	0.05	1.7	0.37
	Euphorbiaceae 5	2.233	0.09	2.3	0.49
	Euphorbiaceae 6	0.727	0.03	1.1	0.24
	Euphorbiaceae 7	0.137	0.01	0.6	0.12
	Euphorbiaceae 8	0.078	*	0.6	0.12
	Euphorbiaceae 9	0.283	0.01	0.6	0.12
	Euphorbiaceae 10	7.349	0.28	3.4	0.73
	Euphorbiaceae 11	0.270	0.01	0.6	0.12
	Euphorbiaceae 12	0.213	0.01	0.6	0.12
	Euphorbiaceae 13	1.461	0.06	1.1	0.24
	Euphorbiaceae 14	0.114	*	0.6	0.12
	Euphorbiaceae 15	0.087	*	0.6	0.12
Fagaceae	*Castanopsis* sp 2	2.214	0.09	0.6	0.12
	Lithocarpus pusillus	1.429	0.06	1.1	0.24
	L. sp 1	6.344	0.25	2.3	0.49
	L. sp 3	0.196	0.01	0.6	0.12
	L. sp 4	7.446	0.29	1.1	0.24
	Fagaceae 1	0.269	0.01	0.6	0.12
	Fagaceae 2	0.489	0.02	0.6	0.12
Flacourtiaceae	*Hydnocarpus woodii*	0.190	0.01	0.6	0.1
	H. sp 1	11.763	0.45	3.4	0.73
	H. sp 3	0.294	0.01	0.6	0.12
Guttiferae	*Callophyllum* sp 2	4.881	0.19	1.7	0.37
	Garcinia bancana	0.179	0.01	0.6	0.12
	G. cornea	1.092	0.04	1.7	0.37
	G. cowa	0.449	0.02	0.6	0.12
	G. dulcis	1.289	0.05	1.7	0.37
	G. parvifolia	0.420	0.02	1.1	0.24
	G. sp 5	0.135	0.01	0.6	0.12
	G. sp 7	0.0876	*	0.6	0.12
	Mesua borneensis	3.202	0.12	1.7	0.37
	M. sp 1	2.968	0.11	1.1	0.24
Hypericaceae	*Cratoxylum glaucum*	0.437	0.02	0.6	0.12
Lauraceae	*Cinnamomum* sp.	0.233	0.01	0.6	0.12
	Cryptocarya sp.	3.224	0.12	0.6	0.12
	Dehaasia firma	1.194	0.05	1.1	0.24
	D. incrassata	0.656	0.03	0.6	0.12
	D. sp 1	3.812	0.15	1.7	0.37
	Endiandra sp 2	2.270	0.09	1.1	0.24
	Eusideroxylon zwageri	22.809	0.88	1.7	0.37
	Lauraceae 1	0.355	0.01	0.6	0.12
	Lauraceae 2	0.319	0.01	0.6	0.12
	Lauraceae 4	0.166	0.01	0.6	0.12
	Lauraceae 6	0.145	0.01	0.6	0.12
	Lauraceae 7	0.260	0.01	0.6	0.12
	Lauraceae 8	11.654	0.45	2.9	0.61
	Lauraceae 9	1.877	0.07	0.6	0.12
	Lauraceae 10	0.100	*	0.6	0.12

Table III-4 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	Lauraceae 11	0.174	0.01	0.6	0.12
	Lauraceae 12	0.214	0.01	0.6	0.12
	Lauraceae 13	0.085	*	0.6	0.12
	Lauraceae 14	1.156	0.05	0.6	0.12
Lecythidiaceae	*Barringtonia* sp.	3.262	0.13	2.3	0.49
Leguminosae	*Dialium indicatum*	5.256	0.20	2.9	0.61
	D. indum	23.689	0.91	2.9	0.61
	D. patens	0.226	0.01	0.6	0.12
	D. sp 1	10.694	0.41	2.9	0.61
	Koompassia malaccensis	36.338	1.40	3.4	0.73
	K. excelsa	2.405	0.09		
	Pithecellobium clypearia	2.297	0.09	0.6	0.12
	Sindora beccariana	3.088	0.12	0.24	0.12
	S. coriaceae	6.487	0.25	0.6	0.12
Linaceae	*Ctenolophon parvifolius*	0.229	0.01	0.6	0.12
Loganiaceae	*Strychnos ignatii*	0.189	0.01	0.6	0.12
Magnoliaceae	*Talauma* sp.	1.331	0.05	1.1	0.24
Melastomataceae	*Pternandra rostrata*	1.470	0.06	1.7	0.37
	Memecylon laevigatum	0.122	0.01	0.6	0.12
	M.. laurinum	0.462	0.02	1.1	0.24
Meliaceae	*Aglaia ganggo*	0.437	0.02	0.6	0.12
	A. sp 1	1.880	0.07	1.7	0.37
	A. sp 2	0.975	0.04	0.6	0.12
	Chisocheton sp 1	44.167	1.70	8.6	1.83
	C. sp 2	0.665	0.03	1.1	0.24
	Dysoxylum sp.	6.326	0.24	2.3	0.61
	Sandoricum sp.	0.488	0.02	0.6	0.12
	Walsura sp 1	0.757	0.03	1.1	0.24
	W. sp 2	0.087	*	0.6	0.12
Moraceae	*Artocarpus anisophyllus*	1.066	0.04	1.7	0.37
	A. dadah	1.099	0.04	1.1	0.24
	A. elasticus	3.359	0.13	0.6	0.12
	A. integer	0.456	0.02	0.6	0.12
	A. nitidus	1.150	0.04	1.7	0.37
	A. odoratissimus	5.131	0.20	2.3	0.61
	A. sp 1	1.086	0.04	1.1	0.24
	A. sp 3	1.005	0.04	0.6	0.12
	A. sp 7	0.571	0.02	1.1	0.24
	Ficus stupenda	0.228	0.01	0.6	0.12
	Prainea limpato	0.396	0.02	0.6	0.12
Myristicaceae	*Gymnacranthera contracta*	0.137	0.01	0.6	0.12
	G. sp 1	15.129	0.58	2.9	0.73
	G. sp 2	0.228	0.09	0.6	0.12
	Horsfieldia sp 1	8.470	0.33	2.9	0.73
	Knema latericia	1.112	0.04	1.1	0.24
	K. latifolia	0.171	0.01	1.1	0.24
	Myristica elliptica	0.701	0.03	1.1	0.24

Table III-4 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	M. villosa	0.087	*	0.6	0.12
	M. sp 1	2.392	0.09	2.3	0.49
	Myristicaceae 1	0.115	*	0.6	0.12
	Myristicaceae 2	0.185	0.01	0.6	0.12
	Myristicaceae 3	0.165	0.01	0.6	0.12
	Myristicaceae 4	0.506	0.02	0.6	0.12
	Myristicaceae 5	1.966	0.08	1.1	0.24
	Myristicaceae 6	0.144	0.01	0.6	0.12
	Myristicaceae 7	0.690	0.03	0.6	0.12
Myrtaceae	*Eugenia ecostulata*	0.117	0.01	0.6	0.12
	E. leucoxla	0.387	0.02	1.1	0.24
	E. papillosa	1.438	0.06	0.6	0.12
	E. sp A	0.747	0.03	1.1	0.24
	E. sp B	0.084	*	0.6	0.12
	E. sp 1	3.214	0.12	1.7	0.37
	E. sp 4	0.268	0.01	0.6	0.12
	E. sp 8	0.203	0.01	0.6	0.12
	E. sp 9	0.185	0.01	0.6	0.12
	E. sp 10	9.441	0.36	1.7	0.37
	E. sp 11	0.196	0.01	0.6	0.12
	E. sp 12	0.187	0.01	0.6	0.12
	E. sp 16	1.358	0.05	0.6	0.12
	E. sp 17	35.774	1.38	5.7	1.22
	Syzygium lineatum	0.161	0.01	0.6	0.12
Olacaceae	*Ochanostachys amentacea*	2.971	0.12	2.3	0.49
Palmaceae	*Oncospermum horridum*	0.138	0.01	0.6	0.12
Polygalaceae	*Xanthophyllum affine*	27.970	1.08	6.3	1.34
	X. griffithii	0.552	0.02	0.6	0.12
	X. stipitatum	2.214	0.09	1.1	0.24
	X. sp 2	2.746	0.11	1.1	0.24
	X. sp 3	0.523	0.02	0.6	0.12
Rhamnaceae	*Zizyphus angustifolius*	0.102	*	0.6	0.12
Rhizophoraceae	*Pellacalyx* sp.	0.092	*	0.6	0.12
Rosaceae	*Parastemon spicatum*	0.129	0.01	0.6	0.12
	P. urophyllus	4.268	0.16	1.1	0.24
	Prunus javanica	0.082	*	0.6	0.12
Rubiaceae	*Nauclea excelsa*	1.767	0.07	0.6	0.12
	N. sp 2	0.092	*	0.6	0.12
	Porterandia anisophylla	0.622	0.02	1.1	0.24
	Wenlandia sp 2	0.129	0.01	0.6	0.12
	Rubiaceae 4	0.106	*	0.6	0.12
	Rubiaceae 5	0.078	*	0.6	0.12
Rutaceae	*Euodia* sp 1	0.107	*	0.6	0.12
	E. sp 2	0.010	*	0.6	0.12
Sapindaceae	*Lepisanthes* sp 1	0.091	*	0.6	0.12
	Mischocarpus pentapetalus	0.141	0.01	0.6	0.12
	Nephelium cuspidatum	1.500	0.06	1.7	0.37

Table III-4 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	N. maingayi	0.608	0.02	0.6	0.12
	N. sp 1	0.588	0.02	0.6	0.12
	Pometia pinnata	5.764	0.22	1.7	0.37
	Xerospermum noronhianum	1.812	0.07	1.1	0.24
	Sapindaceae 1	0.084	*	0.6	0.12
Sapotaceae	*Ganua boerlageana*	0.093	*	0.6	0.12
	G. kingiana	8.398	0.32	2.9	0.73
	G. motleyana	4.367	0.17	2.9	0.73
	G. sp 2	0.675	0.03	1.1	0.24
	G. sp 3	0.093	*	0.6	0.12
	Madhuca mangifera	16.217	0.63	2.9	0.73
	Palaquium calophyllum	1.956	0.08	1.1	0.24
	P. microphyllum	0.363	0.01	0.6	0.12
	P. quercifolium	1.231	0.05	1.1	0.24
	P. sp 1	0.229	0.01	0.6	0.12
	Payena leeri	0.669	0.03	0.6	0.12
	Planchonella sp.	0.255	0.01	0.6	0.12
	Sapotaceae 1	0.636	0.03	0.6	0.12
	Sapotaceae 2	2.297	0.09	0.6	0.12
Sterculiaceae	*Heritiera simplicifolia*	0.274	0.01	0.6	0.12
	H. sumatrana	2.297	0.09	0.6	0.12
	Pterospermum sp 1	0.092	*	0.6	0.12
	Scaphium macropodum	1.851	0.07	1.1	0.24
	Sterculia sp 1	0.982	0.04	1.7	0.37
	S. sp 2	0.624	0.02	1.1	0.24
	Steculiaceae 4	0.233	0.01	0.6	0.12
	Sterculiaceae 5	0.158	0.01	0.6	0.12
Symplocaceae	*Symplocos barringtoniifolia*	0.937	0.04	1.1	0.24
Theaceae	*Adinandra dumosa*	0.517	0.02	0.6	0.12
Thymelaceae	*Gonystylus affinis*	8.321	0.32	4.0	0.86
	G. sp 1	28.350	1.09	8.0	1.71
	G. sp 2	2.542	0.10	2.3	0.49
Tiliaceae	*Microcos* sp.	0.085	*	0.6	0.12
	Pentace excelsa	0.329	0.01	0.6	0.12
	P. laxiflora	2.235	0.09	1.1	0.24
Ulmaceae	*Gironniera nervosa*	0.126	0.01	0.6	0.12
Verbenaceae	*Teijsmanniodendron* sp.	1.014	0.04	0.6	0.12
	Vitex quinata	27.600	1.07	5.7	1.22
Violaceae	*Rinorea* sp.	1.095	0.04	1.1	0.24
Unidentified		1477.368	7.07	-	-

Total number of identified trees in plots = 735

Total number of unidentified trees in plots = 83

* Value < 0.01

Table III- 5 Basal area, density and relative density of identified tree species in heath forest vegetation plots (Area = 0.5 ha).

Family	Species	Basal Area	% of BA	Density	Relative Density
Anacardiaceae	*Buchanania* sp.	0.105	0.05	2	0.19
	Campnosperma auriculatum	0.097	0.05	2	0.19
	Gluta aptera	0.467	0.22	6	0.57
	G. beccarii	2.426	1.12	24	2.29
	G. pubescens	0.026	0.01	2	0.19
	Koordersiodendron pinnatum	0.012	0.01	2	0.19
	Melanochyla angustifolia	0.020	0.01	2	0.19
	Parishia maingayi	0.097	0.05	6	0.57
	Semecarpus heterophyllus	0.019	0.01	2	0.19
	Swintonia acuta	0.014	0.01	2	0.19
	S. foxworthyi	2.102	0.97	16	1.53
	S. schwenkii	0.032	0.02	2	0.19
	Anacardiaceae 4	0.032	0.02	2	0.19
	Anacardiaceae 5	0.023	0.01	2	0.19
	Anacardiaceae 6	0.099	0.05	2	0.19
	Anacardiaceae 7	0.022	0.01	2	0.19
Annonaceae	*Cyathocalyx* sp.	0.050	0.02	4	0.38
	Polyalthia glauca	0.013	0.01	2	0.19
	Annonaceae 5	0.093	0.04	6	0.57
	Annonceae 7	0.040	0.02	4	0.38
Burseraceae	*Dacryodes rostrata*	0.542	0.25	8	0.76
Casuariniaceae	*Casuarina* sp.	0.692	0.32	12	1.15
Celastraceae	*Bhesa paniculata*	1.672	0.77	18	1.72
	Lophopetalum glabrum	11.530	5.30	28	2.68
	L. rigidum	0.023	0.01	2	0.19
Dipterocarpaceae	*Cotylelobium lanceolatum*	0.760	0.35	12	1.15
	C. sp	0.375	0.17	8	0.76
	Dipterocarpus eurynchus	0.068	0.03	2	0.19
	D. kerrii	0.030	0.01	2	0.19
	D. sp 3	0.008	*	2	0.19
	D. sp 6	0.930	0.43	8	0.76
	Hopea mesuoides	30.464	14.02	68	6.50
	H. micrantha	11.372	5.23	46	4.40
	H. vaccinifolia	0.066	0.03	2	0.19
	H. sp	0.083	0.04	2	0.19
	Shorea albida	97.486	44.85	62	11.85
	S. coriaceae	6.194	2.85	26	2.45
	S. havilandii	3.013	1.39	26	2.45
	S. induplicata	0.516	0.24	10	0.96
	S. venulosa	0.011	0.01	2	0.19
	S. sp 10	5.776	2.66	18	1.72
	S. sp 12	0.811	0.37	4	0.38
	Vatica coriaceae	0.113	0.05	6	0.57
	V. rotata	0.043	0.02	4	0.38
	V. sp 4	0.016	0.01	2	0.19
Ebanaceae	*Diospyros ferruginea*	0.010	0.01	2	0.19

Table III-5 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	D. turfosa	0.083	0.04	4	0.38
	D. sp 3	0.011	0.01	2	0.19
Euphorbiaceae	*Baccaurea bracteata*	0.380	0.18	8	0.76
	Macaranga brachythyrsa	0.613	0.28	6	0.57
Fagaceae	*Castanopsis* sp.	0.196	0.09	8	0.76
	Lithocarpus ferrugineus	0.009	*	2	0.19
	L. pusillus	0.088	0.04	4	0.38
Guttiferae	*Callophyllum nodosum*	0.191	0.09	8	0.76
	C. teysmannii	0.016	0.01	2	0.19
	C. sp 2	0.015	0.001	2	0.19
	Garcinia	1.585	0.73	14	1.34
	*G.*sp1	2.591	1.19	22	2.10
	*G.*sp2	0.182	0.08	8	0.76
	*G.*sp3	0.013	0.01	2	0.19
	*G.*sp4	0.282	0.13	6	0.57
	*G.*sp5	0.010	0.01	2	0.19
	*G.*sp6	0.018	0.01	2	0.19
	*G.*sp7	0.045	0.02	4	0.38
	Mesua beccariana	0.517	0.24	4	0.38
	M. sp 1	0.009	*	2	0.19
	M. sp 2	2.267	1.04	22	2.10
Icaniaceae	*Stemonurus* sp.	0.734	0.33	14	1.34
	Icaniaceae 1	0.010	0.01	2	0.19
Lauraceae	*Alseodaphne albifrons*	0.090	0.04	6	0.57
	Dehaasia firma	0.019	0.01	2	0.19
	Lauraceae 9	0.561	0.26	8	0.76
	Lauraceae 14	0.016	0.01	2	0.19
Leguminosae	*Archiodendron* sp.	0.025	0.01	2	0.19
	Dialium indum	3.921	1.80	44	4.21
	Sindora coriaceae	0.235	0.11	6	0.57
Melastomataceae	*Memecylon sp.*	0.116	0.05	6	0.57
	Pternandra teysmanniana	0.501	0.23	8	0.76
Meliaceae	*Sandoricum caudatum*	2.542	1.12	16	1.53
Myristicaceae	*Horsfieldia oligocarpa*	0.011	0.01	2	0.19
Myrtaceae	*E.*sp4	0.283	0.13	2	0.19
	*E.*sp5	1.957	0.90	18	1.72
	*E.*sp6	0.153	0.07	2	0.19
	*E.*sp7	0.111	0.05	2	0.19
	*E.*sp8	0.011	0.01	2	0.19
	*E.*sp9	0.036	0.02	2	0.19
	*E.*sp10	0.010	0.01	2	0.19
	*E.*sp11	1.315	0.61	10	0.96
	*E.*sp12	1.133	0.52	14	1.34
	*E.*sp13	0.056	0.03	4	0.38
	*E.*sp14	0.035	0.02	2	0.19
	*E.*sp15	0.023	0.01	2	0.19
	Tristania grandifolia	0.010	0.01	2	0.19

Table III-5 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	T. stellata	8.043	3.70	42	4.02
	T. whiteana	2.041	0.94	30	2.87
Sapindaceae	*Lepisanthes divaricata*	0.903	0.42	14	1.34
	Xerospermum laevigatum	0.010	0.01	2	0.19
Sapotaceae	*Madhuca elmeri*	0.012	0.01	2	0.19
	M. sp 1	0.013	0.01	2	0.19
	M. sp 2	0.643	0.23	12	1.15
	Palaquium hexandrum	0.036	0.02	2	0.19
	P. microphyllum	0.025	0.01	2	0.19
	P. quercifolium	0.010	0.01	2	0.19
	P. sp 1	0.413	0.19	6	0.57
	Sapotaceae 1	0.018	0.01	2	0.19
	Sapotaceae 2	0.020	0.01	2	0.19
	Sapotaceae 3	0.019	0.01	2	0.19
Sterculiacae	Sterculiaceae 1	0.009	*	2	0.19
Symplocaceae	*Symplococos cochinchinensis*	0.031	0.01	2	0.19
Theaceae	Theaceae 1	0.163	0.08	6	0.57
Thymelaceae	*Gonystylus xylocarpus*	3.530	1.62	13	2.49

Total number of identified trees in plots = 523

* Value < 0.01

Table III- 6 Basal area, density and relative density of identified tree species in secondary forest vegetation plots (Area = 1.25 ha).

