Socioecology of Cat Ba Langurs (*Trachypithecus poliocephalus*): Implications for Conservation

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Statement of originality

The work presented in this thesis is, to the best of my knowledge and belief, original and my own work except where otherwise acknowledged. This material has not been submitted either in whole or in part, for a degree at this or any other university.

Rebecca Lynne Hendershott

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Dr Ben Rawson, Prof Colin Groves, and Dr Alison Behie in the field, Cat Ba Island
Photo taken Aug 2014 by R Hendershott

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Mr Nguyen Cam and myself on our boat
Photo taken Jan 2015 by B Kimitsuka

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Abstract

Cat Ba langurs (*Trachypithecus poliocephalus*), endemic to Cat Ba Island (Vietnam), are a member of the limestone langur group (*francoisi* species-group) found in Laos, Vietnam, and China. With less than 75 individuals in the world, these Cat Ba langurs are Critically Endangered. This dissertation represents the first long-term behavioural study of the species (549 contact hours across 11 months), and provides socioecological information for two groups (n=17-20) living on the Cua Dong fjord, which can be used in conservation management. Like most other colobines, the majority of the Cat Ba langur diet is leaves (84% of their dietary budget). This may explain their activity budget, which is primarily inactivity (55% of their activity budget), followed by foraging (19%) and social behaviour and locomotion (12% each). Activity and dietary budgets vary seasonally, with animals spending more time in social behaviours in the wet season, when they eat more fruit, and more time in foraging in the dry season, when leaves are ingested more, suggesting they are energy maximisers. In addition, age differences were found, with adults spending the most time in social behaviours and resting. Social behaviour primarily includes grooming and playing with others - play is more common in younger animals, while older animals tend to groom more. Overall, they spend 58% of their days not in proximity to any other langurs. Adult males spend the most time alone, and seem to avoid young langurs. Disputes tend to be between adult females, and two females only tend to come together if there is a young langur acting as a 'social glue'. Home ranges varied between groups with the larger group's range being 50ha compared to just 22ha for the smaller group. In both areas, rocks and sparsely covered areas are used most often, which is due to the shrubby, discontinuous vegetation. Most of the langurs' observable time is spent on exposed slopes (47%), followed by steep cliffs (38%), summits (11%), valleys (3%), and the ground (1%); this varied seasonally, likely to balance foraging needs with thermoregulation. The langurs used 22 sleeping sites, including ledges (61%) and caves (17%). When newborn, Cat Ba langurs are bright orange. They start to lose this natal coat as an infant, and become much darker during the young juvenile stage. As individuals age, they also become more independent and start to forage and locomote more on their own. These reported behaviours can be used to create a baseline for activity budgets, home range size, and habitat use, and development and maturation that can be used for comparative purposes in future studies. Results find that animals are behaviourally similar to other related species and their biggest threat is likely their small, fragmented population structure. To combat this, I support habitat protection, patrols, and enforcement; education and training; habitat corridors; and limiting the human population, as these support an entire ecosystem while teaching locals the importance of biodiversity, reducing resource competition, and fragmentation from infrastructure, and providing a means for the langurs themselves to disperse.

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Abbreviations

A	adult
AF	adult female
AM	adult male
ANU	Australian National University
BLM	binomial linear model
^{0}C	degrees Celsius
CBLCP	Cat Ba Langur Conservation Project
CBNP	Cat Ba National Park
cm	centimetre
df	degrees of freedom
EPRC	Endangered Primate Rescue Center
F	female
FFI	Fauna & Flora International
GLM	generalised linear model
GPS	global positioning system
ha	hectre
IMI	intermembral index
IUCN	International Union for Conservation of Nature
kg	kilograms
km	kilometres
K-S	Komolgorov-Smirnov test
LM	linear model
M	male
m	metres
MCP	minimum convex polygon
mm	millimetre
mya	millions of years ago
N	number of observations (scans)
p	p-value of statistical test
SE	standard error
SMART	Spatial Monitoring and Reporting Tool
SA	subadult
TWG	Technical Working Group
UN	United Nations
UNESCO	United Nations Educational, Scientific and Cultural Organization
USD	currency ($) for USA
UTM	Universal Transverse Mercator (coordinate system)
VND	currency (đồng) for Vietnam
Y	young

Chapter 1: Introduction

1.1 Introduction

Cat Ba langurs [*Trachypithecus poliocephalus* (Trouessart 1911)] are Critically Endangered (Bleisch et al. 2008a) Asian colobines endemic to Cat Ba Island in northeastern Vietnam. Very little is known about these karst-dwelling, folivorous langurs. An initial census was done in 1998-2000 and found only 104-135 individuals (Nadler and Ha Thang Long 2000), which then reportedly declined to less than half in the following six years, leaving an estimated 64 individuals (Nadler et al. 2007), although some estimates place the population as low as the 40s in this decade (Leonard 2014; Table 7.1, Chapter 7, for a full historical account of species numbers). Currently the global population consists of three breeding populations [two on Cat Ba Island, and one ex-situ at the Endangered Primate Rescue Center (EPRC) in Cuc Phong, 120km south of Hanoi], and one isolated group of five females, totalling 63 animals as of September 2014 (Lees et al. 2014).

While poaching is responsible for the species' decline to dangerously low numbers on the island, poaching of Cat Ba langurs has been brought under control through ongoing Cat Ba Langur Conservation Project (CBLCP; established in 2001) and Cat Ba National Park (CBNP) efforts (Stenke and Chu Xuan Canh 2004). Although the last documented poaching of Cat Ba langurs was in 2004 (N Leonard pers. comm. 2015), other taxa are still illegally hunted on the island; additionally there is continual habitat destruction, isolation of langur groups due to fragmentation, and the associated danger of inbreeding or demographic stochasticity due to extremely low population numbers and lack of dispersal opportunities between breeding populations. Tourism, the associated infrastructure, and a growing local population also threaten the langurs' habitat and the animals themselves (Stenke and Chu Xuan Canh 2004). All of this makes long-term species viability questionable (Lees et al. 2014).

Known as limestone langurs, the *francoisi* superspecies group of langurs contains species that are all Endangered or Critically Endangered: Delacour's langur (*Trachypithecus delacouri),* Laotian langur (*Trachypithecus laotum),* Hatinh langur *(Trachypithecus hatinhensis*), Indochinese black langur (*Trachypithecus ebenus*), François' langur (*Trachypithecus francoisi*), Cat Ba langur, and white-headed langur *(Trachypithecus* *leucocephalus)* (Groves 2007). The latter three are the northern group, divided from the southern group by the Red River (Groves 2007). Cat Ba and white-headed langurs are the most closely related taxa (Roos 2003; Roos 2004), still being considered as subspecies by some authorities (Wang et al. 1997; Huang et al. 2002; Roos 2004; Roos et al. 2007; Nadler 2010). This study considers the two as full species, based on recent publications of Asian primate taxonomy (Groves 2004; Groves 2007; Roos et al. 2014).

Limestone langurs all have challenges to their locomotion, resources, and habitat usage. The limestone formations are steep and sharp (Sterling et al. 2006), with poor soil quality and stunted vegetative growth (Urich 1989; Day and Chenoweth 2004; Clements et al. 2006). Studies have shown that white-headed langurs have increased terrestrialism as an adaptation to the karst mountains (Huang and Li 2005); this locomotion on such sharp vertical rock substrates has been dubbed 'petrous' (Workman and Schmitt 2012).

Limestone langurs may be attracted to the karst habitat because of the presence of caves, or because they are reliant on limestone-endemic food species for mineral acquisition (Nadler and Ha Thang Long 2000; Grueter and Ding 2006). However, over half of plant species consumed are not endemic to limestone (but are endemic to Eastern Asia) (Workman 2010b), suggesting that this niche specialisation does not account for why these monkeys are found only on limestone (Li and Rogers 2005b). Some researchers suggest that limestone langurs do not choose limestone karst, but that they have been marginalised by human impacts to this environment (which humans cannot cultivate or live on as easily) (Li and Rogers 2005a; Workman 2010a). There is evidence to suggest that the limestone langurs prefer continuous forests with higher vegetation coverage, and avoid the shrubby areas that can make up a third of their habitat (Li and Rogers 2005b; Hu 2007; Zeng et al. 2013).

Others suggest that limestone langurs are adapted specifically to karst. When found in areas that abut nonlimestone karst, they seem to primarily continue to use the karst habitat (C Groves pers. comm. 2015), and they have a preference the under-canopy vegetation and shrubby forests (Nadler and Ha Thang Long 2000). For example, Indochinese gray langurs (*Trachypithecus crepusculus*), the closest species to the limestone langur group (Roos et al. 2007; Liedigk et al. 2009), live mostly in evergreen, semievergreen, mixed moist deciduous, bamboo, and woodland forests, but can also live on limestone karst forests (Bleisch et al. 2008b). Their use of such a variety of habitat types compared to the *francoisi* superspecies-group suggests that the latter may be choosing to primarily use karst habitat even when other suitable habitat types are available, although this is an area that requires further study.

This dissertation will investigate the socioecology of the Cat Ba langur, including their activity and dietary budget, ranging patterns and habitat use, social behaviour, and young development, and considers the implications the results have for the conservation of this species. It will also address seasonal differences that may impact any of these variables. As no long-term studies have been conducted on the Cat Ba langur up until this point, this study will be crucial for learning more about this species and helpful in making conservation decisions on their behalf.

1.2 Research Aims

With such dangerously low population numbers, historical hunting, and a disturbed, fragmented habitat, the Cat Ba langur is considered Critically Endangered (Bleisch et al. 2008a) and has consistently been on the Top 25 Most Endangered Species List (2000-2016) (Leonard et al. 2016b). Despite this, however, there have been no long-term studies of this species; the only published papers/chapters on Cat Ba langurs focus on short-term, broad overviews (Nadler and Ha Thang Long 2000; Schneider et al. 2010) and conservation options (Stenke and Chu Xuan Canh 2004; Schneider et al. 2010), with a few papers mentioning genetic work undertaken to define their taxonomy (Roos 2004; Liu et al. 2013a). Their long-term behavioural activity budget, how they move and use their habitat, social behaviour, and young development were completely undocumented before the start of this study. This study thus aims to answer basic uncertainties about the species so as to make them comparable to other limestone langurs (on which research is also scant) and to aid in important conservation planning.

Until more is known about Cat Ba langurs, conservation plans can only be made based on what is known from closely related species, potentially making unnecessary or inappropriate assumptions. Due to the low number of individuals left of this species globally, it is imperative that action is taken now to gain a full understanding of their behaviour and ecology. Knowledge gained from this study will be useful for captive breeding, translocations, protection of habitat, and understanding conditions that are conducive to reproduction. Therefore, this study is critical to the preservation of Cat Ba langurs.

1.3 Research Limitations

Although the animals studied are habituated to human presence from afar (they live in an area that is in visual proximity to local people's floating villages, fishing and tourist boats, shellfish collectors, kayakers, etc.), they are not accustomed to being followed on foot or at close proximity. For this reason, and difficulties in doing follows on limestone karst terrain, all observations were made from a boat, following existing protocols (Workman 2010a; Agmen 2014; Phan Duy Thuc et al. 2014). Accurately being able to census and see animals in karst environments has been a consistent problem for researchers (Li and Rogers 2007; Haus et al. 2009; Han et al. 2013). Proximity between the monkeys and myself ranged from 50-300m. This, in combination with boat movement, made details of observations difficult. Often I could determine only age class, making consistent individual IDs of the monkeys not possible throughout the year.

As with all research, there is threat of observer bias. The data collection schedule used introduced one bias: due to the boat driver contract of only being out eight hours a day, this means I focused observations around periods when the animals were most visible (i.e. not when they were resting in dense foliage in the middle of the day: Li et al. 2003; Li and Rogers 2004a; Zhao and Pan 2006; Zhou et al. 2007a), as other researchers have done (Long et al. 1998; Jin et al. 2015). This will overestimate activity levels. Secondly, the habitat restricted visibility, thus behaviours that occur in more open or visible habitat will be overrepresented. This is a common problem for primate researchers (Huang et al. 2003; Li and Rogers 2004a; Li and Rogers 2006; Li and Rogers 2007; Li et al. 2009; Rawson 2009; Workman and Schmitt 2012; Agmen 2014), and suggests that this study is comparable given this bias in visibility.

This study is based on 17-23 animals in the Cua Dong breeding population, living at the southeast end of Cat Ba Island. While the sample size is small, it still accounts for approximately a third of all remaining Cat Ba langurs. In addition, as populations are living in fragmented and degraded habitat, reproduction (Yeager and Kirkpatrick 1998), group structure (Sterck 1998; Sterck 1999), ranging (Wasserman and Chapman 2003;

Phiapalath and Suwanwaree 2010), diet (Li and Rogers 2006) and activity budgets (Li and Rogers 2004a; Phiapalath and Suwanwaree 2010) may be impacted by the difficulty of dispersal and lower resource availability. That being said, this is the environment they have been in for a long time, and studying how animals are behaving in isolated environments (where decisions are limited) is informative and comparable to other limestone langurs who are also suffering from declining populations and habitat.

1.4 Permissions Obtained

Approval was granted by The Australian National University Animal Experimentation Ethics Committee (Animal Ethics Protocol Number: A2013/18) for dates 1/7/13 – 30/6/16. While this ethics protocol is for the larger research project, where the principal investigator is Dr Alison Behie, I was included as a co-investigator. A research permit on the ground was supported by Hai Phong’s People’s Committee. Research was approved by all relevant agencies: Australian National University (ANU), Fauna & Flora International (FFI), CBLCP, CBNP, and the local government.

1.5 Thesis Outline

This thesis contains seven chapters that will address the behaviour and socioecology of Cat Ba langurs in hopes of adding to our knowledge of limestone langurs and conservation planning. The current chapter provides background on the justification for the thesis as well as a review of what is known about Cat Ba langur taxonomy, distribution, anatomy, activity and dietary budgets, home range, life history and reproduction, and social structure; and current and historical threats to the species and conservation. Chapter 2 outlines the study area and general methods used in this study. Chapter 3 investigates activity and dietary budgets used by Cat Ba langurs, and variation within the year, the day, and age-sex classes; this concentrates on four main behaviours (inactivity, social behaviour, locomotion, and foraging) with rare behaviours lumped under ‘other’. Chapter 4 analyses how Cat Ba langurs range, where they sleep, and how they use their habitat. Chapter 5 explores social behaviour variation and proximity within the groups, age, and sex classes. Chapter 6 addresses how young develop behaviourally and physically, with reference to how these factors make them vulnerable. Chapter 7 ties these chapters together by relating results back to conservation efforts of this Critically Endangered species.

The following questions were addressed:

1. What is the activity and dietary budget of the Cat Ba langur (Chapter 3)?
    a. What is the activity budget of the Cat Ba langur (Sections 3.3.1 and 3.4.1)?
        i. How do behaviours differ across time of day (Sections 3.3.1.1 and 3.4.1.1)?
        ii. How do behaviours differ across seasons (Sections 3.3.1.2 and 3.4.1.2)?
        iii. How do behaviours differ across groups (Sections 3.3.1.3 and 3.4.1.3)?
        iv. How do behaviours differ across age classes (Sections 3.3.1.4 and 3.4.1.4)?
        v. How do behaviours differ across sexes (Sections 3.3.1 and 3.4.1.4)?
        vi. What are nursing patterns?
            1. What is the rate of nursing for adult females (Section 3.3.1)?
            2. Do nursing rates differ across time of day (Sections 3.3.1.1 and 3.4.1.1)?
    b. What is the dietary budget of the Cat Ba langur (Sections 3.3.2 and 3.4.2)?
        i. How does diet differ across time of day (Sections 3.3.2.1 and 3.4.2.1)?
        ii. How does diet differ across seasons (Sections 3.3.2.2 and 3.4.2.2)?
        iii. How does diet differ across groups (Sections 3.3.2 and 3.4.2.3)?
        iv. How does diet differ across age classes (Sections 3.3.2 and 3.4.2.3)?
        v. How does diet differ across sexes (Sections 3.3.2 and 3.4.2.3)?
2. What are the ranging patterns of Cat Ba langurs, and how is the habitat used (Chapter 4)?
    a. What is the home range size for the two reproductive groups (Sections 4.3.1 and 4.4.1)?
        i. How much of home ranges overlap?
        ii. Does home range size change seasonally?
    b. What parts of the habitat are most used (Sections 4.3.2 and 4.4.2)?

        i. How does habitat use differ across behaviours (Sections 4.3.2.1 and 4.4.2.1)?
        ii. How does habitat use differ across locomotion types (Sections 4.3.2.2 and 4.4.2.1)?
        iii. How does habitat use differ across seasons (Sections 4.3.2.3 and 4.4.2.2)?
    c. Where do the langurs sleep (Sections 4.3.4 and 4.4.4)?
        i. How many sleeping sites does each group have?
        ii. Were sites reused or used consecutively?
        iii. What are the characteristics of chosen sleeping sites?
            1. Are sites ledges, caves, or trees?
            2. Where do sites occur on a hill? What hill type are they on?
        iv. Do sleeping sites change with season?

3. How do Cat Ba langurs engage socially (Chapter 5)?
    a. What social behaviours do the langurs use (Sections 5.3 and 5.4)?
        i. How do social behaviours differ across groups (Section 5.3)?
        ii. How do social behaviours differ across age classes (Sections 5.3.1 and 5.4.1)?
        iii. How do social behaviours differ across sexes (Sections 5.3.2 and 5.4.1)?
    b. How common is intragroup aggression (Sections 5.3.3 and 5.4)?
    c. How often are langurs within proximity to other group members vs. alone (Sections 5.3.4, 5.3.5, and 5.4.2)?
        i. How does being alone differ across time of day?
        ii. How does being alone differ across seasons?
        iii. How does being alone differ across groups?
        iv. How does being alone differ across age-sex classes?
        v. How does being alone differ across behaviours engage in?
        vi. How many others are in proximity?
            1. Does the number of others in proximity differ across groups?
            2. Does the number of others in proximity differ across age-sex classes?
        vii. What type of huddles are the langurs using?

            1. What is the average huddle size?
            2. Does huddle size differ across groups or age-sex classes?
            3. Are the different age-sex classes associating randomly?

4. How do Cat Ba langur young develop both physically and behaviourally (Chapter 6)?
    a. Is there a birth season or peak (Sections 6.3.1 and 6.4.1)?
    b. Are there significant differences in behaviour by age for young langurs (Sections 6.3.2 and 6.4.2)?
        i. What is the activity budget for young langurs (Sections 6.3.2.1 and 6.4.2)?
            1. Do social behaviours differ for young langurs?
            2. Do 'other' behaviours differ for young langurs?
            3. Does number of others in proximity and time spent alone differ for young langurs?
        ii. What is the dietary budget for young langurs (Sections 6.3.2.2 and 6.4.2)?
        iii. What is the nursing behaviour of young langurs (Sections 6.3.2.2 and 6.4.2)?
        iv. What is the locomotor budget for young langurs (Sections 6.3.2.3 and 6.4.2)?
        v. What is the postural budget for young langurs (Sections 6.3.2.3 and 6.4.2)?
    c. What is the progression of the natal coat loss, and how does this correspond to age (Sections 6.3.3 and 6.4.2)?
5. What are the conservation implications for Cat Ba langurs of this research (Chapter 7)?
    a. What are the options for conservation management, and how effective are they/might they be for the langurs (Section 7.2)?
        i. How effective is habitat protection, patrols, and enforcement for the conservation of Cat Ba langurs (Section 7.2.1)?
        ii. How effective is education and training for the conservation of Cat Ba langurs (Section 7.2.2)?

    iii. How effective are habitat corridors for the conservation of Cat Ba langurs (Section 7.2.3)?
    iv. How effective is limiting the human population for the conservation of Cat Ba langurs (Section 7.2.4)?
    v. How effective is captive breeding for the conservation of Cat Ba langurs (Section 7.2.5)?
    vi. How effective is translocation for the conservation of Cat Ba langurs (Section 7.2.6)?
    vii. How effective is ecotourism for the conservation of Cat Ba langurs (Section 7.2.7)?
b. What are the behavioural indicators of a loss in habitat quality, reduction in food supply, and physiological stress (Section 7.3)?
    i. What do changes in activity budget indicate (Section 7.3.1)?
    ii. What do changes in habitat use and range size indicate (Section 7.3.2)?
    iii. What do changes in development and maturation indicate (Section 7.3.3)?

1.6 Species Overview

1.6.1 Taxonomy

Cat Ba langurs, also known as golden-headed langurs or ‘Cang den dau trang’/‘voọc Cát Bà’ in Vietnamese (Nisbett and Ciochon 1993; Nguyen Cam pers. comm. 2014) are a Critically Endangered (Bleisch et al. 2008a) leaf-eating monkey within the family Cercopithecidae and subfamily Colobinae of Old World monkeys, endemic to a small Vietnamese island – Cat Ba Island.

1.6.1.1 *Colobines*

Early colobines moved into arboreal and folivorous niches by the late Pliocene (Jablonski 2002). They then divided into two tribes: the African (Colobini; which includes the genera *Procolobus, Piliocolobus,* and *Colobus*), and the Asian [Presbytini; which includes the odd-nosed group (*Nasalis, Rhinopithecus*, *Simias*, and *Pygathrix*), and the langur, or leaf, monkeys (*Trachypithecus*, *Presbytis*, and *Semnopithecus)*] (Groves 2001) somewhere around 10.9-15.39 million years ago (Delson 1994; Sterner et al. 2006; Meyer et al. 2011; Roos et al. 2011). The original Asian group then again split around 6.9 million years ago into the odd-nosed and leaf-eating groups (Sterner et al. 2006). The Asian group has retained the primitive features in their molars, premolars, jaw bone, feet bones, and thumb, which were more derived in the African group (Strasser and Delson 1987; Groves 1989).

1.6.1.2 *Asian Colobines*

Debate continues as to the relatedness of the Asian colobines (Karanth 2010), particularly between *Rhinopithecus, Pygathrix,* and *Trachypithecus* (Oates et al. 1994; Wang et al. 1997), although each genera has been shown to be monophyletic (Sterner et al. 2006). There is confusion as to whether or not *Presbytis* is sister taxon to *Trachypithecus* and *Semnopithecus,* or if *Semnopithecus* is sister to the other two, and where these divisions stand in relation to the odd-nosed group of Asian colobines (Strasser and Delson 1987; Groves 1989; Pan and Groves 2004; Sterner et al. 2006; Kirkpatrick 2007; Osterholz et al. 2008; Ting et al. 2008; Meyer et al. 2011; Perelman et al. 2011; Roos et al. 2011). The questionable relatedness among the langurs is a complex issue, possibly due to past hybridisation between them (Osterholz et al. 2008; Roos et al. 2011) or morphological convergence (Perelman et al. 2011). Their perceived relatedness, therefore, depends on what is being tested (e.g. morphology, nuclear vs. mitochondrial DNA), although this does not change the true nature of their evolution and phylogeny.

1.6.1.3 Trachypithecus

While the genus *Trachypithecus* used to be said to include five species-groups, *T. obscurus*, *T. cristatus*, *T. francoisi*, *T. pileatus*, and *T. vetulus* (Groves 2001; Roos 2003), the last two have been found to be genetically closer to the *Semnopithecus* (*T. pileatus* is the result of hybridisation with *Semnopithecus* in the past and retains the *Trachypithecus* genus name, whereas *T. vetulus* should always have been considered part of *Semnopithecus*: Zhang and Ryder 1998; Roos 2003). As a result, *Trachypithecus* now includes only three species-groups (*T. obscurus*, *T. cristatus*, and *T. francoisi* groups) (Harding 2010) that separated 3.17 ± 0.31 million years ago (Roos et al. 2008). The number of species within the genus as a whole is questionable, ranging from 17-20 species (Harding 2010). This study follows the most updated taxonomic list for Asian species in recognising 20 *Trachypithecus* species (Roos et al. 2014).

The *francoisi* species-group of limestone langurs include: Delacour’s, Laotian, Hatinh, Indochinese black, François’, Cat Ba, and white-headed langurs (Groves 2007). All of these animals live on limestone karst mountains (Groves 2007), resulting in similar ecological, locomotor, and nutritional challenges. The *francoisi* species-group can be further divided into the northern (François’, Cat Ba, and white-headed langurs) and the southern (Delacour’s, Laotian, Hatinh, and Indochinese black langurs) groups (Roos 2003; Roos et al. 2007; Figure 1.1), whose ranges are divided by the Red River (Groves 2007).

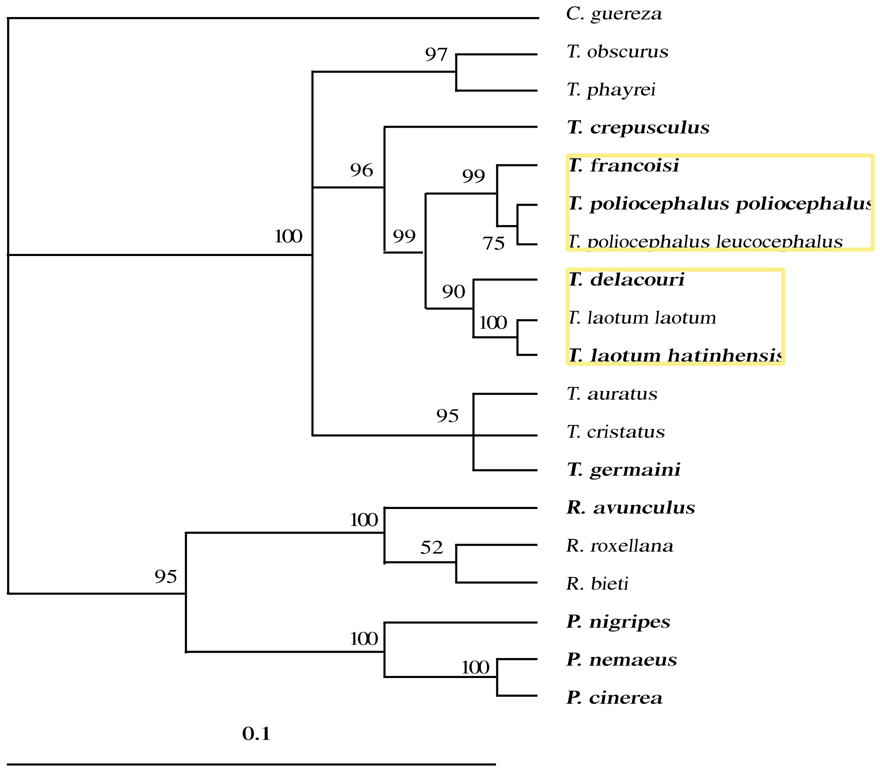


Fig. 2.3-1.
50%-majority-rule consensus tree for the maximum-likelihood method following a molecular clock. Branch lengths are drawn according to the number of substitutions per position with the bar indicating 0.1 substitutions per site. Numbers in the tree indicate bootstrap values in %. Species names in bold represent Vietnamese primates.

Figure 1.1: Phylogeny of limestone langurs (based on cytochrome b analysis), showing that François' (*Trachypithecus francoisi*), white-headed (*Trachypithecus leucocephalus*), and Cat Ba (*Trachypithecus poliocephalus*) langurs are part of the northern species group, while Delacour's (*Trachypithecus delacouri*), Hatinh (*Trachypithecus hatinhensis*), and Laotian (*Trachypithecus laotum*) langurs are part of the southern species group. Black langurs (*Trachypithecus ebenus*) not assessed. Taken, with permission, from Roos (2003).

1.6.1.4 Trachypithecus poliocephalus *and* T. leucocephalus

Given the convoluted phylogenetic relationship of the Asian colobines, it is not surprising that Cat Ba langurs have moved around taxonomically. They were first recognised as a species under the name *Semnopithecus (Lophopithecus) poliocephalus* Trouessart, 1911. The species was later called *Pithecus poliocephalus* ('gray-headed langur') and, based on skulls, it was deemed to be closely related to *P. francoisi, P. laotum,* and *P. delacouri* (Osgood 1932). Thirty years later it was tentatively called *Presbytis (?) francoisi poliocephalus* (Ellerman and Morrison-Scott 1951; Napier and Napier 1967). On the basis of morphological similarities, mainly colour pattern, it was recognised as a subspecies of the southern Indian *Semnopithecus johnii* (now *Trachypithecus johnii*: Groves 2001) (Brandon-Jones 1989; Brandon-Jones 1995).

A similar species, with a whitish head contrasting with a black body, was described in 1955 as *Presbytis leucocephalus* from Guangxi Province, China (Tan 1955). Because of the general colour pattern similarity, backed up more recently by the slightness of their mtDNA differences, the Cat Ba langur and white-headed langurs have often been considered only subspecifically different (*Trachypithecus poliocephalus poliocephalus* and *T. p. leucocephalus*) (Wang et al. 1997; Huang et al. 2002; Roos 2004; Roos et al. 2007; Nadler 2010). However, they are two distinct species based on the Phylogenetic Species Concept (Groves 2004), as the colours and colour patterns are in fact distinct, and they separate in a discriminant analysis (Groves 2007). This separation has recently been accepted by multiple scientists and is thus the taxonomy used in this study (Roos et al. 2014).

In contrast to the finding that Cat Ba and white-headed langurs are sister taxa, there is evidence that Cat Ba (0.50-0.25 million years ago) and white-headed (0.46-0.27 mya) langurs *independently* diverged from François' langurs, achieving genetic separation by geographic barriers (Liu et al. 2013a). As white-headed and François' langurs can hybridise (Liu et al. 2013a), some suggest that white-headed langurs should be a subspecies of François' langurs (Wang et al. 1997; Ding et al. 2000). Regardless of species or subspecies status, both the Cat Ba and white-headed langurs are clearly part of the *francoisi* species-group (Nadler et al. 2003; Roos 2004).

1.6.2 Distribution

1.6.2.1 *Vietnamese Primates*

Vietnam has the richest diversity of primate taxa in Southeast Asia (Nadler 2010). Within the country's borders there are two species of Lorisidae (both genus *Nycticebus*), 18 species of Cercopithecidae (five *Macaca*, eight *Trachypithecus*, three *Pygathrix*, and one *Rhinopithecus*), and six Hylobatidae (*Nomascus*) (Roos et al. 2014). The majority of these species are on the IUCN Red List and classified from Vulnerable to Critically Endangered

(Nadler 2010). Two or three of these primate species (Cat Ba and Delacour's langurs and possibly gray-shanked doucs, *Pygathrix cinerea*) are strictly endemic to Vietnam (Roos et al. 2014) while one other is near endemic (cao-vit gibbon, *Nomascus nasutus*) or may now be endemic due to local extirpations elsewhere (Tonkin snub-nosed langur, *Rhinopithecus avunculus*) (B Rawson pers. comm. 2015). However, political borders have little to do with where nonhuman primates range. If we look at a biogeographically relevant area (east of the Mekong River), over half of the primates are endemic (Groves 2007).

1.6.2.2 *Asian Colobines*

Colobines presumably diverged from cercopithecines, in terms of dental and digestive specialisations and reduced thumbs, while in Africa 19.41-14.7 million years ago (Sterner et al. 2006; Meyer et al. 2011). Asian colobines then entered Eurasia through intact forests in the Late Miocene, making it to eastern Asia by the end of the Miocene (Delson 1994). African colobines range across central and western Africa (Oates et al. 1994).

Ancient Asian colobines are poorly understood, including at what point they diversified (Section 1.6.1). Fossils of Asian colobines are found in south China, Myanmar, Laos, Cambodia, Vietnam, Thailand, peninsular Malaysia, Sumatra, Java, and Borneo (Tougard 2001). Jaw parts and tooth fossils suggest colobines had moved east of Europe by five to seven million years ago (Delson 1994). Primates, and other animals, spread across Southeast Asia over the Sunda Shelf, which connected Java, Borneo, Sumatra, southern China, Southeast Asia, and Taiwan when sea levels were 120m lower than today (Hutchison 1989; Brandon-Jones 1996; Sterling et al. 2006) in the late Middle Pleistocene to Late Pleistocene (Tougard 2001). When sea levels rose again, populations were left on islands (e.g. Java, Sumatra, Taiwan, Borneo).

The Asian colobines now range from 9°S in the Malay archipelago to 35°N in Pakistan (Brandon-Jones 1996). *Pygathrix* ranges from southern Laos and eastern Cambodia to eastern Vietnam, *Nasalis* is in Borneo, *Presbytis* can be found in Southeast Asia, and *Semnopithecus* is in the Indian subcontinent (Oates et al. 1994). This distribution is where ever-wet and seasonal rainforests remained intact during the periods 135,000 and 21-22,000 years ago, when sea-levels fell and much of the forest receded (Brandon-Jones 1996).

1.6.2.3 Trachypithecus

Before the glacial drought in the Pleistocene, *Trachypithecus* ranged from Java north into China and to the eastern provinces of India (Brandon-Jones 1996). *Trachypithecus francoisi*, *T. obscurus*, and *T. cristatus* were isolated from one another due to habitat fragmentation from climate change roughly three million years ago (Roos et al. 2008). During glacial periods, the Sunda Shelf was exposed, allowing for migration; seawater rising during an interglacial period about 11,000 years ago drowned the Sunda Shelf and made its constituent regions inaccessible (Sterling et al. 2006). After the drought, *Trachypithecus'* range was more limited, going from west Java (southern range) to southern China (northern range) to India (western range) (Oates et al. 1994; Brandon-Jones 1996; Nadler et al. 2003; Roos et al. 2014).

This is, roughly, still their range, with the majority living in Southeast Asia (Oates et al. 1994). *Trachypithecus* occur across a large range both geologically and ecologically. They survive in moist and wet lowland forests, dry deciduous forests, mangrove swamps along the coast, and broad-leaved forests in the mountains (Oates et al. 1994). *Trachypithecus* are sympatric with *Presbytis* on the Malaysian and Indonesian islands, with *Nasalis* on Borneo, and with *Pygathrix* in Indochina (Oates et al. 1994).

The eight *Trachypithecus* species within Vietnam include: the gray, margarita (*Trachypithecus margarita*), Indochinese lutung (*Trachypithecus germaini*), François', Cat Ba, Hatinh, Delacour's, and Indochinese black langurs (Groves 2007; Nadler 2010; Roos et al. 2014). The latter five are limestone langurs.

Limestone langurs live on limestone karst mountains around northern Vietnam, central and northern Laos, and southern China (Groves 2007). François' langurs exist in the largest and farthest north area of all the limestone langurs, living in southwest China and northern Vietnam (Bleisch et al. 2008c; Roos et al. 2014; Figure 1.2). White-headed langurs have a much smaller distribution than, and are parapatric with, François' langurs; they live in Guangxi Province, China (Li et al. 2003). Delacour's langurs are in northcentral Vietnam (Roos et al. 2014). Laotian langurs are found in central Laos, just north of Hatinh langurs where these latter extend across the border (Roos et al. 2014). Hatinh langurs are the southernmost limestone langur, occurring in northcentral Vietnam and eastcentral Laos (Roos et al. 2014). Indochinese black langurs are in eastcentral Laos and central Vietnam (Roos et al. 2014).

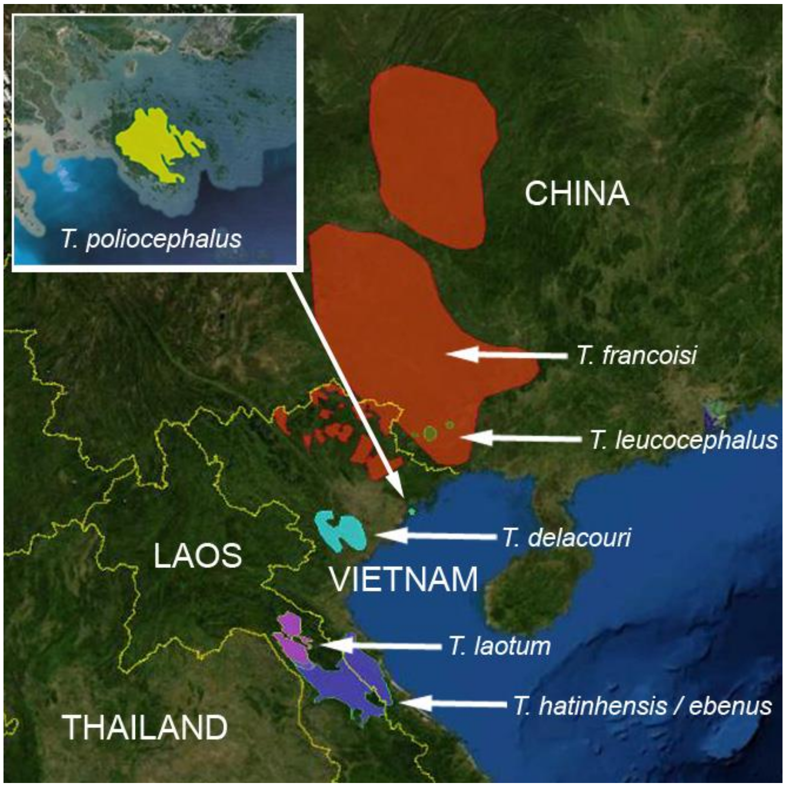


Figure 1.2: Distribution of limestone langurs (*Trachypithecus* spp.). Spatial maps for species provided by IUCN (2015) and compiled on Google Earth. Note: IUCN does not recognise *Trachypithecus hatinhensis* and *Trachypithecus ebenus* as separate species, so their distribution maps are combined (I could not find any more information on their distribution). IUCN also does not recognise *Trachypithecus leucocephalus* and *Trachypithecus poliocephalus* as separate species, but I was able to separate their distribution on the map given that *T. poliocephalus* only occur on Cat Ba Island.

1.6.2.4 Trachypithecus poliocephalus

The Cat Ba langur is limited to Cat Ba Island, northeastern Vietnam. There is no evidence these langurs ever occurred on the mainland, as no suitable limestone habitat is nearby (Nadler et al. 2003). It is suggested that they originally colonised the limestone range when sea levels were lower. Those ranges eventually became islands, cut off from one another (Nadler et al. 2003; Mark 2009). Cat Ba island (20°42'-20°55'N; 106°54'-107°10'E) is the largest of hundreds of islands in the Cat Ba archipelago. As of 2006, roughly half of the 140km^2 island is devoted to the CBNP (Sterling et al. 2006; Schrudde et al. 2010), a subset of which is part of a sanctuary (a strictly protected zone within the CBNP created for langur protection).

There are three populations of Cat Ba langurs on the island as of September 2014; two are reproductive and one is an isolated group of adult females (Lees et al. 2014; Table 1.1). Six groups lie within the sanctuary on the eastern side of the island (total: 31) and four groups are in Cua Dong/Viet Hai on the southeastern side of the island (total: 22) as of September 2014 (note that several births have been recorded since this time and group composition has changed for some groups) (Figure 1.3). It is the animals in Cua Dong that were studied for this current project; Groups A and B comprised 99.9% of scan samples, whereas Group C (a group comprised of bachelor males) were only in the study area from November-December 2014 (0.1% of scan samples); Group D (a lone adult female) was never seen in the study area. The five isolated females are at Hang Cai on the far northwestern side of the island, cutoff from the mainland due to mangrove destruction (Nadler et al. 2003). All three wild populations (58 animals) are completely isolated from one another. In addition to wild populations, there is one group of five langurs in captivity at the EPRC in Cuc Phong National Park. This accounts for all 63 Cat Ba langurs that are left in existence as of September 2014.

Table 1.1: Population size, age-sex classes for Cat Ba langurs as of September 2014, taken from Lees et al. (2014). Note: age classes of ‘newborn’ and ‘young juvenile’ are not used – these individuals are under ‘juvenile’ and ‘infant’.

	Cat Ba langur groups by area												
	Sanctuary						**Cua Dong**				**Hang Cai**	**EPRC (captive)**	total
group	A	B	C	D	E	F	A	B	C	D	A	A	12
adult male	1	1	1	1	1	0	1	1	1	0	0	1	9
adult female	5	4	2	1	1	0	5	2	0	1	5	1	27
subadult male	0	0	0	0	0	1	0	1	2	0	0	1	5
subadult female	4	0	0	0	0	0	0	1	0	0	0	0	5
juvenile	5	1	0	0	0	0	4	2	0	0	0	1	13
infant	1	1	0	0	0	0	1	0	0	0	0	1	4
total	**16**	**7**	**3**	**2**	**2**	**1**	**11**	**7**	**3**	**1**	**5**	**5**	63

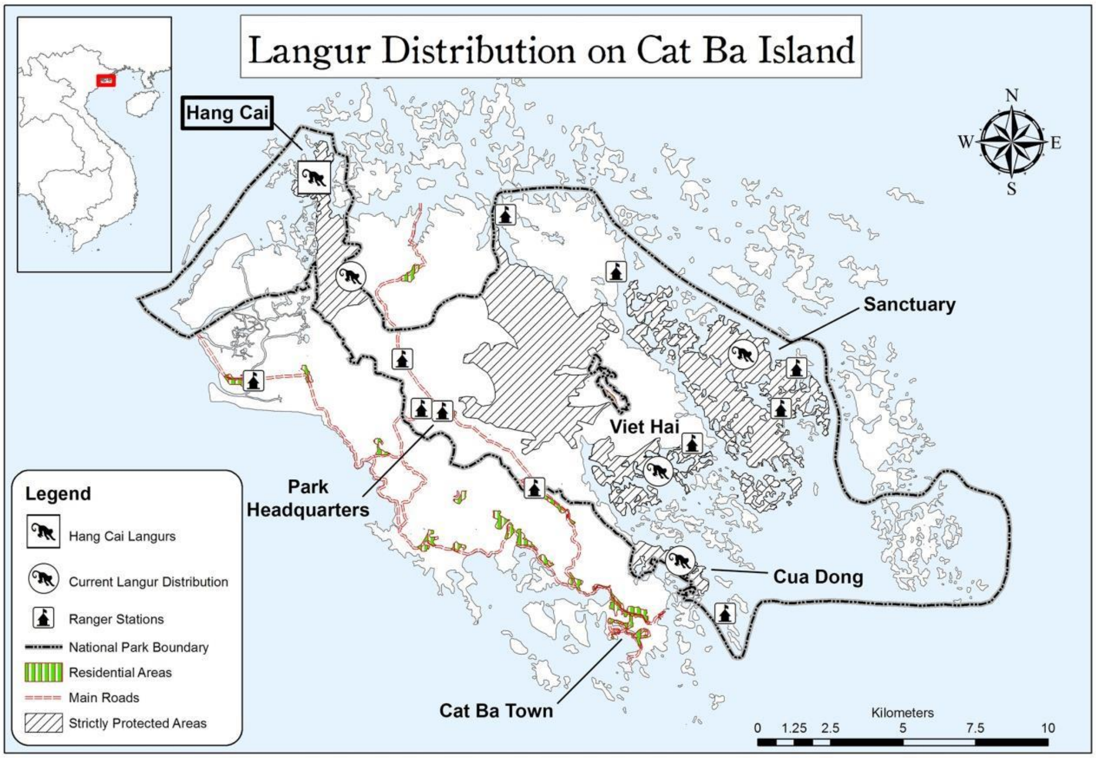


Figure 1.3: Map showing the distribution of Cat Ba langur populations in Cua Dong (southeast), the sanctuary (east), and Hang Cai (northwest) on Cat Ba Island, Vietnam. Map, with permission, from Leonard (2014).

1.6.3 Anatomy

1.6.3.1 *External Morphology*

As with other colobines, langurs have relatively short snouts and eyes farther apart than cercopithecines' (Washburn 1942; Oates and Davies 1994; Fleagle 2013). Colobines have a broad face, deep mandible, and a highly vaulted, but relatively small braincase (Strasser and Delson 1987; Oates and Davies 1994). Asian colobine thumbs are reduced, while they are absent in African colobines (Strasser and Delson 1987; Brandon-Jones 1989; Oates and Davies 1994; Fleagle 2013). The lateral fingers and toes are longer than the medial ones (Washburn 1942), and all fingers and toes are fairly long (Strasser 1992; Nadler et al. 2003); their feet are relatively longer than macaques'(*Macaca* spp.) (Washburn 1942).

Colobines typically have long legs and long tails compared to cercopithecines (Oates and Davies 1994; Fleagle 2013). Compared to cercopithecines, langurs have a slightly shorter humerus and radius and slightly longer femur and tibia (Washburn 1942). They also have a crural index (the ratio of lower leg:thigh length) lower than cercopithecines (Strasser 1992). Langurs have an intermembral index (IMI; the ratio of forelimb:hindlimb length) of 82-83, which fits within the range of Asian colobines (75-94) in general (Fleagle 2013); although limestone langur IMI is on the lower end, at only 76-76.5 (Huang and Li 2005; Workman 2010a). This IMI is associated with a half-arboreal/half-terrestrial form of locomotion (Huang and Li 2005).

This slender body type and long legs are helpful in leaping and running in a forest (Strasser and Delson 1987; Strasser 1992) while the tail may help gain momentum and propel the langur forward, acting as a balance (Burton et al. 1995). How the tail is held while traveling differs both within leaf monkey and even limestone langur species, although there is a general trend for it to move into a high arch when traveling quickly (Stevens et al. 2008). A limestone langurs' ease at navigating their petrous habitat (Huang and Li 2005) is due to them being a behaviourally flexible species (Workman and Schmitt 2012).

Weight for langur species ranges from 5.7kg (female silvered leaf monkeys, *Trachypithecus cristatus*) to 12.8 kg (male capped langurs, *Trachypithecus pileatus*), which is midrange for colobines in general (lightest: 4.2kg female olive colobus, *Procolobus verus;* heaviest: 21.2kg male proboscis, *Nasalis larvatus*) (Oates et al. 1994). Almost a quarter of adult body weight in colobines is stomach contents (Brandon-Jones 1989). Cat Ba langurs weigh 9-11kg (Schrudde et al. 2010), seemingly heavy for their size (Groves 2007). Males have a mean head-body length of 53.7cm while adult females average 53.0cm (Nadler and Ha Thang Long 2000), which is slightly smaller to that seen for François' (54.6cm male and 62.3cm female: Napier 1985; Brandon-Jones 1995; Nadler and Ha Thang Long 2000) and white-headed (61.3cm male and 56.6cm female: Huang and Li 2005; Li and Ma 1980) langurs. The tail is another 85.4cm for male and 85.3cm for female Cat Ba langurs (Nadler and Ha Thang Long 2000). This matches the reported tail length of 83.9-85.8cm (male) and 79.2-87.7cm (female) François' and white-headed langurs (Napier 1985; Brandon-Jones 1995; Nadler and Ha Thang Long 2000; Huang and Li 2005; Li and Ma 1980).

Langurs typically (although not always) live in unimale-multifemale breeding groups (Section 1.6.7). Intrasexual competition occurs in the course of group formation or takeover, but as there is only one male within a reproductive group, intrasexual competition is low on a daily level. It is suggested that males living without extreme intrasexual selection (unimale groups that do not come into contact with other males) have smaller body mass dimorphism than males of modular groups (Grueter and van Schaik 2009). Given that male langurs live in one-male polygynous units (i.e. highly biased sex-ratio) with potentially threatening lone males in proximity (i.e. occasional intrasexual competition), it is expected that they would be sexually dimorphic in order to fight for and defend their females (Mitani et al. 1996; Grueter and van Schaik 2009).

It is therefore interesting that there is little or modest sexual dimorphism between langur sexes, especially *Trachypithecus* (Jay 1963; Leutenegger and Kelly 1977; Burton et al. 1995; Pan and Groves 2004; Huang and Li 2005). This may be because the intrasexual selection that tends towards bigger body size is counteracted by the ecological need for a smaller body size; smaller bodies are more convenient for arboreal living, and they help conserve energy (Leutenegger and Kelly 1977).

Based on predictions for male canine size for unimale mating systems (Leutenegger and Kelly 1977; Plavcan and van Schaik 1992), it is unsurprising that *Trachypithecus* males have large canines (Groves 2001; Jablonski 2002). Male langurs have smaller testes than other primates (adjusting for body weight) (Schultz 1938). As testes size is intimately tied to the promiscuity of female primates (Møller 1988), the small testes of langurs implies that there is not very much intrasexual competition between males for conceptions. The fight for sexual access occurs premating, through group formation and defence (where body and canine dimorphism help), rather than postmating, through sperm competition (where testes size matters).

As with all limestone langurs, these animals are black with a pointed head crest, and species-specific colouration on the head/shoulders and rump/tail (Groves 2007; Figure 1.4). The Cat Ba langur has a distinctive low, wide, and conical crest (Groves 2007); although the lightest coloured area on a Cat Ba langur, it is often tipped with black (Brandon-Jones 1995). All of the limestone langurs also have long, light-coloured hair that goes from ear to ear, resembling a moustache (Groves 2007).

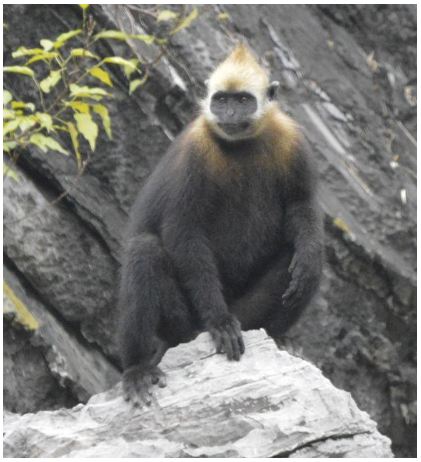
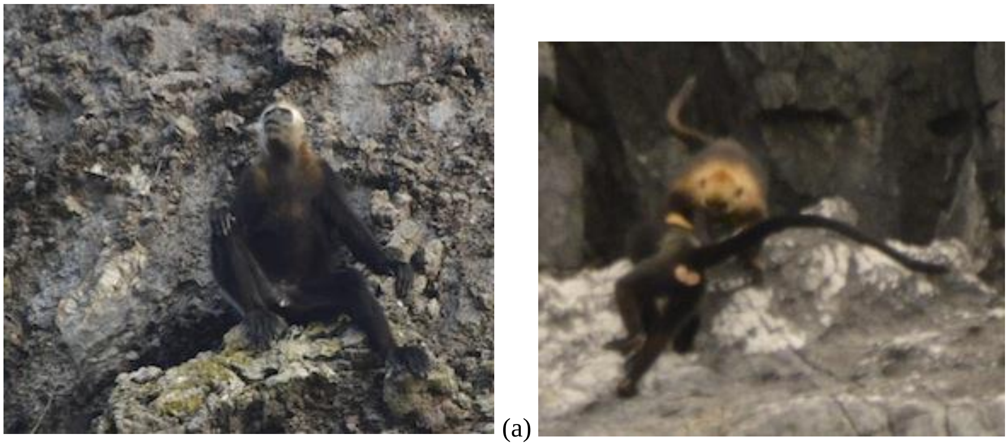


Figure 1.4: Subadult Cat Ba langur where moustache, colouration, and crest are visible. Photo taken Jan 2015 by R Hendershott

In Cat Ba langurs, adult pelage is dark brown/black, with the exception of the bright golden-brown to yellowish-white on their head to shoulders. The back hair appears brown at the roots, and is blacker towards the tips (Brandon-Jones 1995); the hairs are approximately 10-12cm long (Trouessart 1911). There is a V-shaped 'frosted' gray band that goes from the thighs to above the root of the tail on the monkey's back; the roots are the same colour as the body while the terminal 5mm are bright silver-gray (Nadler and Ha Thang Long 2000). This species, like the François' langur, has a back 'cape' of hairs (Nadler and Ha Thang Long 2000). Overall the colouration of Cat Ba langurs is similar to that of Nilgiri langurs (*Trachypithecus johnii*), which was the original reason it was considered a subspecies of *S. johnii* (Brandon-Jones 1995). However, genetic evidence suggests that the Cat Ba and white-headed langurs' pelage colouration is the result of a recent mutation after they had split from the François' langur ancestor (Liu et al. 2013a).

Langurs have little sexual dichromatism with the exception of females having a pubic patch of pale hairs and irregular skin colouration on their inner thighs (Brandon-Jones 1995; Nadler and Ha Thang Long 2000; Figure 1.5). Some report that male Cat Ba langurs have a small amount of yellow-orange hairs surrounding the penis (Brandon-Jones 1995) while others report that this is uncommon (Nadler and Ha Thang Long 2000); if this occurs, it was not apparent to me in this study. The easiest ways to tell an adult female from an adult male are the thigh patches and elongated nipples; testes and penis are difficult to see (Figure 1.6a). Another of the few things that differs between males and females is that the ischial callosities are separated in females (with the vulva between them; Figure 1.5), but joined in males (Brandon-Jones 1989; Figure 1.6b). Natal coats are flamboyant orange, a common feature of most *Trachypithecus* species (Groves 2007; Figure 1.7). Infants are born bright orange with no crest, and then start to change colour as they age. The purpose of being so visually obvious is still being contested, with the main hypothesis centred on it acting as an infanticide avoidance tactic (Treves 1997; Section 6.1.3, Chapter 6).

Figure 1.5: Adult female Cat Ba langur. Note: separated ischial callosities and white thigh patches. Photo taken Aug 2014 by R Hendershott



(a) (b)

Figure 1.6: (a) Adult male Cat Ba langur. Note: lack of thigh patches and small testes. (b) Juvenile male Cat Ba langur playing. Note joined ischial callosities. Photos taken Aug 2014 by R Hendershott

Figure 1.7: Newborn Cat Ba langur clinging to an adult female. Note: coat colour and lack of crest. Photo taken August 2014 by R Hendershott

1.6.3.2 *Specialised Digestion*

Colobines are primarily folivorous with physiological adaptations to a specialised leaf-eating diet. These include specialised salivary glands (Bauchop 1978), dentition (Kay and Hylander 1978; Oates and Davies 1994), stomach morphology (Caton 1999), and extended retention of the food for fermentation purposes (Caton 1999). Colobines have large salivary glands that produce an abundance of saliva, which most likely helps buffer the acidity of the stomach (Bauchop and Martucci 1968; Bauchop 1978; Oates and Davies 1994). As *Trachypithecus* must chew and swallow leaves before eating more (they are called ‘ingestive folivores’: Wright et al. 2008) it is a time consuming activity (Clutton-Brock and Harvey 1977a; Decker 1994). Intake affects the digestibility and speed with which the food passes through the gut in colobines, which in turn limits the amount an individual can eat (Edwards and Ullrey 1999). High cusped teeth with well-developed shear crests and small narrow incisors help in folding, slicing, grinding, and crushing leafy foods (Kay and Hylander 1978; Oates and Davies 1994). The large lower molars help in breaking down leaves and opening seeds (Lucas and Teaford 1994).

The stomach itself is a large, tubular, three-chambered, sacculated organ (Caton 1999). Having such a large stomach allows for food to be retained for longer, increasing fermentation efficiency (Bauchop and Martucci 1968; Parra 1978; Fleagle 2013). Indeed, there is a trend for the size of the stomach and the volume of the colon to be larger in folivorous species (Chivers 1994). The forestomach holds large amounts of food that is mixed with fermentation-aiding microorganisms in a slightly acidic (pH of 5.0-6.7) environment (Bauchop and Martucci 1968; Bauchop 1978). It is here that secondary compounds in the leaves are detoxified (Kay and Davies 1994). The hindgut morphology is similar to that of Cercopithecinae (Caton 1999). It does a similar job fermenting and retaining as much digesta as possible. Therefore, colobines have two fermentation chambers, the former of which is more developed and more efficient than that of Cercopithecinae (Caton 1999; Edwards and Ullrey 1999).

1.6.4 Diet and Activity

Activity budgets for primate species are highly dependent on the availability and location of important food resources as well as the evolved physiology of the species. Leaf-eating primates, such as langurs, have high rates of inactivity due to their high-fibre diet, which takes a lot of time to digest (Clutton-Brock 1977; Stanford 1991a; Dasilva 1992; Oates and Davies 1994; Edwards and Ullrey 1999; Kirkpatrick 2007). They also tend to show high rates of feeding due to the processing of bulky leaves (Clutton-Brock and Harvey 1977a; Decker 1994). They have relatively low rates of social behaviour, which may be due to energy constraints (Brandon-Jones 1989) or because of the nonmonopolisable nature of abundant leaves (Newton and Dunbar 1994). This sort of ubiquitous food source is also expected to lead to an egalitarian social structure (Section 1.6.7) and low levels of between-group competition for resources, making socialisation less important for within-group cohesion in a leaf-eating primate (Wrangham 1980).

This results in colobines spending 25-69% of their time inactive, 17-51% foraging, and less than 16% of their day in social behaviours (Table 1.2). This is different to the activity budget of primarily fruit eating macaques (Thierry 2007), who spend 15-32% of their time inactive, 19-45% of their day foraging, and up to a third of their day engaged in social behaviours (Hanya 2004; Kumar et al. 2007; Alami et al. 2012; Hambali et al. 2012). While foraging rates seem comparable, this is due to macaques spending more time searching for clumped fruits and colobines spending more time processing leaves (Newton 1992; Decker 1994; Agetsuma and Nakagawa 1998).

Table 1.2: Annual activity budgets for some colobines living in the wild. Numbers are percent (%) of each behaviour within the activity budget. Limestone langur data is expanded upon in Table 3.8. A dash (-) signifies that the original study reported a range. All values rounded to nearest integer.

	species	**inactivity/ rest**	**foraging/ feeding**	**social/ grooming**	**locomotion**	**'other'**	source
African	king colobus	61	28	1	9	1	(Dasilva 1992)
	(Colobus polykomos)	34	46	5	15		(McGraw 1998)
	Western red colobus *(Piliocolobus badius)*	30	45	6	19		(McGraw 1998)
	Tana River red colobus (*Piliocolobus rufomitratus*)	49	26	<1	23	2	(Decker 1994)^{a}
	Ugandan red colobus (*Piliocolobus tephrosceles*)	25-30	40-51	5-10	16-29		(Snaith and Chapman 2008)
	olive colobus *(Procolobus verus)*	35	39	7	19		(McGraw 1998)
	ursine colobus	57	26	3	13	1	(Djègo-Djossou et al. 2015)
	(*Colobus vellerosus*)	59	24	3	15		(Teichroeb et al. 2003)
	Angola colobus (*Colobus angolensis ruwenzorii*)	32	42	5	20	1	(Fashing et al. 2007b)
	guerezas	64^{c}	26	7^{b}	2	1	(Fashing 2001a)^{a}
	(*Colobus geureza*)	69	17	6	6	2	(Onderdonk and Chapman 2000)
Asian	Hanuman langurs (*Semnopithecus entellus*)	42	26	7	13	12	(Newton 1992)
	red-shanked doucs (*Pygathrix nemaeus*)	26	43	15	10	7	(Phiapalath and Suwanwaree 2010)
	black-shanked doucs (*Pygathrix nigripes*)	61	27	3	7	2	(Rawson 2009)
	black snub-nosed monkeys	35	39	16^{b}	10		(Long et al. 1998)
	(*Rhinopithecus bieti*)	29	39		19	14	(Grueter et al. 2013)
	capped langurs (*Trachypithecus pileatus*)	40	35	7	18		(Stanford 1991a)
	white-headed langurs (*Trachypithecus leucocephalus*)	52	13	14	15	7^{d}	(Li and Rogers 2004a)
	Delacour's langurs (*Trachypithecus delacouri*)	75	21	2	2	<1	(Agmen 2014)
	François' langurs (*Trachypithecus francoisi*)	52	23	2^{a}	17	6^{d}	(Zhou et al. 2007a)

[a] averaging of two groups
[b] includes groom, greet, social play, infant handling, display
[c] includes vigilance
[d] includes play and/or huddling, which could also be social

Diet also influences locomotion as folivores do not need to travel as far as frugivores to obtain enough food, as leaves are abundant. For example, frugivorous macaques spend 16-18% of their time traveling (Hanya 2004; Kumar et al. 2007; Alami et al. 2012) while folivorous colobines may travel as low as 2% of their activity budgets (Table 1.2). The more an animal concentrates on fruit eating, the more time they must spend moving, whereas the more they concentrate on leaves, the less time they spend moving (Agetsuma and Nakagawa 1998). While diet plays a role in determining activity budget, so do things like body mass: larger and heavier animals feed more to meet energetic demands (Oates 1987).

Colobines are specialised folivores, who have anatomy to allow for a diet high in leafy matter, including a sacculated stomach. They do, however, supplement this diet with a variety of leaves, fruits, flowers, seeds, lichen, bark, gum, insect galls, fungi, pith, roots, sap, and animal matter (Brandon-Jones 1989; Kirkpatrick 2007). Generally, over half of the diet is focused on leaves (30-92%), especially young leaves, with flowers making up 0-19% of the diet, and seeds and fruit contribute 5-49% of the diet (Table 1.3).

Table 1.3: Annual dietary budgets for some colobines living in the wild. Numbers are percent (%) of each food item within the dietary budget. A dash (-) indicates that a range was reported in the original study. Limestone langur data is expanded upon in Table 3.11. All values rounded to nearest integer.

	species	**young leaves**	**mature leaves**	**flowers**	**fruits**	**seeds**	**'other'/ unknown**	source
African	black colobus	18	19			58	5[a]	(McKey 1978)
	(*Colobus satanas*)	21[b]	18	3[c]	53[g]		5	(McKey et al. 1981)
	Tana river red colobus	54	2	20	24		1	(Decker 1994)[d]
	(Piliocolobus rufomitratus)	89	3	1	3	2		(Snaith and Chapman 2008)
	olive colobus	59	11	7	4	14	4	(Oates 1988)
	(Procolobus verus)							
	ursine colobus	32	21	2	33	3	9	(Djègo-Djossou et al. 2015)
	(*Colobus vellerosus*)	40	34	6	8	8	4	(Teichroeb et al. 2003)
	guerezas	24	29	1	37	1	7	(Fashing et al. 2007a)
	(*Colobus guereza*)	61	4	0	15		20	(Onderdonk and Chapman 2000)
Asian	capped langurs	54-70		19[c]	15-16		u/k	(Solanki et al. 2007)
	(*Trachypithecus pileatus*)	16	42	7	24	9	2	(Stanford 1991a)
	Hanuman langurs	17[b]	35	10[c]	25		14	(Newton 1992)
	(*Semnopithecus entellus*)	34[b]	8	27	30			(Hladik 1977)[f]
		50	5	19	26		<1	(Vandercone et al. 2012)[d]
	red-shanked doucs	55		4	34		8	(Phiapalath et al. 2011)
	(*Pygathrix nemaeus*)							
	black-shanked doucs	24	6	9	11	40	10	(Rawson 2009)
	(*Pygathrix nigripes*)							
	black snub-nosed monkeys	16[b]	5[e]		11		68	(Grueter et al. 2010)
	(*Rhinopithecus bieti*)							
	purple-faced langurs	46[b]	51		3			(Hladik 1977)
	(*Trachypithecus vetulus*)	58	5	11	26		0	(Vandercone et al. 2012)
	maroon leaf monkeys	37		11	19	30	3	(Davies and Baillie 1988)
	(*Presbytis rubicunda*)							
	Nilgiri langur	31[b]	27	9	25[g]		8	(Oates et al. 1980)
	(*Trachypithecus johnii*)							
	white-headed langur (*Trachypithecus leucocephalus*)	88		2	7	1	2	(Li et al. 2003)
	Delacour's langur	80		5	9 [g]		6	(Workman 2010a)
	(*Trachypithecus delacouri*)							
	François' langurs	64		4	26	7		(Hu 2007)
	(*Trachypithecus francoisi*)							

[a] leaf + floral buds, leaves of undetermined age
[b] young leaf + open and closed leaf buds or petioles or shoots
[c] flower buds + flowers
[d] averaging of two groups
[e] mature leaves + herbs
[f] only one of two time periods reported
[g] does not differentiate between fruits and seeds

1.6.5 Home Range

Home ranges are areas used by animals in the course of their lives, and are measured by documenting their movements and use of certain areas over time (Worton 1987). They are limited by their proximity to important resources, such as food (Li et al. 2003), sleeping sites (Barton et al. 1992; Zhou et al. 2007b; Zhou et al. 2011), water (Altmann 1974a; Barton et al. 1992; Campos and Fedigan 2009; Zhou et al. 2011; Zeng et al. 2013), and uncommon [but vital] sources such as saltlicks (Pages et al. 2005), bark (Fashing 2001a), or swamp plants (Oates 1978). In general, the minimum size of a home range is set by the need to fulfil daily energy, water, and sleeping requirements, while the maximum size is limited by travel, lack of familiarity, and physiological abilities for consumption and digestion (Kelt and van Vuren 2001). In other words, home range size may be a balance of the benefits of increasing a range and the costs of traveling within that range, which will be dependent on the animal's diet, body size, social organisation, and habitat type.

There is a general trend for more folivorous primates to have smaller home ranges than more frugivorous species, most probably due to the nonclumped and more ubiquitously distributed resources and low energy requirements of leaf-eating animals (Milton and May 1976; Clutton-Brock and Harvey 1977a). Terrestrial species tend to have larger home ranges than arboreal species, although that may be due to the nature of a two-dimensional habitat (Clutton-Brock and Harvey 1977a) or their tendency for a larger body size (Milton and May 1976).

Larger body size (contributing to primate biomass) is correlated with larger home ranges (Milton and May 1976), meaning that larger animals need more space (Kelt and van Vuren 2001) because of metabolic differences (McNab 1963). For example, primates that weigh over 15kg tend to require 6.5-150ha/individual [with the exception of Hanuman langurs, *Semnopithecus entellus*, who are often provisioned (Blaffer Hrdy 1977)], while primates that weigh 1-10kg require 0.1-34ha/individual (an exception being patas monkeys, *Erythrocebus patas*, who need 170 ha/individual), and primates under 1 kg use 0.15-2.4 ha/individual (Milton and May 1976). Similarly, larger group sizes (another form of increasing primate biomass) are also correlated with larger home ranges (Milton and May 1976).

Range use may also be affected by social factors such as proximity to other groups, (especially for unimale groups that are vulnerable to takeovers) (Cowlishaw 1997; Gibson and Koenig 2012), intergroup encounters (Struhsaker 1974), and degree of overlap between neighbouring groups (Martin 1984a). For example, Phayre's leaf monkeys (*Trachypithecus phayrei)* in unimale groups spend significantly less time than expected on home range borders that abut neighbouring groups than those that do not (Gibson and Koenig 2012). Ugandan red colobus (*Piliocolobus tephrosceles*) use a larger variety of their home range in months with more intergroup conflicts (Struhsaker 1974). Encounters between colobine groups occur more often when day (Fashing 2001b) and monthly (Newton 1992) ranges increase. Crowding via high population density limits colobine populations (Davies 1994), even when the ecological carrying capacity is not maximised (Yeager and Kool 2000).

1.6.6 Life History and Reproduction

There is not strict seasonality for births in all Colobinae [some species, e.g. Hanuman langurs, do have strict seasonality to births (Koenig et al.1997)], although there are a few birth peaks in some species, depending on the local climate and food availability (Struhsaker and Leland 1987; Borries et al. 2001; Nadler et al. 2003; Kirkpatrick 2007; Solanki et al. 2007; Qi et al. 2008; Jin et al. 2009a). These peaks tend to coincide with either birth or weaning occurring at times of peak food availability, or else births occurring at the end of peak food availability (Janson and Verdolin 2005). Births are likely in the dry and cold months of November-March for white-headed langurs in China (Jin et al. 2009a).

White-headed langurs first give birth around five to six years of age (Jin et al. 2009a), which is similar in other colobines (Wich et al. 2007; Qi et al. 2008), although later than provisioned Hanuman langurs (Sommer et al. 1992) and earlier than Hanuman langurs living in poor quality habitat (Borries et al. 2001). Hanuman langur females begin cycling around 29 months; they have a reproductive cycle an average of every 24.1 (Sommer et al. 1992) - 26.4 (Borries et al. 2001) days. The general trend is for an Asian female colobines' birth rate/year to be around 0.44-0.49 (Wich et al. 2007; Qi et al. 2008; Jin et al. 2009a), which translates into a female giving birth roughly every other year. There is evidence for long-lived Hanuman langurs, silvered leaf monkeys, and Phayre's leaf monkeys

(*Trachypithecus phayrei*) to experience menopause or reproductive cessation (Sommer et al. 1992; Borries and Koenig 2008; Roberts 2015).

Gestation is around six to seven months in Asian colobines (Newton 1987; Sommer et al. 1992; Borries et al. 2001; Kumar et al. 2005; Kirkpatrick 2007; Solanki et al. 2007). Interbirth intervals are between 15.3-29 months (Newton 1987; Struhsaker and Leland 1987; Newton and Dunbar 1994; Borries et al. 2001; Solanki et al. 2007; Wich et al. 2007; Qi et al. 2008); white-headed langurs' interbirth interval is 18.0-28.4 months (Jin et al. 2009a). Captive (Harley 1985) or provisioned (Sommer et al. 1992) Hanuman langurs have a much shorter interbirth interval and can breed throughout the year when they have consistent resources like human crops to raid (Newton 1987). Losing an infant early on reduces interbirth intervals (Harley 1985; Newton 1987; Struhsaker and Pope 1991; Sommer et al. 1992; Wich et al. 2007; Qi et al. 2008; Jin et al. 2009a; Yang et al. 2009).

Infanticide is a male reproductive strategy used by a number of mammals across a diverse array of taxa (Blaffer Hrdy 1979; Labov 1984; Mock 1984; Packer and Pusey 1984; Struhsaker and Leland 1987; Campagna et al. 1988; Lewison 1998; Borries et al. 1999), including Asian colobines (Sugiyama 1965; Wolf and Fleagle 1977; Newton 1986; Newton 1987; Newton 1994; Moore et al. 2010), and limestone langurs (Li and Rogers 2004b; Hu 2007; Zhao et al. 2011a; Yao et al. 2012). If a male takes over a reproductive group, it is in his own best interests to kill all of the dependent, nursing offspring of the former male where tenure is short (i.e. takeovers are frequent). Doing so causes the females to begin cycling sooner (Sommer et al. 1992), as evidenced by their shorter interbirth intervals (see above), allowing them to be impregnated by the infanticidal male as soon as possible (i.e. the sexual selection hypothesis). This both decreases resource competition for himself and his future offspring, and increases the number of offspring he can sire before he loses his resident male status from another takeover event (Blaffer Hrdy 1979). There is debate as to the efficacy (Harley 1985; Sommer et al. 1992) and intent (Bartlett et al. 1993) of this strategy, but in general alternative hypotheses (such as infanticide as a social pathology or the result of generalised aggression, resource competition, or high population density) to infanticide have not been as supported by the colobine data as infanticide being a sexually selected reproductive strategy (Newton 1986; Struhsaker and Leland 1987; Ross 1993; Blaffer Hrdy et al. 1994; Sussman et al. 1994; Beehner and Bergman 2008) although there are interspecific and population-based differences (Blaffer Hrdy 1979).

