FOREGING ECOLOGY OF PIED CURRAWONGS *Strepera graculina* IN RECENTLY COLONISED AREAS OF THEIR RANGE

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The research reported in this thesis is my own original work except where otherwise acknowledged. Chapter 2 is jointly authored with Andrew Cockburn and Christopher Reid, Chapter 3 is jointly authored with Andrew Cockburn and Robert Magrath. In each case, I am the senior author, and the principal contributor to all aspects of the work. Andrew Cockburn contributed discussion of ideas. Andrew Cockburn and Ross Cunningham contributed statistical analysis.

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Preface

This thesis is written as a series of four papers (Chapters 2 to 5), plus a statement of introduction (Chapter 1) and general discussion and future prospects (Chapter 6). This approach maximises brevity, but some replication of methods and references is inevitable.

ABSTRACT

This thesis addresses the foraging ecology of an Australian passerine, the pied currawong, *Strepera graculina* (Shaw) in recently colonised areas of its range. Pied currawongs are large, black and white birds found throughout the mountain ranges, and the farming, urban and coastal areas of south-eastern Australia. Historically, pied currawongs were exclusively seasonal-altitudinal migrants which congregated and moved to the lowlands or settlements during autumn and winter and returned to the mountains for breeding in spring. However, in the last few decades some pairs have not returned to the mountains in spring, instead they have established the breeding population around settlements. This study was conducted at the Australian National Botanic Gardens, the Australian National University campus and nearby suburbs on the slope of Black Mountain in the Australian Capital Territory. Pied currawongs are found in pairs or family groups during the breeding season (August/September to January/February) and in flocks ranging from twenty to hundreds individuals during seasonal migration (Mar/April to July/August). Males are slightly bigger and have longer bills than females. During the breeding season pied currawongs are territorial and defend an area surrounding their nest site of approximately 8 ha. After becoming independent, the young leave their natal territory and congregate in large flocks.

In this study, I focussed on year round diet, predation on other bird species, the importance of foraging for breeding and for survival of the young, and acquisition of foraging skills in young birds. The year round diet was studied by analysing the regurgitated pellets. The pellet analysis showed that the pied currawong diet varied seasonally. Fruits of introduced bushes especially *Pyracantha* spp. predominate in the autumn and winter diet, while insects dominated the spring and summer diet. The domination of the diet by introduced fruit bearing species supports earlier contentions that the availability of this new

food source may have contributed to a population explosion and increased breeding range. Currawongs travel long distances to gain access to these fruits, and are likely to be important vectors of seed dispersal for some weed species. Bird eggs and vertebrate prey including other bird species were taken only during spring and summer, when the pied currawongs were breeding. The arthropod component of the diet is particularly remarkable, being dominated by large insects, many of which are extremely aggressive (e.g. *Myrmecia* spp.) or usually regarded as toxic (pentatomid bugs, some Coleoptera).

The impact of predation on other bird species was studied by investigating predation on two documented prey species (*Malurus cyaneus* and *Sericornis frontalis*) and estimating the number of broods of other species taken from nest-feeding observations. Pied currawongs were consistent egg predators of the two prey species, though rates of egg predation were low (less than 4% per day). The two prey species are multibrooded and have a longer breeding season than that of the pied currawongs. Pied currawongs were extremely important predators of young in the early part of their breeding season of superb-fairy wrens, and the late part of the breeding season of white-browed scrubwrens. Currawongs also hunt birds. This hunting is done by males, and is concentrated on fledglings during their first days out of nest. Observations of meat delivery by the pied currawongs to nestlings suggest that 39 broods of other species are taken to raise each brood of currawong young. Coupled with the prey consumed by adults, currawongs in their newly colonised range are likely to have an extremely deleterious effect on their bird prey species.

Pied currawongs are monogamous and have long-term pairbonds. In their newly colonised range they have extremely high survival and fledge 1 to 2 young every year. Timing of breeding season did not vary between years, despite high variability in climate. They build the nests and lay eggs between August and September. Incubation takes about 3 weeks and the nestlings appear in October. The young stay in the nest for about one month and fledge between November and December.

Males and females both perform parental care. Only females build the nest, incubate and brood. However, males feed the females during nestbuilding and incubation, and are active in chasing intruders such as ravens and other pied currawongs. Both parents feed and guard their young until they can forage by themselves. Male feeding rates decline during the last half of the nestling period, possibly because males deliver fewer, larger food parcels at this time. Males are active participants in the care of fledglings.

Juvenile pied currawongs require some months to obtain optimal foraging techniques and proficiency. However, in the transition to independence which usually takes about 50 days after fledging, they acquire simple foraging techniques such as foraging from the ground and gleaning on the foliage or canopy. At this stage, they can obtain 80% of total feeds from self foraging.

The pied currawongs are well adapted in recently colonised of their range, as indicated by the wide range and seasonal variation in their diet and by their breeding success. This condition may have altered the behaviour patterns in some pied currawongs. As a consequence, the population of pied currawongs may increase and affect the population of other bird species in recently colonised areas of their range.

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Chapter 1

Introduction

INTRODUCTION

Foraging is always an essential component of the ecology of a species (Kamil *et al.* 1987). Most investigations on foraging behaviour of Australian birds have been based on comparison between species in a whole community in one area (Crome 1978; Thomas 1980; Wooller and Calver 1981; Frith 1984; Recher *et al.* 1985; Ford *et al.* 1986; MacNally 1994) or have investigated particular guilds of closely related, ecologically similar species such as honeyeaters (Keast 1968; Ford and Paton 1977; Brooker *et al.* 1990), pardalotes (Woinarski and Rounsevell 1983) and treecreepers (Noske 1979). However, detailed study of the foraging of a single species in an attempt to understand the interaction of this species with the community in which it lives remains poorly developed for many species.

The following work investigates the foraging ecology of an Australian passerine, the pied currawong, *Strepera graculina* (Shaw) in recently colonised areas of its breeding range. The background of this work stems from growing concern over the impact of this species as its range expands. Formerly, pied currawongs migrated to lowland sites in search of food only during autumn and winter (Roberts 1942; Lamm and Wilson 1966; Strong 1966; Readshaw 1968; Robertson 1969; Wimbush 1969; Vellenga 1980) and returned to the mountain forests to breed in spring (Walsh 1965; Readshaw 1968; Lenz 1990). However, in the last few decades a substantial number of breeding pairs have remained at the lowland sites all year round and have bred there. For example, in the Canberra region currawongs were first recorded nesting in 1965 (Marchant cited by Lenz 1990). In subsequent years, the breeding population in this new range, which includes the Australian National University campus, has increased steadily (Figure 1).

Recher (Recher and Lim 1990, Recher cited by Roberts 1991) blames introduction of fruits which flower in winter for increasing the survival of pied currawong during winter hence causing the population explosion. Since currawongs are also well known to be bird predators, this population explosion could cause declines in the population of other small bird species (Roberts 1991, Allison 1993, Bass 1995, Major *et al.* in preparation). Consequently, Recher (Roberts 1991) suggested a mass poisoning program of currawongs. Such draconian action can only be justified on the basis of high quality data, yet research on the pied currawong is very limited. There are no published data on its demography or reproductive biology. Similarly, although there are numerous anecdotal notes on food eaten by currawong (for a review see Barker and Vestjens 1990), quantitative information on year round diet is not available.

Previous workers have discussed some biological aspects of pied currawongs including morphometric studies on banded birds and museum specimens (Robertson 1969, Wimbush 1969, Vellenga 1980, Robertson and Woodall 1982), their longevity (Nicholls and Woinarski 1988), winter diet (Bass 1995), insect diet (Readshaw 1965, 1968) and bird predation (Priddel and Carlile 1995). Morphometric studies reported that males are heavier and have longer bills than females (Wimbush 1969), and the weight of both male and female fluctuates seasonally (Vellenga 1980). A study on longevity indicated that pied currawongs can live up to 15 years (Nicholls and Woinarski 1988).

In regards to currawong diet, winter diet has been studied during the altitudinal migration in Armidale, New South Wales (Bass 1995). This study strongly supports Recher's hypothesis that the winter diet mostly consists of fruits of introduced plant species and also draws attention to the role of currawongs as potential dispersers of these species (Bass 1990, 1995), as pied currawongs usually regurgitate pellets containing viable seeds of those fruits. The most common introduced fruits that have been dispersed by pied currawongs are *Rosa rubiginosa* (Hatton 1989), *Crataegus monogyna* (Bass 1990), *Pyracantha* spp.(Bass 1990, 1995) and *Ligustrum* spp. (Buchanan 1978, Bass 1995).

The only detailed study of bird predation by currawongs concerns the endangered Gould's petrel *Pterodroma leucoptera leucoptera* on Cabbage Tree Island, New South Wales (Priddel and Carlile 1995). Pied currawongs preyed extensively on adults, causing a 7% decline in the breeding population during the 1992-93 season (Priddel and Carlile 1995). Removal of pied currawongs and their nests on the island reversed the population decline of the Gould's petrels.

By contrast, Readshaw (1965, 1968) reported that currawongs have beneficial effects through predation of stick insects (*Podocanthus wilkinsoni* and *Didymuria violescens*), which occasionally undergo population explosions and defoliation of *Eucalyptus* forests in south-eastern Australia during late summer and autumn. It was found that the number of stick insects that they preyed upon was higher than that of other insectivorous birds.

This thesis addresses three aspects of the foraging ecology of currawongs. First, it investigates seasonal changes in the diet. Second, it assesses the impact of predation on birds, concentrating on two prey-species (superb fairy-wrens *Malurus cyaneus* and white-browed scrubwrens *Sericornis frontalis*). Third, it investigates the important function of foraging for breeding and survival of young currawongs.

The specific aims of the study reported in this thesis are as follows :

1. To document the diet throughout the year and examine the effect of season on variation in the diet (Chapter 2).

2. To describe hunting behaviour and examine the impact of predation in relation to the reproductive cycle of both pied currawongs and their prey (Chapter 3).

3. To investigate reproductive success and breeding behaviour of pied currawongs (Chapter 4).

4. To document early development of foraging skills (Chapter 5).

5. To discuss the conclusions of Chapters 2 to 5 in the context of our current understanding of the foraging ecology of pied currawongs (Chapter 6).

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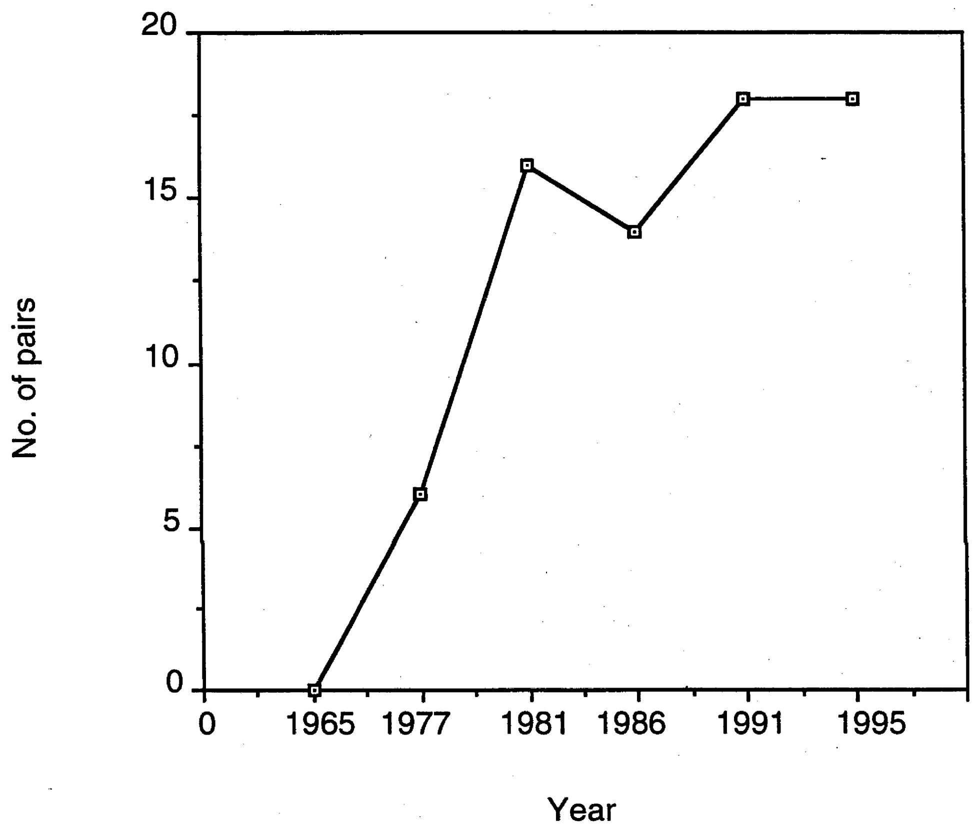
Figure 1. The number of pied currawong breeding pairs recorded at the Australian University campus, between 1965-1995. Data were obtained from Lenz (unpublished data) and this study.



Chapter 2

The diet of pied currawongs *Strepera graculina* in recently colonised areas of their range: I. Seasonal variation

(co-authored by Andrew Cockburn and C.A.M. Reid)

INTRODUCTION

The Pied Currawong *Strepera graculina* is common in eastern Australia from north Queensland through New South Wales to Victoria (Gould 1865; Blakers *et al.* 1984). Historically, the species was an exclusive altitudinal migrant (Strong 1966; Wimbush 1969; Pizzey 1986) congregating at lower altitudes during autumn and winter (Roberts 1942; Lamm and Wilson 1966; Readshaw 1968; Robertson 1969; Bass 1990), probably in search of food (Readshaw 1968; Wimbush 1969), and returning to the mountain forests in spring to breed (Walsh 1965; Readshaw 1968; Lenz 1990). However, in the last few decades a substantial number of breeding pairs have not returned to the mountains; instead they have colonised lowland sites, which were previously occupied only in autumn and or winter. Instead, these pairs have remained at lowland sites all year round, including during the breeding season. For example, in the Canberra region currawongs were first recorded breeding in 1965 (Marchant cited by Lenz 1990). Since then, rapid population growth has taken place from one breeding pair per ca. 40.1 ha at the Australian National University campus in Canberra in 1977 to one per 17.2 ha in 1988 (Lenz 1990). There is now one pair per 8 ha (Prawiradilaga this study).

The spread of this species has prompted concern for two reasons. First, currawongs often eat fruit, and may therefore be a vector for transmission of weeds such as sweet briar *Rosa rubiginosa* (Hatton 1989), firethorn *Pyracantha* sp. (Mulvaney 1986; Bass 1990, 1995) and privet *Ligustrum* sp. (Allison 1993; Bass 1995). Second, currawongs are known predators of nestlings of other species, and are a potential threat to birds which have not previously been exposed to such predation (Recher as interviewed by Roberts 1991; Priddel and Carlile 1995). Alternatively, it has been argued that currawongs may be beneficial and help to control outbreaks of insect pests such as folivorous phasmatids (Readshaw 1965;

1968).

Despite this concern, there is only one study which has demonstrated that currawongs are a pest. Priddel and Carlile (1995) reported that currawongs preyed upon nestlings of the endangered and declining Gould's petrel *Pterodroma leucoptera* on Cabbage Tree Island. When the currawong nests were destroyed, the population of Gould's petrel on this island increased. Further, although there are a large number of anecdotal studies of currawong diet (Appendix 1), no study has accurately characterised the diet throughout the year. In this study we report seasonal changes in the diet of currawongs in parkland and native woodland in Canberra, a region recently colonised by breeding pied currawongs.

MATERIALS AND METHODS

Information on the diet of Pied Currawongs in the vicinity of Canberra, in the Australian Capital Territory, was gathered by examining the contents of regurgitated pellets and the contents of gizzards from dead birds, and by observing foraging birds with binoculars. Direct observations of birds were often useful for diet identification, and particularly for establishing which fruits were taken, and for confirming the bird species preyed upon by currawongs. However, it soon became clear that most currawong feeding took place in tree canopies, where identification of the exact prey taken was almost impossible. Gizzard samples were obtained from three dead specimens of adult birds collected from Mt. Stromlo, Turner and Ainslie (Canberra suburbs); and one dead specimen of a chick (12 days old) from the ANU campus during summer. Since the gizzard samples were small and direct observation was usually unsatisfactory, this study relied most heavily on pellet analysis. The remaining data were mostly useful for confirming items not regurgitated in pellets.

Pellets or pellet fragments collected from one location on the same day were lumped as one sample. Most pellets were found as fragments. Some physical measurements such as size and dry weight were taken from the small number of intact pellets. Three hundred and eleven samples (590 pellets) were collected between September 1992 and May 1994 from three main study sites: 1) the Australian National Botanic Gardens (ANBG) which is a mixture of plantations of Australian plant species, and native vegetation comprising woodland dominated by *Eucalyptus rossii* and *E. macrorhyncha* (Burbidge and Gray 1970) and with a mixed *Stipa/Danthonia/Poa* grassland understorey; 2) the Australian National University (ANU) campus which is open parkland where both tree and shrub species are often introduced; 3) Turner and O'Connor (Canberra suburbs) with mixed suburban gardens. All areas occur on the slopes of Black Mountain (149° 15' E 36° 05' S), the site where pied currawongs were first recorded nesting in the Canberra region. At least one member of most pairs (usually the male as territorial females are very wary of traps) in the main study areas were banded with a metal band and distinguishing colour bands. In these study areas, pellet collections were made at least once a week. Pellet samples were also gathered from Mt. Ainslie, a nearby area of *E. rossii* woodland during one breeding season. During the breeding season most pellets were collected from near the nests. After the young fledged, the collecting of pellets became more difficult because it was hard to find the roosting sites which changed frequently and were very wide-spread. Some birds and their young disappeared from the study areas between December and May, reducing the number of pellets that could be collected.

All pellets were soaked in 70% ethanol, then washed in water, sieved to remove soil and dirt, and then sorted with a low power dissecting microscope. The food items were sorted into plant material (preserved as dried material), arthropod remains (preserved in 70% ethanol), snails (preserved as dried material), vertebrate remains (preserved in 70% ethanol for soft/internal organs and as dry material for bones, teeth, feathers, claws and hairs) and others (preserved as dried material) for further identification.

Identification of the various components in the diet of digested and partly digested material relies upon recognising those structures which resist digestion. Appropriate 'indicators' are given in Table 1. Because of differential digestion and quantity, there was no prospect of accurately estimating the biomass of each prey type nor counting it (Engel and Young 1989). Instead, each type of food was scored as present or absent, and data summarised as the frequency of occurrence in the samples, reflecting the proportion of different food types in the diet (Tatner 1983).

Some fruit skin was identifiable, but most identification of plants relied on characteristics of seeds (Martin and Barkley 1961) and comparison with seeds collected from plants in the field (particularly those frequently fed upon by currawongs) and with reference collections held by the CSIRO Division of Wildlife & Ecology and the Plant Quarantine Laboratory of the CSIRO Division of Plant Industry. Seeds were generally identified to the generic level, though some distinctive seeds could be identified to the species level.