Family	Species	Basal Area	% of BA	Density	Relative Density
Actinidiaceae	*Saurauia nudiflora*	7.007	0.09	4.8	0.86
Anacardiaceae	*Campnosperma* sp.	2.430	0.03	2.4	0.43
	Gluta rostrata	0.113	*	0.8	0.14
	Mangifera sp.	7.078	0.09	3.2	0.57
	Semecarpus rufovelutinus	0.081	*	0.8	0.14
	Swintonia glauca	1.568	0.02	0.8	0.14
	S. spillea	0.240	*	0.8	0.14
Annonaceae	*Cyathocalyx* sp.	5.175	0.07	3.2	0.57
	Mezzettia sp.	0.101	*	0.8	0.14
	Polyalthia sumatrana	0.158	*	0.8	0.14
	Pseudocarpus sp 1	1.046	0.01	1.6	0.28
	Pseuduvaria sp.	0.482	0.01	0.8	0.14
	Annonaceae 1	0.861	0.01	1.6	0.28
	Annonaceae 2	0.272	*	0.8	0.14
Bombaceae	*Durio griffithii*	4.111	0.05	1.6	0.28
	Canarium sp.	0.091	*	0.8	0.14
	Dacryodes sp.	0.574	0.01	1.6	0.28
Dilleniaceae	*Dillenia borneensis*	86.330	1.09	19.2	3.42
	D. grandifolia	1.613	0.02	3.2	0.57
	D. suffruticosa	50.934	0.64	14.4	2.57
Dipterocarpaceae	*Cotylelobium lanceolatum*	0.128	*	0.8	0.14
	Dipterocarpus kerrii	7.083	0.09	1.6	0.28
	Shorea atrinervosa	6.965	0.09	0.8	0.14
	S. beccariana	0.404	0.01	0.8	0.14
	S. crassa	2.904	0.034	1.6	0.24
	S. kunstleri	0.252	*	0.8	0.14
	S. leprosula	21.670	0.41	5.6	1.00
	S. parvifolia	2.043	0.03	1.5	0.28
	S. smithiana	56.718	0.72	8.0	1.43
	Shorea sp 2	0.145	*	0.8	0.14
	Vatica chartaceae	0.399	0.01	1.6	0.28
	V. sarawakensis	0.147	*	0.8	0.14
Ebanaceae	*Diospyros confertiflora*	0.089	*	0.8	0.14
	D. korthalsiana	0.417	0.01	1.6	0.28
	D. nemorosa	0.704	0.01	0.8	0.14
Euphorbiaceae	*Baccaurea bracteata*	1.381	0.02	2.4	0.43
	B. sp	0.105	*	0.8	0.14
	Croton sp.	0.084	*	0.8	0.14
	Endospermum diadenum	0.103	*	0.8	0.14
	Glochidion sp.	1257.454	15.87	81.6	14.55
	Macaranga amissa	217.678	2.75	17.6	3.14
	M. gigantea	105.865	1.34	19.2	3.42
	M. hosei	703.987	8.89	43.2	7.70
	M. hypoleuca	15.233	0.19	5.6	1.00
	M. tanarius	11.666	0.15	8.0	1.43
	M. triloba	0.151	*	0.8	0.14

Table III-6 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	M. sp 1	8.904	0.11	4.0	0.57
	Euphorbiaceae 1	0.129	*	0.8	0.14
	Euphorbiaceae 2	0.091	*	0.8	0.14
	Euphorbiaceae 3	0.147	*	0.8	0.14
	Euphorbiaceae 4	3.781	0.05	1.6	0.28
Fagaceae	*Castanopsis javanica*	0.131	*	0.8	0.14
	Lithocarpus bennetii	0.928	0.01	1.6	0.28
Flacourtiaceae	Flacourtiaceae 1	37.580	0.47	5.6	1.00
Guttiferae	*Garcinia bancana*	0.221	*	0.8	0.14
	G. cowa	0.445	0.01	1.6	0.28
Hypericaceae	*Cratoxylum formosum*	0.129	*	0.8	0.14
	C. glaucum	4385.057	55.36	52.8	9.42
	C. sumatranum	2.892	0.04	4.0	0.71
Lauraceae	*Cryptocarya palawensis*	0.586	0.01	1.6	0.28
	C. sp 1	2.198	0.03	1.6	0.28
	Dehaasia firma	0.079	*	0.8	0.14
	Endiandra sp 1	0.262	0.03	0.8	0.14
	E. sp 2	1.846	0.02	2.4	0.43
	Litsea roxburghii	2.125	0.03	3.2	0.57
	L. sp 1	5.931	0.08	4.0	0.71
	L.. sp 2	0.077	*	0.8	0.14
	L. sp 3	0.194	*	0.8	0.14
	Lauraceae 1	1.713	0.02	0.8	0.14
	Lauraceae 2	0.174	*	0.8	0.14
	Lauraceae 3	0.108	*	0.8	0.14
	Lauraceae 4	0.882	0.01	0.8	0.14
	Lauraceae 16	0.779	0.01	1.6	0.28
Lecythidaceae	*Barringtonia* sp.	0.108	*	0.8	0.14
Leguminosae	*Archidendron ellipticum*	0.498	0.01	1.6	0.28
	Cassia nodosa	0.486	0.01	0.8	0.14
	Castanopsis sp 1	0.208	*	0.8	0.14
	Koompassia excelsa	0.504	0.01	1.6	0.28
Magnoliaceae	*Talauma* sp.	0.106	*	0.8	0.14
Melastomataceae	*Pternandra rostrata*	437.324	5.52	48.0	8.56
Meliaceae	*Chisocheton* sp.	0.133	*	0.8	0.14
	Walsura sp 1	0.098	*	0.8	0.14
Moraceae	*Artocarpus anisophyllus*	0.736	0.01	1.6	0.28
	A. elasticus	1.243	0.02	2.4	0.43
	A. integer	0.277	*	0.8	0.14
	A. kemando	0.139	*	0.8	0.14
	A. nitidus	9.133	0.12	4.8	0.86
	A. odoratissimus	2.105	0.03	2.4	0.43
	A. sp 1	1.053	0.01	1.6	0.28
	A. sp 2	0.261	*	0.8	0.14
	A. sp 3	0.795	0.01	1.6	0.28
	A. sp 4	2.267	0.03	3.2	0.57
	A. sp 5	0.908	*	0.8	0.14

Table III-6 (continued)

Family	Species	Basal Area	% of BA	Density	Relative Density
	Ficus beccarii	0.110	*	0.8	0.14
	F. variegata	4.191	0.05	2.4	0.43
	F. vasculosa	0.077	*	0.8	0.14
	F. sp 3	2.703	0.03	3.2	0.57
	Moraceae 1	0.140	*	0.8	0.14
Myristicaceae	*Gymnacranthera* sp 1	0.085	*	0.8	0.14
	Horsfieldia grandiflora	8.164	0.10	4.0	0.71
Myrtaceae	*Eugenia palyanta*	0.751	0.01	1.6	0.28
	E. sp B	0.133	*	0.8	0.14
	E. sp 1	1.035	0.01	2.4	0.43
	E. sp 2	1.158	0.02	1.6	0.28
	E. sp 3	0.388	0.01	1.6	0.28
	Tristania stellata	2.041	0.03	0.8	0.14
	T. whiteana	37.166	0.47	4.0	0.71
	T. sp 1	1.481	0.02	0.8	0.14
Rubiaceae	*Anthocephalus chinensis*	0.694	0.01	0.8	0.14
	Nauclea orientalis	0.110	*	0.8	0.14
	N. subdita	5.244	0.07	5.6	1.00
	Porterandia sp.	2.372	0.03	2.4	0.43
	Timonius borneensis	31.989	0.40	5.6	1.00
	Wenlandia dasythyrsa	14.482	0.18	6.4	1.14
	Rubiaceae 1	0.086	*	0.8	0.14
	Rubiaceae 2	0.078	*	0.8	0.14
	Rubiaceae 3	0.106	*	0.8	0.14
Rutaceae	*Euodia latifolia*	11.983	0.15	4.8	0.86
Sapindaceae	*Mischocarpus* sp.	0.181	*	0.8	0.14
	Nephelium daedaleum	0.102	*	0.8	0.14
	Paranephelium xestophyllum	0.185	*	0.8	0.14
	Pometia pinnata	4.936	0.06	1.6	0.28
Sapotaceae	*Ganua* sp.	1.148	0.01	0.8	0.14
	Payena endertii	0.770	0.01	0.8	0.14
	Sapotaceae 1	0.079	*	0.8	0.14
Sterculiaceae	Sterculiaceae 1	2.898	0.04	3.2	0.57
	Sterculiaceae 2	0.093	*	0.8	0.14
Symplocaceae	*Symplocos cochinchinensis*	0.092	*	0.8	0.14
Theaceae	*Adinandra dumosa*	12.541	0.16	4.8	0.86
	Ternstroemia sp.	0.107	*	0.8	0.14
Thymelaceae	*Gonystulus* sp 1	0.390	0.01	0.8	0.14
Tiliaceae	*Pentace excelsa*	0.226	*	0.8	0.14
Ulmaceae	*Gironniera subaequalis*	0.092	*	0.8	0.14
Verbenaceae	*Callicarpa cana*	0.414	0.01	1.6	0.28
	Geunsia pentandra	15.954	0.20	8.8	1.57
	Vitex pubescens	0.139	*	0.8	0.14
	V. quinata	1.066	0.01	2.4	0.43
Unidentified		254.356	3.21		

* Value < 0.01

Total number of identified trees in plots = 668

Total number of unidentified trees in plots = 33

Appendix IV

Mammal and Bird Species Identified at Barito Ulu

Between 1988 and 1996, successive field researchers based at the Muara Rekut basecamp compiled a record of mammalian and bird species observed in the Barito Ulu watershed. Mammalian species are listed in Table IV-1 and bird species in Table IV-2. Those species observed by S.B. are denoted by an asterix.

Table IV-1 Checklist of mammalian fauna recorded at Barito Ulu between 1988 and 1996 (Subfamily in brackets).

Order	Family	Genus	Species	Common Name
Insectivora	Erinaceidae	*Echinosorex*	*E. gymnura*	Moonrat*
Scandentia	Tupaiidae	*Tupaia*	*T. dorsalis*	Striped Treeshrew
			T. glis	Common Treeshrew*
			T. gracilis	Slender Treeshrew*
			T. minor	Lesser Treeshrew*
			T. splendidula	Ruddy Treeshrew
			T. tana	Large Treeshrew
Dermoptera	Cynocephalidae	*Cynocephalus*	*C. variegatus*	Colugo (or Flying Lemur)*
Chiroptera	Pteropodidae	*Pteropus*	*P. vampyrus*	Large Flying Fox
		Cynopterus	*C. brachyotis*	Short-nosed Fruit Bat*
		Penthetor	*P. lucasi*	Dusky Fruit Bat*
		Megaerops	*M. ecaudatus*	Tailless Fruit Bat
		Chironax	*C. melanocephalus*	Black-capped Fruit Bat
		Balionycteris	*B. maculata*	Spotted-winged Fruit Bat
	Emballonuridae	*Emballonura*	*E. alecto*	Greater Sheath-tailed Bat*
	Megadermatidae	*Megaderma*	*M. spasma*	Lesser False Vampire
	Nycteridae	*Nycteris*	*N. tragata*	Hollow-faced Bat
	Rhinolophidae	*Rhinolophidae*	*R. borneensis*	Bornean Horseshoe Bat*
			R. sedulus	Lesser Woolly Horseshoe Bat*
			R. trifoliatus	Trefoil Horseshoe Bat
	Hipposideridae	*Hipposideros*	*H. diadema*	Diadem Roundleaf Bat*
		Coelops	*C. robinsoni*	Lesser Tailless Roundleaf Bat
	Vespertilionidae (Vespertilioninae)	*Myotis*	*M. (Selysius) muricola*	Whiskered Myotis*
	Vespertilionidae (Murininae)	*Kerivoula*	*K. papillosa*	Papillose Woolly Bat*
Primates	Loridae	*Nycticebus*	*N. coucang*	Slow Loris*
	Tarsiidae	*Tarsius*	*T. bancanus*	Western Tarsier

Table IV-1 (continued)

Order	Family	Genus	Species	Common Name
	Cercopithecidae	*Presbytis*	*P. rubicunda*	Maroon or Red Leaf Monkey*
		Macaca	*M. fascicularis*	Long-tailed Macaque*
			M. nemestrina	Pig-tailed Macaque
	Hylobatidae	*Hylobates*	*H. agilis albibarbis*	Agile Gibbon*
			H. a. albibarbis x H. muelleri	Hybrid *agilis x muelleri* gibbons*
	Pongidae	*Pongo*	*Pongo pygmaeus*	Orangutan
Pholidota	Manidae	*Manis*	*M. javanica*	Pangolin
Rodentia	Sciuridae (Sciuriae)	*Ratufa*	*R. affinis*	Giant Squirrel*
		Callosciurus	*C. prevostii*	Prevost's Squirrel*
			C. notatus	Plantain Squirrel*
		Sundasciurus	*S. hippurus*	Horse-tailed Squirrel
			S. lowii	Low's Squirrel*
			S. tenuis	Slender Squirrel
			S. jentinki	Jentink's Squirrel
			S. brookei	Brooke's Squirrel
		Lariscus	*L. insignis*	Three-Striped Ground Squirrel*
		Rhinosciurus	*R. laticaudatus*	Shrew-Faced Ground Squirrel
		Nannosciurus	*N. melanotis*	Black-eared Pigmy Squirrel*
		Exilisciurus	*E. exilis*	Plain Pigmy Squirrel*
		Rheithrosciurus	*R. macrotis*	Tufted Ground Squirrel
	Sciuridae (Petauristinae)	*Petaurista*	*P. petaurista*	Red Giant Flying Squirrel
			P. elegans	Spotted Giant Flying Squirrel
	Muridae	*Rattus*	*R. tiomanicus*	Malaysian Field Rat*
			R. exulans	Polynesian Rat*
		Sundamys	*S. muelleri*	Muller's Rat*
		Niviventer	*N. rapit*	Long-tailed Mountain Rat
		Maxomys	*M. surifer*	Red Spiny Rat

Table IV-1 (continued)

Order	Family	Genus	Species	Common Name
			M. whiteheadi	Whitehead's Rat*
			M. rajah	Brown Spiny Rat
		Leopoldamys	*L. sabanus*	Long-tailed Giant Rat
		Lenothrix	*L. canus*	Grey Tree Rat
	Hystricidae	*Trichys*	*T. fasciculata*	Long-tailed Porcupine
		Hystrix	*H. brachyura*	Common Porcupine*
Carnivora	Canidae	*Canis*	*C. familiaris*	Domestic Dog*
	Ursidae	*Helarctos*	*H. malayanus*	Sun Bear*
	Mustelidae	*Martes*	*M. flavigula*	Yellow-throated Marten*
		Mustela	*M. nudipes*	Malay Weasel
		Mydaus	*M. javanensis*	Teledu (Malay Badger)
		Lutra	*L. sumatrana*	Hairy-nosed Otter*
		Aonyx	*A. cinerea*	Oriental Small-clawed Otter**
	Viverridae	*Viverra*	*V. tangalunga*	Tangalung (Malay Civet)*
		Paradoxurus	*P. hermaphroditus*	Common Palm Civet
		Arctictis	*A. binturong*	Binturong (Bearcat)*
		Arctogalidia	*A. trivirgata*	Small-toothed Palm Civet
		Hemigalus	*H. derbyanus*	Banded Palm Civet*
	Herpestidae	*Herpestes*	*H. brachyurus*	Short-tailed Mongoose
			H. semitorquatus	Collared Mongoose
	Felidae	*Neofelis*	*N. nebulosa*	Clouded Leopard
		Pardoelis	*P. marmorata*	Marbled Cat*
		Catopuma	*C. badia*	Bay Cat**
		Prionailurus	*P. bengalensis*	Leopard Cat*
Artiodactya	Suidae	*Sus*	*S. barbatus*	Bearded Pig*
	Tragulidae	*Tragulus*	*T. javanicus*	Lesser Mouse-Deer*

Table IV-1 (continued)

Order	Family	Genus	Species	Common Name
			T. napu	Greater Mouse-Deer*
	Cervidae	*Muntiacus*	*M. muntjak*	Red Muntjac*
			M. atherodes	Bornean Yellow Muntjac*
		Cervus	*C. unicolor*	Sambar Deer (Rusa or Payau)*

* Animals observed (includes both visual and audible detection) by S.B. or A.W. during the 1995-1996 field season.

** Animals observed by S.B. or A.W. and previously not know to occur in the Barito Ulu watershed.

Subfamily is indicated in brackets

Taxonomy follows:

Wilson, D.E. and Reeder, D.A. 1993 *Mammal Species of the World: A Taxonomic and Geographic Reference.* (2nd Edition). Washington and London. Washington and London: Smithsonian Institution Press.

Table IV-2 Checklist of avian fauna recorded at Barito Ulu between 1988 and 1996 (Subfamily in brackets).