Infanticide is especially common in unimale group species (as Cat Ba langurs are: Section 1.6.7) because there is such a disparity in reproductive success between resident males and marginalised males (Struhsaker and Leland 1987). In multimale groups, paternity is not necessarily assured, and an infanticidal male may face a number of resident males willing to protect their potential offspring. The costs are thus not worth the small genetic benefit that may result (Ross 1993). Unimale group males and females, however, must always be on the lookout for lone males or groups of roaming sexually mature males who may possibly takeover the group (a loss to males) or kill group infants (a loss to females). Strange males or males that just took over a group commit the vast majority of observed infanticides (~91%) (Struhsaker and Leland 1987; Borries 1997).

Females have adopted countertactics to minimise the potential loss of their infant, both in the long and short term. A long-term form of infanticide reduction is forming a permanent association with a male (Sterck et al. 1997; van Schaik and Kappeler 1997). Short-term responses to a takeover or potential infanticide include: dispersing with the ousted male if they have a suckling infant (Zhao et al. 2011a); abruptly weaning (Beehner and Bergman 2008; Zhao et al. 2011a) spontaneously aborting if pregnant (Beehner and Bergman 2008); banding together to prevent an assault (Newton 1986; Borries 1997); or soliciting the strange male, even when unable to conceive (known as ‘pseudoestrus’) (Sugiyama 1965; Newton 1986; Brandon-Jones 1989; Ross 1993; van Schaik and Kappeler 1997). Once a female’s infant is killed, those females tend to mate with, and have the infanticidal male sire, their next infants (Newton 1987; Borries 1997; Beehner and Bergman 2008; Yamagiwa et al. 2009).

Cat Ba langurs have a very low reproductive rate; from 2001-2004 there were nine births and three deaths in the censused groups (Stenke and Chu Xuan Canh 2004). The reproductive rate is about one to three offspring per year for the species as a whole (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2008), giving a birth rate of 0.045 infants/reproductive individuals/year (Phan Duy Thuc et al. 2014). In stark contrast to these past years, however, 2014-2016 were an extremely productive time for Cat Ba langurs, with 20 infants being born on the island (Leonard et al. 2016a). This may call into question whether previous birth records accurately reflected reproductive patterns.

1.6.7 Social Structure

Langurs, being mostly leaf eaters, have less within-group competition for resources than cercopithecines (Wrangham 1980), and exhibit a more egalitarian social structure (Li and Rogers 2004b; Jay 1963), with affiliative and fairly benign intragroup interactions (Newton and Dunbar 1994). Note, however, that this may an oversimplification as some colobines do express dominance hierarchies (Blaffer Hrdy 1977; Amarasinghe et al. 2009; Borries et al. 1991) and, in addition to scramble competition, they also have a level of contest competition over limited food (Koenig 2000).

Langurs typically live in unimale-multifemale groups, or in all-male groups, although animals can also be solitary (Newton and Dunbar 1994; Yeager and Kool 2000; Nadler et al. 2003; Li and Rogers 2004b; Kirkpatrick 2007; Jin et al. 2009b). Male takeover and infanticide are associated with this type of grouping pattern (Boggess 1984; Teichroeb and Sicotte 2008; Zhao et al. 2011a), because there is a high potential reproductive benefit in obtaining a group of females, and a very high cost to not having a group in which to breed (Struhsaker and Leland 1987). Therefore, there is intense competition between males to acquire, monopolise, and keep fertile females. Male takeovers occur at an average of every 50.1 group months (range of 29-63 months) in white-headed langurs (Zhao et al. 2011a). Sometimes, when a resident male is ousted from his group, he leaves with the juveniles and infants he (presumably) fathered (Liu et al. 2013b), to save them from the potentially infanticidal male (Zhao and Pan 2006). That being said, extragroup copulations and siring of offspring have been noted in white-headed langurs, suggesting some nonresident males can gain reproductive opportunities (Liu et al. 2013b).

Some consider colobine females to be philopatric (i.e. males disperse at the age of sexual maturity) (Hu 2007; Kirkpatrick 2007) because of the observation of stable female group membership and the presence of solitary and extragroup adults (Struhsaker and Leland 1987; Newton and Dunbar 1994). Other evidence points to colobines being male philopatric, or dual dispersal (Marsh 1979; Moore 1984; Hohmann 1989; Stanford 1991a; Newton and Dunbar 1994; Borries et al. 2004; Li and Rogers 2004b; Jin et al. 2009b). At any rate, female dispersal is not uncommon in colobines (Marsh 1979; Moore 1984), and female-based nepotism or differentiated relationships are unlikely (Wrangham 1980; Moore

1992). A recent review of dispersal patterns shows that all three types of dispersal are seen in both Asian and African colobines, with dual dispersal being the most common (Matsuda et al. 2015). Among the closely related white-headed langur groups, multigenerational females are related (Liu et al. 2013b), suggesting that they either dispersed together or remained in their natal range. This implies that female Cat Ba langurs in a group may likewise be related.

Limestone langur group sizes range from 2-26 individuals. White-headed langurs have an average group size of 5.3-9.1 (Huang et al. 2002; Huang et al. 2003; Li and Rogers 2004b; Li and Rogers 2007; Huang et al. 2008a; Jin et al. 2009b; Yin et al. 2011). However, Laotian langurs living in areas free from hunting have group sizes of 15-25, suggesting this may be the natural, undisturbed state of langur social groups (Steinmetz et al. 2011). On average, unimale white-headed langur groups have one adult male, 5.1 adult females, 0.1 subadult males, 2.6 juveniles, and 2.9 infants (Jin et al. 2009b). This size group is defensible against other males and, thus, fairly stable. The relatively rare multimale groups contain 2-3 adult males, 1-5 adult females, 0-2 subadult males, 0-7 juveniles, and 0-2 infants (Jin et al. 2009b). This large group is deemed transitory and unstable, due to be broken up into unimale units (although multimale groups of *Semnopithecus* are not uncommon: Kirkpatrick 2007). Bachelor groups are smaller than reproductive groups and are comprised of 1.3 adult males, 1.3 subadult males, and 2.6 juveniles (Jin et al. 2009b).

While the lower limit on group size is likely set by predation threat (Wrangham 1980; van Schaik 1983; Anderson 1986; Hill and Lee 1998), the upper limit is thought to either be set by resource competition or infanticide risk. As folivorous species rely on leaves, which are not monopolisable, resource competition suggests they should live in large groups (Clutton-Brock and Harvey 1977b). It is therefore surprising that folivorous species live in such small groups (Janson and Goldsmith 1995). However, folivores do not in fact have ever-abundant resources (van Schaik and van Noordwijk 1988; Snaith and Chapman 2005) and they experience both scramble and contest competition for resources, especially in the dry season (Koenig 2000). They feed selectively, are food-limited, and their resources vary in quality throughout space and time (Koenig 2000; Li et al. 2003; Snaith and Chapman 2005; Borries et al. 2008; Snaith and Chapman 2008; Harris et al. 2009). Thus, the larger the group, the larger the home range (Fashing et al. 2007; Gillespie and Chapman 2001; Oates 1994; Snaith and Chapman 2008; Teichroeb and Sicotte 2009), and the day range (Wrangham et al. 1993), with more energy being put into traveling between food patches (Gillespie and Chapman 2001; Snaith and Chapman 2008). This suggests there are energetic consequences to larger group sizes (i.e. that scramble competition is occurring). Additionally, females in larger groups have lower reproductive success (Borries et al. 2008; Snaith and Chapman 2008; Zhao et al. 2011b) and must spend more time feeding (Teichroeb et al. 2003), while infants develop slower (Borries et al. 2008). Therefore, there are ecological limitations and energetic restrictions to group size (Janson and Goldsmith 1995).

The chance of male takeover and infanticide may be another factor that sets a maximum on overall group size and number of females (Yeager and Kirkpatrick 1998). Large groups are at more of a risk of being taken over, as they present a more desirable target for bachelor males (Janson and Goldsmith 1995; Steenbeek and van Schaik 2001). Group females may be responsible for managing how many females are allowed to join the group, or dispersing females may be less attracted to joining a group with many females (Teichroeb et al. 2009a). Females may also chose to immigrate out of a nonideal group, which is easier for Asian colobines who have nonclumped resources and do not face high predation pressure (Sterck 1999; Kirkpatrick 2007). Therefore, group size is limited by social factors (e.g. infanticidal risk, social stress) as well as ecological ones (e.g. resource availability, predation pressure).

The group size of Cat Ba langurs varies, with reports of 8.6-10.3 in 1990, 5.6-6.7 in 1999 (Nadler and Ha Thang Long 2000), 3.7 in 2004 (Stenke and Chu Xuan Canh 2004), 6.1 in 2010 (Schrudde et al. 2010), and 4.67 in 2014 (Phan Duy Thuc et al. 2014). Currently there are 58 langurs on the island, divided into 11 groups (Lees et al. 2014), giving an average group size of 5.3. It is probable that group sizes used to be larger when there were more langurs, although no information exists pre-1990 (Nadler and Ha Thang Long 2000).

1.7 Conservation Issues of Limestone Langurs

All limestone langurs are under threat of extinction. Laotian langurs are listed as an IUCN Vulnerable species (Timmins and Boonratana 2008); François' (Bleisch et al. 2008c), and Hatinh/Indochinese black langurs (not recognised as separate species by IUCN redlist) (Le Xuan Canh and Timmins 2008) are Endangered; Delacour's (Nadler et al. 2008), and Cat Ba⁄white-headed langurs (not recognised as separate species by IUCN redlist) (Bleisch et al. 2008a) are all Critically Endangered. The major threats to limestone langurs are loss of habitat to agriculture, development, grazing by goats, or quarrying; firewood collection and logging; illegal hunting for traditional medicine, meat, and live capture for the pet trade – all of which are ineffectively monitored with little enforcement of laws (Huang et al. 2002; Nadler et al. 2003; Hu et al. 2004; Le Khac Quyet 2004a; Nadler 2004; Stenke and Chu Xuan Canh 2004; Wang and Jin 2004; Harding 2010; Workman 2010a; Harding 2011).

The Cat Ba langur has been on the Top 25 Most Endangered Species List since 2000 and is listed as Critically Endangered by the IUCN due to their small population size, the effects of hunting, habitat disturbance, and fragmentation (Bleisch et al. 2008a; Leonard et al. 2016b). As of September 2014 there were 63 Cat Ba langurs left in existence, 36 of which were adults, 10 subadults, and 17 younger animals (Lees et al. 2014; Table 1.1).

Hunting was the biggest cause of population decline up until the CBLCP (established 2001) (Schrudde et al. 2010) started and national laws were made against hunting for the sake of conservation and biodiversity (Warne and Tran Lien Phong 2002; Rawson et al. 2011). Langurs are not difficult to catch and/or kill by hunters due to their curiosity and slow movement (Ngoc Mai 2004); they rarely run from people or hunters, even when guns are used in the area (Steinmetz et al. 2011) or after shots are fired (Brandon-Jones 1995). Poachers have been able to take advantage of sleeping cave use; an entire group can be wiped out by hunters putting a net over the cave entrance while they sleep (Nadler 2004; Nguyen Manh Ha 2006). From 1970-1986 an estimated 500-800 Cat Ba langurs were killed by hunters (Nadler and Ha Thang Long 2000). Poachers kill the langurs for traditional medicine, food, and the pet trade, often destined for China (Nadler et al. 2003; Bleisch and Zhang 2004; Tran Thu Hang 2010). The medicinal wine made from langurs is reputedly for digestion, rheumatism, and general health (Tan 1985; Huang et al. 2002).

The current biggest threat to Cat Ba langurs centres not so much on poaching, but on the booming human population and uncontrolled tourism industry on Cat Ba Island. In the 1980s the human population began to grow on Cat Ba Island (Stenke and Chu Xuan Canh 2004; Nguyen Van Quan et al. 2010; Thanh Van Mai and Maani 2010). In the 1990s the economy was based on agriculture and fishing, but since tourism has increased these have declined drastically (Stenke and Chu Xuan Canh 2004; Thanh Van Mai and Maani 2010). Many locals, especially in Cat Ba town (where 70% of locals live: Nguyen Van Quan et al. 2010), cater to the 1.5 million tourists that pass through the island on an annual basis, all of whom require resources (Thanh Van Mai and Maani 2010). At times, their use of these resources are in direct conflict with the langurs' needs. Tourism has caused pollution, an expansion of infrastructure, and overuse of underground water (Thanh Van Mai and Maani 2010). Limestone quarrying has seen habitat literally blown apart (Day and Chenoweth 2004; Nadler et al. 2007). Firewood collection by villagers and forest fires from local honey collectors has furthered the destruction of the forests (Nadler et al. 2007). The overall effect is one of large scale devastation, degradation of the biodiversity, and forest fragmentation.

The consequence of this fragmentation is massive habitat loss and social isolation between langur groups (Schrudde et al. 2010) with groups being isolated from one another since the 1990s (Nadler et al. 2003). This means that animals are not free to disperse and interbreed, limiting gene flow and increasing inbreeding and the effects of genetic drift (Freeman and Herron 2004). This is problematic as a species' ability to survive in the future is highly dependent on their vast stores of genetic variation (Allendorf and Leary 1986; Lacy 1997). One way of measuring this variation is through average hetero- and homozygosity of a population (Ballou et al. 2010). Homozygous (i.e. inbred or those who underwent genetic drift) individuals have lower fertility and mating ability, mortality and survivability, disease resistance, growth rates and development, and stability (Lacy 1997; Cowlishaw and Dunbar 2000). Genetic diversity and heterozygosity is lost in smaller populations, on islands, and among endemic species, much faster than in larger/mainland populations or widely distributed species (Frankham 1998; Ballou et al. 2010). All of these traits describe a number of threatened primates. For example, banded surilis (*Presbytis femoralis femoralis*) in Singapore went through a population bottleneck (a low of 15-20 individuals) due to deforestation and road constructions in the 1970-80s, and the resulting population (~40 individuals) has extremely low genetic diversity (Ang et al. 2012). Out of 141 Tonkin snub-nosed monkeys (*Rhinopithecus avunculus*) tested from a single, fragmented population in Vietnam, there was absolutely no mitochondrial variability on the loci tested (Ang et al. 2016), which suggest that they are living with extremely low levels of genetic diversity. This places this species at extremely high risk of extinction. Therefore, a major threat to Cat Ba langurs is lost genetic variation, which has implications for long-term viability beyond the effects of habitat loss.

Whereas the Cat Ba langurs used to be so abundant that they were shot as pests or for fun, and could be seen all over Cat Ba (Nadler and Ha Thang Long 2000), they are now fragmented into just two breeding populations that cannot expand or disperse beyond their small areas (Nadler et al. 2007; Schrudde et al. 2010). Viability of the species depends upon those subpopulations (one of which is nonreproductive) being able to interbreed. However, the vast distance, lack of habitat corridors, and lack of continuity between the groups makes dispersal incredibly difficult.

Chapter 2: Methods

2.1 Study Site

2.1.1 Geography of Cat Ba Island

Cat Ba Island (20°42'-20°55'N; 106°54'-107°10'E) is one of 366 of islands in the Cat Ba Archipelago, in the south of the famous Ha Long Bay (an UNESCO World Heritage Site as of 1994) in Vietnam (Mark 2009). It is the only location that Cat Ba langurs (*Trachypithecus poliocephalus)* can be found in the wild. In 2004 the Cat Ba Archipelago Biosphere Reserve was created (Schrudde et al. 2010). The island itself is about 140km^2 (Stenke and Chu Xuan Canh 2004) of mature karst landscape with sharp, rugged limestone karst peaks jutting straight up out of the water and coming to a razor sharp point approximately100-200 metres above sea level (Sterling et al. 2006). This scenery is the main draw to Ha Long Bay for tourists.

Southeast Asia has about 400,000km^2 of karst (Clements et al. 2006), 60,000km^2 of which is in Vietnam, covering 18% of the country's land area (Tuyet Do 2001). Limestone, a fossiliferous material, is formed by calcium and magnesium carbonate building up on the ocean floor from marine organisms (Clements et al. 2006). Around 370-224 million years ago there was a shallow sea covering northern Vietnam that allowed for the marine organisms to be deposited up to three kilometres thick in some areas (Sterling et al. 2006). The limestone deposits were distorted when the tectonic plates moved (Nguyen Van Quan et al. 2010)– some of the blocks of deposit eroded, creating hills and valleys and sinkholes (Urich 1989; Mark 2009). Softer materials were lost to mechanical and chemical weathering (Clements et al. 2006). The limestone is covered in white, weathered silt (where magnesium, strontium, and uranium were leached) (Hajna 2003) and orange/brown flowstone (probably organic compounds like fulvic and humic acids runoff from surface leaching, dripping out of cracks in the rocks) (White 1988).

Some limestone karsts are steep mountains while others are conical hills called mogotes (Urich 1989). When rainwater, which traps acids in the atmosphere, contacts limestone, the limestone begins to dissolve (Sterling et al. 2006; Mark 2009). This leads to hollow cavities, or caves, throughout the limestone hills (Mark 2009). Small springs or reservoirs occur underground from the water run off (Urich 1989), although there is no fresh water source on the island. When the corrosion occurs at sea level it leads to foot caves, which can sometimes be navigated by boats. Occasionally these caves collapse, resulting in sinkholes (often grouped or occurring in a line) (Mark 2009). The whole limestone environment is covered in fractures, pockmarks, caves, and short-lived springs (Day and Chenoweth 2004).

2.1.2 Plants on Cat Ba Island

A limestone karst environment is quite harsh in terms of soil quality, forest abundance, and digestibility of associated plants. The porous nature of the limestone makes it difficult for fresh water to be retained in either rock pools or soil, which results in an environment that is fairly dry with irregular, shrubby patches of vegetation (Nisbett and Ciochon 1993; Qin et al. 2012). In addition, the soil is alkaline, low in zinc and phosphorus (Urich 1989), and thin (van Beynen and Townsend 2005), meaning plants have to fight for water on the dry, porous limestone (White 1988; Clements et al. 2006). The Cat Ba Island habitat is classified as ‘tropical moist deciduous’ and ‘karst forest’ (Nisbett and Ciochon 1993). Dipterocarps, a family of evergreen tropical trees, are the primary flora in several limestone karst locations (Nisbett and Ciochon 1993) where the soil is deep enough for them to grow (Clements et al. 2006). Dipterocarps undergo mast fruiting at irregular intervals (Sterling et al. 2006). While these plants are able to survive dry conditions in general, overall growth on limestone karst is stunted (Day and Chenoweth 2004).

In addition to the challenges faced by being on limestone, vegetation on Cat Ba has suffered from logging. There is little primary forest on Cat Ba, as it has mostly been cut down (Nadler and Ha Thang Long 2000). Even the trees on the steep, unproductive karst cliffs have been altered by honey collection and their associated [unintentional] forest fires, which destroys an estimated 15-20% of mountaintop vegetation in Cat Ba National Park (CBNP) each year (Nadler and Ha Thang Long 2000).

On the karst cliffs of Cat Ba Island, langur habitat may be divided into four mountain types, with certain plants commonly found in each type (Nguyen Hiep pers.

comm. 2014). These are here designated ‘steep cliffs’, ‘summits’, ‘exposed slopes’ and ‘valleys’, approximately corresponding to the terms ‘cliffs’ ‘hilltops’, ‘hillsides’ and ‘valley basins’, respectively, used in some other studies (e.g. Zhou et al. 2013a; Huang et al. 2015a). The bottoms of the hills are relatively wet and closed-canopy (Liu et al. 2004), and house the tallest vegetation (Li and Rogers 2005b). The plants are dense and the soil is able to support large trees as well as shrubs, vines, and grass at this low level. This is especially true if the bottom of the hill slopes into a valley, where soil has a chance to gather (Nisbett and Ciochon 1993; Nguyen Van Quan et al. 2010; Yin et al. 2011). Valleys are the moistest, richest areas, with almost all Cat Ba flora represented and, for François’ langurs (*Trachypithecus francoisi*), has the most amount of food species available (Huang et al. 2008b). Exposed slopes have less water than valleys, with the flora scattered. There is only a thin layer of soil (Yin et al. 2011). The flora is still fairly rich, with drought-tolerant, sun-loving plants taking a starring role, such as short grass, vines, and shrubs (Liu et al. 2004). Cliffs present an additional challenge to plants: they must take root in vertical crevices with almost no shade, even less water, and no protection from the elements (sun, wind, rain, monsoons). What sandy soil does occur on these steep slopes is very thin, except for its lining of sinkholes (Liu et al. 2004). The plants on the summit tend to be short due to the dry environment and exposure to harsh elements and not much soil: shrubs, grasses, and other low growing species are found there (Liu et al. 2004; Qin et al. 2012). Often they are succulents, evolved to deal with such harsh conditions.

2.1.3 Nonhuman Animals on Cat Ba Island

Vietnam in general has high species richness, and limestone karst in particular has high species diversity and specialised, endemic species (Clements et al. 2006; Sterling et al. 2006). The Cat Ba Archipelago has the most biodiversity in Vietnam (Nguyen Van Quan et al. 2010). Cat Ba Island is home to 2,380 animal species, 11.8% of which are terrestrial animals (Nguyen Van Quan et al. 2010). There are a number of species that are highly endangered or extinct, existing only as museum specimens or in the memories of poachers.

The presence of others are difficult to confirm, but their appearance on restaurant menus implies they must still be around.

There is little information on Vietnam's karst fauna (Tuyet Do 2001), but from the few sources that do exist (Nadler and Ha Thang Long 2000; Sterling et al. 2006), the authors include the following mammals: serow (*Capricornis maritimus*; rare), wild pigs (*Sus scrofa*; possibly locally extinct), common barking deer (*Muntiacus nigripes*; unconfirmed), leopard cat (*Prionailurus bengalensis*; rare), golden cat (*Catopuma temminickii*; rare), fishing cat (*Prionailurus viverrinus*; rare), ferret badger (*Melogale moschata*; poacher reports), small Indian civet (*Viverricula indica*), common palm civet (*Paradoxurus hermaphrodius*; poacher reports), giant black squirrel (*Ratufa bicolor*), red-bellied squirrel (*Callosciurus erythraeus*), striped tree squirrel (*Tamiops maritimus*), short-tailed porcupine (*Hystrix brachyura*; rare), and several bat species. The only sympatric primate species to Cat Ba langurs on the island is the rhesus macaque (*Macaca mulatta*) (Nadler and Ha Thang Long 2000). The cats and civets may be a predatory threat to Cat Ba langurs (as similarly-sized cats have been known to prey on similarly sized animals in Thailand: Grassman et al. 2005; Borries et al. 2014), although it is unknown if they use the same type of environment (e.g. cliffs and hills).

Twelve amphibians and 20 reptiles have been documented on the island, although no details are provided on what those are (Nadler and Ha Thang Long 2000). Poachers are known to catch multiple species of snake, some of which may be potential predators or threats to the langurs (Nguyen Cam pers. comm. 2014). As evidence of this, there were cases where ex-poachers described cutting open a python (no species documented) and seeing a langur inside, or watching a python fall out of a sleeping cave wrapped around an adult langur (Nguyen Cam pers. comm. 2014). Accidental bites from any of the numerous venomous snakes are not unlikely, as that fate has befallen at least one captive Cat Ba langur at the EPRC (T Nadler pers. comm. 2014).

Overall there is not a great diversity or a large number of birds on the island. Birds documented include: black kites (*Milvus migrans*), large-billed crows (*Corbus macrohynchos*), red-whiskered bulbul (*Pycnonotus jocosus*), plain prinia (*Prinia inornata*), common stonechat (*Sazicola torguata*), olive-backed pipit (*Anthus hodgsoni*), common kingfisher (*Alcedo atthis*), and the Pacific Reef egret (*Egretta sacra*) (Nadler and Ha Thang Long 2000). Some locals report that there used to be large raptors (possibly white-bellied sea eagles; *Haliaeetus leucogaster*) but they have mostly been hunted or stopped coming to

Cat Ba (Nguyen Cam pers. comm. 2014). It is possible that historically large eagles were a threat to infant langurs, but that is unknown. There is evidence that kites are big enough to carry off infants (reported for Hanuman langurs, *Semnopithecus entellus*: Blaffer Hrdy 1977:83). According to Nadler et al. (2003) there are no natural predators (besides humans) on Cat Ba Island for the langurs, but this is contrary to ex-poacher and locals' reports of seeing Cat Ba langurs killed by other species, such as constrictors and raptors.

There were a few animals that I saw repeatedly to interact with or be in proximity to the langurs throughout my study period. These include kites, crows (Figure 2.1), and squirrels (giant black squirrels and an unidentified gray squirrel). Other than these few observations, there was no other evidence of interactions between langurs and other animals. It is, however, still possible that predation by nonhumans is something for which the langurs must remain vigilant and adjust their behaviour accordingly.


(a) (b)

Figure 2.1: Crows (a) swooping on, and (b) chasing langurs; they were successful at getting the langurs to move from the area. Photos taken April 2014 by R Hendershott

2.1.4 Human Population on Cat Ba Island

There is evidence that humans were living in caves on Cat Ba Island 25,000-7,000 years ago (Nguyen Thi Son et al. 1999; Nguyen Van Quan et al. 2010). Although specific numbers are not documented, it is reported that the population of Cat Ba used to be quite low until settlers were brought in after the China-Vietnam war (1978-1979) (Nadler and Ha Thang Long 2000). The people living on Cat Ba Island are predominantly of the major Vietnamese ethnic group, Kinh, and Chinese-Vietnamese (96.17%) (Thanh Van Mai and

Maani 2010). In 1986 there were 5,850 people; 10 years later this had jumped to 8,400 (Nguyen Van Quan et al. 2010). In 1999 there were 12,723 people, or 3,213 families, in seven locations: Cat Ba town – by far the largest community – , Chan Chau, Zuan Dam, Hien Hao, Gia Luan, Phu Long, Viet Hai, and the CBNP headquarters) (Nadler and Ha Thang Long 2000). Ten years later there were 15,500 people living on the island (Thanh Van Mai and Maani 2010); it is projected that by 2020 there will be 20,242 Cat Ba inhabitants (Nguyen Van Quan et al. 2010).

Most Cat Ba Island locals live in poverty, as defined by the United Nations poverty indicator of less than $1USD/day, and have limited education and health care services (Thanh Van Mai and Maani 2010). This puts considerable pressure on families to exploit natural resources (Jha and Bawa 2006) especially for those living in proximity to the biosphere reserve, CBNP, and the buffer zone (Thanh Van Mai and Maani 2010). Exploitation includes cutting trees, collecting firewood, trapping animals, collecting honey, mining limestone, allowing animals to graze, and planting fields (Nadler and Ha Thang Long 2000; Thanh Van Mai et al. 2011). Improving living conditions for local villagers should alleviate some of the pressure locals put on the environment (Nadler et al. 2003).

The majority of locals used to focus their efforts on fishing, aquaculture, and other sources of livelihood from the ocean; now only 40% live in rural areas making their living from agriculture, and there is a disparity in wealth between those living in rural vs. urban settings (Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). In the last 15-20 years, a lot of locals' attention has turned to tourism (Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). Tourism is the most profitable sector of the local economy, bringing in a projected 1,100 billion VND ($69 million USD) in 2015 (Thanh Van Mai and Maani 2010), and most people on the island interact with and earn money from tourists (Nguyen Thi Son et al. 1999). An increase in tourism has increased the number of people who immigrate to Cat Ba for jobs in hotels, restaurants, or tour companies (Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). The rapid development of tourism has led to massive infrastructure development, road construction, overexploitation of fresh water, traffic, pollution, and waste (Nguyen Van Quan et al. 2010; Thanh Van Mai et al. 2011)

In 1999, 50,600 Vietnamese tourists and 20,100 foreign tourists visited the island (Nadler and Ha Thang Long 2000). Ten years later, over one million tourists visited the island (cited in Thanh Van Mai et al. 2011). Roughly 1.6-1.7 million tourists visit the island each year (N Leonard pers. comm. 2016), with an annual growth rate of 22% (Thanh

Van Mai and Maani 2010). Most stay in Cat Ba town, at the southwestern side of the island where the majority of hotels are concentrated. As of 2008, there were 107 hotels with 2,000 rooms able to accommodate 5,000 tourists a day (Thanh Van Mai and Maani 2010).

Tourists tend to hike in CBNP, rock climb, kayak, bike ride, and take day or multiday tours around the bay. Although there is no official, legal, tourism of the langurs (their population is too low for ecotourism: Nadler et al. 2003) it is quite common for tour companies to stop and watch the langurs if they are in an easily visible spot. Without any regulations or lessons on how to act around the langurs, many tourists and tour guides will deliberately try and disturb the langurs in order to get them to move around. Some of the langur groups in the sanctuary are so well habituated to people that quite a number of kayakers reported being able to almost reach out and touch them as they passed by (C Johnson pers. comm. 2014).

2.2 Study Groups Home Range - Cua Dong

Cua Dong is an inlet on the southeastern corner of the island (Figure 2.2). Some areas are calmer and more protected from the elements, humans, and traffic than others within Cua Dong (Figure 2.3). There are coves (that are more sheltered than the hills that face the ocean) present in both langur groups' home range. There is an internal side of the inlet (made up mostly by coves) and an external side, which faces open ocean (made up by coves and mountain faces). It should be noted that although this area is referred to as 'open ocean', there are numerous small islands in the vicinity, probably helping to shield the external side from some wind, rain, and currents.

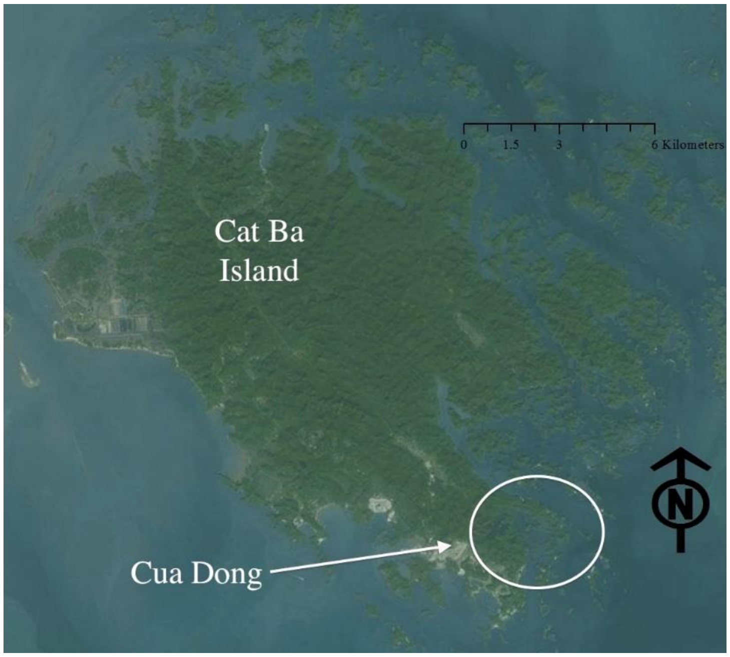


Figure 2.2: Map of Cat Ba Island, northeastern Vietnam. Map source: ArcGIS.

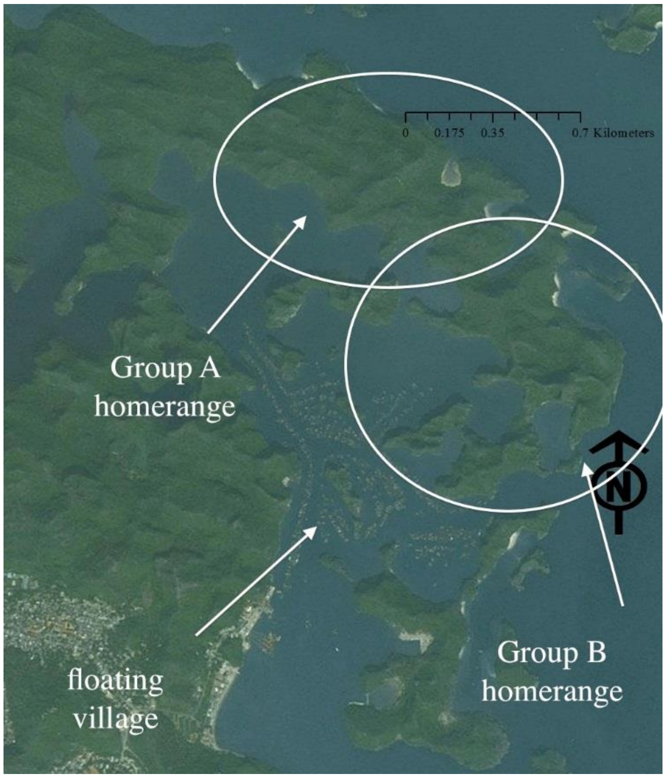


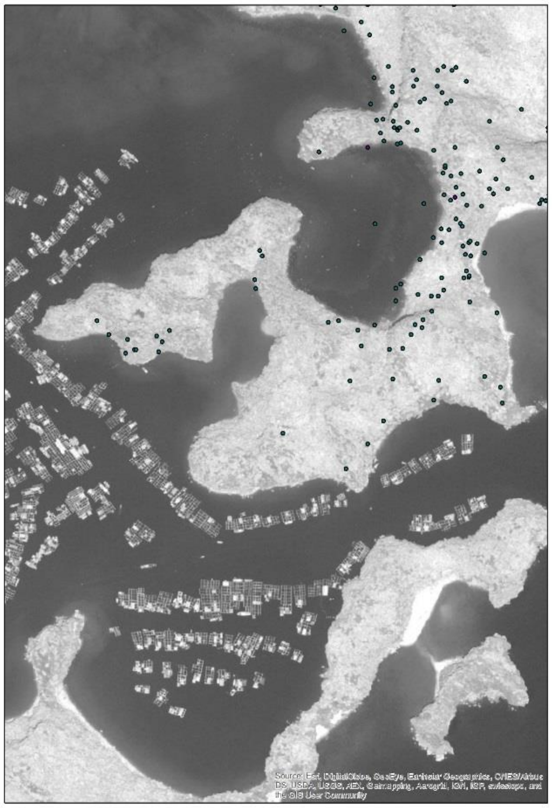
Figure 2.3: Map of Cua Dong with rough home ranges for Groups A and B. Note: coves and hills facing west are more protected than those facing east; there are coves that are more protected than hills facing the ocean directly; and all of Cua Dong is in proximity to humans (floating villages, tourists, traffic, fishing boats, etc.). Map source: ArcGIS.

There are few places in Cua Dong that are easily accessible to humans; some exposed slopes end on beaches, but the majority of the ocean-facing hillsides are cliffs that drop straight down into the water (or are undercut). Very few observations were made from land; most were at low tide when I was able to walk out onto the beach.

Cua Dong lies within the CBNP boundary, covering roughly 1.1km^2. Invasive activities (tree cutting, animal collecting, etc.) are therefore banned and are monitored by the park rangers. However, within the area human presence at water level is quite prominent, and results in high levels of activity. There are hundreds of floating homes, forming vast villages complete with dogs, chickens, cats, children, boats, aquaculture, stores, and copious amounts of waste. These are visible from the internal side of the inlet, and human activity can be heard from all areas of the Cua Dong langurs' home ranges. The external side of the inlet is heavily trafficked by tourist and fishing boats.

Cua Dong was selected as the area for study because of ease of access and because the langurs there are less protected/monitored than the sanctuary populations. Cua Dong lies within the CBNP boundary but outside the specially protected sanctuary zone that has extra patrols. Therefore, my presence along with my boat driver, who is a CBNP ranger, provided an extra layer of protection to these two groups that are exposed to human floating villages (Figures 2.4 and 2.5), boat traffic, tourists (Figure 2.6), and fishermen.

Figure 2.4: Floating homes surrounding Cat Ba langur habitat in Cua Dong. Photo taken March 2014 by R Hendershott



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.5: A satellite image shows sightings of Group B (green dots) in relation to their proximity to floating homes around Cua Dong. Map source: ArcGIS.

Figure 2.6: A tourist kayaker paddles by while a Cat Ba langur female from Group B jumps through water in Cua Dong. Kayakers routinely get within 5-15 metres of this Critically Endangered species. Photo taken January 2015 by R Hendershott

2.3 Cat Ba Langur Conservation Project and Cat Ba National Park

The Cat Ba Langur Conservation Project (CBLCP) works with local people and businesses, government agencies, and international conservation groups to monitor, protect, and spread information about the langurs. Due to the work of the CBLCP and national laws against poaching, known hunting of the species has been eradicated (Schrudde et al. 2010).

As of 2010 there were roughly 200 locals who helped with the various programs associated with the CBLCP (Schrudde et al. 2010). There are unarmed ‘bodyguards’ (some of whom are exhunters of the species) that protect the langurs from poachers (Stenke 2001; Stocking 2003; Schrudde et al. 2010). These ranger guards are also responsible for informing the locals in the communes about why the langurs need protecting and the ecological importance of preserving biodiversity, wild animals, and natural forests (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2010). The CBLCP has a presence in the schools on Cat Ba, teaching children about the importance of saving their endemic species (Le Thi Ngoc Han pers. comm. 2013). Indeed, throughout the course of this study it was often children who showed the most pride and interest in saving their local monkeys.

Cat Ba National Park was established in 1986 and covers 85km^2 – over half of the island (Stenke and Chu Xuan Canh 2004; Sterling et al. 2006; Figure 1.3, Chapter 1). The administration and rangers at CBNP have prioritised saving the Cat Ba langur, and they work closely with CBLCP to provide protection and education to locals and tourists. Within CBNP there is a specially dedicated sanctuary that has been deemed a perfect place to concentrate efforts towards saving this species, set up by CBLCP in 2001 (Schrudde et al. 2010). It is about 8 kilometres long and 3.5 kilometres wide. Extra rangers were hired and ranger stations were built in order to guard access to this sanctuary (Schrudde et al. 2010). This extra surveillance has helped both to protect the langurs, and to keep track of their movements and any births or deaths in known groups.

2.4 Weather on Cat Ba Island

Overall Cat Ba Island is humid with wet southwest monsoons sweeping through April or June to September and a dry northeast monsoon October or November to March or

April (Sterling et al. 2006; Nguyen Van Quan et al. 2010). May to October is quite humid; November to April has early morning fog (Figure 2.4). The summer monsoon is caused by winds coming from the Gulf of Thailand and the Indian Ocean, while the winter winds come from Siberia on their way down south to Australia (Sterling et al. 2006). The most amount of rain falls in July and August (Nadler and Ha Thang Long 2000) while June to August are the hottest months. Humidity ranges from 80-100% (Sterling et al. 2006; Agmen 2014). Previous researchers working on Delacour's langurs (*Trachypithecus delacouri)* in Van Long Nature Reserve (about 80km south of Hanoi) have divided the year into hot, wet summers and cool, dry winters (Workman 2010a; Agmen 2014). Therefore, this study considers Cat Ba to undergo two seasons: wet (May-October) and dry (November-April) so that they are comparable to previous studies.

Unfortunately, weather data could not be directly recorded for this study as the weather station broke multiple times and the weather station in CBNP has been broken since before my study began. Data found online from a weather station at the Hai Phong airport (http://rp5.md/Weather_archive_in_Hai_Phong_%28airport%29) was used to calculate daily average temperatures (Table 2.1). Data found online (www.accuweather.com) from Hanoi provided minimum and maximum daily temperatures (Table 2.1). There is no information on rainfall from either of these sites, although previous publications on Cat Ba report that 1500-1600mm of rain (or roughly 80-90% of annual rainfall) falls during the rainy season (May-October) (Nguyen Van Quan et al. 2010). There is an average annual rainfall of 1700-1800mm (Nadler and Ha Thang Long 2000).

All temperature data (Table 2.1) refer to days that fall within the study period for which I was observing the langurs (180 days between 19 Feb 2014-14 Jan 2015). There were multiple storms/typhoons that swept through the island over the summer (typically there are 1-2 typhoons/year that directly affect the island: Nguyen Van Quan et al. 2010); these were associated with breaks in the data as it was unsafe to be in a boat.

Table 2.1: Temperatures (°C) across the study period, by month (only study days included). Temperature high and low information during the study periods taken from www.accuweather.com, average temperature per day taken from http://rp5.md/Weather_archive_in_Hai_Phong_%28airport%29, average minimum and maximum temperatures and average rainfall per month (across years) from http://www.vietnamembassy.org.uk/climate.html. Average monthly highs and lows (across several years) are listed in parentheses.

month	season	highest (and average daily max) temperature (°C)	lowest (and average daily min) temperature (°C)	average temperature (°C)	average monthly rainfall (mm)
February 2014	dry	24 (21)	9 (13)	17	27
March 2014	dry	30 (24)	14 (18)	20	39
April 2014	dry	32 (29)	20 (21)	25	80
May 2014	wet	40 (32)	21 (22)	28	198
June 2014	wet	38 (33)	24 (25)	30	240
July 2014	wet	37 (32)	24 (26)	30	322
August 2014	wet	37 (32)	24 (25)	28	345
September 2014	wet	35 (31)	24 (24)	29	250
October 2014	wet	34 (28)	20 (23)	28	99
November 2014	dry	32 (25)	15 (19)	22	44
December 2014	dry	28 (21)	8 (16)	17	21
January 2015	dry	24 (20)	9 (12)	17	19

2.5 Data Collection

Between 19 February 2014 and 14 January 2015 I collected data around Cua Dong. This spans 11 months and crosses both seasons (55% of observation days and 53% of contact periods were in winter, 45% of days and 47% of contact periods in summer). Five days a week my boat driver and I would go out looking for the langurs (with some exceptions). This schedule culminated in 549 contact hours[1] across 180 days in the field (Figure 2.7), with an average of just over three hours a day.

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[1] Note: contact was not measured at the minute mark, but rather whether or not langurs were visible at the time of a scan *period* (either the five or ten minute mark). Therefore, all measurements described below use *one scan period = ten minutes*. *Scans* refers to the number of individual scans I was able to scan across all time periods and days. A *scan period* refers to a scan occurring within that ten-minute period (e.g. 7:10-7:20) whereas a *time period* refers to that ten-minute period whether or not a scan was conducted.

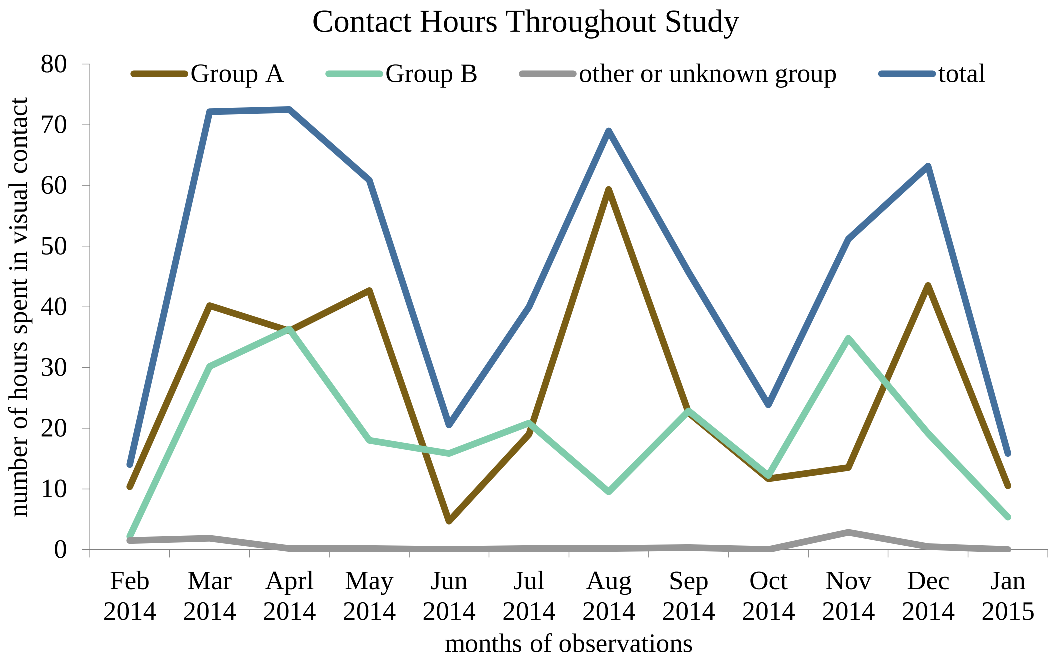


Figure 2.7: Number of hours spent in contact with Cat Ba langurs throughout this study. Over 180 days I was in visual contact with the langurs for 549 hours.

In general the daily protocol was for the boat driver (Nguyen Cam) and myself (hereafter ‘we’) to go out in the boat twice a day. We would leave Ben Beo harbour about 30 minutes before sunrise (about 5:00 in summer, 6:00 in winter) to look for the langurs. If we knew where they slept the night before we would go straight there. Otherwise we started at the edge of the langurs’ home range (determined by ranger/guards reports at the beginning of the project) and slowly drove the boat along the ocean-hill border looking for them. Usually the first indication of their presence was movement - either they jumped on the rocks or a tree branch snapped back.

We stayed with the langurs until we lost sight of them. If they went over the top of a hill or disappeared into the trees we would stay in the area for 30-60 minutes in case they came back over the top or started moving around again. If they did reappear, observations were continued as usual. If they did not reappear in that time, we then continued on looking for the other group. Sometimes we would call langur guards or rangers to ask if langurs had been seen in particular areas recently.

The Cat Ba langurs settle down for a midday sleep (Schneider et al. 2010) typical of limestone langurs (Section 3.4.1.1, Chapter 3), making them very difficult to see and find during this time. Therefore, if the langurs’ location was unknown by 10:00-11:00, we went back to the harbour. This is similar to the methodology used for other limestone langurs, where no observations are made midday (Li et al. 2003; Li and Rogers 2004a; Zhao and Pan 2006; Zhou et al. 2007a). During this time it is presumed that the langurs are fairly inactive, but as they were not visible and we were not out looking for them, this is actually unknown. This resulted in no scans being taken between 14:10-14:50pm, as 14:00 was the latest 'AM' sighting and 15:00 the earliest 'PM' sighting.

For PM data collection, we met again at the harbour between 14:30-16:30pm. The time varied depending on how long we had gone out in the morning and the season and sunset time. The protocol was the same: find and stay with the langurs. If we did not know where they were we started at the beginning of the home range, if we suspected them to be in a certain area we would check there first. The aim was to see where they went to sleep for the night so that we then knew where to start the next morning.

The goal of dividing up the day into two, concentrated contact periods was a matter of time limitation guided by information from other studies on the bimodal distribution of activity in other limestone langurs. With only eight hours a day available to be out in the boat, we had to maximise being able to find, stay with, and record the langurs. This will obviously be a source of bias, but I did try and mitigate these things, by staying with the langurs for as long as I had visual access (and then 30-60 minutes after).

The number of scan *periods* during which visual contact was maintained shows a bimodal distribution (Figure 2.8). This is due to the midday rest or period of inactivity (Section 3.4.1.1, Chapter 3), which has been documented in other langurs (Clutton-Brock 1977) and specifically limestone langurs (Zhao and Pan 2006). 5:00-8:00 has 34% of scan *periods*, 8:00-11:00 has 33%, 11:00-14:00 7%, 14:00-17:00 9%, and 17:00-20:00 16%. The 7:00-7:10 scan *period* was the most successful in terms of number of observations across all observation days. In general 6:30-9:00 was the best time for morning observations, and 17:30 was the best for afternoon observations. One quarter of all days in the field, I could see langurs from 5:40-10:20 and 17:00-18:00.

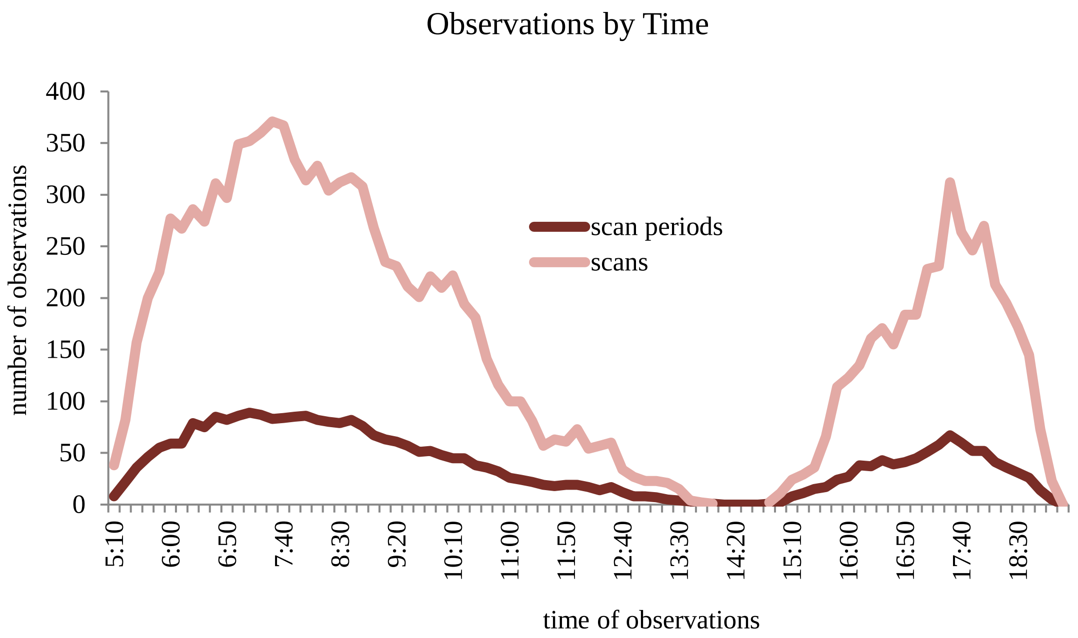


Figure 2.8: Number of scans and scan *periods* during which observations were made across all time periods. Note: bimodal distribution due to a midday rest resulting in lack of visibility.

There was a bias in observations towards Group A (57% of all scan *periods*), followed by Group B (41%; Figure 2.7). This may be due to Group A being more habituated, or because of our daily protocol, wherein we started searching for langurs at the edge of Group A's home range. On two occasions Group C (the bachelor group) was seen and clearly identified, accounting for 1.3% of all scan *periods*. In 1.1% of scan *periods* it was unknown which group I was looking at. On two days I was able to see and record scans for multiple groups during the same scan *period* because of their close proximity. There was a total of 3292 scan *periods* (3292 ten-minute blocks x hr/6 ten-minute blocks = 549 hours).

There were up to four separate contact periods per day. On average, contact was a little over two hours, although this ranged from less than one minute to seven and a half hours (this was the maximum due to the eight-hour-a-day limit on the boat driver contract and associated transfer time to and from the monkeys). There were seven days where there was at least seven hours from beginning to end of contact with a single group, finishing up between noon and 14:00. If we did maintain contact for over seven hours in the morning, or we had used up all eight hours of boat driver time, we did not go out in the afternoon. This happened 21 times throughout the study period.

There were occasions where we were unable to go out on the boat in either the morning or afternoon, due to other obligations. Of the 180 days in the field, 25% were morning outings (this includes outings that lasted the entire eight hour limit), 7.8% were afternoon outings, and 67.2% were days we went out both in the morning and afternoon. We had a high rate of success in daily contact with only 7.2% of all research days resulting in no or very short time with the langurs.

2.6 Behavioural Observations

2.6.1 Study Animals

There were two groups consistently seen in the Cua Dong area (Groups A and B) during my study period. From November - December 2014 a bachelor group of three males (Group C) moved into Group B’s home range although very few scans (n=10) were collected on this group and I was unable to verify the age classes of the bachelor males. In analyses of group differences, only Groups A and B are considered. Group C (a bachelor group) data is included in analyses not based on group differences. Group A grew (from 10 to 13) during the study period, as three individuals were born. Group B remained unchanged (7 individuals). Demographic details for Groups A and B for 2014-2015 can be seen in Table 2.2. Individual identification of those in the same age-sex class was not possible. Identification of age-sex class was based on comparison with the following protocol (Table 2.3), adapted from Agmen (2014), and modified over the pilot period.

Table 2.2: Demographic breakdown of Cua Dong Groups A and B as of Jan 2015.

age-sex class	**# of individuals Group A**	**# of individuals Group B**
adult male	1	1
adult female	5	2
subadult male	0	1
subadult female	0	1
juvenile male	2	1
juvenile female	1	1
young juvenile male	1 (born Aug 2014)	0
young juvenile female	1 (born Jan/Feb 2014)	0
infant male	1 (born Oct/Nov 2014)	0
infant female	0	0
unsexed newborn	1 (born Dec2014/Jan2015)	0
total	13 (10 at the start of the project)	7

Table 2.3: Age-sex classes of langurs used in this study. Chapters 3, 4, and 5 use the broad categories of 'adults', 'subadults', and 'young', while Chapter 6 assesses behavioural differences between the four 'young' age classes (newborn, infant, young juvenile, juvenile).

	age	**definition**		photo reference
adults	adults	Golden-yellow to creamy-white heads, glossy black coat with the possibility of yellow markings around the shoulders. Sexually mature. Full size.		Figure 2.9
		males	Slightly more robust than females. Over 7-8 years old. Penis is white-tipped; no white patches on inner thighs; ischial callosities are joined. May or may not have access to females to mate with.	Figure 1.6, Chapter 1
		females	Has given birth at least once, elongated nipples. Slightly smaller than adult males. Over five years old. White patches on inner thighs and ischial callosities are separated.	Figure 1.5, Chapter 1
subadults	subadults	Mostly adult pelage but with more orange around the neck and shoulders than the more white head of adults. Smaller/slenderer than adults.		Figure 2.10
		males	Penis is white-tipped; no white patches on inner thighs. Testes have descended. Does not have mating access to females. Roughly 3-7 years old.	
		females	White patches on inner thighs. Does not have offspring or elongated nipples. Roughly 3-5 years old.	
young	juveniles	Yellow/orange on extremities, dark torso, brighter orange head than subadults/adults. Still hangs out around females, not fully weaned, 2/3 adult body size, is not carried by adults. Has characteristically large stomach. Roughly 1-3 years old.		Figure 2.11
		males	No white patches on thighs; undescended testes.	
		females	White patches on inner thighs.	
	young juveniles	Yellow/orange extremities, torso is beginning to darken or fully gray. During this time the characteristic belly of leaf-eaters develops. Young juveniles may sometimes be carried, but are much more independent than infants. Roughly 4-12 months old.		Figure 2.12
		males	No thigh patches, undescended testes.	
		females	White patches on inner thighs.	
	infants	Yellow/orange with a slight dulling of orange all over body. Unweaned but eating some solid food. Carried much of the time and rarely gets very far from adult females. Roughly 3-16 weeks old.		Figure 2.13
		males	No thigh patches; undescended testes.	
		females	Thigh patches become visible during this age class.	

newborns	Bright orange/yellow without any darkening. No crest. Unweaned, does not eat any solid foods, and is never off of another langur. Highly desirable to group members; many transfers. Roughly 0-3 weeks old. Sex cannot be determined as newborn is usually held closely.	Figure 2.9

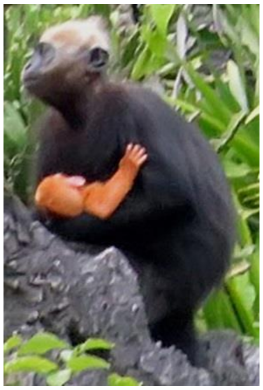


Figure 2.9: Adult female Cat Ba langur holding a newborn. Note: lack of orange on shoulders on adult and bright orange colouration of newborn. Photo taken August 2014 by K Hartwell

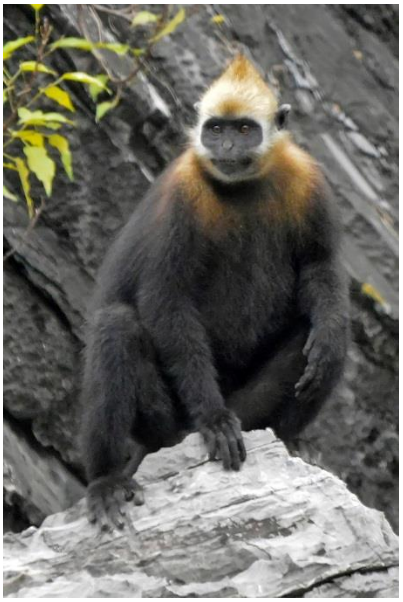


Figure 2.10: Subadult Cat Ba langur. Note: orange colouration on shoulders. Photo taken January 2015 by R Hendershott

Figure 2.11: Juvenile Cat Ba langurs. Note: dark torso with some orange/yellow remaining on the extremities and orange shoulders. Photo taken April 2014 by B Olesen

Figure 2.12: Young juvenile Cat Ba langur. Note: torso is beginning to darken and orange/yellow remaining on the extremities and across the top of the back, as well as the lack of a large abdomen. Photo taken April 2014 by B Olesen

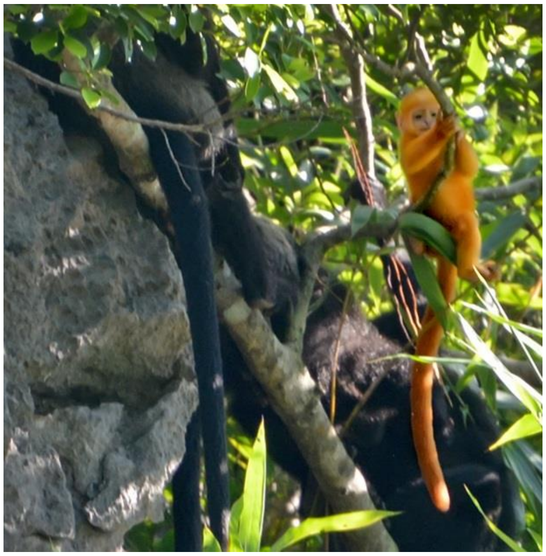


Figure 2.13: Infant Cat Ba langur. Note: pelage is not as bright as newborns' and they have slight locomotor independence from, but close proximity to, adults. Photo taken April 2014 by Nguyen Duc Tho (FFI)

2.6.2 Behavioural Data Collection

Given the difficulty in traversing the limestone karst terrain (Li and Rogers 2007), all observations were made from a boat (Figure 2.14) or low-tide beachs following the protocols of other limestone langur studies (Schneider et al. 2010; Workman 2010a; Agmen 2014; Phan Duy Thuc et al. 2014). Occasionally the boat driver would climb to an internal valley/lake in order to narrow down where the langurs were, but this was not part of the behavioural data-collection phase.

Figure 2.14: Boat driver (Nguyen Cam; left) and myself (middle) observing Cat Ba langurs from a boat. Photo taken April 2014 by B Olesen

I used instantaneous interval scan sampling every ten minutes (Altmann 1974b; Martin and Bateson 2009). Using Canon IS UD 4.5^0 15x50 all-weather binoculars I concentrated on watching the area that contained the most amount of langurs and then visually spiralled out from there for up to 45 seconds (once the timer went off) in order to maximise scans obtained but not bias observations toward flamboyant behaviours (Altmann 1974b). All 10 minutes scans were started on the five or 10 minute mark to avoid a bias towards eye-catching behaviours; scans that started on the five or 10 minute mark are considered the same scan *period* (e.g. a 5:50 scan and 5:55 scan are both part of the 5:50 scan *period*).

Upon first contact, I wrote down the location of the monkeys (taken from a handheld Garmin Etrex 30 GPS of the boat's location and distance from the boat to the monkeys using a Bushnell YardageProSport 450 rangefinder), the group, and the weather. For each scan I wrote down who I could see (age, sex), what they were doing, their posture, the substrate and hill type they were on, the density of the surrounding 10 metre radius of vegetation, and whether or not they were within proximity to another langur. Ad libitum notes (Altmann 1974b; Martin and Bateson 2009) were taken on changes to the weather, mounts, loud calls and other vocalisations, interactions with other species, and newborn/infant transfers. Throughout the year coat colour of the younger langurs was recorded ad libitum. A Philips Voice Tracer voice recorder was used to maximise the amount of information I could collect quickly.

2.6.3 Ethogram

Behaviours used were based off of the following ethogram (Table 2.4), adapted from Niemeyer and Anderson (1983), Sommer and Mendoza-Granados (1995), Arnold and Barton (2001), Fashing (2001a), Li and Rogers (2004a), Zhao et al. (2008), Workman and Schmitt (2012), and Agmen (2014). Behaviours were mutually exclusive; when an individual was doing more than one behaviour (e.g. foraging or masturbating while being groomed) it was the more active behaviour (e.g. foraging, masturbating) than passive (e.g. being groomed) that was recorded. Body postures documented can be seen in Table 2.5.

Table 2.4: Ethogram used in this study in assessing behaviours of langurs.

behaviour	**definition**				
inactivity	Sunbathe, rest, autogroom, scan/vigilance, touching or reaching out to someone (but not infant transfer). No other behaviour on ethogram is being done, with the exception of nursing. A newborn or infant that is on another langur (whose behaviour is observed) and not struggling, being transferred, or being groomed is considered inactive.				
forage	Preparing to eat/manipulating food; searching for food; drinking; masticating; ingesting; rock-lapping. Includes moving less than a body length away to reposition for access to more food. Food items include:				
		leaves	young or mature foliage		
		fruit	fruit or berries (may include seeds)		
		flower	flowers or blossoms		
		water	Licking rocks and/or drinking water from concavities of rocks, drinking ocean water by soaking tail in ocean and then putting that in their mouth or else bending over and putting mouth to ocean level, licking or chewing rocks.		
		stem	stems of vines and leaves		
social	Individuals interact with one another. Includes:				
		groom/ grooming	Individual picks through hair, fingers, toes, or other body parts of another individual. Can be one-way, reciprocal, or a 'chain'.		
				groomer	individual grooming another individual
				groomee	individual receiving the grooming
				both	two individuals mutually grooming one another at the same time
		play social	Individual engaging in repeated social activities such as chasing, wrestling, and mock-biting with other partners. Any play involving another individual, regardless of whether that individual is actively or passively (e.g. letting them jump on body, hang on tail, etc.) involved.		
		vocalise	Making a noise with an individual's mouth. Considered 'continuous' if there is less than a one-minute watch break between bouts. Vocalisation types include:		
				distress call	High pitched squeal, squawk, scream, or cry. Used when in distress (adult females) or to get attention (newborns, infants, young juveniles, and juveniles)
				hoot	a 'who-who' sound, often associated with running and shaking branches
				loud call/ cough/ rasp	A hooting noise with a specific pattern. Often associated with body jolts. Coughing and rasping (a rough barking/coughing) sounds were usually

			used in conjunction with loud calls and therefore all vocalisation analysis lumps these three vocalisations
		other	Barks, grunts, and other less identifiable vocalisations
	mount		An individual does a single or double hind-leg clasp and supports their weight on their arms on the back of the recipient, with or without thrusting, any age or sex. Can be either:
		successful	The recipient allows the mounter to get into position. Does not necessarily include thrusting, intromission, or ejaculation.
		failed	An individual attempts to mount a recipient, but fails due to lack of cooperation from the mounted individual. Includes mounting a sitting individual.
	embrace		Two individuals have ventroventral contact with one or both arms around the other, often accompanied by kneading the fur of the other.
	transfer		Young langur is moved/passed/grabbed from one individual's body to another. Often this is initiated by the recipient, but as the young ages it may also choose to move from one individual to another. Can be either:
		successful	Neither the individual originally holding the young, nor the young, resists the transfer.
		failed	Individual reaches out to take, or tries to grab, young, but is unsuccessful at moving the young to their own body. This may fail due to the individual who has the young turning around or walking away, keeping a tight hold on the young, or resistance from the young itself.
	present/ solicit		Individual stands quadrupedally in front of another individual, occasionally looking over their shoulder, backing up, possibly raising tail. Their anogenital region is placed in front of the recipient of the presentation. Also includes when individual notices another individual approaching who wants to mount, and so gets into position to make that possible.
	harassment of copulation		Approach or contact between nonmating individuals and mounted pair. May or may not prevent the copulation from continuing.
	agonistic behaviours		Includes:
		submission	Individual avoids, or flees, from another individual
		displacement	Individual moves out of the way of another individual who takes their exact spatial location
		aggression	Biting, slapping, lunging, chasing, fleeing
locomotion			Individual goes from one site to another (without chasing), results in a changed spatial position. Does not include repositioning less than a body length away while foraging. Locomotion types include:
	arm swing		Brachiate, drop, pull up. Being suspended by the arms or feet
	drop		An individual suspended from a tree or rock lets go to fall to a lower substrate
	quadrupedal		At least three limbs are on a supporting substrate, with at least two limbs in motion. All four limbs move in a regular pattern above a support, on vertical rock face, or on the ground; includes walking, running, bounding, and galloping
	leap		A movement in which the hind limbs propel the animal across a gap; includes quadrupedal standing then leaping or pumping the body up and down before leaping. Vertical and quadrupedal leaping. Does not include dropping down from a substrate
	climb		Using all four limbs to purposefully climb up or down, tree trunk, branches, vines, or steep rocks. Movements that generally require

			greater mobility of the limbs; all four limbs move in an irregular pattern with abducted arms and knees and with variable hand and foot positions
‘other’ behaviours			Any miscellaneous behaviours not covered under the above categories. Includes:
	adult rejection of young		Female rejects attempts by young to nurse or be held/carried by pushing them away. Individual prevents infant from climbing onto body or forces a young off their body.
	masturbation		Male uses their hands to stimulate an erection; ejaculation unnecessary.
	infant exploration		Infant moves onto nonlangur substrates for short periods of time, practicing limb coordination, grabbing ahold of surrounding objects, and generally exploring. Includes some attributes of play:locomotor and locomote but more shaky and tentative
	infant struggle		Infant attached to another individual is resisting being held. This may involve crying, kicking, trying to get away, or generally being restless.
	play (asocial)		Running and jumping about. Exaggerated movements without ‘purpose’. Includes:
		locomotor/ rotational	Individual moving by locomotion but without a purpose of ‘travel’, no destination, nonoriented. For example: swinging, jumping, rolling around, running
		object	Individual uses hands, feet, or mouth to manoeuvre/hold an object (e.g., branch, leaf etc.). Excludes manipulation of food when the intention is to consume for feeding
nursing			Infant feeding from the mother’s nipples, or mother feeding infant by suckling. Includes young-face-to-adult-breast contact (in a way that is conducive to nipple in mouth contact), whether or not nipple in mouth is seen. Includes when they seem to have fallen asleep in that position.

Table 2.5: Ethogram used in this study in assessing posture use of langurs.

posture	**definition**
stand	Supporting body weight on three or four limbs (three if using the fourth to hold/reach for food/object or while locomoting). Includes crouching.
sit	Weight supported by hind haunches and arms are free. Includes those who are leaning against objects/individuals and those wedged within a vertical crevice.
prone	Animal lies on its belly, side, or back; horizontal to substrate surface.
bipedal	Supporting body weight on back legs. Minimal balancing with arms (e.g. grabbing a branch while foraging on two legs).
suspend	Supporting body weight by one or two limbs above torso; hanging, brachiating, dropping.
cling	Using three or four limbs to support body weight in a vertical position.
leap	Mid-leap or drop, no limbs are in contact with a supporting substrate.
wrestle	Two or more individuals with entwined bodies. Includes standing, sitting, being prone or bipedal, suspended or clinging – so long as they are in a locked embrace with at least one other individual. Occurs while playing socially.

2.6.4 Habitat

Habitat measures include the substrate the langurs were on, how dense the vegetation was, and the hill type at the time of the scan (Table 2.6). For substrates, if an individual is locomoting, it is the substrate they were suspended, clinging, or leaping *from* that counts. The hill types (adapted from Nguyen Hiep pers. comm. 2014) refers to the immediate surrounding area of the individual being observed, not to the entire hillside.

Table 2.6: Ethogram used in this study in assessing how langurs use three habitat type measures: substrate, vegetation coverage, and hill type.

habitat type		**definition**
substrate	*tree*	Any vegetation, including branches, trunks, vines, logs.
	rock	Rocks, whether on the ground or more vertical.
	sand	Lowest level of the strata. Beach that is on a horizontal plane.
	another langur	An individual has their entire body weight supported by another individual. Includes young being held or jumping/playing on adults and anyone who completes a double-hind leg clasp during a mount.
vegetation coverage	*sparse*	More than 60% of surrounding ten metre radius is rocks.
	half	40-60% of surrounding ten metre radius is vegetation or rocks.
	dense	More than 60% of surrounding ten metre radius is vegetation.
hill type	*valley*	Gullies between limestone hills, canyons between two cliffs, or craters with walls that do not face water are considered ‘valley’. Starts to be ‘valley’ at the rim of a crater. Category of ‘valley’ trumps all other hill types. Plant families include: Orchidaceae (*Zeuxinella vietnamica, Paphiopedilum concolor)*, Aquifoliaceae (*Ilex kudingcha)*, Polypodiaceae *(Drynaria bonii)*, Araceae *(Amorphophalus paeoniifolius)*, Arecaceae *(Livistona halongensis*, Asparagaceae *(Dracaena cambodiana)*, Zingiberaceae *(Alpinia calcicola*), Araliaceae *(Schefflera alongensis)*, Balsaminaceae *(Impatiens halongensis)*, Begoniaceae *(Begonia boisiana)*, Fabaceae *(Bauhinia ornate, Sophora tonkinensis)*, Gesneriaceae *(Chirita drakei, C. hamosa, C. halongensis, C. hiepii, C. modesta, Paraboea halongensis)*, Moraceaea *(Ficus alongensis)*, Euphorbiaceae *(Euphorbia antiquorum)*, Menispermaceae *(Stephania rotunda)*, Oleaceae *(Jasminum halongensis)*, Opiliaceae *(Melientha suavis)*, Rubiaceae *(Mussaenda glabra)*, Sapindaceae *(Boniodendron parviflorum)*, Malvaceae *(Sterculia lanceolata, Pterospermum truncalotobatum)*, Urticaceae *(Pilea alongensis)*, Cycadaceae *(Cycas tropophylla).*
	exposed slope	A gradually inclined rock face. ‘Exposed’ refers to the slope being exposed to the ocean (either open or cove), *not* to the rock being exposed on the slope (i.e. visible). Plant families include: Moraceaea *(Ficus alongensis , F. microcarpa , F. orthoneura)*, Sapindaceae *(Boniodendron parviflorum)*, Asparagaceae *(Dracaena cambodiana)*, Rutaceae *(Clausena lansium)*, Malvaceae *(Pterospermum truncalotobatum, Sterculia lanceolata)*, Araliaceae *(Schefflera alongensis)*, Balsaminaceae *(Impatiens halongensis)*, Zingiberaceae *(Alpinia calcicola).*
	steep cliff	An almost vertical rock face. Plant families include: Asparagaceae (*Dracena cambodiana)*, Orchidaceae *(Paphiopedilum concolor, Cymbidium aloifolium)*, Zingiberaceae *(Alpinia calcicola*), Araliaceae (*Schefflera alongensis)*, Gesneriaceae (*Chirita drakei, Paraboea halongensis)*, Moraceaea (*Ficus alongensis)*, Cycadaceae (*Cycas tropophylla)*, Malvaceae (*Pterospermum truncalotobatum)*, Euphorbiaceae *(Euphorbia antiquorum L.)*, Apocynaceae *(Sarcostemma acidum (Roxb.) Voight)*, plus some bamboos and grasses.
	summit	An area that stands above the immediately surrounding hillside. A summit can be very narrow or small, if there is a dropoff in substrate on all neighbouring areas. Plant families include: Cycadaceae (*Cycas tropophylla)*, Gesneriaceae (*Chirita drakei, C. hiepii, C. halongensis, Paraboea halongensis)*, Arecaceae (*Livistona halongensis*).
	ground	Beach, or other horizontal surface, at water-height.