Insect fragments were identified using keys in Naumann *et al.* (1991), by comparison with insect collections in the Australian National Insect Collection (ANIC) and consultations with staff associated with this collection. Insect identification was generally to family but in some cases it was possible to identify genera and species.

Bird and mammal remains were identified using reference collections of the Australian National Wildlife Collections (CSIRO Division of Wildlife and Ecology) and of the Department of Prehistory-A.N.U.. Hair identification used descriptors set out in Brunner & Coman (1974). Reptile bones were identified using keys in Romer (1956) and reference collections in the museum of Division of Botany &

Zoology-A.N.U..

Pied currawong have a diverse diet throughout the year. From this diet, six major food components: plant materials (especially fruits and seeds), arthropods (insects, myriapods, arachnids and crustacea), molluscs, bird remains, bird eggs, and other vertebrate (mammals and reptiles) remains were selected for statistical analysis. All of those food components in each pellet sample were scored as 1 (if present) and 0 (if absent), allowing the use of techniques appropriate for binary data. Pellet samples were grouped into four seasons: autumn (March-May), winter (June-August), spring (September-November) and summer (December-February). Locations were divided into three sites: the Australian National Botanic Gardens, the Australian National University campus and Canberra suburbs (O'Connor and Turner). Mt. Ainslie was excluded from the analysis because the pellet collections from this site were made only for one breeding season. Logistic regression (Collett 1991) was used to examine the effects of season and site on probability of presence of six major diet components. Computation was done using GENSTAT v. 5 (Genstat 5 Committee 1991).

For the diversity of fruits, the number of fruit species present in a sample was from 1 to 4, and for the diversity of insects, the number of insect families present in a sample was from 1 to 12. These diversity data were assumed to have a Poisson distribution (McCullagh and Nelder 1989) and the Poisson regression procedure was used to examine the effect of season on fruit and insect diversity in a sample.

RESULTS

Pied Currawong pellets were cylindrical. Their length varied between 1.4 and 4.0 cm (mean=2.6; s.d.=0.7; n=35), diameter ranges from 0.9 to 1.8 cm (mean=1.3; s.d.=0.3; n=35) and weight between 0.4 and 3.6 grams (mean=1.2;

s.d.=1.1; n=7). Small pellets contained mainly insects; while the biggest and heaviest pellets contained the pulp of fruits and seeds of *Pyracantha* spp.

Between season variation

Currawongs are omnivorous, consuming fruit, invertebrate and vertebrate prey. A large variety of species were taken (Table 2). Here, we concentrate discussion on changes in diversity and frequency of occurrence of the major diet types, and focus particularly on those food types which occurred in many samples (> 10% of samples in any season).

Fruits

Pied Currawongs ate fruit throughout the year, though the proportion of fruit in the diet varied between seasons (χ^2=36.6; df=3; p<0.001). Fruit was most frequent in the winter diet (Figure 1 and Table2). The fruit species present in a sample were more diverse during winter (χ^2=32.8; df=3; p<0.001). Seeds from 23 plant families were identified from the pellets. Most were introduced garden plants. Only five families (Santalaceae (*Exocarpos* spp.), Mimosaceae (*Acacia* spp.), Rosaceae, Araliaceae (*Hedera helix*) and Moraceae (*Morus* spp.)) occurred in at least 10% of the samples. *Acacia* spp. were consumed throughout the year, but were consumed predominantly in the autumn diet. It is likely that *Acacia* seeds were taken to gain access to the ant-attracting elaiosomes attached to the seeds. There is evidence that some of these also attract birds (Davidson and Morton 1984). Fruits from various Rosaceae were taken throughout the year. *Pyracantha* spp.(firethorn) was dominant during autumn, winter and spring and *Prunus* spp. (plum) was dominant during summer (Table 3).

Invertebrates

Arthropods (predominantly insects) were consumed throughout the year (Figure 1), and dominated the autumn, spring and summer diet (χ^2=46.1; df=3; p<0.001).

Thirty one families of insects from nine orders were identified from the samples. The diversity of insects in a sample during spring and summer was higher than during autumn and winter (χ^2=214.1; df=3; p<0.001) (Figure 2). Amongst insects, Coleoptera and Hymenoptera were most important throughout the year (Table 2). Thirteen families of beetles were recorded (Table 4). Some (Scarabaeidae, Curculionidae, Chrysomelidae, Elateridae, Cerambycidae and Carabidae) occurred in all seasons. The most important beetle families were Scarabaeidae, Curculionidae and Chrysomelidae (Table 4) respectively. Most Scarabaeidae were eaten as adults, except for *Diaphonia dorsalis* which was eaten as both larvae and adults. Amongst Scarabaeidae, Melolonthinae and *Anoplognathus* sp. (Christmas beetles) were the most important (Table 5). Melolonthinae were common in the spring diet; however, the Christmas beetles were common in the summer diet. Most Curculionidae (weevils) were taken in adult stages and only *Gonipterus* spp. were eaten as larvae. Among other beetles, only Carabidae were also eaten as larvae as well. Amongst Chrysomelidae, *Trachymela* sp. and *Paropsis* sp. were most important (Table 6).

Hymenoptera in the diet included seven families (Table 7). Most Hymenoptera were eaten as adults, except Pergidae (Symphyta) which were eaten as larvae. Formicidae (ants) and Tiphiidae (wasps) were the most important families and were eaten throughout the year (Table 7). *Myrmecia* spp. (bulldog ants) were the most important (Table 8; Figure 3). The other important ants were *Camponotus* sp., *Rhytidoponera* sp. and *Iridomyrmex* spp. respectively (Table 8).

The most important Tiphiidae were *Heminthynnus* sp., *Diamma* sp. and other tiphiids. Most males in this family are bigger than females with the exception for *Diamma* sp. in which males are smaller (Naumann 1991). All males fly and are common in flowers but females are flightless and crawl on the ground or tree trunk. However, during mating the males pick up females from the ground or tree trunk and carry them to honeydew or flowers in the canopy.

Four families (Pentatomidae, Reduviidae, Coreidae and Cydnidae) of Hemiptera (bugs) were eaten. Pentatomidae (stink bugs) were the most important and were eaten throughout the year (Table 2). All Hemiptera were preyed upon in adult stages.

The most important invertebrates other than insects were Myriapoda (mostly Millipoda) and Mollusca. Both were consumed more often in spring and summer (Table 2).

Vertebrates

Bird and bird-egg remains were common in the spring and summer diet (Table 2). Bird prey included nestlings, fledglings and adults. Detailed identification of bird species will be given elsewhere. Although birds were taken less frequently than fruits or insects, they were much more important than other vertebrates (mammals and reptiles) (Table 2). Mammal and reptile remains were found in the winter, spring and summer diet. Mammals included rodents (*Mus domesticus* and *Rattus rattus* (Muridae)) and echidna (*Tachyglossus aculeatus* (Tachyglossidae)). All reptiles identified were from one family (Scincidae). The presence of *Tachyglossus aculeatus* remains in a winter sample indicated that the bird might have fed on carrion.

Others

Grit fragments were found throughout the year (Table 2).

Between site variation

The three main study sites differed greatly in the relative importance of native and introduced plants. Although plants in the Australian National Botanic Gardens are virtually all native, some pellets collected in this area contained seeds of introduced plant species like *Pyracantha* sp. and *Ligustrum* sp. Thus, currawongs may fly away from the gardens to obtain food from the nearest suburbs (O'Connor and

Turner), approximately 500 m away.

Gizzard analysis

All gizzard samples were collected during summer. The gizzards of adult birds contained items which resembled the items obtained from pellet samples (Table 9). The gizzard of a chick contained plant materials (fibres), insects (Scarabaeidae/Melolonthinae, Orthoptera wings), spiders (Arachninae) and bird/nestling remains of unknown species.

Items consumed that did not appear in pellets

During observations, pied currawongs took some food items that were neither found in the pellet samples nor in the gizzards. These food items comprised earthworms, caterpillars (Lepidopteran larvae), butterflies, cicadas and frogs (Amphibia). Cicadas were consumed very commonly during brief seasonal irruptions in mid to late December.

DISCUSSION

Pellet analysis and its adequacy

The method of analysing regurgitated pellets has been used successfully to determine seasonal variation in the diet of other predatory birds including raptors such as golden eagles *Aquila chrysaetos* (Watson *et al.* 1993), powerful owls *Ninox strenua* (Lavazanian *et al.* 1994), long-eared owls *Asio otus* (Nilsson 1981), and on species with behaviour similar to currawongs such as magpies *Pica pica* (Tatner 1983, Reebs and Boag 1987) and common ravens *Corvus corvus* (Engel and Young 1989, Nogales and Hernandez 1994). However, pellet analysis can only provide a general description of the diet (Marquiss and Booth 1986). Furthermore, direct observations on feeding behaviour have shown that some food items were not represented in the pellets since there are differences in digestibility of food items (Engel and Young 1989).

Currawongs vary their diet seasonally

The diet of pied currawongs varied seasonally (Figure 1, Table 2). Fruits and arthropods were the major constituents throughout the year. However, fruits were dominant during autumn and winter, and insects were dominant in spring and summer.

Since the currawong diet varies seasonally, the body weight of the bird may fluctuate. Major changes in body weight have been indicated by previous studies. Wimbush (1969) and Vellenga (1980) reported that the currawong body weight was highest ca. 400 g (mean=400.6; n=92) between May (late autumn) and June (early winter) and then declined to ca. 290 g (mean=291.5; n=63) into spring (Vellenga 1980). Thus, the body weight of currawongs is lowest when arthropods are consumed and highest when the birds are frugivorous (Figure 1).

The consumption of other birds was confined to spring and summer (Figure 1 & Table 2). However, this will be considered in greater detail elsewhere and will not be discussed further. Grit was common in autumn, spring and summer diet, probably for grinding the hard parts of food (Soler *et al.* 1993), and was least important in winter when the staple diet of currawongs was fruit.

Fruit consumption and its implications

The only native plant species common in currawong diet were *Exocarpos* spp. (Santalaceae) and *Acacia* sp. (Mimosaceae) (Table 2). *Exocarpos* berries were taken in spring and summer, while *Acacia* elaiosomes were only eaten in autumn.

In contrast, the fruit of introduced plants were common throughout the year, consistent with the claim by Recher (Roberts 1991) that pied currawongs are responding to the presence of introduced fruit species. The introduced fruit plants which were important in the diet are *Morus* spp. (Moraceae), *Hedera helix* (Araliaceae) and many species from the Rosaceae family (Table 2 & 3). Fruits of *Morus* spp. were only common in summer, fruits of *Hedera helix* were common in winter and spring, but fruits of Rosaceae were dominant in all seasons (Table 3). Some of these introduced species such as *Pyracantha* spp. (Auld and Medd 1987; Parsons and Cuthbertson 1992) and *Cotoneaster* sp. (Mulvaney 1986) produce fruit at any time of year including winter, and dominated the diet in this season, supporting previous results from Armidale, NSW (Bass 1990, 1995). The introduction of winter-fruiting plants has potentially had a major impact on winter survival of currawongs. In addition, since all regurgitated seeds are viable (Hatton 1989; Bass 1990; Allison 1993), currawongs are important dispersal vectors for weed species (Bass 1990, 1995).

Arthropod consumption and its implications

Arthropods and particularly insects, dominated the diet of currawongs (Table 2). Most insects such as grasshoppers, beetles, ants and wasps have been reported as occurring in pied currawong diet (Appendix 1), but Odonata, Blattodea and Dermaptera (Table 2) have not been recorded previously. Previous studies (Readshaw 1965; 1968) have suggested that pied currawongs are the most important predators of stick insects (Phasmatidae: *Didymuria violescens* and *Podocanthus wilkinsoni*) which cause defoliation of *Eucalyptus* spp. in the mountain forests of eastern Australia. However, stick insects were not an important part of the diet at Black Mountain in the Australian Capital Territory.

Direct observations suggested that several invertebrates were eaten but were not well represented in the pellet samples. These include caterpillars (Lepidopteran larvae), butterflies, cicadas and earthworms (personal observation). Caterpillars, butterflies and earthworms are presumably easily digestible and would not occur in the pellets. In addition, caterpillars and butterflies are often only partly consumed, with wings and external parts being discarded, Cicadas (Homoptera) are taken only during seasonal flushes in summer and often only the abdomens are consumed.

The diet as revealed by pellet analysis is highly unusual. First, currawongs take the majority of their prey (Cerambycidae, Chrysomelidae, Curculionidae Scarabaeidae, and Pentatomidae) from the canopy, as suggested by Recher *et al.* (1985). Second, the classification by MacNally (1994) that currawongs are bark probers is based on an inadequate sample size. Currawongs are very large insectivores in comparison with other bark probers or foliage searchers (Figure 4) and most prey they consume is also very large. For example: *Myrmecia* sp. are the largest ants in Australia (Naumann 1991). Scarabaeidae are between 5 and 25 mm long, Chrysomelidae are between 5 and 15 mm long and Curculionidae are between 7 and 20 mm long. Even among terrestrial prey, the prey taken is unusual. Both Gryllotalpidae (mole crickets) and Tiphiidae (wasps) are uncommon by comparison with other potential prey (Table 2), such common ground-dwelling species like Arachnida, Scorpioninae and ground-dwelling beetles (Carabidae, Staphylinidae and Tenebrionidae).

Most remarkably, many of the very common prey species are quite toxic or difficult to handle. *Myrmecia* sp. (bulldog ants) are highly aggressive ants and secrete formic acid (Roth and Eisner 1962; Piek 1985; Schmidt 1986) and histamine and histamine releasing factors (Holldobler and Wilson 1990). Formic acid may cripple small invertebrates and is painful to humans. Histamine and histamine releasing factors in bulldog ants enhance those effects. Pentatomidae (stink bugs) produce toxic substances in their salivary secretions (Blum 1981; Piek 1985; Aldrich 1988) which are assumed to be poisonous after being ingested (Blum 1981). Some families (Carabidae, Cerambycidae, Staphylinidae and Tenebrionidae) of Coleoptera (beetles) have defensive glands which produce many poisonous chemicals (Crowson 1981; Piek 1985); and Buprestidae (Jewel beetles) contain bitter tasting buprestins A & B (B-D-glucose-1,2,6-triesters with pyrrol-2-carboxylix acid) in their hemolymph (Moore and Brown 1985; Dettner 1987). Also, members of the Chrysomelidae (paropsine beetles) seem to be highly toxic and distasteful to other predators (Selman 1994).

The current study establishes that the diet of pied currawongs in the recently colonised areas of their range varies seasonally. The winter diet is dominated by plants which have been recently introduced. In addition, pied currawongs are important dispersal vectors of those plants since they spread viable seeds over long distances (Bass 1990 and 1995). The summer diet is improved with the availability of Christmas beetles (*Anoplognathus* spp.) (Carne 1957) and cicadas (*Psaltoda moerens*) (Moulds 1990). Changes in the availability of food resources may have contributed to their recent range expansion.

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Table 1. Components used as indicators of the diet items in an analysis of pied currawong pellets and gizzard.

Diet components	**Indicators**
Plant materials	Seed, fruit, flower, bark, leaf, stem, and root remains
Insecta	Heads, elytra, mandibles, thorax, abdomen, antennae, wings, legs and larvae
Myriapoda (Millipoda and Centipoda)	Segmental rings for millipedes and legs for centipedes
Arachnida	Heads and legs
Scorpioninae	Legs and jaws
Crustacea	Exoskeleton fragments
Mollusca	Shell fragments
Birds	Feathers, bones, claws, bird colour and metal bands
Eggs	Bird eggshell fragments
Mammals	Hair, bones, teeth and claws
Reptiles	Bones
Others	Grit, coloured plastic, rubberbands, aluminium foil and stone

Figure 1. Seasonal variation in the frequency with which pied currawongs used five major diet components. Pellet samples were collected in the Australian Capital Territory, September 1992-May 1994. Sample sizes are the number of pellets.

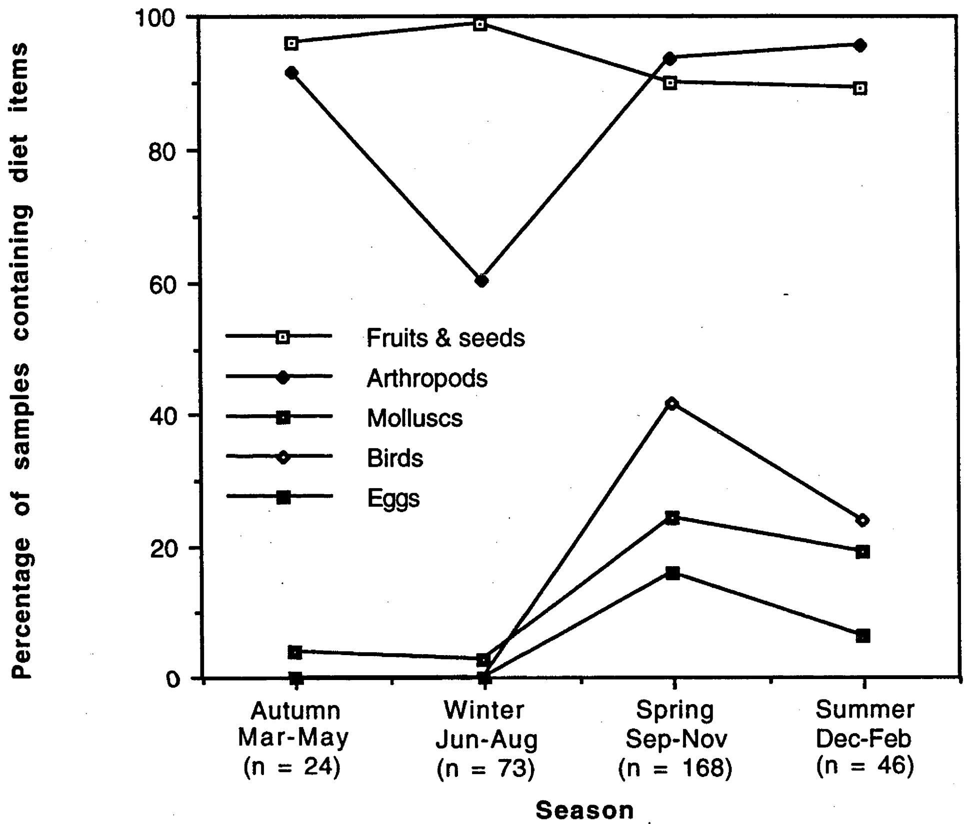


Table 2. Frequency of occurrence of food items found in the currawong pellets throughout the year. Extremely common food items are analysed in greater detail in subsequent Tables.
Note: * = introduced species; # = Australian species, but introduced locally.