Order	Family	Genus	Species	Common Name
Pelecaniformes	Anhingidae	*Anhinga*	*A. melanogaster*	Oriental Darter*
Ardeiformes	Ardeidae	*Butorides*	*B. striatus*	Striated Heron*
		Ixobrychus	*I. sinensis*	Yellow Bittern
	Threskiornithidae	*Pseudibis*	*P. davisoni*	White-shouldered Ibis
Falconiformes	Accipidtridae	*Macheiramphus*	*M. alcinus*	Bat Hawk
		Aviceda	*A. jerdoni*	Jerdon's Baza
		Pernis	*P. ptilorhynchus*	Oriental Honey Buzzard*
		Haliastur	*H. indus*	Brahminy Kite*
		Accipiter	*A. trivirgatus*	Crested Goshawk
		Spizaetus	*S. alboniger*	Blyth's Hawk-Eagle
		Hieraaetus	*H. kienerii*	Rufous-bellied Eagle
		Ictinaetus	*I. malayensis*	Black Eagle*
		Haliaeetus	*H. leucogaster*	White-bellied Fish-Eagle*
		Ichthyophaga	*I. ichthyaetus*	Grey-headed Fish-Eagle*
			I. humilis	Lesser Fish-Eagle*
		Spilornis	*S. cheela*	Crested Serpent-Eagle*
	Falconidae	*Microhierax*	*M. fringillarius*	Black-thighed Falconet*
Galliformes	Phasianidae	*Rhizothera*	*R. longirostris*	Long-billed Partridge
		Arborophila	*A. hyperythra*	Red-breasted Partridge*
		Melanoperdix	*M. nigra*	Black Partridge*
		Rollulus	*R. rouloul*	Crested Wood Partridge
		Lophura	*L. erythrophthalma*	Crestless Fireback*
			L. ignita	Crested Fireback
			L. bulweri	Bulwer's Pheasant*
		Argusianus	*A. argus*	Great Argus
Charadriiformes	Scolopacidae (Tringinae)	*Tringa*	*T. nebularia*	Common Sandpiper*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
Columbiformes	Columbidae (Treroninae)	*Treron*	*T. capellei*	Large Green Pigeon*
			T. curvirostra	Thick-billed Pigeon*
			T. olax	Little Green Pigeon*
	Columbidae (Ptilinopinae)	*Ptilinopus*	*P. jambu*	Jambu Fruit Dove*
	Columbidae (Duculinae)	*Ducula*	*D. aenea*	Green Imperial Pigeon*
	Columbidae (Streptopelinae)	*Macropygia*	*M. emiliana*	Ruddy Cuckoo-Dove
			M. ruficeps	Little Cuckoo-Dove
		Streptopelia	*S. chinensis*	Spotted Dove
		Chalcophaps	*C. indica*	Emerald Dove*
Psittaciformes	Psittacidae	*Psittinus*	*P. cyanurus*	Blue-rumped Parrot
		Loriculus	*L. galgulus*	Malay Lorikeet*
Cuculiformes	Cuculidae (Cuculinae)	*Cuculus*	*C. vagans*	Moustached Hawk-Cuckoo
		Cacomantis	*C. merulinus*	Plaintive Cuckoo*
			C. sepulcralis	Rusty-breasted Cuckoo
		Chrysococcyx	*C. xanthorhynchus*	Violet Cuckoo
	Cuculidae (Phaenicophaeinae)	*Phaenicophaeus*	*P. chlorophaeus*	Raffle's Malkoha
			P. diardi	Black-bellied Malkoha
			P. sumatranus	Chestnut-bellied Malkoha*
			P. javanicus	Red-billed Malkoha*
			P. curvirostris	Chestnut-breasted Malkoha*
	Cuculidae (Centropodinae)	*Centropus*	*C. sinensis*	Common (Greater) Coucal*
			C. bengalensis	Lesser Coucal*
	Cuculidae (Neomorphinae)	*Carpococcyx*	*C. radiceaus*	Sunda-ground Cuckoo
Strigiformes	Tytonidae	*Phodilus*	*P. badius*	Bay Owl
	Strigidae	*Otus*	*O. rufescens*	Reddish Scops Owl

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
		Ketupa	*K. ketupu*	Buffy Fish Owl
		Ninox	*N. scutulata*	Brown Hawk-Owl
		Ninox	*N. scutulata*	Brown Hawk-Owl
		Strix	*S. leptogrammica*	Brown Wood Owl
Caprimulgiformes	Caprimulgidae	*Eurostopodus*	*E. temminckii*	Malaysian Eared Nightjar
		Caprimulgus	*C. macrurus*	Large-tailed Nightjar
		Aerodramus	*A. fuciphagus*	Edible-nest Swiftlet
Apodiformes	Apodidae	*Collocalia*	*C. maxima*	Black-Nest Swiftlet*
			C. esculenta	Glossy Swiftlet
		Hirundapus	*H. caudacutus*	White-throated Needletail
		Rhaphidura	*R. leucopygialis*	Silver-rumped Swift
		Apus	*A. affinis*	House Swift
	Hemiprocnidae	*Hemiprocne*	*H. comata*	Whiskered Tree Swift*
			H. longipennis	Crested (Grey-rumped) Tree Swift
Trogoniformes	Trogonidae	*Harpactes*	*H. diardii*	Diard's Trogon*
			H. kasumba	Red-naped Trogon*
			H. duvaucelii	Scarlet-rumped Trogon
			H. orhophaeus	Cinnamon-rumped Trogon
			H. oreskios	Orange-breasted Trogon
Coraciiformes	Alcedinidae	*Lacedo*	*L. pulchella*	Banded Kingfisher*
		Todirhamphus	*T. chloris*	Collared Kingfisher
		Pelargopsis	*P. capensis*	Stork-billed Kingfisher
		Alcedo	*A. atthis*	Common Kingfisher*
			A. meninting	Blue-eared Kingfisher*
			A. euryzona	Blue-banded Kingfisher*
		Ceyx	*C. erithacus*	Black-backed Kingfisher*

Table IV-2 (continued)

Order	Family	Genus	*Species*	Common Name
			C. rufidorsus	Rufous-backed Kingfisher*
	Meropidae	*Merops*	*M. viridis*	Blue-throated Bee-eater
			M. leschenaulti	Chestnut-headed Bee-eater
		Nyctyornis	*N. amictus*	Red-bearded Bee-eater
	Bucerotidae	*Anorrhinus*	*A. galeritus*	Bushy-crested Hornbill
		Aceros	*A. corrugatus*	Wrinkled Hornbill*
			A. undulatus	Wreathed Hornbill*
			A. comatus	White-crowned Hornbill*
		Anthracoceros	*A. malayanus*	Black Hornbill*
			A. albirostris	Oriental Pied Hornbill*
		Buceros	*B. rhinoceros*	Rhinoceros Hornbill*
			B. vigil	Helmeted Hornbill
Piciformes	Indicatorideae	*Indicator*	*I. archipelagicus*	Malaysian Honeyguide
	Capitonidae	*Calorhamphus*	*C. fuliginosus*	Brown Barbet
		Megalaima	*M. chrysopogon*	Gold-whiskered Barbet*
			M. rafflesii	Red-crowned Barbet*
			M. mystacophanos	Gaudy (Red-throated) Barbet*
			M. henricii	Yellow-crowned Barbet*
			M. pulcherrima	Golden-naped Barbet*
			M. monticola	Mountain Barbet
			M. australis	Little (Blue-eared) Barbet*
			M. eximia	Bornean Barbet
	Picidae (Picumninae)	*Sasia*	*S. abnormis*	Rufous Piculet*
		Picumnus	*P. innominatus*	Speckled Piculet*
	Picidae (Picinae)	*Picus*	*P. puniceus*	Crimson-winged Woodpecker
			P. chlorolophus	Lesser Yellownape
			P. mentalis	Checker-throated Woodpecker

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
			P. miniaceus	Banded Woodpecker
		Celeus	*C. brachyurus*	Rufous Woodpecker*
		Dendrocopos	*D. canicapillus*	Grey-capped Woodpecker*
		Meiglyptes	*M. tristis*	Buff-rumped Woodpecker
			M. tukki	Buff-necked Woodpecker*
		Hemicircus	*H. concretus*	Grey-and-buff Woodpecker
		Dinopium	*D. rafflesi*	Olive-backed Woodpecker*
		Dryocopus	*D. javensis*	White-bellied Woodpecker
		Mulleripicus	*M. pulverulentus*	Great Slaty Woodpecker
		Blythipicus	*B. rubiginosus*	Maroon Woodpecker*
		Chrysocolaptes	*C. lucidus*	Greater Golden Back
		Reinwardtipicus	*R. validus*	Orange-backed Woodpecker*
Passeriformes	Eurylaimidae	*Calyptomena*	*C. viridis*	Green Broadbill*
		Psarisomus	*P. dalhousiae*	Long-tailed Broadbill
		Cymbirhynchus	*C. macrorhynchus*	Black-and-red Broadbill*
		Eurylaimus	*E. ochromalus*	Black-and-yellow Broadbill
			E. javanicus	Banded Broadbill
		Corydon	*C. sumatranus*	Dusky Broadbill
	Pittidae	*Pitta*	*P. arquata*	Blue-banded Pitta
			P. baudi	Blue-headed Pitta*
			P. moluccensis	Blue-winged Pitta
			P. sordida	Hooded Pitta*
	Hirundinidae	*Hirundo*	*H. tahitica*	Pacific Swallow
			H. rustica	Common (Barn) Swallow
	Motacillidae	*Motacilla*	*M. alba*	White Wagtail*
			M. cinerea	Grey Wagtail
			M. flava	Yellow Wagtail*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
	Campephagidae	*Tephrodornis*	*T. gularis*	Large Wood-shrike
		Coracina	*C. striata*	Bar-bellied Cuckoo-shrike
			C. larvata	Sunda Cuckoo-shrike
			C. fimbriata	Lesser Cuckoo-shrike
		Hemipus	*H. hirundinaceus*	Black-winged Flycatcher-shrike
			H. picatus	Bar-winged Flycatcher-shrike
		Pericrocotus	*P. divaricatus*	Ashy Minivet*
			P. flammeus	Scarlet Minivet*
	Artamidae	*Artamus*	*A. leucorhynchus*	White-breasted Wood-Swallow
	Aegithinidae	*Irena*	*I. puella*	(Asian) Fairy Bluebird*
	Chloropseidae	*Aegithina*	*A. viridissima*	Green Iora
		Chloropsis	*C. sonnerati*	Greater Green Leaf-Bird*
			C. cyanopogon	Lesser Green Leaf-Bird
			C. cochinchinensis	Blue-winged Leaf-Bird*
	Pycnonotidae	*Pycnonotus*	*P. eutilotus*	Puff-backed Bulbul
			P. melanoleucos	Black-and-white Bulbul*
			P. atriceps	Black-headed Bulbul*
			P. melanicterus	Black-crested Bulbul*
			P. squamatus	Scaly-breasted Bulbul
			P. cyaniventris	Grey-bellied Bulbul
			P. zeylanicus	Straw-headed Bulbul
			P. flavescens	Pale-faced (Flavescent) Bulbul*
			P. goiavier	Yellow-vented Bulbul*
			P. plumosus	Olive-winged Bulbul
			P. brunneus	Red-eyed Bulbul
			P. simplex	Cream-vented Bulbul
			P. erythrophthalmos	Spectacled Bulbul*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
		Criniger	*C. finschii*	Finsch's Bulbul
		Setornis	*S. criniger*	Hook-Billed Bulbul
		Hypsipetes	*H. criniger*	Hairy-backed Bulbul
		Alophoixus	*A. bres*	Grey-cheeked Bulbul*
			A. ochraceus	Ochraceous Bulbul*
			A. phaeocephalus	Yellow-bellied Bulbul*
		Iole	*I. olivaceae*	Buff-vented Bulbul
		Ixos	*I. malaccensis*	Streaked Bulbul
		Hypsipetes	*H. flavala*	Ashy Bulbul
	Timaliidae (Cinclosomatinae)	*Eupetes*	*E. macrocerus*	Malaysian Rail-Babbler
	Timaliidae (Pellorneinae)	*Pellorneum*	*P. capsitratum*	Black-capped Babbler*
			P. pyrrhogenys	Temminck's Babbler
		Malacocincla	*M. melaccensis*	Short-tailed Babbler*
			M. sepiarium	Horsfield's Babbler*
		Trichastoma	*T. bicolor*	Ferruginous Babbler
			T. rostratum	White-chested Babbler
			T. abbotti	Abbott's Babbler
		Malacopteron	*M. magnum*	Rufous-crowned Babbler*
			M. cinereum	Scaly-crowned Babbler*
			M. magnirostre	Moustached Babbler
			M. affine	Plain (Sooty Capped) Babble
			M. albogulare	White-throated (Grey-breasted) Babbler
	Timalliidae (Pomatorhinae)	*Pomatorhinus*	*P. montanus*	Chestnut-backed Scimitar Babbler*
		Ptilocichla	*P. leucogrammica*	Bornean Wren-Babbler
		Kenopia	*K. striata*	Striped Wren-Babbler
		Napothera	*N. epilepidota*	Small (Eye-browed) Wren-Babbler*
	Timaliidae (Timaliinae)	*Macronous*	*M. gularis*	Striped Tit-Babbler*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
			M. ptilosus	Fluffy-backed Tit-Babbler
		Stachyris	*S. nigriceps*	Grey-throated Babbler
			S. poliocephala	Grey-headed Babbler*
			S. nigricollis	Black-throated Babbler*
			S. leucotis	White-necked Babbler
			S. maculata	Chestnut-rumped Babbler*
			S. erythroptera	Chestnut-winged Babbler
			S. rufifrons	Rufous-fronted Babbler
		Alcippe	*A. brunneicauda*	Brown Fulvetta
		Yuhina	*Y. everetti*	Chestnut-crested Yuhina
			Y. zantholeuca	White-bellied Yuhina*
	Turdidae (Erithacinae)	*Copsychus*	*C. saularis*	Magpie Robin*
			C. malabaricus	White-rumped Shama*
		Trichixos	*T. pyrrhopygus*	Rufous-tailed Shama*
	Turdidae (Enicurinae)	*Enicurus*	*E. leschenaulti*	White-crowned Forktail*
			E. ruficapillus	Chestnut-naped Forktail*
	Turdidae (Turdinae)	*Turdus*	*T. poliocephalus*	Island Thrush
	Sylviidae	*Gerygone*	*G. sulphurea*	Golden-bellied Gerygone
		Urosphena	*U. whiteheadi*	Bornean Stubtail
		Prinia	*P. flaviventris*	Yellow-bellied Wren-Warbler (Prinia)
		Locustella	*L. certhiola*	Pallas's Grasshopper Warbler
		Abroscopus	*A. superciliaris*	Yellow-bellied Warbler
		Orthotomus	*O. atrogularis*	Black-necked (Dark-necked) Tailorbird
			O. sericeus	Red-tailed Tailorbird
			O. ruficeps	Red-headed (Ashy) Tailorbird
	Muscicapidae (Rhipidurinae)	*Rhipidura*	*R. albicollis*	White-throated Fantail*
			R. perlata	Spotted Fantail*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
			R. javanica	Pied Fantail*
	Muscicapidae (Muscicapinae)	*Culicicapa*	*C. ceylonensis*	Grey-headed Flycatcher
		Muscicapa	*M. sibirica*	Sooty (Dark-sided) Flycatcher
		Cyornis	*C. concretus*	White-tailed Flycatcher
			C. superbuss	Bornean Blue Flycatcher*
			C. turcosus	Malaysian Blue Flycatcher*
		Ficedula	*F. dumetoria*	Rufous-chested Flycatcher
		Muscicapella	*M. hodgsoni*	Pygmy Blue Flycatcher
		Rhinomyias	*R. umbratilis*	Grey-chested Flycatcher
			R. ruficauda	Rufous-tailed Jungle Flycatcher
	Muscicapidae (Mnarchinae)	*Philentoma*	*P. pyrhopterum*	Rufous-winged Philentoma*
			P. velatum	Maroon-breasted Flycatcher
		Hypothymis	*H. azurea*	Black-naped Monarch*
		Terpsiphone	*T. paradisi*	Asian Paradise Flycatcher*
	Pachycephalidae	*Pachycephala*	*P. hypoxantha*	Bornean Whistler
	Sittidae	*Sitta*	*S. frontalis*	Velvet-fronted Nuthatch*
	Dicaeidae	*Prionochilus*	*P. thoracicus*	Scarlet-breasted Flowerpecker*
			P. xanthopygius	Yellow-rumped Flowerpecker*
			P. percussus	Crimson-breasted Flowerpecker
			P. maculatus	Yellow-breasted Flowerpecker*
		Dicaeum	*D. chrysorrheum*	Yellow-vented Flowerpecker*
			D. concolor	Plain Flowerpecker
			D. monticolum	Black-sided Flowerpecker
			D. cruentatum	Scarlet-backed Flowerpecker*
			D. trochileum	Scarlet-headed Flowerpecker*
			D. trigonostigma	Orange-bellied Flowerpecker
	Nectarinidae (Nectariniinae)	*Anthreptes*	*A. simplex*	Plain sunbird

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
			A. malacensis	Plain-throated Sunbird
			A. rhodolaema	Red-throated Sunbird
			A. singalensis	Ruby-cheeked Sunbird*
		Hypogramma	*H. hypogrammicum*	Purple-naped Sunbird*
		Nectarinia	*N. sperata*	Purple-throated Sunbird*
		Aethopyga	*A. siparaja*	Crimson Sunbird
			A. mystacalis	Javan Sunbird*
			A. temminckii	Temminck's Sunbird
	Nectariniidae (Arachnotherinae)	*Arachnothera*	*A. longirostra*	Little Spiderhunter
			A. crassirostris	Thick-billed Spiderhunter
			A. robusta	Long-billed Spiderhunter
			A. flavigaster	Spectacled Spiderhunter
			A. chrysogenys	Yellow-eared Spiderhunter
			A. affinis	Grey-breasted Spiderhunter*
			A. juliae	Whitehead's Spiderhunter*
	Zosteropidae	*Zosterops*	*Z. everetti*	Everett's White-Eye
		Oculocincta	*O. squamifrons*	Pygmy White-Eye
	Sturnidae	*Aplonis*	*A. panayensis*	Asian Glossy Starling*
		Acridotheres	*A. cristatellus*	Crested Myna*
		Gracula	*G. religiosa*	Grackle or Hill Myna*
	Ploceidae	*Erythrura*	*E. prasina*	Pin-tailed Parrotfinch
		Lonchura	*L. fuscans*	Dusky Munia
			L. leucogastra	White-bellied Munia
	Dicruridae	*Dicrurus*	*D. aeneus*	Bronzed Drongo
			D. hottentottus	Spangled Drongo
			D. paradiseus	Greater Racket-tailed Drongo*

Table IV-2 (continued)

Order	Family	Genus	Species	Common Name
	Oriolidae	*Oriolus*	*O. xanthonotus*	Dark-throated Oriole*
	Corvidae	*Platylophus*	*P. galericulatus*	Crested Jay*
		Platysmurus	*P. leucopterus*	Black Magpie
		Pityriasis	*P. gymnocephala*	Bornean Bristlehead
		Corvus	*C. enca*	Slender-billed Crow*

* Birds observed by S.B. or A.W. during the 1995-1996 field season.

Taxonomy follows:

Smythies, B.E. 1981 *The Birds of Borneo*. (3rd Edition). Kota Kinabalu and Kuala Lumper: The Sabah Society and The Malayan Nature Society.

MacKinnon, J. and Phillipps, K. 1993 *A Field Guide to the Birds of Borneo, Sumatra, Java and Bali*. Oxford, New York and Tokyo: Oxford University Press.

Appendix V

Food Items Consumed by RBC2

The following table lists the food items consumed by RBC2 over the 60 day observation sample covering the period September 1995 to August 1996.

Table V-1 Length of time and percentage of spent feeding on each food item in RBC2's diet.