Chapter 3: Activity and Dietary Budgets

3.1 Introduction

As activity budgets are highly reliant on available resources (Section 1.6.4, Chapter 1) and immediate needs, primate activity budgets differ throughout days and seasons. For example, primates have feeding peaks throughout the day (Clutton-Brock 1977; Domingo-Roura and Yamagiwa 1999), and this pattern is seen in colobines (Long et al. 1998; Teichroeb et al. 2003; Rawson 2009) and limestone langurs (Huang et al. 2003; Zhou et al. 2007a; Zhou et al. 2010) – all of whom tend to have foraging peaks in the morning and afternoon (however, peaks in feeding may differ seasonally: Zhou et al. 2007a). Sunbathing is another behaviour that typically occurs in the morning for primates (Anderson 1984), including colobines (Oates 1977), and limestone langurs (Huang et al. 2003). Behavioural changes throughout the day are most probably due to temperature variation/thermoregulation (Oates 1987; Hill 2005) and a way of maximising digestion (Clutton-Brock 1977).

Foraging and locomotion is heavily influenced by resource availability (both nutritional content and plant part properties), which changes seasonally. The energy conservation, or time minimising, strategy involves reducing energy expenditure by foraging less at times of low food availability, while energy maximising strategies are those that increase time and energy spent trying to find sufficient resources when resources are scarce (Schoener 1971). King colobus (*Colobus polykomos*) appear to follow an energy conservation strategy, by spending more time resting and less time feeding when preferred seeds are unavailable (Dasilva 1992). In contrast, black snub-nosed monkeys (*Rhinopithecus bieti*) (Grueter et al. 2013) and ursine colobus (*Colobus vellerosus*) (Djègo-Djossou et al. 2015) forage more in the resource-poor season. Guerezas (*Colobus guereza*) travel more (Harris et al. 2009), while Hanuman langurs (*Semnopithecus entellus*) forage and travel more (Newton 1992) at this time of year. This suggests that these species are following an energy maximising strategy. Similarly, limestone langurs rest (40-67% of their activity budget in the dry season vs. 53-84% in the wet season: Huang et al. 2003; Yang et al. 2007; Zhou et al. 2007a; Zhou et al. 2010) and socialise (2% vs. 3%: Zhou et al. 2007a) less, and spend more time traveling (13-46% vs. 7-22%: Huang et al. 2003; Yang et al. 2007; Zhou et al. 2010) and foraging (20-26% vs. 9-19%: Huang et al. 2000; Huang et al. 2003; Zhou et al. 2007a; Zhou et al. 2010) in the dry season. This qualifies these animals as energy maximisers.

Seasonal variation in food supply can also be dealt with by changing and increasing the type of plant parts and species consumed during low food availability (Snaith and Chapman 2007; Zhou et al. 2011), which can affect feeding time and effort (Decker 1994; Dunn et al. 2010). In a metaanalysis of seasonality on primate diet, 70% of species reported on switched their diet, mostly to include more mature leaves, new leaves, and other vegetative matter during times of low resource availability (Hemingway and Bynum 2005). This is more pronounced among some Asian primates, possibly due to their adaptations to the irregular mast fruiting in Southeast Asia across years (van Schaik and Pfannes 2005; Sterling et al. 2006). For example, white-headed langurs (*Trachypithecus leucocephalus*) and François' langurs (*Trachypithecus francoisi*) eat more young leaves in the wet season (64-90% of diet in wet season vs. 10-92% in dry season) and more mature leaves (0-15% vs. 0-37%) in the dry season (Li and Rogers 2006; Hu 2007) in accordance with plant part availability. Although fruit and leaf eating does not show a consistent seasonal trend across limestone langurs, individual langur species do locally adapt to availability (Li and Rogers 2006; Hu 2007; Workman 2010a; Zhou et al. 2013b). If individuals cannot adapt their behaviour or diets, or are energetically constrained, they face increased nutritional stress and reduced reproductive rates (Whitten 1983; Dunbar and Dunbar 1988; Janson and Goldsmith 1995; Snaith and Chapman 2007).

Differences in activity budgets by age and sex reflect differing energetic demands between the sexes, and developmental stages as individuals grow older. Female primates tend to be more social (especially for female-bonded species: Wrangham 1980) and spend more time feeding (Clutton-Brock 1977) than males. For example, among cercopithecines, males spend between 15-25% of their day feeding and 3-11% of their day socialising, while females spend between 21-29% of their day feeding and 5-12% of their day socialising (Key and Ross 1999). Among colobines, females socialise/groom more than males (3-11% of female activity budgets vs. <1-3% of males') while spending less time resting (28-30% vs. 32-37%) (Clutton-Brock 1977; Newton 1992; Key and Ross 1999; Fashing 2001a; Fashing et al. 2007). In Delacour's langurs, females similarly socialise/groom (~9% vs. ~4%) and feed (~33% vs. ~22%) more than males (Workman 2010a).

There are also behavioural differences across ages with adults generally being less active than young animals (Prates and Bicca-Marques 2008; Rawson 2009; Eakins 2010). Young limestone langurs spend more time being social than adults (11-35% of activity budgets for young vs. 1-12% for adults), who spend more time resting (24-52% vs. 44-75%) and feeding (10-21% vs. 20-33%) (Li and Rogers 2004a; Zhou et al. 2007a; Schneider et al. 2010; Agmen 2014).

Contrary to the pattern seen in limestone langurs, a metaanalysis of New and Old World primates shows that juveniles are less efficient at ingesting food, especially leaves, and must spend relatively more time foraging than adults (Janson and van Schaik 1993). Despite mimicking group member foraging patterns, young animals may alter the proportion of certain food items in their diet. As various food items contain varying amounts of minerals, protein, sugar, dry matter weight, energy, fibre, lignin, carbohydrates, and differ in their digestibility, it is expected that young primates would have a different diet than fully grown adult males or reproductive females. This reflects the fact that required nutrients change as individuals age due to a higher metabolic rate and growing body sizes (Rothman et al. 2008), and young avoid hard to process or tough fruits (Janson and van Schaik 1993).

It is important to obtain basic information on behaviours and diet so that future studies can use it as a baseline in assessing the effects of ongoing habitat degradation. As with seasonal fluctuations in resource supply, some primates adopt an energy conservation strategy by decreasing their travel time in disturbed habitats. For example, Sumatran surilis (*Presbytis melalophos*) spend more time resting and less time eating and locomoting in logged habitat (Johns 1986). In contrast, some primates increase energy spent: red-shanked douc (*Pygathrix nemaeus*) groups who experience higher human pressure travel more, stay inactive longer, and sleep less (Phiapalath and Suwanwaree 2010), while white-headed langurs play less and spend more time traveling and feeding, with a more diverse diet that includes less preferred species in degraded habitat (Li and Rogers 2004a; Li and Rogers 2005b; Li and Rogers 2006). Therefore, establishing a reference point of behaviours is important in documenting how animals are having to adjust to a disturbed environment that may have reduced food options (Knight 2001; Arroyo-Rodríguez and Mandujano 2006; Kotler et al. 2007; Searle et al. 2007; Guo et al. 2008; Lindell 2008; Dunn et al. 2010; Berger-Tal et al. 2011). If future studies find a significant difference in activity or dietary budgets, beyond seasonal variation, this may indicate that animals are energetically stressed

(Dunn et al. 2010; Dunn et al. 2013), which has conservation implications as stress affects the ability to gestate and lactate (Yeager and Kirkpatrick 1998; Heistermann et al. 2004).

This chapter explores the activity and dietary budgets of wild Cat Ba langurs (*Trachypithecus poliocephalus*) over a near complete annual cycle (11-month study period). Specifically, it will explore behaviour and diet in relation to time of day, season, group, sex, and age class to provide the first account of behaviours and diets of this Critically Endangered species.

3.2 Methods

3.2.1 Behavioural Data Collection

Using a boat, my boat driver and I went out five days a week from Feb 2014-Jan 2015, resulting in 180 days (or 549 hours) in contact with the langurs. Behavioural data were collected using instantaneous scan samples conducted every ten minutes (Altmann 1974b; Martin and Bateson 2009) on two reproductive groups of Cat Ba langurs in the Cua Dong area of Cat Ba Island. During the scan I started with the area with the highest density of langurs and then spiralled out from there (taking care not to repeat count an individual) for up to 45 seconds so as to maximise scans obtained and not to bias towards flamboyant behaviours (Altmann 1974b).

During each scan I recorded the age-sex class of all visible individuals as well as their behaviour following the ethogram (Tables 2.3 and 2.4, Chapter 2). Some broad behavioural categories (e.g. foraging, social behaviour, locomotion, and ‘other’ behaviours) had subcategories that allowed for more detailed data to be collected and when possible the specific details of feeding and locomotion were recorded. Foraging includes both plant items ingested and water drinking (i.e. water drinking is part of the foraging activity budget), however, water is excluded from further analysis. Foraging also includes short bouts of travel/repositioning to continue foraging and preparing/handling food to consume (Table 2.4, Chapter 2). Not all activity budget categories were inherently mutually exclusive. An individual could be groomed while foraging. In such cases it was the behaviour that the subject animal was more actively engaged in that was counted for the activity budget. For example, foraging would trump passively being groomed.

Study subjects were broken down into adults (n=9; full size, sexually mature, glossy black coat with orange/yellow on heads and/or shoulders), subadults (n=2; smaller than adults, similar colouration to adults except the orange/yellow goes further down the shoulders), and young langurs (n=6-9). Young langurs includes infants (n=1-2 throughout the year; three weeks to four months old, small stomach, orange/yellow dulled over their body), young juveniles (n=0-2 throughout the year; roughly four months to one year old, belly grows, orange/yellow extremities, torso is gray or beginning to darken), and juveniles (n=3 all year; over one year old, smaller than subadults, large stomach, dark torso with orange/yellow on extremities and a brighter orange head than subadults), with some individuals changing within the ‘young’ age classes as they develop (Table 2.3, Chapter 2, for age-sex categories). Females were identifiable by their elongated nipples and white thigh patches. Young langurs were aggregated in this chapter because a detailed analysis of how their behaviour changes across age classes is assessed in Chapter 6.

3.2.2 Data Analysis

Activity and dietary budgets are presented as the mean daily proportion of scans that included each specific behaviour category or the proportion of feeding records that included a specific dietary item. Following existing protocols on similar species (Teichroeb et al. 2003; Hu 2007; Zhou et al. 2007a), day was used as the unit of analysis for independence. For analysis I broke down behavioural activity budgets by time of day and season, as well as by group, age, and sex classes in order to ascertain any differences within each category. In 10% of scans the age is not certain and in 36% the sex is unknown; these are excluded from analysis of age or sex, respectively.

Seasonal behaviours were divided into wet and dry seasons. The winter dry season occurs from the beginning of November until the end of April, and the summer wet season is from the beginning of May until the end of October, during which 80-90% of the year’s rain falls (Section 2.4, Chapter 2). Dividing the year up into two seasons (hot and wet, cool and dry) has been done for other limestone langurs living in geologically/climatologically similar conditions (Workman 2010a; Agmen 2014). In order to assess diurnal patterns to activity and foraging behaviours, the day was divided into five three-hour blocks of time (5:00-8:00, 8:00-11:00, 11:00-14:00, 14:00-17:00, 17:00-20:00), which follows protocols used in previous colobine studies (Oates 1977; Chapman and Chapman 1991; Stanford 1991a). However, observations were not made evenly throughout the three hour blocks (Figure 2.8, Chapter 2). For example, the last time block extends from 17:00-20:00, although the latest scans were 19:05. I retained the three-hour blocks, however, for sake of consistency.

In order to assess whether activity or dietary budgets vary across season, group, age, and sex, I first fit a linear model (LM) with arcsine transformed proportions (similar to Li and Rogers 2004a) as the dependent variable, and behaviours/food, age/sex/group/season/time, and an interaction between the two as the independent factors. If I found that the overall behaviour/food pattern differed between age/sex/group/season/time ($P<0.05$) with this LM, I assessed the differences between ages/sexes/groups/seasons/time periods for each behaviour or food item separately with a binomial logistic model (BLM), using daily observed frequencies out of total numbers of observations. As some analyses were overdispersed, this was accounted for by reporting the more conservative results of a ‘deviance’ model, and is noted in tables throughout the chapter. BLMs provide pairwise comparisons between variables in order to identify where the significant differences lie (e.g. the five time periods or the three age classes); tables for significant pairwise comparisons are provided in the Appendix if BLM posthoc analyses were significant. Note that in reporting pairwise comparisons for time periods, only those that are significantly different than adjacent periods are mentioned.

As I found no evidence that there was a difference of age/sex/group/time in their seasonal responses (Hendershott unpublished data), subgroups were pooled for seasonal analysis. I removed newborns from all analyses because their behaviours were nonindependent. While the foraging category included water drinking (n=26), this was not analysed as part of the dietary budget. I used SPSS 23 for Windows for all analyses, with significance set to $P<0.05$ for two-tailed tests.

3.3 Results

3.3.1 Activity Budget

When all data from groups and seasons is combined, inactivity was the most common behaviour for the Cat Ba langurs, accounting for a mean of 55 ± 1.3% of the day's activity budget. This was followed by foraging (19 ± 1.1%), social behaviour (12 ± 0.7%), locomotion (12 ± 0.9%), and finally 'other' (2 ± 0.2%) (Table 3.1). Almost twice as much time was spent locomoting quadrupedally (65%) as climbing (22%), leaping (11%), drop (1%), and arm swing (<1%) combined (Table 3.1). 'Other' behaviours were primarily asocial play (77%), and explore (19%), with relatively little struggling against being held (2%), rejection from nursing (2%), and masturbation (1%) (Table 3.1). Nursing was included in 8 ± 1.0% of adult females' scans. There was no significant effect of sex on activity budgets (LM: χ^2=9.042, df=4, p=0.060).

Table 3.1: Behavioural categories, listed in order of most common behaviours (newborns excluded), with the mean daily percent (%) that behaviour occupies in the activity budget. Social behaviours are discussed in detail in Chapter 5. Remaining behaviours that comprised less than half a percent of the total activity budgets are combined under 'other' and are discussed in detail in Chapter 6 for young langurs. All values rounded to nearest integer.

behavioural categories	mean daily percent	subcategory behaviour	mean daily percent	sub-subcategory behaviour	percent of scans/ad libitum data
inactivity	55				
foraging	19	leaves	79		
		fruit	7		
		water	6		
		flowers	5		
		stem	3		
social	12	groom	72	*groomer*	51
				groomee	48
				both	1
		social play	18		
		vocalisation	6	*distress*	18
				hoot	3
				loud call	80
		mount	2	*success*	93
				fail	7
		embrace	1		
		present	1		
		infant transfer	<1	*success*	64
				fail	36
		harassment of mounts	<1		
		submission	<1		
		displacement	<1		
		aggression	<1		
locomotion	12	quadrupedal	65		
		climb	22		
		leap	11		
		drop	1		
		arm swing	<1		
other	2	asocial play	77	*locomotor-rotational*	95
				object	5
		explore	19		
		struggle	2		
		rejection	2		
		masturbate	1		

3.3.1.1 *Time Differences in Activity Budgets*

Behaviours were found to vary throughout the day for the Cat Ba langurs (LM: χ^2=95.570, df=16, p<0.001; Figure 3.1); posthoc analyses indicate that this pattern held for foraging, social behaviour, locomotion, and 'other' behaviours (Table 3.2). In both the 5:00-8:00 and 8:00-11:00 time periods inactivity predominated, followed by foraging, social behaviours, locomotion, and 'other' behaviours. During the 11:00-14:00 time period there was a significant increase in foraging while locomotion and social behaviours decreased significantly (Table 1, Appendix). During the afternoon (14:00-17:00), locomotion increased significantly (Table 1c, Appendix). The evening (17:00-20:00) had significantly reduced foraging relative to the previous time period (Table 1a, Appendix). Despite significant variation in ‘other’ behavioural rates throughout the day, no one time period was significantly different from the following or preceding time period (Table 1d, Appendix). Nursing rates changed throughout the day for adult females (BLM: χ^2=12.209, df=4, p=0.016, using a ‘deviance’ model) with 6-8% of scans in the morning (5:00-11:00) including nursing, trending an increase to 11% at midday (11:00-14:00) and then dropping significantly to 4-5% of scans for the rest of the day (14:00-20:00) (Table 2, Appendix). There was no interaction effect of time and season (LM: χ^2=14.376, df=16, p=0.571).

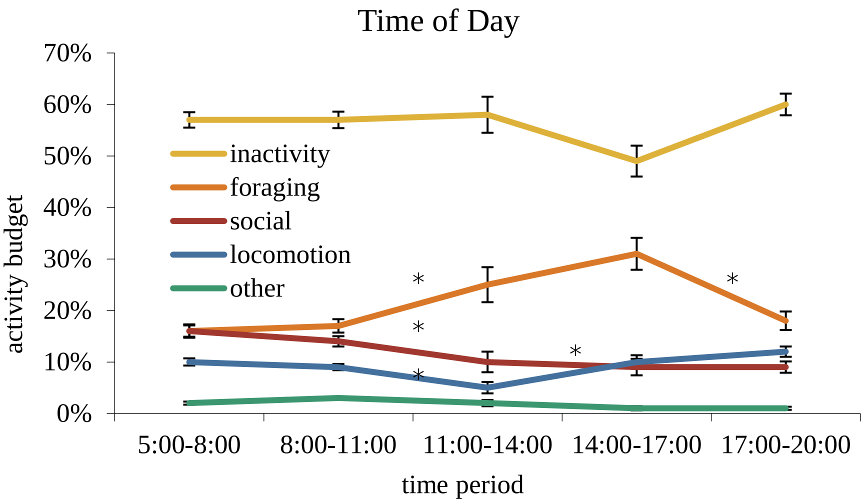


Figure 3.1: Mean daily percent (%) of activity budget ± standard error (SE) each behaviour constitutes in each time period. Foraging, social behaviour, locomotion, and ‘other’ behaviour rates change throughout the day; significant differences to adjacent time periods are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.2, and pairwise comparison p-values can be found in Table 1, Appendix.

Table 3.2: Mean daily percent (%) of activity budget ± SE each behaviour constitutes in each time period. All behaviours assessed with a BLM ‘deviance’ model and df=4. Significant results indicated with asterisk (*). All values rounded to nearest integer. Pairwise comparison p-values can be found in Table 1, Appendix.

	inactivity	**foraging**	**social**	**locomotion**	**other**
5:00-8:00	57 ± 1.5	16 ± 1.3	16 ± 1.1	10 ± 0.7	2 ± 0.3
8:00-11:00	57 ± 1.6	17 ± 1.3	14 ± 1.0	9 ± 0.6	3 ± 0.3
11:00-14:00	58 ± 3.5	25 ± 3.4	10 ± 2.0	5 ± 1.1	2 ± 0.6
14:00-17:00	49 ± 3.0	31 ± 3.1	9 ± 1.6	10 ± 1.3	1 ± 0.4
17:00-20:00	60 ± 2.1	18 ± 1.8	9 ± 1.1	12 ± 1.0	1 ± 0.3
p=	0.051	<0.001*	<0.001*	0.002*	0.012*
χ^2=	9.442	29.941	24.032	16.833	12.846
n=	6163	2007	1413	1050	246

3.3.1.2 *Seasonal Differences in Activity Budgets*

Seasonal differences were found in activity budgets (LM: χ^2=18.643, df=4, p=0.001, Figure 3.2). This pattern held for foraging, social and 'other' behaviours, but not locomotion; seasonal differences in inactivity rates approached significance (Table 3.3). In the wet season, social behaviours increased significantly, while inactivity increased marginally. At the same time, foraging and 'other' behaviours decreased significantly.

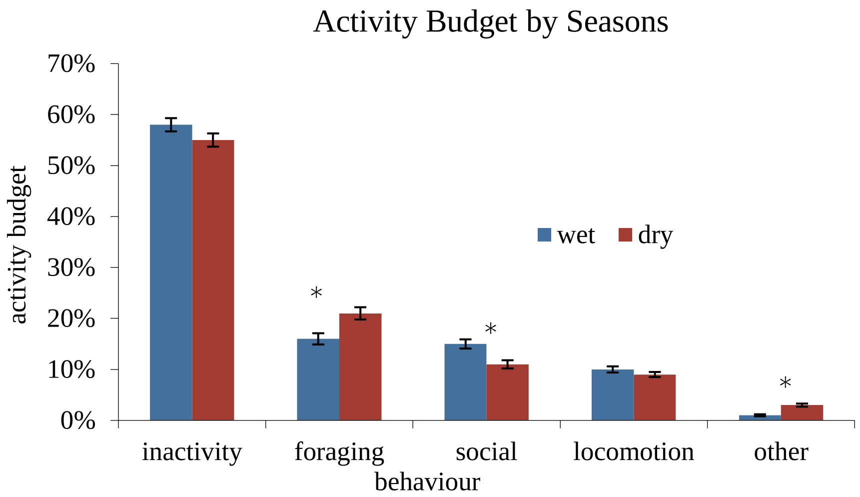


Figure 3.2: Mean daily percent (%) of scans ± SE each behaviour constitutes within the wet (May-Oct) and dry (Nov-Apr) seasons. Behaviours that show significant seasonal differences are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.3.

Table 3.3: Mean daily percent (%) of activity budget ± SE for each behaviour within the wet (May-Oct) and dry (Nov-Apr) seasons. All behaviours assessed with a BLM 'deviance' model and df=1. All values rounded to nearest integer. Significant results indicated with asterisk (*).

	inactivity	**foraging**	**social**	**locomotion**	**other**
wet	58 ± 1.3	16 ± 1.1	15 ± 0.9	10 ± 0.6	1 ± 0.2
dry	55 ± 1.3	21 ± 1.2	11 ± 0.8	9 ± 0.5	3 ± 0.3
p=	0.062	0.001*	0.014*	0.416	<0.001*
χ^2=	3.494	10.988	6.074	0.660	17.749
n=	6163	2007	1413	1050	246

3.3.1.3 *Group Differences in Activity Budgets*

Behaviours were found to be significantly different between the two reproductive groups studied (LM: χ^2=24.497, df=4, p<0.001; Figure 3.3). Posthoc analyses indicate that group differences held for inactivity, foraging, and 'other' behaviours, but not social behaviour or locomotion (Table 3.4). Compared to Group B, Group A (the larger group) spent significantly more time inactive and engaged in ‘other’ behaviours. They spent less time foraging than Group B.

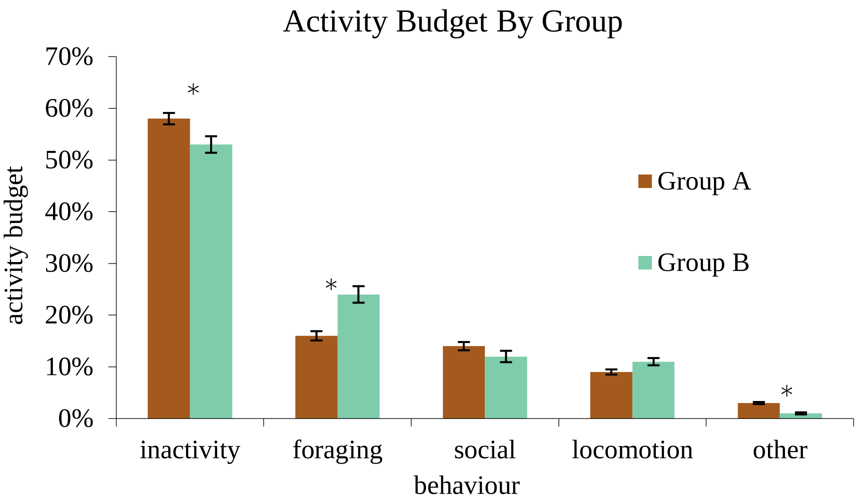


Figure 3.3: Mean daily percent (%) of activity budget ± SE each behaviour constitutes for each of the two main groups. Behaviours that show significant group differences are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.4.

Table 3.4: Mean daily percent (%) of activity budget ± SE for each behaviour within each of the two main groups. All posthoc analyses assessed with a BLM ‘deviance’ model and df=1. All values rounded to nearest integer. Significant results indicated with asterisk (*).

	inactivity	**foraging**	**social**	**locomotion**	**other**
Group A	58 ± 1.1	16 ± 0.9	14 ± 0.8	9 ± 0.5	3 ± 0.2
Group B	53 ± 1.6	24 ± 1.6	12 ± 1.1	11 ± 0.7	1 ± 0.2
p=	0.010*	<0.001*	0.222	0.064	0.001*
χ^2=	6.553	18.331	1.492	3.441	34.411
n=	6111	2000	1409	1044	245

3.3.1.4 *Age Differences in Activity Budgets*

Behaviours were significantly different between age classes (infants, young juveniles, and juveniles are aggregated under ‘young’; LM: χ^2=108.722, df=8, p<0.001; Figure 3.4). This pattern held for all three behaviours that could be assessed (Table 3.5). Young langurs spend a relatively large amount of time locomoting and engaging in ‘other’ behaviours compared to older age classes (Table 3, Appendix). Subadults spend more time foraging than other age classes (Figure 3.4). Compared to young, adults were significantly more social (Table 3a, Appendix), and they had the highest rate of inactivity (Figure 3.4). There was no significant interaction of age and sex on activity budgets (LM: χ^2=12.366, df=8, p=0.136).

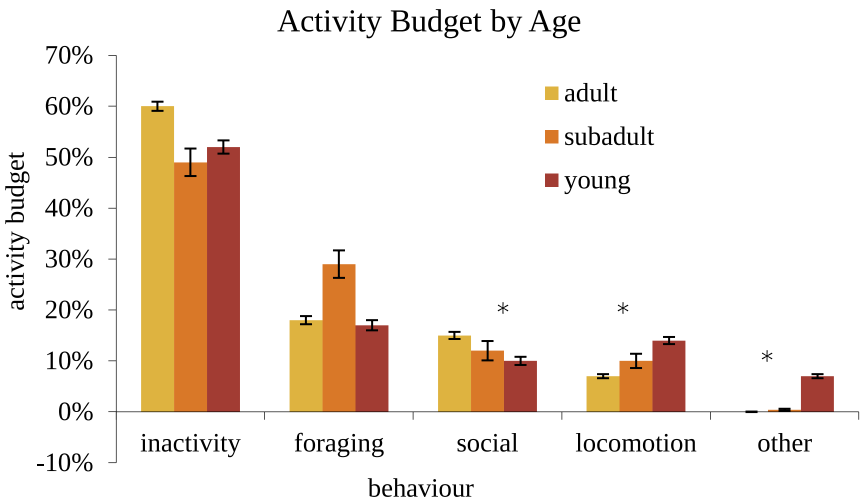


Figure 3.4: Mean daily percent (%) of activity budget ± SE each behaviour constitutes for each age group (the 'young' age group includes infants, young juveniles, and juveniles). Behaviours that show significant age differences are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.5, and pairwise comparison p-values can be found in Table 3, Appendix.

Table 3.5: Mean daily percent (%) of activity budget ± SE for each behaviour within each age class. All analyses are BLM and have df=2. All values rounded to nearest integer. Significant results indicated with asterisk (*). Pairwise comparison p-values can be found in Table 3, Appendix.

	inactivity[b]	**foraging**[b]	**social**[a]	**locomotion**[a]	**other**
adult	60 ± 0.9	18 ± 0.8	15 ± 0.7	7 ± 0.4	<1 ± <0.1
subadult	49 ± 2.7	29 ± 2.7	12 ± 1.9	10 ± 1.4	<1 ± 0.2
young	52 ± 1.3	17 ± 1.0	10 ± 0.8	14 ± 0.7	7 ± 0.4
p=			<0.001*	<0.001*	<0.001*
χ^2=			23.730	71.463	110.016
n=	5722	1875	1358	985	246

[a] assessed with a 'deviance' model

[b] unable to statistically analyse due to low number of observations in some categories

3.3.2 Dietary Budget

The most commonly consumed food was leaves (84 ± 2.8% of foraging scans where the consumed object could be identified), followed by fruit (8 ± 2.8%), flowers (5 ± 1.7%), and finally stems (3 ± 1.2%). The langurs were seen to drink ocean water directly (12% of water consumption), lick rocks and cavities of rock pools (62%), as well as dip their tail in the water in order to drink from it (27%) (Figure 3.5), spending 0.3% of all scans engaged in drinking behaviour. There was no significant effect of group (LM: χ^2=3.442, df=3, p=0.328), age (LM: χ^2=4.585, df=6, p=0.598), or sex (LM: χ^2=0.796, df=3, p=0.851) on dietary budgets.

Figure 3.5: Two young langurs drinking directly from the ocean (left) while an adult (right) licks ocean water off their tail. Photo taken April 2014 by R Hendershott

3.3.2.1 *Time Differences in Dietary Budgets*

Items consumed while foraging differed significantly throughout the day (LM: χ^2=21.284, df=12, p=0.046; Figure 3.6). The only posthoc analysis that was possible was on leaves, which showed diurnal variation (Table 3.6); all other diurnal variation of food items are descriptive only. In the early morning (5:00-8:00) there were relatively low rates of leaf, fruit, and stem eating; and high rates of flower eating. Compared to the previous time period, 8:00-11:00 had less flower eating, and had an increase in stem and leaf consumption. The 11:00-14:00 time period had a significant increase in leaf eating (Table 4, Appendix), and a reduction in stem, flower, and fruit eating. In the afternoon (14:00-

17:00) fruit eating increased. In the evening (17:00-20:00) flowers started being eaten again, fruit eating decreased and stems were not consumed.

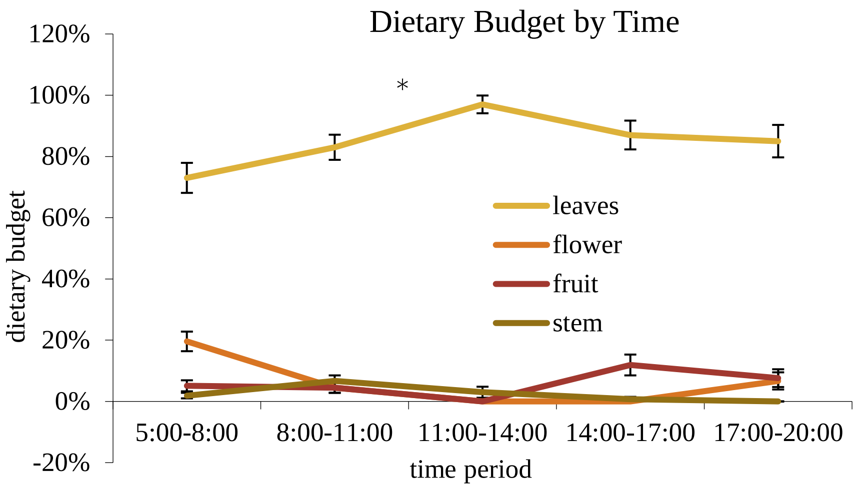


Figure 3.6: Mean daily percent (%) of dietary budget ± SE for each food item within each time period. Food items that show significant variation between adjacent time periods are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.6.

Table 3.6: Mean daily percent (%) of dietary budget ± SE for each food item within each time period. All values rounded to nearest integer. Significant results indicated with asterisk (*). Pairwise comparison p-values for leaf eating can be found in Table 4, Appendix.

	leaves [a]	**flowers**[b]	**fruits**[b]	**stems**[b]
5:00-8:00	73 ± 4.9	20 ± 3.2	5 ± 1.8	2 ± 0.9
8:00-11:00	83 ± 4.1	5± 1.7	5 ± 1.7	7± 1.8
11:00-14:00	97 ± 2.9	0 ± 0.0	0 ± 0.0	3 ± 1.8
14:00-17:00	87 ± 4.7	0 ± 0.0	12 ± 3.4	1 ± 0.8
17:00-20:00	85 ± 5.3	7 ± 2.8	8 ± 2.9	0 ± 0.0
p=	0.069			
χ^2=	8.715			
n=	618	60	46	22

[a] assessed with a BLM ‘deviance’ model, df=4

[b] unable to statistically analyse due to low number of observations in some categories

3.3.2.2 *Seasonal Differences in Dietary Budgets*

Items consumed while foraging differed significantly throughout the year (LM: χ^2=19.422, df=3, p<0.001; Figure 3.7). There was a significant effect of season on leaf and fruit consumption, but not flower or stem consumption (Table 3.7). Leaf eating was significantly more common in the dry season than the wet season, while fruit eating was over seven times more common in the wet season than the dry season.

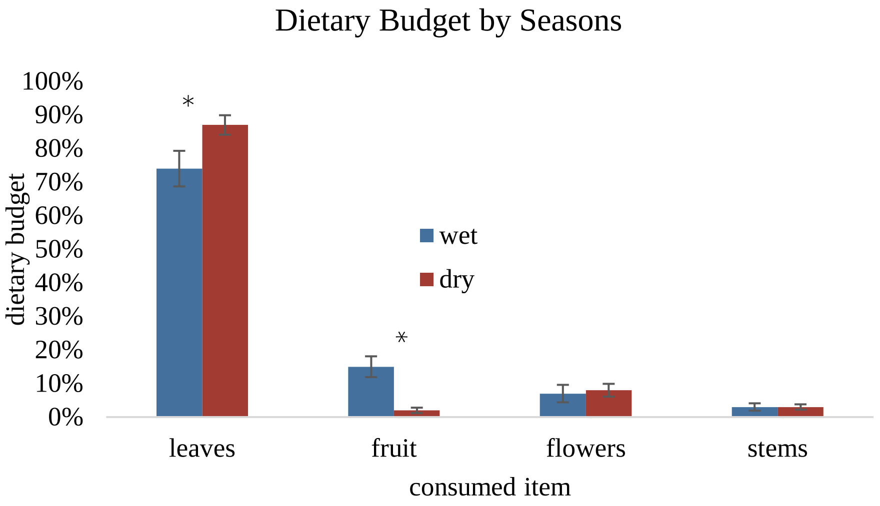


Figure 3.7: Mean daily percent (%) of dietary budget ± SE each food item consumed within the wet (May-Oct) and dry (Nov-Apr) seasons. Food items that show significant seasonal differences are indicated with an asterisk (*). Test statistics and exact values can be found in Table 3.7.

Table 3.7: Mean daily percent (%) of dietary budget ± SE for each food item consumed within the wet (May-Oct) and dry (Nov-Apr) seasons. All poshoc analyses assessed with a BLM 'deviance' model and df=1. All values rounded to nearest integer. Significant results indicated with asterisk (*).

	leaves	**fruits**	**flowers**	**stems**
wet	74 ± 5.3	15 ± 3.1	7 ± 2.6	3 ± 1.1
dry	87 ± 2.9	2 ± 0.8	8 ± 1.9	3 ± 0.8
p=	0.029*	<0.001*	0.732	0.901
χ^2=	4.774	20.605	0.117	0.016
n=	618	46	60	22

3.4 Discussion

3.4.1 Activity Budget

I found that Cat Ba langurs spend 55% of scans inactive, which is likely explained by the high amount of leafy material in their diet (84% leaves) that require animals to spend a considerable part of their day resting to cope with the indigestible fibre in leaves (Dasilva 1992; Kirkpatrick 2007). Inactivity is the most common behaviour for all limestone langurs, ranging from 41-75% of their daily budget (Table 3.8), which roughly fall within the range of other colobines' rates (25-69%) (Table 1.2, Chapter 1), and encompasses the

Cat Ba langur rate. During the dry season, when Cat Ba langurs consume significantly more leaves (Figure 3.7), they also show a [non-significant] trend to spending less time inactive (Figure 3.2). This implies that although the langurs are relying heavily on a leafy diet, they are unable to sit around, inactive and digesting, but must instead spend that time foraging in order to meet energy requirements. A negative relationship between time spent feeding (especially on mature leaves) and time spent inactive has been found in other primates (Clutton-Brock and Harvey 1977a; Oates 1977; Dunbar and Dunbar 1988; Newton 1992; Grueter et al. 2013), suggesting a tradeoff.

Table 3.8: Activity budgets for limestone langurs living in the wild (albeit disturbed habitat) over an annual cycle. Numbers are percent (%) of each behaviour within the activity budget. All values rounded to the nearest integer.

species	**inactivity**	**foraging/ feeding**	**locomotion**	**social**	**'other'**	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	55	19	12	12	2	(this study)
white-headed langurs (*Trachypithecus leucocephalus*)	52	13	15	14[a]	7[c]	(Li and Rogers 2004a)
	46	20	29	4[d]		(Zhou et al. 2010)
Delacour's langurs (*Trachypithecus delacouri*)	61	29	4	6		(Workman 2010a)
	75	21	2	2	<1	(Agmen 2014)
François' langurs (*Trachypithecus francoisi*)	50[b]	27[b]	13[b]	<1[a]	10[b,c]	(Yang et al. 2007)
	41	25	17	5[a]	12[c]	(Hu 2007)
	52	23	17	2[a]	6[c]	(Zhou et al. 2007a)

[a] grooming only
[b] averaging of two groups
[c] includes play and/or huddling, which could also be social
[d] does not differentiate between 'social' and 'other'

Foraging is the second most common behaviour at 19% of Cat Ba langur activity budget, which is within the 13-29% reported across limestone langurs (Table 3.8) and is on the low end of other colobines (17-51%) (Table 1.2, Chapter 1). Time spent foraging (searching for food) and feeding (picking, processing, and ingesting food) depends on the distribution of resources and their quality (Decker 1994). As folivores, colobines eat a bulky diet that requires an extensive amount of feeding time (Decker 1994). Feeding is spread out throughout the day and broken up by resting and digesting, and traveling from one feeding site to the next.

The Cat Ba langurs’ social rate of 12% is relatively high for limestone langurs (Table 3.8), and may be due to the large number of young in this study, or it could reflect my study’s definition of social behaviour which includes groom, social play, vocalise, mount, embrace, transfer, present, harassment, and agnostic behaviours (Table 2.4, Chapter 2); other studies often only report grooming, excluding social play, etc. Among limestone langurs, socialisation and/or grooming ranges from <1%-14% of their activity budgets (Table 3.8), which is similar to social rates in other colobines (1-16%) (Table 1.2, Chapter 1). Typically colobines do not devote a lot of time to social behaviour because of their time-consuming feeding and digesting requirements. Additionally, eating nonmonopolisable sources such as leaves does not require a strong emphasis on socialisation, dominance, and bonding mechanisms in langurs (Section 1.6.7, Chapter 1). Notably, however, Asian colobines can have linear dominance hierarchies and compete over clumped foods (Koenig 2000; Koenig et al. 2004; De Vriest et al. 2016)—especially in captive or provisioned populations (Blaffer Hrdy 1977; Borries et al. 1991; Amarasinghe et al. 2009)—which may be exacerbated by habitat fragmentation (Sterck et al. 1997). Due to the nature of habitat fragmentation and deterioration which limit food resources (Section 7.3, Chapter 7), it is possible that the Cat Ba langurs do experience more significant competition for limited resources, and thus there is stronger emphasis on bonding.

Locomotion, or moving, occupies 12% of Cat Ba langurs' activity budgets, and 2-29% of limestone langur budgets (Table 3.8); other colobines show similar patterns (2-29%: Table 1.2, Chapter 1). As locomotor budgets are often related to habitat and resource distribution and defence for primates (Clutton-Brock and Harvey 1977a; Mitani and Rodman 1979; Pages et al. 2005), locomotion and daily path lengths give an indication as to the amount of competition (van Schaik 1983; van Schaik and van Noordwijk 1988), resource availability (Fashing 2007a; Harris et al. 2009), and habitat quality (Li and Rogers 2005b) for the local primates. Cat Ba langurs have leaping rates that are less than a quarter the rate of leaping locomotion in a white-headed group (11% for Cat Ba vs. 49% for white-headed langurs), and they use climbing slightly more often (22% vs. 17%) (Xiong et al. 2009), which may have to do with differences in habitat and vegetation coverage between sites.

3.4.1.1 *Time Differences in Activity Budgets*

After waking up and moving away from the sleeping site, Cat Ba langurs spend most of their time inactive, foraging, and socialising (Figure 3.1). By the middle of the day, they devote more time to eating. Toward the end of the day they move back to their sleeping sites and resume high levels of inactivity. This is similar to a number of other Asian colobines (Bernstein 1968; Huang et al. 2003; Hu 2007; Zhou et al. 2007a; Rawson 2009; Zhou et al. 2010), including a previous study on Cat Ba langurs (Schneider et al. 2010), that found diurnal variation in activity budgets. Diurnal patterns to activity may be an adaptive strategy for dealing with temperature fluctuations (Oates 1987; Hill 2005) or maximising digestion (Clutton-Brock 1977).

The Cat Ba langurs begin their day around 5:00 in the hot, wet, summer season, but not until 6:00 in the cool, dry, winter season; they are generally moving around before the sun has risen. Primates tend to leave their sleeping sites around dawn, although this can change depending on temperature and light availability (Anderson 1984; Oates 1987; Hu 2007; Xiang et al. 2010).

Cat Ba langurs have relatively high rates of inactivity and social behaviours upon leaving the sleeping site in the morning (Figure 3.1) – especially as they tend to move towards summits or the tops of hills for maximum exposure during this time (Hendershott unpublished data), and summits have high rates of inactivity (Section 4.4.2.1, Chapter 4). Several species, including colobines, sunbathe upon first waking up by orienting themselves towards the sun (Oates 1977; Anderson 1984; Decker 1994), especially in winter when sitting in the sun can be used for thermoregulation purposes. For example, François' and white-headed langurs find sunny spots to sunbathe in winter, often spending time being social while resting on elevated rocks (Huang et al. 2003; Hu 2007).

In the middle of the day Cat Ba langurs spend significantly more time foraging and significantly less time locomoting or socialising compared to the previous time period (Figure 3.1). Cat Ba langurs only have one feeding peak per day, although this may be an artefact of the lumped time periods used in this study (i.e. hourly time blocks may indicate specific feeding peaks that are hidden in three hour time blocks). Many primates [primates in general (Clutton-Brock 1977; Domingo-Roura and Yamagiwa 1999), colobines in general (Long et al. 1998; Teichroeb et al. 2003; Rawson 2009), and limestone langurs (Huang et al. 2003; Hu 2007; Zhou et al. 2007a; Zhou et al. 2010)] have feeding peaks in both the morning and afternoon, although this may differ per season. For example, François' langurs start their morning feeding session earlier and their afternoon session later in the wet season, and tend to concentrate on just one feeding period compared to two peaks in the dry season (Zhou et al. 2007a).

The reduction of locomotion in the middle of the day, found in this study (Figure 3.1), reflects the langurs taking a midday rest. François' langurs rest for two to four hours in the middle of the day (Hu 2007). The length of this rest may be dependent on diurnal temperature fluctuations, and change depending on the season (Hill 2005). For example, white-headed langurs have longer midday rests during the rainy season (Zhou et al. 2010), as was seen in this study. On hot summer days (i.e. wet season) the Cat Ba langurs take a midday rest sometime between 9:00-15:00. In the hot season the midday rest may begin midmorning as a way of avoiding the hottest times of day, as most midday resting occurs in trees with shade (Hu 2007). On one particularly hot day their midday rest began at 6:45. In the cool, winter, dry season the whole day is shorter and starts later, which means the limestone langur midday rest is shorter (usually between 11:00-15:00), and the rests are more likely to occur on rocks (Hu 2007). Note that the midday rest is not reflected in the scan data because I was unable to confirm behaviour when the langurs were completely inactive and hidden in the trees. Therefore, my scans do not show that the langurs were obviously resting during this time; this is a common problem for limestone langur researchers (Hu 2007).

This study found nursing to occur significantly less often after 14:00 compared to the middle of the day. This may reflect the adult females concentrating on foraging and locomotion more during this time period, instead of inactivity and social behaviours during which nursing is more likely occur (Hendershott unpublished data; the latter two behaviours are more likely to occur in relaxed situations and with individuals in proximity: Section 5.3.4, Chapter 5). It is possible that nursing is happening upon settling down to sleep in the evening, as young often huddled with adult females, although I was unable to visually confirm face-to-breast contact due to the huddles and low light.

After the midday rest, there are significantly higher rates of locomotion for Cat Ba langurs, which continues to increase in the evening (Figure 3.1). Foraging decreases significantly as the langurs concentrate on settling down for the night (Figure 3.1). This is in accordance with other limestone langurs, wherein they move toward the sleeping cave in the late afternoon (Huang et al. 2003).

3.4.1.2 *Seasonal Differences in Activity Budgets*

Cat Ba langur activity budgets vary with season; foraging and ‘other’ behaviours increase in the dry season, while social behaviours increase in the wet season (Figure 3.2). This is likely linked to seasonal changes in available resources, which also results in different activity budgets (Gursky 2000; Hanya 2004; van Doorn et al. 2010) and feeding effort (Dunn et al. 2010) for primates. During times of limited resources (the dry season), animals can either reduce their activity levels (i.e. energy conservation) or increase foraging times and ranging distances (i.e. energy maximising) (Schoener 1971; Oates 1987; Hemingway and Bynum 2005). The Cat Ba langur pattern matches that of other limestone langurs, who tend to rest less, and travel and forage more, in the dry season (Table 3.9), as a means to maximise energy budgets when intake is lower. During the wet season, when fruits and young leaves are more available for limestone langurs (Workman 2010a), there is marginally more time for remaining inactive and significantly more time for social behaviour for Cat Ba langurs.

Table 3.9: Activity budgets for limestone langurs living in the wild throughout seasons. Numbers are percent (%) of each behaviour within the activity budget. Only studies that show significant seasonal variation are included. All values rounded to nearest integer; may not add up to 100% because ‘other’ behaviours are not included. Behaviours that show significant seasonal variation are indicated with an asterisk (*).

species	**inactivity**	**foraging /feeding**	**social**[a]	**locomotion**	season	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	58	16*	15*	10	wet	(this study)
	55	21*	11*	9	dry	
white-headed langurs (*Trachypithecus leucocephalus*)	79	14		7*	dry/spring	(Huang et al. 2003)
	84*	9*		7*	wet/summer-autumn	
	67*	20*		13*	wet and dry/winter	
	~53*	~19*		~22*	wet	(Zhou et al. 2010)
	~40*	~21*		~46*	dry	
	84*	9*		7*	wet	(Jin et al. 2009a)
	57*	20*		13*	dry	
François’ langurs (*Trachypithecus francoisi*)	45*	30	0	13*	wet and dry /spring	(Yang et al. 2007)[b]
	63*	21	<1	11*	wet/summer	
	45*	29	1	14*	wet and dry/autumn	
	45*	27	<1	15*	dry/winter	
	42	28*	6	13*	wet and dry /spring	(Hu 2007)
	39	24*	3	20*	wet/summer	
	41	21*	5	18*	wet and dry/autumn	
	42	25*	4	18*	dry/winter	
	55*	19*	3*	17	wet	(Zhou et al. 2007a)
	49*	26*	2*	17	dry	

[a] includes groom, vocalise, sexual behaviour

[b] mean of two groups

Cat Ba langurs forage more in the dry season (Figure 3.2), when there is a greater emphasis on leaf eating (Figure 3.7), which could suggest that more preferred foods are unavailable (Hu 2007). Additionally, feeding time (Decker 1994) and effort (Dunn et al. 2010) increases with an increase in foliage in the diet, as leaves take longer to process than other food items (Clutton-Brock and Harvey 1977b; Parra 1978; Nagy and Milton 1979; Choo et al. 1981; Edwards and Ullrey 1999). Other limestone langurs similarly increase feeding/foraging (Huang et al. 2000; Huang et al. 2003; Zhou et al. 2007a; Zhou et al. 2010) and their daily travel distance (Hu 2007) time in the dry season, when mature leaves dominant the dietary budget. This pattern holds for other langurs; for example, Hanuman langurs spend almost four times as much time feeding in the dry season than the wet season, taking the time from their resting budgets (Newton 1992). Captive studies show that both sexes of white-headed langurs consume more food in the dry season (male: 749g;

female: 640g) than the wet season (male: 659g; female: 591g) (Huang et al. 1997), suggesting that the increased rates of foraging in the dry season reflects increased nutritional or caloric requirements and nutrient content demands, not just increased search and processing time.

Social behaviours occurring more often in the wet season than the dry season for Cat Ba langurs (Figure 3.2) is similar to François' langurs (Zhou et al. 2007a). In the dry season there is more emphasis on foraging, with less time for social behaviour. Less vital/more expendable behaviours, such as socialisation (Dunbar and Dunbar 1988; Dunbar 1992; Alberts et al. 2005), will be sacrificed so that nutritional requirements can be maintained.

Locomotion did not differ by season for Cat Ba langurs (Figure 3.2). This is counter to patterns of other limestone langurs (Huang et al. 2003; Yang et al. 2007; Jin et al. 2009a; Zhou et al. 2010) and colobines (Newton 1992; Fashing 2007b; Harris et al. 2009), who travel more in the dry season in search of adequate food. By increasing their daily path lengths during lean months, colobines are able to maintain a higher intake of quality foods despite the higher locomotor costs (i.e. they are energy maximisers). It may be that Cat Ba langurs are energy limited in the amount they can travel, and instead exhaust nearby available food resources that are of a lower quality and take more foraging time.

'Other' behaviours are primarily those used by young langurs (including asocial play, explore, struggle, rejection, and masturbate) in this study (Figure 3.4). Therefore, the higher rates of 'other' behaviours in the dry season (Figure 3.2) are most probably an artefact of there being more young langurs in Group A in the second dry season included in this study compared to the wet season (Table 6.2, Chapter 6).

3.4.1.3 *Group Differences in Activity Budgets*

Group A spends more time inactive, and using 'other' behaviours, while Group B spends more time foraging (Figure 3.3). Differences in activity budgets between the two groups are counter to what I had anticipated. Group A is larger (n=10-13) with more infants and juveniles, thus I expected them to experience more scramble competition, with associated increased rates of looking for food/feeding and locomotion between feeding patches (van Schaik et al. 1983; van Schaik and van Noordwijk 1988). For example, a group of 22 Arunachal macaques (*Macaca munzala*) spent significantly longer foraging than a neighbouring group of 13 macaques (~37% vs. 22% of their activity budget) (Kumar et al. 2007). Females in a group of 31-33 ursine colobus spent significantly longer feeding in the dry season than females in the group of 8-16 colobus (34% vs. 23% of their activity budget), thus highlighting the seasonal effect of reduced resources and group size (Saj and Sicotte 2007). However, in my study, Group A had lower rates of these behaviours than Group B (n=7). Although densities are similar, Group B lives at a slightly higher density (Group A: 0.2-0.26 individuals/ha; Group B: 0.32 individuals/ha) in a home range less than half the size of Group A's (Table 4.4, Chapter 4), so this could mean they are facing higher scramble competition, and may have to invest more time in finding and procuring (i.e. foraging) these possibly more limited resources. Alternatively, Group A's higher rates of inactivity and lower rates of foraging may reflect an energy reduction/conservation tactic given their higher reproductive demands. The increased rates of 'other' behaviours in Group A are undoubtedly due to the presence of more young langurs in this group that engage in these 'other' subcategories (e.g. exploration, play, rejection, struggle).

3.4.1.4 *Age and Sex Differences in Activity Budgets*

Descriptively, adult Cat Ba langurs showed a trend of spending more time being inactive than subadults and young (Figure 3.4), which matches previous studies on limestone langurs' (Li 1992; Hu 2007; Zhou et al. 2007a; Schneider et al. 2010; Agmen 2014; Table 3.10), colobines' (Rawson 2009; Eakins 2010), and other primates' (Prates and Bicca-Marques 2008) activity budgets. Different age classes will have different requirements, as reproductive adults spend their time differently than developing immatures. Young individuals have less energetic costs in terms of foraging/caloric intake (due to their smaller body size, and most of them still suckling) and locomotion (often being carried), giving them plenty of free time to play or explore while the adults are inactive. Subadult Cat Ba langurs have rates of inactivity more similar to young than adults langurs.

Table 3.10: Activity budgets for limestone langurs broken down by age-sex class. Numbers are percent (%) of each behaviour within the activity budget. All values rounded to nearest integer. Note: A=adult, AM=adult male, AF=adult female, SA=subadult, Y=young

species	**inactivity**	**foraging /feeding**	**social/ grooming**	**locomotion**	**other**	age-sex class	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	60	18	15	7	<1	A	this study
	49	29	12	10	<1	SA	
	52	17	10	14	7	Y	
	69	~17	6	~9		A	(Schneider et al. 2010)
	~48-50	~0-18	33	~18-19		Y	
white-headed langurs (*Trachypithecus leucocephalus*)	66		6	9	19	AM	(Li 1992)
	69		7	10	14	AF	
	48		3	25	23	Y	
	~60	~10	~11[a]	13	~4	A	(Li and Rogers 2004a)
	~45	~2	~23[a]	28	~2	Y	
Delacour's langurs (*Trachypithecus delacouri*)	~70	~21	~4	~5		AM	(Workman 2010a)
	~55	~34	~9	~4		AF	
	~75	~20	~1	~2		A	(Agmen 2014)
	~72	~22	~2	~1		SA	
	~52	~10	~35	~1		Y	
François' langurs (*Trachypithecus francoisi*)	~43	~35	~4[a]	~21		A	(Zhou et al. 2007a)
	~24	~23	~36[a]	~20		Y	

[a] includes playing – unspecified whether this is social or not

Descriptively, subadults forage more than either of the other age classes (Figure 3.4), which is unexpected given they are neither reproductive nor growing significantly (note, however, that this was based on just two individuals in Group B). Surprisingly there is not a detectible difference in foraging rates between young and adult langurs. I had anticipated a difference in foraging rates between adults and young, as adult primates often spend more time feeding than young (Zhou et al. 2007a; Agmen 2014) because larger body sizes necessitate more food consumption and feeding time (Oates 1987), especially for pregnant or lactating females (Clutton-Brock 1977; Dunbar and Dunbar 1988). However, young growing individuals also have high energetic demands that may negate a difference in body size, and they are relatively inefficient foragers, with the result that juveniles spend more time foraging than adults in a metaanalysis of a variety of primate species (Janson and van Schaik 1993). These two factors may negate foraging rate differences, and may account for why rates of foraging are so similar between the two age classes.

I found that social behaviour is significantly more common for adults than young (Figure 3.4), which does not match patterns of high social rates in younger animals seen previously in Cat Ba langurs (Schneider et al. 2010) or limestone langurs (Li and Rogers

2004a; Hu 2007; Agmen 2014; although see Li 1992) and Asian colobines (Newton 1992; Phiapalath and Suwanwaree 2010). This may be due to the four newborns/infants present in Group A, which induced a lot of social interactions between adults, such as transfers and behaviours associated with transfers (e.g. mount/present, embrace, groom: Section 5.4, Chapter 5).

I anticipated that young langurs would be more active/move around more than older age classes, as seen in other Asian colobines (Li 1992; Newton 1992; Rawson 2009; although see Zhou et al. 2007a) and leaf eating primates (Prates and Bicca-Marques 2008), which was borne out by the Cat Ba langur data – young locomote significantly more than older age classes (Figure 3.4). This is due to the young individuals having less need for resting, and apparently investing less in social behaviours, which gives them more time to move around. Subadult Cat Ba langurs have intermediate rates of locomotion, reflecting their tendency to both play and be more active with young group members, and their increased body size that makes them less likely to move without purpose.

‘Other’ behaviours are primarily used by young individuals (Figure 3.4), due to most behaviours being applicable to only young individuals (1% of ‘other’ behaviours were adult oriented; Table 3.1) in this study. Unsurprisingly, there is a massive bias for ‘other’ behaviours to occur in young langurs; as adults never used explore or asocial play, the two most common ‘other’ behaviours. Subadults use ‘other’ behaviours at rates similar to adults.

It is surprising there is no effect of sex on activity budgets, as other studies have found sex differences among colobines, primarily due to differences in nutritional and energetic requirements (due to pregnancy and lactation) (Clutton-Brock 1977; Garber 1987; Dunbar and Dunbar 1988; Key and Ross 1999) and social bonding and vigilance patterns (Clutton-Brock 1977; Newton 1992; Fashing 2001a; Fashing et al. 2007; Hu 2007; Workman 2010a; Witte 2011; Agmen 2014). I believe the lack of sex difference is purely due to a small sample size in which sex was known.

3.4.2 Dietary Budgets

Cat Ba langurs have an annual diet of 84% leaves, which is within the range of limestone langur leaf eating (40-95%; Table 3.11). Young leaves are preferable to mature leaves because they are more digestible, take less time to chew, are a softer texture, have more water and protein and less fibre; they are overall, more nutritious (Hladik 1977; Milton 1979; Oates et al. 1980; Waterman et al. 1980; Choo et al. 1981; McKey et al. 1981; Becker and Martin 1982; Coley 1983; Milton 1984; Davies and Baillie 1988; Chapman and Chapman 2002). This makes then an important item for white-headed langurs (Li et al. 2003; Li and Rogers 2006; Zhou et al. 2011). In general, young leaves are highly preferred by folivores (McKey et al. 1981; Stanford 1991b; Li and Rogers 2006), though less abundant (Milton 1981) than mature leaves. This study did not differentiate between young and mature leaves, which would be an area worthy of further research.

Table 3.11: Annual and seasonal dietary budget for limestone langurs. Numbers are percent (%) of each food item within the dietary budget. Significant seasonal differences indicated with an asterisk (*). All values rounded to nearest integer.

species	**leaves / leaf buds**	**flower/ flower buds**	**fruits**	**seeds**	**‘other’**	season	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	74*	7	15[c]*		3	wet	(this study)
	87*	8	2 [c]*		3	dry	
	84	5	8[c]		3	annual	
white-headed langurs (*Trachypithecus leucocephalus*)	88	2	7	1	2	annual	(Li et al. 2003)
	87	2	8	1	1	annual	(Zhou et al. 2011)[b]
	89	3	9			annual	(Yin et al. 2011)
	91		6[c]			?	(Zhou et al. 2010)
	63-95	0-6	5-35			annual	(Huang et al. 2000)
	89	1	5*		5*	wet	(Zhou et al. 2013b)
	92	1	6*		2*	dry	
	92	<1	4		4	annual	
	79	2	10	0		wet[a]	(Workman 2010a)
	81	8	9	1		dry[a]	
	80	5	9[c]		6	annual[a]	
François’ langurs (*Trachypithecus francoisi*)	79	1	15	2	4	wet	(Hu 2007)
	40	3	43	13	2	dry	
	64	4	26	7		annual	
	95	1	3		2	annual	(Huang et al. 2008b)
	87	1	9[1]		3	annual	(Li et al. 2009)
	53-71	~7-8	~9-17	~5-14	~3-8	annual	(Zhou et al. 2009a)

[a] monthly but not seasonal difference
[b] averaging of two groups
[c] fruits and seeds are undifferentiated

The 8% of Cat Ba langurs’ annual diet devoted to fruit is similar to that of other limestone langurs (3-35%: Table 3.11). Fruit is an energy-rich resource that is more digestible than leaves (Davies and Baillie 1988) and is preferred by some species that can physiologically process it (Hladik 1977; Stanford 1991b; Newton 1992; Bennett and Davies 1994). For colobines this fruit tends to be unripe (Chivers 1994; Waterman and Kool 1994; Davies et al. 1999; Workman and Le Van Dung 2009; Workman 2010a) due to gut microbial flora that cannot digest sugar-rich fruit (Strasser and Delson 1987; Caton 1999). Fruit is not a preferred food for white-headed langurs, although they do feed intensively on some species when they are available (Li and Rogers 2006), a pattern noted observationally for the Cat Ba langurs. Seeds are highly preferred food items by some colobines (McKey 1978; Dasilva 1992) and may be part of Cat Ba langur fruit eating.

Flower eating, at 5% of the Cat Ba langur dietary budget, is similar to what is expected based on studies of other limestone langurs (0-8%: Table 3.11). In a study of Venezuelan red howler monkey (*Alouatta seniculus*) diets, flowers have lower proportions of dry matter, protein, fibre, and acid lignin compared to mature and young leaves, and they have higher proportions of water (Oftedal 1991). Among black howler monkey (*Alouatta pigra*) diets, flowers are particularly high in copper (Behie and Pavelka 2012). In terms of protein-to-fibre, flowers have been found to be a better resource than mature leaves (but not as good as young leaves) at some sites (Waterman and Kool 1994). Therefore, the inclusion of flowers in the diet may be a form of macro or micronutrient or water consumption that is not being otherwise obtained in their diet.

I found that water consumption (i.e. rock lapping, licking rocks, rock gnawing, tail drinking, ocean lapping) does not occur very often (<1% of scans). This relatively low rate is similar to what is reported for Delacour's langurs (*Trachypithecus delacouri*) (Workman 2010a), while François' langurs are observed to drink water only every one-two days (Wang et al. 2011). In general limestone langurs also obtain water from streams and rivers; pools on the ground, in rocks, or in trees; the concavity of leaves, and dew; and within food sources (Brandon-Jones 1989; Huang and Li 2005; Hu 2007); white-headed langur foods have an average of 70 ± 6.4% water content (Zhou et al. 2013b).

3.4.2.1 *Time Differences in Dietary Budgets*

Cat Ba langurs forage on different plant parts throughout the day, although leaves are always consumed more than any other item (Figure 3.6). Diurnal variation in plant part consumption is common for many primates (Oates 1987; Chapman and Chapman 1991; Domingo-Roura and Yamagiwa 1999). Among Cat Ba langurs, flowers are eaten more often in the morning, which then switches to significantly more leaves being eaten in the middle of the day, before the midday rest. Other primates also eat more leaves before sleeping (Oates 1977; Domingo-Roura and Yamagiwa 1999), which may allow for extensive, time-consuming digestion of protein-rich leaves to occur while resting (Clutton-Brock 1977; Wrangham 1977). Geoffroy's spider monkeys (*Ateles geoffroyi*) eat a large amount of leaves in the late morning and late afternoon, right before they sleep; indeed, the time spent eating leaves is related to how much they rest in the following hour, and is negatively related to how far they travel to that night's sleeping site (Chapman and Chapman 1991). Therefore, the leaf eating of Cat Ba langurs may reflect an adaptation for eating items that require a lot of digestion right before sleeping, so that they maximise foraging time.

After the midday rest, fruit becomes more popular in the Cat Ba langurs' dietary budgets. Many primate species concentrate fruit eating early in the day, and sometimes at night (Chivers 1977; Hladik 1977; Rodman 1977; Wrangham 1977; Oates 1987; Chapman and Chapman 1991). This may be an easily digestible adaptation for energy lost while resting (Chivers 1977). Therefore, the fruit eating after the midday rest may reflect a desire for a quick energy source upon waking up.

3.4.2.2 *Seasonal Differences in Dietary Budgets*

It is well known there is seasonal variation in food production and consumption (Li et al. 2003; Hu 2007; Huang et al. 2008b; Workman 2010a; Phiapalath et al. 2011; Table 3.11); thus providing a potential explanation for the pattern of diet differing between seasons for Cat Ba langurs (Figure 3.7). Due to observational constraints, it was difficult to always differentiate between young and mature leaves in this study, but the increased leaf eating in the dry season (Figure 3.7) suggests that leaves – probably mature – were being used as a fallback food. These abundant, but less desirable, resources are typically hard to process physiologically and have low rates of energy payoff, making them part of a 'subsistence' diet, rather than a 'growth' diet (Wrangham 1980; Marshall and Wrangham 2007).

White-headed langurs eat more young leaves in the spring and autumn, or the wet season, when they are more available, whereas mature leaf and fruit consumption increases in the dry season (Li and Rogers 2006; Jin et al. 2009a). Similarly, François' langurs eat significantly more young leaves in wetter seasons, when they are more abundant, and more mature leaves, fruit, seeds, herb roots, and bamboo shoots in the drier seasons (Hu 2007; Zhou et al. 2009a). Delacour's langurs have a peak in young leaf consumption right before the wet season (90% of their diet) and it is lowest in the middle of the wet season (35%) (Workman and Le Van Dung 2010). Fallback species are relied upon in the lean season (Li et al. 2003); for François' langurs this includes consuming rich, fatty, and starchy seeds, petioles, and mature leaves during the dry season (Zhou et al. 2007a; Zhou et al. 2009a).

In the wet season, when fruit is presumably more available (as it is for Delacour's langurs also found in northern Vietnam: Workman 2010a), Cat Ba langurs consume it at much higher rates than during the dry season (Figure 3.7). This is similar to capped langurs (*Trachypithecus pileatus*) who double the amount of fruit eaten in the monsoon months (when the fruit is most abundant) and halve the amount of mature leaves eaten (Stanford 1991b). This pattern of concentrating on leaves in the dry season and fruit in the wet season is also seen in guereza monkeys (Dunbar 1987).

3.4.2.3 *Lack of Group, Age, and Sex Differences in Dietary Budgets*

There is no difference between Groups A and B, the three age classes, or male and female diets of Cat Ba langurs (Section 3.3.2). I suspect this is due to the extremely small number of scans that included sex and/or age *and* details on foraged item. In several other primates, males tend to eat more fruit while females eat more protein-heavy leaves (Garber 1987). Additionally, the categories for foraged items were broad, and a more detailed nutritional analysis may show subtle differences.

However, in a study of mantled howler monkeys (*Allouatta palliata*), a similar result of nondifferential plant part consumption by juveniles and adults is also seen (but plant species consumed do differ), despite the prediction that the different age classes would eat different foods (Raguet-Schofield 2010). A nutritional study in eastern gorillas (*Gorilla beringei*) shows that juveniles eat higher quantities of food, spend longer feeding, with higher rates of protein consumption for their body size than adult males (but a similar amount to adult females, who bear the heavy nutritional cost of gestation, lactation, and carrying of young gorillas) (Rothman et al. 2008). Additionally, they consume more minerals than adults. Interestingly, seasonally-frugivorous gorillas do not show fruit-eating rates to differ between juveniles and adults (Rothman et al. 2008), whereas other reports indicate that fruit is consumed by juveniles at higher rates than adults in other primates (Janson and van Schaik 1993). It may be that if a more detailed foraging analysis were conducted on Cat Ba langurs, micronutrients and protein/energy/fat/carbohydrate, species and plant part proportions may differ between the age classes. If the higher consumption of protein by juvenile gorillas were extrapolated to colobines, then it would be expected that juvenile langurs would consume more young leaves (which have a higher protein to fibre ratio than mature leaves: Milton 1979). The age of the leaves eaten was not assessed in this study and is an important area of research for future studies.

3.5 Summary

Both activity and dietary budgets reflect how animals are able to maximise nutritional intake and limit energy expenditure so that all biological, safety, and social needs are met. In order to create a baseline of behaviours and diet, this study was the first long-term behavioural assessment of the Critically Endangered Cat Ba langur, using 10 minute scan samples across 11 months of observation.

Cat Ba langurs spend 55% of their days being inactive, 19% foraging, 12% in social behaviour, 12% locomoting, and 2% in ‘other’ behaviours. Their diet is 84% leaves, 8% fruit, 5% flower, and 3% stems. The high rates of inactivity and foraging is related to their leafy diet: foliage takes a lot of time to process and requires significant time spent digesting (i.e. inactivity). Behaviours and diet differ throughout the day, partially due to thermoregulation and maximising digestion. Behaviours also differ across ages, reflecting different social and developmental requirements; differences between groups reflect demographic differences. During the dry season Cat Ba langurs spend more time foraging, and they concentrate their foraging on leaves. This is probably in response to a reduction in other, preferred, food availability and reflects the fact that leaves take more time to process than some other food sources. In the wet season the langurs have more time for inactivity and social behaviours, and also consume more fruit. This suggests that the langurs are not as food-limited, and are able to spend more time engaging in ‘expendable’ behaviours. Therefore, Cat Ba langurs can be considered energy maximisers.

It is hoped that results from this chapter can be used as a baseline of behaviours in documenting the continuing effects of habitat degradation (Section 7.3.1, Chapter 7). Detailed observation of how individuals, groups, and species behave and what they eat gives an indication of available food resources, and thus can be used as a proxy measure for habitat quality. This is of key importance to conservation efforts.

Chapter 4: Ranging Patterns and Habitat Use

4.1 Introduction

4.1.1 Ranging

Range size and how a habitat is used can depend on food availability, sleeping sites, water, and other vital resources (Section 1.6.5, Chapter 1). As resources fluctuate seasonally, so too does home range and day travel length. For example, François' langurs (*Trachypithecus francoisi*) (Zhou et al. 2007b), Hanuman langurs (*Semnopithecus entellus*) (Newton 1992), golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Li et al. 2000), and Ugandan red colobus (*Piliocolobus tephrosceles)* (Clutton-Brock 1975) have smaller home ranges at time of year with a higher reliance on leaf eating and lower dietary diversity. However, there is not a simple correlation between proportion of leaves in the diet and home range size in *Presbytis* and *Trachypithecus,* making colobine home ranges quite variable across genera (Bennett and Davies 1994). Additionally, when water is in short supply, ranging patterns (Zhou et al. 2011) and sleeping sites (Wang et al. 2011) of limestone langurs are affected as heavily used areas of the habitat tend to be in close proximity to permanent water resources (Zhou et al. 2011).