Food type	Percentage frequency of occurrence in Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Seeds or fruits				
Liliaceae				
* *Allium* sp.	-	-	0.6	-
Xanthorrhoeaceae				
Lomandra longifolia	-	2.7	-	-
Poacea				
Setaria sp.	-	-	2.4	-
* *Avena* sp.	-	1.4	-	-
Araliaceae				
* *Hedera helix*	-	15.1	10.7	-
Asteraceae				
* *Carthamus* sp.	-	1.4	-	-
* *Carthamus tincticorus*	-	1.4	-	-
Caesalpiniaceae				
Cassia sp.	4.2	4.1	0.6	-
Elaeagnaceae				
* *Elaeagnus* sp.	8.4	-	0.6	-
* *Elaeagnus commutata*	-	-	0.6	-
Fabaceae				
**Phaseolus* sp.	-	-	0.6	-
Gyrostemonaceae				
# *Codonocarpus* sp.	-	-	-	2.2
Malvaceae				
# *Gossypium herbaceum*	-	-	1.2	-
Mimosaceae				
Acacia sp.	29.2	5.5	0.6	-
Acacia implexa	-	-	-	2.2
Moraceae				
* *Morus* sp.	-	-	3.0	17.4
* *Morus australis*	-	-	-	2.2
Myrtaceae				
* *Amomyrtus luma*	-	-	0.6	-
Eucalyptus sp.	-	-	0.6	-
Oleaceae				
* *Ligustrum* sp.	8.4	9.6	-	-
Passifloraceae				
* *Passiflora aurantia*	-	-	-	2.2
Ranunculaceae				
Ranunculus sp.	-	-	1.2	-
Rhamnaceae				
Trevoa trinervia	-	-	1.2	-
* Rosaceae (for detailed analysis see Table 4)	33.3	71.2	25.6	30.4
Rutaceae				
# *Dictamus albus*	4.2	-	-	-
Total samples	**24**	**73**	**168**	**46**

Table 2 (continued). Frequency of occurrence of food items found in the pellets throughout the year. Extremely common food items are analysed in greater detail in subsequent Tables.
Note : * = introduced species; # = Australian species, but introduced locally.

Food type	Percentage frequency of occurrence in Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Seeds or fruits				
Santalaceae				
Exocarpos sp.	-	-	11.9	10.9
Exocarpos cupressiformis	-	-	1.2	-
# *Santalum* sp.	-	1.4	-	-
Sapindaceae				
* *Koelreutia paniculata*	-	1.4	-	-
Solanaceae				
* *Solanum* sp.	-	-	1.2	-
* *Capsicum* sp.	4.2	-	-	-
Vitaceae				
* *Vitis* sp.	4.2	1.4	0.6	-
Unidentified fruits and seeds	16.7	6.8	4.8	13.0
All seeds and fruits	95.8	98.6	89.9	89.1
Animals				
Insects				
Odonata	-	1.4	-	2.2
Blattodea				
Blaberidae	-	1.4	2.4	-
Dermaptera	-	-	1.2	2.2
Orthoptera				
Gryllotalpidae	4.2	-	10.7	8.7
Gryllidae	-	-	0.6	-
Hemiptera				
Coreidae	-	-	-	2.2
Cydnidae	-	-	0.6	-
Pentatomidae	29.2	6.8	23.8	17.4
Reduviidae	-	-	0.6	-
Coleoptera (for detailed analysis see Table 4)	- 64·3	21.9	77.4	86.9
Diptera				
Muscoidea	-	2.7	0.6	-
Phoridae	-	-	-	2.2
Tipulidae	-	-	0.6	-
Sarcophagidae	1.4	-	-	-
Stratiomyidae	-	-	0.6	-
Lepidoptera	-	2.7	2.4	-
Psychidae	-	-	0.6	-
Hymenoptera (for detailed analysis see Table 5)	83.3	24.7	76.2	63
Unidentified insects	12.5	6.8	10.7	8.7
Total insects	91.7	58.9	93.4	95.6
Myriapoda (Millipoda and Centipoda)	8.3	4.1	16.7	10.9
Arachnida	-	8.2	6.5	4.3
Scorpioninae	4.2	-	9.5	-
Total samples	**24**	**73**	**168**	**46**

Table 2 (continued). Frequency of occurrence of food items found in the pellets throughout the year. Extremely common food items are analysed in greater detail in subsequent Tables.
Note: * = introduced species; # = Australian species, but introduced locally.

Food type	Percentage frequency of occurrence in Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Animals				
Crustacea	-	-	5.9	8.7
Mollusca	4.2	2.7	24.4	19.1
Birds	-	-	41.7	23.9
Eggs	-	-	16.1	8.7
Mammals				
Muridae				
* *Mus domesticus*	-	1.4	1.8	-
* *Rattus* sp.	-	-	1.2	2.2
Tachyglossidae				
Tachyglossus aculeatus	-	-	0.6	-
Unidentified mammals	-	-	3.6	2.2
Total mammals	-	1.4	7.1	4.3
Reptiles				
Scincidae	-	1.4	3.6	8.7
Others				
Grit	20.8	4.1	43.4	32.6
Total samples	**24**	**73**	**168**	**46**

Figure 2. Box plot of the diversity of insect families 95% in pied currawong pellet sample for four seasons (September 1992 - May 1994). The box encloses 25th and 75th percentiles, the horizontal line in the box denotes the mean. Vertical lines span the 10-90th percentiles. Circles represent extreme outliers. Sample sizes are the number of pellets.

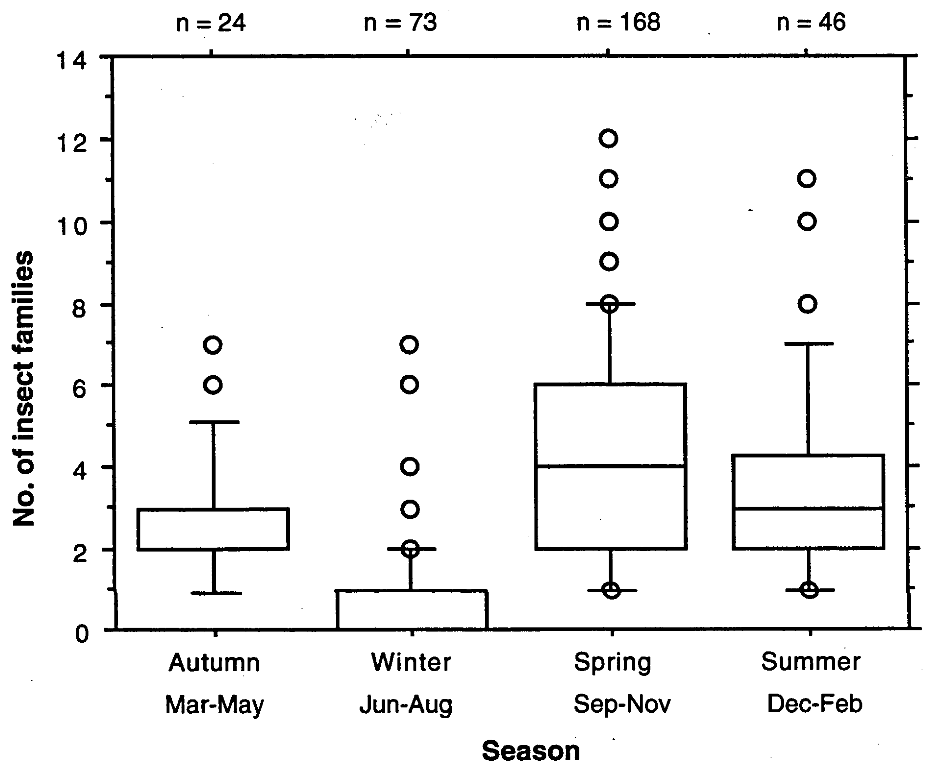


Table 3. Frequency of occurrence of Rosaceae found in the pellets throughout the year (all species were introduced).

Species	Percentage frequency of occurrence in Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Pyracantha sp.	20.8	53.4	14.3	2.2
Rosa sp.	-	13.7	-	-
Rosa rubiginosa	-	2.7	-	-
Rubus sp.	12.5	11.0	0.6	2.2
Prunus sp.	4.2	-	8.9	26.1
Prunus gravesii	-	-	-	2.2
Prunus prostrata	-	-	1.2	-
Prunus hortulana	-	-	-	2.2
Malus spp.	-	12.3	1.8	-
Malus domestica	-	4.1	1.2	-
Cotoneaster sp.	8.4	12.3	2.4	-
Sorbus sp.	4.2	-	1.2	-
Crataegus monogyna	-	9.6	0.6	-
Oemleria cerasiformis	-	-	-	2.2
Total samples	**24**	**73**	**168**	**46**

Table 4. Frequency of occurrence of Coleoptera found in the pellet samples throughout the year.

Family	Habitat	Percentage frequency of occurrence in			
		Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Brenthidae	bark	-	1.4	-	-
Buprestidae	foliage & flowers	4.2	-	1.2	6.5
Carabidae	leaf litter	4.2	4.1	13.1	15.2
Cerambycidae	leaves, flowers, bark	4.2	1.4	16.7	15.2
Chrysomelidae (for detailed analysis see Table 6)	foliage	12.5	4.1	49.4	21.7
Cleridae	bark, foliage	-	-	1.2	-
Curculionidae	bark, leaves	58.3	9.6	46.4	52.2
Elateridae	leaves or bark	4.2	1.4	20.8	6.5
Lucanidae	wood	-	-	3.0	17.4
Passalidae	wood	-	-	0.6	-
Scarabaeidae (for detailed analysis see Table 5)	ground to canopy	8.3	9.6	54.2	69.6
Staphylinidae	leaf litter	8.3	-	23.2	10.9
Tenebrionidae	anywhere	4.2	-	7.1	6.5
Total samples		**24**	**73**	**168**	**46**

Table 5. Frequency of occurrence of Scarabaeidae in the pellet samples throughout the year.

Species	Habitat	Percentage frequency of occurrence in			
		Autumn	Winter	Spring	Summer
		Mar-May	Jun-Aug	Sep-Nov	Dec-Feb
Anoplognathus sp.	leaves	-	1.4	1.8	55.5
Aphodiinae	dung	4.2	-	-	-
Diaphonia dorsalis	flowers & ground	-	-	-	8.3
Dynastinae	roots	-	-	3	-
Melolonthinae	leaves & flowers	8.3	-	38.7	38.9
Onthophagus sp.	dung	-	-	10.7	-
Total samples		**24**	**73**	**168**	**36**

Table 6. Frequency of occurrence of Chrysomelidae in the samples throughout the year (all species are found in the foliage).

Species	Percentage frequency of occurrence in			
	Autumn	Winter	Spring	Summer
	Mar-May	Jun-Aug	Sep-Nov	Dec-Feb
Augomela hypochalcea	-	-	1.2	-
Chalcolampra sp.	4.2	-	-	-
Chrysophtharta sp.	-	-	7.1	-
Dicranosterna immaculata	-	1.4	4.8	2.8
Eboo sp.	-	-	-	2.8
Paropsidis umbrosa	4.2	-	-	-
Paropsis sp.	-	-	24.4	5.5
Paropsisterna sp.	-	-	5.9	-
Trachymela sp.	8.3	-	31.5	11.1
Total samples	**24**	**73**	**168**	**36**

Table 7. Frequency of occurrence of Hymenoptera in the samples throughout the year.

Family	Percentage frequency of occurrence in			
	Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Formicidae (for detailed analysis see Table 8)	83.3	17.8	70.2	52.2
Ichneumonidae	4.2	-	8.9	2.2
Mutillidae	4.2	1.4	-	-
Pergidae	-	-	0.6	-
Vespidae	4.2	1.4	5.3	-
Braconidae	4.2	1.4	-	-
Tiphiidae	4.2	1.4	21.4	15.2
Total samples	**24**	**73**	**168**	**46**

Table 8. Frequency of occurrence of Formicidae in the samples throughout the year. All species can be found both on the ground and in the tree canopy.

Species	Percentage frequency of occurrence in			
	Autumn Mar-May	Winter Jun-Aug	Spring Sep-Nov	Summer Dec-Feb
Amblyopone australis	8.3	1.4	9.5	2.2
Aphaenogaster longiceps	-	-	5.3	-
Camponotus spp.	12.5	5.5	28.6	23.9
Iridomyrmex spp.	16.7	2.7	27.4	6.5
Myrmecia spp.	45.8	4.1	32.1	15.2
Notoncus sp.	-	1.4	1.8	-
Pheidole sp.	8.3	1.4	1.8	-
Rhytidoponera spp.	33.3	1.4	19	13
Total samples	**24**	**73**	**168**	**46**

Figure 3. Frequency of occurrence of *Myrmecia* spp. in the pellets throughout the year. Numbers above bars represent samples sizes.

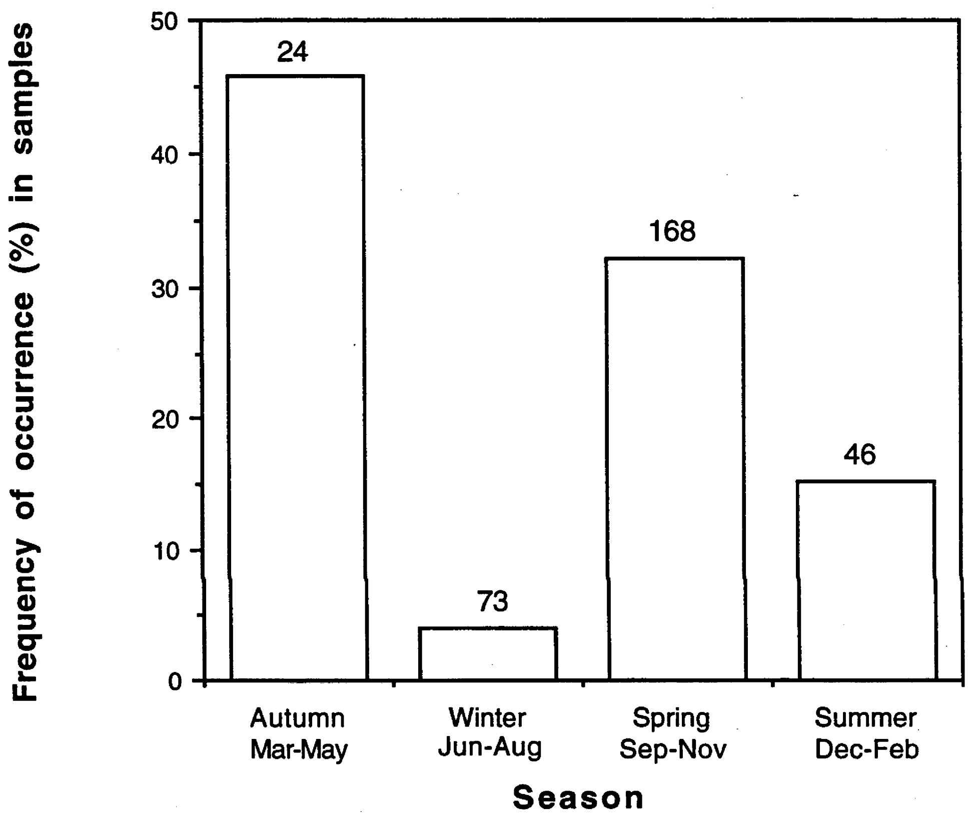
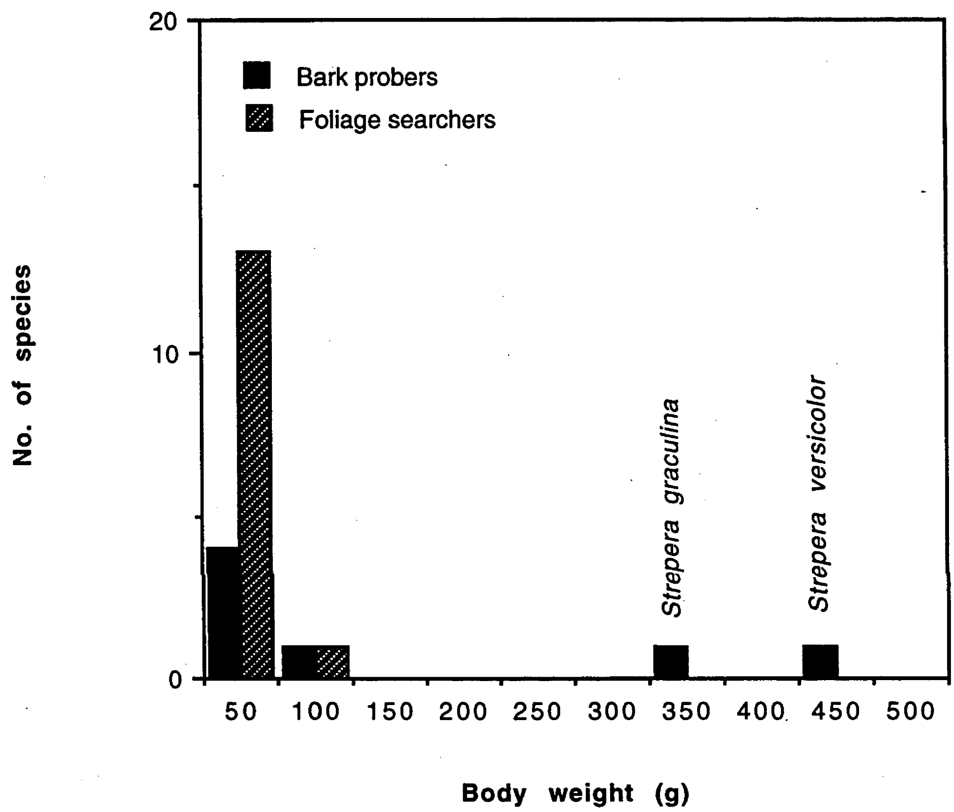


Table 9. Frequency of occurrence of food items found in the gizzards of adult currawongs during summer.

Food items	Percentage frequency of occurrence (%)
Plant materials (bark, flower, pulp of fruits of unknown species and seeds of *Rubus idaeus*)	67
Insects (*Caedicia simplex*/Tettigoniidae, Pentatomidae, Reduviidae, Carabidae, Chrysomelidae, Curculionidae, Scarabaeidae, Staphylinidae)	67
Bird remains (feathers)	33
Total samples	**3**

Figure 4. Body size of pied currawong in comparison with other bark prober and foliage searcher species (after MacNally 1994).
Body weight data were obtained from various sources (Recher *et al.* 1985; Boles 1988; Rogers *et al.* 1990; Longmore 1991; Australian Museum unpublished data; Cockburn unpublished data; Prawiradilaga unpublished data).