Species	Plant part	Total length of feeding time	Percentage of feeding time	Rank
Ficus subgelderi	FIG	1015	4.82	1
Ficus sundaica	FIG	900	4.27	2
Crypteronia griffithii	YL	896	4.25	3
Rhus nodosa	FR	794	3.77	4
Garcinia parvifolia	FR	755	3.58	5
Artocarpus dadah	FR	697	3.31	6
Crypteronia griffithii	FR	519	3.24	7
Eugenia ecostulata	FR	534	2.54	8
Durio malaccensis	YL	522	2.48	9
Dialium patens	YL	466	2.21	10
Ficus villosa	FIG	464	2.20	11
Gnetum gnemon	FR	417	1.98	12
Ficus stupenda	FIG	385	1.83	13
Polyalthia glauca	FR	383	1.82	14
Ficus deltoidea	FIG	371	1.76	15
Gnetum latifolium	FL	365	1.73	16
Paranephelium xestophyllum	FR	346	1.64	17
Artocarpus nitidus	FR	344	1.63	18
Adinandra dumosa	FR	297	1.41	19
Ilex sp.	YL	287	1.36	20
Grewia sp. A	FR	274	1.30	21
Fissistigma manubriatum	FR	268	1.27	22
Arau	YL	238	1.13	23
Baccaurea bracteata	FR	248	1.12	24
Durio griffithii	YL	229	1.09	25
Ficus pellucido-punctata	FIG	225	1.07	26
Parkia speciosa	FR	217	1.03	27
Grewia blattifolia	FR	207	0.98	=28
Durio malaccensis	LB	207	0.98	=28
Xanthophyllum griffithii	YL	203	0.96	30
Gluta curtisii	FL	198	0.94	31
Eugenia leucoxla	FR	180	0.85	32
Xanthophyllum affine	YL	176	0.84	33
Pyridanthe prismatica	FL	175	0.83	=34
Crypteronia paniculata	FL	175	0.83	=34
Ellipeia cuneifolia	FL	171	0.81	36
Gironniera nervosa	FR	169	0.80	37
Garcinia dulcis	FR	166	0.79	38
Dillenia grandifolia	FR	162	0.77	39
Xanthophyllum stipitatum	YL	155	0.74	=40
Gnetum latifoliium	FR	155	0.74	=40
Ficus obscura	YL	153	0.73	42
Pternandra rostrata	FR	149	0.71	43
Ficus sinuata	FIG	144	0.68	44
Gnetum neglectum	FR	132	0.63	45
Willughbeia sp.	FL	131	0.62	=46

Table V-1 (continued)

Species	Plant part	Total length of feeding time	Percentage of feeding time	Rank
Koompassia malaccensis	YL	131	0.62	=46
Artabotrys costatus	FL	130	0.62	=46
Uvaria lobbiana	FL	121	0.57	=49
Ficus bracteata	FIG	121	0.57	=49
Gnetum neglecum	YL	119	0.56	51
Fissistigma manubriatum	FL	115	0.55	52
Ficus chartaceae	FR	114	0.54	53
Shorea crassa	YL	112	0.53	54
Cratoxylum glaucum	YL	107	0.51	55
Parartocarpus bracteatus	FR	106	0.50	56
Eugenia sp B	FR	102	0.48	57
Artocarpus kemando	FR	100	0.47	=58
Ficus excavata	FR	99	0.47	=58
Dialium indum	YL	98	0.47	=58
Garcinia cowa	FL	90	0.43	61
Ficus caulocarpa	FR	89	0.42	=62
Indouchera sp.	FR	88	0.42	=62
Liana June 1	FR	87	0.41	64
Artocarpus elasticus	FR	75	0.36	65
Pentace excelsa	FR	72	0.34	66
Garcinia sp. A	YL	70	0.33	67
Ventilago sp.	YL	66	0.31	=68
Liana Oct 1	YL	65	0.31	=68
Gluta curtisii	YL	64	0.30	70
Rhododendron sp.	FL	61	0.29	71
Oxymitra biglandulosa	FR	60	0.28	=72
Liana Feb 3	FL	60	0.28	=72
Acacia borneensis	YL	60	0.28	=72
Liana Feb 2	YL	59	0.28	=72
Adinandra dumosa	FL	59	0.28	=72
Durio griffithii	LB	59	0.28	=72
Myristica elliptica	FR	58	0.28	=72
Gnetum gnemon	YL	57	0.27	=79
Ficus sp. A	FR	57	0.27	=79
Zizyphus lenticellata	LB	55	0.26	=81
Tree Jan 3	YL	54	0.26	=81
Macrolene sp.	YL	54	0.26	=81
Diospyros borneensis	YL	53	0.25	84
Garcinia sp. B	YL	51	0.24	=85
Arau	FL	51	0.24	=85
Gironniera nervosa	FL	49	0.23	=87
Baccaurea sp.	YL	49	0.23	=87
Lithocarpus pusillus	FR	46	0.22	=89
Diospyros confertiflora	FR	46	0.22	=89
Eusideroxylon zwageri	YL	45	0.21	=91
Clematis sp.	YL	45	0.21	=91
Acacia borneensis	FL	44	0.21	=91

Table V-1 (continued)

Species	Plant part	Total length of feeding time	Percentage of feeding time	Rank
Willughbeia sp.	FR	43	0.20	=94
Mangifera pajang	FR	43	0.20	=94
Wendlandia sp.	FR	42	0.20	=94
Strychnos ignatii	YL	42	0.20	=94
Prainea limpato	YL	42	0.20	=94
Ficus vasculosa	FR	42	0.20	=94
Artocarpus sp. A	FR	42	0.20	=94
Pometia pinnata	FR	41	0.19	=101
Tree July 1	YL	40	0.19	=101
Timonius sp.	FL	40	0.19	=101
Garcina cornea	FR	40	0.19	=101
Embelia sp.	FL	40	0.19	=101
Liana Apr 2	YL	39	0.19	=101
Fagrea ridleyi	YL	38	0.18	=107
Eugenia papillosa	FL	38	0.18	=107
Tristania whiteana	YL	35	0.17	=109
Liana Nov 1	YL	35	0.17	=109
Xerospermum noronhianum	FR	33	0.16	=111
Liana July 3	FR	33	0.16	=111
Swintonia glauca	YL	32	0.15	113
Zizyphus lenticellata	YL	30	0.14	=114
Tree Dec 1	YL	30	0.14	=114
Parartocarpus bracteatus	YL	30	0.14	=114
Hydnocarpus woodii	FR	29	0.14	=114
Xanthophyllum sp. A	YL	28	0.13	=118
Tree Dec 2	LB	28	0.13	=118
Liana Jan 4	FR	28	0.13	=118
Gluta rostrata	YL	28	0.13	=118
Phyllanthus emblica	FR	27	0.13	=118
Desmos dunalii	YL	27	0.13	=118
Calamus pogonacanthus	FR	27	0.13	=118
Tree July 2	FR	26	0.12	=125
Mezzettia havilandi	FR	26	0.12	=125
Psydrax sp.	YL	24	0.11	=127
Garcinia bancana	FR	24	0.11	=127
Shorea kunstleri	YL	23	0.11	=127
Psydrax sp.	FL	23	0.11	=127
Rubus elongatus	FL	22	0.10	=131
Ficus stupenda	LB	22	0.10	=131
Liana Jan 1	YL	21	0.10	=131
Willughbeia sp.	FR	21	0.10	=131
Tree May 1	FR	20	0.09	=135
Szygium lineatum	YL	18	0.09	=135
Dissochaeta sp.	FL	18	0.09	=135
Diospyros ferruginea	FR	18	0.09	=135
Vitis sp.	YL	17	0.08	=139
Hopea griffithii	YL	16	0.08	=139

Table V-1 (continued)

Species	Plant part	Total length of feeding time	Percentage of feeding time	Rank
Dissochaeta sp.	FR	16	0.08	=139
Canarium megalanthum	FL	16	0.08	=139
Artocarpus integer	FR	16	0.08	=139
Sterculiaceae	FR	15	0.07	=144
Payena leeri	FR	15	0.07	=144
Acacia borneensis	YL	15	0.07	=144
Xanthophyllum griffithii	LB	14	0.07	=144
Walsura sp.	YL	14	0.07	=144
Syzygium lineatum	FR	14	0.07	=144
Eugenia sp. A	FR	13	0.06	=150
Zizyphus angustifolius	FR	12	0.06	=150
Palaquium eriocalyx	FR	12	0.06	=150
Gonystylus afinis	FL	12	0.06	=150
Gonystylus borneensis	FL	11	0.05	=150
Erycibe sp.	FR	11	0.05	=150
Tristania grandiflora	FL	10	0.05	=150
Parishia maingayi	FR	10	0.05	=150
Knema latifolia	FR	10	0.05	=150
Gonystylus afinis	YL	10	0.05	=150
Ficus callosa	LB	10	0.05	=150
Crypteronia griffithii	FL	10	0.05	=150
Tree Jan 2	FR	9	0.04	=162
Polyalthia sumatrana	FR	9	0.04	=162
Pegia sarmentosa	YL	9	0.04	=162
Loranthus sp.	FL	8	0.04	=162
Gnetum gnemoides	FR	7	0.03	=166
Liana Apr 1	YL	6	0.03	=166
Shorea parvifolia	YL	5	0.02	=168
Shorea coriacea	FL	5	0.02	=168
Liana May 2	FR	5	0.02	=168
Vatica sumatrana	YL	4	0.02	=168
Desmos dunalii	FR	4	0.02	=168
Diospyros crinitus	YL	4	0.02	=168
Saurauia sp.	FL	3	0.01	=174
Rhus nodosa	LB	3	0.01	=174
Glochidion borneensis	YL	3	0.01	=174
Liana Feb 1	YL	2	0.009	=177
Vatica rassak	LB	1	0.005	=178
Glochidion borneensis	FL	1	0.005	=178

References

Abrams, J.T. 1968 Fundamental approach to the nutrition of the captive wild herbivore. *Symp. Zool. Soc. Lond.* **21**: 41-62.

Ahsan, F. 1994 *Behavioural Ecology of the Hoolock Gibbon* (Hylobates hoolock) *in Bangladesh.* Unpublished PhD thesis, University of Cambridge.

Ahsan, F. 1995 Fighting between two females for a male in the hoolock gibbon. *IJP* **16(5)**: 731-737.

Aldrich-Blake, F.P.G. 1968 A fertile hybrid between two *Cercopithecus* species in the Budongo Forest, Uganda. *Folia primatol.* **9**: 15-21.

Aldrich-Blake, F.P.G. 1970 Problems of social structure in forest monkeys. In J.H. Crook (ed), *Social Behaviour in Birds and Mammals,* 79-101. London: Academic Press.

Aldrich-Blake, F.P.G and Chivers, D.J. 1973 On the genesis of a group of siamang. *AJPA* **38**: 631-636.

Alfred, J.R.B. and Sati, J.P. 1990 Survey and census of the hoolock gibbon in West Garo Hills, Northeast India. *Primates* **31(2)**: 299-306.

Alfred, J.R.B. and Sati, J.P. 1991 On the first record of infanticide in the hoolock gibbon – *Hylobates hoolock* in the wild. *Rec. Zool. Surv. India.* **89(1-4)**: 319-321.

Allaby, M. 1991 *The Concise Oxford Dictionary of Zoology.* Oxford and New York: Oxford University Press.

Altmann, J. 1974 Observational study of behaviour: sampling methods. *Behaviour* **69**: 227-267.

Altmann, J. 1980 *Baboon Mothers and Infants.* Cambridge, Mass.: Harvard University Press.

Altmann, S.A. and Altmann, J. 1970 *Baboon Ecology: African Field Research.* Chicago: University of Chicago Press.

Anderson, E. and Hubricht, L. 1938 Hybridisation in *Tradescantia.* III. The evidence for introgressive hybridization. *Am. J. Botany* **25:** 396-402.

Andrews, P. and Groves, C.P. 1976 Gibbons and brachiation In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 4, 167-218. Basel: S. Karger.

Ashton, P.S. 1982 Dipterocarpaceae. *Flora Malesiana Ser. I.* **9**: 237-552.

Ashton, P.S. 1988 Systematics and ecology of rain-forest trees. *Taxon* **37**: 622-629.

Ave, J.B. and King, V.T. 1986 *Borneo: The People of the Weeping Forest; Tradition and Change in Borneo.* Leiden: National Museum of Ethnology.

Baker, S. and Bynum, E.S. 1989 Preliminary behavioral observations of captive Sulawesi macaques: *Macaca maurus* and *Macaca ochreata* x *brunnescens. AJP* **18(2)**: 133 (abstract).

Baker, S. and Estep, D. 1985 Kinship and affiliative behaviour patterns in a captive group of Celebes black apes (*Macaca nigra*). *J. Comp. Psychol.* **99(3)**: 356-360.

Baldwin, L.A. and Teleki, G. 1976 Patterns of gibbon behavior on Hall's Island, Bermuda: A preliminary ethogram for *Hylobates lar.* In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 4, 21-105. Basel: S. Karger.

Barlow, G. 1988 Monogamy in relation to resources. In C.N. Slobodchikoff (ed), *The Ecology of Social Behavior*, 55-79. San Diego: Academic Press.

Barnes, R.F.W. et al. 1983 The use of pasture by brown hares. *J. Appl. Ecol.* **20**: 179-185.

Bartlett, T.Q. and Brockelman, W.Y. 1996 Gradual replacement of a male pairmate in white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. *AJPA* **99** (Suppl 22): 66 (abstract).

Barton, N.H. and Hewitt, G.M. 1985 Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* **16**: 113-148.

Barton, N.H and Hewitt, G.M. 1989 Adaptation, speciation and hybrid zones. *Nature* **341**: 497-503.

Barton, R.A. and Whiten, A. 1994 Reducing complex diets to simple rules: food selection by olive baboons. *Behav Ecol Sociobiol* **35(4)**: 283-293.

Barton, R.A., Whiten, A., Strum, S.C., Byrne, R.W. and Simpson, A.J. 1992 Habitat use and resource availability in baboons. *Anim. Behav.* **43(5)**: 831-844.

Bellwood, P.S. 1985 *Prehistory of the Indo-Malaysian Archipelago.* London and Sydney: Academic Press.

Bennett, E.L. 1984 *The Banded Langur: Ecology of a Colobine in a West Malaysian Rain Forest.* Unpublished PhD thesis, University of Cambridge.

Bennett, E.L. 1986a *Proboscis Monkeys in Sarawak: Their Ecology, Status, Conservation and Management.* World Wildlife Fund Malaysia and New York Zoological Society.

Bennett, E.L. 1986b Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos. Folia primatol.* **47(1)**: 26-38.

Bennett, E.L. 1988 Proboscis monkeys and their swamp forests in Sarawak. *Oryx* **22(2)**: 69-74.

Bennett, E.L. and Sebastian, A.C. 1988 Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest of Sarawak. *IJP* **9(3)**: 233-255.

Berkson, G. and Chiacumpa, V. 1969 Breeding gibbons (*Hylobates lar entelloides*) in the laboratory. *Lab. Anim. Care* **19**: 808-811.

Bernstein, I.S. 1966 Naturally occurring primate hybrid. *Science* **154**: 1559-1560.

Bernstein, I.S. and Gordon, T.P. 1980 Mixed taxa introductions, hybrids and macaque systematics. In D.G. Lindburg (ed), *The Macaques: Studies in Ecology, Behavior and Evolution,* 125-147. New York: Van Nostrand Reinhold Co.

Bigelow, R.S. 1965 Hybrid zones and reproductive isolation. *Evolution* **19**: 449-458.

Bleisch, W.V. and Chen, N. 1991 Ecology and behavior of wild black-crested gibbons (*Hylobates concolor*) in China with a reconsideration of evidence for polygyny. *Primates* **32(4)**: 539-548.

Bodmer, R.E., Mather, R.J. and Chivers, D.J. 1991 Rain forests of central Borneo – threatened by modern development. *Oryx* **25(1)**: 21-26.

Boinski, S. 1988 Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behav Ecol Sociobiol* **23(3)**: 177-186.

Boggess, J.E. 1979 Troop male membership changes and infant killing in langurs (*Presbytis entellus*). *Folia primatol.* **32**: 65-107.

Booth, C.P. 1968 Taxonomic studies of *Cercopithecus mitis wolf* (East Africa). *National Geographic Society Research Reports* (1963): 37-51.

Bowmaker, J.K., Jacobs, G.H. and Mollon, J.D. 1987 Polymorphism of photopigments in the squirrel monkey: a sixth phenotype. *Proceed. R. Soc. Lond. B* **231**: 383-390.

Breznock, A.W., Harrold, J.B. and Kawakami, T.G. 1977 Successful breeding of the laboratory-housed gibbon (*Hylobates lar*). *Lab. Anim. Science* **27**: 222-228.

Bricknell, S.J. 1982 *The Behaviour in Captivity of Three Species of Gibbon:* Hylobates lar, Hylobates leucogenys *and* Hylobates syndactylus. Unpublished Honours Thesis, Australian National University.

Brockelman, W.Y. 1978 Preliminary report on relations between the gibbons *Hylobates lar* and *H. pileatus* in Thailand. In D.J. Chivers and K.A. Joysey (eds), *Recent Advances in Primatology* Vol 3: *Evolution*, 315-318. London: Academic Press.

Brockelman, W.Y. 1984 Social behaviour of gibbons: Introduction. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 285-290. Edinburgh: Edinburgh University Press.

Brockelman, W.Y. 1997 Extra males in gibbon groups. *Primate Report* (Special Issue) **48-2**: 14.

Brockelman, W.Y. and Gittins, S.P. 1984 Natural hybridisation in the *Hylobates lar* species group: implications for speciation in gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 498-532. Edinburgh: Edinburgh University Press.

Brockelman, W.Y. and Schilling, D. 1984 Inheritance of stereotyped gibbon calls. *Nature* **312:** 634-636.

Brockelman, W.Y. and Srikosamatara, S. 1984 Maintenance and evolution of social structure in gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 298-323. Edinburgh: Edinburgh University Press.

Brockelman, W.Y., Ross, B.A. and Pantuwatana, S. 1974 Social interactions of adult gibbons (*Hylobates lar*) in an experimental colony. In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 3, 137-156. Basel: S. Karger.

Brockelman, W.Y., Reichard, U., Treesucon, U. and Raemaekers, J.J. 1998 Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behav Ecol Sociobiol* **42(5)**: 329-339.

Brown, J.L. 1964 The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**: 160-169.

Brunig, E.F. 1971 On the ecological significance of drought in the equatorial wet evergreen (rain) forest of Sarawak (Borneo). *Erdkunde* **23:** 127-133.

Brunig, E.F. 1974 *Ecological Studies in the Kerangas Forests of Sarawak and Brunei.* Kuching: Borneo Literature Bureau.

Burt, W.H. 1943 Territoriality and home range concept as applied to mammals. *J. Mammol.* **24**: 346-352.

Bynum, E.L., Bynum, D.Z. and Supriatna, J. 1997 Confirmation and location of the hybrid zone between wild populations of *Macaca tonkeana* and *Macaca hecki* in Central Sulawesi, Indonesia. *AJP* **43(3)**: 181-209.

Caldecott, J.O. 1980 Habitat quality and populations of two sympatric gibbons (Hylobatidae) on a mountain in Malaya. *Folia primatol.* **33**: 291-309.

Caldecott, J.O. 1986 An ecological and behavioural study of the pig-tailed macaque. *Contrib. Primatol.* **21**: 1-259 Basel: S. Karger.

Caldecott, J.O and Haimoff, E. 1983 Female solo singing by a wild lar gibbon in Peninsular Malaysia. *Malay Nat. J.* **36(3)**: 167-173.

Camenzind, F.J. 1978 Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. In M. Bekoff (ed), *Coyotes: Biology, Behavior and Management*, 267-294. New York: Academic Press.

Carpenter, C.R. 1940 A field study in Siam of the behaviour and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monogr.* **16**: 1-212.

Carpenter, C.R. 1941 The menstrual cycle and body temperature in two gibbons (*Hylobates lar*). *Anat. Rec.* **7(3)**: 291-296.

Carpenter, C.R. 1942 Societies of monkeys and apes. *Biol. Symposia.* **8**: 177-204.

Caughley, G. 1977 *Analysis of vertebrate populations.* Chichester: Wiley.

Chapman, C. 1988 Patterns of foraging and range use by three species of neotropical primates. *Primates* **29(2)**: 177-194.

Charles-Dominique, P. 1993 Speciation and coevolution: an interpretation of frugivory phenomena. In T.H. Fleming and A. Estrada (eds), *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects,* 75-84. Belgium: Kluwer Academic Publishers.

Chiarelli, B. 1973 Check-list of catarrhina primate hybrids. *J. Hum. Evol.* **2**: 301-305.

Chivers, D.J. 1969 On the daily behaviour and spacing of howling monkey groups. *Folia primatol.* **10**: 48-102.

Chivers, D.J. 1974 The siamang in Malaya: a field study of a primate in tropical rain forest. *Contrib. Primatol.* **4**: 1-335 Basel: S. Karger.

Chivers, D.J. 1975 Daily patterns of ranging and feeding in siamang. In S. Kondo, M. Kawai and A. Ehara (eds), *Contemporary Primatology*, 362-372. Basel: S. Karger.

Chivers, D.J. 1976 Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour* **57**: 116-135.

Chivers, D.J. 1977a The lesser apes. In P. Rainier and G.H. Bourne (eds), *Primate Conservation,* 539-598. New York: Academic Press.

Chivers, D.J. 1977b The feeding behaviour of siamang (*Symphalangus syndactylus*). In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding Behaviour in Lemurs, Monkeys and Apes,* 335-338. London: Academic Press.

Chivers, D.J. 1984 Feeding and ranging in gibbons: a summary. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 267-281. Edinburgh: Edinburgh University Press.

Chivers, D.J and Gittins, S.P. 1978 Diagnostic features of the gibbon species. *Int. Zoo Yb.* **18**: 157-64.

Chivers, D.J. and Hladik, C.M. 1980 Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J. Morph.* **166**: 337-386.

Chivers, D.J. and Raemaekers, J.J. 1980 Long-term changes in behaviour. In D.J. Chivers (ed), *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest,* 209-260. New York: Plenum Press.

Chivers, D.J., Raemaekers, J.J. and Aldrich-Blake, F.P.G. 1975 Longterm observations of siamang behaviour. *Folia primatol.* **23**: 1-49.