Habitat disturbance also affects how primates range (Section 7.3.2, Chapter 7), as disturbance can affect the availability of critical resources and make animals at increased risk of predation and hunting. Among limestone langurs, as habitat quality decreases (predominantly due to anthropogenic disturbance and fragmentation), home range size must increase, as each individual needs a larger area for survival (Li and Rogers 2005b; Hu 2007).

Often habitat fragmentation results in areas that primates are unable to cross, creating isolation of groups and a direct limit on their home range. Despite the fact that limestone langurs can move terrestrially, they are still wary to get too close to human-altered habitats (Li and Rogers 2005a; Zeng et al. 2013; Zhou et al. 2013a). Therefore, limestone langurs living in fragments are surrounded by inhospitable or anthropogenic environments (Huang et al. 2002; Nadler et al. 2003; Hu et al. 2004; Wang and Jin 2004;

Nguyen Manh Ha 2006; Huang et al. 2008a; Schrudde et al. 2010; Han et al. 2013), which creates a direct limit to their ranging. In fact, it is possible that limestone langurs are actually limited to karst habitats solely due to it being inaccessible or unusable to humans (Li and Rogers 2005a; Workman 2010a). In general, continuous, unfragmented, and undeveloped areas are preferred by limestone langurs (Li and Rogers 2005b). Fortunately, the fact that limestone langurs are half-arboreal/half-terrestrial (Huang and Li 2005; Zhou et al. 2013a) may make it easier for them to move between discontinuous canopies (as there is on limestone karst: Section 2.1.2, Chapter 2), unlike more arboreal primates.

4.1.2 Habitat Type: Substrate, Vegetation Coverage, Hill Type

Limestone hills can generally be divided into different regions based on vegetation cover, relative height, and the angle of incline (i.e. valleys, steep cliffs, exposed slopes, and summits). While some claim that limestone langurs prefer the under canopy vegetation and shrubby forests (Nadler and Ha Thang Long 2000), others indicate that limestone langurs avoid shrubby areas and prefer continuous forests with higher vegetation coverage (Li and Rogers 2005b; Hu 2007; Zeng et al. 2013).

Behaviours differ depending on habitat types (Xiong et al. 2009). Dense vegetation with more food options and species are available at lower levels and valleys (Li and Rogers 2004a; Zhou et al. 2013a; Nguyen Hiep pers. comm. 2014), and limestone langurs tend to spend more time foraging in those areas (Li and Rogers 2005b; Schneider et al. 2010), especially when food is less available (Zhou et al. 2013a). However, as lower levels also subject animals to higher predation risk, a tradeoff must be made between safety and food quality (Zhou et al. 2013a).

4.1.3 Sleeping Sites

Primates spend a considerable portion of their lives sleeping, and, because this makes them vulnerable, they need to find appropriate sleeping sites to provide safety from predators and climactic extremes. Other factors that may influence sleeping site selection are parasite avoidance, easy access to food, and visual access to other groups as well as finding a structure that provides a stable platform large enough for the whole group to be in proximity (Anderson 1984; Anderson 1998; Li et al. 2006). The relative value of these variables will differ by species, environment, and season. Overall, sleeping sites may be an important resource that limits group size, size of range (day and home), and whether or not a species occurs in an area (Anderson 1984; Barton et al. 1992).

Unlike most primates (Anderson 1984; Yeager 1990a; von Hippel 1998; Li et al. 2006; Matsuda et al. 2008a; Li et al. 2010; Porter and Garber 2013; Djègo-Djossou et al. 2015), limestone langurs sleep in caves or on ledges rather than trees (Tan 1985; Huang et al. 1992; Rogers 2002; Huang et al. 2003; Grueter and Ding 2006; Zhou et al. 2007b; Zhou et al. 2009b; Li et al. 2011; Wang et al. 2011). This may be due to a lack of large, suitable trees (due to deforestation) (Huang et al. 2003), which are preferred by colobines as sleeping sites (Cui et al. 2006; Djègo-Djossou et al. 2015) but are limited by human-induced fragmentation (Arroyo-Rodríguez and Mandujano 2006). Alternatively, caves may be preferred because they provide better protection from the elements and extreme temperatures, increased safety from predators, and/or increased access to minerals (Nadler et al. 2003; Grueter and Ding 2006).

Through careful selection and reuse, sleeping sites may reduce dangers associated with predation, as escape is easier in known areas (Anderson 1984; Zhou et al. 2009b; Li et al. 2011). White-headed (*Trachypithecus leucocephalus*) (Li et al. 2011) and François' (Zhou et al. 2009b) langurs, as well as other colobines (von Hippel 1998; Matsuda et al. 2008a) choose sites that are difficult for predators to access, and easy to escape from. Observations of langur behaviour before entering a cave suggest that the monkeys are aware of their vulnerability to predators at such times (Zhou et al. 2009b; Li et al. 2011), and some suggest that past predation pressure is why limestone langurs sleep in caves, even when there are no current predators (Huang et al. 2003). However, the only known predators of Cat Ba langurs are humans, who actually take advantage of cave use for catching a whole group at a time (Nadler and Ha Thang Long 2000).

Choosing sleeping sites may also aid in thermoregulation. For example, snub-nosed monkeys (*Rhinopithecus* spp.) face snowy, winter chills as low as -8^{0}C, and choose sleeping trees that are dense with good canopy coverage (and hence help buffer the cold) and face east and southeast (to take advantage of morning sun) (Cui et al. 2006; Li et al. 2006; Xiang et al. 2010). Rock caves may help keep temperatures less extreme (Barrett et al. 2004), protecting sleeping animals from the summer heat and winter chill (Hu 2007), while sleeping on heat-retaining rocks may be an effective way of keeping warm overnight (Anderson 1984). As a result of these advantages, caves and rocky ledges are used by some primates (Zhao and Deng 1988; McGrew et al. 2003; Barrett et al. 2004; Pruetz 2007), including limestone langurs (Huang et al. 2003; Zhou et al. 2009b).

The location of sleeping sites may be determined by quick and easy access to food resources the night before and morning after, which helps reduce travel energy expenditure (Chapman et al. 1989; Zhou et al. 2009b; Xiang et al. 2010; Li et al. 2011; Wang et al. 2011). For example, limestone langurs may choose to sleep nearby food trees, especially in anthropogenically disturbed habitats (Wang et al. 2011), where sleeping sites are associated with heavily-used feeding sites (Zhou et al. 2009b; Li et al. 2011; Zhou et al. 2011). This suggests the langurs may be multiple centre place foragers (Zhou et al. 2009b), meaning that animals are focusing their foraging behaviours around a few central places, including sleeping sites, as a way of reducing travel costs (Chapman et al. 1989).

In this chapter, I assess the size of home range of two groups of Cat Ba langur (*Trachypithecus poliocephalus*), in the Cua Dong region, along with their use of various parts of their habitat (substrates, vegetative coverage, hill type), and their sleeping sites, over an 11 month period. This is put into context by behavioural and locomotor differences in various habitat types. This information is key to conservation management, as home range size and location may shift due to changes in food availability and anthropogenic disturbance. Hence, it can be used as an indicator of habitat quality. Additionally, it is important to understand what areas of a habitat are the most important for key activities (e.g. foraging, sleeping, protection from predators, etc.) so that management can focus their efforts into protecting these biologically important areas.

4.2 Methods

In order to assess home range and habitat type use for the Critically Endangered Cat Ba langur, I observed two reproductive groups (Group A had 10-13 individuals throughout the study, Group B had 7 individuals) in the Cua Dong region of Cat Ba Island from a boat. Between February 2014 and January 2015, I was in visual contact with the langurs for 549 hours over 180 field days. Seasons were divided into wet, hot summers (May-Oct) and cool, dry winters (Nov-Apr) (following Workman 2010b; Agmen 2014).

4.2.1 Home Range

As the internal valleys of the hills on Cat Ba Island are inaccessible, information on ranging patterns can only address ocean-facing range use, which is similar to other studies that face comparable challenges (Schneider et al. 2010; Workman 2010a; Agmen 2014; Phan Duy Thuc et al. 2014). For this study, home range was measured through noting UTM locations whenever the group relocated over 10-20 metres during behavioural observations. I would take my own UTM location (in the boat), and the direction and distance between the langurs and myself, then, using Euclidian geometry, I was then able to obtain UTMs for the langurs' locations. It should be noted that these are approximations only, as the angle of the distance between myself and the langurs could not be exactly calculated (estimated to be from 0-75^0) and their bearing to the boat was approximate (range of up to 23^0). This is methodology was used because I was attempting to capture the group's behaviour, which meant that I could not pinpoint one exact bearing, but instead focused on the centre of the group, while incorporating the majority of the group spread. Additionally, I was unable to measure the vertical angle between myself and the monkeys. Therefore, all locations are approximations only. This is a limitation to data interpretation, however this is a similar methodology to other limestone langur research in rough, vertical terrain (Hu 2007). Locations that were clearly incorrect (over 30 metres from the shore or Cua Dong area) were discarded before analysis. Locations that were calculated (as above) to be in water, but were within 30 metres of the Cua Dong home ranges, were kept; there was no basis to eliminate these points as compared to the error associated with any of the other points.

The langurs' locations were mapped using ArcGIS 10.3.1 with both a minimum convex polygon (MCP) and a modified MCP to account for unusable areas of the habitat (i.e. water covered areas) from April 2014 to Jan 2015. It is widely recognised that home range size varies largely depending on the method of calculation (Decker 1994; Ostro et al. 1999; Boyle et al. 2009; Grueter et al. 2009). Minimum convex polygons may be more useful for animals in forest fragments or those that range far and are territorial, and they are the most accurate for a small number of data points (making them the best option for addressing seasonal changes to home ranges) (Boyle et al. 2009). They, do, however, overestimate home range sizes due to peripheral data points (Worton 1987; Ostro et al. 1999) making adjusted polygons more accurate (Grueter et al. 2009). Therefore, I modified the MCP to eliminate water borders by drawing a polygon around the outermost observation points while still staying on land (i.e. staying in usable areas for the monkeys). As this is not automated and therefore subject to variation, I independently drew a modified MCP ten times and then took the average of those ten polygons. Excluded areas are those that are not usable by the Cat Ba langurs such as ocean borders and a lake in Group A's home range. This is similar to the adjusted polygons presented by Grueter et al. (2009) and used for limestone langurs (Li and Rogers 2005b) with the exception of using a polygon instead of grid cells. Seasonal differences in home range size are discussed with descriptive statistics.

4.2.2 Habitat Use Data Collection

I used instantaneous scan sampling at 10 minute intervals (Altmann 1974b; Martin and Bateson 2009) by initially focusing on the area with the highest density of langurs and then spiralling out from there (for up to 45 seconds), so as to avoid biasing towards eye-catching behaviours (Altmann 1974b) and repeat counting of individuals. Behaviours and habitat use (hill type, substrate used, and vegetative coverage) was noted at the time of scans; in this way the two are linked (Section 3.2, Chapter 3, for more details).

4.2.2.1 *Behaviours and Locomotion*

Behaviours include: inactivity, foraging, social behaviour, locomotion, and 'other'. Locomotion types include drop, arm swing, quadrupdealism, leaping, and climbing (Table 2.4, Chapter 2, for definitions). However, as drop (n=7) and arm swing (n=1) occurred in less than 10 scans each, they are removed from detailed analysis.

4.2.2.2 *Habitat Use*

Substrates include: tree, rock, sand, and another langur (Table 2.6, Chapter 2). However, for this chapter, ‘another langur’ (n=128) was removed as a substrate as these tended to be young clinging to or being carried by an older langur, and ‘sand’ (n=12) was removed as a substrate as sand only occurs at ground level, and therefore all assessment of ‘ground’ includes ‘sand’ use (additionally, all analytical results were the same as ground use: Hendershott unpublished data). The cover of vegetation within a ten metre radius could have been either: sparse (>60% rocks), half (40-60% rocks or trees), or dense (>60% canopy); however, analysis is only conducted on ‘sparse’ and ‘dense’, with all ‘half’ vegetation coverage removed from analysis (n=395). Hill type was based on a quick plant species survey that showed there to be four main areas the langurs use: valleys, exposed slopes, steep cliffs, and summits (Nguyen Hiep pers. comm. 2014). This is similar to categories used in other limestone habitats (Zhou et al. 2013a; Huang et al. 2015a). I added in the category of ‘ground’ when I noted that the langurs came down to ocean level.

It must be kept in mind that for this study, the percent of available substrates, vegetative densities, and hill type in the home range of the groups were not assessed, therefore I cannot say whether or not biases in use is a reflection of langur choice, chance, or observational bias (as I could not confirm behaviours as well when animals were in trees, dense areas, or far away on summits or valleys). Currently, research is being carried out (by K Apthrop) that will address habitat quality and types, and available food resources.

4.2.2.3 *Data Analysis*

Habitat use (substrate, vegetative densities, hill types) is presented as the mean daily proportion of scans that included each specific habitat category. Following existing protocols on similar species (Teichroeb et al. 2003; Hu 2007; Zhou et al. 2007a), day was used as the unit of analysis for independence. Within each day, the number and proportion of observations of each habitat type used were recorded by three variables: behaviour, locomotion type, and season. In order to assess whether habitat use vary across these variables, I fit a linear model (LM) with arcsine transformed proportions, similar to Li and Rogers (2004a) as the dependent variable, and substrate/vegetative coverage/hill type, behaviour/locomotion type/season, and an interaction between the two, as the independent factors.

If I found that the overall habitat use pattern differed between behaviour/locomotion type/season ($P<0.05$), I assessed the differences between behaviour/locomotion type/season for each habitat type separately with a binomial logistic model (BLM), using daily observed frequencies out of total numbers of observations. As some analyses were overdispersed, this was accounted for by reporting the more conservative results of a ‘deviance’ model, and is noted in tables throughout the chapter. Tables for significant pairwise comparisons are provided in the Appendix if posthoc analyses were conducted with a BLM and were significant. I removed newborns from all analyses because their behaviours were nonindependent. I used SPSS 23 for Windows for all analyses, with significance set to $P<0.05$ for two-tailed tests.

4.2.3 Sleeping Sites

Sleeping site data were opportunistically noted during afternoon data collection when I recorded where individuals were settling down to sleep for the night. If I saw a group sit and huddle for the night I noted which group, the boat’s UTM (and distance and direction to sleeping site, so as to calculate site location as described above), the type of sleeping site (cave, ledge, tree), strata height and hill type. If any individuals were still moving when I lost sight of them due to darkness, I did not consider them at their sleeping site, but if I could not see anyone moving around but only could confirm a few langurs at a site, I considered the group to be settled there for the night. It should be noted that the monkeys were often not at the sleeping site when it was light enough to see them the next morning, suggesting that they start moving extremely early (before half an hour before sunrise) or moved very late in the evening - when it was too dark to see.

Occasionally the sleeping site ID was not recorded at the time, although the boat’s location was noted. When entering the data into ArcGIS I realised I was unable to discern whether sites were the same ones or not if they were within 55 metres of each other (especially given the inaccuracy of calculating monkey location in relation to boat distance; Section 4.2.1); this cut off was based on two sleeping sites that I knew were two different spots ~55m apart, while all other sites that were <55m apart I could not verify as being two separate sleeping sites. Therefore, if sites were within 55m of each other (as demonstrated through the mapping software), they are considered the same site. This conservative approach (i.e. having to confirm settling down and site type, lumping sites nearby one another) undoubtedly underestimates the number of sleeping sites and the number of times they were visited. As so few sleeping sites were reliably documented, they are mentioned with descriptive statistics only.

4.2.4 Limitations

There is the ever-present possibility of observer bias that affected my ability to detect langurs and their behaviours in various habitat types (especially in areas with more vegetative coverage). Limited visibility in dense foliage or trees is a common problem for Asian colobine researchers (Huang et al. 2003; Li and Rogers 2004a; Li and Rogers 2006; Li et al. 2009; Rawson 2009; Workman and Schmitt 2012; Agmen 2014). Inactivity and relaxed social behaviours (e.g. grooming) are more difficult to detect in trees or dense foliage, while locomotion and foraging are more eye-catching due to the noise associated with leaping and the langurs sitting at the tops of trees in order to reach foliage. As these results are similar to those of other limestone langurs, who likely had a similar observer bias problem, this suggests the results are valid but should be interpreted conservatively.

4.3 Results

4.3.1 Home Range

Out of the 261 GPS locations gathered for Group A, and the 234 for Group B, home ranges were calculated as 70ha for Group A and 46ha for Group B (using MCP methods) (Figure 4.1). As MCPs are inevitably an overestimation of home range size, I modified the calculation by eliminating water (i.e. unusable) areas. This gives a modified home range size of 50ha for Group A and 22ha for Group B (Figure 4.1). This home range size appears to be complete, as a graph of cumulative range size by month asymptotes after roughly five months of observations for both groups (Hendershott unpublished data).

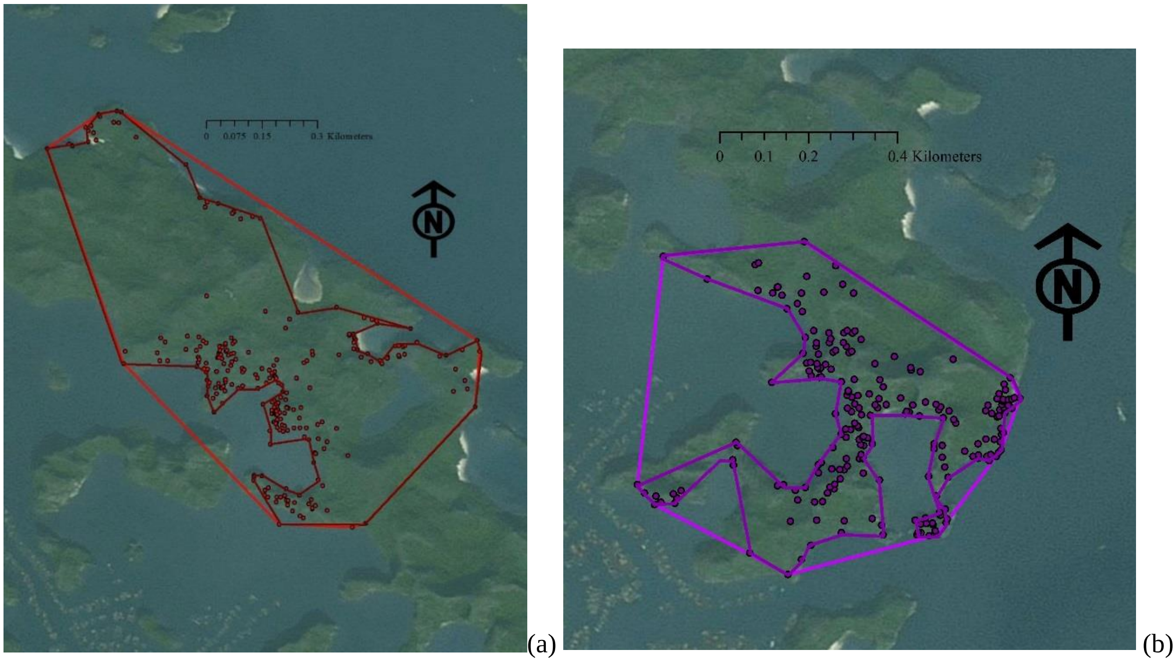


Figure 4.1: Sightings (dots) and minimum convex polygons (MCP) computer generated (outer line) and modified (inner line) for Groups (a) A and (b) B. The computer generated MCP (without modification) shows home ranges are 70ha for Group A and 46ha for Group B (note: unusable water areas included). A modified MCP gives an estimated home range of 50ha for Group A and 22ha for Group B. Map source: ArcGIS.

Throughout the study there were 10-13 individuals in Group A and 7 individuals in Group B (Table 2.2, Chapter 2); this gives a density *within home ranges* of 0.20-0.26 individuals/ha in Group A and 0.32 individual/ha in Group B. Their estimated home range overlap (from the modified MCP) was 5 ha, or 10% of Group A’s home range and 24% of Group B’s home range (Figure 4.2). Both groups had larger home ranges in the wet season than the dry season: Group A ranged within 33ha in the wet season and 22ha in the dry season, while Group B ranged within 21ha in the wet season and 18ha in the dry season.

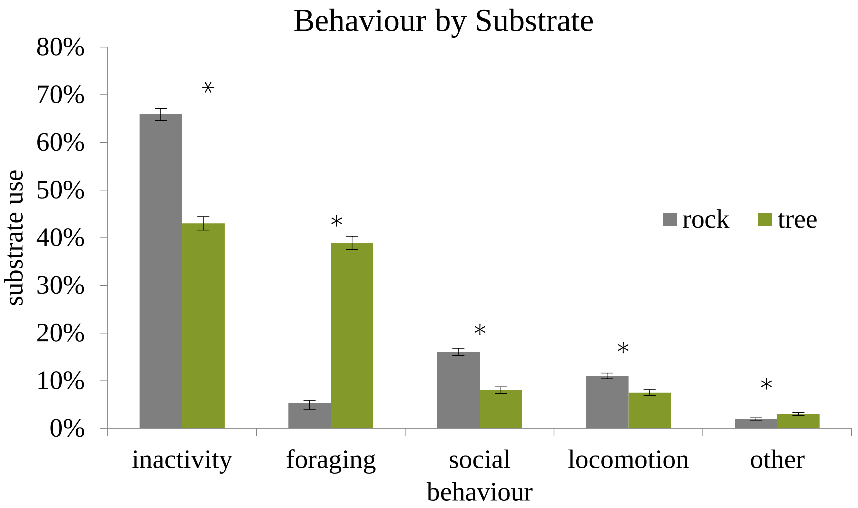
Figure 4.2: A map showing the overlap of Group A (northern range) and Group B (southern range) in Cua Dong. Overlap is 5ha, or 10% of Group A's home range and 24% of Group B's home range. Map source: ArcGIS

4.3.2 Habitat Use

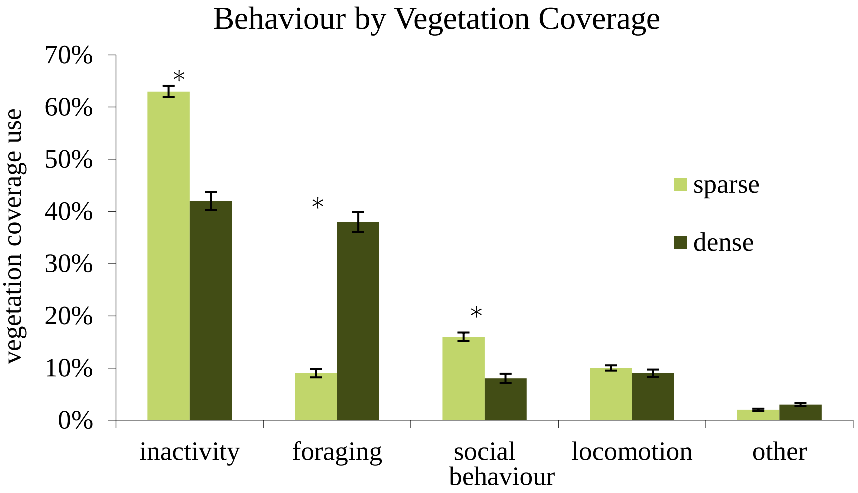
Of 12,834 scans that included information on substrate, the most commonly used substrate was rocks (54 ± 1.8%), followed by trees (46 ± 1.8%). Of 10,621 vegetation coverage scans, the most commonly used coverage is sparse (65 ± 2.2%) then dense (35 ± 2.2%). Of 8,148 scans that include information on hill type, the majority of observations were of langurs on exposed slopes (47 ± 2.9%), followed by steep cliffs (38 ± 2.9%), summits (11 ± 1.8%), in valleys (3 ± 1.0%), and on the ground (1 ± 0.5%).

4.3.2.1 *Behavioural Differences in Habitat Use*

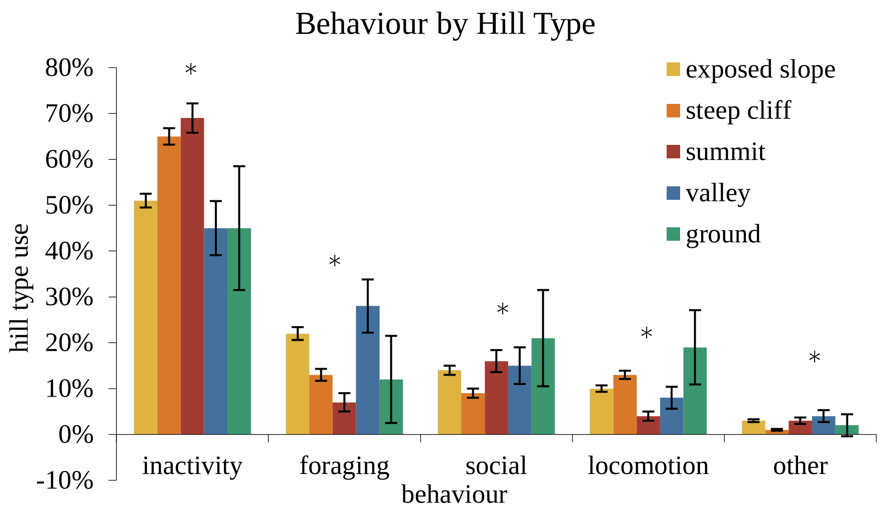
Behaviours differed across substrates (LM: χ^2=501.436, df=4, p<0.001; Figure 4.3a), vegetation coverage (LM: χ^2=328.993, df=4, p<0.001; Figure 4.3b), and hill type (LM: χ^2=132.706, df=16, p<0.001; Figure 4.3c). Posthoc analyses indicate that this pattern was significant for all five behaviours for all three habitat variables, with the exception of locomotion and ‘other’ behavioural rates not changing significantly between sparse or dense vegetation coverage (Table 4.1).



(a)



(b)



(c)

Figure 4.3: Mean daily percent (%) of habitat use ± standard error (SE) that occurred while on/in (a) substrates, (b) vegetation coverages and (c) hill types. An asterisk (*) indicates that behaviours differ significantly across habitat variables. Test statistics and exact values can be found in Table 4.1, and pairwise comparison p-values for hill type can be found in Table 5, Appendix.

Table 4.1: Mean daily percent (%) of habitat use ± SE for each behaviour while on/in each habitat variables, and results of posthoc analyses for each binomial behaviour using a BLM. All values rounded to nearest integer. Substrates and vegetation coverage have a df=1, while hill type has df=4. Significant results indicated with asterisk (*). Pairwise comparison p-values for hill type can be found in Table 5, Appendix.

			dependent variable: behaviour			
			inactivity	**foraging**	**social**	**locomotion**	**‘other’**
independent variables	substrate	**rock**	66 ± 1.1	5 ± 0.5	16 ± 0.8	11 ± 0.6	2 ± 0.2
		tree	43 ± 1.4	39 ± 1.4	8 ± 0.7	8 ± 0.6	3 ± 0.3
		p=	<0.001[a]*	<0.001[a]*	<0.001[a]*	<0.001[a]*	<0.001[a]*
		χ^2=	155.157	414.106	48.714	17.428	19.976
		n=	6022	1968	1365	1023	228
	vegetation coverage	**sparse**	63 ± 1.1	9 ± 0.8	16 ± 0.8	10 ± 0.5	2 ± 0.2
		dense	42 ± 1.7	38 ± 1.9	8 ± 0.9	9 ± 0.7	3 ± 0.3
		p=	<0.001[a]*	<0.001[a]*	<0.001[a]*	0.336[a]	0.255[a]
		χ^2=	102.782	218.967	29.302	0.925	1.297
		n=	4889	1573	1167	825	191
	hill type	**exposed slope**	51 ± 1.5	22 ± 1.4	14 ± 1.0	10 ± 0.7	3 ± 0.3
		steep cliff	65 ± 1.8	13 ± 1.3	9 ± 1.0	13 ± 0.9	1 ± 0.2
		summit	69 ± 3.2	7 ± 2.0	16 ± 2.4	4 ± 1.0	3 ± 0.7
		valley	45 ± 5.9	28 ± 5.8	15 ± 4.0	8 ± 2.4	4 ± 1.3
		ground	45 ± 13.5	12 ± 9.5	21 ± 10.5	19 ± 8.1	2 ± 2.4
		p=	<0.001[a]*	<0.001[a]*	0.002[a]*	<0.001[a]*	<0.001[a]*
		χ^2=	48.911	34.831	16.919	23.853	36.294
		n=	3733	1139	804	670	144

[a] assessed with a ‘deviance’ model

Inactivity, social behaviours, and locomotion were significantly more common on rocks, while foraging and ‘other’ behaviours were significantly more common in trees. Similarly, inactivity and social behaviours were more common in sparsely covered areas and foraging was more common in densely covered areas. Inactivity rates were higher on summits and steep cliffs than on exposed slopes or valleys (Table 5a, Appendix). Foraging was most likely in valleys, followed by high rates on exposed slopes; steep cliffs and summits were used the least often for foraging (Table 5b, Appendix). Social behaviour rates were highest on exposed slopes, followed by summits, and finally steep cliffs have the lowest rate of social behaviours (Table 5c, Appendix). Locomotion rates were significantly highest on steep cliffs, followed by exposed slopes, and finally summits had the lowest rate of locomotion (Table 5d, Appendix). ‘Other’ behaviours were significantly less likely on steep cliffs than exposed slopes, summits, or valleys (Table 5e, Appendix). Therefore, areas with more food options (trees>rocks, dense>sparse, valleys and exposed slopes>summits) were mostly used for foraging purposes, while most other behaviours occured in sparsely covered rocky areas.

4.3.2.2 *Locomotor Differences in Habitat Use*

Across all habitat types, quadrupedalism, and leaping account for the majority of the langurs’ locomotion (Section 3.3.1, Chapter 3). There was a significant effect of substrates (LM: χ^2=70.758, df=2, p<0.001; Figure 4.4a), vegetation coverage (LM: χ^2=58.298, df=2, p<0.001; Figure 4.4b) and hill type (LM: χ^2=80.253, df=8, p<0.001; Figure 4.4c) on locomotion types used by Cat Ba langurs. Posthoc analyses indicate that this significance is due to quadrupedalism and leaping rates being variable on substrates and vegetation coverages (Table 4.2). Quadrupedalism was most common on rocks in sparsely vegetated areas; only quadrupedalism was used on the ground, and constituted more than 80% of locomotion on exposed slopes and summits. Descriptively, climbing was most likely on almost-vertical steep cliffs, and there was a trend for it to occur more often on rocks and sparsely vegetated areas. Leaping was most common in trees and densely vegetated areas, such as valleys.

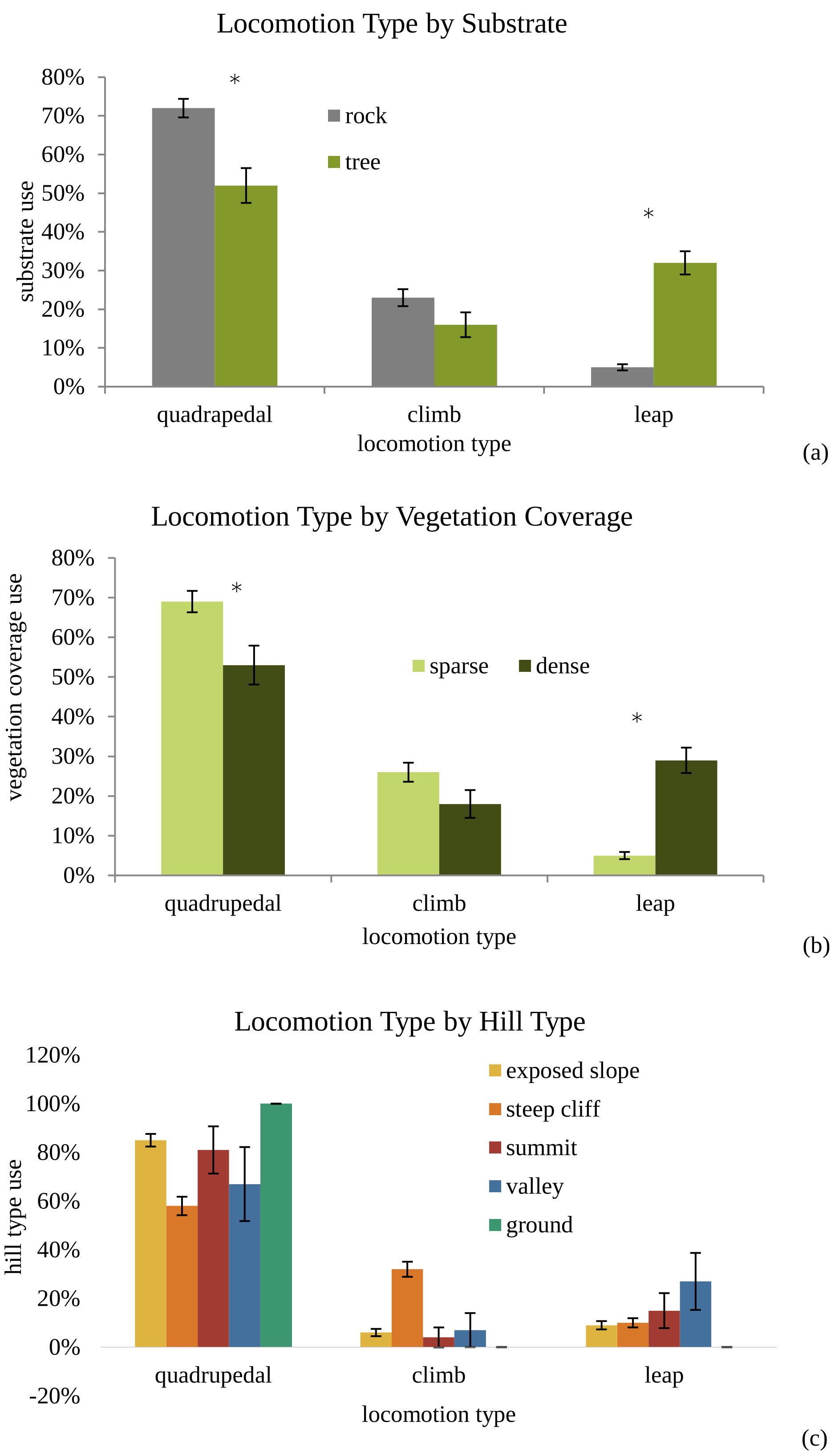


Figure 4.4: Mean daily percent (%) of habitat use ± SE each locomotion type constitutes on/in each (a) substrate, (b) vegetation coverage and (c) hill type. Significant differences across habitat variables indicated with asterisk (*). No posthoc analysis could be run on locomotion type by hill type due to low number of observations in some categories. Test statistics and exact values can be found in Table 4.2.

Table 4.2: Mean daily percent (%) of habitat use ± SE for each locomotion type while on/in each habitat variables, and results of posthoc analyses for each binomial behaviour, using a BLM. Substrates and vegetation coverage have a df=1; hill type unable be statistically analysed due to low number of observations in some categories. Significant results indicated with asterisk (*). All values rounded to nearest integer.

			dependent variable: locomotion type		
			quadrupedal	**climb**	**leap**
independent variables	substrate	**rock**	72 ± 2.4	23 ± 2.2	5 ± 0.8
		tree	52 ± 4.5	16 ± 3.2	32 ±3.0
		p=	<0.001[a]*	0.079[a]	<0.001*
		χ^2=	16.104	3.095	98.649
		n=	611	197	110
	vegetation coverage	**sparse**	69 ± 2.7	26 ± 2.4	5 ± 0.9
		dense	53 ± 4.9	18 ± 3.5	29 ± 3.2
		p=	0.003[a]*	0.097[a]	<0.001*
		χ^2=	8.734	2.753	66.203
		n=	491	179	88
	hill type	**exposed slope**	85 ± 2.6	6 ± 1.5	9 ± 1.7
		steep cliff	58 ± 3.8	32 ± 3.1	10 ± 1.9
		summit	81 ± 9.7	4 ± 4.1	15 ± 7.2
		valley	67 ± 15.2	7 ± 7.0	27 ± 11.7
		ground	100 ± 0.0	0 ± 0.0	0 ± 0.0
		n=	446	106	62

[a] assessed with a ‘deviance’ model

4.3.2.3 *Seasonal Differences in Habitat Use*

There were seasonal differences in use of vegetation coverage (LM: χ^2=11.411, df=1, p=0.001; Figure 4.5a) and hill type (LM: χ^2=30.018, df=4, p<0.001; Figure 4.5b), but there were no seasonal differences in use of substrate (LM: χ^2=0.242, df=1, p=0.623). Posthoc analyses indicate that this significance was maintained across all habitat variables tested, with the exception of exposed slopes not being used differently across seasons (Table 4.3). The wet season included significantly higher use of sparsely covered areas, and steep cliffs, than the dry season. In the dry season the langurs used significantly more densely canopied areas, as well as summits and valleys, than the wet season.

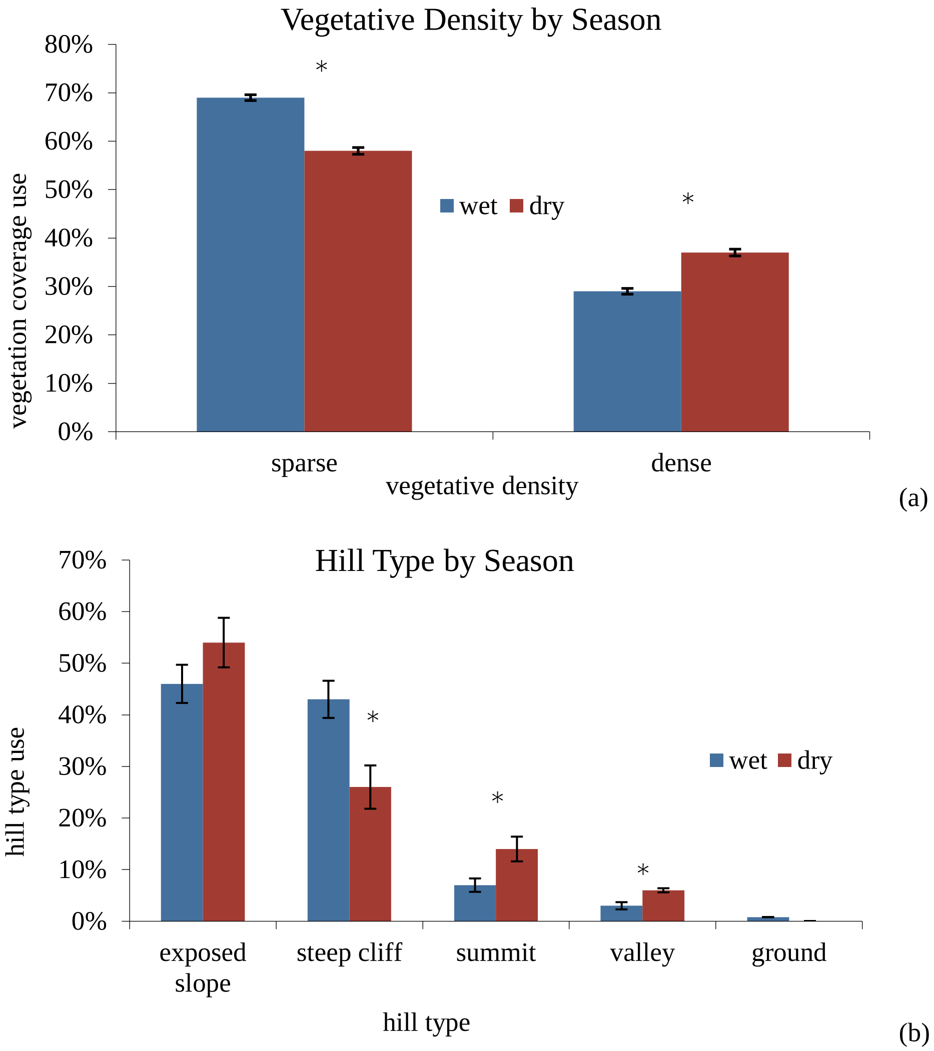


Figure 4.5: Mean daily percent (%) of habitat use ± SE that occur on/in (a) vegetation coverages and (b) hill type that are used in the wet (May-Oct) and dry (Nov-Apr) seasons. An asterisk (*) indicates significantly different use across seasons. Test statistics and exact values can be found in Table 4.3.

Table 4.3: Mean daily percent (%) of habitat use ± SE for the use of each habitat variable in the wet (May-Oct) and dry (Nov-Apr) seasons. All habitat variables that could be assessed were done with a BLM 'deviance' model and df=1. All values rounded to nearest integer. Significant results of posthoc analyses indicated with asterisk (*).

			independent variable: season		posthoc test results		
			wet	**dry**	p=	χ^2=	n=
dependent variables	vegetation coverage	**sparse**	72 ± 2.6	64 ± 2.9	0.030*	4.694	7013
		dense	28 ± 2.6	36 ± 2.9	0.030*	4.694	3243
	hill type	**exposed slope**	46 ± 3.7	54 ± 4.8	0.216	1.532	4007
		steep cliff	43 ± 3.6	26 ± 4.2	0.004*	8.465	3015
		summit	7 ± 1.3	14 ± 2.4	0.006*	7.552	781
		valley	3 ± 0.7	6 ± 1.4	0.028*	4.800	301
		ground[a]	1 ± 0.2	0 ± 0.0			44

[a] unable to statistically analyse due to low number of observations in some categories

4.3.4 Sleeping Sites

A total of 73 nights of reliable, identifiable sleeping sites were recorded during this study; however, as sleeping sites were being discovered right up to the end of the study, there is a high chance that this is not an exhaustive list of used sleeping sites. Conservatively, Group A had 10 sleeping sites (visited on 47 nights) and Group B had 13 (visited on 26 nights) (Table 6, Appendix). This results in an average of each site being used 4.7 times for Group A and 2.0 times for Group B. Group A used two key sleeping sites 13 and 17 times (64% of all Group A sleeping sites) – no other sites were used more than four times by either group. There were 14 reused sites, divided evenly between the two groups. Of the seven sites reused by Group A, they were revisited after an average of 59 days; the seven sites reused by Group B were revisited after an average of 57 days. Group A was the only group observed to use sites on two consecutive nights (four times), but this was most probably a result of methodology (I was not always with the same group in the evening, time limitations, and stringent criteria). One ledge was used by both groups, months apart.

Sleeping sites were sometimes spread out (the group separated at night) but more often the whole group huddled together on one substrate/site type. The majority of identifiable sleeping sites were ledges (61%; Figure 4.6), followed by caves (17%; Figure 4.7) and ledges + caves (group spread between them; 17%), and finally ledges + trees (4%). Given the number of observations of use of each sleeping site type (i.e. the number of nights a site was seen to be used), it seems that caves were preferentially selected (as they make up 27% of observations but only 17% of sleeping sites) and ledges are not as preferred (they are 49% of observations but 61% of sleeping sites), while ledges + caves (18%) and ledges + trees (5%) are similar to the percent of sleeping sites the langurs were observed to use (17% and 4%, respectively).

Figure 4.6: Cat Ba langurs in Group B (circled) settled on a sleeping ledge in the middle of a sparsely vegetated area of a steep cliff. Photo taken Dec 2014 by R Hendershott

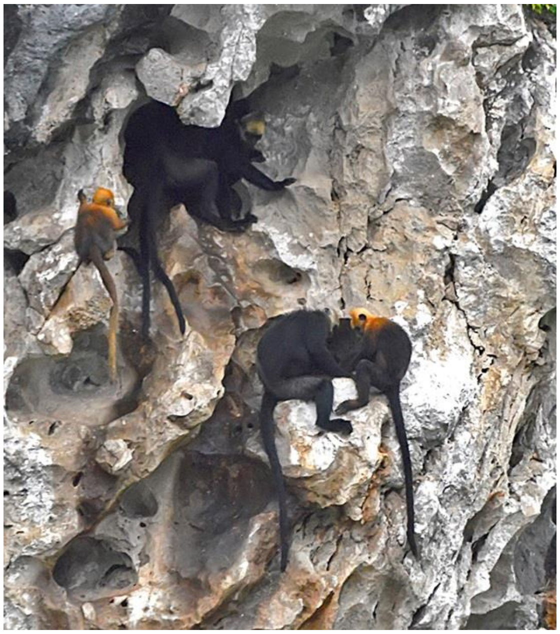


Figure 4.7: Cat Ba langurs sitting and socialising at the vertical entrance to a cave before retiring for the night. Note: entrance (where several adult langurs are gathered, to the left) is a hole below a vertical shaft. Photo taken August 2014 by R Hendershott

The majority of sleeping sites were in the middle of the hill (71%), and occasionally in the lower third (19%), or upper third (10%). Ninety-five percent of sleeping sites were surrounded by sparse canopy coverage (Figures 4.6 and 4.7), and only 5% dense coverage. All sleeping sites, for both groups, were on steep cliffs (Figures 4.6 and 4.7; Table 6, Appendix). Group B’s sleeping sites had higher rates of being in low (25% for Group B vs.

11% for Group A) or upper (17% vs. never observed) stratums, and only Group B was seen to use an area densely vegetated.

There does not seem to be seasonal variation in sites chosen (although the data set is relatively small), with the possible exception of Group A returning to one ledge five times in August, right after a newborn showed up in the group. Caves, which includes instances of both the whole group being in one cave, or the group spread between caves and ledges, represented 39% of sleeping sites in the dry season and 35% of sleeping sites in the wet season. Ledges, which includes both when the whole group uses a ledge and when a group is spread between ledges and trees, were used at the same rate in the wet and dry seasons (59%). Trees (with groups spread out between ledges and trees) were more commonly used in the wet (6%) than the dry (2%) season. Langurs settled down to sleep earlier in the winter dry season (16:45-18:30) than in the summer dry season (17:50-19:00).

4.4 Discussion

4.4.1 Home Range

Among the Cua Dong Cat Ba langurs, the home range of Group A (50ha) is over twice the size of that of Group B (22ha) (Figure 4.1). This may be due to the larger group size of Group A (10-13 individuals) vs. Group B (7 individuals), as larger groups need more resources, and thus have a wider ranging patterns, than smaller groups (van Schaik et al. 1983; Isbell 1991). An increase in range or daily travel distance in larger groups is also suggested to indicate the presence of within-group scramble competition, although this is not always found for species with less rigid dominance hierarchies (Isbell 1991; Fashing 2001a; Teichroeb et al. 2003). It is also possible that the Cat Ba langurs in Group A require more resources for their higher reproductive output (three infants were born in Group A, none in Group B, during this study), including gestation and lactation. Thus, as evidenced by their higher reproductive output, Group A's travel costs to scramble competition may be offset by higher food consumption or higher food quality. Conversely, Group B's reproduction may have been limited by their smaller range and available resources. Additionally, it may be that Group B is unable to expand because of boundaries to their home range set by the water and the presence of Group A. Group A may not be able to expand farther up the fjord due to human presence, which also makes dispersal north to Viet Hai difficult (Section 7.2.3, Chapter 7). This is a problem if the Cua Dong populations grow beyond the home range's carrying capacity, or for individuals attempting to disperse and/or migrate.

Home range size in Asian colobines is extremely variable, ranging between 2-3500ha, although it tends to be the snub-nosed monkeys that have the especially large ranges, the rest range within roughly 100ha (Newton and Dunbar 1994; Kirkpatrick 1998; Kirkpatrick 2007). In *Presbytis* and *Trachypithecus* the home range is anywhere from 2.5-84ha, and home ranges for colobines are variable across taxa (Bennett and Davies 1994). The Cat Ba langur home range sizes found here are thus similar to those found for other limestone langurs (Table 4.4), who have similar body masses (Section 1.6.3.1, Chapter 1).

Table 4.4: Home ranges (ha) for limestone langurs; ranges cover ≥12 months unless otherwise stated. If one study reports on multiple groups, they are separated by commas (,), if a range is reported they are represented by a dash (-).

species	**home range size (ha) per group**	**group size**	**individual per area (ha)**	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	50, 22	10-13, 7	0.20-0.26, 0.32	(this study)[b,c]
white-headed langurs (*Trachypithecus leucocephalus*)	24, 34[a]	14-18, 11	0.58-0.75, 0.32	(Zhou et al. 2011)[d]
	16, 17, 26, 27, 28, 32, 32, 36, 48	11.5, 4.0, 7.5, 12.0, 4.5, 6.0, 14.5, 9.5, 10.0	0.72, 0.24, 0.29, 0.44, 0.16, 0.19, 0.45, 0.26, 0.21	(Li and Rogers 2005b)[b]
François' langurs (*Trachypithecus francoisi*)	46, 50, 56, 76, 111	8-11, 10-11, 8, 9-12, 14-19	0.17-0.24, 0.20-0.22, 0.14, 0.12-0.16, 0.13-0.17	(Hu 2007)[d]
	19	4-7	0.21-0.37	(Zhou et al. 2007b)[d]
	69	10-12	0.14-0.17	(Zhou et al. 2009b)[d]
	56, 78, 119			(Wang et al. 2011)[f,h]
Delacour's langurs (*Trachypithecus delacouri*)	74[e]-80[b], 60[b]-77[e]	1, 1		(Elser et al. 2015)[g]
	1020, 284, 720	1,1,1		(Agmen 2014)[d,g]

[a] monthly home range
[b] measured using a MCP or modified MCP
[c] range size is based on nine months of observations
[d] measured using quadrats/cells/grids
[e] measured using kernel density
[f] no information provided on how home range size was calculated/measured
[g] individuals who were in the process of forming a spatial map, exploring, and settling into a home range post-release; no group size applicability; not an annual range
[h] no information on group size provided

Studies of other colobines show that home range size is reduced when animals include more leaves or other fallback foods in their diet (Clutton-Brock 1975; Newton 1992; Li et al. 2000; Zhou et al. 2007b; Grueter et al. 2013; González Monge 2016). In this study, the Cat Ba langurs eat more leaves in the dry season (Figure 3.7, Chapter 3) thus the corresponding smaller home range is expected. This is due to the decreased need for searching and traveling for leaves, as they are more evenly distributed than fruit. When the langurs eat more fruit (in the wet season: Figure 3.7, Chapter 3) they must travel and range farther in search of the clumped and seasonally-dependent resource (Schoener 1971; Grueter et al. 2013).

It is unknown if the home ranges calculated for Cat Ba langurs reflects their optimum habitat size or a marginalisation by human activities. Groups of other langur species living in fragmented and disturbed habitat have larger home ranges, most probably because they have to travel farther per day in poor quality habitats to find adequate food resources (Li and Rogers 2005b; Hu 2007). Langurs in fragmented forests are also known to have to travel through open forest, bush patches, and farm land, whereas those in better habitat tend to stay in closed forests (Hu 2007).

The density of Cat Ba langurs found in this study (0.20-0.32 individuals/ha) is high compared to other langurs, but this is most probably due to this study's measure only considering animals within a known home range, not animals across available habitat, which is how densities are measured in other studies (Li et al. 2007; Haus et al. 2009). This is an important area for future study for Cat Ba langurs to get a better sense of overall population density. Other than methodological differences between studies, the high population density may reflect that these groups have been isolated to Cua Dong relatively recently, and have not yet reduced to carrying capacity (Dunbar 1987; Decker 1994).

Trachypithecus species have been shown to have a wide range of density patterns, ranging from 0.02 Phayre's leaf monkeys (*Trachypithecus phayrei*)/ha to 3.45 Javan lutungs (*Trachypithecus auratus*)/ha (Newton and Dunbar 1994). White-headed langurs in fragmented habitat occur at a rate of 0.08-0.17 individuals/ha (cited in Huang et al. 2003). François' langur density is constantly dropping due to habitat loss and hunting; there are currently 0.006 individuals/ha, which is half the density it had been in a survey 12 months prior and a 90% reduction since the early 1980s (Hu et al. 2004; Li et al. 2007). Within a home range, the density of Cat Ba langurs (0.20-0.32 individuals/ha) is within the range of other limestone langurs (0.12-0.75 individuals/ha) (Table 4.4).

The 10-24% range overlap of Cat Ba langurs found in this study (Figure 4.2) qualifies them as being somewhat tolerant of known neighbouring groups, although the fact that they were never seen in the same place at the same time suggests that this tolerance may only extend spatially, rather than temporally, as seen in white-headed langurs (Li and Rogers 2005b). Colobines are known to be relatively tolerant of neighbouring groups (although some *Trachypithecus* species do actively defend territories: Gibson and Kenig 2012), as demonstrated through overlapping home ranges and occasional proximity (Clutton-Brock 1975; Oates 1977; Oates 1978; Stanford 1991a; Newton 1992; Kirkpatrick 2007), which has even been suggested as the foundation of multilevel social band formation (Yeager and Kirkpatrick 1998). Among *Trachypithecus*, ranges overlap from 1-83% (Table 4.5); among Asian colobines range overlap is anywhere from 0-100% (Kirkpatrick 2007). Interestingly, the Cat Ba langurs did not seem to avoid the area of overlap; they even shared a sleeping site (Section 4.3.4).

Table 4.5: Percent (%) of range that overlaps for colobines. If one study reports on multiple groups, they are separated by commas (,), if a range is reported they are represented by a dash (-). As instances of limestone langurs are rare, other colobine species were used to contextualise the results of this study.

species	**range overlap (%)**	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	1, 24	(this study)
white-headed langurs (*Trachypithecus leucocephalus*)	2-38	(Li and Rogers 2005b)
François' langurs (*Trachypithecus francoisi*)	1, 11, 19, 74, 83	(Hu 2007)
Silvered leaf monkeys (*Trachypithecus cristatus*)	'only a few trees'	(Bernstein 1968:6)
Phayre's leaf monkeys *(Trachypithecus phayrei)*	3, 6	(Gibson and Koenig 2012)
Hanuman langurs (*Semnopithecus entellus*)	50	(Newton 1992)
guereza (*Colobus guereza*)	49-83 74 of quadrats had other groups seen	(Fashing 2001a) (Oates 1977)
Western red colobus (*Piliocolobus badius*)	10-20	(Davies et al. 1999)
king colobus *(Colobus polykomos)*	4	

4.4.2 Habitat Use

Rocks and sparsely covered areas are used frequently by Cat Ba langurs (54-65% of observations; Section 4.3.2, Figure 4.8). This is not surprising given the petrous limestone karst habitat; karst tends to have shrubby, stunted, and discontinuous vegetation (Nisbett and Ciochon 1993; Day and Chenoweth 2004; Liu et al. 2004). Some studies on limestone langurs find that rocks are the most common substrate used, yet other studies report trees to be more common (Table 4.6). Shrubby hills make up 34% of François' langur habitat (Zeng et al. 2013), and are more common in disturbed forests (Hu 2007). François' langurs prefer habitat with high tree canopy density and high vegetation cover (Zeng et al. 2013), indicating that while limestone langurs spend much time on rocks with discontinuous forests, this may be an artefact of marginalisation over preference (Li and Rogers 2005a). It is possible that Cat Ba langurs are forced to use sparsely vegetated areas due to habitat degradation and fragmentation.

Figure 4.8: Cat Ba langurs on a sparsely vegetated area of a steep cliff. Photo taken July 2013 by R Hendershott

Table 4.6: Substrate use by limestone langurs. Numbers are percent (%) of substrate use. Note: this study excludes 'other' in analyses.

species	**trees**	**rocks**	**other**	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	46	53	1	(this study)
white-headed langurs (*Trachypithecus leucocephalus*)	24	76[a]		(Huang and Li 2005)[b]
	70	30[a]		(Xiong et al. 2009)[b]
François' langurs (*Trachypithecus francoisi*)	61	39[a]		
	53	47		(Zhou et al. 2013a)[b]
Delacour's langurs (*Trachypithecus delacouri*)	21	79		(Workman and Schmitt 2012)[c]

[a] rock+ground

[b] specifically while locomoting

[c] for consolidated posture and locomotor categories

I found that the langurs spend almost half their time on exposed slopes, which have more food options than steep cliffs due to soil accumulation on the gradual hillside (Liu et al. 2004; Yin et al. 2011). Steep cliffs, common on limestone karst, are where the Cat Ba langurs spend over a third of their time, especially around waking up or settling down times of day. The langurs spend 11% of their time on summits, often to soak up the morning sun. The 3% rate of valley use is most certainly an underestimate, as visibility was limited when the monkeys moved into valleys. Cat Ba langurs spent ≤1% of scans on sand or the ground.

It is unknown if Cat Ba langurs are using certain areas of their habitat disproportionate to their availability. Valleys have the most dense, tallest, and richest vegetation, because this is where soil can accumulate on karst (Nisbett and Ciochon 1993; Li and Rogers 2004a; Huang et al. 2008b; Nguyen Van Quan et al. 2010; Yin et al. 2011). This better vegetation makes valleys the most suitable (Zeng et al. 2013) and preferred (Hu 2007) habitat for François' langurs. That being said, it has been found that François' langurs spend more time than expected on cliff-hilltops (roughly equivalent to this study's 'summit') and less than expected on the hillside ('exposed slope') (Zhou et al. 2013a). Another study found that areas with lower elevation and steeper slopes are used more, with valleys being the most suitable habitat despite only covering 25% of their habitat (Zeng et al. 2013). Additionally, there are local-scale preferences for bamboo and mixed conifer-broadleaf forests, while coniferous forests and shrubby areas are used less than their availability (Zeng et al. 2013). Closed canopied areas in François' langurs' home range are used the most intensively (Hu 2007).

4.4.2.1 *Behaviours, Locomotion Types, and Habitat Use*

My results show that inactivity is more likely on rocks, in sparsely vegetated areas, and on steep cliffs or summits (Figure 4.3), which is in accordance with a previous study on Cat Ba langurs that found resting is more common on hills and cliffs (Schneider et al. 2010). The high rate of inactivity on highly sun-exposed areas, such as summits and sparsely covered areas, may be a form of sunbathing (Figure 4.9), especially on cold mornings (Section 4.4.2.2). The high rate of inactivity on steep cliffs reflects that limestone langurs take several breaks *en route* to their sleeping sites (Huang et al. 2004; Nguyen Manh Ha 2006; Hu 2007; Wang et al. 2011), which are on steep cliffs (Section 4.3.4).

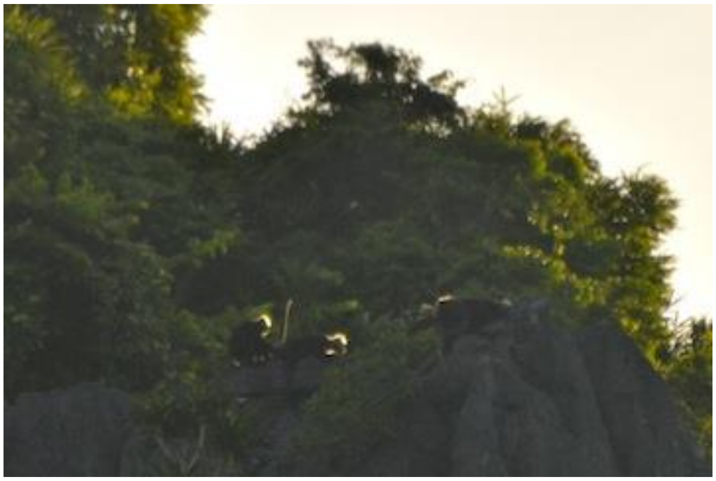


Figure 4.9: Cat Ba langurs in Group A sitting on a summit while inactive and socialising in order to bask in the morning sun. Photo taken Aug 2014 by R Hendershott

In opposition to this, white-headed langurs rest more in densely vegetated areas in low strata (Li and Rogers 2005b), and resting langurs are said to prefer dense bush vegetation (Nadler and Ha Thang Long 2000). However, other studies of limestone langurs show similar results to this study, in that langurs spend the majority of their maintenance activities (inactivity, locomotion, social behaviours) on rocks (Xiong et al. 2009; Workman and Schmitt 2012). Typically, the Cat Ba langurs did take their midday rest in dense trees, but this was not reflected in the scan data because I could not confirm their presence or activities once they disappeared into dense vegetation; therefore it is likely that the midday nap did take place in dense areas.

I found foraging rates to be higher in trees (Figure 4.10), in more densely covered areas, and in valleys and exposed slopes (Figure 4.3); this may be because gradually inclined slopes, especially those with a vegetated basin, have a higher degree of vegetative coverage than nonvalley hill type due to soil accumulation. Delacour’s langurs (*Trachypithecus delacouri)* spend slightly more time in trees (52%) than on rocks (48%) when feeding (Workman and Schmitt 2012). Other studies on limestone langurs indicate that feeding typically takes place at low and mid-level hill strata (Li and Rogers 2005b; Huang et al. 2008b; Schneider et al. 2010), with the langurs preferring lower elevation habitat (Zeng et al. 2013), which includes valleys. The bias for eating at lower levels may possibly be due to the vegetation being denser and taller at lower levels, with more species diversity and overall better feeding options (Li and Rogers 2004a; Huang et al. 2008b; Zhou et al. 2013b; Nguyen Hiep pers. comm. 2014).

Figure 4.10: Cat Ba langurs in Group B sit in a tree on an exposed slope to forage on flowers. Photo taken March 2014 by R Hendershott

I found social behaviour to be more likely on rocks, in sparsely covered areas, and on nonsteep cliff hill type (Figure 4.3). This may be a combination of sunbathing intermixed with social grooming and playing, which is most comfortable on nonvertical surfaces. A previous study on Cat Ba langurs found that social behaviour declines the closer to ground level the langurs move (Schneider et al. 2010), suggesting they are less safe at lower levels. Interestingly, the high rates of social play on sand were primarily by young langurs (Hendershott unpublished data), who seemed excited to have the opportunity to play on a flat surface.

Locomotion commonly occurs on rocks for the Cat Ba langurs in my study (Figure 4.3), which is in contrast to a previous claim that Cat Ba langurs prefer to move through vegetation (Nadler and Ha Thang Long 2000). I also found that locomotion rates are highest on steep cliffs (Figure 4.11), where sleeping sites are concentrated (Table 6, Appendix), and on the ground, which was only used (by adults) for moving between hills quadrupedally. Adults generally crossed beaches quickly, as the ground is risky in terms of predators and poachers which is supported by the fact that limestone langurs act nervous at ground level (Li and Rogers 2005a; Zhou et al. 2013a). Conversely, young Cat Ba langurs took the opportunity to play socially on the flat sandy surface, which may indicate they are less vigilant of predators/hunters (Janson and van Schaik 1993). In addition, it is possible that young langurs, born after hunting rates declined dramatically due to the efforts of the Cat Ba Langur Conservation Project (Section 2.3, Chapter 2), do not have experience with predators or hunters, and so are less concerned with these potential dangers compared to adults who have lived through intense hunting pressures.

Figure 4.11: Cat Ba langurs locomoting quadrupedally along petrous, rocky, and almost vertical steep cliffs of limestone karst. Photo taken April 2014 by R Hendershott

Other studies confirm that locomotion commonly occurs on rocks (Huang and Li 2005; Workman and Schmitt 2012). When locomoting in the valley basin limestone langurs mostly stay in the upper strata and avoid coming down to the ground (Zhou et al. 2013a), but they may also run on the ground to get between hills (Li and Rogers 2005a). The high rate of rock use for travel purposes is also documented for white-headed langurs, who spend over half their time walking quadrupedally on rocks (Huang and Li 2005). This, plus an intermediate intermembral index (a ratio of front limbs to hind limbs), has led to the conclusion that limestone langurs are specially adapted for territorialism in their primarily rocky, petrous, environment (Huang and Li 2005). This study supports that distinction, as most locomotion took place on the petrous rocks.

I found that langurs use different forms of locomotion to move around their habitat (Figure 4.4). Quadrupedal locomotion is most likely on rocks and sparsely vegetated areas; descriptively, there are high rates on exposed slopes and summits. Climbing is most common on steep cliffs (Figure 4.12), showing a trend that it occurs more often on rocks. This is most often in traveling to and from sleeping sites. Delacour's langurs similarly spend more time climbing on rocks than trees (Workman and Schmitt 2012). The trend towards higher rates of climbing on rocks is logical given the rockface that necessitates life lived on an almost vertical surface much of the time (especially on steep cliffs); climbing and careful quadrupedalism along sharp, vertical karst may be the way that the limestone langurs have most behaviourally adapted to their petrous environment (Workman and Schmitt 2012). Leaping typically occurs in trees and densely covered areas, as it is an efficient means of moving around the canopy. A similar pattern is seen in white-headed (Huang and Li 2005) and Delacour's (Workman and Schmitt 2012) langurs, while François' langurs leap more in valleys (which have dense vegetation cover) (Zhou et al. 2013a).

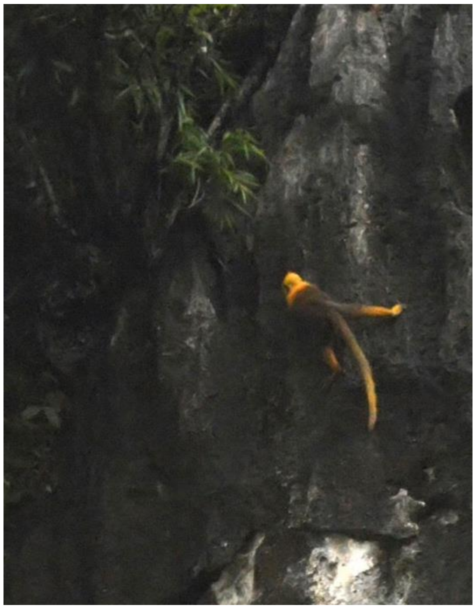


Figure 4.12: Young Cat Ba langur locomoting by climbing along rocky, sparsely covered, steep cliffs of limestone karst. Photo taken August 2014 by R Hendershott

4.4.2.2 *Seasonal Differences in Habitat Use*

In the cold, dry winter, summits are used more often (Figures 4.5 and 4.13). This is possibly in order to sunbathe (which occurs more often in winter: Hu 2007), absorb as much retained heat as possible from the rocks (Huang et al. 2003), and to sit with maximum sun exposure (Stelzner and Hausfater 1986) by moving to the tallest part of the hill. This suggests that the habitat is being used for thermoregulatory purposes, as has been seen in other limestone langurs (Huang et al. 2003; Hu 2007; Zhou et al. 2007a). In addition to summits, densely covered areas and valleys are used more often in the dry season by Cat Ba langurs (Figure 4.5). This may be due to the dry season resulting in limited food supply, which requires the langurs to go into more vegetated areas (dense > sparse; valleys

> cliffs) in search of adequate food resources. Indeed, they spend more time foraging in the dry season (Figure 3.2, Chapter 3) and foraging happens most commonly in valleys and on exposed slopes (Figure 4.3). François' langurs will also use predator-risky but food-rich hillsides and valley basins more often in the dry season when young leaves and fruit availability declines (Zhou et al. 2013a).

Figure 4.13: Cat Ba langurs from Group B take time to socialise and rest on a sun-exposed summit in the cold dry season. Photo taken April 2014 by R Hendershott

4.4.3 Sleeping Sites

Cat Ba langurs were observed to sleep in trees (and rocks) during the daytime, but mostly on rockfaces at night (there was one observation of Group B settled down while spread out between ledges and trees, the rest being all ledges, caves, or ledges + caves). Cat Ba langurs move towards their sleeping sites around sunset by climbing and clinging along the steep rock face, taking short breaks to eat and rest along the way. Often they moved in single file, fairly quiet except for youngsters' distress calling to be carried and an occasional dispute among females as they settle down for the night (Section 5.3.3, Chapter 5). Similarly, before entering a sleeping site, other limestone langurs rest, groom, play, or feed within 10 metres for about 10-60 minutes (Huang et al. 2004; Nguyen Manh Ha 2006; Hu 2007; Wang et al. 2011; Figure 4.7). They are usually silent and vigilant while heading towards a sleeping cave (Zhou et al. 2009b; Li et al. 2011), and wait until dark to enter

(Huang et al. 2004). It takes 3-16 minutes for the whole group to settle down at a sleeping site, and 3-12 minutes to leave in the morning (Huang et al. 2004; Huang and Li 2005; Wang et al. 2011).

The Cat Ba langurs often arrive at a sleeping site after the sun has gone down (typically 20-40 minutes after; hence the limited visibility) and leave in the morning before the sun rises (>15 minutes) – therefore their settling and waking times are seasonally dependent. Among primates in general, and Asian colobines in particular, the time that individuals enter or leave a sleeping site is dependent on the season/light availability (Anderson 1984; Oates 1987; Huang et al. 1992; Huang et al. 2004; Nguyen Manh Ha 2006; Hu 2007; Xiang et al. 2010). For example, snub-nosed monkeys arrive at sleeping sites 10-42 minutes after sunset, sleep for longer and leave their sleeping sites later in the cold season, especially if snow falls during the night (Li et al. 2010; Xiang et al. 2010; Zhang et al. 2011). Similarly, limestone langurs enter and settle into their sleeping sites later at night, and leave them earlier in the morning, in hot summers; in the cool winter, on the other hand, they prefer caves, settle earlier, and leave later in the morning (Huang et al. 2004; Nguyen Manh Ha 2006; Hu 2007; Li et al. 2011; Wang et al. 2011). It is interesting that no seasonal pattern emerges for Cat Ba langur sleeping site types, although this may be due to small sample size.

In this study the order in which individuals entered and left the cave was not noted, but based on personal observation I can say that the male often waited until the rest of the group was settled before he himself would join the huddle. Among proboscis monkeys (*Nasalis larvatus)*, the adult male typically moves from the sleeping tree last, but occasionally first (Yeager 1990b). Among black snub-nosed monkeys (*Rhinopithecus bieti*), adult males enter sleeping trees last (Cui et al. 2006; Li et al. 2010). Among François' langurs, the adult male usually leaves the cave first in the mornings, and will enter a cave first in the evening if it is new or has not been used in a while, suggesting he is acting as a protector to the group by exploring potentially dangerous situations before the rest of the group (Huang et al. 2004).

Usually once most primates have settled down for the night, there is little moving until they wake up in the morning, unless disturbed (Anderson 1984). Interestingly, there was one night where I observed Group B get stuck on a small high-tide island at night. This small island is in a highly human-trafficked area and makes the langurs extremely vulnerable. When I returned the next morning before sunup (at a lower tide), the langurs had moved far into the heart of their range, suggesting that they had crossed soon after the tide was low enough to jump across (approximately 3:00) and then settled the rest of the night in a more safe area of their home range.