Appendix 1. Previous records on food of Pied Currawongs

Food types	Sources
Plant	
Pinaceae	
Seeds of *Cedrus atlantica*	Lepschi (1993)
Agavaceae	
Fruits of *Cordyline australis*	Lepschi (1993)
Cupressaceae	
Juniperinus communis	Lepschi (1993)
Grass/Poaceae	Buchanan (1978a); Barker and Vestjens (1990)
Zea mays	Barker and Vestjens (1990)
Digitaria sangunalis	Lepschi (1993)
Philesiaceae	Barker and Vestjens (1990)
Smilacaceae	Barker and Vestjens (1990)
Anacardiaceae	
Fruits of *Rhus* sp.	Lepschi (1993)
Schinus areia	Barker and Vestjens (1990)
Apocynaceae	
Fruits of *Alyxia* sp.	Knight (1989)
Araliaceae	
Hedera helix	Lepschi (1993)
Asteraceae	
Hypochaeris sp.	Barker and Vestjens (1990)
Stalks of *Taraxacum* sp.	Lepschi (1986a)
Ebenaceae	
Fruits of *Diospyres kaki*	Roberts (1942); Smith *et al.* (1984)
Elaeocarpaceae	
Elaeocarpus reticulata	Barker and Vestjens (1990)
Epacridaceae	
Flowers of *Styphelia tubiflora*	Barker and Vestjens (1990)
Ericaceae	
Fruits of *Arbutus unedo*	Lepschi (1993)
Fabaceae	
Fruits of *Sophora japonica*	Lepschi (1993)
Fagaceae	
Quercus palustris	Lepschi (1993)
Lauraceae	
Fruits of *Cinnamomum camphora*	Smith *et al.* (1984); Barker and Vestjens (1990)
Loranthaceae	Barker and Vestjens (1990)
Malvaceae	
Fruits of *Lagunaria patersonii*	Smith *et al.* (1984)
Meliaceae	
Fruits of *Melia azedarach*	Smith *et al.* (1984)
Mimosaceae	
Albizia julibrissin	Lepschi (1993)
Fruits of *Albizia lophanta*	Smith *et al.* (1984)
Moraceae	
Fruits of *Ficus* sp.	Rose (1973); Smith *et al.* (1984); Knight (1986); Barker and Vestjens (1990)
Fruits of *Ficus rubiginosa*	Barker and Vestjens (1990)
Fruits of *Morus nigra*	Roberts (1942); Smith *et al.* (1984); Barker and Vestjens (1990); Lepschi (1993)
Fruits of *Morus alba*	Lepschi (1993)

Food types	Sources
Myrtaceae	
Fruits of *Acmena smithii*	Barker and Vestjens (1990)
Fruits of *Eucalyptus caesia*	Smith *et al.* (1984)
Fruits of *Eugenia coolminiana*	Barker and Vestjens (1990)
Oleaceaea	
Fruits of *Ligustrum* sp.	Walsh (1965); Vellenga (1966); Rose (1973); Buchanan (1978b); Smith *et al.* (1984); Bass (1990); Barker and Vestjens (1990)
Orchard fruits	Roberts (1942); Macdonald (1973)
Orchidaceae flower	Barker and Vestjens (1990)
Leaves of *Cryptostylis erecta*	Buchanan (1978a)
Leaves of *Acianthus* sp.	Buchanan (1978a)
Phytolaccaceae	
Phyolacca octandra	Barker and Vestjens (1990)
Phytolacca sp.	Barker and Vestjens (1990)
Pittosporaceae	
Pittosporum undulatum	Barker and Vestjens (1990)
Proteaceae	
Persoonia pinifolia	Barker and Vestjens (1990)
Persoonia sp.	Barker and Vestjens (1990)
Rosaceae	
Fruits of *Cotoneaster* sp.	Mulvaney (1986); Barker and Vestjens (1990)
Fruits of *Cotoneaster microphyllus*	Lepschi (1993)
Fruits of *Crataegus monogyna*	Bass (1990); Barker and Vestjens (1990)
Cydonia oblonga	Barker and Vestjens (1990)
Fruits of *Fragaria* sp.	Barker and Vestjens (1990)
Fruits of *Pyracantha* sp.	Mulvaney (1986); Bass (1990); Lenz (1990)
Fruits of *Pyracantha angustifolia*	Lepschi (1993)
Fruits of *Pyracantha fortuneana*	Lepschi (1993)
Fruits of *Rosa rubiginosa*	Hatton (1989)
Fruits of *Malus* sp.	Smith *et al.* (1984); Barker and Vestjens (1990)
Fruits of *Prunus* sp.	Barker and Vestjens (1990)
Fruits of *Prunus cerasifera*	Lepschi (1993)
Fruits of *Pyrus communis*	Barker and Vestjens (1990)
Santalaceae	
Fruits *Exocarpos stricta*	Buckingham (1986); Barker and Vestjens (1990)
Solanaceae	
Solanum nigrum	Lepschi (1993)
Sterculiaceae	
Brachychiton populneum	Lepschi (1993)
Vitaceae	
Fruits of *Ampleopsis brevipendunculata*	Lepschi (1993)
Vitis sp.	Barker and Vestjens (1990)
Invertebrate	
Cocoons	Roberts (1942)
Mantodea	Barker and Vestjens (1990)
Plecoptera	Barker and Vestjens (1990)
Grasshoppers	Gould (1865); Rose (1973)
Tettigoniidae & Acrididae	Barker and Vestjens (1990)
Phasmatidae	
Stick insects *Didymuria violescens* and *Podocanthus wilkinsoni*	Readshaw (1965; 1968); Barker and Vestjens (1990)

Food types	Sources
Hemiptera	Barker and Vestjens (1990)
Cicadidae	Barker and Vestjens (1990)
Green Monday Cicadas *Cyclochila australasiae*	Veerman (1986)
Coleoptera/ Beetles	Roberts (1942); Rose (1973); Buchanan (1978b) Barker and Vestjens (1990)
Grubs	Gould (1865); Roberts (1942); Recher (1976)
Carabidae (*Harpalides* sp.)	Barker and Vestjens (1990)
Lucanidae	Barker and Vestjens (1990)
Scarabaeidae	Barker and Vestjens (1990)
Scarabaeinae	Barker and Vestjens (1990)
Rutellinae (*Anoplognathus* sp.)	Barker and Vestjens (1990)
Elateridae	Barker and Vestjens (1990)
Cerambycidae	Barker and Vestjens (1990)
Chrysomelidae (*Paropsis* sp.)	Barker and Vestjens (1990)
Curculionidae	Barker and Vestjens (1990)
Hymenoptera	
Formicidae (ants)	Roberts (1942); Rose (1973; Buchanan (1978b); Lepschi (1993); Buckingham (1994)
Camponotus sp.	Barker and Vestjens (1990)
Chalcoponera sp.	Lepschi (1993)
Iridomyrmex sp.	Buckingham (1994)
Myrmecia sp.	Barker and Vestjens (1990)
Chalcoponera sp.	Lepschi (1993)
Pheidole sp.	Lepschi (1993)
Pergidae larvae	Reid (unpublished data)
Ichneumonidae	Barker and Vestjens (1990)
Lepidoptera	
Caterpillars	Roberts (1942); Rose (1973); Recher (1976); Edgecombe (1984)
Psychidae	Barker and Vestjens (1990)
Arctiidae	Barker and Vestjens (1990)
Diptera	
Calliphoridae (*Lucilia* sp.)	Barker and Vestjens (1990)
Stratiomydae	Lepschi (1986b); Reid (unpublished data)
Molluscs	Recher (1976); Barker and Vestjens (1990)
Arachnida	Roberts (1942); Barker and Vestjens (1990)
Lycosidae (wolf spider)	Lepschi (1993)
Scorpioninae	Barker and Vestjens (1990)
Crustacea	Recher (1976); Barker and Vestjens (1990)
Mictyris longicarpus &*Macrophthalmus setosus*	Recher (1976); Barker and Vestjens (1990)
Vertebrate	
Amphibia *Bufo marinus*	Bekker (1985)
Aves	
Procellariidae	
Pterodroma leucoptera	Priddel and Carlile (1995)
Pterodroma solandri	Cockburn (unpublished data)
Columbidae	
Streptopelia chinensis	Cooper and Cooper (1981); Miller & Naisbitt (1994)
Muscicapidae	
Pachycephala rufiventris	Bridges (1994)

Turdus merula	Metcalf (1988)
Nestlings of *Petroica multicolor*	Robinson (1990)
Nestlingsof *Manorina melanophrys*	Poiani (1991)
Pardalotidae (nestlings of *Pardalotus punctatus*)	Wood (1993)
Maluridae (nestlings of *Malurus cyaneus*)	Nias (1986)
Acanthizidae (*Acanthiza pusilla*)	Metcalf (1988)
Nestlings of Yellow-rumped thornbill (*Acanthiza chrysorrhoa*)	Ebert (personal communication)
Meliphagidae	
Anthocaera carunculata	Cooper and Cooper (1981)
Phylidonyris novaehollandiae (fledglings)	McFarland (1986)
Zosteropidae (*Zosterops lateralis*)	Metcalf (1988); Lepschi (1993)
Passeridae (*Passer domesticus*)	Taylor (1986); Metcalf (1988); Lepschi (1993)
Sturnidae	
Sturnus vulgaris	Taylor (1986); Butterfield (1988)
Acridotheres tristis	Debus cited by Cooper and Cooper (1981)
Corcoraciidae (*Corcorax melanorhamphos*)	Manuel (1991)
Artamidae (nestlings of *Artamus superciliosus*)	Recher and Schulz (1983)
Cracticidae (fledgling of*Gymnorhina tibicen*)	Cooper and Cooper (1981)
Mammals	
Rattus sp.	Cooper and Cooper (1981); Knight (1989)
Pseudocheirus langinosus	Cooper and Cooper (1981)
Reptile	
Scincidae	Rose (1973); Recher (1976); Pizzey (1986); Barker and Vestjens (1990)
Lygosomo quoyii	Debus cited by Cooper and Cooper (1981)
Tilliqua scincoides	Debus cited by Cooper and Cooper (1981)

Chapter 3

The diet of pied currawongs, *Strepera graculina* in recently colonised areas of their range: II. Predation on birds

(co-authored by Andrew Cockburn and Robert D. Magrath)

INTRODUCTION

Pied currawongs *Strepera graculina* have recently expanded their range (Lenz 1990). Because they prey upon other vertebrates, including birds, it has been suggested that this expansion may lead to a decline in population of small birds (Recher and Lim 1990; Major *et al.* in preparation). Although there are many reports of pied currawong predation on other birds (Cooper and Cooper 1981; Recher and Schulz 1983; McFarland 1986; Nias 1986; Taylor 1986; Butterfield 1988; Metcalf 1988; Ford 1989; Robinson 1990; Manuel 1991; Poiani 1991; Roberts 1991; Langmore and Mulder 1992; Wood 1993; Bridges 1994; Miller and Naisbitt 1994), only one published study has proved that currawongs are an important predator (Priddel and Carlile 1995). They showed that pied currawongs preyed upon the adults of endangered Gould's petrel *Pterodroma leucoptera leucoptera* on Cabbage Tree Island, New South Wales, and thus caused the decline in its population. However, in a recent long-term study on the diet of pied currawongs, we showed that birds were a major part of the diet of currawongs in urban areas throughout the breeding season (Chapter 2).

In this paper we expand on these results by analysing the pattern of predation on birds and bird eggs in greater detail. We examine: 1) the technique used by currawongs to hunt prey and the sexual differences in foraging tactics; 2) the timing of predation in relation to the reproductive cycle of both predator and two prey species; and 3) the vulnerability of young prey birds. We conclude by discussing the probable impact of currawongs in newly colonised areas of their range.

MATERIAL AND METHODS

Study area

Pellet collections and feeding observations of pied currawongs were made in the Australian National Botanic Gardens (ANBG), the Australian National University (ANU) campus and in Turner and O'Connor (Canberra suburbs on the slope of Black Mountain), in the Australian Capital Territory (ACT) (149° 15'E 36° 05'S).

Prey species

In order to estimate prey availability, we took advantage of very detailed demographic and reproductive data collected simultaneously from two of the commonest bird species in the ANBG: superb fairy-wrens *Malurus cyaneus* and white-browed scrubwrens *Sericornis frontalis*. It is likely that the only species which occurs in similar density is the eastern spinebill *Acanthorhynchus tenuirostris*, and the only species with comparable biomass are crimson rosellas *Platycercus elegans* and red wattlebirds *Anthochaera carunculata*.

(1) Superb fairy-wrens (*Malurus cyaneus*) are small cooperatively breeding birds, weighing between 8 and 11 g. In the study area they breed from early September to early March. They can fledge three broods in a year but in the event of predation will lay as many as eight clutches (Green *et al.* 1995). Clutch sizes vary between two and four with a mode of three eggs (Rowley 1965). Females incubate eggs for 14 days. Nestlings fledge after 12 days.

During the study, there were approximately 80 territories containing marked individuals in and around the ANBG. Regular visits (at least two or three times a week) to the breeding territories were conducted to inspect colour-banded birds, and nest building activity, and to follow the fate of each clutch and brood.

(2) White-browed scrubwrens (*Sericornis frontalis*) are another small cooperative breeder, weighing between 11 and 15 g. In the study area they breed from early July to late January. Most clutches are of 3 eggs. The mean incubation period is 18.5 days and nesting period is 15 days. Nestlings were banded in the nest when 9-10 days old. There were about 50 territories in the study area. Similar observations to those for the fairy-wrens were also carried out on the marked scrubwren population.

Data collection

<u>Pellet samples</u>

Pellets are regurgitated by pied currawongs and contain the undigested part of food. The main analysis of diet was based on pellet samples which were collected throughout three breeding seasons (1992 until early 1995). Methods of pellet analysis are described in detail in a companion paper (Chapter 2).

<u>Observations</u>

General observations on feeding behaviour were conducted during regular visits to the nest sites or breeding territories. These observations included descriptions of hunting behaviour, prey species seen to be eaten by currawongs, and identification of feather or skeleton remains under the nests.

In order to estimate the prey consumed by nestling currawongs, systematic feeding observations were made on marked pied currawong pairs in the ANBG and the ANU Campus during the 1993/94 and 1994/95 breeding seasons. These intensive observations recorded the rate at which bird meat was delivered to the nestlings. Each nest was watched every day for an hour period to record the frequency of visits and the types of food brought by both parents to feed their nestlings. Observations were as evenly distributed as possible throughout daylight hours. Nineteen nests were observed for 303 hours during the 1993/94 and 1994/95 seasons.

Data analysis

Pellet analysis and identification of prey species

In a companion paper, diet was compared between seasons, revealing that birds were only preyed upon by pied currawongs during spring and early summer. In order to gain more detailed information, in this paper all of the data were divided into half-month intervals. Each month was grouped into early (day 1 to 15) and late (day 16 to end of month).

Bird remains in pellets were identified predominantly by the shape of bird bones. Fragmented bones and feathers could not be identified. Whenever possible, bird bones were identified to species using reference collections of the Australian National Wildlife Collections (CSIRO Division of Wildlife and Ecology) and of the Department of Prehistory - A.N.U.. If species identification could not be made, the bird bones were categorised into passerine and non-passerine by the morphology of the tarsometatarsus (van Tets personal communication), and their size was classified as small, medium and large (small was estimated to be less than 50 g, medium was between 51 and 100 g and large was more than 101 g). The age of birds preyed upon could sometimes be estimated from the morphology of the bones and feathers. Growing or young bones are chalky and young feathers are short, fluffy and usually without a rachis (van Tets personal communication). Identification of bones of the two well studied prey species in the pellet samples was assisted by the presence of metal and colour bands of these species, which were placed on *M. cyaneus* nestlings of 7 days of age and on *S. frontalis* nestlings of 9 days of age.

When pied currawongs were seen with avian prey in the field, an effort was made to identify the prey species. However, if species identification was impossible, the prey was only classified according to its size.

Predation on eggs and studied birds

Demographic data for superb fairy wrens and white-browed scrubwrens were analysed from the three breeding seasons (1992/93, 1993/94 and 1994/95) over which feeding data were obtained from pied currawongs. The number of total eggs present in the nests and those preyed upon as well as the number of surviving and eaten nestlings for both species were counted for each day. The total number of eggs for a half-month interval is defined as the number of egg-days. Predation rate on eggs or young per day was calculated by taking the number of eggs or young being preyed upon over the total number of eggs or young available on the same day. Also, the mean predation rate per day was calculated for a half-month interval.

Pied currawongs maintain breeding territories from the nestbuilding phase in August and September until their young fledge in early December. The breeding territory was defined by territorial defense of each pair. The last spots where the breeding pairs defended against other conspecific birds or other bird species were considered as the edge of their territory. These spots were then plotted in the maps as the border of territories. All activities of each pair such as collecting nest material and foraging during this period are confined to these areas. In the main study area (ANBG), the territories ranged between 4.5 and 11.6 ha (mean=7.9; s.d.=2.3; n=6).

To estimate the detailed impact of predation on studied birds, the number of fairy wren and scrubwren broods available and being preyed upon were calculated using currawong territory maps and grid references for the nests of the prey species for two seasons (1993/94 and 1994/95). The availability of these studied prey species in each currawong territory was then compared with the total predation occurring in that territory between September and December.

RESULTS

Hunting and feeding behaviour

Although the diet of pied currawongs is dominated by insects and fruit, they hunt vertebrates, in particular birds, opportunistically at any time of day. When hunting, they may suddenly attack birds on the ground, sneak up to and rob nests in bushes, or pursue a bird in the canopy or in the air. Thirty-three successful hunts were seen. Most successful hunting and killing is done solitarily by males (91%); occasionally females help to drive the prey (6%) but females rarely kill solitarily (3%). Calls which are similar to alarm calls are usually given by pied currawongs during pursuit and attack. Possibly, these calls function to stir up and frighten the prey.

Once they have captured a bird, they grasp its head or nape. When they fly with their prey, and if the prey is small, they usually grasp it in their bill, but if the prey is large, they carry it using both feet. In order to kill the prey, they either decapitate it, or pound it on the ground or a tree branch and peck it to death. After that, they always pluck the belly feathers of the prey, slit its stomach, and eat the internal organs first. They will then eat the muscle tissue on the breast, rump and elsewhere. If the prey is an adult bird, they usually leave its head, wings and skeleton. However, if the prey is a nestling, it seems that it is eaten whole except for the head. No skulls have been found in pellets.

The males often share their prey items with the females (73.2%; n=41). The males also feed some of these prey items to their young in the nest, often via the female (68.3%; n=41). They never bring an entire large bird to the nest. Instead, they always cache it away from nest (100%; n=38), and make several trips to feed their young. When bringing meat to the young, they are very cautious as they never fly directly to the nest, but instead pause several times to look around. Sometimes the meat which is going to be fed to the nestlings is torn in tiny pieces and formed into boluses. However, it is still unclear whether the meat is first eaten and then regurgitated. A feeding session can cease before the prey item is completely consumed. The males then cache the remaining prey on the ground or on a high branch of a tree (Prawiradilaga 1994). Females actively seek out such caches and eat them when they locate them.

Species and size of birds eaten

Sixteen bird species were identified as prey either from pellet analysis or feeding observations (Table 1). However, most of the bird remains in the pellets could not be identified. This was particularly true of observations at the nest, where bird prey was usually presented as finely chopped meat. The ability to identify *Malurus cyaneus* and *Sericornis frontalis* was enhanced because of the recovery of the bands of these species in pellet samples. Small species were more often found in pellets than the medium and large species (Table 1).

Predation pattern

(1) Egg predation

Pellet analysis indicated that predation on eggs was concentrated between early October and late December and peaked in late October and early November (Figure 1a). Egg predation began earlier and was most common in the 1993 breeding season, and was of shortest duration in the 1994 breeding season.

Figures 2a and 3a show the number of superb fairy-wren and white-browed scrubwren eggs available in the study area during three breeding seasons. Both species bred for about 7 months except in 1994/95 when severe drought shortened the breeding period. However, the scrubwren breeding season started and finished about six weeks earlier than the fairy-wren season.