Choudhury, A. 1990 Population dynamics of hoolock gibbons (*Hylobates hoolock*) in Assam, India. *AJP* **20(1)**: 37-41.

Choudhury, A. 1991 Ecology of the hoolock gibbon (*Hylobates hoolock*), a lesser ape in the tropical forests of north-east India. *J. Trop. Ecol.* **7(1)**: 147-153.

Ciani, A.C., Stanyon, R., Scheffrahn, W. and Sampurno, B. 1989 Evidence of gene flow between Sulawesi macaques. *AJP* **17**: 257-270.

Clarke, B.C. 1966 The evolution of morph-ratio clines. *Am. Nat.* **100**: 389-402.

Clutton-Brock, T.H. 1972 *Feeding and Ranging Behaviour of the Red Colobus*. Unpublished PhD thesis, University of Cambridge.

Clutton-Brock, T.H. 1975 Ranging behaviour of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Anim. Behav.* **23**: 706-722.

Clutton-Brock, T.H. 1977 Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 539-556. London: Academic Press.

Clutton-Brock, T.H. and Harvey, P.H. 1977 Primate ecology and social organisation. *J. Zool. Lond.* **183**: 1-39.

Clutton-Brock, T.H. and Harvey, P.H. 1979 Home range size, population density and phylogeny in primates. In I. Bernstein and E.O. Smith (eds), *Primate Ecology and Human Origins: Ecological Influences on Social Organisation*, 201-214. New York: Garland.

Clutton-Brock, T.H. and Parker, G.A. 1995 Sexual coercion in animal societies. *Anim. Behav.* **49**: 1345-1365.

Coe, M.J., Cumming, D.H. and Phillipson, J. 1976 Biomass and production of large herbivores in relation to rainfall and primary production. *Oecologia* **22**: 341-354.

Coolidge, H.J. 1984 Foreword. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, ix-x. Edinburgh: Edinburgh University Press.

Cowlishaw, G. 1992 Song function in gibbons. *Behaviour* **121**: 131-153.

Cowlishaw, G. 1996 Sexual selection and information content in gibbon song bouts. *Ethology* **102(4)**: 272-284.

Creel, N. and Preuschoft, H. 1976 Cranial morphology of the lesser apes: a multivariate statistical study. In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 4, 219-303. Basel: S. Karger.

Creel, N. and Preuschoft, H. 1984 Systematics of the lesser apes: A quantitative taxonomic analysis of craniometric and other variables. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 562-613. Edinburgh: Edinburgh University Press.

Cronin, J.E., Sarich, V.M. and Ryder, O. 1984 Molecular evolution and speciation in the lesser apes. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 467-485. Edinburgh: Edinburgh University Press.

Curtin, R.A. 1977 Langur social behavior and infant mortality. *Kroeber Anth. Soc. Pap.* **50**: 27-36.

Curtin, R.A. 1982 Range use of gray langurs in Highland Nepal. *Folia primatol.* **38(1-2)**: 1-18.

Curtin, R.A. and Dolhinow, P. 1978 Primate social behavior in a changing world. *Am. Sci.* **66**: 468-475.

Curtin, R.A. and Dolhinow, P. 1979 Infanticide among langurs - a solution to overcrowding? *Science Today* **13**: 35-41.

Dahl, J.F. and Nadler, R.D. 1989 The external genitalia of female gibbons. *AJP* **18**: 141-142.

Dahl, J.F. and Nadler, R.D. 1992 The external genitalia of female gibbons *Hylobates (H.) lar*. *Anat. Rec.* **232**: 572-578.

Dasilva, G.L. 1992 The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J. Anim. Ecol.* **61(1)**: 79-91.

Dao, V.T. 1983 On the North Indochinese gibbons (*Hylobates concolor*) (Primates, Hylobatidae) in North Vietnam. *J. Hum. Evol.* **12(4)**: 367-372.

Davies, A.G. 1984 *An Ecological Study of the Red Leaf Monkey (*Presbytis rubicunda*) in the Dipterocarp Forest of Northern Borneo.* Unpublished PhD thesis, University of Cambridge.

Davies, G. and Payne, J. 1982 *A Faunal Survey of Sabah.* Kuala Lumper: WWF Fund Malaysia.

Davies, A.G., Bennett, E.L. and Waterman, P.G. 1988 Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol. J. Linn. Soc.* **34(1)**: 33-56.

Delacour, J. 1933 On the Indochinese gibbons (*Hylobates concolor*). *J. Mammal.* **14**: 17-73.

De Moor, P.P. and Steffens, F.E. 1972 The movements of vervet monkeys (*Cercopithecus aethiops*) within the ranges as revealed by radio-tracking. *J. Anim. Ecol.* **41**: 677-687.

Deputte, B.L. 1982 Duetting in male and female songs of the white-cheeked gibbon (*Hylobates concolor leucogenys*). In C.T. Snowdon (ed), *Primate Communication*, 67-93. New York: Cambridge University Press.

De Valois, R.L. and Jacobs, G.H. 1968 Primate colour vision. *Science* **162**: 533-540.

Dixson, A.F. 1977 Observations on the displays, menstrual cycles, and sexual behaviour of the "black ape" of Celebes (*Macaca nigra*). *J. Zool.* **182**: 63-84.

Dobzhansky, T. 1970 *Genetics of the Evolutionary Process.* New York: Columbia University Press.

Dolhinow, P. 1978 A behavior repertoire for the Indian langur monkey (*Presbytis entellus*). *Primates* **19(3)**: 449-472.

Dowsett-Lemaire, F. 1988 Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Terre et la Vie* **43(3)**: 251-281.

Dunbar, R.I.M. 1983 Structure of gelada baboon reproductive units. IV. Integration at group level. *Z. Tierpsychol.* **63(4)**: 265-282.

Dunbar, R.I.M. 1988 *Primate Social Systems.* London and Sydney: Croom Helm.

Dunbar, R.I.M. and Dunbar, P. 1974a On hybridization between *Theropithecus gelada* and *Papio anubis* in the wild. *J. Hum. Evol.* **3**: 187-192.

Dunbar, R.I.M. and Dunbar, P. 1974b Ecology and population dynamics of *Colobus guereza* in Ethiopia. *Folia primatol.* **21**: 188-209.

Dunbar, R.I.M. and Dunbar, P. 1988 Maternal time budgets of gelada baboons. *Anim. Behav.* **36(4)**: 970-980.

Dunbar, R.I.M. and Sharman, M. 1983 Female competition for access to males affects birth rate in baboons. *Behav Ecol Sociobiol* **13(2)**: 157-159.

Ellefson, J.O. 1968 Territorial behaviour in the common white-handed gibbon, *Hylobates lar* Linn. In P.C. Jay (ed), *Primates: Studies in Adaptation and Variability*, 180-199. New York: Holt, Rinehart and Winston.

Ellefson, J.O. 1974 A natural history of white-handed gibbons in the Malayan peninsula. In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 3, 1-136. Basel: S. Karger.

Emlen, S.T. and Oring, L.W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215-223.

Endler, J.A. 1973 Gene flow and population differentiation. *Science* **179**: 243-250.

Endler, J.A. 1977 *Geographic Variation, Speciation, and Clines.* Princeton, New Jersey: Princeton University Press.

Erhart, E.M., Overdorff, D.J. and Bramblett, C.A. 1996 Behavioral development of male hybrid *Cercopithecus* monkeys. *AJPA* (Suppl 22): 102 (abstract).

Estrada, A. and Coates-Estrada, R. 1984 Fruit eating and seed dispersal by howling monkey (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *AJP* **6**: 77-91.

Estrada, A. and Coates-Estrada, R. 1986 Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In A. Estrada and T.H. Fleming (eds), *Frugivores and Seed Dispersal*, 93-104. Dordrecht: Dr W. Junk.

Fairbanks, L.A. and McGuire, M.T. 1984 Determinants of fecundity and reproductive success in captive vervet monkeys. *AJP* **7(1)**: 27-38.

Fischer, J.O. and Geissmann, T. 1990 Group harmony in gibbons: comparison between white-handed gibbon (*Hylobates lar*) and siamang (*H syndactylus*). *Primates* **31(4)**: 481-494.

Fooden, J. 1969 Color-phase in gibbons. *Evolution* **23**: 627-644.

Fossey, D. and Harcourt, A.H. 1977 Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding Behaviour in Lemurs, Monkeys and Apes*, 415-447. London: Academic Press.

Fox, G.J. 1984 The conservation of gibbons in American zoos. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 74-78. Edinburgh: Edinburgh University Press.

Frisch, J.E. 1965 Trends in the evolution of the hominoid dentition. *Bibl. Primat.* **3**: 1-130.

Froehlich, J.W. and Supriatna, J. 1996 Secondary intergradation between *Macaca maurus* and *M. tonkeana* in South Sulawesi, and the species status of *M. togeanus*. In J.E. Fa and D.G. Lindburg (eds), *Evolution and Ecology of Macaque Societies*, 43-70. Cambridge: Cambridge University Press.

Froehlich, J.W., Supriatna, J. and Froehlich, P.M. 1991 Morphometric analyses of *Ateles:* systematic and biogeographic implications. *AJP* **25(1)**: 1-22.

Galdikas, B. 1988 Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *IJP* **9(1)**: 1-35.

Ganzhorn, J.U. 1992 Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia* **91(4)**: 540-547.

Garber, P.A. 1984 Proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi*. *IJP* **5(1)**: 1-15.

Garber, P.A. 1993 Feeding ecology and behaviour of the genus *Saguinus*. In A.B. Rylands (ed), *Marmosets and Tamarins: Systematics, Behaviour and Ecology*, 273-295. Oxford: Oxford University Press.

Garza, J.C. and Woodruff, D.S. 1992 A phylogenetic study of the gibbons (*Hylobates*) using DNA obtained noninvasively from hair. *Molecular Phylogenetics and Evolution* **1(3)**: 202-210.

Gatinot, B.L. 1978 Characteristics of the diet of West African red colobus. In D.J. Chivers (ed), *Recent Advances in Primatology* Vol 1: *Behaviour*, 253-255. New York: Academic Press.

Gautier-Hion, A. 1980 Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.* **49**: 237-269.

Gautier-Hion, A., Gautier, J.P. and Quris, R. 1981 Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Terre et la Vie* **35**: 511-536.

Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. and Thiollay, J.M. 1985 Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65(3)**: 324-337.

Geissmann, T. 1984 Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pileatus* x *H. lar*). *Folia primatol.* **42(3-4)**: 216-235.

Geissmann, T. 1986 Mate change enhance duetting activity in the siamang gibbon (*Hylobates syndactylus*). *Behaviour* **96(1-2)**: 17-27.

Geissmann, T. 1991 Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.) *AJP* **23(1)**: 11-22.

Geissmann, T. 1993 *Evolution of Communication in Gibbons (Hylobatidae).* Inaugural-Dissertation, Universität Zürich.

Getty, T. 1987 Dear enemies and the prisoner's dilemma: why should territorial neighbours form defensive coalitions? *Amer. Zool.* **27**: 327-336.

Gittins, S.P. 1978a The species range of the gibbon *Hylobates agilis.* In D.J. Chivers and K.A. Joysey (eds), *Recent Advances in Primatology* Vol 3: *Evolution*, 319-321. London: Academic Press.

Gittins, S.P. 1978b Hark! The beautiful song of the gibbon. *New Scientist* **80**: 832-834.

Gittins, S.P. 1979 *The Behaviour and Ecology of the Agile Gibbon* (Hylobates agilis). Unpublished PhD thesis, University of Cambridge.

Gittins, S.P. 1980 Territorial behaviour in the agile gibbon. *IJP* **1**: 381-399.

Gittins, S.P. 1982 Feeding and ranging in the agile gibbon. *Folia primatol.* **38(1-2)**: 39-71.

Gittins, S.P. 1984a The vocal repertoire and song of the agile gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 354-375. Edinburgh: Edinburgh University Press.

Gittins, S.P. 1984b Territorial advertisement and defence of gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 420-424. Edinburgh: Edinburgh University Press.

Gittins, S.P. and Raemaekers, J.J. 1980 Siamang, lar and agile gibbons. In D.J. Chivers (ed), *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest*, 63-105. New York: Plenum Press.

Gittins, S.P. and Tilson, R.L. 1984 Notes on the ecology and behaviour of the hoolock gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 258-266. Edinburgh: Edinburgh University Press.

Glander, K.E. 1982 The impact of secondary compounds on primate feeding behavior. *Ybk. Phys. Anth.* **25**: 1-18.

Glaser, D. 1993 The effects of sweeteners in primates. In M. Mathlouthi, J.A. Kanters and G.G. Birch (eds), *Sweet-Taste Chemoreception*, 353-363. London: Elsevier.

Glaser, D. 1994 Distribution of thaumatin tasters. In M. Witty and J.D. Higginbotham (eds), *Thaumatin*, 183-191. Boca Raton: CRC Press.

Glaser, D., Hellekant, G., Brouwer, J.N. and van der Wel, H. 1978 The taste responses in primates to the proteins thaumatin and monellin and their phylogenetic implications. *Folia primatol.* **29**: 56-63.

Glaser, D., van der Wel, H., Brouwer, J.N., Du Bois, G.E. and Hellekant, G. 1992 Gustatory responses in primates to the sweetener aspartame and their phylogenetic implications. *Chem. Senses* **17(3)**: 325-335.

Glaser, D., Tinti, J.M. and Nofre, C. 1995 Evolution of the sweetness receptor in primates. I. Why does alitame taste sweet in all prosimians and simians, and aspartame only in old world simians? *Chem. Senses* **20(5)**: 573-584.

Goodman, M., Porter, C.A., Czelusniak, J., Page, S.L., Schneider, H., Shoshani, J., Gunnell, G. and Groves, C.P. 1998 Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Molecular Phylogenetics and Evolution* **9(3)**: 585-598.

Goosen, C. 1987 Social grooming in primates. In G. Mitchell and J. Erwin (eds), *Comparative Primate Biology* Vol 2 Part B: *Behavior, Cognition and Motivation*, 107-131. New York: Alan R. Liss.

Goustard, M. 1984 Patterns and functions of loud calls in the concolor gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 404-415. Edinburgh: Edinburgh University Press.

Grant, V. 1963 *The Origin of Adaptations.* New York: Columbia University Press.

Gray, A.P. 1971 *Mammalian Hybrids.* Commonwealth Agricultural Bureaux, Farnham Royal, Slough.

Greenaway, C. 1991 *A Study of the Behavioural Ecology of* Hylobates muelleri x Hylobates agilis *Hybrid Gibbons, 1991.* Project Barito Ulu Report.

Greig-Smith, P. 1964 *Quantitative Plant Ecology.* New York: Plenum Press.

Groves, C.P. 1967 Geographic variation in the hoolock or white-browed gibbon (*Hylobates hoolock* Harlan 1834). *Folia primatol.* **7**: 276-283.

Groves, C.P. 1971 Geographic and individual variation in Bornean gibbons, with remarks on the systematics of the subgenus *Hylobates. Folia primatol.* **14**: 139-153.

Groves, C.P. 1972 Systematics and phylogeny of gibbons. In D.M. Rumbaugh (ed), *Gibbon and Siamang* Vol 1, 1-89. Basel: S. Karger.

Groves, C.P. 1980 Speciation in *Macaca:* The view from Sulawesi. In D.G. Lindburg (ed), *The Macaques: Studies in Ecology, Behavior and Evolution*, 84-124. New York: Van Nostrand Reinhold Co.

Groves, C.P. 1984 A new look at the taxonomy and phylogeny of the gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 542-561. Edinburgh: Edinburgh University Press.

Groves, C.P. 1993 Speciation in living hominoid primates. In W.H. Kimbel and L.B. Martin (eds), *Speciation, Species Concepts, and Primate Evolution*, 109-121. New York: Plenum Press.

Groves, C.P. and Wang Y. 1990 The gibbons of the subgenus *Nomascus* (Primates, Mammalia). *Zool. Res.* **11(2)**: 147-154.

Hadidian, J. 1980 Yawning in the old world monkey, *Macaca nigra* (Primates: *Cercopithecidae). Behaviour* **75**: 133-147.

Haimoff, E.H. 1983 *Gibbon Songs: An Acoustical, Organisational, and Behavioural Analysis.* Unpublished PhD thesis, University of Cambridge.

Haimoff, E.H. 1984a Acoustic and organisational features of gibbons songs. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 333-353. Edinburgh: Edinburgh University Press.

Haimoff, E.H. 1984b The organisation of song in the agile gibbon (*Hylobates agilis*). *Folia primatol.* **42(1)**: 42-61.

Haimoff, E.H. 1984c The organisation of song in the Hainan black gibbon (*Hylobates concolor hainanus*). Primates **25(2)**: 225-235.

Haimoff, E.H. 1985 The organisation of song in Müller's gibbon (*Hylobates muelleri*). *IJP* **6(2)**: 173-192.

Haimoff, E.H. and Gittins, S.P. 1985 Individuality in the songs of wild gibbons (*Hylobates agilis*) of Peninsular Malaysia. *AJP* **8(3)**: 239-247.

Haimoff, E.H. and Tilson, R.L. 1985 Individuality in the female songs of wild Kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia primatol.* **44**: 129-137.

Haimoff, E.H., Gittins, S.P., Whitten, A.J. and Chivers, D.J. 1984 A phylogeny and classification of gibbons based on morphology and ethology. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 614-632. Edinburgh: Edinburgh University Press.

Haimoff, E.H., Yang, X-J, He, S-J and Chen, N. 1986 Census and survey of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Folia primatol.* **46(4)**: 205-214.

Haimoff, E.H., Yang, X-J, He, S-J and Chen, N. 1987 Preliminary observations of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Primates* **28(3)**: 319-335.

Hall, J.C. 1993 *Managing the Tropical Rain Forest: Swiddens, Housegardens and Trade in Central Kalimantan.* Unpublished PhD Thesis, Oxford Brookes University.

Hall, K.R.L 1966 Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. *J. Zool.* **148**: 15-87.

Hall, L.M., Jones, D. and Wood, B. 1996 Evolutionary relationships between gibbon subgenera inferred from DNA sequence data. *Biochemical Society Transactions* **24(3)**: 416S.

Halliday, R.B., Barton, N.H. and Hewitt, G.M. 1983 Electrophoretic analysis of a chromosomal hybrid zones in the grasshopper *Podisma pedestris. Biol. J. Linn. Soc.* **19**: 51-62.

Hanwell, A.S. and Peaker, M. 1977 Physiological effects of lactation on the mother. *Symp. Zool. Soc. Lond.* **41**: 297-311.

Harrison, M.J.S. 1983a Patterns of range use by the green monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. *Folia primatol.* **41(3-4)**: 157-179.

Harrison, M.J.S. 1983b Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. *Behav Ecol Sociobiol* **12(1)**: 85-94.

Harrison, M.J.S. 1984 Optimal foraging strategies in the diet of the green monkey, *Cercopithecus sabaeus*, at Mt. Assirik, Senegal. *IJP* **5(5):** 435-471.

Harrison, M.J.S. 1985 Time budget of the green monkey, *Cercopithecus sabaeus:* some optimal strategies. *IJP* **6(4)**: 351-376.

Harrison, R.G. 1990 Hybrid zones: windows on evolutionary process. *Oxford Surv. Evol. Biol.* **7**: 69-128.

Harrison, R.G. 1993 Hybrids and hybrid zones: historical perspective. In R.G. Harrison (ed), *Hybrid Zones and the Evolutionary Process*, 3-12. New York and Oxford: Oxford University Press.

Harrisson, T. 1984 *World Within: A Borneo Story* (2nd ed). Oxford: Oxford University Press.

Harrisson, T. and Harrisson, B. 1971 *The Prehistory of Sabah.* Kota Kinabalu: Sabah Society.