Group A and Group B used 10 and 13 different sleeping sites, respectively, which is slightly more sleeping sites per group than those reported for other limestone langurs (Table 4.7). Group A used a smaller amount of sites more often, resulting in a higher average number of nights spent at each site. One of these sites was shared between the two groups (in an area of home range overlap), although there was a temporal separation, as noted for François' langurs (Hu 2007). The number of sleeping sites a species uses depends on a number of variables. For example, territorial forest-dwellers and semiterrestrial species tend to have fewer sleeping sites than multimale forest or woodland-dwelling groups (Anderson 1984).

Table 4.7: Sleeping site use by limestone langurs. Cave and ledge numbers are percent (%) of each site type within observed sleeping sites. Note: in this study there were specifically 4 caves and 14 ledges, but there were 22 sleeping sites of all types (caves, ledges, ledge+cave, ledge+tree).

species	**cliff caves**	**cliff ledges**	**# of groups in study**	**sites/ group**	**maximum consecutive use (nights)**	source
Cat Ba langurs (*Trachypithecus poliocephalus*)	4	14	2	12.5	2	(this study)
white-headed langurs (*Trachypithecus leucocephalus*)	17	1	2	9	3	(Li et al. 2011)
	32		6	5.3	4	(Huang et al. 2003)
François' langurs (*Trachypithecus francoisi*)	6	17	2	11.5	4	(Zhou et al. 2009b)
	6 [A]		1	6	5	(Zhou et al. 2007b)
	23 [A]		3	7.7	6	(Wang et al. 2011)
	4	1	1	5	7	(Huang et al. 2004)
	15	u/k	5	3	5	(Hu 2007)

[A] unspecified cliff location

Sleeping site use is not divided evenly. Group A revisited sites, including on consecutive nights, more often than Group B. In fact, just two sites account for 64% of all sleeping site nights for Group A. In François' langurs at the Fusui Nature Reserve in China, one study found that four out of six sites were used in 96% of observations (Zhou et al. 2007b), while another study found that seven out of 23 sites are used in 64% of observations (Zhou et al. 2009b). Cat Ba langurs use more ledges than caves, but caves seem to be used disproportionately (Table 6, Appendix) (it is unknown if this is more or less than expected given the Cua Dong habitat). This is similar to François' langurs who, despite having more ledges used as sleeping sites, spent more nights than expected in caves, demonstrating a preference (Zhou et al. 2009b).

Cat Ba langur sleeping sites were spread throughout their visible home range (i.e. along ocean-facing borders) and typically nearby areas where foraging was concentrated (Figure 4.14). Limestone langurs sleep on rocky ledges and caves close by main feeding sites and water sources during dry periods (Hu 2007; Zhou et al. 2007b; Zhou et al. 2009b; Li et al. 2011; Wang et al. 2011), and commonly used areas of the home range (Grueter and Ding 2006; Hu 2007; Zhou et al. 2011), probably as a way to reduce travel costs. Observationally I can confirm that sleeping sites were often near the last feeding area, although it is hard to tell if the site was chosen first and foraging occurred along the way, or if the langurs concentrated on eating and then scrambled to find a sleeping site when the sun went down. If the langurs do show a preference for sleeping sites close to main feeding sites, they may be multiple central place foragers (Chapman et al. 1989; Hu 2007; Zhou et al. 2009b). I cannot confirm whether or not these sites were concentrated in core areas, but there was at least one site in a zone of home range overlap used by the two groups.

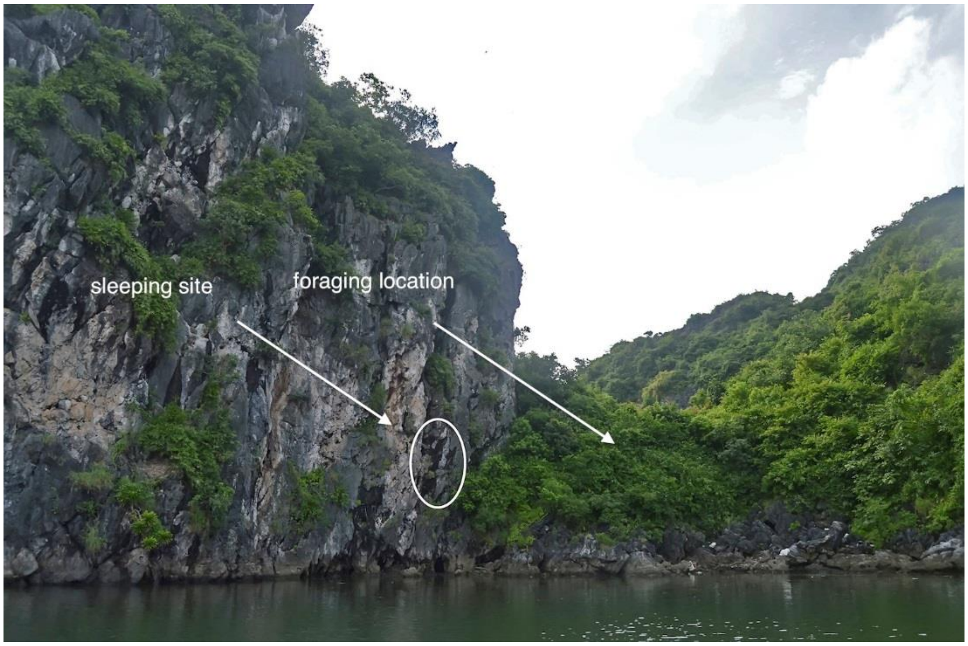


Figure 4.14: Many of the sleeping sites for the Cat Ba langurs were nearby areas where intense foraging occurred the afternoon before or morning after. Here a ledge in the lower third of the steep cliff is nearby a valley where the animals foraged extensively. Photo taken August 2014 by R Hendershott

Both Cat Ba langur groups reuse sites, on average, every couple of months. Sleeping sites may not be used consecutively because of an increased chance of parasitic infection (Hausfater and Meade 1982) or to create unpredictable patterns for predators (Blaffer Hrdy 1977). Group A was seen to reuse four different ledges/ledges + cave on two consecutive nights; this is a low number of nights of consecutive use compared to other limestone langurs (Table 4.7). In contrast, others report that Cat Ba langurs use a cave for a week at a time (Nadler and Ha Thang Long 2000), which was definitely not seen in this study (as I often searched for them at night in areas I saw them use the night before). Consecutive use of a sleeping area may be a reflection of low predation pressure (Liu and Zhao 2004), although more observations of nighttime sleeping choices would undoubtedly increase evidence of consecutive use. Group B seemed less predictable in their sleeping sites, whereas Group A concentrated theirs in a smaller number of areas. It is possible that Group A, with newborns present in the group, felt more protective or threatened, and returned to reliable sites as a safety precaution. This was most notable right after a newborn was born into the group in August, when Group A reused the site (although not necessarily consecutively) that was the farthest away from Group B. It may be that Group A returned there while a vulnerable newborn was present in the group, so as to maximise distance between themselves and neighbouring Group B (and reducing risk of infanticide).

Sleeping sites should allow for the ability to detect and escape predators (Anderson 1984). Several factors point to sleeping sites being selected for their predator-safe properties (Figure 4.15). For example, the Cat Ba langurs have multiple caves whose entrances are a vertical hole below the shaft (Figure 4.7). This would certainly have the effect of helping to reduce the risk from terrestrial predators (Barrett et al. 2004). Historically, golden (*Catopuma temminickii),* leopard *(Prionailurus bengalensis*), and fishing (*Prionailurus viverrinus*) cats as well as small Indian (*Viverricula indica*) and common palm (*Paradoxurus hermaphrodius*) civits have been reported on Cat Ba Island (Nadler and Ha Thang Long 2000), and may have been a terrestrial predation threat to the langurs before they were poached at such high rates. The potential threat from avian predators (such as white-bellied sea eagles, *Haliaeetus leucogaster,* or black kites, *Milvus migrans*, also found on the island: Nadler and Ha Thang Long 2000) would also be reduced through the use of caves.

Figure 4.15: Sleeping sites should allow for good predator detection, such as good visibility (i.e. sparse vegetation coverage) and difficulty of access for terrestrial predators (i.e. on a steep cliff, mid strata). These traits are exemplified in this sleeping ledge used by Group B. Photo taken August 2014 by R Hendershott

I found that all sleeping sites are on steep cliffs (Table 6, Appendix), a pattern also seen in François' langurs, who choose to sleep on cliffs with greater than a 60^0 angle (Huang et al. 2004; Wang et al. 2011; although see Hu 2007). Presumably this limits the number of predators who can reach such locations. An anecdote from a langur guard supports this: he said that he watched a large python slowly working its way up the vertical cliff, towards a sleeping group of Cat Ba langurs; when it got about 5-10 metres directly below the group it was unable to ascend the remaining distance due to the smooth rock directly below the langurs, which was covered in mineral runoff and excreta and no ledges or niches (note, however, that there also anecdotes of poachers killing pythons and finding langurs inside) (Nguyen Cam pers. comm. 2014). Additionally, caves on steep cliffs are very difficult for human poachers (the main predators of Cat Ba langurs) to access, and hunters have been known to die and be injured in attempts to catch langurs in caves on practically vertical rockfaces (Nadler and Ha Thang Long 2000). François' langurs select caves that are not necessarily the safest from nonhuman predators, but are undisturbed by humans (Hu 2007), suggesting that humans do influence where limestone langurs are choosing to sleep.

I found the majority of sleeping sites are in the middle of a steep cliff (Table 6, Appendix). White-headed langurs sleep in caves and ledges in the middle or top of the cliffs (Huang et al. 2003; Li et al. 2011). A similar pattern is seen in François' langurs, although they seem to have a preference for sleeping at low-level cliffs (Zhou et al. 2009b). In undisturbed habitat François' langurs tend to sleep in the lower portion of the cliff, whereas sites are more evenly distributed between upper and lower cliff strata in disturbed habitat (Wang et al. 2011). Interestingly, Group B used upper and lower cliff strata for sleeping more than Group A. This may, however, reflect home range differences. Alternatively, if the middle of a cliff is the safest, Group A may have been more conservative because of their higher percent and number of vulnerable young.

There is no clear pattern of sleeping site type by season for Cat Ba langurs (Table 6, Appendix). Results are divided for François' langurs: they reportedly use ledges more commonly in the dry (Zhou et al. 2009b) *and* the wet (Hu 2007) seasons. Caves are cooler in summer, warmer in winter, and have more stable temperatures than outside (Barrett et al. 2004; Hu 2007; Pruetz 2007), suggesting that they may be used for thermoregulation and to escape extreme temperatures. This again suggests that there is a predicted seasonality and temperature-dependency in sleeping site selection.

If nighttime sleeping sites are reflective of predation pressure, the different pattern of sleeping in trees during the day may suggest that the Cat Ba langurs are not in as risky a situation at that time, and that therefore their predators are nocturnal (such as cats or civits). Similarly, golden snub-nosed monkeys sleep in trees in large clusters at night to avoid predators, but may also sleep on the ground in smaller clusters during the day (Zhang et al. 2011).

The vegetation surrounding a sleeping site may be used strategically by primates. Sparse canopy coverage around sleeping sites, most often used by Cat Ba (Figure 4.6) and François' (Hu 2007) langurs, may allow for earlier detection of predators (Wang et al. 2011). Dense canopy cover may help protect/buffer against the cold or provide more concealment from predators (Anderson 1984; Li et al. 2006). François' langurs' sleeping sites tend to be in closed forests (Hu 2007). Interestingly, François' langurs sleeping sites are surrounded by shrubs and rocks in undisturbed habitat, while in disturbed habitat there are more trees (as well as shrubs and rocks) surrounding the sleeping site (Wang et al. 2011). This may be due to a reduction in predators in disturbed habitat.

Therefore it appears that sleeping sites are selected by limestone langurs for both their protection from predators and extreme climatic conditions, with the possibility that they are opting to sleep near food resources (Nadler and Ha Thang Long 2000; Zhou et al.

2009b; Wang et al. 2011). Overall Group B was less predictable, more often spread out across multiple sites, using upper and lower strata more than Group A. This may reflect the lack of vulnerable newborns and infants in the group, the lessened cohesiveness of this group (as evidenced by their splitting shortly after the study period: Nguyen Cam pers. comm. 2015), or their perceived predation risk being lower.

4.5 Summary

This chapter aimed to establish a home range size, patterns of habitat use, and characteristics of sleeping sites for two groups of Critically Endangered Cat Ba langurs living in Cua Dong, southeast Cat Ba Island. This was accomplished through noting GPS locations of groups whenever they moved large distances, and then using a modified minimum convex polygon to determine the extent of that ranging. During 10 minutes scan samples, the behaviour and locomotion type were noted, as well as the substrates the langurs were on, the vegetation coverage within a 10 metre radius of the langur, and the hill type the langurs were on. This data was assessed through linear models. Data collection encompassed 11 months of observations, or 549 hours in visual contact with the langurs.

The home range of Cat Ba langurs is similar to that of other limestone langurs, with the larger group (A) having over double the area of the smaller group (B), with a small region of overlap. Home ranges are larger in the wet season, presumably in an effort to locate clumped fruit resources. Rocks are used more often than trees and sparse areas more than densely vegetated areas for Cat Ba langurs. Exposed slopes are almost half of all hill type used, steep cliffs are over a third, and summits, valleys, and the ground are used less than 15% of the time. Cat Ba langurs adapt their behaviours and locomotion types to the habitat they are in, and they use different parts of their habitats at different times of the year. This may be partly due to different habitat types aiding in thermoregulation during extreme temperatures, balanced with the need for foraging. The timing of going to the sleeping cave is seasonally dependent. Compared to other limestone langurs, the two Cat Ba langur groups observed in this study use more sleeping sites per group, and use them for fewer consecutive nights than those of other limestone langurs, suggesting predation pressure may be low. A high percent of these are ledges, rather than caves, and there seemed to be preferred sites that were used much more often than others. There is evidence that sleeping sites are selected based on their safety from [historical] predators and for thermoregulatory purposes.

It is hoped that this information can be useful in creating a baseline for home range size; changes in location and size can be used as a proxy measure of habitat disturbance and degradation, as animals respond to a loss of food resources or anthropogenic pressures. Additionally, conservation management should be focused on protecting areas that are key food, safety, and sleeping resources (Chapter 7).

Chapter 5: Social Behaviour

5.1 Introduction

Socialisation is a key component to group cohesion. It unites group members and solidifies their alliances, creating a well-defined social group. Due to their egalitarian social structure (Section 1.6.7, Chapter 1) and their nonmonopolisable diet, colobines spend little time engaged in social activities/grooming, ranging from <1-15% (Table 1.2, Chapter 1).

Affiliative social behaviours seen in colobines include grooming, playing with others, mounting and presenting, embracing, and infant handling and transferring, while agonistic social behaviours include aggression, displacement, and submission (Niemeyer and Anderson 1983; Arnold and Barton 2001; Fashing 2001a; Li and Rogers 2004a; Agmen 2014). Aggression within a group often takes the form of biting, slapping, lunging, and chasing from the aggressor and submission or fleeing by the individual experiencing aggression, although aggression is often relatively mild (Newton and Dunbar 1994).

Compared to other behaviours in the activity budget, affiliation within a group is thought to be somewhat expendable, called the ‘dispensable social time hypothesis’ (Alberts et al. 2005). This means that when more time is needed for digesting, foraging, or locomoting, it usually comes at the cost of being social (Dunbar and Dunbar 1988; Dunbar 1992), hence the low rates of social behaviour in colobines. Therefore, as social behaviours are more expendable than some other necessary behaviours, they are often affected by availability of resources: when habitat quality is poor grooming rates decline for primates (Lehmann et al. 2007). Play rates also decline at times of the year when langurs consume more leaves (Sommer and Mendoza-Granados 1995) or in poorer-quality habitats (Li and Rogers 2004a; Hu 2007).

Dispersal patterns also have large implications for socialisation. If primates remain in their natal group, there is the chance for long-term, kin-based relationships, coalitions, and alliances (Wrangham 1980). Although the dispersal patterns of Asian colobines are uncertain and variable, it is possible that both females and males disperse (Section 1.6.7, Chapter 1). This biases against sex-based coalitions and alliances as individuals are unlikely to be related. Therefore, a detailed analysis of social behaviour and affiliations between the sexes can be used as a proxy for dispersal patterns.

In the absence of more overt social behaviours, proximity is often used as an indicator of tolerance, social availability, familiarity (Chapais 2001), and degree of social integration (Silk et al. 2003). As it is a passive rather than active form of socialisation, it is rarely reported (Sussman et al. 2005), although proximity has been correlated to a number of sociopositive behaviours (Kasper and Voelkl 2009) such as food sharing (de Waal and Brosnan 2006), grooming (Seyfarth 1980; King et al. 2011), and the transmission of cultural traditions (Bonnie and de Waal 2006). Additionally, proximity can be used by primates to assess degree of kinship, which then translates into nepotistic altruism (Chapais 2001). Adult female yellow baboons (*Papio cycnocephalus*) that spend more time in proximity to and/or grooming other adults have higher infant survival rates (Silk et al. 2003), thus demonstrating the importance of social integration and proximity to reproductive success.

Proximity can thus serve as a crude proxy measure of social interactions among group members (Whitehead 1997), despite providing more limited information than a full account of the details and nature of these interactions (Whitehead and Dufault 1999). Additionally, it is important to consider measurements that are biologically significant to the animals themselves (Whitehead and Dufault 1999). As someone within arm's reach is someone that can be groomed, embraced, mounted, or attacked quickly, proximity is an important measure of social tolerance, and often requires some sort of communication upon approach to indicate affiliative intentions (Maestripieri 1997). Although proximity may be an inappropriate measure of social cohesion in species that typically have a very small group spread, it is still a helpful, if not rough, measure of tolerance in species that typically have a larger group spread.

Documenting the rate and type of social behaviours along with the proximity individuals are found in can be informative of alliances, bondedness, and dispersal patterns, all of which have implications for conservation. For example, for captive management (Novak 2004; Hosey 2005), reintroduction, or translocations to work, conservationists must consider typical group structure and relationships and natural dispersal patterns. Negative effects of captivity can also potentially be mitigated with knowledge of an animals' natural behavioural repertoire (Visalberghi and Anderson 1993). For instance, if adult females actively avoid being in proximity, they should not be the starting point for artificial group creation. This is true for adults in general, who have a harder time adjusting to social grouping after isolation than subadult or juvenile individuals (Reinhardt et al. 1995). Individuals that are overly aggressive toward one another or xenophobic should not be trapped together or with strangers in captivity (Reinhardt et al. 1988; Visalberghi and Anderson 1993; Reinhardt et al. 1995) while those who are naturally solitary should not be placed in a group (Novak and Suomi 1988). If males are the dispersing sex, then they are probably more able to handle translocating to a new location and finding resources and group mates than females; if females are philopatric, they may be unwilling to accept strange females. Therefore dispersal patterns must be taken into consideration (Novak and Suomi 1988). Overall, it is important to document social behaviours and affiliations as a baseline for comparisons to future, degraded habitats and unnaturally housed captive animals in order to verify they are compatible.

This chapter aims to assess the differences in social behaviours of Cat Ba langurs (*Trachypithecus poliocephalus)* in relation to group, age, and sex. It will also investigate the nature of intragroup disputes. The results can then be used for the management of captive, relocated, and translocated individuals as well as documenting expendable time (thus providing a proxy measure of habitat quality) and providing evidence about dispersal patterns.

5.2 Methods

5.2.1 Behavioural Data Collection

Observations of behaviour and proximity (including huddles) of the Critically Endangered Cat Ba langur took place from Feb 2014-Jan 2015 in the Cua Dong area of Cat Ba Island, Vietnam, resulting in 549 hours in visual contact (Section 2.5, Chapter 2). Social behaviours were recorded from a boat using 10 minute instantaneous scan samples (Altmann 1974b; Martin and Bateson 2009), and included the behaviours listed in Table

5.1. Agonistic behaviours (n=5) and harassment of mounts (n=4) occurred in <10 scans each, and were therefore removed from further analysis.

Table 5.1: Social behaviours recorded in the course of this study on Cat Ba langurs.

behaviour	**definition**	
groom	Individual picks through hair, fingers, toes, or other body parts of another individual. Can be one-way, reciprocal, or a 'chain'. Includes:	
	groomer	individual grooming another individual
	groomee	receiving the grooming from someone else
social play	Individual engaging in repeated social activities such as chasing, wrestling, and mock-biting with other partners. Any play involving another individual.	
vocalise	Making a noise with an individual's mouth. This is considered social as it serves as a mechanism for intergroup spacing and territoriality (Blaffer Hrdy 1977; Newton and Dunbar 1994; Oates 1994), and has been considered part of the social behavioural repertoire by other colobine researchers (Stanford 1991a; Agmen 2014). Includes:	
	distress call	high pitched squeal, squawk, scream, or cry used in distress or to get attention
	hoot	a 'who-who' sound, often associated with running and shaking branches, used by adults
	loud call/ cough/ rasp	a hooting noise with a specific pattern; often associated with body jolts
	'other'	barks, grunts, and other less identifiable vocalisations
mount	An individual does a single or double hind-leg clasp and supports their weight on their arms on the back of the recipient, with or without thrusting. Includes:	
	successful	recipient allows the mounter to get into position
	failed	mountee did not cooperate
embrace	Two individuals have ventroventral contact with one or both arms around the other, often accompanied by kneading the fur.	
transfer	Newborn or infant is moved/passed/grabbed from one individual's body to another. Refers to both the individuals transferring and the young being transferred. Includes:	
	successful	individual holding the young, nor the young themselves, resist the transfer
	failed	individual reaches out to take or grab the young, but is unsuccessful at moving the infant to their own body due to resistance by the individual holding the young or the young themselves
present/ solicit	Individual stands quadrupedally in front of someone, occasionally looking over their shoulder, backing up, possibly raising tail.	
harassment	Approach or contact between nonmounted individuals and mounted pair which may or may not prevent the mount from continuing.	
agonistic behaviours	Includes:	
	submission	avoiding and fleeing
	displacement	an individual moving so another can take their location
	aggression	biting, slapping, lunging, chasing

In addition to scan data, vocalisations, mounts, transfers, fights, and aggression were recorded ad libitum and details mentioned descriptively. Behaviours are discussed in order of their percent within the social budget scan data, with the exception of all sexual behaviours (presentations, mounts, and harassments) being considered together in the discussion.

Age classes included adult (black coats with yellowish head and shoulders; older than five years; n=9), subadult (smaller than adults, with more orange around neck and shoulders; between three and 5-7 years old; n=2), and young (flamboyant orange to mostly adult coloured with orange/yellow remaining on limbs and tail; 0-36 months; infants, young juveniles, and juveniles are combined under 'young'; n=6-9) (Table 2.3, Chapter 2, for descriptions of age categories). Newborns were excluded from all analyses due to their nonindependence. The data comes from the two reproductive groups in Cua Dong [Group A=10-13 individuals (one adult male, five adult females, four to seven young); Group B=7 individuals (one adult male, two adult females, two subadults, two young) (Table 2.2, Chapter 2)]. Group C was never observed to use social behaviours.

5.2.2 Intragroup Aggression (ad libitum data)

Intragroup aggressive interactions were limited to 'outings' (one full observation period) so as to reduce the chance that multiple aggressive encounters in the same morning or afternoon period were counted more than once, as they could not necessarily be counted as independent events. For example, if there were multiple squabbles between adult females within a two hour period it may be that they are due to the same underlying group tension for that time period. Context was determined based on whether the disputes occurred while settling down to sleep at night or over access to a newborn (note that these contexts are not mutually exclusive and are descriptive only; these were the only two identified contexts for disputes). Newborn disputes took the form of an individual trying to monopolise the newborn, and then getting slapped, mounted, chased, or screeched at. Sleeping disputes were when individuals were trying to settle down for the night on either caves or ledges, but then left abruptly when screaming, slapping, or chasing occurred. Due to the low number of aggressive events observed, all statistics are descriptive only.

5.2.3 Proximity and Huddles

When individuals were within an arm's length of another langur, they were defined as being in proximity, regardless of whether or not they were actually touching, which is a definition that has previously been used in primate studies (Boccia et al. 1982; Stanford 1991a; Melfi and Thomas 2005; Bonnie and de Waal 2006). When individuals were not within arm's reach of any other group members, they were classified as 'alone'. All scans, including those in which individuals were not in proximity, were used in calculating the average number of others in proximity. Based on the proximity scans I then converted the data into huddle groups. A 'huddle' is defined as more than one individual in proximity (Ogawa and Takahashi 2003; Li et al. 2010). Average huddle size reflects how many other individuals someone surrounds themselves with *when in a huddle*. A huddle may include individuals who are not directly within proximity to each other, but who are in mutual proximity to other individuals within a huddle (Figure 5.1). For example, if seven langurs are sitting in a line *or* if they are sitting in a circle, both are considered a huddle, despite the fact that the first and last langurs in a line are not in arm's reach to one another.

Figure 5.1: Huddles are defined as when two or more individuals are in proximity (i.e. within arm's reach) to each other or are mutually in proximity to another langur. To the left there is a young langur not in a huddle, while on the right there are six langurs in a huddle. Note: young (left side of the huddle) and adult female (on the right side of the huddle) are both part of the same huddle despite not being in arm's reach to one another. Photo taken Nov 2014 by R Hendershott

In order to remain conservative with estimates of huddles and being in proximity to others, if I could not confirm that an individual was within arm's reach of someone else, I did not write it down. This possibly creates a Type II error (i.e. false negative) bias toward rates of being alone (as the default is 'alone' unless noted otherwise), and possibly results in an underestimation of huddle sizes and number of others in proximity. For example, when settling down to the sleeping site for the evening, usually the whole group would huddle together along a skinny ledge or shallow cave. With the sun going down and a limited viewpoint (from a boat), I may only have been able to confirm seeing the first row or two of langurs (Figure 5.2). Despite not seeing any langurs still moving around the rockface, I could not (with confidence) confirm that anyone beyond the visible langurs were involved in a huddle.

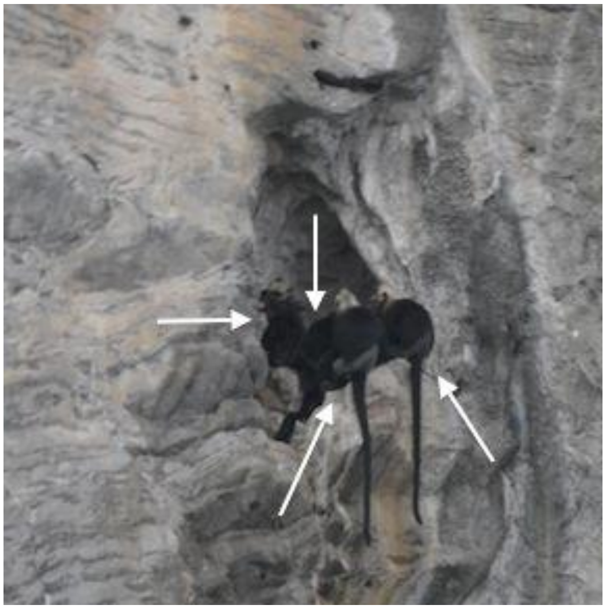


Figure 5.2: This study has a Type II bias in huddle sizes (with being alone the default state), and all huddle sizes should be considered as being ‘at least’ that number of individuals. For example, in this photo of the langurs at a sleeping cave, I could confirm four langurs (indicated with arrows) but there is the possibility that other langurs were within arm’s reach but not visible to me from the boat. Photo taken Nov 2014 by R Hendershott

Huddles of the exact same size and composition were counted (in Microsoft Excel 14.5.3) and the total size of each composition is listed, as well as all other possible age-sex combinations that could have been possible. Because there was an unmanageable number of dyads, triads, etc. when every age-sex class is used, age-sex classes were narrowed down to adult female, adult male, subadults, and young. Only huddles wherein the participants could be narrowed down to one of these four age-sex classes were included, in case there was a bias in detecting and documenting certain age-sex classes, as done by Saj and Sicotte (2007). Due to the effect newborns have on drawing individuals together (Section 6.3.2.1, Chapter 6), huddles involving a newborn were excluded from analysis. Given the differing size and demography of Group A compared to Group B, the two were separated for all analyses of huddles.

5.2.4 Data Analysis

Social budgets are presented as the mean daily proportion of scans that included each specific behaviour category. Following existing protocols on similar species

(Teichroeb et al. 2003; Hu 2007; Zhou et al. 2007a) day was used as the unit of analysis for independence. For analysis I broke down behavioural activity budgets by group, age, and sex classes in order to ascertain any differences within each category. I used SPSS 23 for Windows for all analyses, with significance set to $P<0.05$ for two-tailed tests.

In order to assess whether social budgets vary across group, age, and sex, I first fit a linear model (LM) with arcsine transformed proportions (similar to Li and Rogers 2004a), as the dependent variable, and behaviours, group/age/sex, and an interaction between the two, as the independent factors. If I found that the overall behavioural pattern differed between group/age/sex ($P<0.05$) with this LM, I assessed the differences between group/age/sex for each behaviour separately with a binomial logistic model (BLM), using daily observed frequencies out of total numbers of observations. As some analyses were overdispersed, this was accounted for by reporting the more conservative results of a 'deviance' model, and is noted in tables throughout the chapter. BLMs provide pairwise comparisons between variables in order to identify where the significant differences lie (e.g. the three age classes). Tables listing p-values for significant pairwise comparisons are provided in the Appendix if posthoc analyses were conducted with a BLM and were significant.

The likelihood of being found alone (i.e. not in proximity to anyone) is compared across time, seasons, groups, age, sex, and behaviours with a binomial linear model. Time is broken down into three-hour time blocks, although observations were not made evenly throughout the three-hour blocks (Section 3.2.2, Chapter 3). The winter dry season occurs from the beginning of November until the end of April, and the summer wet season is from the beginning of May until the end of October (Workman 2010a; Agmen 2014).

Average number of others in proximity is calculated from Microsoft Excel 14.5.3, and is assessed with a generalised linear model (GLM). In order to assess average huddle sizes for each age-sex class, any huddle that includes at least one of a 'target' age-sex class is considered part of that age-sex classes huddle data. For example, a huddle of an adult male (AM), two adult females (AF), and a subadult (SA) is included in the data set for AM, AF, and SA, but not young (Y). To compare the cumulative distribution of huddle sizes by age-sex class I used a two-sample Komolgorov-Smirnov test (K-S) (e.g. AM vs. AF, AF vs. Y, Y vs. AM).

Huddle composition gives an idea of who associates with whom, and whether or not this is dependent on the age-sex class of other huddle members. Unfortunately, due to the lack of individual identification and visual limitations, an index of association measure, nearest neighbour and maintenance of proximity scores were not possible to record. A hypergeometric distribution was used to assess the expected chance that a huddle is composed of each possible age-sex class demographic (i.e. in order to answer whether or not AM and AF huddle together more than expected, regardless of who else is in the huddle); this was calculated for each age-sex class combination. This analysis allows for the differentiation of the likelihood that, for example, an adult male is associated with an adult female above chance (based on the individuals remaining in the group excluding the adult male) and the likelihood that an adult female is associating with an adult male above chance (based on remaining group mates, excluding one adult female); therefore dyadic huddles do not necessarily have to have the same results for each participant. Huddles larger than two individuals could not be statistically analysed via a hypergeometric distribution for Group B, and huddles larger than three individuals could not be assessed for either group due to expected counts being below five (a requirement for a chi-square test due to distortion: Gravetter and Wallnau 2011). Therefore, only dyadic (both groups) and triadic (Group A) huddles can be assessed for whether or not they occur more or less than chance.

In Group A, the group composition changed throughout the study, resulting in two extreme 'expected' values (one for the beginning and one for the end of the study). The observed rate was compared against the least extreme expected rate. For example, the observed rate of adult females associating with young (in dyadic huddles) is 63%, and this is compared to the upper expected extreme (55%), and not the lower expected value (44%). The chance/random rate for all associations is compared to the observed rates through contingency tables. This was done for each age-sex class of each huddle size (e.g. did adult males associate randomly in dyadic huddles, young in triadic huddles, etc.?). If this is significant, further posthoc chi-square tests were used to assess which age-sex class was responsible for this significance (e.g. did the adult males associate with adult females more than chance?). Only the most conservative chi-square and p-value are listed; this information can be found in tables throughout results.

5.3 Results

Social behaviours were the third most common type of behaviour recorded in this study, comprising 12% of the Cat Ba langurs' activity budget (Section 3.3.1, Chapter 3). All further analyses and discussion in this chapter were only done within the context of all *social* behaviours, not all behaviours. There were 1,413 scans that included known social behaviours. The most common social behaviour was grooming (72 ± 2.6% of Cat Ba langur social budget or 8% of their activity budget); followed by playing with others (18 ± 2.2% of social budget or 2% of activity budget); vocalising (6 ± 1.6% of social budget); mounting (2 ± 0.6% of social budget); embracing and presenting (1% each of social budget); and then transferring a newborn/infant, harassing a mounted pair, and aggression, displacement, and submission behaviours (<1% each of social budget). As some of these behaviours occurred in less than 10 observations—harassment (n=4) and agonistic [submission (n=3), displacement (n=1), and aggression (n=1)]—they were removed from detailed analysis. Social behaviours did not differ between the two reproductive groups (LM: χ^2=1.857, df=6, p=0.932).

As far as vocalisations are concerned, ad libitum data (n=612 vocalisations) indicated that 62% of calls were loud calls/coughs/raspberry sounds (used exclusively by adult males), followed by distress vocalisations (28%; used by young and/or adult females), hoots/coos (8%; used by adults typically during intergroup encounters), and 2% were 'other' types of calls. Ad libitum data indicate that mounts (n=314) were predominantly sociosexual (64%; i.e. not an adult male mounting an adult female), with only 36% being sexual. Roughly a quarter of mounts (26%) were failed, because the mountee was not standing/presenting quadrupedally in order for the mounter to complete the double hind-leg clasp. It appears that Cat Ba langurs employed both single and multiple-mounts, although sexual mounts were more likely to include multiple mounts (81% of successful mounts occur within three minutes of another mount whereas only 48% of successful sociosexual mounts are within three minutes of another mount). Transfers were also recorded ad libitum (n=174); 67% of transfers were successful, and transfers were concentrated on newborns (68%) and infants (32%).

5.3.1 Age Differences in Social Behaviours

There was a significant effect of age on social behaviours (LM: χ^2=616.536, df=12, p<0.001; Figure 5.3). This pattern holds for groom and play, but not for embrace; it could not be assessed for vocalise, mount, present, or transfer (Table 5.2). When young, social play was almost two-thirds the social budget, which was significantly reduced to less than a third the rate as they become subadults and grooming rates significantly more than double (Table 7, Appendix). There was no difference between adults and subadults in grooming behaviour, but adults played significantly less than subadults. Therefore, grooming was more common in older individuals, while social play was more common in younger individuals.

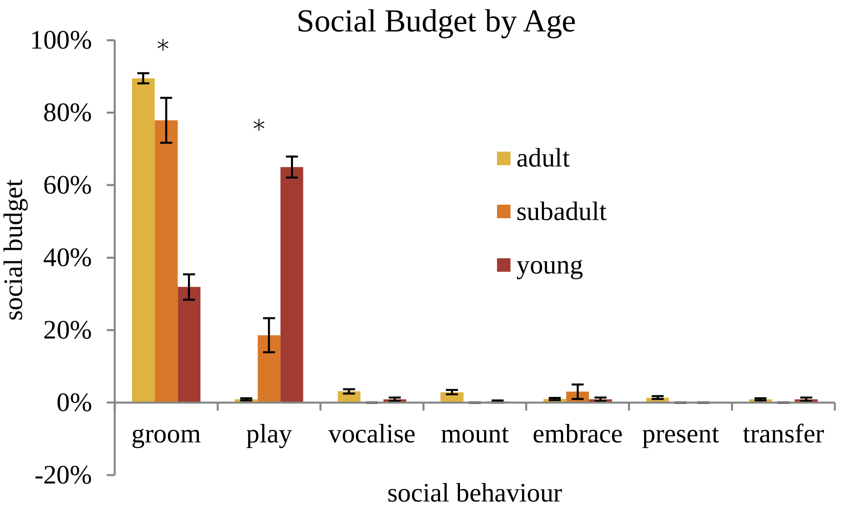


Figure 5.3: Mean daily percent (%) of social behaviours ± standard error (SE) used by the different age classes. Social behaviours that show significant differences between age classes are indicated with an asterisk (*). Test statistics and exact values can be found in Table 5.2, and pairwise comparison p-values can be found in Table 7, Appendix.

Table 5.2: Mean daily percent (%) of social behaviours ± SE used within each age class. For all analyses (BLM), df=2. All values rounded to nearest integer. Significant results indicated with asterisk (*). Pairwise comparison p-values can be found in Table 7, Appendix.

	groom[a]	**play**[a]	**vocalise**[b]	**mount**[b]	**embrace**	**present**[b]	**transfer**[b]
adult	90 ± 1.4	1 ± 0.3	3 ± 0.6	3 ± 0.6	1 ± 0.3	1 ± 0.4	1 ± 0.3
subadult	78 ± 6.2	19 ± 4.7	0 ± 0.0	<0 ± <0.1	3 ± 2.0	<0 ± <0.1	0 ± 0.0
young	32 ± 3.5	65 ± 2.9	1 ± 0.5	<1 ± 0.3	1 ± 0.5	<0 ± <0.1	1 ± 0.5
p=	<0.001*	<0.001*			0.127		
χ^2=	177.741	186.663			4.123		
n=	1005	246	32	28	15	13	11

[a] assessed with a ‘deviance’ model

[b] unable to statistically analyse due to low number of observations in some categories

5.3.2 Sex Differences in Social Behaviours

There was a significant effect of sex on social behaviours (LM: χ^2=239.502, df=6, p<0.001; Figure 5.4). This pattern holds for groom and social play, but not mount or transfer (Table 5.3). It could not be assessed in vocalise, embrace, or present, although it is notable that no males were seen to present or embrace during scans, and no females vocalised during scans. Females used grooming significantly more than males, while males used social playing significantly more than females.

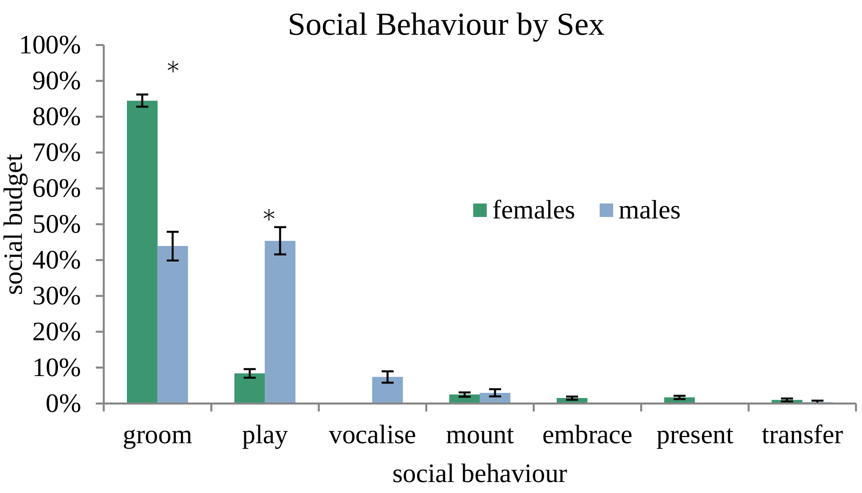


Figure 5.4: Mean daily percent (%) of social behaviours ± SE used by the different sexes. Social behaviours that show significant differences between sexes are indicated with an asterisk (*). Test statistics and exact values can be found in Table 5.3.

Table 5.3: Mean daily percent (%) of social behaviours ± SE used within each sex. All analyses (BLM) have df=1. All values rounded to nearest integer. Significant results indicated with asterisk (*).

	groom[a]	**play**[a]	**vocalise**[b]	**mount**	**embrace**[b]	**present**[b]	**transfer**
females	85 ± 1.7	8 ± 1.2	0 ± 0.0	3 ± 0.6	2 ± 0.4	2 ± 0.5	1 ± 0.4
males	44 ± 4.0	45 ± 3.8	7 ± 1.6	3 ± 1.0	0 ± 0.0	0 ± 0.0	<1 ± 0.4
p=	<0.001*	<0.001*		0.121			0.334
χ^2=	86.056	99.307		0.728			0.932
n=	782	189	20	28	12	13	9

[a] assessed with a ‘deviance’ model

[b] unable to statistically analyse due to low number of observations in some categories

5.3.3 Intragroup Aggression

Intragroup aggression was extremely rare in Cat Ba langurs. Only one scan included aggression, and only one included a displacement. There were three scans that included submission. These five scans of agonism comprised <1% of the social activity budget. Ad libitum data also show disputes occurred in only 21, or 7%, of data collection sessions, and it is this ad libitum data that is described in this section. Although 58% of my contact time with langurs was in Group A, Group A had 90% of disputes, suggesting that disputes were occurring disproportionately in Group A. Disputes tended to occur on different days, although there were two days that had disputes in the morning *and* the afternoon.

In the 10 cases in which context could be determined for Group A agonism recorded ad libitum (neither of the two events in Group B had clear contexts), six centred around the individual holding a newborn, and the other four occurred while settling down to sleep at night. No recorded disputes were over food or occurred in a feeding context. The presence of newborn and young infants seemed to increase group tension and interaction levels, as transfer attempts were often associated with grooming, mounting, presenting, slapping, chasing, wrestling, grabbing, fleeing, and vocalising.

Disputes (where the age-sex class of participants was known; n=16) were almost always between or involving adult females (88% with adult females, 13% with unsexed adults). On four occasions (25%) the adult male seemed to mediate fights, but on one occasion (6%) he was chased by adult females. In both groups disputes were equally divided between seasons (Group A: 55% in the wet season; Group B: 50% in wet season).

5.3.4 Proximity

In over half (58%) of daily activity budgets, individuals were not in proximity to someone else (i.e. they were ‘alone’). The chance that an individual was alone changes according to season (χ^2=3.904, df=1, p=0.048), group (χ^2=46.100, df=1, p<0.001), age and sex (age: χ^2=38.924, df=2, p<0.001; sex: χ^2=48.025, df=1, p<0.001; interaction of age and sex: χ^2=173.952, df=5, p<0.001); and across behaviours (χ^2=638.286, df=4, p<0.001).

Rates of being alone did not differ across time periods (χ^2=3.810, df=4, p=0.432). All analyses were BLM with a ‘deviance’ model.

In the dry season (54 ± 1.7%) there was a significantly higher chance of being alone compared to the wet season (50 ± 1.7%). Group A langurs (47 ± 1.3%) were significantly less likely to be found alone than Group B langurs (62 ± 1.8%). Subadults were alone significantly more often than young langurs, and adults were alone significantly less often than all other age classes (Table 5.4; Table 8a, Appendix). Males were significantly more likely to be found alone than females (Table 5.4). An interaction of age and sex indicates that among females, adults were found alone significantly less often than subadults or young (Table 5.4, Figure 5.5; Table 8b, Appendix). Among males, adults and subadults were found alone significantly more than young (Table 5.4, Figure 5.5; Table 8b, Appendix). Adult males were alone significantly more than adult females (Table 5.4, Figure 5.5; Table 8b, Appendix). In contrast, young females showed a trend towards spending more time alone than young males (Table 5.4, Figure 5.5; Table 8b, Appendix).

Table 5.4: Mean daily percent (%) of alone time (i.e. not in proximity) ± SE for the six age-sex classes. All values rounded to nearest integer.

	adult	**subadult**	**young**	all ages
female	37 ± 1.1	56 ± 4.4	55 ± 2.0	42 ± 1.2
male	65 ± 2.3	65 ± 4.1	50 ± 1.8	57 ± 1.7
all sexes	47 ± 1.1	64 ± 3.1	55 ± 1.4	58 ± 1.4

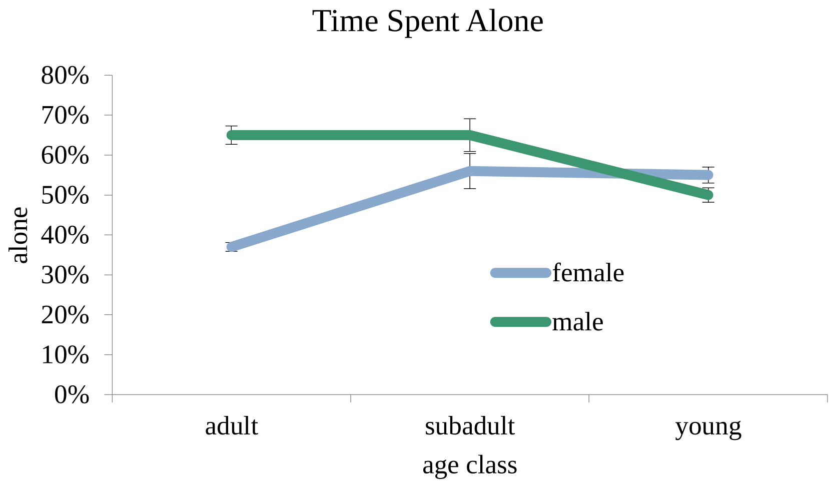


Figure 5.5: Mean daily percent (%) of alone time (i.e. not in proximity) ± SE for the six age-sex classes. There is a significant interaction effect of age, sex, and an interaction of age *and* sex for time spent alone. Exact values can be found in Table 5.4, and pairwise comparison p-values can be found in Table 8, Appendix.

Langurs spent the most amount of time alone while locomoting (88 ± 1.7%), followed by foraging (83 ± 1.4%), 'other' behaviours (61 ± 5.2%), and inactivity (44 ± 1.1%); they spent the least amount of time alone when using social behaviours (15 ± 1.6%), with significant differences between all behaviours (Table 9, Appendix). This indicates that animals engaging in social behaviours and inactivity spent over half their time surrounded by others, while animals engaging in locomotion, foraging, and 'other' behaviours spent over half their time alone.

An individual in Group A was surrounded by a significantly higher number of others in proximity (average 1.5 individuals) than Group B (0.86 individuals) (GLM: χ^2=331.755, df=1, p<0.001). With both groups combined, the average number of others in proximity was 1.3 individuals. There was an effect of age-sex class on number of others in proximity (GLM: χ^2=241.738, df=3, p<0.001; Table 5.5). Across groups and on average, the adult females were surrounded by significantly more individuals than young, and both adult females and young were surrounded by significantly more individuals than adult males and subadults (Table 10a, Appendix). When the groups were assessed separately, this pattern held for both Group A (GLM: χ^2=112.644, df=2, p<0.001; Table 10b, Appendix) and Group B (GLM: χ^2=44.058, df=3, p<0.001; Table 10c, Appendix). In both groups, adult females were surrounded by the highest average number of others (Table 5.5). In Group A, the young were also surrounded by significantly more langurs than the adult male (Table 10b, Appendix). This suggests that, for these two groups, adult females were the most social (in terms of proximity) and the adult males and subadults were the least social.

Table 5.5: The average number of other langurs in proximity (i.e. within arm's reach) and average huddle size for Groups A, B, and both groups combined.

age-sex class	group	**average others in proximity**	**average huddle size**
adult females	Group A	1.8	3.0
	Group B	1.3	3.2
	both groups	1.7	3.0
adult males	Group A	1.1	3.9
	Group B	1.0	3.7
	both groups	1.0	3.9
subadults	Group B	0.9	3.3
young	Group A	1.4	3.1
	Group B	0.9	3.1
	both groups	1.3	3.1

5.3.5 Huddles

Of 2,210 huddles documented throughout the study period, the majority were of two individuals (54%); followed by three (21%); four (11%); five (6%), six (3%), seven (2%), eight (1%), and nine, 10, and 12[2] (<1% each). Note that Group B could not possibly be in huddles larger than seven, as that was their group size. The more animals there were in a huddle, the less often I observed huddles of that size, with a similar trend between both groups (Figure 5.6), although this could not be assessed with a K-S test because of the differing group sizes. Despite the differences in group sizes, the average huddle size was 2.9 for both groups.

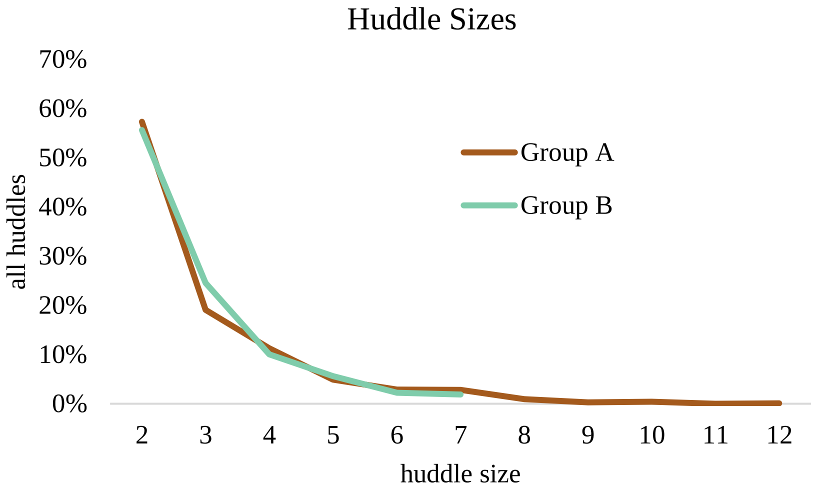


Figure 5.6: Percent (%) of observations of each huddle size for each reproductive group.
Note: huddles larger than seven were not possible in Group B.

There were 1,624 observed huddles in Group A and 586 in Group B. When huddles involving an individual of an unknown age-sex class or newborns were removed [Group A: 586 (36%) involve an unknown or newborn; Group B: 288 (49%) involve an unknown], the resulting matrix includes 1,038 huddles for Group A and 298 huddles in Group B to be assessed for composition. The different age-sex classes engaged in huddles of various sizes at variable rates. In Group A, the average huddle size was largest for those that included an adult male, followed by young and adult females (Table 5.5). In Group B, average huddle

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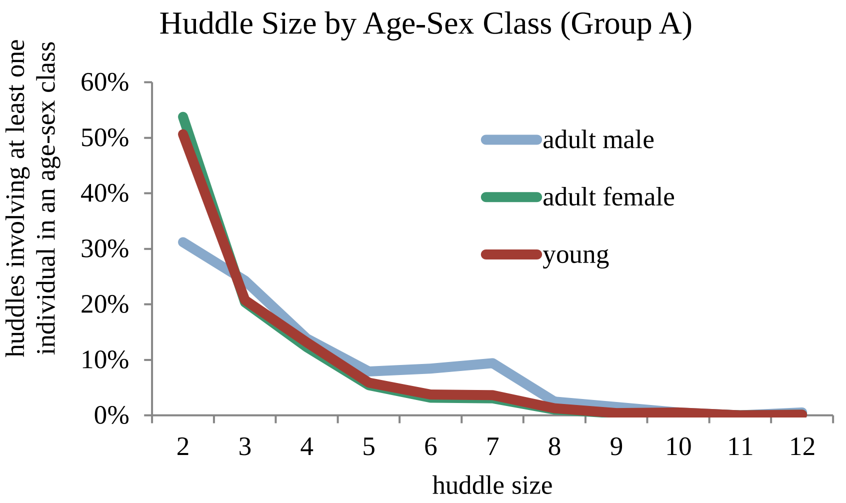
[2] A huddle of 11 was not observed.

sizes were again highest when the adult male was part of a huddle, followed by subadults, adult females and young (Table 5.5). For both groups, the distribution of huddle sizes were significantly different between the adult male and adult females/young langurs (Figure 5.7; Table 11, Appendix). Adult males tended not to engage in dyadic huddles as often as other age-sex classes, but huddled together in larger groups more often (Figure 5.7). This all demonstrates that adult males tended not to join huddles until they were larger (>2 *other* individuals).



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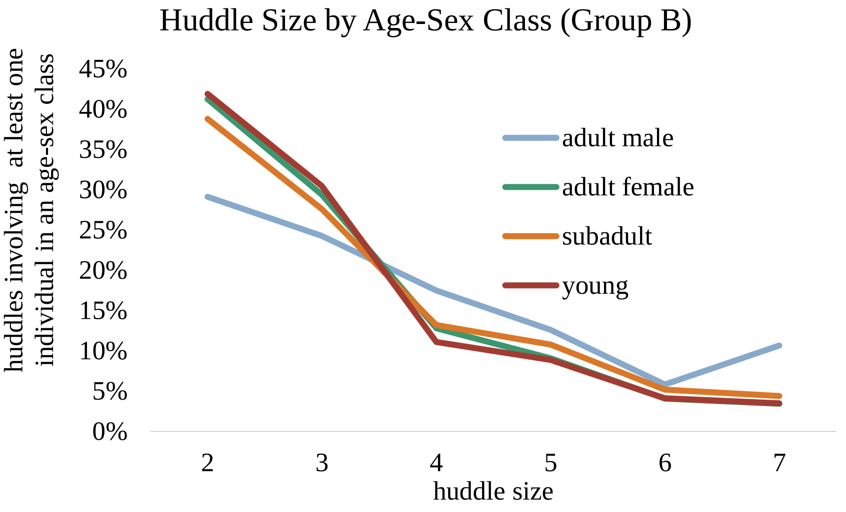
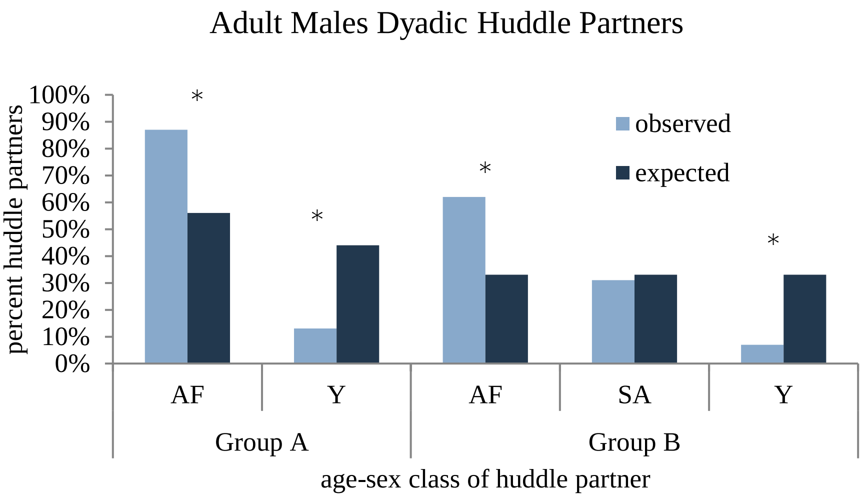


(b)

Figure 5.7: Percent (%) of huddle sizes involving at least one of a target age-sex class across all possible huddle sizes in (a) Group A and (b) Group B. In both groups the adult male has a significantly different huddle size distribution than adult females and young langurs.

In dyadic huddles, the adult male did not choose his huddle partner randomly (Group A: χ^2=25.714, df=1, p<0.001; Group B: χ^2=13.296, df=2, p=0.001; Figure 5.8a,

Table 5.6; Table 12, Appendix) with adult males spending significantly more time in proximity to adult females, and significantly less time in proximity to young, than chance. In Group B the adult male associated with subadults at chance levels. In dyadic huddles, adult females did not choose their huddles partners randomly (Group A: χ^2=20.854, df=1, p<0.001; Group B: χ^2=15.565, df=2, p=0.001; Figure 5.8b, Table 5.6; Table 12, Appendix). They associated with young at rates higher than chance and other adult females and subadults less than chance. In both groups adult females associated with the adult male at chance levels. In dyadic huddles, subadults (Group B) were in proximity to others randomly (χ^2=1.826, df=2, p=0.609). Young did not associate randomly in either group (Group A: χ^2=90.447, df=1, p<0.001; Group B: χ^2=23.161, df=2, p<0.001; Figure 5.8c, Table 5.6; Table 12, Appendix). In both groups young were around adult females more than expected and around adult males less than expected. In Group A the young associated with one another less than expected, but in Group B their rate of association was at chance levels. Young were in proximity to subadults at chance levels in Group B.



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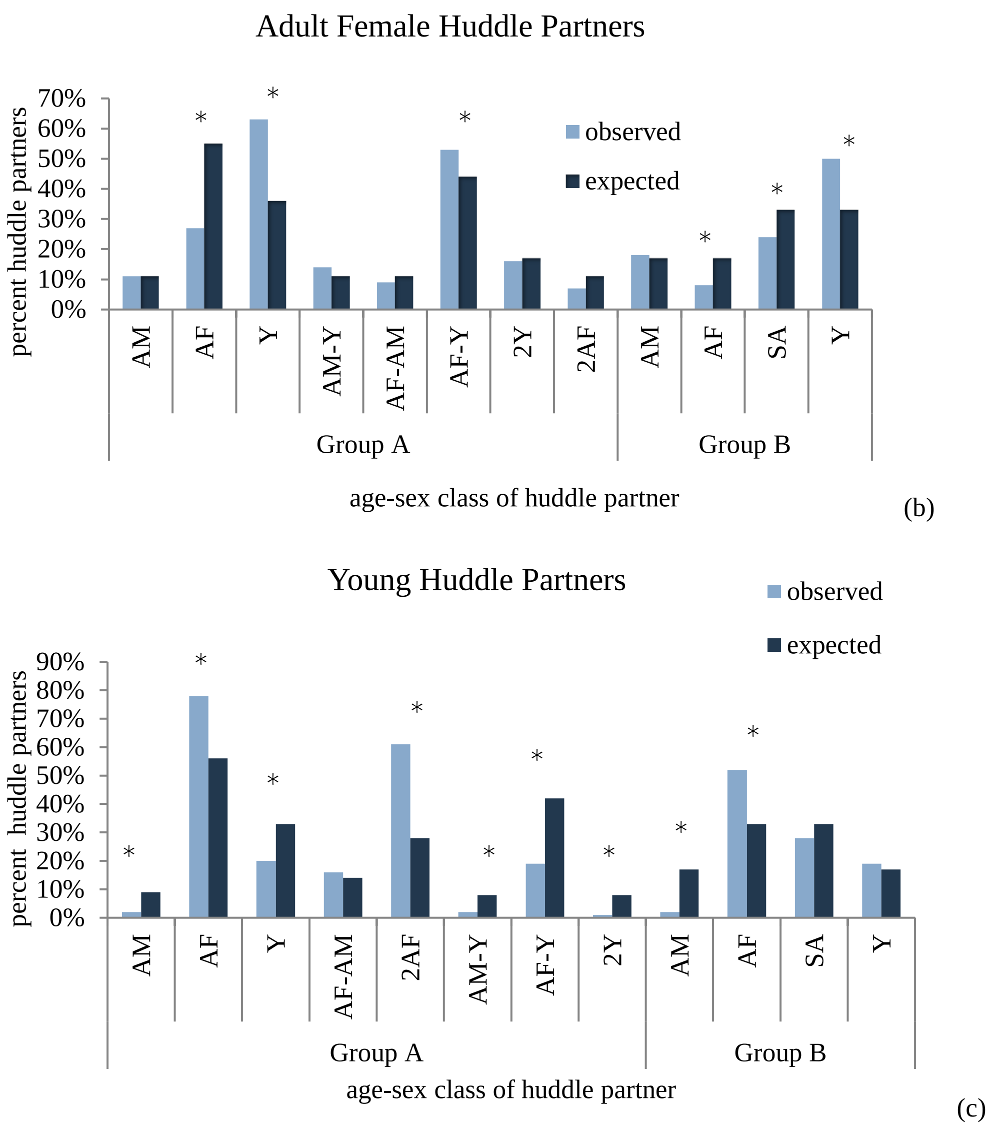

Figure 5.8: Expected versus observed rate of association for all target individuals that did not associate randomly within a specific huddle size (see text). This includes (a) adult male, (b) adult female, and (c) young dyadic associations in both groups; and (b) adult female and (c) young triadic associations in Group A. Posthoc differences and test values of rates of association within a particular huddle size that are statistically significant can be found in Table 5.6 and Table 12, Appendix, and are indicated with an asterisk (*). Note: AM=adult male, AF=adult female, SA=subadult, Y=young

Table 5.6: Results of posthoc comparisons between observed huddles of two (both groups) and three (Group A) and the likelihood that that huddle occurred by chance given the group's demographics. Dyads and triads that show significantly higher or lower rates of occurrence than chance are indicated with an asterisk (*). The 'target' age-sex class is the age-sex class used as a basis of comparison. Subadults are not included as a target age class for dyadic interactions, nor adult males for triadic interactions, as initial analysis indicated there was no significant difference in their choice of huddle partners. The rate of observation vs. chance is shown in Figure 5.8. Note: the chance of a huddle is different for each age-sex class. For example, an adult female being around an adult male (the target age-sex class) is different than an adult male being around an adult female (the target age-sex class).

'target' age-sex	interacting age-sex class	group	p=	χ^2=	n=	if significant, more or less than chance?
AM	**AF**	A	<0.001*	25.714	55	more
		B	0.001*	10.765	18	more
	SA	B	0.792	0.070	9	
	Y	A	<0.001*	25.714	8	less
		B	0.003*	9.127	2	less
AF	**AM**	A	0.851	0.035	55	
		B	0.721	0.127	18	
	AF	A	<0.001*	20.767	135	less
		B	0.020*	5.411	8	less
	SA	B	0.048*	3.917	24	less
	Y	A	0.003*	13.017	317	more
		B	<0.001*	12.506	50	more
	2AF	A	0.108	2.588	14	
	AF-AM	A	0.444	0.585	18	
	AF-Y	A	0.016*	5.862	102	more
	AM-Y	A	0.192	1.696	27	
	2Y	A	0.847	0.038	31	
Y	**AM**	A	<0.001*	24.814	8	less
		B	<0.001*	14.901	2	less
	AF	A	<0.001*	84.640	317	more
		B	<0.001*	14.486	50	more
	SA	B	0.251	1.318	27	
	Y	A	<0.001*	33.611	80	less
		B	0.618	0.249	18	
	2AF	A	<0.001*	93.799	102	more
	AF-AM	A	0.377	0.782	27	
	AF-Y	A	<0.001*	36.11	31	less
	AM-Y	A	0.006*	7.622	4	less
	2Y	A	0.001*	11.039	2	less

Triadic huddles could only be assessed in Group A, due to low numbers of expected values in Group B. In huddles with two others, the Group A adult male associated randomly (χ^2=3.546, df=2, p=0.170). Adult females (χ^2=15.443, df=4, p=0.004) and young (χ^2=106.588, df=4, p<0.001) did not associate randomly (Figures 5.8b,c; Table 5.6; Table 12, Appendix). Adult females in triadic huddles were more likely than chance to be found in proximity to another adult female and young. They randomly associated with all other dyads. Young in triadic huddles were more likely to associate with two females than by chance. They were less likely than chance to be found in proximity to: the adult male and another young langur, an adult female and another young langur, and two other young langurs. Their likelihood of being around an adult female and the adult male was at chance levels.

Although I could not statistically verify that the difference between observed and expected was significant for huddles over two (for Group B) or three (for Group A) individuals, there were a few patterns that emerge in the data (especially noticeable in Group A; Table 12, Appendix). There was a trend for the adult male not to associate with large numbers of young, especially on his own, but when adult females were part of the huddle the adult male would be around a small number of young. Additionally, adult females and young were often found in large groups together, although it was uncommon for females to be around more young than there are adult females in the huddle.

5.4 Discussion

In a previous chapter I found that Cat Ba langurs spend 12% of their activity budgets engaging in social behaviour, which may be due to the high number of young in Group A, especially newborns, who are extremely attractive to females colobines (Chapter 6). Newborn presence results in a large number of interactions – not just from transfers and handling, but also by increasing associated grooming, mounts/presentations, embrace, close proximity, and aggression in attempts to obtain or monopolise the newborn. For example, embracing (Slater et al. 2007) and, especially, grooming (Henzi and Barrett 2002; Gumert 2007; Tiddi et al. 2010; Yu et al. 2013) are traded with mothers for newborn/infant access in a number of primates. Additionally, this study found that disputes tend to focus around access to newborns. Therefore, a number of social behaviours are involved in newborn attraction across primates and among Cat Ba langurs, with the most common one being grooming.

Grooming makes up 72% of Cat Ba langur social interactions (Figure 5.9), and 8% of their day, a relatively high rate compared to some other colobines where it is commonly only 0-5% of activity budgets (Dunbar 2010; Matsuda et al. 2012a) and to other limestone langurs where it is typically less than 6% (Hu 2007; Yang et al. 2007; Zhou et al. 2007a). That being said, it is on par with white-headed langurs' (*Trachypithecus leucocephalus*) grooming rates of 14% (Li and Rogers 2004a). Other studies have similarly found that despite not being a common behaviour, grooming does account for the majority of social interactions for colobines (Kirkpatrick 2007; Rawson 2009; Matsuda et al. 2012a; Djègo-Djossou et al. 2015). Grooming of others is an important part of many catarrhines primates' social lives, and serves primarily a social purpose (Dunbar 1991), although it may also serve a hygienic function (Borries 1992). Across primates, it is associated with reconciliation (necessary for groups to stay together after an aggressive episode) (de Waal 2000), and among Asian colobines may be used as a form of post-conflict appeasement (Arnold and Barton 2001). Overall it has been found to help group member cohesion (Matsuda et al. 2015) and to aid in tension reduction (McKenna 1978). This is most probably due to a release of neuroendocrines (endorphins, oxytocin and vasopressin) that create a 'psychological environment of trust' (Dunbar 1991:263).

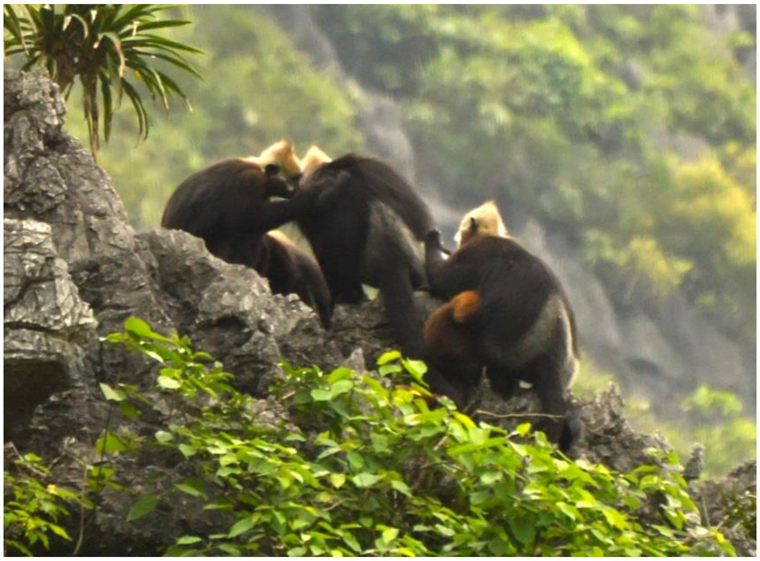

Figure 5.9: Grooming in Group B. Photo taken April 2014 by R Hendershott

Social play (e.g. wrestling and chasing; Figure 5.10) is the second most common form of socialisation for Cat Ba langurs (18% of social budget), as has been found for other limestone langurs (Hu 2007; Agmen 2014) and African colobines (Djègo-Djossou et al. 2015). It is the most common form of play (Hendershott unpublished data) and takes up 2% of Cat Ba langurs' total activity budget. Playing with others is an important developmental stage for young animals that helps prepare for future situations, such as intrasexual competition and sexual interactions, predatory techniques or antipredatory evasion techniques; it also bonds and integrates group mates with one another while teaching appropriate forms of communication (Bekoff 1972; Poirier and Smith 1974; Byers 1984; Chalmers 1984; Hole and Einon 1984; Martin 1984b).

Figure 5.10: Two juveniles males playing socially in Group A. Photo taken August 2014 by R Hendershott

Vocalisations make up 6% of the Cat Ba langurs' social budget, or 1% of their entire activity budgets. This low rate is also seen in Delacour's langurs (*Trachypithecus delacouri)*, who vocalise <1% of their activity budgets (Agmen 2014). Vocalisations were often directed intragroup among the Cat Ba langurs, although there were times the adult male would perch on a summit, orient himself away from his group, and then loud call towards a neighbour's home range, or females would hoot while displaying during intergroup encounters.

Sexual behaviour is necessary for reproduction in primates and is typically initiated through a solicitation. I found presentations to make up 1% of Cat Ba langur social budgets. In order to solicit, females present the hindquarters while lowering the tail, often accompanied by a head-shake or head-shudder (Bernstein 1968; Blaffer Hrdy 1977; Srivastava et al. 1991; Sommer et al. 1992; Kirkpatrick 2007). It is also possible that a male solicits by displaying his erect penis to a female, although a female must still present in order to be mounted (Solanki et al. 2007). Interestingly, there was one observation of the adult male displaying his erection and then masturbating while an adult female groomed him, but no mounting occurred. Masturbation has been noted for other Asian colobines

(Bernstein 1968; Clarke 1991), including François' langurs (*Trachypithecus francoisi*) (Hu 2007).

I found mounts to make up 2% of Cat Ba langur social budgets. Mounting behaviour occurs fairly infrequently; given observation time (Section 5.2.1) sexual mounts occur once every 5.3 observation hours or 0.03 mounts/hour/female (a mount every 38 observation-hours for each female). This is with each mount counted separately, which likely overestimates ejaculations: Asian colobines have been described as both single (golden snub-nosed monkey, *Rhinopithecus roxellana*: Clarke 1991) and multimount ejaculators [doucs, *Pygathrix nemaeus* and *P. nigripes* (Hollihn 1973; Rawson 2009) and silvered leaf monkey, *Trachypithecus cristatus* (Bernstein 1968)], and some species are described as using both single and multiple mounts [proboscis, *Nasalis larvatus* (Hollihn 1973; Yeager 1990a; Murai 2006) and capped langurs, *Trachypithecus pileatus* (Stanford 1991a)]. Cat Ba langurs seemed to use both tactics, although sexual mounts were more likely to involve multiple mounts (ejaculation could not be confirmed in any observations). Note, however, that almost a fifth of successful sexual interactions only include a single mount, so this does not appear to be uncommon for the Cat Ba langurs. Ad libitum data indicate that most mounts are sociosexual, and all successful mounts look similar (meaning it is not easy to tell whether or not the mount is sociosexual or sexual in nature). Therefore, a quick observation without knowledge of the age-sex classes of participants may give a biased measure of mating rates.