Predation of superb fairy-wren eggs (Figure 2b) was consistently higher than that of white-browed scrubwren eggs (Figure 3b). In both species, the period of egg predation was shorter in 1994/95, reflecting the short breeding season of the prey that year. The predation rate of superb fairy-wren eggs in 1992 (Figure 2b) reflected the pattern of egg availability in the same year (Figure 2a). However, in 1993/94 and 1994/95 the peaks of egg predation of superb fairy-wren occurred before the highest egg availability, though there was a secondary peak in early February when egg availability was declining. Predation on white-browed scrubwren eggs peaked after the peaks of egg availability (Figures 3a and 3b).

(2) Bird predation

As for egg predation, pellet analysis showed that predation on birds commenced earlier in 1993/94 than in the other two seasons. In the three seasons, birds were largely preyed upon between early October and early December (Figure 1b). Apart from an anomalous record in late December 1992, predation on birds peaked in late November and then declined to negligible levels by late December.

Figures 4a and 5a describe the number of nestlings and fledglings of the fairy wrens and scrubwrens per day available in the study area during three years breeding seasons. Like eggs, the availability of young birds of both species in 1993/94 was higher than in 1992/93 or 1994/95, with one peak (early January) in fairy wrens (Figure 4a) and two peaks (late August and late November) in scrubwrens (Figure

5a). Figures 4a and 5a showed that fewer young of both species were available and for a shorter period in the drought year of 1994/95.

Pied currawongs mostly preyed upon nestlings and fledglings of the two studied species (Table 2). Recovery of metal and colour bands of these two species from pellet analysis indicated only one adult (a white-browed scrubwren) was killed. One or two day old fledglings were most likely to be preyed upon.

The high predation rate of young birds after late December (Figures 4b and 5b) cannot be attributed to currawongs, as they had ceased to prey upon birds coincident with the completion of their breeding season. Presumably, other predators such as snakes or lizards increased predation at this time.

Estimation of total prey eaten by a pair of currawong throughout breeding season based on bird meat delivery to the nest

Bird meat was delivered to the nest in 9.2% of nest watches (n=303 hours), with similar frequencies in each year (χ^2=0.5; df=1; p $\simeq$ 0.5). When meat was delivered during a nest watch, it was usually delivered many times (5.0 $\pm$ 3.4 (s.d.); n=28; effect of year; t=0.4, p=0.7), because parents tear up their prey before presenting it to the young, and because they are likely to take all young from any nest that they encounter. Assuming that each nest watch where meat was brought to the nest represents a predation event, that predation largely involves birds, either an entire brood, a fledgling or occasionally an adult bird, that there are 14 hours of feeding during October and November, and that the nestling period is 30 days, then each pair of currawongs will kill about 39 broods of other species to raise one brood. The total impact is likely to be much greater, because parents continue to feed their young other birds for a period after fledging, and they consume birds (and eggs) themselves, and males feed females with bird meat during incubation.

Estimation of superb fairy-wren and white-browed scrubwren broods available and being preyed upon in the pied currawong territory

Demographic data from two breeding seasons (1993/94 and 1994/95) showed that the number of superb-fairy wren broods available in each currawong territory was higher than the number of broods of white-browed scrubwrens (Table 3). However, the predation rate on the scrubwren broods was higher than on the fairy-wren broods during the two seasons (Table 4). For both species, 45% and 89% of nests are lost to predators during the peak period of nest predation.

DISCUSSION

Sexual difference in hunting behaviour of pied currawong

There are sexual differences in the hunting behaviour of pied currawongs. Males do almost all hunting and killing of avian prey while females only hunt occasionally. This study supports Recher's (1979) opinion that the foraging behaviour of breeding pied currawongs differs between males and females. Furthermore, Recher (1979) speculated that since the males are larger and have a stronger beak, they specialise on large food items, while females collect small food items in order to maximise the utilization of food resources in their territory.

The relationship between body size and feeding habits has been recognised in other bird species (Selander 1966, Morse 1980, Jehl and Murray 1986, Newton 1992). In most species, males are larger than females (Hill 1944, Jehl and Murray 1986, Aulen and Lundberg 1991), but in raptors females are larger (reversed sex dimorphism; Jehl and Murray 1986, Newton 1992). Sexual differences in bill size are the most important influence on foraging differences (Aulen and Lundberg 1991). Although the bills of male pied currawongs are longer than those of females (Wimbush 1969), further research on the foraging behaviour of marked and sexed individual birds is still required to identify the sex-based differences in behaviour of this species.

Pied currawong breeding season and predation pattern

There was no variation in the timing of pied currawong breeding during the three years of the study. Even though there was a severe drought in the 1994/95, pied currawongs still bred at the same time as in the previous years ($F_{2,11}$=0.3; p=0.7; Table 5). The breeding pairs built the nests, laid eggs and incubated in August and September, they cared for nestlings in October and cared for fledglings in November and December.

The predation patterns of eggs and birds followed the breeding pattern of pied currawongs. Pellet analysis indicated that the rates of egg and bird predation peaked between late October and late November (Figures 1a, b) when pied currawongs had large nestlings or young dependent fledglings. Also, the rate of egg predation peaked earlier (late October and early November) than the bird predation (late November).

In relation to the prey species, the pied currawong breeding season began at the same time as the breeding season of the fairy wrens, the commonest prey species in the area. Virtually, all other small birds produce fledglings before fairy wrens. Similar evidence has been reported for sparrowhawks (*Accipiter nisus*), the commonest small raptors in European woodlands in which their breeding pattern coincides with the the breeding patterns of their prey species (Newton and Marquiss 1982).

Impact on prey species

This study provides the strongest available evidence that the population expansion of pied currawongs is likely to have a strongly deleterious impact on populations of bird species that are taken as prey. Pied currawongs prey frequently upon young (nestlings and fledglings) of a large number of species (Table 1). Adults probably feed young from about 40 broods of other species to each brood of their own nestlings, and also consume additional young to feed themselves and their fledglings.

During the period when pied currawongs are nesting, between 45% and 89% of all broods of nestlings of the two well-studied small passerines are taken by predators (Tables 3 and 4). The 89% loss of white-browed scrubwren nests is particularly remarkable, given the notoriously cryptic nests of these species. At least some predation might be attributable to other predators, but several lines of evidence suggest that pied currawongs are the dominant predators. First, mammalian predation is likely to be slight. Cats and foxes are controlled within the ANBG study area, though probably exert some effect before they are shot. However, the position of some fairy-wren nests (at the forks of delicate branches some height from the ground) and the lack of damage to nests during the course of predation suggests birds or reptiles as the culprit. A study in a nearby region of the ACT which monitored predation of artificial eggs using automatic photography (Gardner 1995), suggests that nest visits are dominated by pied currawongs and grey shrike-thrushes (*Colluricincla harmonica*). Pied currawongs are considerably more abundant than shrike-thrushes at the ANBG, and in any case are presumably more likely to take large nestlings and fledglings. There is evidence of significant predation by eastern brown snakes (*Pseudonaja textilis*), but observational evidence (A. Cockburn, personal observation) suggests that this is confined to summer, presumably because of the greater activity of snakes at this time. Coupled with the data from pellet analysis (Figure 1), these observations suggest that pied currawongs dominate predation during September to December, though reptiles may be more important thereafter, at least in areas where foxes and cats are routinely shot.

Such extreme rates of predation are likely to exert a harmful impact on host species, both by reducing juvenile recruitment, and by extending the breeding season of species which continually lay replacement clutches. One fairy-wren which initated 8 clutches produced more than three times its own body weight in eggs during the course of the season, and did not survive the following winter. The impact on rare species, and those with more conspicuous nests seems, likely to be even more deleterious. We therefore conclude that increases in the number of pied currawongs should be considered in any attempt to analyse negative changes in the population densities of bush birds in eastern Australia.

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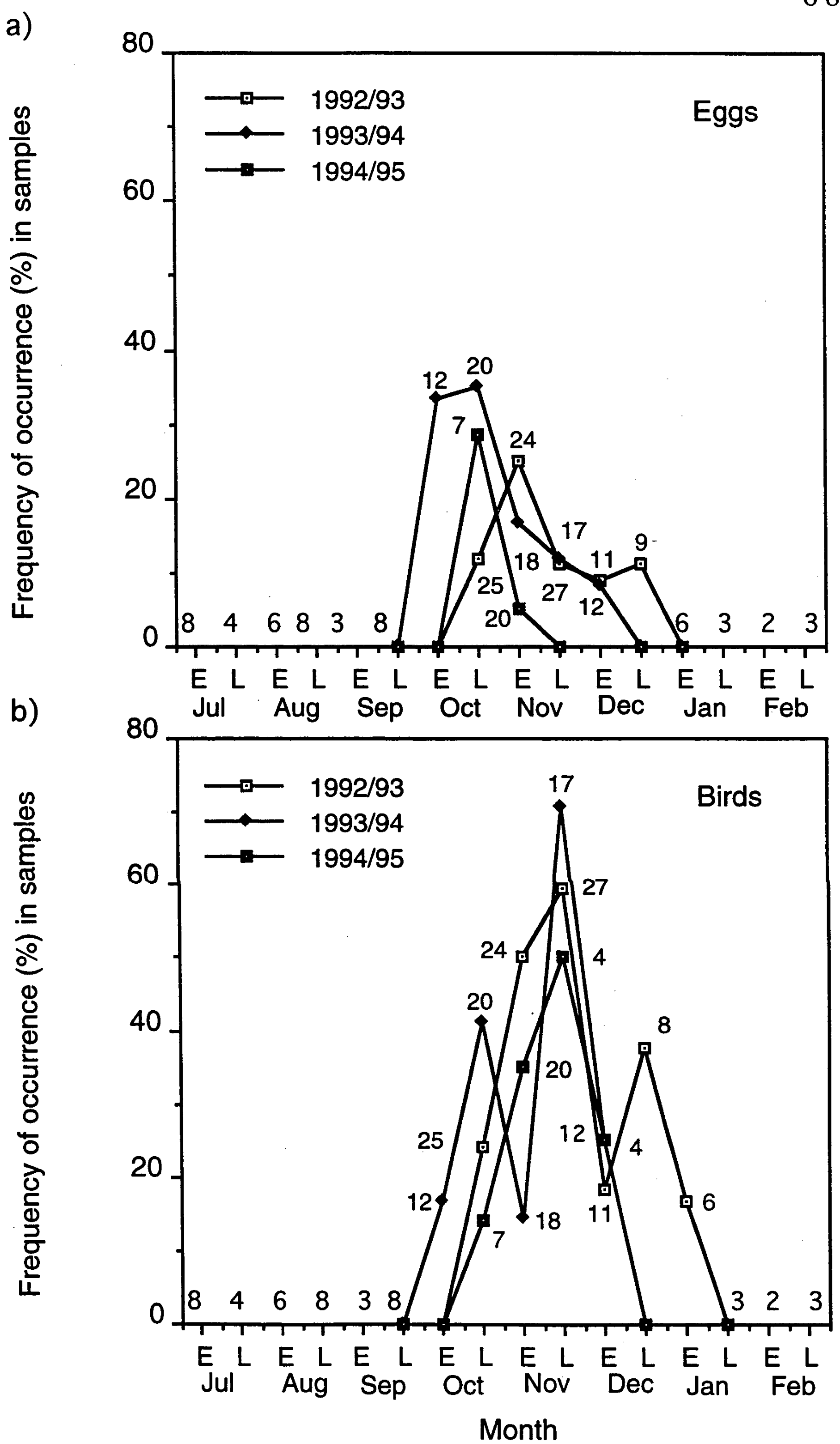
Table 1. Bird prey species identified from pellet samples and feeding observations.

<u>Note</u>: Y= young; A = adult

Size	Species	Number of occurrence in:	
		Pellets (n=85)	Observations (n=49)
Small (< 50 g)	Duckling (Anatidae)	-	1
	Rhipidura leucophrys (A)	-	1
	Myiagra sp. (A)	-	1
	Malurus cyaneus (Y, A)	15	1
	Sericornis frontalis (Y, A)	10	1
	Gerygone fusca (A)	-	1
	Passer domesticus (A)	1	-
	Unidentified species (Y, A)	25	7
	Total	51	13
Medium (51-100 g)	*Turdus merula* (A)	3	2
	Anthochaera carunculata (A)	4	1
	Acridotheres tristis (A)	2	-
	Sturnus vulgaris (Y, A)	3	4
	Grallina cyanoleuca (A)	-	1
	Unidentified species (Y, A)	4	-
	Total	16	8
Large (> 101 g)	*Columba domestica* (A)	-	3
	Geophaps lophotes (A)	-	1
	Platycercus elegans (A)	-	3
	Corcorax melanorhamphos (Y, A)	-	3
	Gymnorhina tibicen (Y)	1	-
	Total	1	10

Figure 1a. Egg predation by pied currawongs during three breeding seasons (1992/93-1994/95) based on pellet analysis. Sample sizes are the number of pellets considered. Sample sizes above x axis represent total samples for 3 years. Axes are scaled to facilitate comparison with subsequent figures.

Figure 1b. Bird predation by pied currawongs during three breeding seasons (1992/93-1994/95) based on pellet analysis. Sample sizes are the number of pellets considered. Sample sizes above x axis represent total samples for 3 years. Axes are scaled to facilitate comparison with subsequent figures.



a)
Frequency of occurrence (%) in samples
1992/93
1993/94
1994/95
Eggs
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
b)
Frequency of occurrence (%) in samples
1992/93
1993/94
1994/95
Birds
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
Month

Figure 2a. Availability of superb fairy-wren eggs during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

Figure 2b. Predation of superb fairy-wren eggs during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT. Numbers represent total number of egg-days (see text).
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

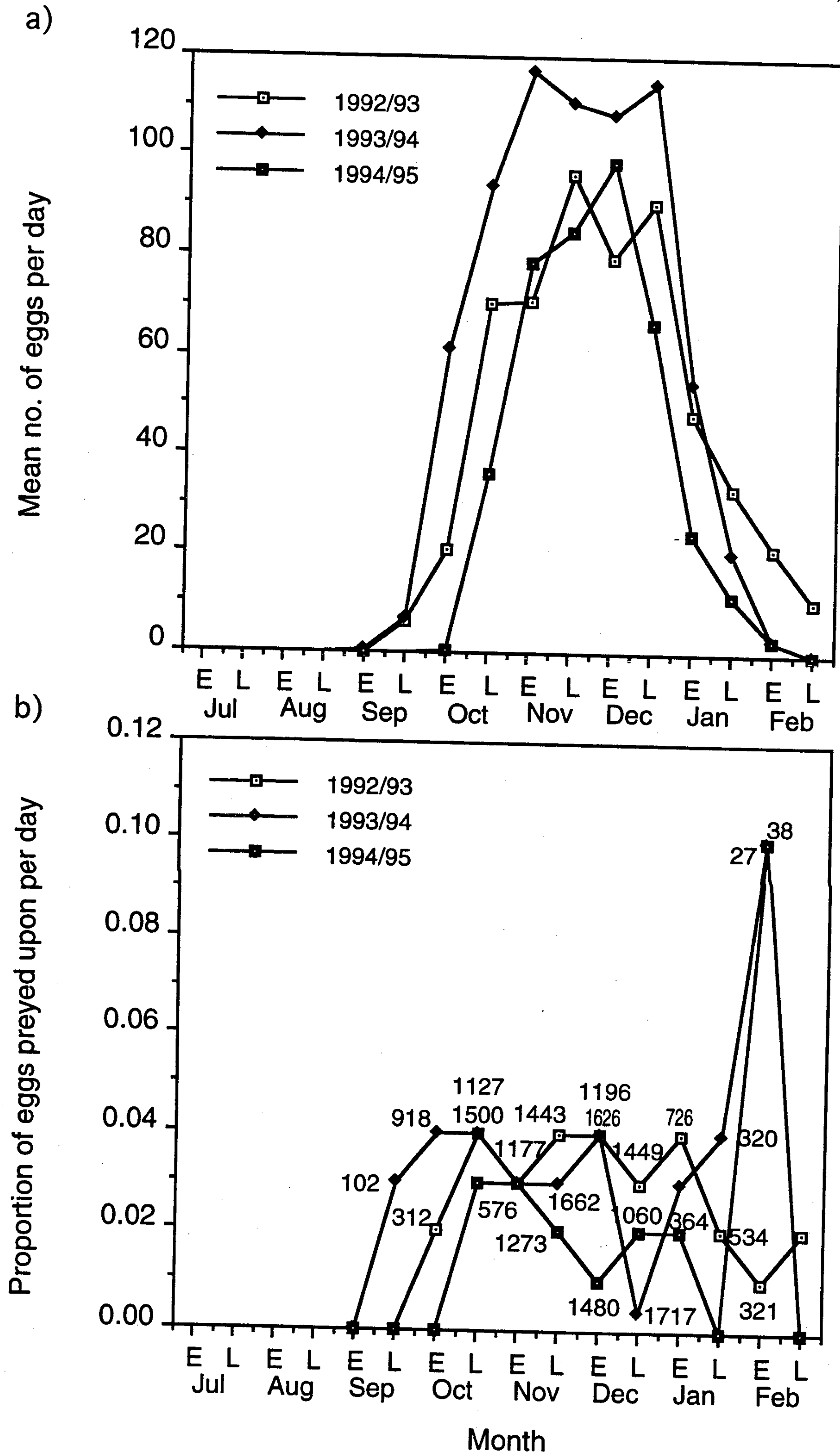

a)
120
100
80
60
40
20
0
Mean no. of eggs per day
1992/93
1993/94
1994/95
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
b)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion of eggs preyed upon per day
1992/93
1993/94
1994/95
38
27
1127
1196
918
1500
1443
1626
726
1177
1449
320
102
576
1662
312
1060
364
1273
534
1480
1717
321
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
Month

Figure 3a. Availability of white-browed scrubwren eggs during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

Figure 3b. Predation of white-browed scrubwren eggs during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT. Numbers represent total number of egg-days (see text).
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