Harvey, P.H. and Clutton-Brock, T.H. 1981 Primate home-range size and metabolic needs. *Behav Ecol Sociobiol* **8**: 151-155.

Hayashi, S., Hayasaka, K., Takenaka, O. and Horai, S. 1995 Molecular phylogeny of gibbons inferred from mitochondrial DNA sequences: Preliminary report. *J. Mol. Evol.* **41(3)**: 359-365.

Hayes, V.J., Freedman, L. and Oxnard, C.E.. 1990 The taxonomy of savannah baboons: an odontomorphometric analysis. *AJP* **22(3)**: 171-190.

Heiduck, S. 1997 Food choice in masked Titi monkeys (*Callicebus personatus melanochir*): selectivity or opportunism? *IJP* **18(4)**: 487-502.

Henzi, S.P., Byrne, R.W. and Whiten, A. 1992 Patterns of movement by baboons in the Drakensburg Mountains: primary responses to the environment. *IJP* **13(6)**: 601-629.

Herrera, C.M. 1984 A study of avian frugivores, bird-dispersed plants, and their interaction in mediterranean scrublands. *Ecol. Monog.* **57**: 305-331.

Hewitt, G.M. 1979 *Animal Cytogenetics. III. Orthoptera.* Stuttgart: Gebruder Borntraeger.

Hewitt, G.M. 1985 The structure and maintenance of hybrid zones – with some lessons to be learned from alpine grasshoppers. In J. Gosalvez, C. Lopez-Fernandez, and C. Garcia de la Vega (eds), *Orthoptera I*, 15-54. Madrid: Fundacion Ramon Areces.

Hewitt, G.M. 1988 Hybrid zones – natural laboratories for evolutionary studies. *Trends Ecol. Evol.* **3**: 158-167.

Hewitt, G.M. 1989 The subdivision of species by hybrid zones. In D. Otte and J.A. Endler (eds), *Speciation and its Consequences*, 3-12. Massachusetts: Sinauer Assoc Ins.

Hewitt, G.M. 1993 After the ice: *Parallelus* meets *Erythropus* in the Pyrenees. In R.G. Harrison (ed), *Hybrid Zones and the Evolutionary Process*, 140-164. New York and Oxford: Oxford University Press.

Hewitt, G.M. and Barton, N.H. 1980 The structure and maintenance of hybrid zones as exemplified by *Podisma pedestris*. In R.L. Blackman, G.M. Hewitt, and M.A. Ashburner (eds), *Insect Cytogenetics*, 149-170. Symp. R. Entomol. Soc 10.

Hill, C.A. 1967 A note on the gestation period of the siamang. *Int. Zoo. Ybk.* **7**: 93-94.

Hinde, R.A. 1975 Interactions, relationships and social structure in non-human primates. In S.Kondo (ed), *Proceed. Symp. 5th Congr. Inter. Prim. Society*, 13-24. Tokyo: Japan Science Press.

Hladik, C.M. 1977 A comparative study of feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus.* In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 323-353. London: Academic Press.

Hladik, C.M. 1978 Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. In G.G. Montgomery (ed), *The Ecology of Arboreal Folivores*, 51-72. Washington DC: Smithsonian Institution.

Hoffman, C.L. 1986 *The Punan: Hunters and Gatherers of Borneo.* Studies in Cultural Anthropology, No. 12. Ann Arbor: UMI Research Press.

Hohmann, G. 1988 Analysis of loud calls provides new evidence for hybridisation between two Asian leaf-monkeys (*Presbytis johnii, Presbytis entellus*). *Folia primatol.* **51**: 209-213.

Hohmann, G. 1991 New evidence for hybridization in *Presbytis johnii* and *Presbytis entellus. J. Bombay Nat. Hist. Soc* **88(3)**: 315-319.

Herzog, M.O. and Hohmann, G.M. 1984 Male loud calls in *Macacca silenus* and *Presbytis johnii*. *Folia primatol.* **43(4)**: 189-197.

Hohmann, G., Herzog, M. and Wothe, K. 1986 The brown langurs of South India: Evidence of hybridization in feral *Presbytis johnii* and *P. entellus*. *Primate Report* **14**: 256 (abstract).

House, J. 1991 *Relationship of Soil Type to the Mosaic Pattern of Floristic Variation in Lowland Rain Forest in Central Kalimantan, Indonesia.* Unpublished Honours thesis, University of London.

Howe, H.F. and Estabrook, G.F. 1977 On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* **111**: 817-826.

Howe, H.F. and Smallgood, J. 1982 Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* **13**: 201-228.

Hrdy, S.B. 1974 Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia primatol.* **22**: 19-58.

Hrdy, S.B. 1977 *The Langurs of Abu: Female and Male Strategies of Reproduction.* Cambridge, Mass.: Harvard University Press.

Hrdy, S.B. 1979 Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *J. Ethol. Sociobiol.* **1**: 13-40.

Hu, Y., Hu, H-W and Yang, D-H. 1989 The studies on ecology in *Hylobates leucogenys. Zool. Res.* **10**(Suppl): 61-67.

Hubbs, C.L. 1955 Hybridisation between fish species in nature. *Syst. Zool.* **4**: 1-20.

Inger, R.F. 1966 The systematics and geography of the amphibians of Borneo. *Fieldiana Zool.* **52**: 1-402.

Isbell, L.A. 1983 Daily ranging behavior of red colobus (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. *Folia primatol.* **41(1-2)**: 34-48.

Islam, M.M. and Feeroz, M.A. 1992a *Ecology and Behaviour of Hoolock Gibbons of Bangladesh.* Dhaka, Bangladesh: MARC.

Islam. M.M. and Feeroz, M.A. 1992b Ecology of hoolock gibbon of Bangladesh. *Primates* **33(4)**: 451-464.

Itani, J. 1972 A preliminary essay on the relationships between social organization and incest avoidance in nonhuman primates. In F.E. Poirier (ed), *Primate Socialization*, 165-171. New York: Random House.

Itani, J. 1982 Intraspecific killing among non-human primates. *J. Soc. Biol. Struct.* **5**: 361-368.

Iwamoto, T. 1979 Feeding ecology. *Contrib. Primatol.* **16**: 279-330. Basel: S. Karger.

Iwamoto, T. and Dunbar, R. 1983 Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *J. Anim. Ecol.* **52(2)**: 357-366.

Jacob, J. 1974 Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**: 413-417.

Jacobs, G.H. 1996 Primate photopigments and primate color vision. *Proc. Natl. Acad. Sci. USA* **93(2)**: 577-581.

Jacobs, G.H., Neitz, J. and Neitz, M. 1993 Genetic basis of polymorphism in the color vision of platyrrhine monkeys. *Vision Res.* **33(3)**: 269-274.

Janson, C.H. 1983 Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* **219**: 187-189.

Janson, C.H., Stiles, E.W. and White, D.W. 1986 Selection of plant fruiting traits by brown capuchin monkeys: a multivariate approach. In A. Estrada and T.H. Fleming (eds), *Frugivores and Seed Dispersal*, 83-92. Dordrecht: W. Junk Publishers.

Janzen, D.H. 1980 When is it coevolution? *Evolution* **34**: 611-612.

Jay, P. 1963 The Indian langur monkey (*Presbytis entellus*). In C.H. Southwick (ed), *Primate Social Behaviour*, 114-123. Princeton, N.J.: D. Van Nostrand Company, Inc.

Jay, P. 1965 The common langur of North India. In I. DeVore (ed), *Primate Behavior: Field Studies in Monkeys and Apes*, 197-249. New York: Holt, Rinehart, and Winston.

Jolly, A. 1972 *The Evolution of Primate Behaviour.* New York: MacMillan.

Jolly, C.J. and Brett, F. 1973 Genetic markers and baboon biology. *J. Med. Primatol.* **2**: 85-99.

Jolly, C.J., Wolley-Barker, T., Beyene, S., Disotell, T.R. and Phillips-Conroy, J.E. 1997 Intergeneric hybrid baboons. *IJP* **18(4)**: 597-627.

Julliot, C. 1996a Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *AJP* **40(3)**: 261-282.

Julliot, C. 1996b Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *IJP* **17(2)**: 239-258.

Julliot, C. and Sabatier, D. 1993 Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *IJP* **14(4)**: 527-550.

Kappeler, M. 1984a Vocal bouts and territorial maintenance in the moloch gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 376-389. Edinburgh: Edinburgh University Press.

Kappeler, M. 1984b Diet and feeding behaviour of the moloch gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 228-241. Edinburgh: Edinburgh University Press.

Kar-Gupta, K. and Kumar, A. 1994 Leaf chemistry and food selection by common langurs (*Presbytis entellus*) in Rajaji National Park, Uttar Pradesh, India. *IJP* **15(1)**: 75-93.

Kartawinata, K. 1978 The "kerangas" heath forest in Indonesia. In J.S. Singh and B. Gopal (eds), *Glimpses of Ecology*, 145-152. Jaipur: International Scientific Publications.

Kartawinata, K. 1980 Note on a kerangas (heath) forest at Sebulu, East Kalimantan. *Reinwardtia* **9**: 429-447.

Kawai, M. and Sugawara, K. 1976 Hybridization and the evolution of primates. I. Social structure of a hybrid baboon group between *Papio anubis* and *Papio hamadryas*. *Shizen* **31**: 48-57.

Kawakami, T.G. and Kollias, G.V. 1984 Breeding and rearing lar gibbons in captivity. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 44-50. Edinburgh: Edinburgh University Press.

Kay and Davies, A.G. 1994 Digestive physiology. In A.G. Davies and J.F. Oates (eds) *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, 229-249. Cambridge: Cambridge University Press.

Key, K.H.L. 1968 The concept of stasipatric speciation. *Syst. Zool.* **17**: 14-22.

Key, K.H.L. 1981 Species, parapatry, and the morabine grasshoppers. *Syst. Zool.* **30**: 425-58.

Kinzey, W.G. 1987 Monogamous primates: a primate model for human mating systems. In W.G. Kinzey (ed), *The Evolution of Human Behaviour: Primate Models*, 105-114. Albany: State University Press.

Kinzey, W.G. and Gentry, A.H. 1979 Habitat utilization in two species of *Callicebus*. In R.W. Sussman (ed), *Primate Ecology: Problem-oriented Field Studies*, 89-100. New York: John Wiley.

Kinzey, W.G. and Norconk, M.A. 1990 Hardness as a basis of fruit choice in two sympatric primates. *AJPA* **81(1)**: 5-15.

Kleiman, D.G. 1977 Monogamy in mammals. *Quart. Rev. Biol.* **52**: 39-69.

Knight, R.S. and Siegfried, W.R. 1983 Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia* **56**: 405-412.

Kool, K.M. 1993 The diet and feeding behaviour of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *IJP* **14(5)**: 667-700.

Kottelat, M. 1982 A small collection of fresh-water fishes from Kalimantan, Borneo, with descriptions of one new genus and three new species of Cyprinidae. *Revue Suisse Zool.* **89**: 419-437.

Kummer, H. 1968 *Social Organisation of Hamadryas Baboons.* Chicago: University of Chicago Press.

Kummer, H. 1971 *Primate Societies: Group Techniques of Ecological Adaptation.* Chicago: Aldine-Atherton.

Kummer, H. and Kurt, F. 1963 Social units of a free living population of hamadryas baboons. *Folia primatol.* **1**: 4-19.

Kummer, H., Goetz, W. and Angst, W. 1970 Cross-species modifications of social behavior in baboons. In J.R. Napier and P.H. Napier (eds), *Old World Monkeys: Evolution, Systematics, and Behavior*, 226-231. New York: Academic Press.

Lack, D. 1946 Competition for food by birds of prey. *J. Anim. Ecol.* **15**: 123-129.

Lack, D. 1947 *Darwin's Finches.* London: Cambridge University Press.

Lan, D-Y. 1993 Feeding and vocal behaviours of black gibbons (*Hylobates concolor*) in Yunnan: a preliminary study. *Folia primatol.* **60(1-2)**: 94-105.

Langub, J. 1974 Adaptation to a settled life by the Punan and Penan of the Belaga sub-district. In J. Rosseau (ed), *The Peoples of Central Borneo*, 295-302. *Sarawak Mus. J. Special Issue* Vol 22.

Laws, J.W. and Vonder Haar Laws, J. 1984 Social interactions among adult male langurs (*Presbytis entellus*) at Rajaji Wildlife Sanctuary. *IJP* **5(1)**: 31-50.

Lee, P.C. 1983 Ecological influences on relationships and social structure. In R.A. Hinde (ed), *Primate Social Relationships: An Integrated Approach*, 225-229. Oxford: Blackwell Scientific Publications.

Lee, P.C. 1984 Ecological constraints on the social development of vervet monkeys. *Behaviour* **91(4)**: 245-262.

Leighton, D.R. 1987 Gibbons: territoriality and monogamy. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds), *Primate Societies*, 135-145. Chicago and London: University of Chicago Press.

Leighton, M. 1993 Modelling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *IJP* **14(2)**: 257-313.

Leighton, M. and Leighton, D.R. 1983 Vertebrate responses to fruiting seasonality within a Bornean rain forest. In S.L. Sutton, T.C. Whitmore and A.C. Chadwick (eds), *Tropical Rain Forest: Ecology and Management* Vol 2, 181-196. Oxford: Blackwell Scientific Publications.

Levey, D.J., Moermond, T.C. and Denslow, J.S. 1984 Fruit choice in neotropical birds: the effect of distance between fruits and preference patterns. *Ecology* **65**: 844-850.

Liu, Z-H, Zhang, Y-Z, Jiang, H-S and Southwick, C. 1989 Population structure of *Hylobates concolor* in Bawanglin Nature Reserve, Hainan, China. *AJP* **19(4)**: 247-254.

Lochowski, T. 1991 *Feeding and Ranging Behaviour in Gibbon Groups at Barito Ulu, 1991.* Project Barito Ulu Report.

MacKinnon, J.R. 1974 The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.* **22**: 3-74.

MacKinnon, J.R. 1978 *The Ape Within Us.* New York: Holt, Rinehart and Winston.

MacKinnon, J.R. and MacKinnon, K.S. 1978 Comparative feeding ecology of six sympatric primates in West Malaysia. In D.J. Chivers and J. Herbert (eds), *Recent Advances in Primatology* Vol 1: *Behaviour*, 305-321. London: Academic Press.

MacKinnon, J.R. and MacKinnon, K.S. 1980 Niche differentiation in a primate community. In D.J. Chivers (ed), *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest*, 167-190. New York: Plenum Press.

MacKinnon, J. and MacKinnon, K. 1986 *Review of the Protected Area System in the Indo-Malayan Realm.* Gland: IUCN.

MacKinnon, K., Hatta, G., Halim, H. and Mangalik, A. 1996 *The Ecology of Kalimantan* The Ecology of Indonesia Series: Vol III. Hong Kong: Periplus Editions Ltd.

McKey, D. 1975 The ecology of coevolved seed dispersal systems. In L.E. Gilbert and P.H. Raven (eds), *Coevolution of Animals and Plants*, 159-191. Austin and London: University of Texas Press.

McKey, D. and Waterman, P.G. 1982 Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Doula-Edea Reserve, Cameroon. *Folia primatol.* **39(3-4)**: 264-304.

McKey, D.B., Gartlan, J.S., Waterman, P.G. and Choo, G.M. 1981 Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* **16**: 115-146.

McConkey, K.R. 1999 *Gibbons as Seed Dispersers in the Rain-forests of Central Borneo.* Unpublished Ph.D. thesis, University of Cambridge.

Ma ,S and Wang, Y. 1986 The taxonomy and distribution of gibbons in southern China and its adjacent region – with a description of three new subspecies. *Zool. Res.* **7**: 393-409.

Ma, S., Wang Y-X and Poirier, F.E. 1988 Taxonomy, distribution and status of gibbons (*Hylobates*) in southern China and adjacent areas. *Primates* **29(2)**: 277-286.

Maples, E.G., Haraway, M.M. and Hulto, C.W. 1989 Development of coordinated singing in a newly formed siamang pair (*Hylobates syndactylus*). *Zool Biol* **8:** 367-368.

Maples, W.R. 1972 Systematic reconsideration and a revision of the nomenclature of Kenya baboons. *AJPA* **36**: 9-20.

Marler, P. and Tenaza, R. 1977 Signalling behaviour of apes with special reference to vocalization. In T.A. Sebeok (ed), *How Animals Communicate*, 965-1033. Bloomington and London: Indiana University Press.

Marks, D.L., Swain, T., Goldstein, S., Richard, A and Leighton, M. 1988 Chemical correlates of rhesus monkey food choice: the influence of hydrolyzable tannins and free amino acids. *J. Chem. Ecol.* **14(1)**: 213-235.

Marsh, C.W. 1981a Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana River, Kenya. *Folia primatol.* **35**: 147-178.

Marsh, C.W. 1981b Ranging behaviour and its relation to diet selection in Tana River red colobus (*Colobus badius rufomitratus*). *J. Zool. Lond.* **195**: 473-492.

Marshall, J.T. and Brockelman, W.Y. 1986 Pelage of hybrid gibbons (*Hylobates lar* x *H. pileatus*) observed in Khao Yai National Park, Thailand. *Nat. Hist. Bull. Siam Soc.* **34(2)**: 145-157.

Marshall, J.T. and Marshall, E. 1976 Gibbons and their territorial songs. *Science* **193**: 235-237.

Marshall, J. and Sugardjito, J. 1986 Gibbon systematics. In J. Erwin (ed), *Comparative Primate Biology* Vol 1: *Systematics, Evolution, and Anatomy*, 137-185. Alan R. Liss, Inc.

Marshall, J.T. Jr, Ross, B.A. and Chantharojvong, S. 1972 The species of gibbon in Thailand. *J. Mammol.* **53**: 479-486.

Marshall, J.T., Sugardjito, J. and Markaya, M. 1984 Gibbons of the lar group: relationship based on voice. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 533-541. Edinburgh: Edinburgh University Press.

Mather, R. 1992 *A Field Study of Hybrid Gibbons in Central Kalimantan, Indonesia.* Unpublished PhD thesis, University of Cambridge.

Matthews, L.H. 1946 Notes on the genital anatomy and physiology of the gibbon (*Hylobates*). *Proc. Zool. Soc. Lond.* **116**: 339-364.

Mayr, E. 1942 *Systematics and the Origin of Species.* New York: Columbia University Press.

Mayr, E. 1963 *Animal Species and Evolution.* Cambridge, Mass.: Belknap Press of Harvard U.P.

Mayr, E. 1970 Diverse approaches to systematics. *Evol. Biol.* **4**: 1-38.

Mayr, E. and Ashlock, P.D. 1991 *Principles of Systematic Zoology* (2nd ed). New York: McGraw-Hill, Inc.

Medway, Lord. 1972 The phenology of tropical rainforest in Malaya. *Biol. J. Linn. Soc.* **4**: 117-146.

Medway, Lord. 1977 *Mammals of Borneo* (2nd ed). Kuala Lumpur: Royal Asiatic Society, Malaysian Branch.

Milton, K. 1979 Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* **114**: 362-378.

Milton, K. 1980 *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics.* New York: Columbia University Press.

Milton, K and May, M.L. 1976 Body weight, diet and home range area in primates. *Nature* **259**: 459-462.

Mitani, J.C. 1984 The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behav Ecol Sociobiol* **15(3)**: 225-229.

Mitani, J.C. 1985a Gibbon song duets and intergroup spacing. *Behaviour* **92(1-2)**: 59-96.

Mitani, J.C. 1985b Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets. *IJP* **6(2)**: 193-200.

Mitani, J.C. 1987a Species discrimination of male song in gibbons. *AJP.* **13(4)**: 413-423.

Mitani, J.C. 1987b Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behav Ecol Sociobiol* **20(4)**: 265-269.