Harassment of mounts is <1% of Cat Ba langur social budget, and approximately one-third of mounts are harassed (Hendershott unpublished data). Harassment of mounts has been noted for other colobine species (Stanford 1991a; Newton and Dunbar 1994; Fashing 2007b; Li and Zhao 2007); for example, Hanuman langur (*Semnopithecus entellus*) mounts are interrupted almost half (48%) the time (Newton 1987). It may be that adult females (i.e. sexual competitors) harass other matings between females and the resident male as a form of reproductive competition for sperm; conception for any one female is less likely the more females the harem male mates with (Sommer et al. 1992). Similarly, among golden snub-nosed monkeys, conception is negatively correlated with the number of females the harem male mates with that day; groups with more females have more sexual harassment, and females that conceive during the mating season harass others at higher rates, suggesting a hormonal control (Qi et al. 2011).

The Cat Ba langurs spend 1% of their social budget embracing. Embracing is a common behaviour for primates, often seen during times of heightened tension (de Waal 2000; Shimooka and Nakagawa 2014) and accompanied by specific vocalisations or facial expressions (Thierry 1984; Maestripieri 1996; Shimooka and Nakagawa 2014). In Cat Ba langurs embraces are used to gain access to a newborn or infant, to calm down young individuals (as distressed and crying young often ran to an adult female, who embraced them as they stopped crying), and during times of heightened tension (during disputes). Embraces are part of grooming bouts. Among macaques (*Macaca* spp.), females often initiate embraces during aggressive or grooming episodes, and those who embrace the most are those who get into the most conflicts (Thierry 1984; Maestripieri 1996; Shimooka and Nakagawa 2014). Among Hanuman langurs, embracing occurs while playing, when feeling threatened, or during sexual excitement (Weber 1973), and they are sometimes associated with same-sex mounts (Sommer et al. 2006). Overall embraces seem to reduce tension, anxiety, aid in appeasement, and prolong grooming interactions (Shimooka and Nakagawa 2014) and tend to occur during greeting, sexual harassment, tension, or aggression (see sources within Thierry 1984). They can also be used for reconciliation (Ren et al. 1991; Arnold and Barton 2001) and to signal benign intent (Slater et al. 2007).

Transfers occurred for 1% of the Cat Ba langur social budgets; they are indicative of intense group member interest in newborns and infants. Overall these transfers are concentrated around the first few weeks of a newborn's life, with a gradual decline in interest and transfers as the newborn transitions into being an infant and gains more independence.

I found that less than 1% of social behaviour is agonistic in nature. Agonistic behaviours are extremely uncommon in Cat Ba langurs and colobines in general (Jay 1963; Ren et al. 1991; Li and Rogers 2004b; Matsuda et al. 2012a; Djègo-Djossou et al. 2015), especially compared to cercopithecines (Newton and Dunbar 1994). Given observation time (Section 5.2.1), agonistic interactions for Cat Ba langurs occur at a rate of one every 110 hours of observation. Among ursine colobus (*Colobus vellerosus*), agonistic interactions occur every 2-38 hours (Saj and Sicotte 2007) – and 94% of interactions are affiliative (Djègo-Djossou et al. 2015) – while the rate among Western red colobus (*Piliocolobus badius*) females is once every five hours, and among king colobus (*Colobus polykomos*) females once every 1.7 hours (Korstjens et al. 2002). The relative rarity of these dominance-related behaviours suggests that Cat Ba langurs do not have a strict hierarchy, but this needs to be assessed with individual recognition and closer visual access. While some researchers have detected a hierarchy in colobines living in unusually dense, provisioned, or captive situations (Blaffer Hrdy 1977; Borries et al. 1991; Amarasinghe et al. 2009; although see Koenig 2000 and Koenig et al. 2004), others have found results more similar to my finding that dominance interactions are rare, hierarchies are weak, and/or there is no discernible female hierarchy (Jay 1963; McKenna 1979; Stanford 1991a; Stanford 1992; Li and Rogers 2004a; Rawson 2009; Matsuda et al. 2012a).

Among Cat Ba langurs, most agonistic interactions (especially between adult females) centred around settling down to sleep or access to a newborn. Similarly, proboscis monkey females have been reported to aggress against other females while settling down at night (Yeager 1990b). It is interesting that Cat Ba langurs do not have agonistic interactions in a feeding context. Often aggressive interactions between colobine females occur while feeding (Korstjens et al. 2002; Koenig et al. 2004); in capped langurs it has been noted that intragroup aggression is lowest when leaves are most available, suggesting that aggression is related to competition for resources (Stanford 1991b). Over half of displacements between gray langur (*Semnopithecus*) females are over food, and high-ranking females are better fed, resulting in higher fecundity (Borries et al. 1991) and infant survival (De Vries et al. 2016). The fact that the Cat Ba langurs do not have agonistic interactions while feeding may indicate that there is not significant contest competition occurring or that animals spread out enough to reduce competition.

The Cat Ba langur male in Group A was observed to mediate fights between adult females; he typically did this by chasing one of the females so that they separated. Male mediation of female fights is also seen in other Asian colobines (Yeager 1990b; Ren et al. 1991; Matsuda et al. 2012a). For example, most agonistic interactions in proboscis monkeys are about displacement (in general and during feeding) and threats by the male while mediating fights (Matsuda et al. 2012a).

5.4.1 Age and Sex Differences in Social Behaviours

Female, and older, Cat Ba langurs spend significantly more time grooming than males, and younger langurs (respectively) (Figures 5.3, 5.4, and 5.11). Since grooming is the primary social currency for colobines and Cat Ba langurs (Kirkpatrick 2007; Rawson 2009; Matsuda et al. 2012a; Djègo-Djossou et al. 2015; Section 5.3), rates of grooming between individuals gives a measure of their relationship and can serve as a proxy for how various relationships are valued. Female Cat Ba langurs invest more in their relationships than males by spending more time grooming, possibly because limestone langur females are related due to female philopatry or parallel dispersal in a dual-dispersal species (Li and Rogers 2004b; Hu 2007; Jin et al. 2009b). Female-philopatric species have higher rates of female-female grooming than male-philopatric (Lehmann et al. 2007) or dual-dispersal (Matsuda et al. 2015) species; males in these latter societies are more peripheral to the group's social network and females are more central (Zhang et al. 2012; Matsuda et al. 2015). Indeed, grooming interactions are higher among colobine females than between males and females; when females and males do engage in grooming bouts it tends to be around copulations, and females groom males significantly more and longer than males groom females (Mitchell and Tokunaga 1976; McKenna 1978; Struhsaker and Leland 1987; Yeager 1990b; Stanford 1991a; Newton and Dunbar 1994; Hu 2007; Kirkpatrick 2007; Rawson 2009; Workman 2010a; Witte 2011; Matsuda et al. 2012a; Kumar and Solanki 2014).

Figure 5.11: The adult male (top, right) sits sentry while two juveniles play socially (middle) and a group of adult females groom (bottom, left) in Group A. Photo taken March 2014 by R Hendershott

It was clear in my observations that female Cat Ba langurs with newborns were highly attractive social stimulants, and are frequently the targets of grooming interactions. This is partially demonstrated by the large number of others in proximity to newborns (Section, 6.3.2.1, Chapter 6), who are always carried by someone else. Therefore, attraction to a newborn results in the female holding them also receiving attention (especially in attempts at transfers). Similarly, a female proboscis monkey in possession of an infant is a highly desirable target for grooming, and these females receive more grooming than they give (Yeager 1990b).

Social play is more common in male, and younger, langurs (Figures 5.3, 5.4, and 5.11). This is expected as social play is the primary way young animals learn about and interact with their group mates (Bekoff 1972; Fagen 1974; Poirier and Smith 1974; Blaffer Hrdy 1977). This also seems to reflect that young males in Group A have same-sex social peers with whom they interact (the young in Group A include two juveniles and two younger males, and one juvenile and one younger female; Group B includes two juveniles, one of each sex: Table 2.2, Chapter 2), as this heavily influences play opportunities and rates (Chalmers 1984; Fagen 1993; Watts and Pusey 1993).

Ad libitum data indicates that almost all age classes (excluding infants and newborns) participate in mounting behaviour to varying degrees. This includes both sexual (an adult male mounting an adult female) and sociosexual (all other dyads) mounts; sociosexual mounts are two-thirds of all mounts. Females initiate mounts (females were seen to present more often than males), with a number of their solicitations being ignored by the adult male. Females direct their solicitations to both adult males and adult females, although adult males are more common. Female-dominant solicitation and male denial has been documented in other colobines (Bernstein 1968; Newton 1987; Brandon-Jones 1989; Yeager 1990a; Newton and Dunbar 1994; Li and Zhao 2007; Solanki et al. 2007). In fact, Hanuman langur females solicit 4.5x as often as mounts actually occur (Sommer et al. 1992). If a male does not respond to a solicitation, the female may persist and reorient (Bernstein 1968). Indeed, there were many times I saw a female present, then look back at the male, who would look at her briefly, and then turn away. The female would then back up closer to the adult male, or move around so that she was again in front of him. In these cases another adult female would often mount the presenting female. In Hanuman langurs, most solicitations are directed to the resident male (Newton 1987); when a female mounts a female, it is more common for the mountee to be soliciting a female mounter than a male mounter (Sommer et al. 2006). In a François' langur group, the adult female was much more likely to solicit the subadults or juvenile than be solicited herself (Huang et al. 2015b).

Roughly one-third of Cat Ba langur mounts are harassed (Hendershott unpublished). Harassment of mounts are entirely done by juveniles throughout scans, but I did also observe adult females interrupting mounts occasionally. Infants and juveniles have been observed to interrupt proboscis monkey mounts as well (Yeager 1990a). In 48% of Hanuman langur copulations the individuals are harassed, primarily by adult, subadult, and juvenile females (Newton 1987); infants may slap or bite the mounting male, who generally ignores him/her (Jay 1963). A similar pattern of female-biased harassers (76-100%) is found in golden snub-nosed monkeys (Li and Zhao 2007; Qi et al. 2011).

Female, but not male, Cat Ba langurs attend to distressed young, and each other, through embracing. Similarly, embraces among macaques are typically a female affiliative affair (Maestripieri 1996; Maestripieri 1997; Shimooka and Nakagawa 2014). Young are often embraced when distressed or during moment of heightened tension (Figure 5.12) and adult females embrace when approached by another, often accompanied by fear grimacing and followed/preceded by sociosexual mounts. Female Cat Ba langurs were the only ones observed to embrace during scans (Figure 5.4).

Figure 5.12: The subadult female (Crowley) embracing the juvenile male (Longbottom) while sitting during a moment of heightened tension in Group B. Note: fear grimace. Photo taken January 2015 by R Hendershott

Although unreflected in the scan data of Cat Ba langurs, ad libitum data indicates that transfers are primarily done between females (Hendershott unpublished data). Adult female, juvenile female, and young juvenile females are the most interested in handling newborns/infants. Adults are more successful than young age classes in obtaining a newborn or infant in a transfer, most probably because mothers are resistant to transferring their vulnerable offspring to inexperienced handlers (Jay 1963; Kumar et al. 2005).

My ad libitum data on intragroup aggression indicates that it is primarily between adult females. In Delacour's langurs, young have a larger percent of affiliative interactions than adults (Agmen 2014), perhaps because of a social tolerance associated with young that still have their natal coat (Alley 1980). Additionally, it is adult females who bear the heavy cost of gestation and lactation, suggesting they will be most affected by intragroup competition and, thus, have higher rates of disputes with one another than other age-sex classes.

5.4.2 Proximity and Huddles

Cat Ba langurs spend over half of their time out of arm's reach of another langur and are, on average, in proximity to 1.3 other langurs (Table 5.5). Measuring proximity to others (i.e. engaging in a huddle) is used as a proxy for tolerance, preference, relationships, bondedness, and even dispersal/philopatry patterns (Packer 1979; Stanford 1991a; Cords 1997; Sueur et al. 2011; Matsuda et al. 2012b; Zhang et al. 2012). Rates of being in proximity often correlate with rates of grooming between individuals (King et al. 2011) or general sociopositive interactions (Cords 1997). Thus, the time an animal spends in proximity to another individual can indicate how independent or asocial they are.

When Cat Ba langurs huddle together, their average huddle size is almost three. Huddle size is a measure of the group coming together, typically during times of inactivity or social behaviour, or else when settling down at a sleeping site. Therefore, huddle size and composition provides a picture of which individuals are most bonded and those who interact affiliatively. Interestingly, animals were found alone more often in the cold, dry season and less often in the hot, wet season, which suggests that huddling for warmth cannot account for this difference. However, huddling to avoid exposure to rain may explain the seasonal differences in rates of being alone.

5.4.2.1 *Behaviour and Proximity and Huddles*

Certain behaviours naturally accommodate being next to someone else or being alone, and not all social behaviours require proximity (for example, social play, vocalisations, presenting, and agnositic behaviours can all occur without being in proximity). When inactive/resting or being social, a Cat Ba langur is more likely to be next to someone else, which may be seen as a passive form of socialisation. In contrast, foraging and locomotion are more likely when alone. Spreading out while foraging may be a mechanism for reducing scramble competition between individuals (van Schaik et al. 1983; Saj and Sicotte 2007); the exception to this is young, who may stay close to more experienced foragers to watch what they eat (Janson and van Schaik 1993). Capped langur females also spread out to eat as far as the tree crown allows (Stanford 1991a). Locomotion does not necessitate individuals be alone, but the chance is much higher that individuals would not be within arm's-reach of another while moving. For example, in capped langurs locomotion is often single-file, resulting in larger group spread than at other times (Stanford 1991a). Limestone langurs also travel single-file along the rock face (Zhou et al. 2009b), although I observed that the whole Cat Ba langur group does not necessarily travel concurrently.

5.4.2.2 *Age and Sex Differences in Proximity and Huddles*

I found that adult males have larger average huddle sizes while having fewer others in proximity than other age-sex classes (Table 5.5); this indicates that they are generally around fewer individuals and, when they do join a huddle, these are larger (typically for longer rest or night time periods). Along with subadult males, they are found alone more than any other age-sex class (65%). Similarly, adult male capped langur spend 86% of scans alone (Stanford 1991a), and adult male proboscis monkeys have greater average distances to nearest neighbours than adult females (Yeager 1990b). At night, adult male black snub-nosed monkeys (*Rhinopithecus bieti*) sleep alone significantly more than any other age-sex class (Li et al. 2010). For many colobines, males are more peripheral than females, especially in female philopatric or dual dispersal groups (Matsuda et al. 2012b; Matsuda et al. 2015). This all suggests a lack of emphasis on social relationships.

Among Cat Ba langurs, adult females and adult males associate at rates that are more than chance for the male, but at chance for the females (Figure 5.8), which suggests that males are seeking out females. Colobine males tend to interact with females only through grooming and mating, and during infanticidal attacks; they are not particularly pair-bonded (Newton and Dunbar 1994), resulting in random association rates for male and female adult capped langurs (Stanford 1991a). In contrast, Western red colobus adult females are surrounded by adult males significantly more than chance (Korstjens et al. 2002).

Adult male Cat Ba langurs appear to avoid proximity to young unless there is another individual present (e.g. group size increases, typically at the nighttime sleeping spot) (Figure 5.8, Table 5.6). Similarly, other colobine adult males passively tolerate but do no interact with young group members (Bernstein 1968; Hu 2007), except for occasional aggression (although this changes if he leaves the group with juveniles and infants during a takeover) (Zhao and Pan 2006). Interestingly, golden snub-nosed monkey males will interact dyadically with juveniles during the day, but associate with them at night only if an adult female is present (Zhang et al. 2011). This implies that adult males may incidentally end up close to young in attempts to be close to adult females, but that they are not necessarily choosing to be next to them. Therefore, although colobine males do not engage very often with adult females, they are their sole source of integration (via grooming) into the group, and their relationship to young occurs incidentally while bonding to adult females (Matsuda et al. 2015).

Adult Cat Ba langur females are often surrounded by others, making them the most social age-sex class in this aspect, although their huddle sizes are generally small as they engage intensively with a few individuals at a time (Table 5.5). Females are often central to a colobine group (Matsuda et al. 2015). Adult female capped langurs spend 59% of scans out of proximity to another animal (Stanford 1991a), a rate much higher than Cat Ba langurs (37%; Figure 5.5), which is even more surprising given the Type II error (Section 5.2.3) and that ‘proximity’ is defined as ‘within two metres’ for capped langurs but just ‘arm’s reach’ for Cat Ba langurs (this difference remains unexplained, as group size and number of young, as well as climate and vegetation, are similar between the two studies, although differences in habitat quality, predation, and food patch size may explain proximity differences). The majority of these huddles are with young langurs, who adult females associate with at rates higher than chance both dyadically (both groups) and triadically (Group A) (Figure 5.8b, Table 5.6). This is because the young are still somewhat dependent on adult females for nursing, transport, keeping warm, and overall safety. François' langur females spend most of their grooming time on young group members (Hu 2007). In capped langurs the majority of social affiliation (i.e. proximity) comes in the form of mother-infant dyads (Stanford 1991a). In golden snub-nosed monkeys adult females and young are found together at the centre of the group (Zhang et al. 2012), and they are the most common form of nighttime sleeping huddles (Li et al. 2010; Zhang et al. 2011).

It is extremely interesting that dyadic huddles involving two adult females occur at rates below chance in both groups of Cat Ba langurs, but two females huddling with a young occurs above chance in Group A (Figure 5.8b). This implies that adult females are not actively seeking each other out (dyadically), but will engage in huddles if a young group member is involved (triadic huddles). Therefore the young are acting as a sort of 'social glue' keeping the females in proximity to one another. This may have been mitigated through newborn/infant transfer, which has been proposed to help bond females in dual-dispersal groups (Matsuda et al. 2012a). Indeed, newborns and infants are a source of attraction that clearly brought the Cat Ba langur females closer together, at least spatially.

I found that subadults, independent of caretakers but not yet reproductive, are found alone almost two-thirds of their time (Table 5.4); they are more solitary than adults or young. Among golden snub-nosed monkeys, subadults are described as neither being protected by others, nor having the responsibility to protect others, which results in the subadult male(s) loosely following adult male patterns, and subadult female(s) being randomly spatially distributed throughout the group (Zhang et al. 2012). Among François' langurs, subadult males are less associated with group members and tend to stay peripheral to the group (Hu 2007). Subadult Cat Ba langurs' average huddle size is intermediate (Table 5.5), indicating they do engage more in huddles than adult males, but less than adult females and young. Their average number of others in proximity is low, partly due to the smaller group size in Group B, which is the only group to contain subadults, and partly due to their incomplete social integration.

It does appear that subadults are less connected and assimilated into Cat Ba social groups; they associate with adult females less than chance, and all other age-sexes at rates expected by chance (Figure 5.8). This result may be different if a subadult female (only in Group B in this study) were in a group with newborns or infants (only in Group A in this study), as subadult females are well known to be interested in transfers and handling infants (Jin et al. 2015), which would increase a subadult female's rates of association and bonding. The fact that the subadult male trends towards being found alone more often than the subadult female (Figure 5.5) may indicate that he is on the verge of dispersal, as seen in François' langur groups (Hu 2007), but his lack of loud calling suggests he is not yet mature enough to be seen as a threat by the resident male (Hohmann 1989).

Young Cat Ba langurs are surrounded by others 45% of daily observations (Table 5.4), which is within the diverse rate (7-58%) of young capped langurs (Stanford 1991a), and follows a pattern of decreasing within young age categories (Section 6.3.2.1, Chapter 6). Their huddle sizes are similar to those of adult females, though they are surrounded by fewer individuals than adult females on average (Table 5.5). Young do not necessarily maintain proximity with one another: In Group A two young were found in proximity less than chance (no effect in Group B), and *two* young are around an adult male, an adult female, or another young less than chance (Figure 5.8c). The young individuals in Group A includes much younger individuals (newborns, infants, and young juveniles) who do not engage as often with social behaviours as juveniles (Figure 6.1, Chapter 6), whereas the two juveniles in Group B played, groomed, and rested together, which probably accounts for the difference between groups. In golden snub-nosed monkeys, juveniles interact/associate with other juveniles more often during the day than at night (Zhang et al. 2011). In contrast, juvenile male black snub-nosed monkeys frequently huddle together at night (Li et al. 2010). Therefore, there may be temporal variation in proximity between young.

I found that adult males are more solitary than their female counterparts (Figure 5.5), as they have little interest in socialising/grooming or handling/being around young. When young, however, there is a trend for males to spend more time in proximity to someone else than are young females (Figure 5.5), and they often play socially (Figure 5.10). This may be because the two young males in Group A were close in age, and were often seen playing, wrestling, and traveling together. In contrast the young females did not have same-age female peers, an important factor in young socialisation patterns (Watts and

Pusey 1993). This result is still surprising, however, given that young female primates are often nearby to adult females in order to groom and due to their attraction to newborn or infant group members (Jay 1963; Poirier and Smith 1974; Blaffer Hrdy 1977; Young et al. 1982; Fagen 1993).

5.4.2.3 *Group Differences in Proximity and Huddles*

Individuals in the Group B are less likely to be in proximity to other group members, both because of the smaller group size, and the fewer number of young langurs that maintain close proximity to adult females. Average huddle sizes and number of others in proximity are larger for all age-sex classes in Group A (Table 5.5), reflecting their overall larger group size. Huddle sizes, as a percent of all huddles observed, are similar between the two groups, with the exception of Group A having the possibility of huddles larger than seven (Figure 5.6). The composition of huddle dyads, as well as the expected percent, are obviously different between the two groups, as Group B also has subadults, and the percent expected by chance between the two groups are different given their demography.

It is hoped that this information is used in captive breeding and translocation attempts. As females seem to avoid one another, a group of just females will not make a stable starting point for group cohesion. However, if one or more females have an infant, this may help with bonding. As males spend more time alone, and may possibly be the dispersing sex, they are probably better able to handle translocation attempts. It is important to understand the social behaviours of a species before trapping them in captivity with one another.

5.5 Summary

Social behaviour is key to group living primate cohesion. In this chapter, I assess social behaviours and proximity of Cat Ba langurs through 10 minute scan samples over an 11 month period. Cat Ba langurs interact socially in a variety of ways, with grooming being the most common, followed by play, vocalisations, presentations + mounts +

harassment, embraces, transfers, and agonistic interactions (aggression, displacement, submission). Dominance and aggressive interactions are rare.

Individuals in different age-sex classes have different ways of socialising. Adult males are quite solitary, only joining huddles when everyone is coming together, and tending to avoid young. Adult females are much more social in terms of being surrounded by others, especially young. They both groom more and are the only ones initiating disputes. Subadults are fairly independent. Young are often found around adult females and – when older – each other, but rarely around the adult male. As newborn/infants are highly attractive to group females, there was much interest in transferring a newborn/infant by all age females. Because of their demographic differences, Group A gets in more disputes within the group, and can be found in larger huddles. Group B is smaller, and individuals are found alone more often. Their smaller average huddle size and likelihood of being in proximity is due to their smaller group size and fewer proportion of young, dependent group members.

The rate and type of social behaviour can indicate strength of relationships, dispersal patterns, and provides information as to how captive animals should be grouped. Additionally, as it is an expendable behaviour that relies on food availability, and, thus, habitat quality, documenting social behaviour rates can be informative of animals that are having to exert more energy into more necessary behaviours to obtain sufficient food resources (Section 7.3.1, Chapter 7).

Chapter 6:
Newborn through Juvenile Development

6.1 Introduction

Among young primates, documenting behavioural development through changes in activity budgets, diet, nursing, locomotion and postures can aid in identifying key developmental stages, such as the point at which individuals are most vulnerable to malnutrition or infanticide due to weaning or inability to locomote on their own. Assessing physical development of young primates creates a ‘species average’ for life history, and depends on events such as dental eruption, skeletal fusion and growth plates, body mass and fat, brain and nervous system development, motor skills, and muscular coordination (Bolter and Zihlman 2007). Tracking the eventual shift in natal coat colouration can be another indicator of attraction to newborns and infants by group members and the vulnerable period for infanticide. Thus, there is a strong relationship between both behavioural (e.g. vulnerability and independence) and physical (e.g. natal coat transformation and locomotion skills) development.

Pelage, along with physical and behavioural development, can be affected by food availability and habitat quality. This is because as individuals become nutritionally stressed due to lack of resources or stressful environments, their growth and development will be retarded (Janson and Goldsmith 1995; Mori et al. 1997; Cowlishaw and Dunbar 2000; Koenig 2002; Borries et al. 2008; Zhou et al. 2010). This can then affect long-term survival and reproduction (Altmann 1998). Support for this idea comes from the fact that animals tend to mature faster in captivity than in the wild, as captive animals are generally better nourished and face lower social, physical, and predatory stress (Bolter and Zihlman 2007). In the wild, Phayre’s leaf monkey (*Trachypithecus phayrei*) infants transition to an adult coat later in larger groups than in smaller groups, possibly as a result of the increased scramble competition their mothers experienced over the course of their development (Borries et al. 2008). This scramble competition and maternal nutritional stress affects milk quality and/or quantity (Hinde and Milligan 2011), resulting in developmental retardation (Altman et al. 1970; Martorell 1999; Altmann and Alberts 2005; Keenan et al. 2013).

Some young primates play less in poorer-quality habitat (Barrett et al. 1992; Sommer and Mendoza-Granados 1995), including limestone langurs (Li and Rogers 2004a; Hu 2007). Overall, poor habitat quality can lead to later maturation and a delayed start to reproduction (Cowlishaw and Dunbar 2000), presumably due to the reduced food availability in degraded habitat (Johns 1986; Medley 1993; Tutin 1999; Arroyo-Rodríguez and Mandujano 2006; Wong et al. 2006; Guo et al. 2008; Dunn et al. 2010; Wang et al. 2011).

Therefore, a reduction in resource availability can cause the natal coat to be lost later and a reduction in play and highly-energetic activities for young animals. It is thus important to study the behavioural and physical ontogeny of individuals as a reflection of resource availability, vulnerability to infanticide, and age-specific mortality. All of this information can then be used to better improve population viability analyses and conservation management.

6.1.1 Births

Many primates show seasonality in their reproductive patterns, including Asian colobines (Struhsaker and Leland 1987; Brockman and van Schaik 2005; Kumar et al. 2005; Solanki et al. 2007; Jin et al. 2009a). Seasonality of births may have to do with food availability at critical key developmental stages, ensuring that the most vulnerable stage has the best access to resources. For example, weaning may be timed so that it occurs when food is most available, or birth may be timed so that it happens when food is either most available or at the end of peak availability (Janson and Verdolin 2005). If resources are consistent (e.g. human crops to raid), breeding may not show seasonality (Newton 1987).

There are, however, other factors that influence birth seasonality. Species distribution plays a role through differences in habitat types. The mast fruiting common in Southeast Asia (van Schaik and Pfannes 2005; Sterling et al. 2006) may cause primates in this area to be more opportunistic, with less obvious seasonal variation because of between-year differences in food availability (Janson and Verdolin 2005). Additionally, there are differences in birth seasonality based on life history characteristics: small animals that breed multiple times a year, and large animals that cannot fit a breeding cycle into a year, may not be subject to birth seasonality, although, at a moderate size, births should be highly seasonal (Janson and Verdolin 2005). Finally, diet plays a role in birth seasonality: while frugivores are the most dependent on the seasonal availability of preferred foods, gumnivores have more consistent resources and show the least amount of birth seasonality, and folivores have intermediate birth seasonality as their resources are not constant throughout the year but are subject to less variation in availability (Janson and Verdolin 2005).

Some primates have biased sex-ratios at birth (Johnson 1988; Hiraiwa-Hasegawa 1993; Silk and Brown 2008; Zhao et al. 2009), which may reflect a conception or zygote vitality bias that is adaptive based on mother's body condition. This includes differences across maternal rank (Paul and Kuester 1990), with factors like sexual dimorphism and food availability interacting with maternal rank (Schino 2004), or dispersal patterns and competition with neighbours (Johnson 1988; Singleton and van Schaik 2002; Silk and Brown 2008). Nonetheless, there remains no consistent pattern of birth ratios across primates, as adaptive traits differ between species (Hiraiwa-Hasegawa 1993) and there may be interactive effects (Packer et al. 2000; Schino 2004).

6.1.2 Behavioural Development

6.1.2.1 *Activity Budget*

How an individual spends its time is likely to change with age, as maturational and developmental changes dictate basic needs and abilities. For example, as white-headed langur (*Trachypithecus leucocephalus*) infants age, they spend less time in physical contact with their mothers, more time exploring their environment, and more time feeding (Zhao et al. 2008). For the first week they cling to their mother or a handler/allomother, and then at as early as five months of age, mothers start regularly rejecting an infant from nursing or being carried around, but maintain guarding behaviour over them. By 21 months they are frequently rejected as they are fully weaned (Zhao et al. 2008). Infants start exploratory play around two months, which then turns into social play after three months of age; social play peaks around 16 months (Zhao et al. 2008).

In a study on the development of a captive male spectacled langur (*Trachypithecus obscurus),* four phases are noted: the Maternal Care period (0-20 days), the Individualisation period (21-70 days), the Socialisation period (71-240 days), and the Juvenile period (over 240 days) (Horwich 1974). During the first period there are high rates of maternal behaviours and nipple contact, which corresponds to my study's 'newborn' period. The Individualisation period is when the langur begins to explore, spends less time in contact with the nipple, and gains locomotor skills. During this time solitary play rates are high. This corresponds to the present study's 'infant' period. The Socialisation period is when play starts to be social, and the majority of pelage change happens; this corresponds to the end of the present study's 'infant' period and the majority of the 'young juvenile' period. During the final stage, the Juvenile period, there is increased independence with less reliance on contact with the mother. This spans this study's end of 'young juvenile' period and beginning of the 'juvenile' period.

6.1.2.2 *Dietary Budgets and Nursing Behaviour*

Nursing is key to immature mammalian survival. The relatively long immature period of primates that is accompanied by frequent contact with the mother for nursing (compared to other mammals: Janson and van Schaik 1993), requires primates to produce relatively dilute milk (i.e. high water content, low in protein and energy) as a means to help alleviate energetic costs of lactation to the mother (Hinde and Milligan 2011). Among langurs, infants have fairly constant access to the nipple (Blaffer Hrdy 1977) with the exception of when they are carried by nonlactating adults. Milk quality, composition, and quantity may vary with the sex of the offspring, and the maternal experience of the mother (Hinde 2009; Hinde and Milligan 2011).

Weaning is an important time in the life of both a mother and her offspring. The mother is withdrawing resources so that she can invest in future offspring, while it is in the infant's best interest to be nursing as long as possible (Trivers 1974; Maestripieri 2002). The conflict of interest between mother and offspring takes the form of maternal rejection, particularly at the time that she returns to estrus (Zhao et al. 2008) or when resources are limited (Maestripieri 2002). Infants are the main initiators of contact while the mothers resist such demands (Blaffer Hrdy 1977). In langurs the rejection can be mild, such as just moving away or holding off the infant (Jay 1963; Blaffer Hrdy 1977). As the infant ages, the female may become more aggressive and threatening in her rejection.

Infants in larger social groups are sometimes weaned later, possibly as a result of scramble competition (Borries et al. 2008). Alternatively, later weaning may be a consequence of poor environment (Kirkpatrick 2007). Either way, juvenile primates can limit the costs of a larger body size during times of limited resources (i.e. when highly vulnerable to starvation) by slowing their rate of growth (Janson and van Schaik 1993) via prolonged nursing, presumably of lower quality milk due to nutritional stress.

To aid in quick growth rates (which are higher in folivores than nonfolivores of similar body size), protein-heavy food items are expected to be consumed at higher rates than those who are not putting as much energy into growth (Leigh 1994; Rothman et al. 2008). For folivores, protein comes primarily from young leaves (Milton 1979). As langurs often consume fruit that is unripe (which is less digestible than ripe fruit) (Chivers 1994; Waterman and Kool 1994; Workman and Le Van Dung 2009; Workman 2010a), it is expected young langurs' efforts would go into leaves over fruit, especially if that fruit is harder to process (Janson and van Schaik 1993).

6.1.2.3 *Locomotor and Postural Budgets*

Newborns of most primate species can cling to their mother from birth (Dunbar and Badam 1998), although the mother may help hold the infant in place when she walks or runs (Jay 1963; Blaffer Hrdy 1977). White-headed langur infants start trying to move onto nonlangur substrates around 3-5 weeks of age, although they lack the strength and coordination to break contact until 4-5 weeks of age (Zhao et al. 2008). Among captive red-shanked doucs (*Pygathrix nemaeus*), interest in the environment starts at about two weeks of age, and by the fifth week they are able to move around on their own (Yeong et al. 2010). Sitting and standing often are the first postures observed once individuals start to gain independence; this then progresses to poorly coordinated quadrupedal walking or bipedal leaping forms of locomotion (Dunbar and Badam 1998). This initial 'shaky-ness' and inaccuracy in locomotion patterns reflects developmental limitations (Workman and Covert 2005).

At approximately 3-7 months of age Hanuman langurs (*Semnopithecus entellus*) are primarily moving around by hopping or leaping; by the time they are around a year old they are able to use standard adult postures which, again, start out uncoordinated and gradually become more refined (Dunbar and Badam 1998). Captive red-shanked doucs are locomoting independently by 8-13 weeks of age (Yeong et al. 2010). White-headed langurs start leaping around 6-7 weeks of age (Zhao et al. 2008); around one year old (what the present study considers the 'juvenile' period), white-headed langurs master moving and leaping on the steep limestone karst (Huang and Li 2005). Juveniles have the skills, strength, and coordination to locomote like adults, although they have a larger locomotor repertoire than adults (Dunbar and Badam 1998; Covert et al. 2004; Workman and Covert 2005).

6.1.3 Pelage and Physical Ontogeny

Natal coats of Cat Ba langurs (*Trachypithecus poliocephalus)* are flamboyant orange, a common feature of the genus *Trachypithecus* (Blaffer Hrdy 1976; Oates and Davies 1994; Groves 2001; Nadler et al. 2003). The distribution of natal coat colouration has been used as a way of teasing apart relatedness between species (Nadler et al. 2003) and different ages within a species (Treves 1997).

As an infant starts spending more time away from its mother (i.e. gaining independence) its coat begins to change colour (Horwich 1974; Stanford 1991a); infant handlers lose interest in infants at this stage (Jay 1963), which has been estimated to happen at about four months of age in Cat Ba langurs (Schrudde et al. 2010). Across primates, once the change is complete, weaning begins (Treves 1997) – or, in the case of François' langurs (*Trachypithecus francoisi*), has completed (at 12-14 months of age) (Hu 2007).

While the exact reason for this visually obvious age-dependent coat colouration is unknown, there are several hypotheses. Two of these relate to infanticide-avoidance: infant defence and paternity cloaking (Treves 1997). The infant defence hypothesis states that the orange coat is meant to contrast with all adult pelage in order to signify to potentially infanticidal males that the group will come together to protect such a vulnerable group member (Treves 1997). The paternity cloaking hypothesis states that having bright orange infants removes any phenotypic paternity identifiers and protects infants from harm from any adult male who may recognise the infant as not being his own (Treves 1997).

Other hypotheses focus on the care-eliciting effects the orange coat seems to have on group members. Group members are highly attracted to natal coats, and it has been suggested that this would be a psychological and evolutionary tactic to induce caretaking by promoting interest and tolerance, preventing aggression, and creating a safe social environment when the youngsters are at their most vulnerable (Alley 1980). Nonetheless, flamboyant natal coats are certainly not a prerequisite for receiving interest and tolerance. In general it does seem that natal coats are being used to signal vulnerability and dependency to others, as they are common in species with high rates of infant-handling wherein newborns are attractive to group members (Blaffer Hrdy 1976), and the natal colouration does seem to elicit caretaking responses (Alley 1980).

This chapter addresses the patterns of development for Cat Ba langurs from birth through the juvenile period (approximately 1-3 years of age) by assessing their activity, postural, locomotor, and dietary budgets. This is done across the four age classes in order to document behavioural development. Additionally, these behavioural and age differences will be related to changes in pelage colouration from bright orange to the adult coat colour of black with an orange/yellow head/shoulders. This information can be used for both censusing and monitoring normal behavioural and pelage development by park rangers and conservation management teams and provide information on vulnerable periods that may increase age-specific mortality.

6.2 Methods

Data were collected on two reproductive groups of Cat Ba langurs living on the Cua Dong fjord of Cat Ba Island (northeastern Vietnam). Observations were made from a boat, as is standard for research on primates living on steep limestone karst (Workman 2010a; Agmen 2014; Phan Duy Thuc et al. 2014). Behavioural data were collected through instantaneous scan samples every 10 minutes (Altmann 1974b; Martin and Bateson 2009).

I initially focused on the area with the highest density of langurs and then visually spiralled out from there for up to 45 seconds. This was done to avoid repeat counting of individuals, to prevent a bias in documenting flamboyant behaviours, and to ensure that the scan was as instantaneous as possible.

Newborns, infants, and young juveniles were individually identifiable as there was typically only one in each age class at a time. Group A included three juveniles and between one and three other young individuals that changed young age classes throughout the study (Table 6.1). Group B had two juveniles throughout the study. Thus, this small sample size must be kept in mind when interpreting significant results.

Table 6.1: Group A's demographic breakdown of young group members throughout the study period. Group A had three individuals born during the study period, while Group B remained unchanged with two juveniles (one male, one female). Arrows indicate that it is the same individual that changed age classes throughout the study. Note: M=male, F=female

as of…	**newborn**	**infant**	**young juvenile**	**juvenile**
21 Feb 2014	0	1 (F)	0	3 (1F, 2M)
5 May 2014	0	0	1 (F)	3 (1F, 2M)
4 Aug 2014	1 (M)	0	1 (F)	3 (1F, 2M)
22 Aug 2014	0	1 (M)	1 (F)	3 (1F, 2M)
7 Nov 2014	1 (M)	1 (M)	1 (F)	3 (1F, 2M)
13 Nov 2014	0	2 (M)	1 (F)	3 (1F, 2M)
3 Dec 2014	0	1 (M)	2 (1F, 1M)	3 (1F, 2M)
3 Jan 2015	1 (u/k)	1 (M)	2 (1F, 1M)	3 (1F, 2M)

6.2.1 Births

Births were noted ad libitum. Data on births come from the three individuals born into Group A during the study period and one individual born into Group A less than a month before the study period (Le Ngoc Nghi pers. comm. 2014). Birth dates for the three born during the study period are assumed to be between the last time all group members were counted with no newborn present and the first sightings of the newborn; this ranged from 4-12 days. Two individuals were born while I was away from the island, which is why the birth ranges are so large. Due to the low number of births, only descriptive statistics can be provided.

6.2.2 Behavioural Data Collection

Behavioural development was documented through scans, as was nursing. Behavioural categories recorded include: inactivity, foraging, social, locomotion, and ‘other’. While foraging the langurs may consume leaves, flowers, fruit, stems, or water. Water was removed from foraging analyses, while stem eating occurred at rates too low for detailed analysis for young langurs (n<10). Locomotion includes quadrupedalism, climbing, leaping, dropping, or arm swinging; these latter two locomotion types occurred <10 times each, and are therefore removed from detailed analysis. Postures include: sitting, standing, clinging, leaping, lying prone, wrestling, suspending, and standing bipedal. Within social behaviours, young langurs were seen to use: play, groom, transfer, harass, vocalise distress, embrace, mount, and submission. Within ‘other’ behaviours, young langurs were seen to use: asocial play, explore, struggle, and rejection. The overall activity budgets do not directly correspond to ‘young’ behaviours in Chapter 3 as Chapter 3 excluded newborns from analyses. Note that throughout this chapter I am assessing different age classes over the course of 11 months of observation, and that while some individuals (n=3) changed age classes, analyses are focusing on comparing age classes, not documenting the development of the same individuals as they cross age classes.

At the time of the scan, it was also noted if a young was nursing. Other studies use time spent on an adult female’s ventrum as a proxy measure of suckling (Zhao et al. 2008), although I used the much more conservative definition of confirmed face-to-breast contact (Table 2.4, Chapter 2). This is because during initial observations it became clear that young often cling to adults without nursing, and I did not want to overestimate time spent nursing.

Young langur behaviours are assessed for an overall activity budget (with breakdowns of ‘social’ and ‘other’ behaviours) as well as foraging, posture and locomotion. Activity, dietary, postural, and locomotor budgets are presented as the mean daily proportion of scans that included each specific behaviour category. Following existing protocols on similar species (Teichroeb et al. 2003; Hu 2007; Zhou et al. 2007), day was used as the unit of analysis for independence.

In order to assess whether the three to four young age classes vary across these various budgets, I first fit a linear model (LM) with arcsine transformed proportions (similar to Li and Rogers 2004), as the dependent variable, and behaviours/food/postures/locomotion type, age, and an interaction between the two as the independent factors. If I found that the overall behaviour/food/postures/locomotion type pattern differed between young age classes ($P<0.05$) with this LM, I assessed the differences between ages for each behaviour, food item, posture, and locomotion type separately with a binomial logistic model (BLM), using daily observed frequencies out of total numbers of observations. As some analyses were overdispersed, this was accounted for by reporting the more conservative results of a 'deviance' model, and is noted in tables throughout the chapter. BLMs provide pairwise comparisons between variables in order to identify where the significant differences lie (e.g. the three age classes); tables for significant pairwise comparisons are provided in the Appendix if posthoc analyses were conducted with a BLM and were significant. The results of pairwise comparisons within the posthoc tests are only mentioned if they are significantly different to adjacent age classes.

Proximity (being within arm's reach of other langurs) and number of other individuals in proximity were noted at the time of scans (Section 5.2.3, Chapter 5 for more details). Analyses of time spent alone (not in proximity) vs. near some other langur (in proximity) is done with a BLM, while average number of others in proximity are assessed with a generalised linear model (GLM). There was one scan in which I could see the newborn but could not tell if anyone was in proximity due to visual obstructions; I consider this scan inaccurate as the animal was too young to be alone at that age. Therefore, I removed this scan from the dataset; statistical results were unaffected.

A rate was obtained for nursing; rejections occurred at such low levels that they are mentioned only descriptively. Similarly, a breakdown of social and 'other' behaviours is simply descriptive, although overall differences were assessed with a LM. I used SPSS 23 for Windows for all analyses, with significance set to $P<0.05$ for two-tailed tests.

6.2.3 Pelage and Physical Ontogeny

Age-related changes to coat colouration and body size were noted ad libitum in between scans, and are mentioned only descriptively in this chapter. These descriptions of natal coats progressing into adult colouration were aggregated across individuals, due to small sample size [this is based on five juveniles, who remained juveniles for the entire study period, and four individuals that developed and changed age classes (newborn – young juvenile) in the course of the study period: Table 6.1]. As birth dates were not known exactly for the three individuals born during the study period (range: 4 to 12 days), descriptions of pelage colouration are narrowed down by month.

6.3 Results

On the basis of behavioural data, pelage colour, physical characteristics, and attractiveness to other group members, four 'young' age categories were created: newborn (roughly 0-3 weeks), infant (roughly 3-16 weeks old), young juvenile (roughly 4-12 months old), and juvenile (estimated 1-3 years old) (Table 2.3, Chapter 2). Although multiple aspects were used to determine age classes, coat colouration was the main emphasis so that brief observations (by survey team members or National Park staff) could still be informative of age classes (Altmann et al. 1981). Behavioural developments closely matched stages of coat colouration.

Initial exploration of the data indicates that 81% of all newborn scans for which identity was known were of Simba, followed by Jordan (10%), and Brock (9%); 8% of newborn scans could not be narrowed down to an individual (Table 6.2 for name references). Forty-four percent of all infant scans for which identity were known were of Simba, followed by Jessie (42%), and Brock (15%); 19% of infant scans could not be narrowed down to an individual. Young juvenile scans were focused on Jessie (83% of scans for which identity are known) and Simba (17%), with only 2% of young juvenile scans not being narrowed down to an individual. In contrast, scans of juveniles are of completely different individuals (two of whom are in Group B): Longbottom (42% of known juvenile scans), Minerva (36%), and Mitty (22%); two-thirds of all scans could not be narrowed down to an individual. This was primarily due to two male juveniles in Group A that I could not tell apart (Tweedledee and Tweedledum), who comprised 29% of all 'unknown' juvenile scans. The variation in scans of each individual were primarily due to differences in observation time (e.g. Brock was only observed on four different days; Jessie had the longest observed period of being a young juvenile) and my inability to confirm sex among the three juveniles in Group A.

Table 6.2: Young langurs included in analyses from Groups A and B, their birth dates, and the times during the study in which they were considered each age class. Note: u/k=unknown

	sex	group	born	**newborn period**	**infant period**	**young juvenile period**	**juvenile period**
Jordan	u/k	A	31 Dec 2014 – 3 Jan 2015	birth – end of study			
Brock	male	A	27 Oct 2014 – 7 Nov 2014	birth – 11 Nov 2014	13 Nov 2014 – end of study		
Simba	male	A	1 Aug 2014 – 4 Aug 2014	birth – 21 Aug 2014	22 Aug 2014 – 2 Dec 2014	3 Dec 2014 – end of study	
Jessie	female	A	Jan-Feb 2014	u/k	21 Feb 2014 – 29 April 2014	5 May 2014 – end of study	
Mitty	female	A	Jan-Feb 2013[a]	u/k	before July 2013[b]	u/k	before Feb 2014
Tweedledee	male	A	Jan-Feb 2013[a]	u/k	before July 2013[b]	u/k	before Feb 2014
Tweedledum	male	A	Jan-Feb 2013[a]	u/k	before July 2013[b]	u/k	before Feb 2014
Minerva	female	B	u/k	u/k	u/k	u/k	before July 2013[b]
Longbottom	male	B	u/k	u/k	u/k	u/k	before July 2013[b]

[a] based on CBNP ranger information (Le Ngoc Nghi pers. comm. 2013)
[b] estimated based on pilot work July-Aug 2013

6.3.1 Births

Two births in Group A occurred in the dry winter season, one in the wet summer season, and one right on the border between seasons (Table 6.2). A female (Jessie) was born January-February 2014, before the study period began; she was still mostly orange and being carried most of the time when I first saw her late February 2014. A male (Simba) was born 1 August – 4 August 2014. Another male (Brock) was born 27 October – 7 November 2014. An unsexed newborn (Jordan) was born 31 December 2014-3 January 2015. At the end of the study (January 2015) both Jessie and Simba were ‘young juveniles’, Brock was an ‘infant’, and Jordan was still a ‘newborn’. Of the three individuals that could be sexed, one was female and two were male.

6.3.2 Behavioural Development

6.3.2.1 *Activity Budget*

For all young combined, the most common behaviour was inactivity (51 ± 1.8%), followed by social behaviour (19 ± 0.9%), foraging (18 ± 1.4%), locomotion (17 ± 1.4%), and finally ‘other’ (5 ± 0.5%). The most common social behaviour was social play (52 ± 3.3%), followed by grooming [43 ± 4.3% (28 ± 4.8% of their daily grooming budget is them grooming someone else vs. 72 ± 4.8% of them being groomed)], transfer (1 ± 0.6%), vocalise [1 ± 0.5% (all of which are distress vocalisations)], embrace (1 ± 1.0%), mount [1 ± 1.0% (all of which are failed)], harass (<1 ± 0.2%), and submission (<1 ± 0.3%). The most common ‘other’ behaviour for young langurs was asocial play [75 ± 4.3% (96 ± 1.9% of their daily asocial play budget was locomotor-rotational play vs. 4 ± 1.9% object play) and exploration (20 ± 3.9%), with a small amount of struggling against being held (4 ± 1.7%) and rejection [1 ± 1.3% (all of which was adult females rejecting juveniles)].

There was a significant effect of age on activity budgets (χ^2=367.490, df=12, p<0.001; Figure 6.1). This held for all five behaviours (Table 6.3). As newborns were – by definition – unable to forage or locomote, newborns were removed from posthoc analyses of foraging and locomotion by age. In the first stage of life (i.e. newborns) inactivity rates were significantly higher than all other young ages (Table 13a, Appendix). Comparatively, infants were significantly less inactive and used ‘other’ behaviours at over 17 times the newborn rate (Table 13, Appendix); they also used foraging and locomotion, which newborns never did. Young juveniles’ rates of foraging and locomotor behaviours increased significantly compared to infants while ‘other’ behaviours used decreased (Table 13, Appendix). Juveniles foraged and socialised significantly more than young juveniles, while using locomotion and ‘other’ behaviours significantly less (Table 13, Appendix).

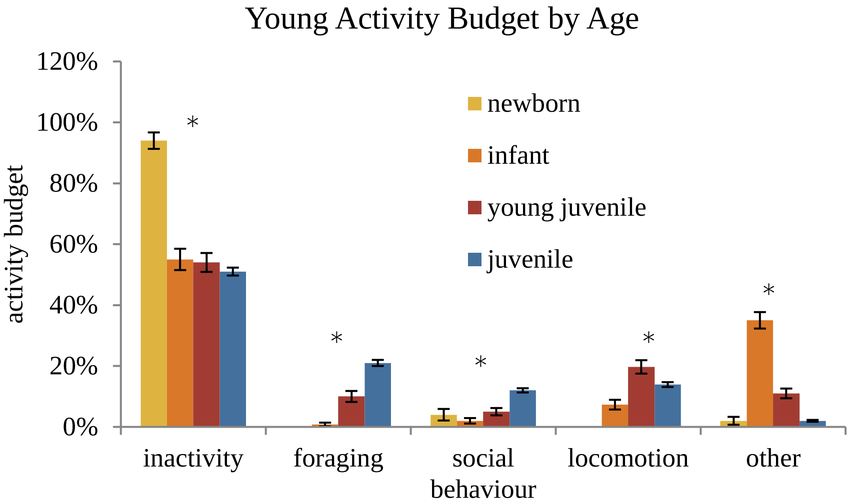

Figure 6.1: Mean daily percent (%) of activity budget ± standard error (SE) for each behaviour within each young age class. Behaviours that show significant differences across ages are indicated with an asterisk (*). Test statistics and exact values can be found in Table 6.3, and pairwise comparison p-values can be found in Table 13, Appendix.

Table 6.3: Mean daily percent (%) of activity budget ± SE for each behaviour within each young age class. A dash (-) indicates that newborns did not forage or locomote, by definition, and were therefore removed from posthoc analysis of those behaviours. All behaviours assessed with a BLM ‘deviance’ model. All values rounded to nearest integer. Significant results indicated with asterisk (*). Pairwise comparison p-values can be found in Table 13, Appendix.

	inactivity	**foraging**	**social**	**locomotion**	**‘other’**
newborn	94 ± 2.7	-	4 ± 1.9	-	2 ± 1.3
infant	55 ± 3.5	1 ± 0.6	2 ± 0.9	7 ± 1.6	35 ± 2.7
young juvenile	54 ± 3.1	10 ± 1.8	5 ± 1.2	20 ± 2.2	11 ± 1.6
juvenile	51 ± 1.3	21 ± 1.0	12 ± 0.7	14 ± 0.8	2 ± 0.3
p=	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
df=	3	2	3	2	3
χ^2=	33.958	38.709	33.447	17.483	284.874
n=	1918	593	350	480	238

There were significant age differences in langurs' use of social behaviours (LM: χ^2=11.896, df=3, p=0.008). Transfer (n=6), vocalise (n=4), harass (n=4), embrace (n=3), mount (n-1), and submission (n=1) were removed from analysis due to low number of observations in some categories. This leaves groom and play as the two main social behaviours of young langurs, but posthoc analysis could not be run due to low number of observations in some categories. Descriptively, grooming/being groomed was 100 ±0.0% of newborn, 43 ± 27.3% of infant, 25 ± 12.9% of young juvenile, and 33 ± 4.0% of juvenile social budgets; social play was 0 ± 0.0% of newborn, 57 ± 27.3% of infant, 75 ± 12.9% of young juvenile and 67 ± 4.0% of juvenile social budgets. Thus, the general trend was for play to peak at the young juvenile stage but generally increase with age, and newborns to only engage socially by being groomed.

There were significant age differences in young langurs' use of 'other' behaviours (LM: χ^2=128.613, df=2, p<0.001). Struggle (n=7) and rejection (n=2) were removed from analysis due to low number of observations in some categories; asocial play and explore were the two main 'other' behaviours of young langurs (they were not used by newborns at all), but posthoc analysis could not be run due to low number of observations in some categories. Explore seemed to be used by infants (49 ± 4.8%) as a precursor to gaining mobility and independence (Figure 6.2). It was not used by the older age classes at all, who spent 100% of their 'other' budget playing asocially (compared to the infant rate of 51 ± 4.8%).

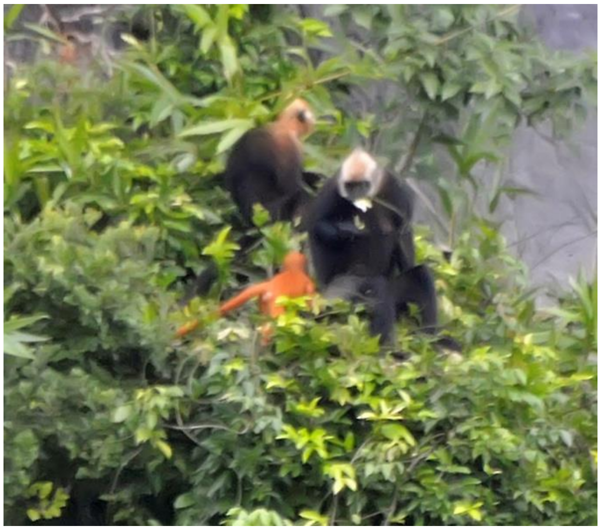

Figure 6.2: An infant male (within two months of birth), Simba, exploring his environment while the adult female just carrying him concentrated on eating. Photo taken September 2014 by R Hendershott

The younger the individual, the more the average number of others in proximity to each age class increased, with significant differences between all five age-group categories (GLM: χ^2=187.716, df=4, p<0.001; Table 14a, Appendix). A newborn was, on average, surrounded by 2.3 other individuals, followed by infants (1.9), young juveniles (1.5), and juveniles (Group A: 1.2, Group B: 0.86, combined: 1.1). Time spent alone (i.e. with no other langurs in proximity) also had a relationship with age (BLM: χ^2=98.688, df=3, p<0.001) (newborns removed from analysis as they were never alone, by definition). Juveniles in both groups spent 60-63% of their time alone (Group A: 60 ± 1.6%, Group B: 63 ± 2.2%), young juveniles 50 ± 3.0%, and infants 26 ± 2.8%, with significant differences between all age classes, except juveniles in the two groups (Table 14b, Appendix). Therefore, time spent alone increased as langurs age.

6.3.2.2 *Dietary Budget and Nursing Behaviour*

Young langurs' diet was made up of leaves (85 ± 3.6%), fruit (6 ± 2.6%), flowers (6 ± 2.5%), and stems (3 ± 1.3%); stems were removed from analysis as young langurs consumed them on only five occasions. There were no significant difference in dietary budgets (nursing excluded) for young langurs (LM: χ^2=5.739, df=4, p=0.219). There were no significant differences in nursing rates (independent of diet) among young langurs (BLM: χ^2=6.087, p=0.107, using a 'deviance' model). Newborns and infants spent 3-4% of their time nursing. Comparatively, young juveniles and juveniles seemed to nurse more (6-8%), but this is undoubtedly due to an observer bias: it was easier to confirm face-to-breast contact in older individuals (who were generally independent) than younger individuals (who spend the majority of their time on another's ventrum). Indeed, there are differences among young age classes in their rates of being on another langur (although this could not be assessed statistically): newborns spent 91 ± 2.2% of their time on another langur, infants 19 ± 1.7%, young juveniles 1 ± 0.4%, and juveniles <1± 0.1%. The only individuals who were rejected from nursing were the oldest young age class—juveniles—who were rejected twice (<1% of scans); no further analysis was possible on rejection rates.

6.3.2.3 *Locomotor and Postural Budget*

Ad libitum notes indicate that Simba was first seen off of any older langur at 14-18 days of age, and Brock at 7-17 days of age, though still keeping a hand on the older langur's thigh, arm, or tail. At 22-26 days of age Simba was first seen to move far enough away from another langur that he was not touching them. It was around this time that Simba was first seen to choose who held him, by moving from one individual to another on his own. Brock, at 24-36 days old, was seen to be left on a rock, and he locomoted independently after the group.

Locomotion for young langurs included quadrupedalism (59 ± 3.1%), climb (27 ± 2.9%), leap (12 ± 1.9%), drop (1 ± 0.8%), and arm swing (<1 ± 0.3%); drop (n=4) and arm swing (n=1) were removed from analyses due to low number of observations in some categories. There was no significant difference in types of locomotion for young langurs (LM: χ^2=2.028, df=4, p=0.731).

Young langurs used all of the postures that older animals used. Their postural budget includes sit (69 ± 1.6%), stand (16 ± 1.3%), cling (8 ± 1.1%), leap (2 ± 0.3%), suspend (2 ± 0.7%), wrestle (1 ± 0.3%), lie prone (1 ± 0.3%), and bipedalism (1 ± 0.3%). Newborns only used cling as 100% of their postural budget, and were therefore removed from further analyses of posture. There was a significant effect of age on postures used for the young age classes (LM: χ^2=331.615, df=14, p<0.001; Figure 6.3). This pattern held for sit, stand, cling, and suspend, but not leap, lie prone, wrestle, or bipedal postures (Table 6.4), although none of the pairwise comparisons for suspend were significant (Table 15d, Appendix). Newborns used only cling postures, as they spent this part of their life always on another langur. Infants sat and stood most commonly, followed by cling. Comparatively, young juveniles used higher rates of sitting and lower rates of standing (Table 15, Appendix); they also used lying prone and wrestling (while playing socially), but this was not used by younger age classes. Juveniles had even higher rates of sitting and lower rates of standing and clinging (Table 15, Appendix). In general sitting was more common in older individuals, while standing and clinging was less common.

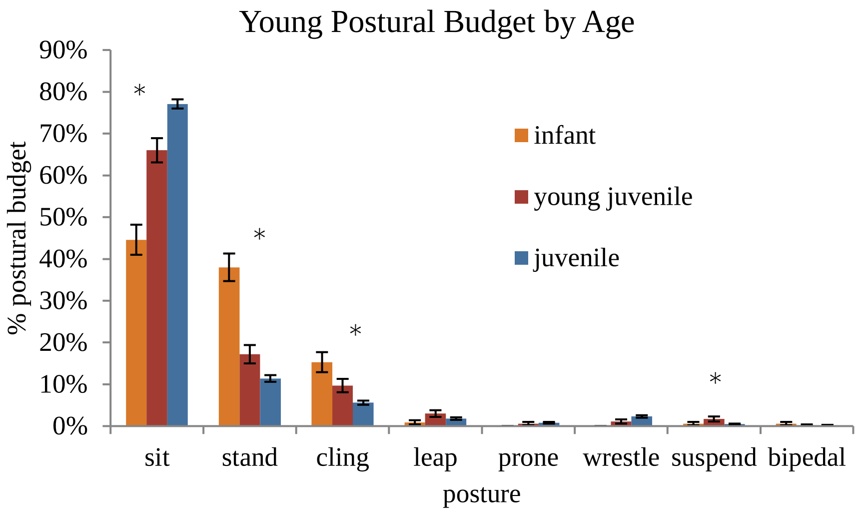

Figure 6.3: Mean daily percent (%) of activity budget ± SE for each posture within each young age class (newborns excluded as they only use cling postures). Postural types that show significant differences between age classes are indicated with an asterisk (*). Test statistics and exact values can be found in Table 6.4, and pairwise comparison p-values can be found in Table 15, Appendix.

Table 6.4: Mean daily percent (%) of activity budget ± SE for each posture within each young age class. All postures assessed with BLM and have df=2. All values rounded to nearest integer. Significant results indicated with asterisk (*). Pairwise comparison p-values can be found in Table 15, Appendix.

	sit[a]	**stand**[a]	**cling**[a]	**leap**	**prone**[b]	**wrestle**[b]	**suspend**	**bipedal**
infant	45 ± 3.6	38 ± 3.3	15 ± 2.4	1 ± 0.5	0 ± 0.0	0 ± 0.0	1 ± 0.4	1 ± 0.4
young juvenile	66 ± 2.9	17 ± 2.2	10 ± 1.6	3 ± 0.8	1 ± 0.4	1 ± 0.5	2 ± 0.6	<1 ± 0.2
juvenile	77 ± 1.1	11 ± 0.8	6 ± 0.5	2 ± 0.3	1 ± 0.2	2 ± 0.3	1 ± 0.1	<1 ± 0.1
p=	<0.001*	<0.001*	<0.001*	0.097			0.032*	0.695
χ^2=	84.699	93.786	30.608	4.659			6.885	0.727
n=	2423	497	238	64	24	63	24	15

[a] assessed with a ‘deviance’ model

[b] unable to statistically analyse due to low number of observations in some categories

6.3.3 Pelage and Physical Ontogeny

I noted the gradual shift of pelage colouration and growth in abdomen size for young Cat Ba langurs (Table 6.5). This information is based on three individuals who changed age classes throughout the study (Jessie, Simba, Brock), one individual who was only observed as a newborn (Jordan), and five individuals who began and ended the study as juveniles (Longbottom, Minerva, Mitty, Tweedledee, and Tweedledum). It is separated by parts of the body (torso/body; exposed skin; head, neck, and shoulders; limbs; and tail) and age-month.

Table 6.5: Pelage colouration and physical characteristics of Cat Ba langurs as they age. The first month includes the newborn and infant age classes, 2-3 month olds are infants, 4 month olds are infants and young juveniles, 5-11 month olds are part of the young juvenile stage, and individuals older than one year are in the juvenile stage. Note: 'n' refers to the number of langurs this description is based on

	torso/body	**exposed skin (face, ears, hands, feet)**	**head, neck, shoulders**	**limbs (arms, legs)**	**tail**
born (n=3) Figure 6.4a	bright orange	pink-gray; small bald spot on forehead			
1 month (n=3) Figure 6.4b	orange coat begins to fade slightly; extremely skinny		duller orange than rest of torso; dark-tipped hairs where crest develops		
2 months (n=3) Figures 6.4c and 6.4d	becoming more pale (still fairly bright)	darkens	crest darkens	arms and legs are a more pale orange than torso	
3 months (n=2) Figures 6.4e and 6.4f		dark gray		middle of arm is duller orange than rest of the arm with some dark hairs	small black spot/stripe above the tail; underneath the tail is more dark and gray than the top
4 months (n=2) Figure 6.4g	lighter shade of orange with dark gray/black undercoat reaching from shoulder blades down the back; gray saddle becomes visible	black	beginnings of moustache	arms and legs lighter colour than torso	basal third of tail is dark/black; rest of tail is orange
5 months (n=2)	back is dark; definite saddle; orange spot between shoulder blades; abdomen is still skinny			arms and legs are orange; upper legs to knees are darker than lower legs	bottom 2/3 of tail are still orange
6-7 months (n=1) Figure 6.4h	dark back with slight orange tinge; orange spot between shoulder blade remains; abdomen begins to grow		shoulders and neck are pale orange	blanched thigh patches on females; lower arms and upper legs are dark (from knee to ankle is dull	top 1/3-2/3 of tail is gray; underside continues to darken

				orange, from ankle down is paler)	
8-9 months (n=1) Figure 6.4i		black	back of the neck is lighter orange than top of the head	bottom of forearms are darker while the tops are more orange	bottom of tail lightens
9-10 months (n=1)	lower back almost black			arms get darker	dark patches of hair on tip of tail
10-11 months (n=1)	upper back still lighter than lower back			most of arms and legs are dark (except for orange patches on top of wrists and feet)	tail has some light patches in the lower half
12-36 months (n=5) Figure 6.4j	darker but still more faded orange, and the black is more orange-brown, than adults; light gray saddle; orange spot between shoulder blades; front of body is mostly orange; fully distended abdomen	not as leathery looking as adults	crest with dark tip visible; head is lighter orange/yellow than the rest of the body, extending down neck, chest, shoulders	arms are mostly black except back of upper arms is lighter and more orange than the rest of the body; shoulder to outside elbows being orange/brown (upper shoulders are mostly light orange with a 'V' of darker hairs crossing laterally in profile); orange spots on forearms and tops of hands; lower half of leg is pale orange and/or dark with orange spots on top of feet	dark brown/gray basal area, rest of tail is gray, dull yellow, orange; underside is black/gray


(c)


(d)


(e)


(f)


(g)


(h)


(i) (j)

Figure 6.4: Pelage development from the newborn to juvenile age classes. (a) Newborn male (Simba) within a week of birth. Note: pink hands, face, and ears. Photo taken August 2014. (b) Infant male (Simba), aged 24-27 days, exploring his environment. This was the first time Simba was observed off of another langur while staying close to an adult. Note: slightly duller coat colour (especially on the head) and the skinny abdomen. Photo taken August 2014 by Kieu Tuyet Nga. (c) Orange infant female (Jessie) at one to two months old (seen here clinging to an adult female). Note: darkening of torso and face and ears. Photo taken March 2014. (d) Infant male (Brock) at one to two months. Note: gray face and hands and increased independence. Photo taken December 2014. (e) Infant male (Brock) within three months of birth. Note: darkening coat colouration and lack of thigh patches (which allows for sexing). Photo taken January 2015. (f) Infant male (Simba) at three months old. Note: dark hands and face and the darkening at the bottom of the base of the tail. Photo taken November 2014. (g) Young juvenile male (Simba) within four months of birth. Note: dark undercoat on torso and orange limbs, plus darkening at base of tail. Photo taken December 2014. (h) Young juvenile female (Jessie) within six to seven months of birth. Note: obvious thigh patches and orange tinge to dark back, arms are darker on lower half, legs are lighter on lower half, tail darker than when younger. Photo taken August 2014. (i) Young juvenile female (Jessie) at 9-10 months old. Note: large abdomen and dark tip of the tail, torso and parts of limbs are almost black with some orange spots. Photo taken November 2014. (j) The juvenile male in Group B (Longbottom), at least one year old. Note: orange spots on forearms, wrists, knees, and tops of feet, while rest of body is a lighter version of adult colouration. Abdomen is fully distended and the moustache is developed. Photo taken January 2015. All photos taken by R Hendershott unless otherwise noted.

6.4 Discussion

This chapter aims to document a number of factors associated with young development, including birth patterns, as well as behavioural, dietary, and locomotor independence throughout young age classes. This is done by noting how often each age class uses each behaviour and the amount of time spent alone or in proximity. Finally, my goal is to relate these behavioural developments to changes in the natal coat. In this way, brief observations of young animals can be informative of their level of dependence, which can, in turn, be related to infanticidal and other mortality risks. This discussion will focus on age classes, and specific behavioural and pelage changes that occur within each age class (as contrasted with the results, which focused on activity, dietary, and locomotor/postural budgets and pelage changes separately). This is done in order to link specific threats and vulnerabilities with coat colouration and development.

6.4.1 Births

The four Cat Ba langur individuals born just before or during the study period have a birth date narrowed down to one or two months. Two (Jordan and Jessie) were in the dry winter season, one (Simba) in the wet summer season, and one was on the border between seasons (Brock) (Table 6.2). Given such a small sample size, no clear pattern of a birth season is evident. In 47 birth records from the Cat Ba Langur Conservation Project starting in 2007, births do seem to occur throughout the year, although 26% happen in February, and they are more often in the early dry and early wet seasons (Leonard et al. 2016a). Of 20 births recorded for François' langurs, spread out across the year, 55% occurred in February and March (Hu 2007). Similarly, white-headed langurs tend to conceive when food is abundant, in the rainy seasons of May through September, resulting in a birth peak in the dry and cold months of November to March (Jin et al. 2009a). As it is during the rainy season that females are able to increase the percent of young leaves in their diets, it seems that they are able to build up the necessary resources to support a pregnancy (Jin et al. 2009a); additionally, it means that females are starting to lactate in early spring, when young leaves again become widely available (Hu 2007). Capped langurs (*Trachypithecus pileatus*) mate and have high rates of female solicitations in the dry and cool winters, with birth peaks from December through April (over half of all births being in February and March) (Sommer et al. 1992; Kumar et al. 2005). This reproductive pattern is related to available foods, although any fluctuations or disturbances in seasons and habitat can affect the mating and birth patterns and breeding success (Solanki et al. 2007). For example, Hanuman langurs also have a tendency for birth peaks, but they are able to breed throughout the year (Blaffer Hrdy 1977), possibly because this species in India is often provisioned.

6.4.2 Behaviour and Pelage

This study agrees with previous observations on other limestone langurs that individuals are born bright orange, start to lose the flamboyant colouration within a few months, and have mostly achieved adult colouration by one year of age. The gradual shift from an orange natal coat to adult colouration has been documented for other Asian colobines (Horwich 1974; Blaffer Hrdy 1977; Hu 2007; Agmen 2014). In general the progression of coat colouration is similar among the species (although timing may differ), and tends to coincide with increased independence (Jay 1963; Blaffer Hrdy 1976; Stanford 1991a; Treves 1997; Hu 2007; Schrudde et al. 2010). Colouration may, however, be affected by available resources/habitat quality (Borries et al. 2008) or infanticide risk (Bădescu et al. 2016), and not every individual will follow the same timeline for maturation (Altmann et al. 1981). Typically, however, the colour shift is completed by six months of age (Treves 1997; Borries et al. 2008). Documenting coat transitions is a noninvasive means of assessing development (Treves 1997).