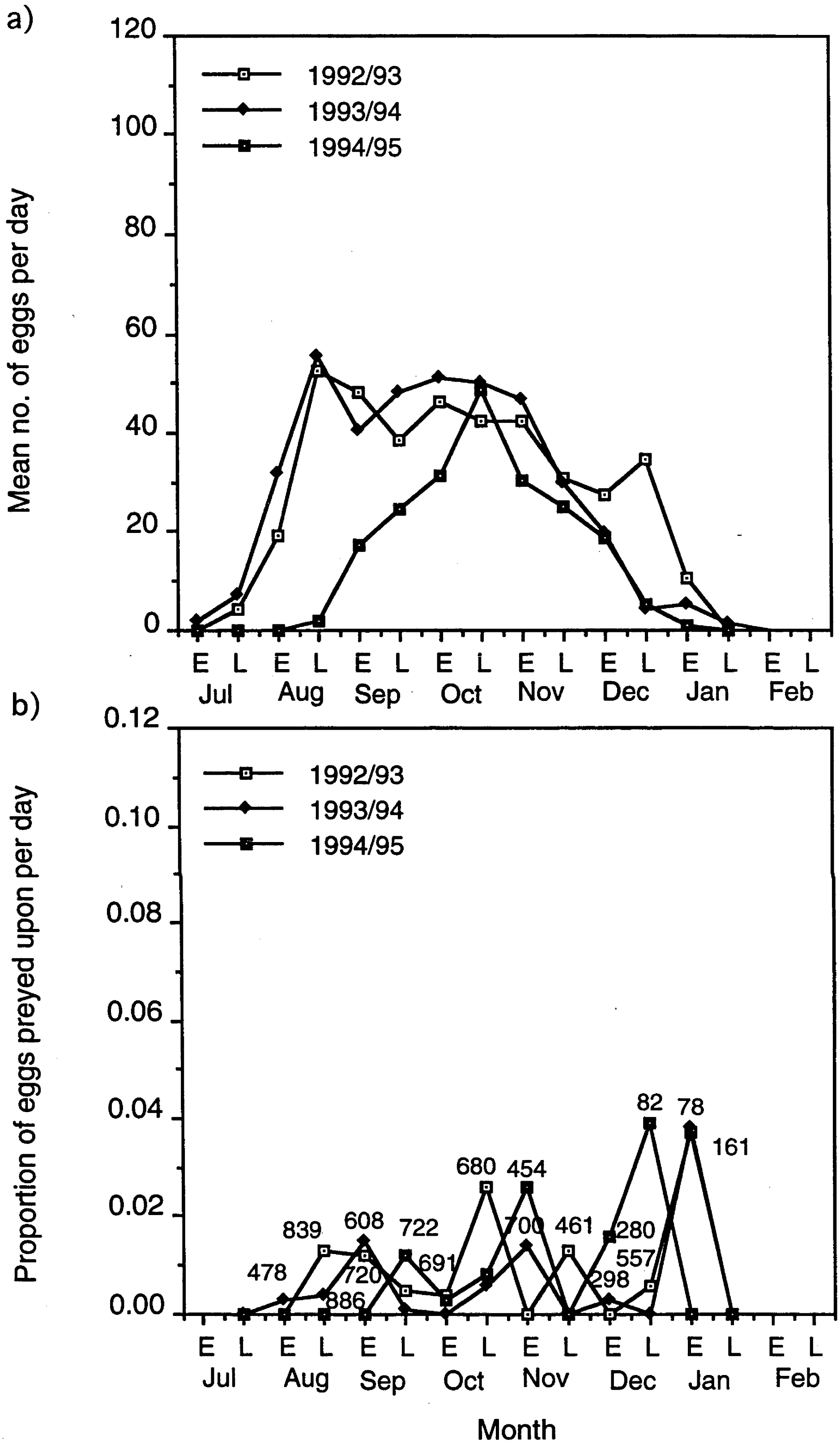

a)
Mean no. of eggs per day
120
100
80
60
40
20
0
1992/93
1993/94
1994/95
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
b)
Proportion of eggs preyed upon per day
0.12
0.10
0.08
0.06
0.04
0.02
0.00
1992/93
1993/94
1994/95
82
78
161
680
454
839
608
722
700
461
280
478
720
691
557
298
386
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
Month

Figure 4a. Availability of superb fairy-wren young during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
<u>Note</u> : E = early (day 1 to 15); L = late (day 16 to end of month)

Figure 4b. Predation of superb fairy-wren young during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
<u>Note</u> : E = early (day 1 to 15); L = late (day 16 to end of month)

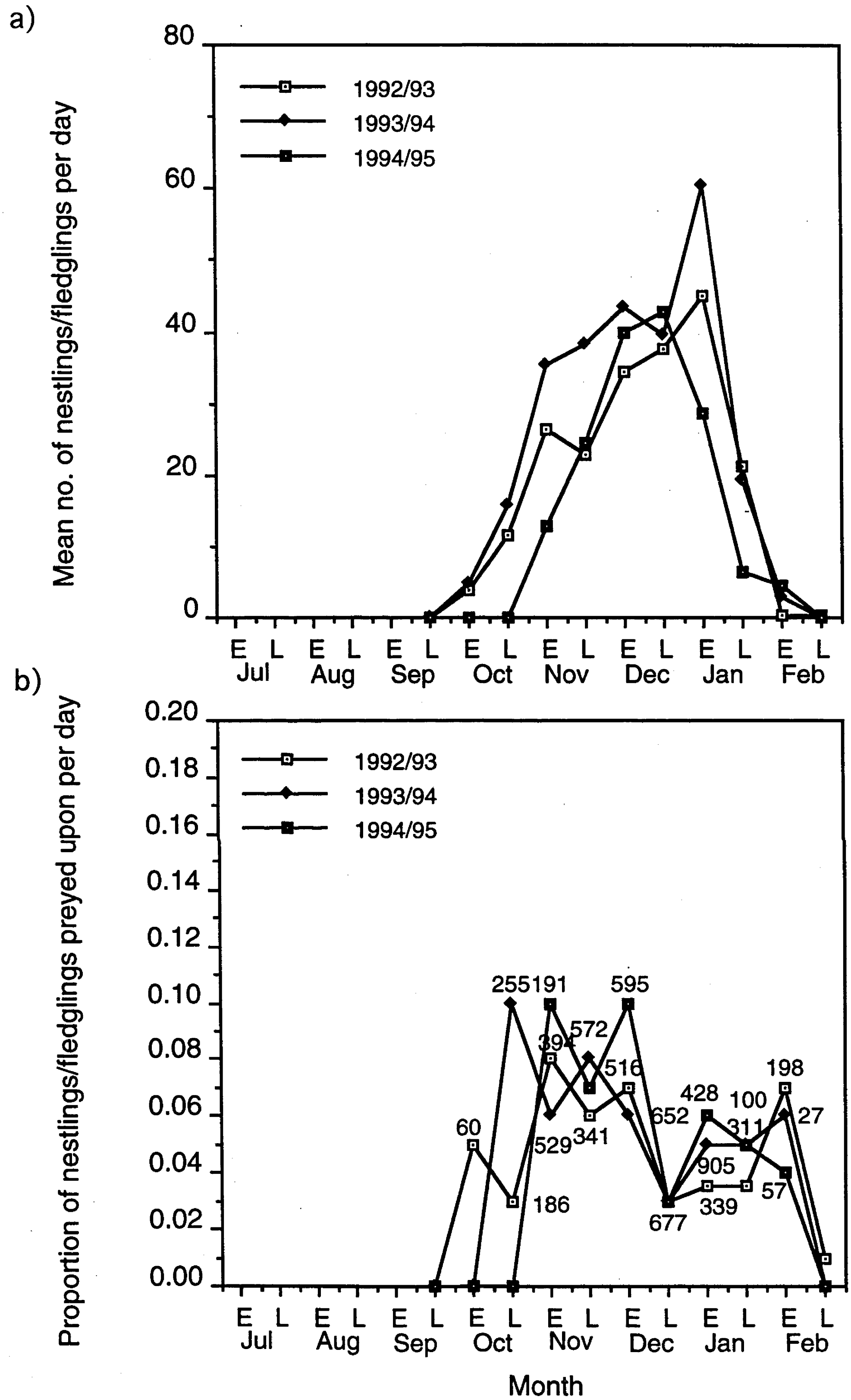

a)
80
60
40
20
0
1992/93
1993/94
1994/95
Mean no. of nestlings/fledglings per day
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
b)
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
1992/93
1993/94
1994/95
Proportion of nestlings/fledglings preyed upon per day
255
191
595
394
572
516
198
428
100
652
311
27
60
529
341
905
57
186
339
677
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
Month

Figure 5a. Availability of white-browed scrubwren young during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

Figure 5b. Predation of white-browed scrubwren young during three breeding seasons (1992/93-1994/95) at the Australian National Botanic Gardens, Canberra, ACT.
Note : E = early (day 1 to 15); L = late (day 16 to end of month)

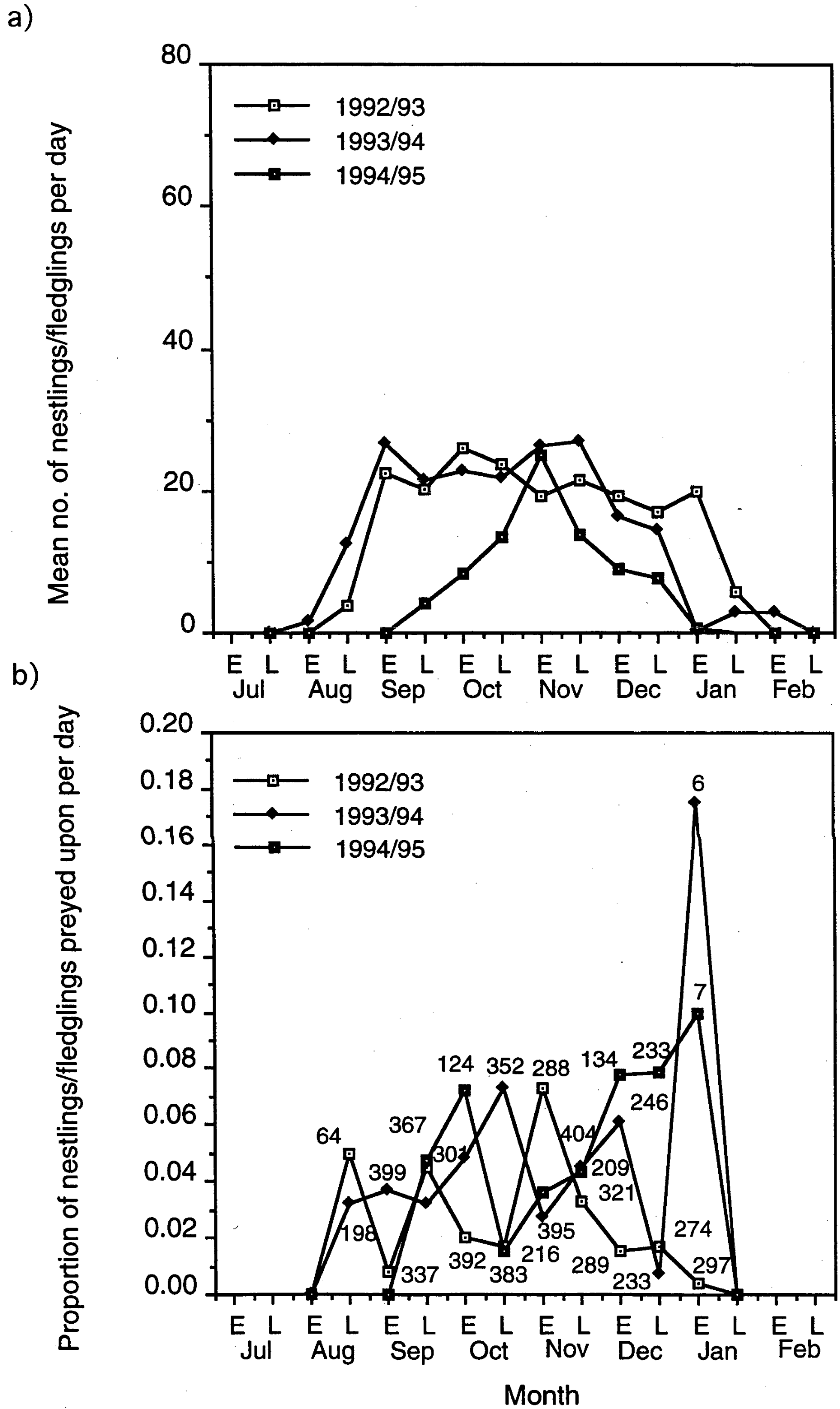

a)
80
60
40
20
0
Mean no. of nestlings/fledglings per day
1992/93
1993/94
1994/95
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
b)
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion of nestlings/fledglings preyed upon per day
1992/93
1993/94
1994/95
6
7
124 352 288 134 233
246
64 367
404
399 301
209
321
198
395
274
392 216
337 383 289 297
233
E L E L E L E L E L E L E L E L
Jul Aug Sep Oct Nov Dec Jan Feb
Month

Table 2. Predation on two prey species based on recovery of their metal and colour bands in the pellets collected in the ANBG for three breeding seasons (1992/93 - 1994/95).

Age of birds	Number of samples containing identified metal and colour bands of: Fairy-wren	Scrubwren
Nestlings	8	1
Fledglings day 1 or 2	3	2
Fledglings after day 2	1	1
Adult	0	1
Unknown	8	7
Total samples	**20**	**12**

Table 3. Numbers of broods of the two prey species available in six pied currawong territories at the ANBG for two breeding seasons.

Territory No.	Total No. of broods available in 1993/94		1994/95	
	Fairy-wren	Scrubwren	Fairy-wren	Scrubwren
1	21	11	21	12
2	16	5	16	4
3	17	12	9	7
4	19	8	8	12
5	13	14	11	4
6	15	5	7	1
Mean ± s.e	15.5 ± 1.7	9.2 ± 1.5	12.3 ± 2.1	6.7 ± 1.9

Table 4. Estimation on broods of the two prey species eaten in six pied currawong territories at the ANBG for two breeding seasons.

Territory No.	Total No. of broods eaten in 1993/94		1994/95	
	Fairy-wren	Scrubwren	Fairy-wren	Scrubwren
1	11	10	16	9
2	5	1	7	4
3	9	7	4	7
4	4	4	4	11
5	5	7	5	4
6	8	3	2	1
Mean ± s.e.	7 ± 1.1	5.3 ± 1.3	6.3 ± 2	6 ± 1.5
Rate (%)	45	58	51	89

Table 5. Breeding season of pied currawongs in the study areas during three years.

Year	Date of nestbuilding (mean ± s.d.)	Date of incubation (mean ± s.d.)	Date of hatching (mean ± s.d.)	Date of fledging (mean ± s.d.)
1992	16 September ± 38 days* (n=6)	19 September ± 7 days (n=4)	26 October ± 12 days* (n=6)	22 November ± 11 days (n=9)
1993	10 September ± 24 days* (n=4)	22 September ± 15 days* (n=6)	12 October ± 13 days (n=9)	14 November ± 14 days (n=9)
1994	1 September ± 15 days (n=4)	16 September ± 8 days* (n=6)	17 October ± 10 days* (n=7)	18 November ± 11 days (n=8)

Note:
* Including second attempt

Chapter 4

Reproductive biology of pied currawongs, *Strepera graculina* in newly colonised areas of their breeding range

INTRODUCTION

The pied currawong (*Strepera graculina*) is one of the Australo-Papuan passerines that has not yet been the subject of an intensive and long term study. Although it has been suggested that pied currawong population may be increasing (Recher and Lim 1990), the population dynamics of this species are not clearly understood. The only information on the demography of pied currawong is a study on longevity of banded birds in south-eastern Australia which reported a high survival of some adults (Nicholls and Woinarski 1988). Studies on the reproductive biology of pied currawongs, including brood size, number of surviving and independent young, and reproductive behaviour may provide key information for demography of the species and evidence of population increase.

Pied currawongs are monogamous (Lack 1968). Monogamy is common among birds (Lack 1968, Emlen and Oring1977, Møller 1986) and characterised by biparental care (Oring 1982, Wickler and Seibt 1983, Mock and Fujioka 1990). Such biparental care is seldom shared equally and the female parent commonly contributes more than the male one (Lack 1968, Trivers 1972, Clutton-Brock 1991). Although the absence of male care during nestling period can cause a decline in growth rate and survival of young until fledging in some passerines (Greenlaw and Post 1985, Wolf, Ketterson and Noran 1988, Bart and Tornes 1989), the importance of male care after the post-fledging period until foraging independence has not yet been investigated (Bart and Tornes 1989).

Based on his observation on one breeding pair of pied currawongs for one season, Recher (1976) reported that this pair was engaged in reproductive activities for five to six months and both parents provided care for the young until fledging. However, the biparental care for this species has not been investigated sufficiently. In this paper, I examine the breeding success of urban pied currawongs over three seasons and examine biparental care by observing male and female contributions in raising their brood throughout the breeding period commencing from nest building until their young become independent.

MATERIAL AND METHODS

Study species

The pied currawong is a large (ca. 345 gr) passerine in the tribe Artamini, subfamily Corvinae, family Corvidae (Sibley and Ahlquist 1985; Sibley *et al.* 1988; Sibley and Ahlquist 1990) which is common throughout eastern Australia (Gould 1865; Blakers *et al.* 1984). It occupies eucalypt forests, woodlands and suburbs (Slater 1976, Lenz 1990).

The pied currawong is omnivorous, with a diet dominated by insects and fruit; but during the breeding season it includes other vertebrates, and particularly birds (Chapter 2). Foraging is opportunistic and involves walking, pecking and digging from the ground or vegetation, bark probing, gleaning from canopy, sally-flycatching from the ground or elevated perches, and hawking flights (Chapter 5).

Study area

The study was conducted at adjoining sites in the Australian National Botanic Gardens (ANBG) and the Australian National University campus, Canberra, Australian Capital Territory (149^{0}15' E 36^{0}05'S) for three breeding seasons (1992, 1993 and 1994). The habitat in the Australian National Botanic Gardens (40 Ha) is a mixture of plantations of Australian plant species, and native vegetation comprising woodland dominated by *Eucalyptus rossii* and *E. macrorhyncha* and with a mixed *Stipa/Danthonia/Poa* grassland understorey. The habitat in the Australian National University campus (280 Ha) comprises open parkland where both tree and shrub species are often introduced.

Data collection and analysis

Birds were caught by walk-in house trap (crow trap) and bal-chatri traps (McClure 1984), both baited with meat. The captured birds were then marked with unique colour bands. The behaviour of these captured birds was observed in the field and their sex was determined from copulations and incubation (n=12). Although temporary residents or migratory birds were easily caught, birds occupying permanent territories proved very difficult to capture. In general, it was only possible to catch the male of the territorial pairs, presumably because they are more inquisitive or bold.

Breeding pairs and nest sites were located by walking through territories and observing nestbuilding and other reproductive activities. During the incubation and nestling periods, nest condition was checked from a distance and by observing the behaviour of the breeding pairs during systematic observations conducted every second day.

Nest failure was usually detected within a couple of days. Clutch sizes could not be determined as most nests were very high and pied currawongs proved sensitive to human disturbance by repeatedly attacking observers. Brood size was determined at the point when young were visible at the rim of the nest. The survival of young after fledging was followed as closely as possible until the time they became nutritionally independent. Most young are independent by seven weeks after fledging. Because birds range widely and start to aggregate into flocks, it was hard to locate young and their family by 5 weeks after fledging, so I used the number of young surviving to five weeks after fledging as a measure of breeding success.

Time-activity budgets of the marked-breeding pairs were made from observations at sufficient distance to ensure that the presence of the observer was ignored by the birds. Observations were spread as evenly as possible over all daylight hours and throughout the breeding season. Observations on nestbuilding, mate guarding, incubation, mate feeding, nest visits, removal of faecal sacs, parental guarding, and territorial defence by each pair were carried out in systematic observations of one hour duration. Data were gathered every second day. Observations started following a 5 minutes acclimatisation period after I arrived in the territory.