Mitani, J.C. 1988 Male gibbon (*Hylobates agilis*) singing behavior: natural history, song variations and function. *Ethology* **79(3)**: 177-194.

Mitani, J.C. 1989 Orangutan activity budgets: monthly variations and the effects of body size, parturition and sociality. *AJP* **18(2)**: 87-100.

Mitani, J.C. 1990 Demography of agile gibbons (*Hylobates agilis*). *IJP* **11(5)**: 411-424.

Mitani, J.C. and Marler, P. 1989 A phonological analysis of male gibbon singing behaviour. *Behaviour* **109(1-2)**: 20-45.

Mitani, J.C. and Rodman, P.S. 1979 Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol* **5**: 241-251.

Moermond, T.C. and Denslow, J.S. 1983 Fruit choice in neotropical birds: effect of fruit type and accessibility on selectivity. *J. Anim. Ecol.* **52**: 407-420.

Mohnot, S.M. 1971 Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae), in western India. *Mammalia* **35**: 175-198.

Mollon, J.D. 1989 "Tho she kneel'd in that place where they grew." The uses and origins of primate colour vision. *J. Exp. Biol.* **146**: 21-38.

Mollon, J.D., Bowmaker, J.K. and Jacobs, G.H. 1984 Variations in colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proc. R. Soc. Lond. B* **222**: 373-399.

Mootnick, A. 1984 Census of gibbons in North America. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 61-73. Edinburgh: Edinburgh University Press.

Mowry, C.B., Decker, B.S. and Shure, D.J. 1996 The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Procolobus badius rufomitratus*). *IJP* **17(1)**: 63-84.

Mturi, F.A. 1993 Ecology of the Zanzibar red colobus monkey, *Colobus badius kirkii* (Gray, 1968), in comparison with other red colobines. In J.C. Lovett (ed), *Biogeography and Ecology of the Rain Forests of East Africa*, 243-266. Cambridge: Cambridge University Press.

Müeller-Dombois, D. and Ellenberg. H. 1974 *Aims and Methods of Vegetation Ecology*. New York: Wiley and Sons.

Nagel, U. 1971 Social organisation in a baboon hybrid zone. In S. Kummer (ed), *Proceedings of the 3rd International Congress of Primatology* Vol 3: *Behavior*, 48-57. Basel: S. Karger.

Nagel, U. 1973 A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia primatol.* **19**: 104-165.

Napier, J.R. and Napier, P.H. 1967 *A Handbook of Living Primates*. London and New York: Academic Press.

Newton, P. 1992 Feeding and ranging patterns of forest Hanuman langurs. *IJP* **13**: 245-285.

Oates, J.F. 1977 The guereza and its food. In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 275-321. London: Academic Press.

Oates, J.F. 1988 The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. *IJP* **9(5)**: 457-478.

Oates, J.F., Waterman, P.G. and Choo, G.M. 1980 Food selection by the south Indian leaf monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* **45**: 45-56.

Oki, J. and Maeda, Y. 1973 Grooming as a regulator of behaviour in Japanese macaques. In C.R. Carpenter (ed), *Behavioral Regulators of Behavior in Primates*, 149-163. Lewisburg, Penn.: Bucknell University Press.

Osorio, D. and Vorolyev, M. 1996 Colour vision as an adaptation to frugivory in primates. *Proc. R. Soc. Lond.* B **263**: 593-599.

Packer, C. 1975 Male transfer in olive baboons. *Nature* **255**: 219-220.

Packer, C. 1979 Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* **27**: 1-36.

Palombit, R. 1992 *Pair Bonds and Monogamy in Wild Siamang* (Hylobates syndactylus) *and White-handed Gibbon* (Hylobates lar) *in Northern Sumatra*. Unpublished Ph.D thesis, University of California, Davis.

Palombit, R. 1994a Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. *Behaviour* **128(1-2)**: 65-101.

Palombit, R. 1994b Extra-pair copulations in a monogamous ape. *Anim. Behav.* **47(3)**: 721-723.

Palombit, R. 1995 Longitudinal patterns of reproduction in wild female siamang (*Hylobates syndactylus*) and white-handed gibbons (*Hylobates lar*). *IJP* **16(5)**: 739-760.

Palombit, R. 1996 Pair bonds in monogamous apes: A comparison of the siamang *Hylobates syndactylus* and the white-handed gibbon *Hylobates lar*. *Behaviour* **133**: 321-356.

Palombit, R. 1997 Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia primatol.* **68(6)**: 321-337.

Parathasarathy, M.D. and Rahaman, H. 1974 Infant-killing and dominance assertion among the Hanuman langur. *Abstr. 5th Congr. Int. Primatol. Soc.*, August 21-24, 1974 at Nagoya, Japan. p 34.

Paterson, H.E.H. 1985 The recognition concept of species. In S. Vrba (ed), *Species and Speciation*, 21-29. Transvaal Museum Monograph No 4, Transvaal, Pretoria.

Patton, J.L. 1993 Hybridisation and hybrid zones in pocket gophers (Rodentia, Geomyidae). In R.G. Harrison (ed), *Hybrid Zones and the Evolutionary Process*, 290-308. New York and Oxford: Oxford University Press.

Payne, J. 1980 Competitors. In D.J. Chivers (ed), *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest*, 261-277. New York: Plenum Press.

Payne, J. 1988 *Orangutan Conservation in Sabah.* WWF International Project No. 3759.

Payne, J., Francis, C.M. and Phillipps, K. 1985 *A Field Guide to the Mammals of Borneo.* Kota Kinabalu: The Sabah Society and WWF Malaysia.

Peace, W.J.H. and MacDonald, F.D. 1981 An investigation of the leaf anatomy, foliar mineral levels, and water relations of trees of a Sarawak forest. *Biotropica* **13**: 100-109.

Petit, O. and Thierry, B. 1992 Affiliative function of the silent bared-teeth display in Moor macaques (*Macaca maurus*): further evidence for the particular status of Sulawesi macaques. *IJP* **13(1)**: 97-105.

Petit, O. and Thierry, B. 1994a Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Anim. Behav.* **48(6)**: 1427-1436.

Petit, O. and Thierry, B. 1994b Reconciliation in a group of crested macaques. *The Dodo, J. Wildlife Pres. Trust* **30**: 89-95.

Phillips-Conroy, J. and Jolly, C.J. 1981 Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. *AJPA* **56**: 115-129.

Phillips-Conroy, J.E. and Jolly, C.J. 1986 Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. *AJPA* **71(3)**: 337-350.

Phillips-Conroy, J.E., Jolly, C.J. and Brett, F.L. 1991 Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. *AJPA* **86(3)**: 353-368.

Phillips-Conroy, J.E., Jolly, C.J., Nystrom, P. and Hemmalin, H.A. 1992 Migration of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. *IJP* **13(4)**: 455-476.

Polyak, S. 1957 *The Vertebrate Visual System.* Chicago: Chicago University Press.

Portman, O.W. 1970 Nutritional requirements (NRC) of nonhuman primates. In R.S. Harris (ed), *Feeding and Nutrition of Nonhuman Primates*, 87-115. New York: Academic Press.

Post, D., Hausfater, G. and McCuskey, S.A. 1980 Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia primatol.* **34**: 170-195.

Prance, G.T. 1982 *Biological Diversification in the Tropics.* New York: Columbia University Press.

Proctor, J., Anderson, J.M., Fogden, S.C.L. and Vallack, H.W. 1983 Ecological studies in four contrasting rain forests in Gunung Mulu National Park, Sarawak. I. Forest Environment. *J. Ecol.* **71**: 237-260.

Prouty, L.A., Buchanan, P.D., Pollitzer, W.S. and Mootnick, A.R. 1983 Bunopithecus: a genus-level taxon for the hoolock gibbon (*Hylobates hoolock*). *AJP* **5(1)**: 83-87.

Raemaekers, J.J. 1977 *Gibbons and Trees: Ecology of the Siamang and Lar Gibbons.* Unpublished PhD thesis, University of Cambridge.

Raemaekers, J. 1978a Changes through the day in the food choice of wild gibbons. *Folia primatol.* **30**: 194-205.

Raemaekers, J.J. 1978b Sharing of food resources between two gibbon species in the wild. *Malay. Nat. J.* **31(3)**: 181-188.

Raemaekers, J. 1979 Ecology of sympatric gibbons. *Folia primatol.* **31**: 227-245.

Raemaekers, J. 1980 Causes of variation between months in the distance travelled daily by gibbons. *Folia primatol.* **34**: 46-60.

Raemaekers, J. 1984 Large versus small gibbons: relative roles of bioenergetics and competition in their ecological segregation in sympatry. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 209-218. Edinburgh: Edinburgh University Press.

Raemaekers, J.J., Raemaekers, P.M. and Haimoff, E.H. 1984 Loud calls of the gibbon (*Hylobates lar*): repertoire, organisation and context. *Behaviour* **91(3)**: 146-189.

Raemaekers, J.J. and Raemaekers, P.M. 1985 Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. *Anim. Behav.* **33(3)**: 481-493.

Ralls, K. 1977 Sexual dimorphism in mammals: avian models and unwarranted unanswered questions. *Am. Nat.* **111**: 917-938.

Rasmussen, D.R. 1979 Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). I. Sleeping sites, impregnable females, births, and male emigrations and immigrations. *Anim. Behav.* **27**: 1098-1112.

Reichard, U. 1995 Extra-pair copulation in a monogamous gibbon (*Hylobates lar*). *Ethology* **100(2)**: 99-112.

Reichard, U. and Sommer, V. 1997 Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation, and the concept of infanticide. *Behaviour* **134(15-16)**: 1135-1174.

Rhine, R.J., Forthman, D.L., Stillwell-Barnes, R., Westlund, B.J. and Westlund, H.D. 1979 Movement patterns of yellow baboons (*Papio cynocephalus*): The location of subadult males. *Folia primatol.* **32**: 241-251.

Rijksen, H.D. 1978 *A Field Study on Sumatran Orangutans* (Pongo pygmaeus abelii *Lesson 1827): Ecology, Behaviour and Conservation.* Wageningen, Netherlands: H. Veenman and Zonen BV.

Rijksen, H.D. 1981 Infant killing, a possible consequence of a dispute leader role. *Behaviour* **78**: 138-167.

Ripley, S. 1967 Intertroop encounters among Ceylon gray langurs (*Presbytis entellus*). In S.A. Altmann (ed), *Social Communication Among Primates*, 237-253. Chicago: Chicago University Press.

Ripley, S. 1980 Infanticide in langurs and man: Adaptive advantage or social pathology? In M.N. Cohen, R.S. Malpass and H.G. Klein (eds), *Biosocial Mechanisms of Population Regulation*, 349-390. New Haven and London: Yale University Press.

Rodman, P. 1977 Feeding behaviour of orangutans of the Kutai Nature Reserve, East Kalimantan. In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 383-413. London: Academic Press.

Rogers, M.E., Maisels, F., Williamson, E.A., Fernandez, M. and Tutin, C.E.G. 1990 Gorilla diet in the Lope Reserve, Gabon: a nutritional analysis. *Oecologia* **84(3)**: 326-339.

Rosenzweig, M.L. 1968 Net primary productivity of terrestrial communities: prediction from climatological data. *Am. Nat.* **102**: 67-74.

Rowell, T.E. 1972 Female reproduction cycles and social behavior in primates. *Adv. Study. Behav.* **4**: 69-104.

Rudran, R. 1973 Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia primatol.* **19**: 166-192.

Rudran, R. 1978 Socioecology of the blue monkeys (*Cercopithecus mitis Stuhlmanni*) of the Kibale Forest, Uganda. *Smith. Contr. Zool.* **249**: 1-88.

Samuels, A. and Altmann, J. 1986 Immigration of a *Papio anubis* male into a group of *Papio cynocephalus* baboons and evidence for an *anubis-cynocephalus* hybrid zone in Amboseli, Kenya. *IJP* **7(2)**: 131-138.

Schilling, D. 1984a Gibbons in European zoos, with notes on the identification of subspecies of concolor gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 51-60. Edinburgh: Edinburgh University Press.

Schilling, D. 1984b Song bouts and duetting in the concolor gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 390-403. Edinburgh: Edinburgh University Press.

Schultz, A.H. 1933 Observations on the growth, classification and evolutionary specialisations of gibbons and siamangs. *Human Biology* **5:** 212-255, 385-428.

Sellato, B. 1989 *Hornbill and Dragon.* Elf Aquitaine Indonesie-Elf Aquitaine Malaysia.

Seth, P.K. and Seth, S. 1986 Ecology and behaviour of rhesus monkeys in India. In J.G. Else and P. Lee (eds), *Primate Ecology and Conservation*, 89-103. Cambridge: Cambridge University Press.

Sheeran, L.K. 1993 *A Preliminary Study of the Behavior and Socio-Ecology of Black Gibbons (*Hylobates concolor*) in Yunnan Province, People's Republic of China.* Unpublished PhD thesis, The Ohio State University.

Short, L.L. 1969 Taxonomic aspects of avian hybridisation. *Auk* **86**: 84-105.

Shotake, T. 1981 Population genetical study of natural hybridization between *Papio anubis* and *Papio hamadryas. Primates* **22**: 285-308.

Shotake, T., Nozawa, K. and Tanabe, Y. 1977 Blood protein variation in baboons: Gene exchange and genetic differentiation between *Papio anubis, Papio hamadryas* and their hybrids. *Jpn. J. Genet.* **52**: 223-237.

Sigg, H., Stolba, A., Abegglen, J.D. and Dasser, V. 1982 Life history of hybrid baboons: Physical development, infant mortality, reproductive parameters, and family relationships. *Primates* **23(4)**: 473-487.

Skutch, A.F. 1980 Arils as food of tropical American birds. *Condor* **82**: 31-42.

Slatkin, M. 1973 Gene flow and selection in a cline. *Genetics* **75**: 733-756.

Smith, M.F. and Patton, J.L. 1984 Dynamics of morphological differentiation: temporal impact of gene flow in pocket gopher populations. *Evolution* **38**: 1079-1087.

Smith, M.F. et al. 1983 *Thomomys bottae* gophers of the central Rio Grande Valley in New Mexico: local differentiation, gene flow and historical biogeography. *Occ. Pap. Mus. Southwest. Biol.* **2**: 1-16.

Smuts, B.B. and Smuts, R.W. Male aggression and social coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Adv. Study. Behav.* **22**: 1-63.

Smythies, B.E. 1981 *The Birds of Borneo* (2nd ed). Kuala Lumpur: The Sabah Society and the Malayan Nature Society.

Snodderly, D.M. 1979 Visual discriminations encountered in food foraging by a neotropical primate: implications for the evolution of color vision. In E.H. Burtt Jr (ed), *The Behavioral Significance of Color*, 239-279. New York: Garland STPM Press.

Snow, D.W. 1971 Evolutionary aspects of fruit eating by birds. *Ibis* **113**: 194-202.

Sommer, V. 1987 Infanticide among free-ranging langurs (*Presbytis entellus*) at Jodhpur (Rajasthan/India): Recent observations and a reconsideration of hypotheses. *Primates* **28(2)**: 163-197.

Sommer, V. and Reichard, U. 1998 Rethinking monogamy: the gibbon case (in prep).

Sourd, C. and Gautier-Hion, A. 1986 Fruit selection by a forest guenon. *J. Anim. Ecol.* **55(1)**: 235-244.

Southwick, C.H. and Southwick, K.L. 1983 Polyspecific groups of macaques on the Kowloon Peninsula, New Territories, Hong Kong. *AJP* **5(1)**: 17-24.

Southwick, C.H., Beg, M.A. and Siddiqi, M.R. 1965 Rhesus monkeys in north India. In I. DeVore (ed), *Primate Behavior: Field Studies in Monkeys and Apes*, 111-159. New York: Holt, Rinehart and Winston.

Southwick, C.H., Siddiqi, M.F., Farooqui, M.Y. and Pal, B.C. 1974 Xenophobia among free-ranging rhesus groups. In R. Holloway (ed), *Primate Aggression, Territoriality, and Xenophobia*, 185-209. New York: Academic Press.

Srikosamatara, S. 1980 *Ecology and Behaviour of the Pileated Gibbon* (Hylobates pileatus) *in Khao Soi Dao Wildlife Sanctuary, Thailand.* Unpublished M.Sc thesis, Mahidol University.

Srikosamatara, S. 1984 Ecology of pileated gibbons in south-east Thailand. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 242-257. Edinburgh: Edinburgh University Press.

Srikosamatara, S. and Brockelman, W.Y. 1983 Patterns of territorial vocalisation in the pileated gibbon (*Hylobates pileatus*). In P.K. Seth (ed), *Perspectives in Primate Biology*, 19-22. New Delhi: Today and Tomorrow's Printers and Publishing.

Srikosamatara, S. and Brockelman, W.Y. 1987 Polygyny in a group of pileated gibbons via a familial route. *IJP* **8(4)**: 389-393.

Stanford, C.B. 1991 The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. *Contrib. Primatol.* **26**: 1-179 Basel: S. Karger.

Stebbins, G.L. 1950 *Variation and Evolution in Plants.* New York: Columbia University Press.

Stebbins, G.L. 1959 The role of hybridisation in evolution. *Proc. Am. Philos. Soc.* **103**: 231-251.

Steubing, R.B. 1991 A checklist of the snakes of Borneo. *Raffles Bull. Zool.* **39:** 323-362.

Stiles, E.W. 1980 Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *Am. Nat.* **116**: 670-688.

Struhsaker, T.T. 1967 Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli game reserve, Kenya. *Ecology* **48**: 891-904.

Struhsaker, T.T. 1970 Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys. In J.R. Napier and P.H. Napier (eds), *Old World Monkeys: Evolution, Systematics, and Behavior*, 365-444. New York: Academic Press.

Struhsaker, T.T. 1974 Correlates of ranging behavior in a group of red colobus monkeys (*Colobus badius tephrosceles*). *Amer. Zool.* **14**: 177-184.

Struhsaker, T.T. 1975 The Red Colobus Monkey. Chicago: The University of Chicago Press.

Struhsaker, T.T., Butynski, T.M. and Lwanga, J.S. 1988 Hybridization between redtail (*Cercopithecus ascanius schmidti*) and blue (*C. mitis. stuhlmanni*) monkeys in the Kibale Forest, Uganda. In A. Gautier-Hion, F. Bourliere and J-P Gautier (eds), *A Primate Radiation: Evolutionary Biology of the African Guenons*, 477-497. Cambridge: Cambridge University Press.

Sugardjito, J. 1988 Preliminary field observation on agile gibbon (*Hylobates agilis*) of Tanjung Puting National Park, Central Kalimantan. *Rimba Indonesia* **22(1-2)**: 75-82.

Sugardjito, J., te Boekhorst, I.J.A., and van Hooff, J.A.R.A.M. 1987 Ecological constraints on the grouping of wild orang-utans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *IJP* **8(1)**: 17-41.

Sugawara, K. 1979 Sociological study of a wild group of hybrid baboons between *Papio anubis* and *Papio hamadryas* in the Awash Valley, Ethiopia. *Primates* **20**: 21-56.

Sugawara, K. 1982 Sociological comparison between two wild groups of anubis-hamadryas hybrid baboons. *African Study Monogr.* **2**: 73-131.

Sugawara, K. 1988 Ethological study of the social behavior of hybrid baboons between *Papio anubis* and *P. hamadryas* in free-ranging groups. *Primates* **29(4)**: 429-448.

Sugiyama, Y. 1965a Behavioral development and social structure in two troops of Hanuman langurs (*Presbytis entellus*). *Primates* **6**: 213-247.

Sugiyama, Y. 1965b On the social change in Hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates* **6**: 381-418.

Sugiyama, Y. 1966 An artificial social change in a hanuman langur troop (*Presbytis entellus*). *Primates* **7**: 41-72.