The behaviours of young individuals are dictated by their inexperience, vulnerability, and dependence. Young animals must learn how to forage and locomote appropriately without putting themselves at risk. Risks come in the form of malnutrition/starvation, mistreatement, predation, and infanticide (Altman et al. 1970; Blaffer Hrdy 1979; Struhsaker and Leland 1987; Janson and van Schaik 1993; Borries et al. 1999; Gould et al. 1999; Strier 2003; Bolter and Zihlman 2007; Shelmidine et al. 2013). The first stage of life is a time of high vulnerability for primates; commonly only a third to half of primates survive this stage (Altmann et al. 1977; Blaffer Hrdy 1977; Sussman 1991; Decker 1994; Debyser 1995; Alberts and Altmann 2003; Bolter and Zihlman 2007; Teichroeb and Sicotte 2008). Roughly a third of captive silvered leaf monkey (*Trachypithecus cristatus*) (Shelmidine et al. 2013), a third of Hanuman langur (Rajpurohit and Sommer 1991), 22% of golden snub-nosed monkey (*Rhinopithecus roxellana*) (Qi et al. 2008) and 43-48% of Thomas langur (*Presbytis thomasi)* (Wich et al. 2007) infants die in their first year. Sixteen percent of white-headed langurs do not live beyond their 20th month (Jin et al. 2009a). In a rough estimate of infant mortality between 2007-2016, 11% of Cat Ba langur infants did not survive, while there is an average of 3.2 surviving young per year between 2001-2016 (Leonard et al. 2016a). This may be due to Cat Ba langurs population growth not being dependent on density (as there are too few langurs for crowding to be an issue, as it may be in other species), although I suspect it has more to do with inconsistent censusing of the Cat Ba langur population. Since birth records are patchy and only limited censuses have been conducted, it is likely that births (and then subsequent deaths) were overlooked.

Young primates are extremely susceptible to a loss of resources and environmental conditions, partially due to poorer maternal body condition resulting in poorer lactational performance (Altmann and Alberts 2005), and partially due to their inefficient foraging (Janson and van Schaik 1993), combined with their higher nutritional requirements per kilogram compared to adults (Martorell 1999). Restriction of diet during gestation and lactation in mammals leads to lower birth weights, delayed growth, higher rates of mortality and susceptibility to disease and infections, smaller adult size, and retarded cognitive development and competence (Altman et al. 1970; Martorell 1999; Keenan et al. 2013). It has consistently been shown that captive animals, and wild animals with access to provisioned foods, grow faster and mature earlier, with shorter interbirth intervals, and sexual dimorphism that is obvious at a younger age, than those without access to high quality resources (Altmann et al. 1977; Harley 1985; Altmann and Alberts 1987; Newton 1987; Sommer et al. 1992; Mori et al. 1997; Altmann and Alberts 2005). This indicates that limited resources and increased ecological pressures limit growth, and suggests that young primates suffer greatly from environmental disturbance that limits food supply. For example, ring-tailed lemur (*Lemur catta*) infants experiencing a prolonged drought had a mortality rate that rose from 48% (12 months pre-drought) to 80% (six months after the drought) (Gould et al. 1999). Young juvenile grivet monkeys (*Chlorocebus aethiops*) are underrepresented in groups after habitat disturbance resulted in fewer food resources (Struhsaker 1973). Black howler monkeys (*Alouatta pigra*) that lost available food resources due to a hurricane had a positive correlation between infant survival and fruit availability in the following years, presumably due to an improvement in maternal body condition (Behie and Pavelka 2015).

Overall, infant and young primates are at high risk of predation due to their lack of vigilance and awareness about predators, poor motor skills and strength, and small body size, all of which can be behaviourally combatted by avoiding areas of high predation risk (i.e. staying in the middle of the group) (Janson and van Schaik 1993). Additionally, their play groups can take them away from adults, making them easier targets for predators

(Hausfater 1976). Although it is difficult for researchers to directly observe predation (Miller and Treves 2007), there are a few first-hand observations (Sampaio and Ferrari 2005; Matsuda et al. 2008b; Borries et al. 2014), and there are studies that assess predation from the predator's perspective, primarily via fecal analysis or looking at raptor nest refuse (Hausfater 1976; Struhsaker and Leakey 1990; Stanford et al. 1994; Mitani et al. 2001; Sanders et al. 2003; Surbeck et al. 2009). The only observed case of predation by tufted capuchin monkeys (*Cebus apella*) on another primate was on an infant titi monkey (*Plecturocebus moloch*) (Sampaio and Ferrari 2005). In two direct observations of predation on proboscis monkeys (*Nasalis larvatus*) by clouded leopards (*Neofelis diardi*), one was a juvenile and one was an infant (although the authors conclude that all age-sex classes may be at risk of predation) (Matsuda et al. 2008b). Adult male yellow baboons (*Papio cynocephalus*) stalk and prey on specifically juvenile vervet monkeys (*Cercopithecus pygerythrus*) (Hausfater 1976). Juvenile Ugandan red colobus (*Piliocolobus tephrosceles*) face an increased risk of predation over other age classes (Struhsaker and Leakey 1990; Stanford et al. 1994; Stanford 2002), possibly due to their independence without fully formed adult skills. However, this pattern is not always consistent across primates (Struhsaker and Leakey 1990; Mitani et al. 2001; Sanders et al. 2003). Overall, there is evidence to suggest that young animals are at more risk of predation than older animals, as they are taken at 1.3-17.2x the rate of adult group members (Janson and van Schaik 1993). The low rates of consecutively reusing sleeping sites may be a method for reducing predation or infanticide risk of vulnerable group members (Section 4.4.3, Chapter 4).

In addition to general vulnerability due to dependence/immobility, newborn and unweaned primates living in unimale-multifemale groups may be targeted by infanticidal males; 71% of infant ursine colobus (*Colobus vellerosus*) deaths are due to suspected infanticide (Teichroeb and Sicotte 2008). This is seen in many species of primates (Fossey 1984; Moos et al. 1985; Struhsaker and Leland 1987; Harcourt and Stewart 2007; Beehner and Bergman 2008; Yamagiwa et al. 2009), and langurs in particular (Blaffer Hrdy 1977; Wolf and Fleagle 1977; Newton 1986; Newton 1987; Ross 1993; Newton 1994; Borries 1997; Moore et al. 2010). Specifically, male takeover and/or infanticide is documented in white-headed langurs (Zhao et al. 2011b; Yin et al. 2013), and François' langurs (Hu 2007), the closest relatives to Cat Ba langurs (Nadler et al. 2003; Roos 2003). This suggests that as long as a Cat Ba langur is nursing, it is at risk of being killed as a reproductive tactic by a nonpaternal male (Section 1.6.6, Chapter 1).

This period of high vulnerability to infanticide coincides with bright natal coat and high interest and caretaking by adult females (Horwich 1974; Blaffer Hrdy 1976; Alley 1980; Stanford 1991a; Teichroeb and Sicotte 2008; Kumar and Solanki 2014; Jin et al. 2015). Overall, it is unclear what the relationship is between natal coat colouration, infanticide risk, and attraction to young by older group members (Blaffer Hrdy 1976; Ross and Regan 2000). There is evidence that mothers may enhance investment in their infant, resulting in a faster loss of the natal coat, if they are at higher risk of infanticide, suggesting that there is an effect of infanticide on coat colouration (Bădescu et al. 2016). It does seem that bright orange natal coats can mask paternity and signal that infants will be highly protected due to the intense interest at this stage by adult females (Treves 1997).

Among Asian colobines, older group members (especially females) are highly interested in being around and handling younger group members (Blaffer Hrdy 1977; Hu 2007; Jay 1963; Jin et al. 2015; Kumar and Solanki 2014; Kumar et al. 2005; Stanford 1991a; Stanford 1992; Yao et al. 2012; Xi et al. 2008). This is safe only for species with a more egalitarian social structure, as large rank differences would make it dangerous for low-ranking individuals to risk their infant being mistreated when held by higher-ranking individuals; thus, transfers and handling by nonmothers is more common among colobines than despotic cercopithecines (Maestripieri 1994; McKenna 1979; Thierry 2007). The purpose, or benefits, of infant handling by nonmothers has been extensively explored (Blaffer Hrdy 1976; Dolhinow and DeMay 1982; Maestripieri 1994; Newton and Dunbar 1994; Paul and Kuester 1996; Silk 1980; Silk 1999), and will not be the focus of this discussion. As young langurs begin to lose their natal coat and gain independence, there is decreased interest by group members (Blaffer Hrdy 1976; Hu 2007; Jay 1963; Stanford 1991a; Treves 1997; Ross and Regan 2000).

The lack of differences across young ages in diet and locomotion types is probably due to a combination of broad food categories/locomotion types and a limited number of scans in which age and food item/locomotion type could be ascertained. In contrast to the expectation that time spent nursing decreases as individuals age and start adding in solid foods to their diet (e.g. Kumar and Solanki 2014), there is a trend for higher rates of nursing for young juvenile and juvenile Cat Ba langurs than for newborn or infant langurs in this study. Rather than reflecting a true biological rate of nursing, I suspect this is due to observer bias: I was unable to confirm face-to-breast contact (my definition of nursing) when young, clinging langurs were permanently on an adult female's ventrum (often the adult female would hunch over the small langur, limiting visibility). It was more obvious, however, when active, more independent langurs would bound over to an adult female and start nursing in the midst of playing, foraging, etc. Therefore, the higher rate of nursing in the two older young age classes probably reflects the ease of confirming nursing in those age classes compared to confirming face-to-breast contact for age classes that spend most of their day on another's ventrum (whether they are suckling or not). This is a common problem for researchers (Zhao et al. 2008; Agmen 2014); hence the use of clinging to a ventrum as a proxy for suckling in white-headed langurs, who spend less time on another langur's ventrum as they age (Zhao et al. 2008).

6.4.2.1 *Newborns*

Cat Ba langurs (Figure 2.9, Chapter 2; Figure 6.4a), as with other limestone langurs (Hu 2007; Agmen 2014), are born bright orange or golden with gray-pink or gray-white exposed skin. It is common for langur infants to cling to the mother's ventrum and move very little, completely dependent, in their first week of life (Jay 1963; Blaffer Hrdy 1977; Hu 2007; Zhao et al. 2008). Accordingly, when Cat Ba langurs are first born and bright orange, they cling to others inactively, with very little social interaction beyond passively being groomed. When Simba was first born, the adult female carrying him would walk tripedally, holding him to her ventrum with one hand. This is in accordance with Hanuman and capped langur newborns who are supported at first, and then by 7-10 days old are adequately able to hold/cling to another langur, without additional support (Jay 1963; Blaffer Hrdy 1977; Kumar et al. 2005). Adult females providing extra clinging support for newborns was not observed for the other two Cat Ba langur individuals born during the study, possibly because they were older when first observed. Newborn Cat Ba langurs never put any food items in their mouths beyond nursing. They are always carried by someone else, and are never found alone. This is similar to François' langurs, where those less than a month old are never left alone (Hu 2007). As in red-shanked doucs (Yeong et al. 2010), capped (Stanford 1991a; Kumar and Solanki 2014) and white-headed (Zhao et al. 2008) langurs, the rate of being next to someone else declines as individuals get older.

The only ‘other’ behaviour Cat Ba langur newborns use is struggling against being held (Hendershott unpublished data). The majority of spectacled langur struggling against being held occurs from days 5-45, which corresponds to the high maternal care period (Horwich 1974). Notably, there was one obvious instance of ‘maternal punishment’ (Blaffer Hrdy 1977) observed in Group A, not captured in the scans. This was in August 2014, when Simba was still a newborn. He was crying incessantly while struggling to get away; the adult female holding him shook him, bit him gently, barked, then let him go back to clinging. His crying did not stop, and she repeated the shaking, biting and barking multiple times; this lasted 17 minutes. Afterwards Simba did not seem injured.

It is at this newborn stage, which coincides with the flamboyant natal coat, that individuals are most attractive to other group members (Figure 6.5), and most at risk of infanticide (Blaffer Hrdy 1977; Hu 2007; Jay 1963; Jin et al. 2015; Kumar and Solanki 2014; Kumar et al. 2005; Stanford 1991a; Stanford 1992; Yao et al. 2012; Xi et al. 2008). Therefore, beyond vulnerabilities to poor resource availability, newborn Cat Ba langurs are both highly at risk of infanticide, and highly protected by group members due to this risk.

Figure 6.5: A newborn (Simba at 4-9 days old) acts as a social attractant for adult females in the group. Photo taken Aug 2014 by R Hendershott

6.4.2.2 *Infants*

In both this study (Figure 6.4b), and among other langurs (Blaffer Hrdy 1977; Hu 2007), infants start changing colouration within the first month of life. As with other limestone langurs (Hu 2007; Agmen 2014), in the first few months the exposed skin areas darken, dark hairs start to show up on the body, and the beginnings of the mustache and crest start to develop (Figures 6.4c,d). In Cat Ba langur infants the tail does not become completely black until after a year of age, and does not start changing until the third month (Table 6.5; Figures 6.4e,f). This is later than François' langur infants whose tail is three-quarters blackish in the first month (Hu 2007), or Delacour's langur (*Trachypithecus delacouri*) infant whose tail is mostly black by two weeks of age (Agmen 2014). Note, however, that the Delacour's langurs studied were in captivity (Agmen 2014), and captivity is known to increase rates of maturation (Altmann et al. 1981). As with Cat Ba langurs, most of the coat of the Delacour's langur infant became a darker orange, while the head and abdomen did not darken as much at two months old, but started to by three months (Agmen 2014). The face is black by two to four months of age (Blaffer Hrdy 1977; Hu 2007; Agmen 2014; Figures 6.4e-g).

Cat Ba langur infants are more independent and active than newborns, spending more time away from others, and are starting to explore, forage, and locomote on their own (Figure 6.1). Similarly, François' langur infants start to explore and play but stay close to their mother (Hu 2007). Delacour's langurs are first seen to move independently around two weeks of age (Agmen 2014) which is the border of the Cat Ba langur newborn and infant period. Exploration and interest in the surrounding environment shows up at around 1-5 weeks of age in Asian colobines (Yeong et al. 2010; Kumar and Solanki 2014); white-headed langur infants aged 3-6 weeks show interest in other group members (especially other infants) (Zhao et al. 2008) while month old François' langurs start to engage with other young group members (Hu 2007). Cat Ba langur infants start to play (specifically locomotor-rotational play; Hendershott unpublished data), which may help in practicing coordination (Wilson and Kleiman 1974).

The 74% rate of being in proximity for infant Cat Ba langurs is similar to the 75% rate for capped langurs' (Kumar and Solanki 2014) and the 60-100% rate for red-shanked doucs (Yeong et al. 2010) clinging to someone else in their first three months. Group members seem less interested in handling infant (than newborn) Cat Ba langurs, and infants are used less often for transfers (than newborns) (Hendershott unpublished data). This reflects the fact that colobines have decreased interest in handling older young (Kumar and Solanki 2014; Jin et al. 2015). Infants' decreased role as an attractant for other group members is reflected in their lower rate of number of others in proximity compared to newborns. The Cat Ba langur infant period roughly corresponds to the spectacled langurs' individualisation and socialisation period (Horwich 1974).

Infant Cat Ba langurs start to become independent by reducing their time on older langurs, increasing standing rates (Figure 6.3), and starting to test their ability to move on their own, which matches patterns of other Asian colobines (Zhao et al. 2008; Yeong et al. 2010). Young white-headed langurs are carried less, and move more independently, as they age (Zhao et al. 2008). Despite Cat Ba infants locomoting on their own, they are still usually carried between long distances (>20 metres) or precarious locations; even when off another langur, they rarely get very far from adult females. Similarly, one-two month old François' langur infants are still mostly carried, although they start to explore their use of limbs (Hu 2007). This locomotion is extremely uncoordinated and clumsy, a common developmental stage (Dunbar and Badam 1998; Workman and Covert 2005). As individuals mature they gain locomotor skills, possibly as a result of changing musculoskeletal dimensions and balancing (Turnquist and Wells 1994), and clearly become more confident in their movements. However, they also adopt more passive postures (such as sitting) than their younger counterparts (who used high rates of standing and clinging) (Figure 6.3).

I found that infants started to test foods, but relied predominantly on nursing for their nutrition. Similarly, month old François' (Hu 2007) and Delacour's (Agmen 2014) langur infants, 1-2 month old white-headed langurs (Tan 1985), and 2-3 month old Hanuman langur (Jay 1963) and red-shanked douc (Yeong et al. 2010) infants begin putting solid foods in their mouth. In spectacled langurs, four to six teeth erupt by about three weeks of age (Horwich 1974), which coincides with the start of infants starting to test solid foods.

Cat Ba langur infants seem to pay close attention to what their mothers forage on, trying out food items they saw them eat. Overall, primate infants learn what foods to eat through both trial and error (small taste tests teach them palatability and toxicity), and watching their mothers and group mates (Janson and van Schaik 1993). As Cat Ba langurs age, they tend to eat more often on their own. The rate of foraging on solid foods increases steadily for capped (Stanford 1991a) and François' (Hu 2007) langurs and there is a positive linear relationship between age and feeding time in white-headed langurs (Zhao et al. 2008). In this study, young Cat Ba langurs follow a similar pattern, with foraging rates increasing in young juveniles and juveniles (Figure 6.1).

Infant Cat Ba langurs are highly dependent on adults, but they are starting to gain independence. At the same time, their natal coat is dulling/being lost and other group members are less interested in handling them. This puts infant Cat Ba langurs at a heightened risk of infanticide and predation, as they start to explore but are still highly uncoordinated; they wander away from protective group individuals, and those individuals are less attracted to them. Additionally, trauma is more likely as infants wander away from protective adults (Shelmidine et al. 2013). This means that they face a higher risk of being targeted by predators or strange males (particularly due to their reliance on nursing) and are at higher risk of accidental trauma.

6.4.2.3 *Young Juveniles*

Around four months of age Cat Ba langurs change from being infants to being young juveniles, during which time their extremities and torso continue to darken (Figure 6.4g). Months 4-5 are similarly marked by drastic changes in François' langurs, with individuals turning almost completely back within five days (from 125-130 days), although the head and shoulders still retain some yellow fur (Hu 2007). For Hanuman langurs, adult colouration is reached by 5-6 months of age (Blaffer Hrdy 1977). Months 6-12 have continual darkening of colouration in Cat Ba langurs, female thigh patches become visible (Figure 6.4h), and the characteristic leaf-eaters' abdomen grows (Figure 6.4i).

I found that young juveniles spend even more time foraging, and moving around on their own (Figure 6.1), although they are still carried occasionally across dangerous areas (Figure 6.6), as reported for other limestone langurs (Hu 2007). Although they are locomoting more independently, young juveniles start to sit more than infants, and stand less (Figure 6.3), reflecting the trend that animals become more sedentary and use more passive postures as they age (Prates and Bicca-Marques 2008; Eakins 2010). Young juveniles no longer 'explore' their environment on shaky limbs (as this seems limited to only the first months of venturing off of another langur), but are more confident in their movements, which are practiced during play. The Cat Ba langur young juvenile period roughly corresponds to mid-way through the spectacled langurs' socialisation period (Horwich 1974). Young juvenile Cat Ba langurs spend almost twice the amount of time alone as infants. Similarly, in capped langurs, individuals 4-12 months of age spend roughly 30-63% of their time in proximity or contact with others, which is a dramatic drop from the 97-80% they are next to someone as a newborn to three month old (Stanford 1991a); by one year individuals are spending 80% of their time away from mothers (Kumar and Solanki 2014).

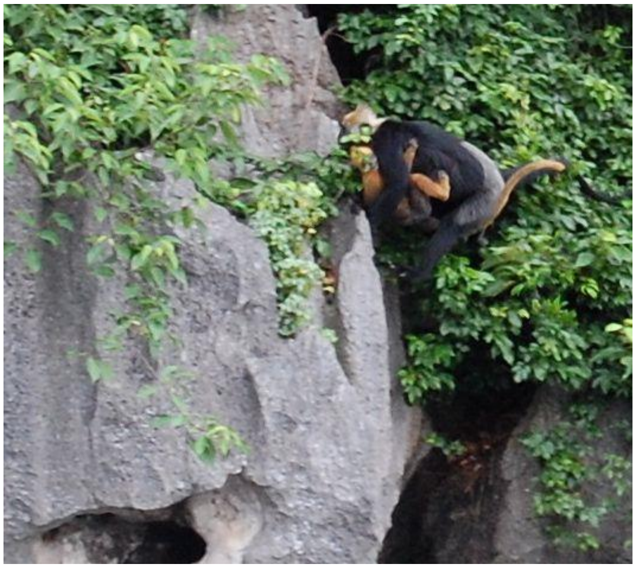

Figure 6.6: A young juvenile being carried across a precarious gap. Photo taken Aug 2013 by R Hendershott

The young juvenile stage is the point when the most dramatic pelage changes are occurring for Cat Ba langurs. They are not as reliant on nursing due to their increased exploration of appropriate food items, and they are much more mobile and coordinated than infants. Thus, young juveniles are presumably at less risk of infanticide [as the effects of lactational amenorrhea are reduced (Elias et al. 1986; McNeilly et al. 1994), which is proposed to be a key factor in infanticide (Blaffer Hrdy 1979)], but possibly still at high risk of predation, due to their independence and reduction in proximity to others, combined with inexperience (Janson and van Schaik 1993). Additionally, no transfers occur with young juveniles (Hendershott unpublished data), indicating that they are past the stage that group members are attracted to.

6.4.2.4 *Juveniles*

After one year old, the species-typical moustache, saddle, and crest has developed in Cat Ba (Table 6.5) and François' (Hu 2007) langurs, while their bodies continue to darken (Figure 6.4j). Although colouration is similar to adults, there is still some orange left on the torso, neck and shoulders, and extremities (Hu 2007; Figure 6.4j). As these juveniles continue to age they grow in body size. Subadults have fully descended testes (Table 2.3, Chapter 2). In Hanuman langurs, after the juvenile period, in the transition to subadulthood, male testes grow larger (Blaffer Hrdy 1977). By about four years of age, the testes have descended and canine teeth have erupted (Blaffer Hrdy 1977). Individuals reach adult size by about year five (Brandon-Jones 1989).

Juvenile Cat Ba langurs are more independent than young juveniles, spending more time foraging (though not necessarily weaned), and socialising more (Figure 6.1). They locomote less and are never carried by others. They use less ‘other’ behaviours, primarily due to the shift from asocial play to social play (Hendershott unpublished data). A higher rate of activity and locomotion in younger juveniles compared to older juveniles is also seen in silvered leaf monkeys (Eakins 2010) or between infants and juveniles in François’ langurs (Hu 2007).

The only cases of denied nipple access that I observed occurred for juveniles, who, with predicted ages of 12-36 months, were old enough to be weaned (but might still nurse for comfort). White-headed (Zhao et al. 2008), François’ (Hu 2007) and capped (Kumar and Solanki 2014) langur mothers begin rejecting their infants around 2-5 months, but they maintain a guarding behaviour over them. Rejection in white-headed langurs declines between 6-17 months, and then rises sharply at 18-21 months (Zhao et al. 2008). Young François’ langurs are weaning at 12-14 months (Hu 2007), while white-headed langur young are fully weaned by 19-21 months of age (Zhao et al. 2008). In red-shanked douc young this ranges from 4-11 months, and by 15-18 months, the two red-shanked douc young for which there are records had been completely weaned (Yeong et al. 2010). For Hanuman langurs this is 6-20 months (Blaffer Hrdy 1977), or, in poor quality environments, between 20-30 months (Borries et al. 2001).

Cat Ba langur juveniles are also more passive in their postures, with higher rates of sitting, and lower rates of standing and clinging than young juveniles (Figure 6.3). Juvenile Cat Ba langurs (over a year old) are sure-footed when navigating the petrous habitat, and are never carried. This is similar to Hanuman (Dunbar and Badam 1998), François’ (Hu 2007), and white-headed (Huang and Li 2005) langurs’ locomotor abilities at this stage. Six month old François’ langurs spend over half of their locomotor time moving independently, and by 11-12 months they are carried only 2% of locomotor time (Hu 2007). At about 17-21 months white-headed langurs are no longer carried by their mothers (Zhao et al. 2008). It appears that, although juveniles can locomote on their own, the limestone karst environment requires extensive locomotor practice, as animals over a year old can still have difficulties navigating the vertical, pointed rockfaces.

The increased time foraging among Cat Ba langur juveniles (Figure 6.1) was expected as small bodied, weaned juveniles spend a significant portion of their day foraging (Janson and van Schaik 1993), in order to sustain the skeletal, muscular, brain, and fat growth that is occurring as their body transitions to the adult form (Bolter and Zihlman 2007). Due to their highly energetic physiological demands, juveniles are especially susceptible to starvation if resources are hard to come by (Janson and van Schaik 1993; Rothman et al. 2008); indeed, juvenile white-headed langurs suffer the greatest mortality of all age classes (Burton et al. 1995). Juveniles have high rates of being found alone, and the lowest average number of others in proximity of any young age classes.

Juvenile Cat Ba langurs are past the stage of relying on nursing, thus making them relatively free from risk of infanticide. Juvenile primates are generally able to travel and forage on their own (although they retain close relationships with their mother and siblings), meaning that they must compete with other langurs for resources (Bolter and Zihlman 2007). As a result, when resources are limited, as many as half of juveniles will not survive (Bolter and Zihlman 2007). Juvenile Cat Ba langurs no longer rely on their mothers for nutrition or locomotion, and instead must establish their social role within the group. This means that they are particularly susceptible to a loss of resources, as seen seasonally (van Schaik and Pfannes 2005; Li and Rogers 2006; Zhou et al. 2009a; Workman 2010a) and in degraded habitats (Johns 1986; Arroyo-Rodríguez and Mandujano 2006; Wong et al. 2006; Dunn et al. 2010). Therefore, particular attention should be paid to monitoring juvenile mortality, as they may be the first indicators of a reduction in resources.

6.5 Summary

This chapter assesses the development of young Cat Ba langurs by looking at birth patterns, activity budgets, proximity, diet and nursing behaviours, locomotor and postural budgets, and pelage shifts; this is put into context by noting the threats which each age class (newborn, infant, young juvenile, and juvenile) faces and the implications for survivability.

Using instantaneous scan samples at 10 minute intervals, the data cover 180 days in the field, or 549 hours in visual contact with langurs.

Cat Ba langurs are born throughout the year. Newborns are bright orange and are highly attractive to group members. As they age and gain independence, infants are less attractive for transfers, but spend more time away from others, testing foods, their locomotive skills and play behaviours. Their coat and skin begins to darken, and the beginnings of species-specific characteristics emerge. Young juveniles are yet still more independent, spend more time alone, and start building up social relationships, playing socially more often. Young juveniles' coats are darker than infants', female thigh patches become visible, and their abdomen grows. Juveniles are the most independent of the young age classes, spending more time foraging and socialising and less time playing; they are able to easily move around the steep rockface. Juveniles still nurse, and were the only age class observed to be rejected. Their rate of locomotion decreases compared to those of younger individuals. Juveniles' coats are similar to that of adults, although some orange remains on the limbs, back, and shoulders. Newborns and infants are at the highest risk of infanticide. They are also at risk of predation due to their small body size, and are particularly vulnerable to the body state of their mother. Young juveniles and juveniles are also at risk of predation, but more so because of their playful, clumsy nature without a full repertoire of adult vigilance and attention. Juveniles, due to being weaned and competition with older group members, are most susceptible to a drop in resource availability, making them the age class that can be most indicative of a reduction in foods from the habitat.

It is my goal that this information is helpful in assessing how individuals develop, and by concentrating on pelage shifts it should make it easier for inexperienced rangers and surveyors to estimate births and ages. This will aid in population viability analyses and documentation of age-specific mortality and censusing. Additionally, the pace of development may be indicative of habitat quality or infanticide risk (Section 7.3.3, Chapter 7).

Chapter 7: Implications for Conservation

7.1 Introduction

In previous chapters I reported on the activity and dietary patterns (Chapter 3), home range size and habitat use (Chapter 4), social behaviours (Chapter 5) and ontogeny (Chapter 6) of Cat Ba langurs (*Trachypithecus poliocephalus*). Given the lack of data available on this species, this information can be used as a baseline of how these animals behave, interact with one another, and utilise their environment. Thus, through comparison with this data researchers can document how the langurs are being affected by on-going habitat loss, degradation, and fragmentation. This study cannot directly address conservation issues, as that was not the focus or aim, although the results from this first long-term behavioural study on Cat Ba langurs can be used to make inferences about conservation policy on Cat Ba Island.

Cat Ba langurs are Critically Endangered (Bleisch et al. 2008a) and have been on the Top 25 Most Endangered Primates list since 2000 (Leonard et al. 2016b) due to continuing threats such as hunting and habitat loss (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2010). Around the beginning of the twentieth century, there were an estimated 2,400-2,700 Cat Ba langurs on the island (Nadler and Ha Thang Long 2000), although when only optimal habitat is considered this number drops to 1,545 (Phan Duy Thuc et al. 2014); locals report that Cat Ba and some of the close islands used to be densely covered in langurs (Mittermeier et al. 2009). By the beginning of this century, there were possibly as low as 40 or as many as 135 langurs left on the island, and the population has generally hovered at less than 70 since that time (Table 7.1). There has been a massive decline in the last year (Leonard et al. 2016a). Group size has declined as the population has dwindled (Section 1.6.7, Chapter 1).

Table 7.1: Historical population numbers for Cat Ba langurs. A dash (-) signifies 'high' and 'low' counts of individuals.

	# of individuals	**# of groups**	source
early 20th century	2400-2700/ 'thousands of langurs'		(Nadler and Ha Thang Long 2000)
1999-2000	104-135	21-22	(Nadler and Ha Thang Long 2000)
	40-53 (30-40 of which were assumed to be adults)		(Nadler et al. 2003; Schrudde et al. 2010; Leonard et al. 2016a)
	40-60		(Lees et al. 2014)
2001-2003	59-63 (50 are adults)	7	(Stenke and Chu Xuan Canh 2004)
2003	40		(Leonard 2014)
2004	59		(Stenke and Chu Xuan Canh 2004)
2006	64	11	(Nadler et al. 2007)
2010	48-53		(Leonard 2014)
	60-70	11	(Schrudde et al. 2010)
2013	50-56	12	(Phan Duy Thuc et al. 2014; Leonard et al. 2016a)
2014	63 (58 in the wild, 5 in captivity)	12	(Lees et al. 2014)
	61		(Leonard 2014)
2015	64-70		(Leonard et al. 2016a)
2016	51-54		(Leonard et al. 2016a)

As of 2014 there were five captive individuals at the Endangered Primate Rescue Center (EPRC) as well as the 58 in-situ on Cat Ba Island which are divided into three subpopulations (Lees et al. 2014). Of these 63 animals, 84% are in reproductive groups, divided into two subpopulations (in the sanctuary and Cua Dong). Within the two free-living reproductive subpopulations, there are only eight adult males and 21 adult females contributing to the current breeding pool, a mere 46% of the global population (Table 7.2). Under pessimistic population-viability model scenarios there is an estimated 11% probability that the species will go extinct in the next 100 years without human intervention or subpopulation connectivity; chances of subpopulation extinction are even higher for the Cua Dong and captive populations in isolation (Lees et al. 2014; Table 7.2). Even this bleak outlook is probably over-optimistic, however, as the model assumes no hunting or on-going habitat loss or destruction, both of which are real possibilities.

Table 7.2: Number of individuals that fall within each age-class category for the four subpopulations of Cat Ba langurs (as of 2014), and their ‘optimistic’, ‘best guess’ and ‘pessimistic’ chances of extinction over the next 100 years without management (50 years for captive population). Table and extinction risks from a population viability analysis (Lees et al. 2014).

	sanctuary	**Cua Dong**	**Hang Cai**	**captive**	total
adult male	5	3	0	1	9
adult female	13	8	5	1	27
subadult	5	4	0	1	10
immature	8	7	0	2	17
total	31	22	5	5	63
percent of global population	49%	35%	8%	8%	100%
‘optimistic’ chance of extinction	0.3%	2.4%	0%	95%	0%[a]
‘best guess’ chance of extinction	1.6%	8.6%	0%	98%	0%[a]
‘pessimistic’ chance of extinction	10.6%	40.5%	0%	100%	10.7%[a]

[a] no connectivity between the three subpopulations

Logical fears for such a dwindling population include sustained loss of genetic diversity, inbreeding, and susceptibility to environmental or demographic stochasticity events; all of which arise from a small population size (Caughley 1994). Some argue, however, that long before a population crashes due to loss of genetic diversity or the effects of demographic stochasticity, extrinsic factors (e.g. overhunting, habitat loss) will cause extinction (Caughley 1994; Harcourt 1995). Either way, Cat Ba langurs are clearly vulnerable and deserving of strenuous conservation efforts.

Unfortunately, conservation efforts are difficult to spearhead in developing countries, as higher economic growth and external debt, energy use, human population density and growth, relatively lower standards of living, and certain socioeconomic policies and local traditions of a country (i.e. reliance on forest resources) are reflected in high loss of forests (Harcourt 1996; Sodhi et al. 2004; Jha and Bawa 2006; Laurance 2007) and species (Ehrlich 1994). This is in contrast to areas with lower economic growth and poorer countries with external debt (Harcourt 1996; Sodhi et al. 2004; Laurance 2007), periods with lower energy use (Ehrlich 1994), areas with lower human population density and growth (Harcourt 1996; Sodhi et al. 2004; Jha and Bawa 2006; Laurance 2007), and countries with higher standards of living (Jha and Bawa 2006). Additionally, there is a trend for countries with higher population growth, lower quality of life, and lower per capita gross national product to be more corrupt (Smith et al. 2003), and for that reason suffer from higher deforestation rates (Laurance 2007). Corrupt countries are significantly less effective at preventing logging and land conversion in reserves (Wright et al. 2007), with the result that such corrupt countries have significantly fewer bird and mammal species (Smith et al. 2003).

Southeast Asia holds about 9% of the world's population on 3% of the world's land (Duckworth et al. 2012). Vietnam is considered a 'lower middle income' country (WB 2015), with 11.3% living in poverty in 2012 (WFB 2017). The government is severely corrupt, based on a composite index from reputable sources (surveys, assessments, etc.) of perceived corruption of the public sector; it ranked 31/100 relative to other countries assessed for corruption (lower numbers indicate more corrupt countries) (TI 2016). The current population of Vietnam is over 94 million people (305 people/km^2), representing 1.3% of the world's population, with a 1.07% growth rate (WM 2016). Roughly 66-80% of Vietnamese people live in rural areas and depend on environmental resources (Tuyet Do 2001; Warne and Tran Lien Phong 2002; WM 2016). This has led to the loss of half of Vietnam's forests in the last half century (Warne and Tran Lien Phong 2002), with only 1% of its remaining forests being primary vegetation (GFRA 2016). Although the quality of life has increased in Vietnam over the past 30-40 years (Jha and Bawa 2006; HDR 2015), deforestation rates have remained high, despite the general trend of an inverse relationship in other countries (Jha and Bawa 2006). This may be because the Vietnamese government is hesitant to limit the growing economy by strictly enforcing regulations ever since the Doi Moi Renovation policy was enacted in 1986, which has led to a quick economic growth to the detriment of the environment (Boll 2013).

Logging, clearcutting for agriculture, industrial developments that degrade ecosystems and invite invasive species, forest fires, pollution, and unsustainable harvesting of forest animals and plants are common problems in Vietnam (Warne and Tran Lien Phong 2002). For this reason, Vietnam's wildlife and forests are suffering (Workman 2004), with unsustainable resource exploitation and environmental damage (Boll 2013), from a growing population (Tuyet Do 2001), corruption (TI 2016), poverty (Dasgupta et al. 2005), poor enforcement of laws with little institutional framework, and high reliance on forest resources (Warne and Tran Lien Phong 2002).

Vietnam has implemented a number of national-level environmental and biodiversity conservation laws, such as the National Plan for Environmental and Sustainable Development and the Tropical Forestry Action Program in 1991, the Law on Environmental Protection in 1994, the National Environment Action Plan and the Biodiversity Action Plan in 1995 and 2007, and a Government Decree 32/2006/ND-CP in 2006 (which includes all Vietnamese limestone langurs as deserving of special protection) (Warne and Tran Lien Phong 2002; Hanh H Dang et al. 2003; Rawson et al. 2011).

Additionally, they have ratified a number of international treaties relating to environmentalism, such as the Convention on International Trade in Endangered Species (1994), the Convention on Biological Diversity (1994), and the United Nations Framework Convention on Climate Change (1994) (Warne and Tran Lien Phong 2002; Rawson et al. 2011).

Unfortunately, there is little infrastructure and insufficient personnel to carry out ambitious conservation plans and, despite a number of institutions that claim to help with environmental protection, efficiency is suffering from lack of oversight and coordination (Warne and Tran Lien Phong 2002; Duckworth et al. 2012). Individual agencies (such as the Ministry of Agriculture and Rural Development, The Ministry of Natural Resources and Environment, the Ministry of Science, Technology and Environment, and the National Conservation Strategy) often do not exchange information, and there are constant internal arguments about who has what power and responsibility (Warne and Tran Lien Phong 2002; Boll 2013). Overall, meetings and working groups are convened in order to 'give the appearance of action, but there are no enforcement or deterrent mechanisms to back up the words' which effectively gives a 'false sense of action' (Boll 2013:11).

In addition to local Vietnamese' reliance on forest resources, East Asian (Duckworth et al. 2012), especially Chinese (Bleisch and Zhang 2004; Corlett 2007), population and wealth is ever-growing and their demand for wildlife and associated products (including monkey balm and monkey wine) is insatiable, draining the biodiversity throughout Southeast Asia. Cat Ba langurs have been heavily hunted in the past, both for domestic consumption and for sale across the Chinese border in the form of monkey balm or wine (for traditional medicine), food, and the pet trade (Nadler et al. 2003). Despite national-level protections, illegally-trapped Vietnamese primates flood over the border into China (Li and Li 1998; Bleisch and Zhang 2004). Over 90% of wildlife products traded across the Mong Cai border region are illegal; in three months there are 34,000 shipments of internationally protected animals (Robertson 2013). Primates (including Vietnamese), such as Tonkin snub-nosed monkeys (*Rhinopithecus avunculus*), macaques (*Macaca assamensis*, *M. mulatta*, *M. fascicularis*, *M. arctoides*), and François' langurs (*Trachypithecus francoisi*), can be found in wildlife markets and high-end restaurants in border regions of China (Li and Li 1998; Li and Wang 1999). Brokers – often criminals involved in human and drug trafficking across the border (Bennett 2011; Duckworth et al. 2012) – face minimal fines if caught, but rely more heavily on bribing corrupt officials

(Boll 2013; Robertson 2013). This is possible because of the lack of resources, insufficient laws and regulations, underpaid and limited staff, a weak judicial system, systematic corruption, and officials who are unaware of or unconcerned with the biological severity and loss that this trade represents (Li and Wang 1999; Bennett 2011; Duckworth et al. 2012; Boll 2013; Robertson 2013). Staff need to be taught the dire consequences of breaking wildlife protection laws so that these crimes can be seen as serious environmental hazards (Bennett 2011), while a long-term solution is to reduce consumer demand and implement better enforcement systems (Duckworth et al. 2012).

Ever since the Cat Ba langur population decline was first documented by Nadler and Ha Thang Long (2000), there have been a number of conservation management options that have been considered, and new ideas are always being generated. In the course of this study (2014) a Technical Working Group (TWG) was convened that included Cat Ba National Park (CBNP), the Cat Ba Langur Conservation Project (CBLCP), Fauna & Flora International (FFI), the EPRC, various experts and government officials, and myself. The goal of the TWG is to decide on appropriate and feasible conservation management strategies to protect the remaining Cat Ba langurs.

A few management options have been enacted since 2000, with variable results, while there are other management options that have not been explored. In Section 7.2 I will discuss the two methods being used that have been positive for the conservation of the Cat Ba langur, and two additional methods that should be considered. I will critique two methods that I do not consider to be a good use of limited funds, and consider ways of formalising a third. In Section 7.3 I will then explore ways of using the previous four chapters' results to document how the langurs may be affected by the continual loss, degradation, and fragmentation of habitat. Therefore, evidence for success or failure to protect and buffer the langurs from anthropogenic changes to their habitat and interactions with humans can be measured through behaviours and diet, home range and habitat use, and developmental/maturational progression.

7.2 Conservation Management of the Cat Ba Langur

There are several approaches currently being undertaken by the CBNP, CBLCP, EPRC, FFI, and local governments to ensure the viability of the small Cat Ba langur population. I fully support a number of these efforts, as they have proven effective across primates and, especially, Cat Ba langurs.

These successful efforts address the declining-population paradigm, in which the cause of population decline (hunting, habitat loss and degradation) is managed through habitat protection, patrols, enforcement, and education and training (Caughley 1994). Additionally, there are a few methods not currently being exercised that may be beneficial, including the creation of habitat corridors and limiting the ever-growing human population and infrastructure. The Cat Ba langur conservation efforts that I do not fully support include captive breeding and translocations, neither of which address the cause of the decline (Rabinowitz 1995; Cowlishaw and Dunbar 2000). Ex-situ conservation is significantly more expensive, and requires much more time and space per animal saved, than in-situ conservation (Caughley 1994; Cowlishaw and Dunbar 2000). Additionally, it only works one species at a time. It is better to put energy into conserving habitat than caring for the social, physical, and environmental enrichment and resources of a species (Newberry 1995; Nijman 2004). An additional management consideration is formalising ecotourism of the langurs. The remainder of this section addresses each management method in turn.

7.2.1 Habitat Protection, Patrols, Enforcement

One of the most effective ways of saving species in the wild is patrolling on behalf of forest/wildlife protection; this supports an entire, interdependent community of plants and animals. It is only through creating adequate protection that Southeast Asian biodiversity stands a chance (Sodhi et al. 2004). All parts of reserves – even those not used very frequently – need intense protection (Nadler 2004). If a forest fragment is unprotected, there is not much value in investing conservation efforts into it (Chapman et al. 2007a).

The efficacy of protected areas is contingent on regularly conducted patrols *and* enforcement; forest quality and conservation goals are correlated with enforcement efforts in a range of countries (Bruner et al. 2001; Gibson et al. 2005; Leverington et al. 2010). In other words, it is not enough to just establish a protected area. They require appropriate management, and it may be better to focus on increasing management of already established areas rather than creating new protected spaces (Leverington et al. 2010; Harrison 2011). The best form of enforcement is a high density of park guards, while using a bonus system (for information that leads to arrest or confiscation) in combination with investigative rangers (who investigate reports of illegal activity) has also been found to be an effective and efficient method for preventing poaching (Jachmann and Billiouw 1997; Bruner et al. 2001).

As law enforcement budgets are inversely related to poaching rates (Jachmann and Billiouw 1997), it is unfortunate that developing countries such as Vietnam may put less money and effort into enforcing laws protecting animals and forests, with the added problem of corruption and bribery (Nadler et al. 2003; Workman 2004). Even with adequate funding, there may be mismanagement of funds (the emphasis is on infrastructure, rather than patrols, which I consider to be a better use of funds on behalf of habitat protection), leading to ineffective enforcement of rules. In a global analysis of protected areas, only 22% have sound, sustainable, and effective management (Leverington et al. 2010); many of Southeast Asia's protected areas are not managed effectively, and need more intensive law enforcement (Duckworth et al. 2012).

The benefits of protection and patrols are evidenced by healthier forests and higher animal abundance. Protected tropical and subtropical forest reserves suffer from less logging, land conversion, and deforestation than unprotected areas (Wright et al. 2007; Nagendra 2008; Brooks et al. 2009; Spracklen et al. 2015). It is estimated that protection prevents 10-13% of deforestation that would have occurred otherwise, although forest loss even within protected areas is particularly high in Asia due to pastures and cattle grazing, environmental effects, and firewood extraction by local people (Andam et al. 2008; Nagendra 2008; Spracklen et al. 2015). Poaching decreases with an increase in antipoaching patrols and guards (Jachmann and Billiouw 1997; Hilborn et al. 2006). Hose's langurs (*Presbytis hosei*) living in a pristine National Park in East Borneo that had no protection from hunting suffered a 50-80% decline in population density over a seven-year period, indicating that even short periods of unrestricted hunting can be devastating to large vertebrates regardless of habitat quality (Nijman 2005)[3].

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[3] Unfortunately, there is no comparable data on population declines of this species in pristine habitats without hunting.

When areas are adequately protected, primates are found at higher densities and habitat is lost at a much lower rate compared to unprotected areas (Cowlishaw and Dunbar 2000). For example, white-headed langurs (*Trachypithecus leucocephalus*) living in areas that are effectively patrolled have larger population sizes (Li and Rogers 2007). In addition, since the creation of a strongly protected nature reserve for the previously-hunted Delacour's langurs (*Trachypithecus delacouri)*, the langur population has increased, and the animals have started acting less shy and are easier to see, indicating they may feel less threat (Nadler 2004).

Unfortunately, patrols by park rangers in developing countries often occur less than required compared to days rangers spend working (although note that there is no international standard for patrol days) (Bell 1985). For example, rangers in Lake Malawi National Park (Malawi, Africa) patrol less than seven days a month, resulting in an underestimation of the amount of illegal firewood collectors (Abbot and Mace 1999). Rangers have little incentive to actually conduct patrols, as there is rarely much oversight in isolated ranger stations (this is something I personally observed on Cat Ba Island; Gibson et al. 2005; Robinson et al. 2010), and when patrols are conducted they tend to concentrate on easily accessible areas (Robinson et al. 2010; Plumptre et al. 2014). In a study on the patrol efforts of the Greater Virunga Landscape (Democratic Republic of the Congo, Africa), patrols were concentrated within three kilometres of ranger stations, covering only 22% of the landscape; while illegal activities are rarer in those areas, the majority of the area is unmonitored (Plumptre et al. 2014). As it is the park rangers who are typically responsible for enforcing conservation policies, rangers are able to selectively choose for who and when laws are enforced, and how much to document in the process; fines and prosecution can potentially be avoided with bribes, with rangers liable to err on the side of reduced paperwork and personal efforts (Gibson et al. 2005; Robinson et al. 2010). Rangers often want to avoid social conflicts with individuals in the same communities, and are more likely to be sympathetic to small-scale resource extractions, such as firewood collection, as they understand the need for such activities by locals (Robinson et al. 2010). Additionally, the fines imposed for poaching or forest exploitation may be so low that it does little to deter the behaviours or compensate for the ecological costs (Abbot and Mace 1999; Robinson et al. 2010).

Roughly half of Cat Ba Island is designated as National Park, including a sanctuary created on behalf of the langurs (Schrudde et al. 2010; Figure 7.1). Both the CBNP and

CBLCP work together in supporting rangers with equipment, boats, educational material, and floating ranger stations in order for them to patrol the protected areas (Schrudde et al. 2010). There is also a community-based group of unarmed langur guards and forest protection groups that aid in langur protection by destroying traps, monitoring human impacts, and educating locals (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2010). These efforts aid in preventing hunting and forest exploitation that would degrade the quality of langur habitat. They have been largely successful at preventing poaching – with the last documented langur poaching in 2004 (N Leonard pers. comm. 2014). However, the loss of 10-19 animals in the last year represents a suspiciously high adult mortality rate (3.3-6.3x the normal)[4] (Leonard et al. 2016a).

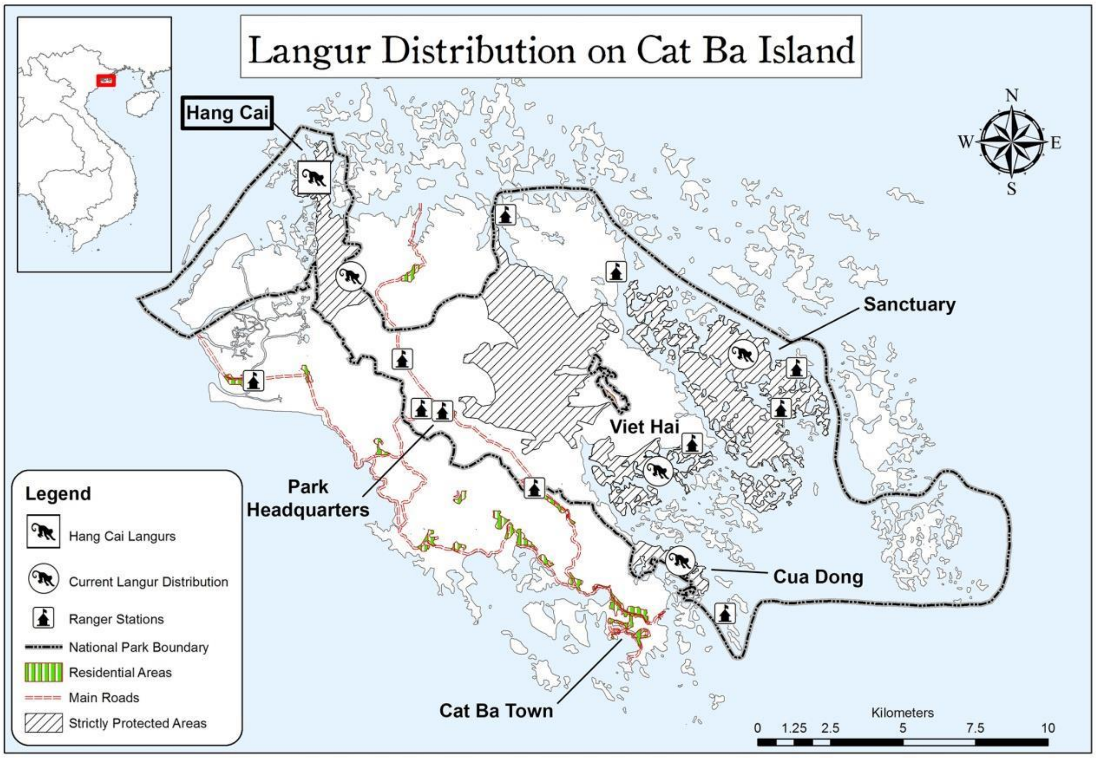

Figure 7.1: Map showing the distribution of langur populations, National Park boundaries and ranger stations, roads and human settlement areas on Cat Ba Island, northeastern Vietnam. Map, with permission, from Leonard (2014).

In addition to direct threats to the langurs themselves, their habitat is being degraded and lost at a rate of 0.1ha/year on the island while regeneration is less than a tenth of that

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[4] Unfortunately I am unable to assess this startling loss in any more detail and all queries should be directed to the CBLCP.

rate (Phan Duy Thuc et al. 2014). Before the 1960s, Cat Ba Island had relatively pristine primary forest cover; since then a large amount has been logged (stopped in 1986 partly due to the creation of CBNP, and partly because commercial timber supplies had been exhausted) (Nadler and Ha Thang Long 2000). Some particularly fertile areas (i.e. valleys that are used for food by the langurs) have been turned over to agriculture (Nadler and Ha Thang Long 2000; Figure 7.2). Although there is an estimated 90km^2 of available habitat on the island (Phan Duy Thuc et al. 2014), the two Cat Ba langur reproductive populations are restricted to ~15km^2 of protected space (1.1km^2 in Cua Dong and 13.9km^2 in the sanctuary: Figure 7.3). Threats to Cat Ba langur habitat quality by local villagers include wood-cutting and honey collection (which can result in whole mountain sides being burned) (Nadler and Ha Thang Long 2000; Nadler 2004).

(a) (b)

Figure 7.2: A valley basin that has been converted to (a) housing and (b) agriculture, which contributes to habitat fragmentation for Cat Ba langurs. Photos taken Feb 2014 by R Hendershott

Figure 7.3: Outline of the sanctuary (eastcentral side of Cat Ba Island) and Cua Dong (southeast), where 53 langurs in reproductive groups (Lees et al. 2014) live within just 15km^2 (of the estimated 90km^2 of available habitat: Phan Duy Thuc et al. 2014). Map source: ArcGIS.

This degradation of forests is partly due to locals' reliance on forest resources, as people on the island are poor, with 40% living in rural areas; this includes people living in poverty in the biosphere reserve (Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). For example, many local people, throughout Vietnam as well is in southern China, cannot afford gas or electric stoves, and therefore rely on cooking with firewood daily. This is 90% of families living around François' langur habitat (Hu 2007) and can amount to 850kg of wood/person each year (McElwee 2010). I witnessed illegal firewood collection from langur habitat in Cua Dong on multiple occasions, suggesting that this is a threat to langur habitat quality. Firewood collectors reduce the amount of decaying plant material, resulting in soil erosion on limestone karst (van Beynen and Townsend 2005), while fires consume the thin layer of soil that builds up (Harding and Ford 1993). This explains why conservation efforts for white-headed langurs in southern China include not only the cessation of tree felling (Li et al. 2003) but also firewood collection (Li and Rogers 2006) from fragmented habitats. Although beyond the scope of this chapter, an economic improvement and access to cooking fuel for locals will result in a reduction of reliance on forest resources.

Honey collection is another detrimental resource extraction, as up to one-fifth of Cat Ba langur karst hills are accidently burned each year in the process (Nadler and Ha Thang Long 2000). The island lost 4.5ha/year between 2004-2011 from wildfires (cited in Phan Duy Thuc et al. 2014:14). Limestone karst takes centuries to recover from disturbance such as fire (Harding and Ford 1993), because the porous nature of karst does not allow for soil accumulation, which means that fires and firewood collection destroy the vegetative duff that provides the foundation for plant growth (van Beynen and Townsend 2005). As with many other areas, an improvement in living conditions for locals on the island and a reduction of poverty should alleviate natural resource exploitation (Nadler et al. 2003; Thanh Van Mai et al. 2011). Given my observations of unpunished firewood collection around Cua Dong, I recommend that park rangers take forest degradation through small-scale extraction of firewood more seriously. This could start with warnings and documentation of those who engage in illegal activities, with fines for repeat offenders.

As in other developing countries, underpaid rangers on Cat Ba often forgo patrols due to lack of motivation, apathy, and claims that they do not have appropriate equipment or boat fuel (Nadler and Ha Thang Long 2000; N Leonard pers. comm. 2014). This makes enforcement another setback. In the course of this study, I witnessed several illegal activities, such as branch and tree cutting, dynamite fishing, and the use of under-water breathing apparatuses to collect protected marine life. The people engaging in these behaviours were rarely interrupted, scolded, cited, or fined; when people were chastised, they were rarely punished or even documented. Rangers seem hesitant to get their village neighbours into trouble (Nadler and Ha Thang Long 2000). Even when rangers do attempt to impose fines on someone caught selling illegal wildlife, the fines are minimal compared to the amount they would make selling the products (N Leonard pers. comm. 2014), making the risk worth the potential benefit.

Although the local Cat Ba villagers have now been educated about the value of their endemic monkey, and there have not been any documented poachings since 2004 (N Leonard pers. comm. 2014), there is always the threat that nonlocals view the remaining 60+ langurs as economically valuable enough to kill. This is especially so considering the high amount of illegal wildlife trade that occurs on Cat Ba (Schrudde et al. 2010) and its proximity to China with its demand for wildlife products (Li and Li 1998; Li and Wang 1999; Nadler et al. 2003; Bleisch and Zhang 2004; Tran Thu Hang 2010). In the course of this study the park rangers were told that some Chinese businessmen had put out a request for Cat Ba langurs, so to be extra vigilant for questionable activity (Nguyen Cam pers. comm. 2014). Unfortunately, in a 2016 census there was a suspiciously dramatic loss of langurs (Leonard et al. 2016a). Thus, patrols are key to ensuring that poaching remains a thing of the past.

In addition to local villagers' small-scale resource exploitation on the island, island-wide limestone quarrying and infrastructure development threaten conservation goals and langur habitat (Nadler and Ha Thang Long 2000; Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). For example, mining activity, rampant along the west coast of Cat Ba Island, is incredibly destructive to limestone karst, as it destroys caves, changes the water table and flow, creates sinkholes, and overall destroys the entire ecosystem (van Beynen and Townsend 2005). Protection and enforcement are effective at saving specific areas, but it does nothing for the overall Cat Ba ecosystem; that requires a shift in governmental policies and a compromise of economic gain with long-term biodiversity.

It is of vital importance that the remaining langur habitat and forests of Cat Ba Island are under heavy protection, and that there are penalties for those who illegally harvest natural resources or disturb wildlife. Extending the borders of CBNP may be effective, but only if there is enforcement of the boundary (Nadler et al. 2003). Some suggest that all of Cat Ba Island should be considered langur habitat and conserved (Schrudde et al. 2010). Conservation programs and patrol groups should remain community based (Le Khac Quyet 2004b), as they have been for Cat Ba langurs in the past (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2010). Gun confiscation policies must be enforced (Li and Rogers 2005a), preferably at the local level (Nadler 2004). Logging and forest conversion needs to be banned or heavily monitored (Ha Thang Long 2004). Paraphernalia and evidence of animal trade must be regularly monitored in villages' neighbouring protected areas, and legal fines imposed (Nadler 2004).

The conservation efforts on behalf of CBNP, CBLCP, and others are working, to an extent. However, they could be much more effective with stricter enforcement and more regularly conducted patrols (Nadler 2004; Workman 2004). Some suggest there needs to be a push for newly protected areas or special 'species conservation areas' (Nadler 2004). However, before dedicating newly protected areas, the government needs to refocus its energy on: *actually* conducting patrols of the already established protected areas, following through with warnings and fines, and enhancing cooperation with locals in developing sustainable forest usage or other alternative forms of livelihood. Furthermore, economic policies need to be reconsidered, as habitat destruction is also occurring on an industry and political-wide scale through tourism development and limestone quarrying. It is not enough to pay lip service to saving their flagship species: methods need to be put in place to document who has received a warning and appropriate punishment doled out to those who repeatedly cut firewood, collect protected marine resources, and illegally collect honey. The process of transparent recording of patrol effort and threats is something that is being started through Spatial Monitoring and Reporting Tool (SMART) enforcement (B Rawson pers. comm. 2016); this makes it easier to track repeat offenders and improve the efficacy of patrol routes due to the constantly updated database (Plumptre et al. 2014; Critchlow et al. 2016).

Rangers may be motivated and supported by receiving positive community publicity (Long et al. 2004; Streicher 2004) or financial rewards (Cowlishaw and Dunbar 2000), as well as a basic understanding of why they are doing their jobs. This means that all CBNP rangers need to undergo training as to why conservation efforts are important, lessons in basic species biology, and how to use the open-access SMART system for documenting locations that need extra protection and people who continually break wildlife laws. They should be commended during community events, with their efforts and accomplishments to be a source of community pride. In order to improve their quality of life, the ranger stations that are falling apart need repairs. Money needs to go towards boat fuel, GPSs and other tools that aid rangers' ability to do their jobs. Finally, a financial reward system for preventing illegal harvesting or punishing repeat offenders would create a direct benefit for individual rangers to put effort into conducting patrols.

Money can be sourced by reprioritising how the funds are spent. Although infrastructure may increase morale and working conditions, my approach is that rather than building new, expansive, and expensive CBNP headquarters for administration purposes (which I observed in the course of this study, 2014), the money could be redirected into paying the people who are actually carrying out the patrols and their required equipment. Although increased patrolling and enforcement requires funds, the benefits are priceless in terms of biodiversity, conservation, and preserving a part of the locals' culture.

7.2.2 Education and Training

In order to increase effectiveness, enforcement should be used in conjunction with education programs (Corlett 2007). Appropriately, the second strategy that is currently being successfully enacted on behalf of the langurs is conservation education. Educating local people on environmental decisions and consequences helps foster new ways of interacting with the environment and an appreciation of conservation, including a sense of pride (Peters and Matarasso 2005; Trewhella et al. 2005). Overall, rangers (Cowlishaw and Dunbar 2000; Long et al. 2004; Streicher 2004; Harrison 2011), locals (Wallis and Lee 1999; Le Khac Quyet 2004b; Nadler 2004; Thanh Van Mai et al. 2011), and tourists (Forestell 1993; Orams and Hill 1998; Wallis and Lee 1999; Ngoc Mai 2004; Stenke and Chu Xuan Canh 2004; Section 7.2.7) all need to be educated as to why biodiversity, forest health, disease risks, and conservation matter, as well as which animals cannot be hunted, what activities count as illegal, and what effects tourism and increasing populations are having on the island's ecology.

Rangers are often inexperienced and unknowledgeable about basic animal behaviour and ecology. They are told to confiscate illegal animals, but often do not know what to do with them (Streicher 2004). There are rarely adequate facilities and resources for their immediate care, despite animals often being dehydrated, stressed, injured, and/or malnourished at the time they are confiscated (Tran Thu Hang 2010). The people tasked with protecting and patrolling must be educated on biological matters, such as primate identification, how to handle confiscated animals, species-specific characteristics, and a background of conservation biology, to do their jobs effectively (Cowlishaw and Dunbar 2000; Long et al. 2004; Streicher 2004). The experienced CBNP rangers are very good at finding langurs, but they lack fundamental behavioural and ecological knowledge about their charges. It would be beneficial for them to be aware of basic ethograms, activity and dietary budgets, habitat use, and development presented in this thesis so that they are better able to locate langurs, identify age-sex classes in order to estimate birth dates, document abnormal or unusual behaviours (such as infanticide or increased rates of aggression), and increase interest in watching the langurs during their patrols (which will improve the information they are collecting on behalf of the CBNP and CBLCP). It is hoped that an investment in learning about these Critically Endangered species will increase interest and motivation in the rangers' jobs.

The CBLCP has local guards who are responsible for informing the locals in the communes about why the langurs need protecting and the ecological importance of biodiversity (Stocking 2003; Stenke and Chu Xuan Canh 2004; Schrudde et al. 2010). These guards visit homes of known forest exploiters in order to provide an informal education as to how damaging their behaviours are to the forests, as well as organise educational broadcasts to be played through village loudspeakers (Schrudde et al. 2010). However, it may help to take advantage of newer media formats that are less controlled by the government (e.g. internet blogs and social media) to reach more people (Mol 2009).

In northcentral Vietnam, education of community members leads to an improvement of environmental knowledge and attitudes, as well as more efficient agroforestry and animal husbandry skills, which empowers locals (Peters and Matarasso 2005). Therefore, it is education that is key to promoting concern for the state of Cat Ba's wildlife and forests, although direct evidence of knowledge leading to behaviour change with ultimate conservation implications is difficult to demonstrate.

In addition to less formalised environmental education methods, the CBLCP created a school-based education program that has created pride in children in their island's endemic, flagship species (Figure 7.4). An environmental education program targeted at school children in Brazil was successful in raising interest and knowledge in the local Endangered black lion tamarin (*Leontophithecus chrysopygus*) and habitat conservation, as students gained an appreciation for the species and environment they had previously taken for granted (Padua 1994). Similarly, school children in Uganda learnt and retained environmental education for years, with results possibly indicating that they spread this information within their community (Kuhar et al. 2010). Both these studies suggest that hunting (Padua 1994) and snare trapping (Hashimoto et al. 2007; Kuhar et al. 2010) have declined as a result of the education program. In order to truly call the CBLCP education program successful, there needs to be some metric of behaviour change and conservation benefits.

Figure 7.4: A family watches a group of langurs from their floating home. The young boy showed keen interest in seeing the langurs after having learnt about them in school. Photo taken Aug 2013 by R Hendershott

I support the continuation of a personal education program by local community members, and the formalised education programs for school-age children, although how this relates to behaviour change and conservation goals needs to be assessed. Nonetheless, it is the adults who are responsible for forest exploitation on behalf of their families, and there is little documentation of who the repeat offenders are. Therefore, education programs that target general adult audiences are imperative, lest it take a generation before the local population has an ingrained sense of the value of biodiversity and conservation (Peters and Matarasso 2005). I recommend that all tour operators are taught appropriate behaviours when around the langurs, so that they too can be educated as to why illegal ecotourism is detrimental to the langurs (Section 7.2.7).

7.2.3 Habitat Corridors

An option that has not been given much consideration on behalf of the Cat Ba langurs is that of habitat corridors, which can serve to increase the likelihood of dispersal, and, thus, genetic diversity, between free-living animals. This can be done by connecting habitat fragments with natural, vegetated corridors. Increasing connectivity allows for migration, which decreases inbreeding depression and genetic drift, and helps to mitigate demographic stochasticity (Simberloff and Cox 1987). Modelling of samango monkeys (*Cercopithecus* cf. *mitis*) in forest fragments indicates that in the long term (800-1500 years) habitat corridors are the best way to enhance monkey presence in these areas (Swart and Lawes 1996). In fact, low population growth rates combined with corridors increases survival probability more than high growth without corridors. Reintroduction/restocking of groups helps species population numbers only when the density of monkeys is low and the area is not at carrying capacity, and only in the short term (500 years). Therefore, this model indicates that forest patch connectivity is far more important, in the long term, than reintroduction (including translocation or captive breeding for release).

Overall, it is not necessary for an area to be ideal habitat or pristine (those less than a few hundred metres wide are unlikely to retain primary habitat characteristics anyway), so long as it is safe and sufficiently vegetated, and connects populations (Lovejoy et al. 1986; Cowlishaw and Dunabr 2000). This makes corridors a relatively cheap and effective way of increasing subpopulation connectivity, as animals passively expand their range into areas with food. Fortunately, some primates regularly venture into noninhabitable areas (the landscape 'matrix' and corridors), primarily those that are most vegetated and similar to their natural habitat (Estrada and Coates-Estrada 1996; Umapathy and Kumar 2000; Anderson et al. 2007; Pozo-Montuy et al. 2011; Benchimol and Peres 2014). This indicates that it is not unreasonable for primates to use corridors, despite it not being the highest quality habitat.

Cat Ba langurs are living in fragments surrounded by ocean, human settlements, and agriculture, all of which limits their ability to disperse and migrate. Nonetheless, there have been cases of the monkeys crossing areas that were thought to be impassable (N Leonard pers. comm. 2016; Figure 7.5), so there is the chance that the anthropogenic matrix is not completely limiting to the langurs. Either way, Cua Dong is ~10km away from the sanctuary (Figure 7.6), separated by villages and roads, making it unlikely that individuals are free to interbreed. This isolation could be lessened by providing corridors for dispersal. In a population viability analysis for Cat Ba langurs, the population is found to grow much faster if the subpopulations are able to move freely betwixt one another, and within 100 years there could be as many as 450 langurs if dispersal were not a limiting factor (Lees et al. 2014). Habitat corridors have not, to my knowledge, been implemented as a management strategy, despite them being a low-cost, effective means of providing habitat connectivity between isolated populations, and having been recommended previously (Stenke and Chu Xuan Canh 2004).

Figure 7.5: A bachelor male langur (circled) crossing an area inhabited by humans and dogs. Note: proximity to park rangers (in boat). It was previously thought that this human settlement was a barrier for the langurs. Photo taken Jan 2015 by R Hendershott

Figure 7.6: The Cua Dong and sanctuary Cat Ba langur populations (outlined in black) may be more likely to disperse and interbreed if they are connected with a vegetated and protected corridor (10.2km) that follows ridgetops and avoids human infrastructure (shown here as a white line).

Although corridors may not be a viable strategy to connect all groups on the island (the Hang Cai group is too far away for dispersal to happen within a reasonable time frame), a well-protected corridor from Cua Dong to the sanctuary would be a relatively inexpensive way of facilitating dispersal between the two breeding populations without stressful human contact. The corridor would be most effective if it followed the uncultivated or undeveloped hills, especially as the langurs need to use steep cliffs for sleeping sites (Section 4.4.3, Chapter 4) and limestone karst ridges are safer from human disturbance due to their inaccessibility (Nadler 2004). Difficult-to-access areas cannot be underappreciated: in Asia, 40% of the reduction in deforestation in protected areas is due to inaccessibility of geography/terrain (steep slope and higher elevation) rather than legal status (although legal status did have an effect) (Spracklen et al. 2015). Thus, protection of a corridor can be a passive denial for infrastructure development, limestone quarrying, road construction, etc. in areas that are fairly inaccessible, and, thus, relatively protected anyway. Corridors around limestone karst hills may also be used by other species (Furey et al. 2010), increasing their effectiveness at overall habitat and ecosystem conservation.

The first step for this process is to assess what makes for preferred habitat for Cat Ba langurs (currently being assessed by K Apthorp), and what the key food resources are (currently being assessed by K Ruskins). Results from the habitat assessment across the island will help in deciding the value and placement of corridors for Cat Ba langurs. As Cat Ba langurs must disperse a long distance (Figure 7.6), they will require resources *en route*; this means that a corridor should be wide enough to contain adequate food and sleeping sources while still providing protection from the elements and predation (Harrison 1992). If the potential corridors lack sufficient food resources but are otherwise appropriate habitat, the corridor should be planted with food species. The CBLCP has worked on some planting projects already (N Leonard pers. comm. 2014), so I recommend that these should focus on food trees along a potential corridor. As Cat Ba langurs are relatively comfortable with traveling and engaging in most behaviours on rocks, and spend significant time in sparsely vegetated areas (Section 4.4.2, Chapter 4), it is not critical that the corridor be fully vegetated with dense canopy coverage.

However, even with a variety of surrounding matrices and corridors around a habitat fragment, the area and quality of the fragment itself is the most important feature in long-term viability for forest-dwelling species (Hodgson et al. 2011). This suggests that Cat Ba langurs may benefit from suboptimal forests that connect populations, but that this should not take away from focusing on improving the habitat within established fragments and home ranges.

7.2.4 Limited Human Population

Although, historically, hunting caused a decrease in Cat Ba langur numbers, these animals are now confronted with uncontrolled population growth on the island. Cat Ba Island is a popular tourist destination, resulting in a large amount of national and international tourism, as well as Vietnamese immigrating to Cat Ba in order to tap into the tourism trade (Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). This means that both the local and tourist population is increasing. A high density of humans can be detrimental to the surrounding wildlife and environment; high population growth and density is associated with high rates of deforestation (Harcourt 1996; Jha and Bawa 2006; Laurance 2007) and, ultimately, is responsible for the majority of extinctions (Pimm et al. 1995). The high population, immigration, and tourism on the island result in a competition for resources with langurs (Thanh Van Mai and Maani 2010), roads that divide up langur habitat and create accessibility for humans (Le Khac Quyet 2004b; Le Khac Quyet and Nguyen Vu Khoi 2010; Figure 7.7), forest conversion to agriculture and settlement areas (Stenke and Chu Xuan Canh 2004; Figure 7.2) with a resulting destruction and fragmentation of langur habitat, and social isolation of langur populations (Day and Chenoweth 2004; Nadler et al. 2007; Schrudde et al. 2010). Therefore, a growing human population makes it unlikely that the Cat Ba langurs can breed, disperse, and thrive without human intervention.

Figure 7.7: Roads divide forested mountainsides. This road in (a) leads to Cat Ba town while (b) is heading towards the National Park. Photo taken (a) Sept 2014 and (b) Feb 2014 by R Hendershott

Beyond tourism and infrastructure, locals create environmental concerns. The borders of Cat Ba Island are littered with environmentally destructive floating homes. I noticed that marine farming and floating villages have resulted in massive deposits of waste and pollution, exploitation, and overtaxing of an already-strained marine ecosystem (Nadler and Ha Thang Long 2000). The langurs drink from the heavily polluted seawater (Figure 7.8), which is often covered with a sheen of oil.