During the nest building period, records were made on the number of female building visits, the males feeding the female, males and females chasing intruders and the length of time the male guarded the female.

During incubation, records were made on the length of time females incubated the eggs, the extent of male attendance, the rate of male feeds to the incubating female, and whether males or females chased intruders.

In the nestling phase, records were kept on the rate of feeding visits by males and females, removal of faecal sacs by males and females and whether males or females chased intruders.

After the young fledged, each family was followed and watched for an hour period to quantify post-fledging care. The frequency that both parents provisioned their young and the length of time they spent with their young were recorded. Because the young moved within a wide area, a long time searching prior to observations was needed to locate them. Therefore, observations on post-fledging care were less regular and frequent. Summary data are presented in tables and figures as rates or proportion of time per hour.

RESULTS

Survival of adults

During the three-year study, no mortality of banded territorial birds was recorded in the area. Seven marked pairs nested in the area for 3 years and three marked pairs for 2 years. Thus, while it was impossible to estimate life table statistics, it is clear that urban pied currawongs are long lived.

Breeding season

The pied currawongs in this study defended their breeding territory between August and early December. They built their nest and laid eggs in September. The eggs hatched in October, and the young fledged between November and early December, and they became independent from mid January onwards. Even though there was a severe drought in the 1994 season, there was no delay in the timing of breeding (Table 1).

Pied currawongs have long term pair-bonds. Although females were not always marked, observations on banded birds indicated that these pairs stayed together and bred over three seasons.

Breeding performance of pied currawong

Nesting success

A total of seventeen pairs of breeding pied currawongs were observed. Of these pairs, seven were observed for three seasons, and three for two seasons. The remaining pairs were only observed for one season because they moved their nests outside the study site, or their nests could not be located. The breeding performance of ten to twelve pairs was assessed every year (Table 2). Currawongs raise only one brood each year. In the 1992 season, three pairs lost their first clutch. Two pairs renested, but these second clutches also failed. In the 1993 season, one pair failed to rear a first clutch but successfully raised a second brood. In the 1994, two pairs failed with their first clutch. Only one pair renested successfully.

Brood size and independent young

Brood sizes ranged from 1 to 3 (Table 3). Although there was no significant difference between years ($F_{2,30}$=0.3; P=0.8), the low brood size in the 1994 may be related to a severe drought in this year. The proportion of young surviving to independence in the 1994 was also low (Table 4).

Nest failure

During three seasons, nest failure occurred either during incubation (4 out of 8) or at the nestling stage (4 out of 8). During incubation 75% (3 out of 4) of nest failures were caused by storms which blew the nests out of the tree. The other nest failure during incubation could have been caused by an unknown predator, since only eggshells of three fertilised eggs were found under the damaged nest. At the nestling stage, nest failure was probably caused by predation. Potential nest predators which often visited pied currawong territories and prompted strong retaliation from the breeding pair were Australian ravens *Corvus coronoides* and other pied currawongs. Three of 4 cases of nest failure just occurred after hatching (day 1 or 2) and the last case occurred at the end of nestling period.

Young mortality in successful clutches

Mortality of young during the nestling and post-fledging stages was similar over three seasons (Table 4). Eight out of 13 cases of nestlings mortality were probably caused by partial predation or starvation in the nest, 3 nestlings disappeared after storms, 1 nestling fell out of the nest, was injured and then died of starvation, and 1 nestling died while being removed from the nest for banding.

After fledging, 6 out of 12 young disappeared, possibly because of predation, 3 young were abandoned by their parents and died of starvation, 1 young was drowned, 1 young disappeared after a storm and 1 young died after being attacked and injured by an unknown species. Most young (8 out of 12) that disappeared did so within 1 week of fledging (Table 4).

Reproductive behaviour

Nest sites and building

Pied currawongs build bowl nests with an outer ring of between 28-37 cm (mean=32; s.d.=3.7; n=4) and an inner ring of diameter 15-17 cm (mean=15.4; s.d.=1.2; n=4), and 4-6 cm deep (mean=5.2; s.d.=1; n=4). The nests were made of twigs of *Eucalyptus* spp., *Acacia* spp. or any other species available in the territory, and lined with root fibres, grass and bark.

The nests were usually located in *Eucalyptus* trees, but in the 1992 breeding season one nest was found in a willow tree (*Salix babylonica*) at the Australian National University campus. They were placed at the far end of a fork branch of a tree between 5.5 and 17 m (mean=12.6; s.d.=3.1; n=15) above the ground. Nest building took between three weeks and one month. Nest-building activity was assigned arbitrarily to two periods: Early (up to the stage when the nest consisted a shallow platform, made of big twigs and visible from a distant) and Late (when the nest was almost in bowl shape).

Nestbuilding was done exclusively by females. During the Early period, building visits occurred more frequently than in the Late period (t=10.2; p=0.002, Table 5). Males exhibited close mate guarding when females were collecting nest material, they also fed females. The proportion of time spent guarding per hour by male during the Late period of nest building was higher than during the Early period (Figure 1). However, the feeding rates per hour by males were similar throughout the nestbuilding period (Figure 2).

<u>Copulation</u>

Copulations are very brief and last about a second. Seven of eight copulations occurred on the nest during nestbuilding, but one copulation was observed during the incubation period. Copulatory behaviour can be initiated either by the male (n=5) or female (n=3) performing pre-copulatory displays. These displays involve spreading and quivering of the wings accompanied by soft-chittering calls and tail wagging. Then, both birds synchronise the displays and soon the female solicits and raises her tail while the wings are still fully spread. The male with opened and quivered wings moves closer to the female. He then mounts the female, grabs her beak and copulates. There does not appear to be any post-copulatory display. After copulation, the male flies off and sometimes gives calls while the female wags her tail, shakes and preens.

Incubation

Incubation was carried out by the female. It took about 21 days. As incubation progressed the female spent more time incubating (Figure 3, $F_{1,24}$=3.6; p=0.07). During incubation the male guarded the nest by perching on the nest tree or nearby tree and chasing intruders. He also brought a variety of food and fed the incubating female. The proportion of time spent for guarding and feeding rate by male per hour in the third week of incubation period was higher than in the earlier weeks (Figures 1 and 2). Male guarding was important when the female was off the nest to forage or to stretch, preen and defaecate. When guarding, the male sometimes checked the eggs by looking into the nest but he never touched the incubated eggs.

Feeding of nestlings

Although Recher (1976) believed that incubation in pied currawongs only commences when all eggs are laid, in this study hatching was observed to be asynchronous and occurred over 2 days suggesting that incubation also starts asynchronously. During observations, the hatching process was recorded by the chick calls and the number of opened beaks when parents brought food to the nest. Both parents contributed food from the first day of hatching, but males usually gave food to the female who then transferred it to the nestlings. After the first few days the males fed nestlings directly. For the first two weeks, males fed nestlings at comparable rates to females (Figure 4). Thereafter, female feeding tended to increase, while male feeds declined sharply (Figure 4, $F_{1,56}$ = 5.4; p = 0.02). All major food types recorded in the diet (Chapter 2) were presented to the young.

Pied currawongs never brought food directly to the nest from the foraging or caching site. They usually stopped or perched a few times with the food in their beak and looked around. Then if they felt secure, they flew to the nest and fed the young.

Brooding of nestlings

Only females brooded nestlings. The length of brooding declined with nestling age ($F_{3,28} = 21.04$; $p < 0.0001$), though at least some brooding continued until the young fledged (Figure 5).

Nest sanitation

Both parents removed faecal sacs from the nest. The removal rate per hour by males (mean=0.11; s.e.=0.04; n=71 hours) and by females (mean=0.24; s.e.=0.04; n=71) was similar (t=1.7; p=0.08).

Territorial defence

During the breeding period, pairs confined activities such as the collection of nest material and foraging to the territory. The territory size ranged between 5.2 and 12.1 ha (mean=7.9; s.d.=2.1; n=11). Both sexes defended the territory, but territorial chases by males were an order of magnitude more frequent than chases by females (Tables 6 & 7). During incubation, the frequency of repulsions per hour by the male alone was significantly higher than by the female alone or by both male and female together ($F_{2,132}$=7.2; p< 0.001).

The most common targets of chases were other pied currawongs (33%); Australian magpies (25%) and Australian ravens (16%) (Table 8). Because breeding pairs of pied currawongs were also attacked by Australian magpies and red wattlebirds, interactions with these species need not reflect the risk of nest predation.

Care of fledged young

The care of fledglings took about seven weeks. Probably in response to hatching asynchrony, fledging took place over two days. During this period parents had to care for both fledged young and the young which remained in the nest. Once all young were fledged, they started to follow their parents and the family moved throughout the territory.

During the post-fledging period the male parents increased the feeding rates and guarding time when they had more than one young to raise, and provided more care than the female (Figures 6 and 7). Instead of feeding their young, both parents also took them to walk and forage on the ground or to forage on foliage. Only the male parents were observed to hunt and prey upon other bird species while they accompanied their young. Detailed information on the development of foraging skill in young pied currawongs is presented elsewhere (Chapter 5).

DISCUSSION

Breeding success of urban pied currawongs

Successful breeding by urban pied currawongs is certainly contributing to the increase in currawong numbers. This study shows that the adult birds have a high survival rate ($\simeq$ 100%) and that their breeding success is high. During the study period each pair successfully raised about 1.7 young per year (Table 4), despite one of the most severe droughts ever recorded in the region. Therefore, the number of pied currawongs is not just increasing as a consequence of increased production in their original breeding range. Reproduction and high survival in their new range are major contributors to the changes.

Reproductive behaviour of pied currawongs

Both male and female pied currawongs contribute care throughout the breeding period. Nestbuilding, incubation and brooding were undertaken by females alone. However, the males contribute during this time via territorial defence and feeding the females during nestbuilding and incubation (Figures 1 and 2). Such sex differences are common among passerines (Regelmann and Curio 1986).

Contrary to Recher's (1976) findings, this study shows that the males did not carry nest material or help to build the nest. Perhaps, Recher had a problem with identification of the sex of each bird as his observed pair was unbanded, and the brood patch on the female belly would not have been developed during the nestbuilding period.

The length of incubation period found in this study (about 3 weeks) is similar to that previously reported by Recher (1976). The proportion of time spent incubating in the third week of the incubation period increased sharply (Figure 3). Possibly, this is because the male increased his feeding rate to the incubating female (Figure 2).

During the nestling period, the females tended to increase the feeding rate as the young grew older (Figure 4) and as the brooding rate dropped (Figure 5). However, the males tended to reduce the feeding rate with nestling age (Figure 4), possibly because they delivered larger loads in the form of the bird meat to the nests. During the post-fledging period, the males's care seemed to increase when they had more than 1 young to raise. The male feeding rate and proportion of time spent guarding increased with the number of young (Figures 6 and 7). Also, the male parents seemed to demonstrate successful hunting and killing when they accompanied their young in the absence of the female. Possibly, at this time the male care is important since most young of predatory birds begin to learn prey recognition and hunting in the period of transition to independence (O'Connor 1984).

Nest defense

Pied currawong males were more active than females in defending their territory throughout the breeding period (Tables 6 & 7, Figure 7). They also guarded the females during the nestbuilding and incubation periods. Male guarding of females activity peaks late in the nestbuilding period (Figure 1), probably as a defence against extra-pair copulation (Birkhead and Møller 1992).

In conclusion, the urban pied currawongs breed successfully and contribute to the increase of population of pied currawong. The pied currawongs in this study had a regular breeding season and raised one brood between August and December.

The male and female pied currawongs cooperated extensively in caring for their offspring throughout the breeding season. The role of the female parents appears to be most important during nestbuilding until the fledging phase and the role of the male parents appears to become more important during post-fledging phase.

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Table 1. Breeding season of pied currawongs in the study areas during three years (1992-1994).

Year	Date of nestbuilding (mean ± s.d.)	Date of incubation (mean ± s.d.)	Date of hatching (mean ± s.d.)	Date of fledging (mean ± s.d.)
1992	16 September ± 38 days* (n=6)	19 September ± 7 days (n=4)	26 October ± 12 days* (n=6)	22 November ± 11 days (n=9)
1993	10 September ± 24 days* (n=4)	22 September ± 15 days* (n=6)	12 October ± 13 days (n=9)	14 November ± 14 days (n=9)
1994	1 September ± 15 days (n=4)	16 September ± 8 days* (n=6)	17 October ± 10 days* (n=7)	18 November ± 11 days (n=8)

Note:

* Including second attempt

Table 2. Nesting success by pied currawongs during three breeding seasons (1992-1994).

Year	No. of observed pairs (nests)	No. of nest failure	No. of pairs laid second clutch	No. of successful pairs
1992	12 (14)	5	2	9 (75%)
1993	10 (11)	1	1	10 (100%)
1994	12 (13)	2	1	11 (92%)

Table 3. Brood size of pied currawongs during three breeding seasons (1992-1994).

Year	Brood size			Mean ± s.e.
	1	2	3	
1992	4	1	6	2.2 ± 0.3
1993	0	3	7	2.7 ± 0.3
1994	2	3	6	1.7 ± 0.2
Total	6	7	19	2.2 ± 0.2
(%)	18.7	21.9	59.4	

Table 4. Production of young pied currawongs during three breeding seasons (1992-1994).

Year	Total no. of nestlings in successful clutches (no. of clutches)	Young mortality in successful clutches	Mortality of fledglings in the first 5 weeks	Total no. of independent young
1992	24 (9)	4 (17%)	1 (5%)	19 (79%)
1993	27 (10)	3 (11%)	6 (25%)	18 (67%)
1994	26 (11)	6 (23%)	5 (25%)	15 (58%)
Total	77 (30)	13 (17%)	12 (19%)	52 (67%)

Table 5. Nestbuilding behaviour of female pied currawongs.

Nestbuilding phase	No. of nests	Nestbuilding visits per hour ± s.e.	Total observations (hours)
Early	4	7.3 ± 0.8	25
Late	6	4.3 ± 0.7	12

Figure 1. Male guarding during the nestbuilding and incubation period. Numbers represent total observation hours.
Vertical lines depict standard errors.

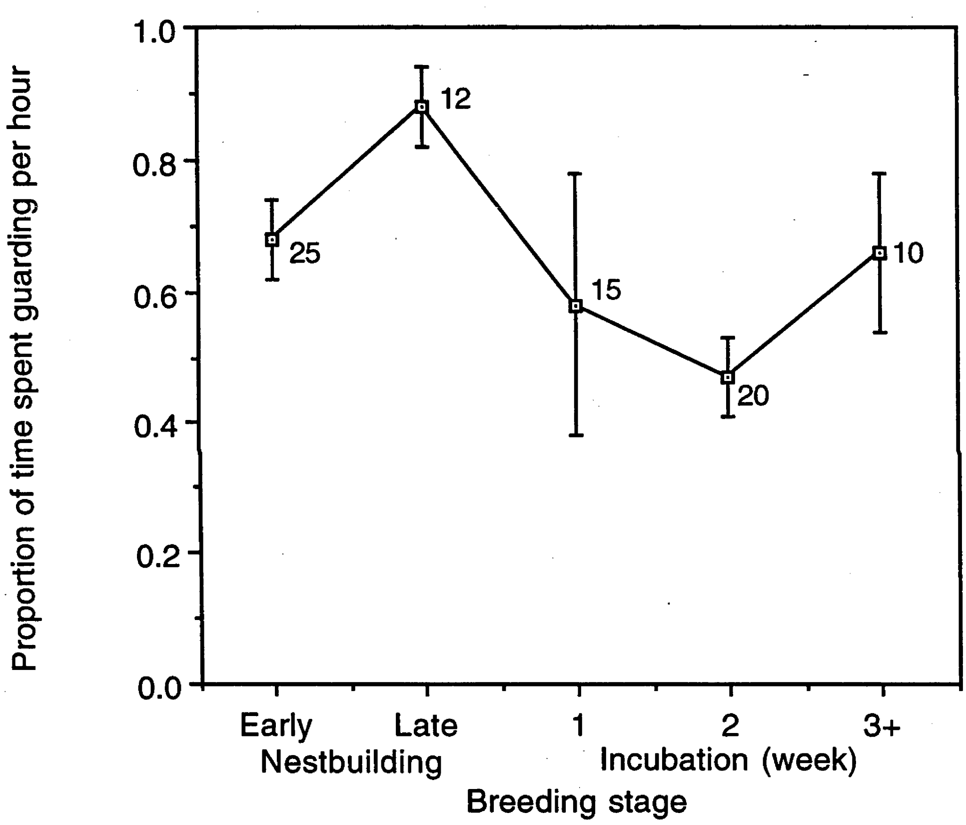


Figure 2. Rate of male feeds to the female (± s.e.) per hour during the nestbuilding and incubation period. Numbers represent total observation hours.

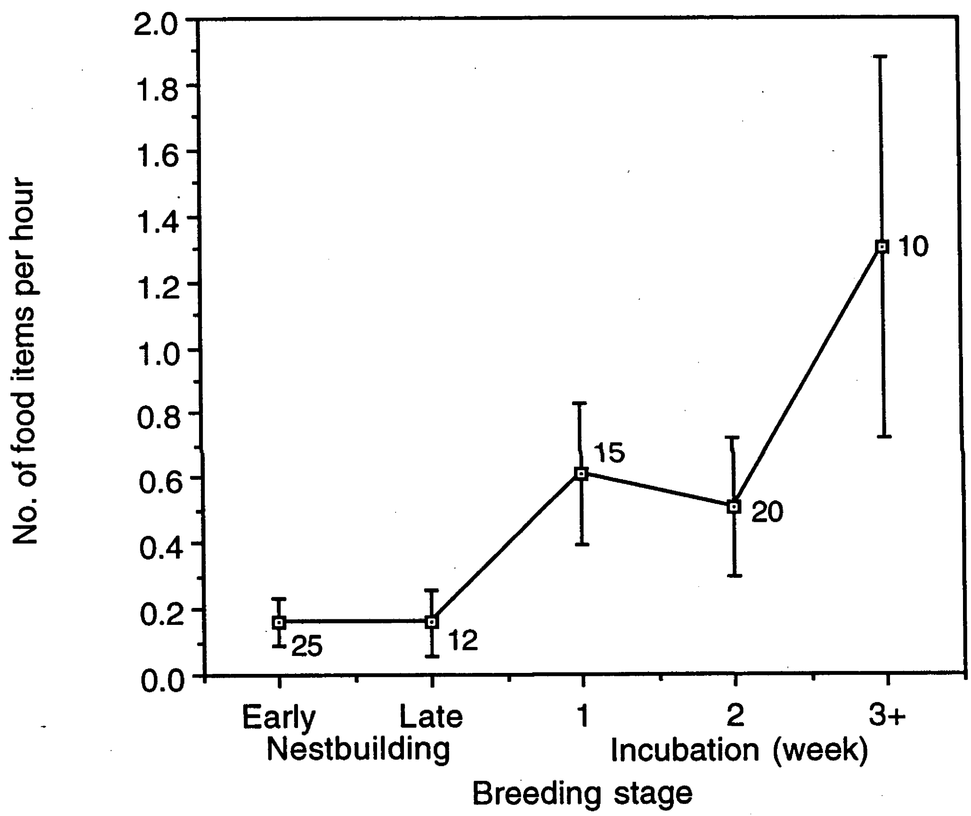


Figure 3. Incubation behaviour of female pied currawongs (n=11).
Numbers near points denote total observation hours.
Vertical lines depict standard error.