Sugiyama, Y. 1984a Some aspects of infanticide and intermale competition among langurs, *Presbytis entellus*, at Dharwar, India. *Primates* **25**: 423-432.

Sugiyama, Y. 1984b Proximate factors of infanticide among langurs at Dharwar: a reply to Boggess. In G. Hausfater and S.B. Hrdy (eds), *Infanticide: Comparative and Evolutionary Perspectives*, 311-314. New York: Aldine.

Supriatna, J. 1991 *Hybridization Between* Macaca maurus *and* Macaca tonkeana*: A Test of Species Status Using Behavioural and Morphogenetic Analyses*. Unpublished PhD thesis, University of New Mexico.

Supriatna, J., Manullang, B.O. and Soekara, E. 1986 Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan. *Primates* **27(2)**: 185-190.

Supriatna, J., Froehlich, J.W., Costin, C. and Erwin, J. 1990 Secondary intergradation between *Macaca maurus* and *Macaca tonkeana* in Sulawesi Selatan. *AJP* **20(3)**: 236.

Suwanvecho, U. and Brockelman, W.Y. 1997 Status and roles of subadult males in gibbon groups. *Primate Report* (Sp. Iss. **48-2**): 38-39.

Suwanvecho, U. and Brockelman, W.Y. 1998 Status and roles of subadults in gibbon groups. *Abstracts from the 17th Congr. Inter. Prim. Society.* August 10-14 1998. Antananarivo, Madagascar.

Suzuki, A. 1979 The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. In I. Bernstein and E.O. Smith (eds), *Primate Ecology and Human Origins: Ecological Influences on Social Organization*, 153-173. New York: Garland.

Szalay, F.S. and Delson, E. 1979 *Evolutionary History of the Primates.* New York: Academic Press.

Takasaki, H. 1981 Troop size, habitat quality, and home range area in Japanese macaques. *Behav Ecol Sociobiol* **9**: 277-281.

Templeton, A.R. 1989 The meaning of species and speciation: A genetic perspective. In D. Otte and J.A. Endler (eds), *Speciation and its Consequences*, 3-27. Massachusetts: Sinauer Assoc Ins.

Tenaza, R.R. 1975 Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Folia primatol.* **15**: 201-211.

Tenaza, R.R. 1976 Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Z. Tierpsychol.* **40**: 37-52.

Tenaza, R.R. 1985 Songs of hybrid gibbons (*Hylobates lar* x *H. muelleri*). *AJP* **8(3)**: 249-253.

Terborgh, J. 1983 *Five New World Primates.* Princeton, NJ: Princeton University Press.

Thierry, B. 1984 Clasping behaviour in *Macaca tonkeana. Behaviour* **89(1-2)**: 1-28.

Thierry, B. 1985 Patterns of agonistic interaction in three species of macaque (*M. mulatta, M. fascicularis, M. tonkeana*). *Aggressive Behaviour* **11(3)**: 223-233.

Thierry, B. 1986 Affiliative interference in mounts in a group of Tonkean macaques (*Macaca tonkeana*). *AJP* **11(1)**: 89-97.

Tilson, R.L. 1979 On the behaviour of hoolock gibbons (*Hylobates hoolock*) during different seasons in Assam, India. *J. Bombay Nat. Hist. Soc.* **76:** 1-16.

Tilson, R.L. 1981 Family formation strategies of Kloss's gibbons. *Folia primatol.* **35:** 259-287.

Ungar, P.S. 1995 Fruit preferences of four sympatric primate species at Ketambe, North Sumatra, Indonesia. *IJP* **16(2)**: 221-245.

van der Pilj, L. 1972 *Principles of Dispersal in Higher Plants.* Berlin: Springer-Verlag.

van Schaik, C.P. and Dunbar, R.I.M. 1990 The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* **115(1-2)**: 30-62.

van Schaik, C.P. and Mirmanto, E. 1985 Spatial variation in the structure and litterfall of Sumatran rain forest. *Biotropica* **17**: 196-205.

van Tuinen, P. and Ledbetter, D.H. 1983 Cytogenetic comparison and phylogeny of three species of Hylobatidae. *AJPA* **61(4)**: 453-466.

Vehrencamp, S.L. 1983 A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**: 667-82.

Walters, J.R. 1987 Transition to adulthood. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds), *Primate Societies*, 358-369. Chicago: University of Chicago Press.

Walters, J.R. and Seyfarth, R.M. 1987 Conflict and cooperation. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker (eds), *Primate Societies*, 306-317. Chicago: University of Chicago Press.

Waser, P. 1977 Feeding, ranging, and group size in the mangabey *Cercocebus albigena.* In T.H. Clutton-Brock (ed), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes*, 183-222. London: Academic Press.

Waser, P.M. and Waser, M.S. 1977 Experimental studies of primate vocalization: specializations for long-distance propagation. *Z. Tierpsychol.* **43**: 239-263.

Watanabe, K. and Brotoisworo, E. 1982 Field observation of Sulawesi macaques. *Kyoto University Overseas Research Report on Studies on Asian Non-Human Primates.* **2**: 3-9.

Watanabe, K. and Matsumura, S. 1991 The borderlands and possible hybrids between three species of macaques (*M. nigra, M. nigrescens* and *M. hecki*) in the northern peninsula of Sulawesi. *Primates* **32**: 365-369.

Watanabe, K., Lapasere, H. and Tantu, R. 1991a External characteristics and associated developmental changes in two species of Sulawesi macaques, *Macaca tonkeana* and *Macaca hecki*, with special reference to hybrids and the borderland between the species. *Primates* **32**: 61-76.

Watanabe, K., Matsumura, S., Watanabe, T. and Hamada, Y. 1991b Distribution and possible intergradation between *Macaca tonkeana* and *M. ochreata* at the borderland of the species in Sulawesi. *Primates* **32**: 369-385.

Waterman, P.G. 1984 Food acquisition and processing by primates as a function of plant chemistry. In D.J. Chivers, B.A. Wood and A. Bilsborough (eds), *Food Acquisition and Processing in Primates*, 177-211. Oxford: Blackwell Scientific Publications.

Waterman, P.G. and Choo, G.M. 1981 The effects of digestibility reducing compounds in leaves on food selection by some Colobinae. *Malaysian Appl. Biol.* **10**: 147-162.

Waterman, P.G., Ross, J.A., Bennett, E.L. and Davies, A.G. 1988 Comparison of floristics and leaf chemistry in two Malaysian rain-forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biol. J. Linn. Soc.* **34**: 1-32

West, K. 1981 *The Behavior and Ecology of the Siamang in Sumatra.* Unpublished M.A. Thesis, University of California, Davis.

Wheelwright, N.T. and Janson, C.J. 1985 Colors of fruit displays of birds dispersed plants in two tropical forests. *Am. Nat.* **126**: 777-799.

Wheelwright, N.T. and Orians, G.H. 1982 Seed dispersal by animals: Contrast with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* **119**: 402-413.

Whitmore, T.C. 1984 *Tropical Rain Forests of the Far East* (2nd ed). Oxford: Clarendon Press.

Whitten, A.J. 1980 *The Kloss Gibbon in Siberut Rain Forest.* Unpublished PhD thesis, University of Cambridge.

Whitten, A.J. 1982a Diet and feeding behaviour of Kloss gibbons on Siberut Island, Indonesia. *Folia primatol.* **37**: 177-208.

Whitten, A.J. 1982b The ecology of singing in Kloss gibbons on Siberut Island, Indonesia. *IJP* **3(1)**: 33-51.

Whitten, A.J. 1982c Home range use by Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Anim. Behav.* **30**: 182-198.

Whitten, A.J. 1982d Numerical analysis of tropical rain forest, using floristic and structural data, and its application to an analysis of gibbon ranging behaviour. *J. Ecol.* **70**: 249-271.

Whitten, A.J. 1984a The trilling handicap in Kloss gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 416-419. Edinburgh: Edinburgh University Press.

Whitten, A.J. 1984b Ecological comparisons between Kloss gibbons and other small gibbons. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman, and N. Creel (eds), *The Lesser Apes: Evolutionary and Behavioural Biology*, 219-227. Edinburgh: Edinburgh University Press.

Whitten, P.L. 1983 Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *AJP* **5(2)**: 139-159.

Wickler, W. 1980 Vocal duetting and the pair bond. I. Coyness and partner commitment. A hypothesis. *Z. Tierpsychol.* **52**: 201-219.

Wilkinson, R., Dutson, G., Sheldon, B., and Darjono, Y. R. N. 1991 *A Systematic List of Avifauna of the Barito Ulu Region.* PBU Report.

Wilson, E.O. and Bossert, W.H. 1971 *A Primer of Population Biology.* Stamford, Conn: Sinauer Associates, Inc.

Wilson, M.F. and Whelan, C.J. 1990 The evolution of fruit color in fleshy-fruited plants. *Am. Nat.* **136**: 790-809.

Wolfheim, J.H. 1983 *Primates of the World: Distribution, Abundance, and Conservation*. Seattle: University of Washington Press.

Woodruff, D.S. 1973 Natural hybridization and hybrid zones. *Syst. Zool.* **22**: 213-218.

Wrangham, R.W. 1981 Drinking competition in vervet monkeys. *Anim. Behav.* **29**: 904-910.

Wrangham, R.W. and Waterman, P.G. 1981 Feeding behaviour of vervet monkeys on *A. tortilis* and *A xanthophloea*: with special reference to reproductive strategies and tannin production. *J. Anim. Ecol.* **50**: 715-731.

Wrangham, R.W., Conklin, N.L., Etot, G., Obua, J., Hunt, K.D., Hauser, M.D. and Clark, A.P. 1993 The value of figs to chimpanzees. *IJP* **14(2)**: 243-256.

Yang, D-H, Zhang, J-Y and Chun, L. 1987 Preliminary survey on the population and distribution of gibbons in Yunnan Province. *Primates* **28(4)**: 547-549.

Yeager, C.P. 1989 Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *IJP* **10(6)**: 497-529.

Yoshiba, K. 1967 An ecological study of hanuman langurs, *Presbytis entellus*. *Primates* **8**: 127-154.

Yoshiba, K. 1968 Local and intertroop variability in ecology and social behavior of common Indian langurs. In P.C. Jay (ed), *Primates: Studies in Adaptation and Variability*, 217-242. New York: Holt, Rinehart and Winston.

ERRATA

The following discrepancies have been detected in the text subsequent to the production of the thesis.

I. Page 2, para 1, sentence 4 - The range of the hoolock gibbon in India is not confined to Assam alone but covers other NE states including Arunachal Pradesh, Nagaland, Manipur, Mizoram, Tripura and Meghalaya. The western limit of their range is delimited by both the Brahmaputra and Dibang Rivers.

II. Page 33, para 2, sentence 1 - refer to thesis by House, 1991 in *References*.

III. Page 34 - The total number of rainy days in the annual period totalled 229.

IV. Page 38, para 1 - the species of otter and cat first described in the Barito Ulu watershed by the author are, respectively, the Oriental small-clawed otter (*Aonyx cinerea*) and Bay Cat (*Catopuma badia*).

V. Page 38, para 2 - nine, rather than eight, differential *types* of primate resided in the Barito Ulu watershed. However, only eight species *per se* were discussed as gibbons in the watershed were hybrid forms rather than full species.

VI. Page 49, para 2 - a total of 1459 minutes were spent following the focus groups.

VII. Page 49, Table 2-5 - Schedule of observation hours for focus group
Total number of hours spent following RBC1 in March 96 equals 25.2, not 27.3
Total number of hours spent following RBC1 and RBC2 over the annual period are in the wrong columns - total for RBC1 = 286.1 hours; total for RBC2 = 1028.5 hours.
Total number of hours spent following RBC3 = 82.1, not 82.0
Total number of hours spent following RBC5 = 62.4, not 62.1
Total number of hours spent following all study groups over the annual period equals 1459.1, not 1460.1. See table below.

Table 2-5 Schedule of observation hours for focus groups: Sep 1995- Aug 1996

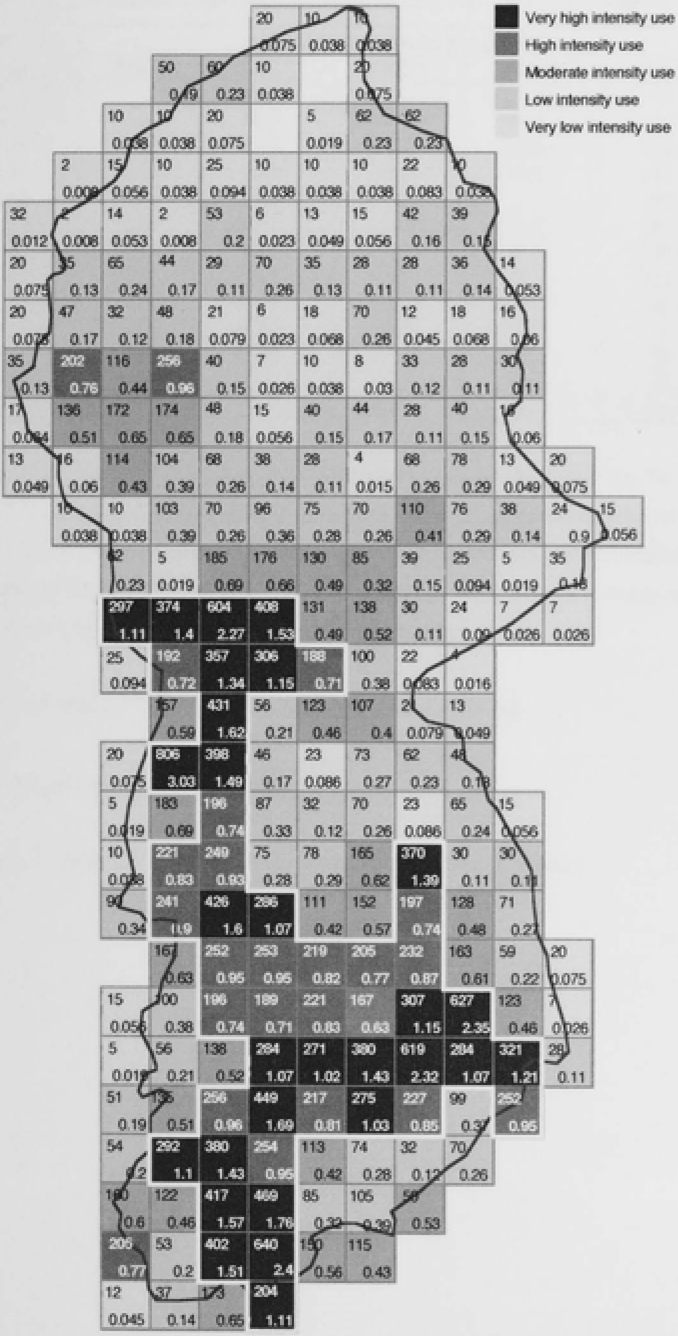
	Observation hours per group				
	RBC1	RBC2	RBC3	RBC5	Total
September 95	-	70.6	-	-	70.6
October 95	31.2	84.3	7.1	8.2	130.8
November 95	24.5	96.5	11.5	10.5	143.0
December 95	27.5	95.2	10.4	10.2	143.3
January 96	27.0	53.1	7.5	-	87.6
February 96	25.0	118.1	8.0	5.5	156.6
March 96	25.2	99.2	10.5	4.3	139.2
April 96	33.1	98.4	12.4	9.1	153.0
May 96	31.1	106.3	10.2	9.3	156.9
June 96	31.3	95.4	4.5	5.3	136.5
July 96	30.2	69.2	-	-	99.4
August 96	-	42.2	-	-	42.2
Total	286.1	1028.5	82.1	62.1	1459.1

VIII. Page 76, para 3 - Calculating the average feeding time for the group from the total feeding times measured for each individual in the group does, on occasion, introduce bias. However, the author wished to discuss group feeding averages and considered the methodology described on page 76 as the most appropriate tool to use. Furthermore, group members tended to spend comparable lengths of time.

IX. Page 131, Table 5-6 - Hollongapar is in India, not Bangladesh.

X. Page 136, Figure 5-6 - see next page.

XI. Page 227, Table 8-5 - Duration of duets and solos is given in minutes.



					20 0.075	10 0.038	10 0.038					
			50 0.19	60 0.23	10 0.038		20 0.075					
		10 0.038	10 0.038	20 0.075		5 0.019	62 0.23	62 0.23				
	2 0.008	15 0.056	10 0.038	25 0.094	10 0.038	10 0.038	10 0.038	22 0.083	10 0.038			
32 0.012	2 0.008	14 0.053	2 0.008	53 0.2	6 0.023	13 0.049	15 0.056	42 0.16	39 0.15			
20 0.075	35 0.13	65 0.24	44 0.17	29 0.11	70 0.26	35 0.13	28 0.11	28 0.11	36 0.14	14 0.053		
20 0.075	47 0.17	32 0.12	48 0.18	21 0.079	6 0.023	18 0.068	70 0.26	12 0.045	18 0.068	16 0.06		
35 0.13	202 0.76	116 0.44	256 0.96	40 0.15	7 0.026	10 0.038	8 0.03	33 0.12	28 0.11	30 0.11		
17 0.064	136 0.51	172 0.65	174 0.65	48 0.18	15 0.056	40 0.15	44 0.17	28 0.11	40 0.15	16 0.06		
13 0.049	16 0.06	114 0.43	104 0.39	68 0.26	38 0.14	28 0.11	4 0.015	68 0.26	78 0.29	13 0.049	20 0.075	
	10 0.038	10 0.038	103 0.39	70 0.26	96 0.36	75 0.28	70 0.26	110 0.41	76 0.29	38 0.14	24 0.9	15 0.056
		62 0.23	5 0.019	185 0.69	176 0.66	130 0.49	85 0.32	39 0.15	25 0.094	5 0.019	35 0.13	
		297 1.11	374 1.4	604 2.27	408 1.53	131 0.49	138 0.52	30 0.11	24 0.09	7 0.026	7 0.026	
		25 0.094	192 0.72	357 1.34	306 1.15	188 0.71	100 0.38	22 0.083	4 0.016			
			157 0.59	431 1.62	56 0.21	123 0.46	107 0.4	21 0.079	13 0.049			
		20 0.075	806 3.03	398 1.49	46 0.17	23 0.086	73 0.27	62 0.23	48 0.18			
		5 0.019	183 0.69	196 0.74	87 0.33	32 0.12	70 0.26	23 0.086	65 0.24	15 0.056		
		10 0.038	221 0.83	249 0.93	75 0.28	78 0.29	165 0.62	370 1.39	30 0.11	30 0.11		
		90 0.34	241 0.9	426 1.6	286 1.07	111 0.42	152 0.57	197 0.74	128 0.48	71 0.27		
			167 0.63	252 0.95	253 0.95	219 0.82	205 0.77	232 0.87	163 0.61	59 0.22	20 0.075	
		15 0.056	100 0.38	196 0.74	189 0.71	221 0.83	167 0.63	307 1.15	627 2.35	123 0.46	7 0.026	
		5 0.019	56 0.21	138 0.52	284 1.07	271 1.02	380 1.43	619 2.32	284 1.07	321 1.21	28 0.11	
		51 0.19	136 0.51	256 0.96	449 1.69	217 0.81	275 1.03	227 0.85	99 0.37	252 0.95		
		54 0.2	292 1.1	380 1.43	254 0.95	113 0.42	74 0.28	32 0.12	70 0.26			
		160 0.6	122 0.46	417 1.57	469 1.76	85 0.32	105 0.39	58 0.53				
		206 0.77	53 0.2	402 1.51	640 2.4	150 0.56	115 0.43					
		12 0.045	37 0.14	173 0.65	204 1.11							

Figure 5-6 Total amount of time and proportion of time RBC2 spent in each home range quadrat during the 60 day sample period. Core ranging area is outlined in broad white line.