Figure 7.8: Cat Ba langurs regularly encounter human rubbish (left), which may increase risks of disease transmission, and drink from the polluted seawater. Photo taken April 2014 by R Hendershott

In addition to indirect effects of habitat degradation and pollution, langurs living near floating villages include daily interactions (i.e. visual and auditory contact) with dogs, fishermen or shellfish-collectors, and washed up rubbish (which the langurs play with or chew on). In all areas of their home range in Cua Dong area, langurs are exposed to people shouting, boat engines, and dogs barking (Figures 7.9 and 7.10). In the areas facing the ocean they are also exposed to tourists in kayaks, junk ships, and large fishing trawlers (Section 2.2, Chapter 2). Noise and light pollution are ever-present.

Figure 7.9: The langurs living in Cua Dong are exposed to (a) large boats and dogs and (b) traffic and floating villages in their daily lives. Photos taken July-Aug 2013 by R Hendershott

[redacted]

[redacted]

Figure 7.10: The Cua Dong langurs live in close proximity to floating villages, which results in their constant exposure to engines, pollution, light, and dogs. This can be seen (a) from above and (b) at water level. Photo (a) taken Jan 2015, (b) taken August 2013 by R Hendershott

This proximity to human settlement places primates at risk of disease transmission (Wallis and Lee 1999); indeed, in documented cases of human to nonhuman ape disease outbreaks, they were most likely a result of interactions with the local human populations (Muehlenbein and Ancrenaz 2009). Ursine colobus (*Colobus vellerosus*) groups living near human settlements have more parasites that are similar to human parasites than those that do not cross paths with humans as often, suggesting anthropozoonotic transmission (Teichroeb et al. 2009b).

Limiting infrastructure development and the cessation of road construction is the most effective and drastic form of allowing the Cat Ba langur population to recover (Nadler et al. 2003), as it reduces resource competition, fragmentation, and interactions with humans, all of which may alleviate stress (Chapman et al. 2006; Chapman et al. 2007b; Martínez-Mota et al. 2007; Rangel-Negrín et al. 2009; Jaimez et al. 2012; Dunn et al. 2013; Rimbach et al. 2013). This then has reproductive and viability implications for animals (Yeager and Kirkpatrick 1998; Heistermann et al. 2004; Charbonnel et al. 2008). Low-level land should be uncultivated, and native, natural vegetation should be restored (Nadler et al. 2003), allowing for an increase in habitat quality and connectivity between limestone hills. Although providing more high-quality, connected habitat and less disturbance from humans does not directly translate into a population increase, it has the effect of allowing for animals to disperse more easily, without the pressures of interacting with humans, and may increase the likelihood of reproduction and survival.

The CBNP and local government officials claim to want to protect wildlife (especially the langur, which is a flagship species for the island: Schrudde et al. 2010), although goals of economic development limit the efficacy of these efforts, as officials are unwilling to enact any policy that limits tourism or revenue, and continue to encourage infrastructure development (Thanh Van Mai et al. 2011). As an example of governmental priorities for development, roads and buildings are ever-increasing in order to accommodate the 15,000-20,000 people already living on the 140km^2 island and the 1.5 million tourists that visit each year (Nguyen Van Quan et al. 2010; Thanh Van Mai and Maani 2010; Thanh Van Mai et al. 2011). This infrastructure development divides limestone hills, making it difficult for Cat Ba langurs to move through valleys (Figure 7.7). Despite the drain this is placing on the island, there is a resort currently being built that is to accommodate an *additional* 50,000 tourists at any one time (Le Thi Ngoc Han pers. comm. 2015). The local government has plans to increase the number of tourists to five million annual visitors by 2025, and 10 million annual visitors by 2050 (N Leonard pers. comm. 2016). Accommodating this many tourists means that more people will immigrate to tap into the tourism industry, possibly increasing the island population to five times its current amount (N Leonard pers. comm. 2016). This creates increased pressures on natural resources, and decreases the natural beauty of the island, which is the primary reason tourists visit (Thanh Van Mai et al. 2011). This is a common problem for tropical countries (Harrison 2011).

The suggestion of limiting roads and infrastructure and uncultivating valuable valleys is, however, idealistic and unrealistic, given the growing population, their dependence on foods from valleys, and governmental goals of economic growth. As more and more land is mined, more and more houses and roads are being built, and increasing tourism and tourism revenue are primary goals for government officials, a bigger threat than the *current* exploitation of natural resources is an *increasing* population, which threatens *ever more* increases in exploitation.

7.2.5 Captive Breeding

Animals bred in captivity can be used to restock wild populations, reintroduce a species to an area from which it has gone extinct, or introduce a species to an area where it has never occurred (IUCN/SSC 2013; IUCN/SSC 2014), and they can function as a pool of genetic diversity for wild populations. Unfortunately, despite long term financial and time investments, it is not unusual for captive breeding programs to fail in creating long-term viability (Cowlishaw and Dunbar 2000). This is partially due to small population sizes, disease transmission, and animals that are behaviourally unprepared for life in the wild.

Captive populations should be large enough that they can survive environmental and demographic stochasticity, and be behaviourally competent so they can successfully reproduce in a self-sustaining manner (Cowlishaw and Dunbar 2000; Ballou et al. 2010). Ideally, captive populations are supplemented with individuals from wild populations in order to maintain genetic diversity, although removing breeding individuals from the wild breeding pool may be detrimental to viability for those species with an extremely low population size in the wild (Cowlishaw and Dunbar 2000; Ballou et al. 2010).

Genetic drift and inbreeding of captive animals needs to be monitored (Cowlishaw and Dunbar 2000; Ballou et al. 2010), especially as inbreeding in captivity affects primates. For example, a captive red-shanked douc langur (*Pygathrix nemaeus*) died from an autosomal dominant trait (pectus excavatum) that was presumably expressed due to inbreeding (Sedgwick 1981). Captive inbred ring-tailed lemurs (*Lemur catta*) suffer higher parasitism, immunosuppression, dehydration, and die earlier from diseases (Charpentier et al. 2008). Although the captive (i.e. less stressful) environment generally buffers animals from harsh ecological conditions, and, thus, the effects of inbreeding, it also has the effect of masking deleterious traits that could then be devastating upon release (Jiménez et al. 1994; Hedrick and Kalinowski 2000; Reed et al. 2002; Armbruster and Reed 2005). Fortunately, an improvement in enclosure and husbandry can lead to a reduction in inbreeding depression (Kalinowski et al. 2000).

Captive care runs the risk of disease transmission (especially if artificially crowded: Dobson and May 1986), so care must be taken to ensure that this risk is minimised (IUCN/SSC 2014). This is especially dangerous for animals that are to be released back into the wild, as the wild population is vulnerable to diseases the released animals may bring *and* because the released animals may be immunologically naïve to wild disease outbreaks and particularly vulnerable due to the stress of the release (Viggers et al. 1993; Wallis and Lee 1999; Kock et al. 2010). Disease transmission has been documented for Delacour's langurs at the EPRC who were moved from captivity to a semiwild enclosures (Hoan-Vu Do 2009), indicating that fears about captive animals introducing additional disease to populations once released are well-founded. This means that animals slated for release need extensive health screenings (Viggers et al. 1993).

For captive animals destined for release into the wild, there is an extreme importance for animals to have regular social interactions with conspecifics and be maternally raised, allowing for the opportunity for breeding, rearing, antipredation, foraging, and navigating skills to develop through species-specific social and structural enrichment (Snowdon 1989; Newberry 1995; Buchanan-Smith 1997; Cowlishaw and Dunbar 2000; Little and Sommer 2002; Mallapur and Choudhury 2003; Novak 2004; Hosey 2005; Kenyon et al. 2010). The psychological welfare of the animals must be taken into consideration (Novak and Suomi 1988); this includes reducing the stress inherent in captivity (Rangel-Negrín et al. 2009), and monitoring rates of nonnatural, abnormal, and undesirable behaviours (Mallapur and Choudhury 2003).

There have been a number of successful primate introductions from captivity, including breeding with wild populations (Britt et al. 2004; Kierulff et al. 2012). Releases of limestone langurs from the EPRC have occurred in the last decade. Hatinh langurs (*Trachypithecus hatinhensis*) have undergone the first stage of release, by being moved to a semiwild enclosure (Vogt and Forster 2010), while Delacour's langurs have been fully reintroduced to the wild (Agmen 2014; Elser et al. 2015). Although the animals have survived throughout the above study periods, it is unclear how successful they have been at contributing to the breeding population.

Cat Ba langurs are prime candidates for captive breeding from a conservation perspective (Nadler et al. 2003; Stenke and Chu Xuan Canh 2004) due to their low population numbers and genetic diversity, and threats to their habitat. The only place where Cat Ba langurs exist outside of Cat Ba Island is at the EPRC located in Cuc Phuong National Park, northcentral Vietnam. The founder population of Cat Ba langurs come from confiscations from illegal markets and poachers (Nadler 2012) and have since been part of a breeding program with the long-term goal of supplementing wild populations (Nadler and

Ha Thang Long 2000). Of the five Cat Ba langurs at the EPRC, three are the result of close-familial breeding, and all five langurs are related (Figure 7.11).

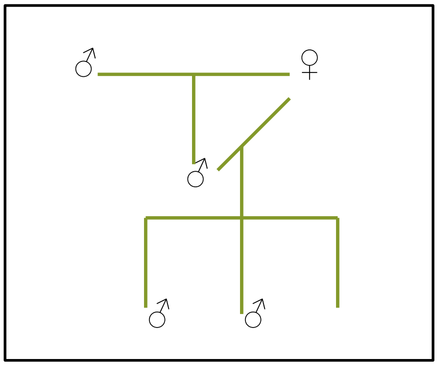

Figure 7.11: Parentage and breeding diagram for the five captive Cat Ba langurs. The original male (now deceased) and female were confiscated from the wild and the three young langurs (two males, one unsexed) are the result of mother-son breeding. Information from T Nadler pers. comm. 2014.

This small, inbred population of captive Cat Ba langurs is inviable in the long term, with an – at best – 95% chance of extinction in the next 50 years without further management (Lees et al. 2014; Table 7.2). Viability could be enhanced by outbreeding (Hedrick and Kalinowski 2000), which either requires more animals coming into captivity or else the release of these animals into the wild breeding population. As the wild population is already at dangerously low numbers, and considering the risk of disease transmission (Cowlishaw and Dunbar 2000; Ballou et al. 2010), capturing wild Cat Ba langurs and placing them into captivity cannot be recommended. Population viability modelling indicates that adding the five wild, isolated, Hang Cai adult females to the captive group still results in a 51% chance of extinction for the captive population, which is a risky move considering extinction risk is reduced to a more manageable level when those five females are moved to one of the other wild-living populations (Lees et al. 2014).

As the captive Cat Ba langur population is too small and too inbred to sustain itself, and since wild-to-captive immigrants are [hopefully] unlikely to appear/be confiscated, my suggestion is that efforts should be made to immediately prepare for the release (i.e testing for diseases) of these five animals, so they can outbreed and start to contribute to the long-term survival of this species. To ensure a smooth transition to life in the wild, the enclosures for captive Cat Ba langurs should be structurally complex and as similar to the release environment as possible. To encourage locomotor skills, which can take a year to develop (Huang and Li 2005; Zhao et al. 2008; Section 6.4.2, Chapter 6), a limestone karst habitat needs to be provided so that animals can practice moving around this petrous environment. Social partners and families should occur in a natural grouping, to ensure adequate adaptations to survival. Based on social affiliations, adult female Cat Ba langurs should ideally not be made the core social group, as they are not highly bonded (they will interact, however, if there are young present) (Section 5.4.2.2, Chapter 5).

Unfortunately, there do not seem to be any plans for releasing these captive Cat Ba langurs in the near future, given the already precarious state of the captive population (T Nadler pers. comm. 2014). We are therefore left with wild animals that cannot be moved to captivity and captive animals that are not being moved to the wild. It is considered a success that the langurs at the EPRC breed (and the number they have in captivity has increased), but a failure that these langurs cannot be used to supplement wild populations (as there are no plans for release). Therefore, the contribution of the captive population to the species long-term conservation through captive breeding is, at present, severely limited. However, if these animals were to be released, they may provide a useful contribution to increasing genetic and demographic diversity. I recommend that plans be started to behaviourally train the five captive Cat Ba langurs for living in the wild, so that they can be released as soon as they are competent and have been assessed for communicable diseases. The captive animals are not contributing to the breeding pool, and cannot be considered an insurance policy of genetic diversity for the species.

7.2.6 Translocations

Another approach that has been strongly supported (Stenke and Chu Xuan Canh 2004) and enacted (R Passaro pers. comm. 2013) for the Cat Ba langurs is capturing and translocating isolated animals into breeding populations. Translocations are a common way of moving threatened/vulnerable/destructive (Imam et al. 2002; Strum 2005), or isolated (Medici et al. 2003; Donati et al. 2007) populations to an area that is more protected, of higher quality, or with a higher carrying capacity than their original location (Caughley 1994; IUCN/SSC 2013). Translocations function to increase genetic diversity and the breeding pool size, a problem for Cat Ba langurs (Section 1.7, Chapter 1). They are helpful as it only takes one (Ralls et al. 1986) or a few (Spielman and Frankham 1992) individuals to move between groups to maintain genetic diversity. Translocations between wild populations are simpler and cheaper than releasing from captivity, as they require less preparation and training for the animals, less infrastructure and people, and no provisioning (Medici et al. 2003); wild-caught animals tend to fare better in translocations than captive-bred animals (Griffith et al. 1989).

There have been a number of successful primate translocations, followed by breeding in the wild, including: black lion tamarins (Medici et al. 2003), Venezuelan red howler monkeys (*Alouatta seniculus*) (Richard-Hansen et al. 2000), rhesus macaques (*Macaca mulatta*) (Imam et al. 2002) and olive baboons (*Papio anubis*) (Strum 2005). To increase success, animals need to be physically and behaviourally competent, with the ability to find food (which requires learning and memorising a new spatial map) (Teixeira et al. 2007). Translocating a large number of individuals in a social group at a time is more successful than individual translocations, although the benefit does become asymptotic (Griffith et al. 1989).

Translocations do have some constraining factors, including cost, stress, and disease transmission. For example, it is estimated that a translocation of golden lion tamarins (*Leontopithecus rosalia*) cost $4,600-22,000USD for each surviving individual (Medici et al. 2003). Additionally, the capturing, undergoing of veterinary exams, transportation, release, and monitoring of individuals can be extremely stressful, leading to increased susceptibility to disease and even death (Struhsaker and Siex 1998; Meijaard and Nijman 2000; Teixeira et al. 2007; Kock et al. 2010). For olive baboons in poor physical condition, translocation results in higher rates of diseases than those in better physical condition, although it seems they are able to build up an immunity over time (Strum 2005). In the course of translocating/introducing 67 Zanzibar red colobus (*Piliocolobus kirkii*), almost 6% died during capture or translocation (Struhsaker and Siex 1998). Of 84 proboscis monkeys (*Nasalis larvatus*) captured for a translocation, a whopping 15% died during capture (Meijaard and Nijman 2000). There is also the risk of disease transmission from one subpopulation to another, which may be particularly detrimental (with additive effects) due to the stress of the translocation itself, and, ultimately, may negate the positive effects of translocation (Kock et al. 2010; IUCN/SSC 2013). Both the translocated individuals and the resident individuals need to be assessed for diseases by veterinarians. Overall, translocation can be extremely expensive, stressful, and not guaranteed of success.

Translocations of Cat Ba langurs have had mixed results. In 2012 the CBLCP successfully translocated two isolated Cat Ba langurs from an unprotected area of the island to the sanctuary (R Passaro pers. comm. 2013). A more recent (2013-2014) attempt at translocating five isolated, potentially postreproductive females (in Hang Cai, at the north end of the island) was not successful, as the langurs could not be trapped (R Passaro pers. comm. 2013). The topic of the first several TWG meetings for these same five langurs was the planning and organisation of another attempt (Leonard 2014). Population viability models indicate that adding these five females to the sanctuary, Cua Dong, or captivity reduces both extinction risk and the degree of inbreeding within those subpopulations, most notably in captivity where extinction risk for the next 50 years is almost halved (from 98% to 51%) (Lees et al. 2014).

Current plans for translocation have been shelved because an adult male has found his way to the [previously assumed to be isolated] island of Hang Cai (N Leonard pers. comm. 2016), thus reducing lost reproductive opportunities. At this point we should wait and see if these females start to breed, and then consider translocations of them and their offspring in the future if they are successful. However, before any more translocations are attempted for the Cat Ba langurs, a detailed analysis of important habitat and resource availability (currently being undertaken by K Apthorp and K Ruskin) is necessary as well as making sure that the area they are being moved to is well protected.

7.2.7 Ecotourism

Ecotourism is a popular option for boosting the local economy and growing respect for a threatened species (Chapman and Peres 2001), as it can lead to effective environmental and species protection, increased revenue, and attitude shifts towards conservation priorities by local communities (Krüger 2005; Yu et al. 2010). Primates (Cowlishaw and Dunbar 2000) and other flagship species (Krüger 2005) are often used as the focus of ecotourism, although langurs are as such popular subjects for ecotourism as are some other charismatic primate species (Nadler and Ha Thang Long 2000; Krüger 2005).

Yet, despite supposedly providing financial support for conservation purposes, ecotourism of primates is not necessarily an ecologically or behaviourally sustainable option (Chapman and Peres 2001). Only 63% of ecotourism projects[5] worldwide are considered to be sustainable, but this figure drops to 41% in Asia and 39% for islands; primary causes of unsustainability are negative effects on the flagship species, insufficient revenue, habitat alteration on behalf of tourists, too many tourists permitted at one time, and lack of local involvement (Krüger 2005). Often local people do not end up benefiting, and ecotourism funds do not get put into conservation (Kinnaird and O'Brien 1996). Overall, tourism negatively affects primates throughout Vietnam, primarily through infrastructure, roads, noise, pollution, and traffic (Stenke and Chu Xuan Canh 2004; Dinh Thi Phuong Anh et al. 2010; Le Khac Quyet and Nguyen Vu Khoi 2010), but also by creating a demand for rare and exotic souvenirs (including illegal forest resources) (Workman 2004).

Even once primates are habituated, contact with tourists (Kinnaird and O'Brien 1996; Behie et al. 2010; Maréchal et al. 2011) and the associated management practices (Berman et al. 2007) can be stressful, resulting in changed behaviour (Kinnaird and O'Brien 1996; Grossberg et al. 2003; Klailova et al. 2010) as well as increased disease transmission via direct contact, coughing, sneezing, spitting, and open wounds (Cowlishaw and Dunbar 2000; Muehlenbein et al. 2010). For example, in a study of silverback western lowland gorilla (*Gorilla gorilla gorilla*), a decrease in gorilla-human distance is associated with increased aggression, resting, and monitoring, and a decrease in foraging behaviour (Klailova et al. 2010). Chimpanzees (*Pan troglodytes*) have suffered population declines due to respiratory disease outbreaks as a result of habituation (Köndgen et al. 2008; Pusey et al. 2008); exposure to researchers predicts subadult mortality better than deforestation rate (cited in Köndgen et al. 2008). In addition to large-bodied apes, olive baboons and mantled howler monkeys (*Alouatta palliata*) have suffered from anthroponic disease outbreaks (Wallis and Lee 1999).

It is unfortunate that Cat Ba langurs are so vulnerable that they cannot be used as an ecotourist attraction until their population has increased to a viable and sustainable level (Nadler et al. 2003; Stenke and Chu Xuan Canh 2004), especially considering the dependence locals have on tourism (Section 2.1.4, Chapter 2). The tourism trade on the island is, however, relatively unregulated: despite there being 44 tour agencies operating, only two are legally licensed to operate (N Leonard pers. comm. 2016), and although there

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[5] I was not able to find any comparable statistics on primate ecotourism.

is not any ‘official’ Cat Ba langur tourism on the island, there is completely uncontrolled incidental tourism occurring. ‘Incidental tourists’, who briefly visit a site for a nonecotourism reason (e.g. archeology or geology) and end up seeing wildlife, are less interested in environmental education and conservation values, and more interested in making wildlife react/move, than those who are specifically ecotourists (Grossberg et al. 2003).

The Cat Ba tourists often go into protected areas without ever knowing they are not supposed to be there (N Leonard pers. comm. 2014), while they often approach to within 2-10 metres of the langurs (C Johnson pers. comm. 2014), which is much closer than I ever got (50-300 metres). In the course of this study, sometimes up to five tourist boats (driven by local fishermen) would stop when they saw our boat near langurs, and crowd the langurs (Figure 7.12), shouting or throwing things and getting much closer than I ever did. When CBNP staff working on my project asked them to leave, they would ignore him, and he had no further power. This is a very serious problem, and the CBNP staff should have more enforcement authority to prevent such harassment (Section 7.2.1).

Figure 7.12: Tourists (left and centre) illegally being shown langurs by a local tour operator (right). Photo taken Dec 2014 by R Hendershott

These interactions are particularly worrisome as there is a chance that tourists are a source of stress for the Cat Ba langurs, as seen in other primates, which may have repercussions for reproduction and population viability (Berman et al. 2007; Chapman et al. 2007b; Martínez-Mota et al. 2007; Rangel-Negrín et al. 2009; Behie et al. 2010; Jaimez et al. 2012; Dunn et al. 2013; Rimbach et al. 2013). For example, black howler monkeys

(*Alouatta pigra*) that are regularly exposed to tourists have higher cortisol/stress levels (Behie et al. 2010). Tibetan macaques (*Macaca thibetana)* tend to respond to loud tourists with threats (Ruesto et al. 2010) and are generally more aggressive, especially toward infants, when exposed to tourists (resulting in increased infant mortality) (Berman et al. 2007). Barbary macaque (*Macaca sylvanus)* stress levels go up when aggressive encounters with tourists increase, and males self-scratch (i.e. are more anxious) the more tourists that are present (Maréchal et al. 2011). The higher stress levels may be an artefact of humans introducing highly contested food items (Hosey 2005) or due to environmental unpredictability (Behie et al. 2010), possibly caused by habitat modification.

Therefore, while the benefits of tourism are financial for those living in Cat Ba town, the cost is one of biointegrity and biodiversity for the island. The ecological impact of tourists' presence must be considered before ecotourism can be considered a viable option for Cat Ba langurs (Stenke and Chu Xuan Canh 2004); yet, despite their vulnerability, tourism of the langurs *is* occurring – with no funds going towards conservation – and needs to be controlled. At this point, Cat Ba tourists are completely uneducated on how to act around wildlife, and they are often unaware that their actions or poor health may be detrimental to local primates. If they were trained in appropriate behaviours, it may result in animals that are less stressed by tourist presence, and a better experience for the tourists themselves. Reducing the impacts of human interactions can be achieved by teaching tour operators appropriate behaviours when they are near langurs (possibly through the CBLCP education program), while tourists can be educated through informational posters, brochures, literature, and informal lectures about why they should not ask to see langurs (Grossberg et al. 2003; Muehlenbein et al. 2010) and appropriate behaviours to use when around animals. All parties need to understand how to reduce impacts on already threatened wildlife through their daily interactions.

There is evidence that tourists benefit from education about appropriate behaviours when around wild (Orams and Hill 1998) and captive (Zager 2011) animals, and increased awareness of the environmental synergy that is an interconnected ecosystem (Forestell 1993). For example, tourists who engage in feeding wild dolphins (*Tursiops truncates* and *Sousa chinensis*) are less likely to disturb the animals by touching them, and receive fewer cautions from staff, if they have undergone an educational program before starting to feed the animals (Orams and Hill 1998). When chimpanzee zoo visitors are provided with informational signage on friendly chimpanzee behaviours or a trained docent, visitor behaviour leads to more positive interactions between the captive and visiting primates (Zager 2011). Training tourists in conservation issues can make them effective ambassadors for conservation.

There is no easy solution to the issue of illegal ecotourism on Cat Ba Island. There is the risk that by training tour operators and tourists of appropriate behaviours that this may signal that langur tourism is condoned. This may then lead to increased interactions and habituation, which is dangerous considering the risk of poaching. Alternatively, providing no guidelines does not prevent the incidental ecotourism from occurring. Therefore, some very basic rules need to be established to reduce negative impacts on the langurs. Tourist groups should be limited in size and proximity (Kinnaird and O'Brien 1996; Wallis and Lee 1999; Cowlishaw and Dunbar 2000; Muehlenbein et al. 2010; Ruesto et al. 2010; Maréchal et al. 2011), their visit should have a limited duration (Muehlenbein et al. 2010), and they should only approach via boats, as langurs move farther away from approaches on land (Nadler and Ha Thang Long 2000). They should avoid eating, spitting, blowing their noses, smoking, and leaving rubbish, and should use facemasks, gloves, hand washing, and shoe disinfectant if they get close to the animals (Muehlenbein et al. 2010). Noise levels and aggressive behaviours need to remain low so as to minimise disturbance (Ruesto et al. 2010; Maréchal et al. 2011), which can be mediated by a trained guide (Orams and Hill 1998). Tourists and tour operators need to be informed of appropriate behaviours, while emphasising that they should not seek out the langurs due to their vulnerability. I do not support the langurs being used for ecotourism purposes, but acknowledge that the unregulated access is a problem that must be dealt with.

7.3 Behavioural Indicators of Habitat Degradation

Animal behavioural studies can aid in conservation management efforts (Knight 2001; Kotler et al. 2007; Lindell 2008). Documenting animal behaviour, especially over time in response to habitat loss, degradation, and fragmentation, may be the first step to assessing individual health, stress, and habitat quality (Searle et al. 2007). These signs can come about before population declines or measures of habitat quality are assessed, thus providing an early warning system for conservation management (Searle et al. 2007; Lindell 2008; Berger-Tal et al. 2011). Foraging behaviour, in particular, can be a helpful indicator of habitat quality (with higher availability of foods indicating a higher quality habitat); foraging and travel time is dictated by food availability, so animals in lower quality habitat may alter their foraging behaviour to accommodate the increase in scramble competition and reduced food availability (Kotler et al. 2007; Lindell 2008).

Degraded forests may not have as many food resources as more pristine forests (Johns 1986; Medley 1993; Tutin 1999; Arroyo-Rodríguez and Mandujano 2006; Wong et al. 2006; Guo et al. 2008; Dunn et al. 2010; Wang et al. 2011). For example, François' langur habitat that is fragmented, cultivated, and open has fewer plant species and food resources, and smaller plant sizes, compared to less disturbed habitat that has greater vegetation coverage with larger and taller trees that produce food for the langurs on a more consistent basis (Hu 2007). A reduction in food availability or quality due to anthropogenic modification can necessitate increased time traveling across a larger range in search of high-quality resources, which can be physiologically stressful. For example, both poor-quality diets among Ugandan red colobus (*Piliocolobus tephrosceles*) (Chapman et al. 2007b), and increased travel time in mantled howler monkeys (Dunn et al. 2013), are associated with increased stress levels. Ugandan red colobus (Chapman et al. 2006; Chapman et al. 2007b), howler monkeys (*Alouatta* spp.) (Martínez-Mota et al. 2007; Dunn et al. 2013), gray-cheeked mangabeys (*Lophocebus ugandae*) (Jaimez et al. 2012), and spider monkeys (*Ateles* spp.) (Rangel-Negrín et al. 2009; Rimbach et al. 2013) that live in small forest fragments have higher stress levels (measured via cortisol and fecal glucocorticoid levels) than those living in larger fragments or continuous forests.

Additionally, dietary stress from limited resource supply can lead to reduced immune system efficacy, which increases susceptibility to diseases (Yeager and Kirkpatrick 1998) and parasitic infections (Holmes 1995; Gillespie et al. 2005). This can be seen in Ugandan red colobus (Chapman et al. 2007b). Parasitic infections and reduced food availability resulted in a population decline for this species (Chapman et al. 2006). Among black howler monkeys, a reduction in fruit availability leads to a decrease in population density; at the same time, parasitic infections and less fruit availability lead to increased stress, which also decreased population density (Behie and Pavelka 2013). Furthermore, stressed animals may be cognitively impaired, limiting their ability to find food or problem solve (Teixeira et al. 2007).

Social and environmental stress can ultimately lead to a decline in population size for primates, as females may be unable to conceive (Wingfield and Sapolsky 2003;

Heistermann et al. 2004), carry, and nurse infants (Yeager and Kirkpatrick 1998), especially if their body fat reserves are limited (Mori 1979; Mori et al. 1997). A reduction in habitat quality or sufficient food resources may lead to later maturation and a delayed start to reproduction, resulting in lower lifetime fecundity and increased mortality rates (especially for low-ranking or young individuals) (Mori 1979; Sugiyama and Ohsawa 1982; Altmann et al. 1993; Mori et al. 1997; Cowlishaw and Dunbar 2000). Tana river mangabeys (*Cercocebus galeritus*) living in disturbed forests have lower reproductive success (Mbora et al. 2009), while guerezas (*Colobus guereza*) have higher reproductive rates in habitats with more trees (Dunbar 1987). Among white-headed langur groups, those in higher quality habitat have more young group members (Li and Rogers 2005a), suggesting that such groups thrive better than those in lower quality habitat.

Cat Ba langurs have reportedly low reproductive success (Stenke and Chu Xuan Canh 2004; Schrudde et al. 2008; Mittermeier et al. 2009): between 2001 and 2012 there were 2.4-2.7 births/year, or 0.045 births/female/year (Phan Duy Thuc et al. 2014; Leonard et al. 2016a), which is one-tenth the rate reported for white-headed langurs (0.47 births/female/year) (Jin et al. 2009a). Thus, it is possible that Cat Ba langurs are exhibiting low fecundity due to chronic stress, which may be a result of exposure to humans and reduced food availability (due to a degraded habitat). This ultimately makes animals more vulnerable to disease transfer and malnutrition, resulting in a population decline. Although there have been several Cat Ba langur births reported since 2014, the population as a whole seems to have declined to just over 50 individuals in the last year (Leonard et al. 2016a). This demonstrates the importance not only on increasing birth rates, but also decreasing mortality at vulnerable life stages (Section 6.4.2, Chapter 6).

The remainder of this section addresses how animals may alter their behaviours, habitat use, and development as a result of habitat change, all of which may indicate that animals are stressed.

7.3.1 Activity Budgets

Animals' activity budgets are often altered in disturbed habitats, both due to a reduction in resources and exposure to humans. For example, red-shanked douc groups which experience higher human pressure travel more, stay inactive longer, and sleep less (Phiapalath and Suwanwaree 2010). Sumatran surili (*Presbytis cf. melalophos*) spend more time resting and less time eating and locomoting in logged habitat (Johns 1986). François' langurs have been found to both increase (Huang et al. 2007) and decrease (Hu 2007; Yang et al. 2007) rates of inactivity in lower-quality or disturbed habitat. Some species trade inactivity for more travel (Yang et al. 2007) and vigilance (Phiapalath and Suwanwaree 2010). The differences between species may reflect energy conservation vs. maximising strategies (Schoener 1971; Oates 1987; Hemingway and Bynum 2005) or the type of disturbance (e.g. immediate human threat vs. a general degradation of habitat). The increased time spent traveling and reduced time spent inactive is a pattern seen in the dry vs. wet seasons for limestone langurs (Section 3.4.1.2, Chapter 3), suggesting they are continuing their energy maximising strategy during not only *times* of low food resources but also *places*.

Social time may depend on habitat quality. For example, Japanese macaques (*Macaca fuscata*) living in a resource poor environment spend less time grooming (as they must spend more time foraging) than those living in an environment with more resources (Agetsuma and Nakagawa 1998). This is found across primates, where habitats with more available resources allow for more social grooming time (Lehmann et al. 2007) and social time in general (Dunbar 1992). Gelada baboon (*Theropithecus gelada*) young play more when there are more food options (Barrett et al. 1992), while young grivet monkey (*Chlorocebus aethiops*) play rates correlate with monthly rainfall patterns, and, thus, available energy from food (Lee 1984). Similarly, play rates increase when fewer leaves are in a langur's diet (Sommer and Mendoza-Granados 1995), and when habitat quality increases for limestone langurs (Li and Rogers 2004a; Hu 2007). Social activities in general increase for François' langurs in high-quality habitat (Huang et al. 2007). In this study the Cat Ba langurs spend less time socialising in the dry season, which is when leaves are eaten at higher rates (Sections 3.4.1.2 and 3.4.2.2, Chapter 3), indicating that langurs may have more disposable energy for social behaviours when their diet does not include so many [presumably mature] leaves.

Similar to seasonal variation in food supply, colobine options for handling disruption to food resources due to habitat fragmentation and disturbance include increasing or decreasing dietary diversity (including eating more exotic species or fallback foods) (Johns 1986; Li and Rogers 2006; Wong et al. 2006; Chapman et al. 2007a; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Hu 2007; Guo et al. 2008; Li et al. 2009) and increasing feeding time (Li and Rogers 2006; Huang et al. 2007). Often this means animals are stressed by eating lower-quality mature leaves – which are less digestible (Waterman et al. 1980; Davies and Baillie 1988) and take longer to process (Milton 1984) than other plant parts – and having to devote more of their activity budget to finding adequate nutrition. Feeding effort (time spent feeding and traveling divided by time spent inactive) and stress increase for groups that rely more heavily on leaves (Dunn et al. 2010).

Thus, attention must be paid to how the Cat Ba langurs are spending their time. It is unknown how or if the subjects of this study have changed their behaviour, or how their diet has shifted, to accommodate human disturbance, but if future studies find an activity budget for Cat Ba langurs that indicates significantly increased foraging (especially on mature leaves) and reduced inactivity and social behaviours due to increased needs for foraging and travel, the animals may be pushing the limit of their energy budgets. As foraging time is a necessity that cannot be forgone (Searle et al. 2007) (and this dictates time spent moving), social and resting time are more dispensable (Dunbar and Dunbar 1988; Dunbar 1992). Therefore, care should be taken to document how foraging, locomotion, inactivity, and social behaviours (as a proportion of the activity budget) shift with a changing environment. Assessing these changes against a baseline (this study) can help to identify if animals are becoming physiologically stressed (Searle et al. 2007). Given the high rates of inactivity and social behaviours by adults (Figure 3.4, Chapter 3), this age class may be the most sensitive indicator of disturbance.

7.3.2 Habitat Use and Range Size

Primates can become locally extinct and/or have their home range limited by the total area available in a habitat fragment (Lovejoy et al. 1986; Harcourt and Doherty 2005; Benchimol and Peres 2014), especially species on islands or ones that require large home ranges (Cowlishaw and Dunbar 2000; Benchimol and Peres 2014). While some primates decrease their home range size in fragmented/degraded habitats due of the lack of areas that can be utilised, inability to cross between fragments, and/or increased crowding (Decker 1994; Tutin et al. 1997; Onderdonk and Chapman 2000; Bicca-Marques 2003), others increase how far they travel/range in search of adequate food resources as they need more space per individual for survival (Sussman 1991; Mbora et al. 2009; Phiapalath and Suwanwaree 2010).

Limestone langurs tend to respond with the latter, energy-maximising strategy. White-headed langurs living in poor quality, disturbed habitat increase their range and eat foods from a wider range of species (Li and Rogers 2005a). Interestingly, studies have found that François' langurs in fragmented and disturbed habitats spend more time traveling (Yang et al. 2007) across larger ranges, as they must cross open forests, bush patches, and farmlands (Hu 2007) but François' langurs in another part of China decrease time spent moving in lower-quality habitats (Huang et al. 2007). Regardless of travel time, ranges in higher quality habitat can be as small as 46ha (0.24 individuals/ha) while those in poorer quality habitat can be as large as 111ha (0.13 individuals/ha) for François' langurs (Hu 2007). This may be due to food distribution, canopy coverage or tree size, or other aspects of their microhabitats.

The home ranges for the two Cat Ba langur groups are similar to those of other limestone langurs living in degraded and fragmented habitat (Section 4.4.1, Chapter 4). The fact that the home ranges increase in the wet season indicates that the langurs are having to increase the areas searched for more widely dispersed food items (such as fruit, which is eaten at higher rates in the wet season: Section 3.4.2.2, Chapter 3). If future studies show a dramatic increase in home range size beyond seasonal variation, this may be indicative of preferred foods being less available due to habitat disturbance. Current work on habitat quality and historical patterns of ranging (being done by K Apthrop) will help elucidate how typical the two Cua Dong groups I studied are, as well as providing a baseline for range contraction/expansion with increasing human pressures.

In addition to home range size, habitat disturbance can affect how animals use their remaining habitats, including differences across microhabitats (Schwarzkopf and Rylands 1989). For example, logging has resulted in a shift in home ranges away from disturbed areas for golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Guo et al. 2008) and margarita langurs (*Trachypithecus margarita*) (González Monge 2016). Golden snub-nosed monkeys do not use areas with highly preferred food availability if they have been disturbed by humans (Li et al. 2000). Limestone langurs may be limited by available sleeping sites (Zhou et al. 2007; Huang et al. 2008a; Zhou et al. 2011), access to rare plant foods (Li et al. 2003), and water (Zhou et al. 2011). Therefore, the presence or absence of these factors may influence home range size and location. For example, limestone langurs rely on steep cliffs for sleeping ledges and caves, and the availability of these areas may create a safety limitation (in terms of predation risk) on ranging (Section 4.4.3, Chapter 4).

Limestone langurs are not averse to discontinuous canopies or life on both rocks and trees (Section 4.4.2, Chapter 4), given the stunted, discontinuous, and shrubby limestone karst habitat (34% of François' langur habitat: Zeng et al. 2013). Although it is suggested that limestone langurs prefer these shrubby forests (Nadler and Ha Thang Long 2000), this may be a result of marginalisation (Li and Rogers 2005a), especially as more thorough analysis of habitat preferences for limestone langurs indicate the desirability of high vegetation coverage and continuous forests, and the undesirability of shrubby areas (Li and Rogers 2005b; Hu 2007; Zeng et al. 2013). François' langurs use closed canopied areas within their home ranges more intensively than other parts of their habitat (Hu 2007). Cat Ba langurs often use sparsely covered areas and rocks (Figure 7.13), with over half their time spent in these shrubby areas (Section 4.4.2, Chapter 4). However, given the preference of other limestone langurs for denser vegetation, this suggests that these animals may respond positively to an increase in vegetation, and reduce their home range size. This could be helped by conservation projects focusing on planting trees, which would increase food options and provide a more desirable habitat, which then may increase reproduction (Dunbar 1987).

Figure 7.13: Langurs sitting on rocks in a sparsely covered area of their habitat. The langurs spend a lot of time in areas that can be called ‘shrubby’. Photo taken Aug 2014 by R Hendershott

Valleys and lower levels of limestone karst hills have the densest and tallest vegetation and greatest species diversity (Section 2.1.2, Chapter 2), resulting in these areas having the best food options for limestone langurs (Li and Rogers 2004a; Huang et al. 2008b; Zhou et al. 2013b; Nguyen Hiep pers. comm. 2014). Therefore, it is these areas where langurs concentrate their foraging efforts (Li and Rogers 2005a; Huang et al. 2008b; Schneider et al. 2010; Section 4.4.2.1, Chapter 4). Unfortunately, these limited areas are used for human agriculture (Figure 7.2) precisely *because* they are the lushest and most productive areas. Additionally, I did see people accessing uncultivated valleys in Cua Dong, primarily for firewood collection.

The destruction of valley habitat creates a direct limit to where the langurs can range. Limestone langurs are wary of coming down to ground level (Li and Rogers 2005a; Zhou et al. 2013a; Section 4.4.2.1, Chapter 4) or getting too close to cultivated valleys (Zeng et al. 2013), presumably because of dangers from humans and dogs. In fact, François’ langrus avoid using food-rich but predator-risky areas (Zhou et al. 2013a). Therefore, ideally, valleys should be left alone or uncultivated (Nadler et al. 2003) to ensure that the langurs have adequate food resources and to reduce fragmentation and isolation of social groups. Additionally, all activities that are occurring within langur home ranges – especially valleys – need to be heavily monitored.

7.3.3 Development and Maturation

Being food limited due to seasonal fluctuations in resource supply, competition, and/or habitat degradation can lead to changes in timing of development. This can include losing the natal coat slower when mothers face high scramble competition (Borries et al. 2008), playing less (Barrett et al. 1992; Sommer and Mendoza-Granados 1995; Li and Rogers 2004a; Hu 2007), and delayed maturation and a reduction in reproduction (Sugiyama and Ohsawa 1982; Altmann et al. 1993; Janson and Goldsmith 1995; Mori et al. 1997; Cowlishaw and Dunbar 2000; Koenig 2002; Borries et al. 2008). For example, unprovisioned female Japanese macaques living in a resource-poor environment develop their first perineal swelling almost three years later than provisioned females (Mori et al. 1997), while baboons (*Papio* spp.) grow larger, develop canines and testes (for males), and reach menarche (for females) at a younger age in captivity or with supplemented food than in the wild (Altmann et al. 1981; Altmann et al. 1993). Among Phayre's leaf monkeys (*Trachypithecus phayrei*), infants living in large groups lose their natal coat roughly six weeks slower, and are weaned three months later, than those in smaller groups (Borries et al. 2008). This is presumably due to the scramble competition the mothers face, resulting in lower energetic net gain for those living at higher densities. Alternatively, this could have to do with a shift in maternal investment due to a perceived infanticidal risk (Bădescu et al. 2016).

The Cat Ba langurs appear to lose their natal coat slightly later than Delacour's (Agmen 2014) and François' (Hu 2007) langurs, suggesting they may be exposed to poorer quality habitat than the other species (Section 6.4.2, Chapter 6; Figure 7.14), or face reduced infanticidal risk (Bădescu et al. 2016) due to the lack of dispersal between isolated subpopulations. It should be noted, however, that the Delacour's study is based on captive infants (Agmen 2014) and there is a high amount of individual variation in maturation rates (Altmann et al. 1981). However, it is fairly common for langurs to be done with their pelage shift by six months of age (Borries et al. 2008), thus demonstrating that Cat Ba langurs appear to be outside of the normal developmental timing for langurs. Regardless, documenting how Cat Ba langur infants develop in the sanctuary/Cua Dong and over time may be indicative of a reduction or improvement of habitat quality, depending on the rate at which individuals lose their natal coats, engage in play behaviour, and mature to a reproductive age. Additionally, monitoring these developmental stages in relation to birth rates can help determine if there is higher-than-expected mortality of young animals, which may be a cause for stunted population growth.

Figure 7.14: The pelage progression of Cat Ba langurs may be subject to the quality of the habitat. Here a 1-2 month old infant with an entirely orange tail clings to an adult female; in other limestone langurs 1-2 month old infants are reported to have darkened or mostly black tails (Section 6.4.2, Chapter 6). Photo taken March 2014 by R Hendershott

7.4 Conclusion

Long-term solutions need to be addressed for the conservation of Cat Ba langurs. This includes increasing patrols and enforcement, educating the local villagers about the importance of the langurs and other poached species, providing sustainable economic support for locals, educating and motivating rangers to actively conduct patrols and issue fines, and providing corridors for isolated subpopulations. A drastic intervention that is unlikely to be enacted due to economic priorities, but would be beneficial to the langurs, is limiting infrastructure development. I recommend that once the captive langurs have been assessed for diseases and are behaviourally competent, they should be released so that they can contribute to the wild population’s reproduction. Ecotourism is a complicated issue, but overall it would be beneficial for tour operators and tourists to be educated about how to minimise their impact on the wildlife, and this should be added to the CBLCP education agenda.

Evidence for the efficacy of these methods can be documented through significant differences in activity and dietary budgets, habitat use and home range size, and young development and maturation rates. If there are significant differences in these measurements, this may indicate individuals are being physiologically stressed by a decreased availability of resources and habitat degradation, and is therefore deserving of more intensive research into stress levels and how they relate to the ongoing loss and degradation of habitat. Conversely, improvements in habitat quality and food supply due to conservation efforts could result in a reduction of stress levels in the future.

This dissertation represents the first long-term behavioural study on the Critically Endangered Cat Ba langur, which gives us essential information regarding their behaviour, habitat use and development. Given the importance of immediate conservation action due to low population numbers and continuing threats to their habitat, this thesis will add value by creating a baseline of Cat Ba langur behaviour; this existing record can then be used to assess behavioural, ranging, or developmental changes due to either on-going habitat degradation or improvements in habitat quality due to conservation efforts. This study has also placed this species into a phylogenetic context, by relating all results to those of other, closely related, limestone langurs living in Laos, Vietnam, and China. By assessing developmental stages and clearly delineating age classes by coat colouration, this study will aid census workers who will be able to more accurately monitor and age individuals. These censuses are key to tracking population growth and decline by age-sex class, which help inform on conservation management. When this information is used in conjunction with the ongoing nutritional and habitat quality studies, it will aid in conservation management, as efforts can be focused on preserving the most critical parts of their habitat and food sources before this species experiences another devastating population decline.

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Appendix

Table 1: P-values for pairwise comparisons noting significant differences in behavioural rates between time periods, done for each of the behaviours that showed significant differences across time periods [(a) foraging, (b) social, (c) locomotion, and (d) ‘other’]. The percent (%) time spent in each behaviour in each time period can be found in Figure 3.1 and Table 3.2, Chapter 3. Significant differences indicated with an asterisk (*); only significant differences compared to adjacent time periods are reported in the chapter.

foraging	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.491	0.015*	<0.001*	0.341
8:00-11:00	0.491	n/a	0.039*	<0.001*	0.703
11:00-14:00	0.015*	0.039*	n/a	0.198	0.083
14:00-17:00	<0.001*	<0.001*	0.198	n/a	<0.001*
17:00-20:00	0.341	0.703	0.083	<0.001*	n/a

(a)

social	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.380	0.010*	0.001*	<0.001*
8:00-11:00	0.380	n/a	0.046*	0.010*	<0.001*
11:00-14:00	0.010*	0.046*	n/a	0.842	0.633
14:00-17:00	0.001*	0.010*	0.842	n/a	0.770
17:00-20:00	<0.001*	<0.001*	0.633	0.770	n/a

(b)

locomotion	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.546	0.001*	0.725	0.028*
8:00-11:00	0.546	n/a	0.005*	0.463	0.008*
11:00-14:00	0.001*	0.005*	n/a	0.006*	<0.001*
14:00-17:00	0.725	0.463	0.006*	n/a	0.195
17:00-20:00	0.028*	0.008*	<0.001*	0.195	n/a

(c)

‘other’	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.437	0.818	0.018*	0.007*
8:00-11:00	0.437	n/a	0.492	0.003*	0.001*
11:00-14:00	0.818	0.492	n/a	0.177	0.178
14:00-17:00	0.018*	0.003*	0.177	n/a	0.881
17:00-20:00	0.007*	0.001*	0.178	0.881	n/a

(d)

Table 2: P-values for pairwise comparisons noting significant differences in nursing between time periods for adult females. The percent time spent nursing in each time period can be found in Section 3.3.1.1, Chapter 3. Significant differences indicated with an asterisk (*); only significant differences compared to adjacent time periods are reported in the chapter.

nursing	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.259	0.075	0.531	0.071
8:00-11:00	0.259	n/a	0.210	0.160	0.005*
11:00-14:00	0.075	0.210	n/a	0.048*	0.010*
14:00-17:00	0.531	0.160	0.048*	n/a	0.522
17:00-20:00	0.071	0.005*	0.010*	0.522	n/a

Table 3: P-values for pairwise comparisons noting significant behavioural differences between age classes, done for each of the behaviours that showed significant differences across age classes that could be assessed [(a) social, (b) locomotion, and (c) ‘other’]. The percent (%) time spent in each behaviour by each age class can be found in Figure 3.4 and Table 3.5, Chapter 3. Significant differences indicated with an asterisk (*).

social	adult	subadult	young
adult	n/a	0.062	<0.001*
subadult	0.062	n/a	0.388
young	<0.001*	0.388	n/a

(a)

locomotion	adult	subadult	young
adult	n/a	0.078	<0.001*
subadult	0.078	n/a	0.006*
young	<0.001*	0.006*	n/a

(b)

‘other’	adult	subadult	young
adult	n/a	0.150	<0.001*
subadult	0.150	n/a	<0.001*
young	<0.001*	<0.001*	n/a

(c)

Table 4: P-values for pairwise comparisons noting significant differences in leaf consumption rates between time periods. The percent time spent consuming leaves within each time period can be found in Figure 3.6 and Table 3.6, Chapter 3. Significant differences indicated with an asterisk (*); only significant differences compared to adjacent time periods are reported in the chapter.

leaves	5:00-8:00	8:00-11:00	11:00-14:00	14:00-17:00	17:00-20:00
5:00-8:00	n/a	0.109	<0.001*	0.042*	0.096
8:00-11:00	0.109	n/a	0.006*	0.566	0.790
11:00-14:00	<0.001*	0.006*	n/a	0.063	0.046*
14:00-17:00	0.042*	0.566	0.063	n/a	0.801
17:00-20:00	0.096	0.790	0.046*	0.801	n/a

Table 5: P-values for pairwise comparisons noting significant differences in how behaviours are used on various hill types, done for each of the behaviours that showed significant differences across hill types [(a) inactivity, (b) foraging, (c) social, (d) locomotion, and (e) 'other' behaviours]. The percent time spent in each behaviour on each hill type can be found in Figure 4.3c and Table 4.1, Chapter 4. Significant differences indicated with an asterisk (*).

inactivity	exposed slope	ground	steep cliff	summit	valley
exposed slope	n/a	0.662	<0.001*	<0.001*	0.346
ground	0.662	n/a	0.155	0.083	0.991
steep cliff	<0.001*	0.155	n/a	0.196	0.002*
summit	<0.001*	0.083	0.196	n/a	<0.001*
valley	0.346	0.991	0.002*	<0.001*	n/a

(a)

foraging	exposed slope	ground	steep cliff	summit	valley
exposed slope	n/a	0.300	<0.001*	<0.001*	0.298
ground	0.300	n/a	0.876	0.637	0.147
steep cliff	<0.001*	0.876	n/a	0.011*	0.014*
summit	<0.001*	0.637	0.011*	n/a	0.001*
valley	0.298	0.147	0.014*	0.001*	n/a

(b)

social	exposed slope	ground	steep cliff	summit	valley
exposed slope	n/a	0.479	<0.001*	0.412	0.859
ground	0.479	n/a	0.230	0.621	0.549
steep cliff	<0.001*	0.230	n/a	0.005*	0.148
summit	0.412	0.621	0.005*	n/a	0.761
valley	0.859	0.549	0.148	0.761	n/a

(c)

locomotion	exposed slope	ground	steep cliff	summit	valley
exposed slope	n/a	0.285	0.021*	<0.001*	0.392
ground	0.265	n/a	0.435	0.067	0.185
steep cliff	0.021*	0.435	n/a	<0.001*	0.062
summit	<0.001*	0.067	<0.001*	n/a	0.159
valley	0.392	0.185	0.062	0.159	n/a

(d)

'other'	exposed slope	ground	steep cliff	summit	valley
exposed slope	n/a	0.772	<0.001*	0.941	0.443
ground	0.772	n/a	0.441	0.761	0.519
steep cliff	<0.001*	0.441	n/a	<0.001*	0.009*
summit	0.941	0.761	<0.001*	n/a	0.507
valley	0.443	0.519	0.009*	0.507	n/a

(d)

Table 6: Sleeping sites of Cat Ba langurs reliably identified in the course of this study. In calculating preference, the number of sites of each type is used as the 'expected' rate of site type available to the langurs, while the 'observed' rate is based on the number of times the site type was observed to be used. Note: C=cliff, L=ledge, T=tree, IN=internal, EX=external, N=north, E=east, S=south, W=west, NE=northeast, NW=northwest, SE=southeast, low=lower third of mountain, mid=middle third of mountain, upp=upper third of mountain, SP=vegetation is sparse (less than half of surrounding 10m radius is covered), DEN=vegetation is dense (more than half of surrounding 10m radius is covered), SC=steep cliff

code	used by which group?	times used in wet season (May-Oct)	times used in dry season (Nov-April)	type	IN/EX part of Cua Dong	direction facing	strata	surrounding vegetation	hill type
2	B	0	1	C	IN				
4	B	1	2	L	EX	SE	low	SP	SC
5	A	1	3	L	IN	N	mid	SP	SC
7	B	0	2	L	IN		mid	SP	
8	A	1	1	L	IN		mid	SP	SC
9	B	0	2	L	IN	E	mid	SP	
10	B	2	1	C + L	IN	NE	mid	SP	SC
11	A	3	1	C + L	IN		mid	SP	SC
12	A	8	9	C	IN	NW-W	mid	SP	SC
14	B	3	1	L + T	IN		mid	SP	SC
15	A	9	4	L	IN		mid	SP	SC
16	A+B	1 (Group B)	2 (Group A)	L	IN		mid	SP	SC
17	A	1	0	L	IN		mid	SP	SC
18	A	1	0	L	EX	NE	low	SP	SC
19	B	1	0	L	IN		upp	DEN	SC
20	B	0	1	L	IN		mid	SP	SC
21	A	2	0	C + L	EX		mid	SP	SC
22	B	1	1	L	IN		mid	SP	SC
23	B	2	2	C + L	EX	E	low	SP	SC
26	B	0	1	C	EX	E	low	SP	SC
27	A	0	1	L	EX	N	mid	SP	SC
29	B	0	1	C	EX	S-SE	upp	SP	SC

Table 7: P-values for pairwise comparisons noting significant differences in (a) grooming and (b) social playing rates between age classes for those behaviours with significant age variation. The percent (%) time spent grooming or socially playing by each age class can be found in Figure 5.3 and Table 5.2, Chapter 5. Significant differences indicated with an asterisk (*).

groom	adult	subadult	young
adult	n/a	0.061	<0.001*
subadult	0.061	n/a	<0.001*
young	<0.001*	<0.001*	n/a

(a)

social play	adult	subadult	young
adult	n/a	<0.001*	<0.001*
subadult	<0.001*	n/a	<0.001*
young	<0.001*	<0.001*	n/a

(b)

Table 8: P-values for pairwise comparisons noting significant differences in rates of being proximate or alone between (a) age and (b) age-sex classes. The percent (%) time spent alone within each age or age-sex class can be found in Table 5.4 and Figure 5.5, Chapter 5. Significant differences indicated with an asterisk (*).

proximity/alone	adult	subadult	young
adult	n/a	<0.001*	<0.001*
subadult	<0.001*	n/a	<0.008*
young	<0.001*	<0.008*	n/a

(a)

proximity/alone	adult male	adult female	subadult male	subadult female	young male	young female
adult male	n/a	<0.001*	0.870	0.094	<0.001*	0.001*
adult female	<0.001*	n/a	<0.001*	<0.001*	<0.001*	<0.001*
subadult male	0.870	<0.001*	n/a	0.130	0.001*	0.020*
subadult female	0.094	<0.001*	0.130	n/a	0.198	0.766
young male	<0.001*	<0.001*	0.001*	0.198	n/a	0.077
young female	0.001*	<0.001*	0.020*	0.766	0.077	n/a

(b)

Table 9: P-values for pairwise comparisons noting significant differences in time spent alone or in proximity across behaviours. The percent (%) time spent alone while engaging in each beahviour can be found in Section 5.3.4, Chapter 5. Significant differences indicated with an asterisk (*).

proximity/alone	inactivity	forage	social	locomotion	'other'
inactivity	n/a	<0.001*	<0.001*	<0.001*	0.001*
forage	<0.001*	n/a	<0.001*	0.015*	<0.001*
social	<0.001*	<0.001*	n/a	<0.001*	<0.001*
locomotion	<0.001*	0.015*	<0.001*	n/a	<0.001*
'other'	0.001*	<0.001*	<0.001*	<0.001*	n/a

Table 10: P-values for pairwise comparisons noting significant differences in average number of others in proximity between age-sex classes for (a) both groups combined, (b) Group A, and (c) Group B. The average number of others in proximity within each age-sex class can be found in Table 5.5, Chapter 5. Significant differences indicated with an asterisk (*).

others in proximity (both groups combined)	adult male	adult female	subadult	young
adult male	n/a	<0.001*	0.190	0.003*
adult female	<0.001*	n/a	<0.001*	<0.001*
subadult	0.190	<0.001*	n/a	<0.001*
young	0.003*	<0.001*	<0.001*	n/a

(a)

others in proximity Group A	adult male	adult female	young
adult male	n/a	<0.001*	0.002*
adult female	<0.001*	n/a	<0.001*
young	0.002*	<0.001*	n/a

(b)

others in proximity Group B	adult male	adult female	subadult	young
adult male	n/a	0.002*	0.530	0.278
adult female	0.002*	n/a	<0.001*	<0.001*
subadult	0.530	<0.001*	n/a	0.491
young	0.278	<0.001*	0.491	n/a

(c)

Table 11: P-value of differences in huddle size distributions between huddles that involve at least one individual of a particular age-sex class. Huddle distribution sizes assessed with Komolgorov-Smirnov test for Group A^{a} and Group B ^{b}. Significant results indicated with an asterisk (*). Note: AM=adult male, AF=adult female, SA=subadult, Y=young.

	AM	AF	SA	Y
AM	n/a	<0.001^{a}*/ 0.020^{b}*	0.170^{b}	<0.001^{a}*/ 0.007^{b}*
AF	<0.001^{a}*/ 0.020 ^{b}*	n/a	0.964^{b}	0.787^{a}/1.0^{b}
SA	0.170^{b}	0.964^{b}	n/a	0.701^{b}
Y	<0.001^{a}*/ 0.007^{b}*	0.787^{a}/1.0^{b}	0.701^{b}	n/a

[a] Group A

[b] Group B

Table 12: All observed and possible huddles for (a) Group A and (b) Group B (Groups A and B are separated due to their differing demography and group numbers). All numbers refer to the percent (%) of huddles of that size that the target age-sex class engaged in (for example, in Group A, 11% of adult female dyadic huddles were with the adult male, 63% with a young langur, and 27% with another female, accounting for 100% of adult female huddles of two), and can be seen in Figure 5.8, Chapter 5. All values rounded to the nearest integer. Expected values are calculated through a hypergeometric distribution. In Group A the expected values are given as ranges from the beginning to the end of the study, as three individuals were born into the group during this period. If a particular huddle composition is not possible at the beginning of the study (e.g. five young could not huddle together when there were only four young in the group) the expected value is 0%. In Group A huddles of 11 and 13 were never observed. An asterisk (*) indicates that the observed value is significantly different from the most conservative expected value. Note: AM=adult male, AF=adult female, SA=subadult, Y=young; O=observed rate of association, E=expected or chance rate of association.

huddle size	huddle composition	n=	adult male		adult females		young	
			O	E	O	E	O	E
2	AF-AM	55	87*	45-56	11	9-11		
	AF-Y	317			63*	44-55	78*	45-56
	2AF	135			27*	36-44		
	2Y	80					20*	33-45
	AM-Y	8	13*	44-55			2*	9-11
3	AF-AM-Y	27	55	55-56	14	11	16	9-14
	2AF-AM	18	37	18-28	9	7-11		
	2AF-Y	102			53*	44	61*	18-28
	2Y-AM	4	8	17-27			2*	8-9
	2Y-AF	31			16	17-27	19*	42-45
	3AF	14			7	11-17		
	3Y	2					1*	8-18
4	AM-3AF	5	18	6-12	4	4-7		
	AM-2AF-Y	19	68	36-48	16	15-19	18	6-12
	AM-AF-2Y	4	14	36-45	3	7-9	4	15-18
	AM-3Y	0	0	5-12			0	4-6
	4AF	7			6	2-5		
	3AF-Y	34			29	22-29	32	6-12
	2AF-2Y	39			34	29-36	37	30-36
	AF-3Y	8			7	5-12	8	18-30
	4Y	1					1	1-6
5	AM-4AF	3	19	2-4	6	1-3		
	AM-3AF-Y	6	38	18-32	12	11-19	13	3-8
	AM-2AF-2Y	6	38	45-48	12	18-19	13	15-24
	AM-AF-3Y	1	6	16-30	2	3-6	2	12-15
	AM-4Y	0	0	1-5			0	1-3
	5AF	1			2	0-1		
	4AF-Y	11			22	7-13	23	2-4
	3AF-2Y	17			33	27-29	36	15-24
	2AF-3Y	6			12	13-24	13	24-30
	AF-4Y	0			0	1-5	0	4-15

	5Y	0					0	0-2
6	AM-5AF	0	0	0-1	0	0-1		
	AM-4AF-Y	2	12	6-16	7	5-13	7	1-4
	AM-3AF-2Y	11	65	32-48	37	19-29	37	11-24
	AM-2AF-3Y	4	24	32-43	13	13-17	13	22-24
	AM-AF-4Y	0	0	4-16	0	1-3	0	4-11
	AM-5Y	0	0	0-1			0	0-1
	AF-5Y	0			0	0-1	0	0-5
	2AF-4Y	0			0	3-13	0	8-22
	3AF-3Y	8			27	19-26	27	22-24
	4AF-2Y	4			13	13-19	13	5-12
	5AF-Y	1			3	1-3	3	0-1
	6Y	0					0	0-<1
7	AM-5AF-Y	0	0	1-5	0	1-5	0	0-1
	AM-4AF-2Y	11	58	16-36	38	9-29	38	5-18
	AM-3AF-3Y	7	37	43-48	24	23-29	24	22-36
	AM-2AF-4Y	1	5	12-32	3	5-15	3	12-22
	AM-AF-5Y	0	0	0-6	0	0-2	0	0-5
	AM-6Y	0	0	0-<1	0	0-<1	0	0-<1
	5AF-2Y	0			0	2-7	0	1-4
	4AF-3Y	2			7	15-19	7	11-18
	3AF-4Y	7			24	7-23	24	12-22
	2AF-5Y	1			3	0-9	3	0-11
	AF-6Y	0			0	0-1	0	0-1
8	AM-5AF-2Y	1	20	5-17	10	5-17	10	2-8
	AM-4AF-3Y	3	60	30-56	30	24-44	30	15-42
	AM-3AF-4Y	1	20	28-45	10	17-27	10	28-30
	AM-2AF-5Y	0	0	0-18	0	0-7	0	0-15
	AM-AF-6Y	0	0	0-2	0	0-<1	0	0-2
	5AF-3Y	1			10	6-11	10	3-8
	4AF-4Y	3			30	11-18	30	14-15
	3AF-5Y	1			10	0-11	10	0-15
	2AF-6Y	0			0	0-1	0	0-3
9	AM-5AF-3Y	2	67	12-44	67	12-44	67	6-33
	AM-4AF-4Y	0	0	45-56	0	36-44	0	30-56
	AM-3AF-5Y	1	33	0-36	33	0-22	33	0-30
	AM-2AF-6Y	0	0	0-6	0	0-2	0	0-6
	5AF-4Y	0			0	9-11	0	6-11
	4AF-5Y	0			0	0-15	0	0-15
	3AF-6Y	0			0	0-4	0	0-6
10	AM-5AF-4Y	1	100	27-100	25	27-100	25	18-100
	AM-4AF-5Y	0	0	0-55	0	0-44	0	0-45
	AM-3AF-6Y	0	0	0-18	0	0-11	0	0-18
	5AF-5Y	2			50	0-11	50	0-9
	4AF-6Y	1			25	0-7	25	0-9
12	AM-5AF-6Y	1	100	100	100	100	100	100

(a)

huddle size	huddle composition	n =	adult male		adult females		subadults		young	
			O	E	O	E	O	E	O	E
2	AM-AF	18	62*	33	18	17				
	AM-SA	9	31	33			13	17		
	AM-Y	2	7*	33					2*	17
	2AF	8			8*	17				
	AF-SA	24			24*	33	35	33		
	AF-Y	50			50*	33			52*	33
	2SA	9					13	17		
	SA-Y	27					39	33	28	33
	2Y	18							19	17
3	AM-2AF	5	26	7	8	7				
	AM-AF-SA	7	37	27	12	13	14	13		
	AM-AF-Y	5	26	27	8	13			10	13
	AM-2Y	0	0	7					0	7
	AM-2SA	0	0	7			0	7		
	2AF-SA	6			10	13	12	7		
	2AF-Y	4			7	13			8	7
	AF-SA-Y	26			43	27	51	27	52	27
	AF-2SA	2			3	7	4	13		
	AF-2Y	5			8	7			10	13
	2SA-Y	5					10	13	10	7
	SA-2Y	3					6	7	6	13
	AM-SA-Y	2	11	27			4	13	4	13
4	AM-2AF-SA	7	41	10	26	10	32	5		
	AM-2AF-Y	2	12	10	7	10			12	5
	AM-AF-2SA	1	6	10	4	5	5	10		
	AM-AF-SA-Y	6	35	40	22	20	27	20	35	20
	AM-AF-2Y	1	6	10	4	5			6	10
	2AF-2SA	2			7	5	9	5		
	2AF-SA-Y	1			4	20	5	10	6	10
	2AF-2Y	2			7	5			12	5
	AF-2SA-Y	5			19	10	23	20	29	10
	AF-SA-2Y	0			0	10	0	10	0	20
	2SA-2Y	0					0	5	0	5
	AM-2SA-Y	0	0	10			0	10	0	5
	AM-SA-2Y	0	0	10			0	5	0	10
5	AM-2AF-2SA	1	8	7	6	7	7	7		
	AM-2AF-SA-Y	5	38	27	29	27	36	13	31	13
	AM-2AF-2Y	3	23	7	18	7			19	7
	AM-AF-2SA-Y	3	23	27	18	13	21	27	19	13
	AM-AF-SA-2Y	1	8	27	6	13	7	13	6	27
	2AF-2SA-Y	1			6	13	7	13	6	7
	2AF-SA-2Y	2			12	13	14	7	13	13
	AF-2SA-2Y	1			6	7	7	13	6	13
	AM-2SA-2Y	0	0	7			0	7	0	7
6	AM-2AF-2SA-Y	1	17	33	13	33	13	33	13	17
	AM-2AF-SA-2Y	5	83	33	63	33	63	17	63	33
	AM-AF-2SA-2Y	0	0	33	0	17	0	33	0	33
	2AF-2SA-2Y	2			25	17	25	17	25	17
7	AM-2AF-2SA-2Y	11	100	100	100	100	100	100	100	100

(b)

Table 13: P-values for pairwise comparisons noting significant differences in behaviour rates between young age classes, done for each of the five behaviours that showed significant differences across age classes [(a) inactivity, (b) foraging, (c) social, (d) locomotion, and (e) 'other' behaviours]. Note that newborns were removed from posthoc analysis of foraging and locomotion, as they could not engage in these behaviours by definition. The percent (%) time spent in each behaviour by each young age class can be found in tables in Figure 6.1 and Table 6.3, Chapter 6. Significant differences indicated with an asterisk (*).

inactivity	juvenile	young juvenile	infant	newborn
juvenile	n/a	0.333	0.304	<0.001*
young juvenile	0.333	n/a	0.904	<0.001*
infant	0.304	0.904	n/a	<0.001*
newborn	<0.001*	<0.001*	<0.001*	n/a

(a)

foraging	juvenile	young juvenile	infant
juvenile	n/a	<0.001*	<0.001*
young juvenile	<0.001*	n/a	<0.001*
infant	<0.001*	<0.001*	n/a

(b)

social	juvenile	young juvenile	infant	newborn
juvenile	n/a	<0.001*	<0.001*	<0.001*
young juvenile	<0.001*	n/a	0.056	0.568
infant	<0.001*	0.056	n/a	0.439
newborn	<0.001*	0.568	0.439	n/a

(c)

locomotion	juvenile	young juvenile	infant
juvenile	n/a	0.015*	<0.001*
young juvenile	0.015*	n/a	<0.001*
infant	<0.001*	<0.001*	n/a

(d)

'**other**'	juvenile	young juvenile	infant	newborn
juvenile	n/a	<0.001*	<0.001*	0.919
young juvenile	<0.001*	n/a	<0.001*	<0.001*
infant	<0.001*	<0.001*	n/a	<0.001*
newborn	0.919	<0.001*	<0.001*	n/a

(e)

Table 14: P-values for pairwise comparisons noting significant differences in (a) average number of others in proximity and (b) time spent in proximity/alone between young age classes. The number of others in proximity and time spent alone within each age class can be found in Section 6.3.2.1, Chapter 6. Significant differences indicated with an asterisk (*).

others in proximity	juvenile (Group A)	juvenile (Group B)	young juvenile	infant	newborn
juvenile (Group A)	n/a	<0.001*	<0.001*	<0.001*	<0.001*
juvenile (Group B)	<0.001*	n/a	<0.001*	<0.001*	<0.001*
young juvenile	<0.001*	<0.001*	n/a	<0.001*	<0.001*
infant	<0.001*	<0.001*	<0.001*	n/a	0.010*
newborn	<0.001*	<0.001*	<0.001*	0.010*	n/a

(a)

proximity/alone	juvenile (Group A)	juvenile (Group B)	young juvenile	infant
juvenile (Group A)	n/a	0.263	0.002*	<0.001*
juvenile (Group B)	0.263	n/a	<0.001*	<0.001*
young juvenile	0.002*	<0.001*	n/a	<0.001*
infant	<0.001*	<0.001*	<0.001*	n/a

(b)

Table 15: P-values for pairwise comparisons noting significant differences in postural rates between young age classes, done for each of the four postures that showed significant differences across age classes [(a) sit, (b) stand, (c) cling, and (d) suspend]. Newborns were removed from posthoc analysis of posture, as they were only observed to cling to another langur. The percent (%) time spent in each posture by each age class can be found in Figure 6.3 and Table 6.4, Chapter 6. Significant differences indicated with an asterisk (*).

sit	juvenile	young juvenile	infant
juvenile	n/a	0.001*	<0.001*
young juvenile	0.001*	n/a	<0.001*
infant	<0.001*	<0.001*	n/a

(a)

stand	juvenile	young juvenile	infant
juvenile	n/a	0.013*	<0.001*
young juvenile	0.013*	n/a	<0.001*
infant	<0.001*	<0.001*	n/a

(b)

cling	juvenile	young juvenile	infant
juvenile	n/a	0.018*	<0.001*
young juvenile	0.018*	n/a	0.052
infant	<0.001*	0.052	n/a

(c)

suspend	juvenile	young juvenile	infant
juvenile	n/a	0.059	0.912
young juvenile	0.059	n/a	0.128
infant	0.912	0.128	n/a

(d)