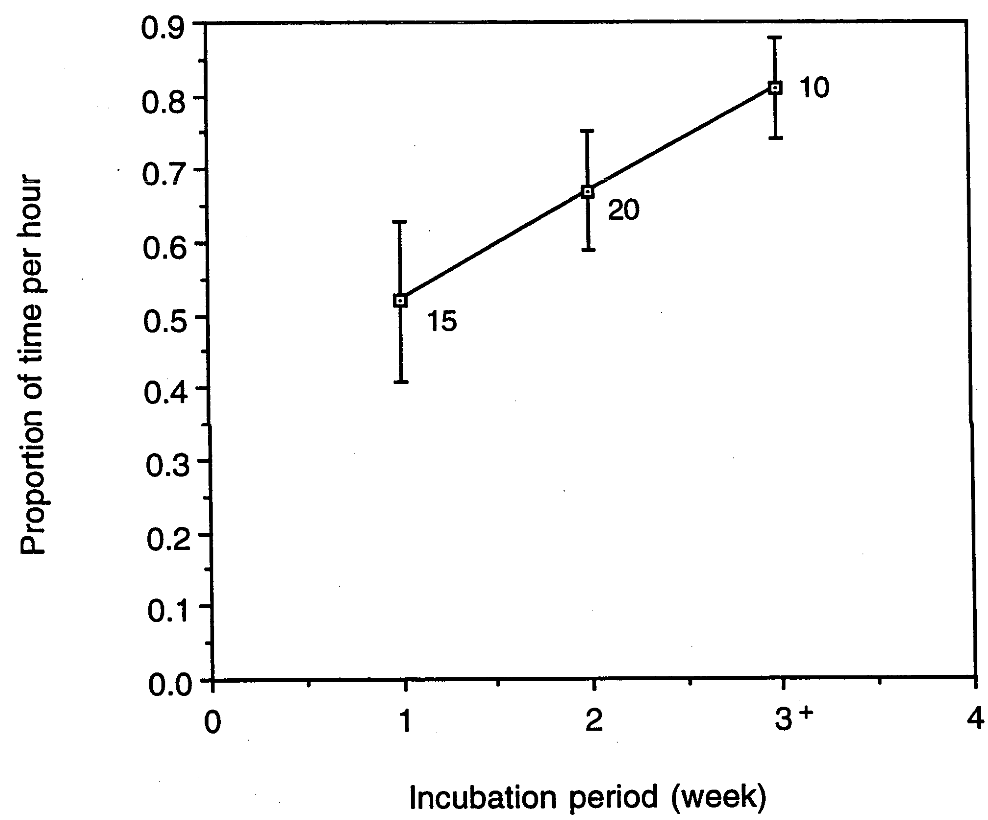


Figure 4. Number of feeding visits per hour by male and female pied currawongs (n=8 pairs). Numbers represent total observation hours. Vertical lines depict standard errors.

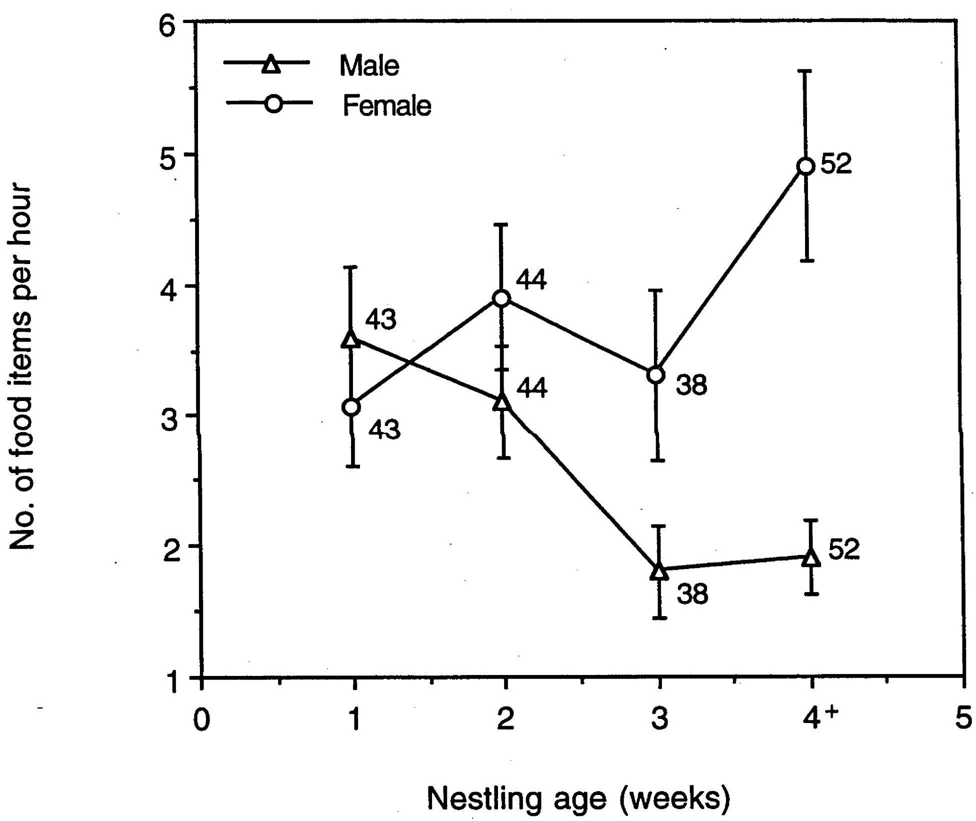


Figure 5. Brooding behaviour of female pied currawongs (n=8).
Numbers represent total observation hours.
Vertical lines depict standard errors.

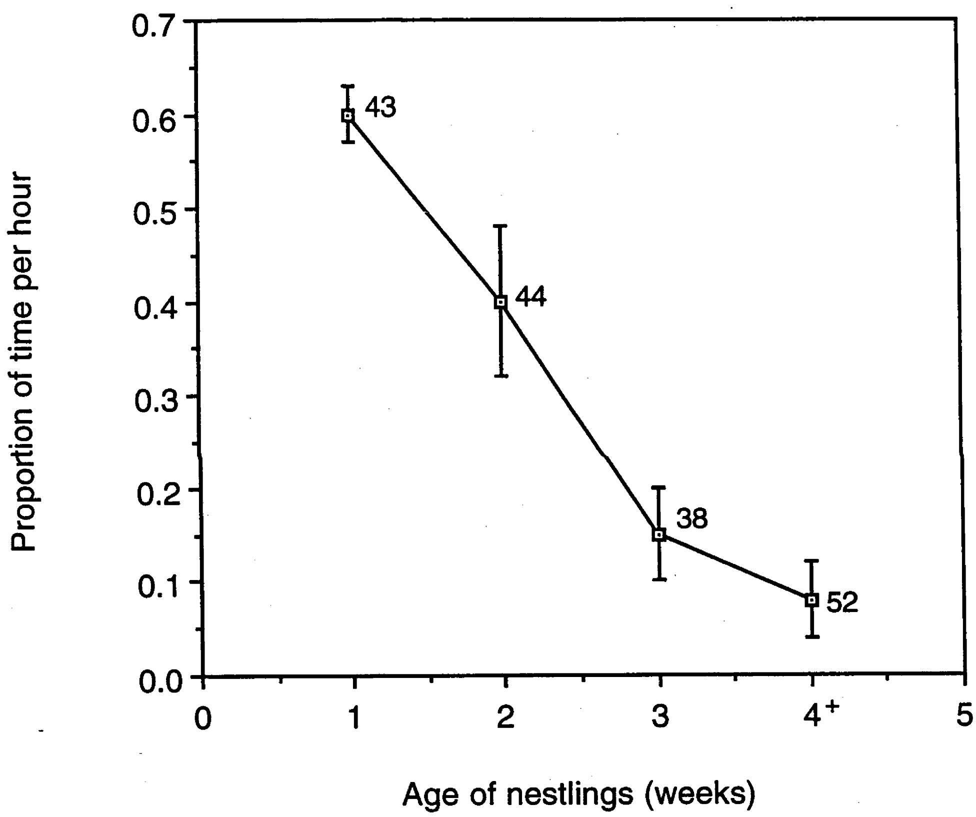


Table 6. Rates of attacks by male and female pied currawongs (n=8 pairs) on other birds intruding on their territory during nestbuilding and incubation period.

Breeding phase	Rate of attacks per hour ± s.e.			Total observations pairs (hours)
	Male	Female	Both	
Nestbuilding	0.3	0	0.3	6 (37)
Incubation	0.54 ± 0.17	0.02 ± 0.02	0.09 ± 0.05	11 (45)

Table 7. Rates of attacks by male and female pied currawongs (n=8 pairs) on other birds intruding on their territory during nestling phase.

	Frequency of repulsions per hour ± s.e. by:			Total observations (hours)
Nestling phase	Male	Female	Both	
1 week	0.5 ± 0.3	0.06 ± 0.04	0.09 ± 0.09	32
2 week	0.1 ± 0.06	0.04 ± 0.03	0.08 ± 0.05	34
3 week	0.3 ± 0.14	0.03 ± 0.03	0.03 ± 0.03	29
4 week	0.11 ± 0.06	0.04 ± 0.04	0	27

Table 8. Bird species and frequency of chases (n=134) by pied currawongs.

Bird species	Frequency of chases (%)
Predatory	
Australian ravens *Corvus coronoides*	16.4
Brown goshawk *Accipiter fasciatus*	0.8
Australian magpies *Gymnorhina tibicen*	24.6
Laughing kookaburras *Dacelo gigas*	3
Other pied currawongs	32.8
Non-predatory	
Maned ducks *Chenonetta jubata*	2.2
Crimson rosellas *Platycercus elegans*	2.2
Sulphur-crested cockatoos *Cacatua galerita*	2.2
Galahs *Cacatua roseicapilla*	1.5
Red-wattlebirds *Anthochaera carunculata*	10.4
Australian magpie-larks *Grallina cyanoleuca*	3.7

Figure 6. Feeding fledgling rates per hour by male and female pied currawongs. Vertical lines depict standard errors. Numbers represent total observation hours.

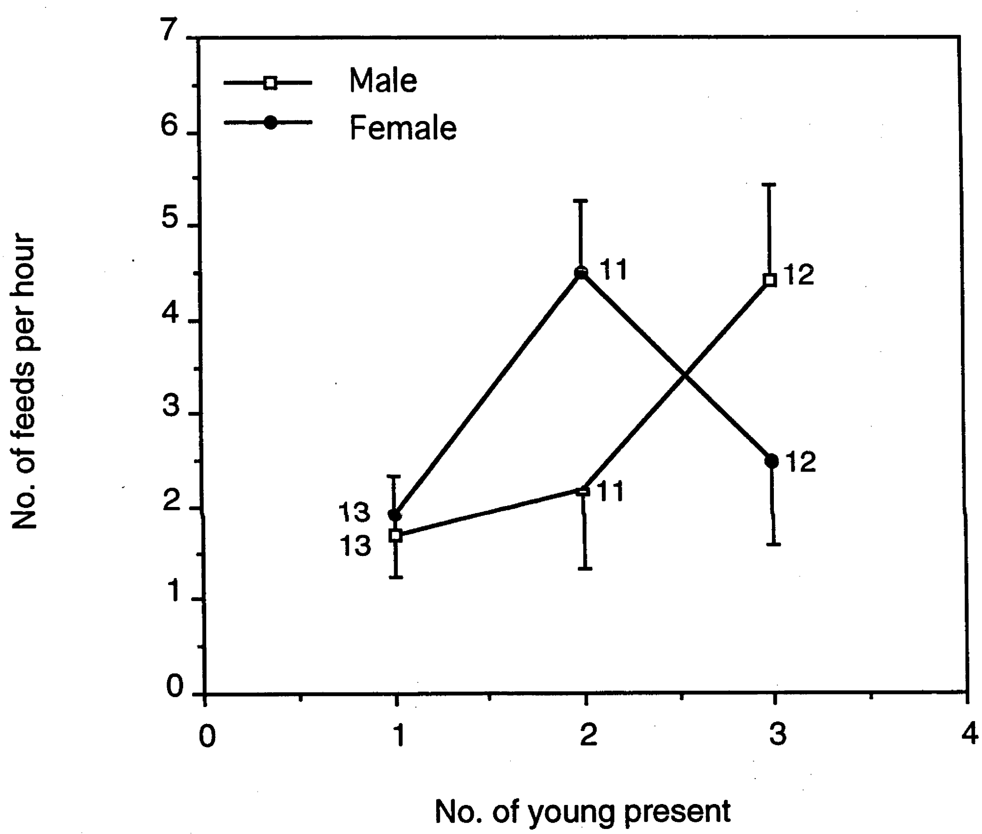
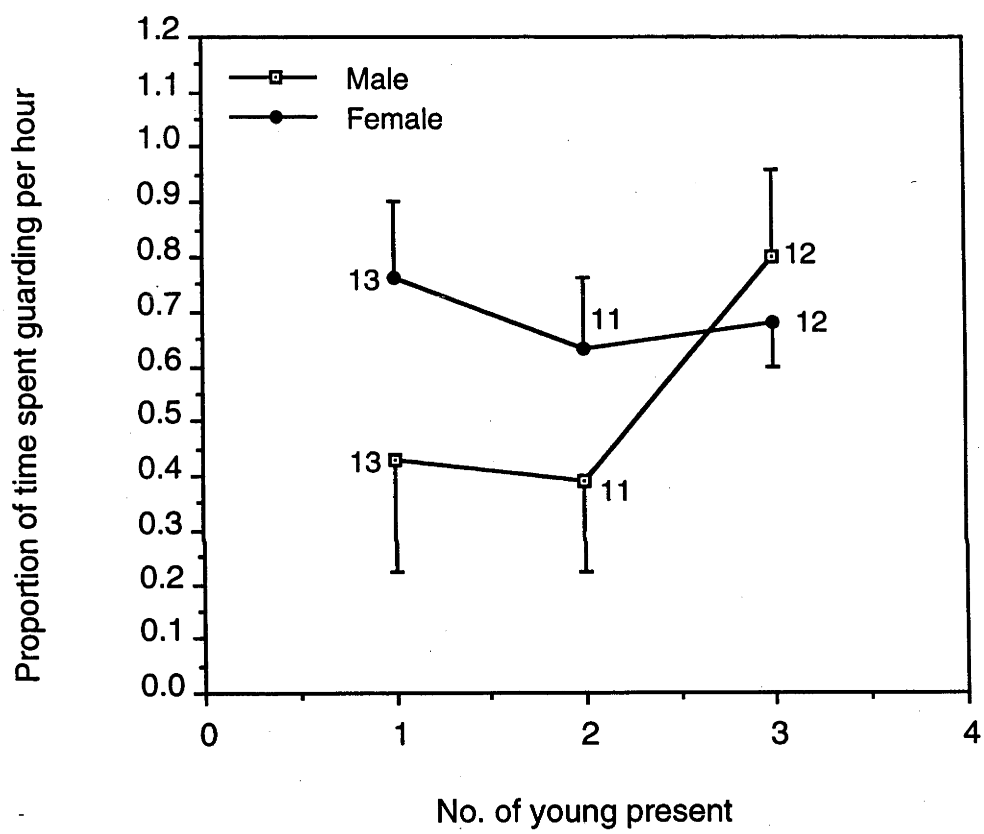


Figure 7. Guarding fledgling by male and female pied currawongs. Vertical lines depict standard errors. Numbers represent total observation hours.



Chapter 5

Early development of foraging skills in pied currawongs, *Strepera graculina*.

INTRODUCTION

Young passerines are typically among the least well developed birds at birth (Starck 1993). Most studies of parental care in passerines have focussed on the nestling period, in part because of the difficulties in observing young after they leave the nest. Only a few studies have quantified parental care after fledging until young become independent (for reviews see Davies 1976; Moreno 1984; Heinsohn 1991). However, it is during this period that the young acquire important skills including predator avoidance, social interaction with competitors (Brown 1975), and in particular foraging proficiency (Wunderle 1991). The period after fledging is often a time of extremely high mortality (Lack 1954), and post-fledging care during the transition to independence is a critical component of parental investment (Drent & Daan 1980; Weathers & Sullivan 1989).

The length of parental care after fledging varies between species (Davies 1976; O'Connor 1984). It can be shorter or longer than that of the nestling period (Skutch 1976; Heinsohn 1991), and appears to be determined by the length of time required by the young to master foraging (Davies 1976; Davies & Green 1976; Moreno 1984), and by interaction between offspring and parents (Davies 1976). Davies (1978) emphasized that reduction in food supply to the young ("parental meanness") triggered the onset of offspring independence.

Several studies have showed that young birds are less successful at capturing prey than adults (Norton-Griffiths 1969; Recher & Recher 1969; Orians 1969; Edwards 1989). Improvement of foraging skills over time has been demonstrated in young of predatory species such as Loggerhead Shrike *Lanius ludovicianus* (Smith 1973), American Kestrel *Falco sparverius* (Muller 1974), Reed Warbler *Acrocephalus scirpaceus* (Davies & Green 1976), Spotted Flycatcher *Muscicapa striata* (Davies 1976) and Yellow-eyed Junco *Junco phaeonotus* (Weathers &

Sullivan 1989). This improvement could be due to developmental maturation of morphological traits or learning (Marchetti & Price 1989; Wunderle 1991).

The transition to foraging independence in pied currawongs is of particular interest. This is because their diet at the time of fledging is dominated by toxic or highly aggressive prey such as bulldog ants (*Myrmecia* spp.), stinkbugs (Pentatomidae) and chrysomelids (Chrysomelidae), as well as nestlings and fledglings of other birds which require skill to locate and kill.

In this paper, I examine the transition to foraging independence in juvenile pied currawongs. I examined the interaction between the young and their parents and how juveniles achieve foraging independence.

METHODS

The biology of Pied Currawongs

Pied currawongs are large (290-410 g) omnivores (tribe Artamini, subfamily Corvinae, family Corvidae) (Monroe & Sibley 1993) and are monogamous. They can live as long as 14 years (Nicholls & Woinarski 1988).

Their diet throughout the year is dominated by insects and fruit. However, during the breeding season it includes vertebrates, particularly other bird species (Chapter 2).

The foraging mode of Currawongs is opportunistic. Their foraging method varies from walking and foraging from the ground or vegetation (Brown & Veltman 1987), digging soil (personal observation), probing bark (Recher 1979; MacNally 1994), gleaning from the canopy (Ford et al. 1986, personal observation), sallying from the ground or elevated perches, robbing bird nests (Brown & Veltman 1987; Gardner 1995) and hawking flights (personal observation). They forage alone, in pairs, or in flocks during their seasonal migration. Paired birds have been recorded to hunt cooperatively, though hunting is dominated by the male (Chapter 4). They also occasionally cache food (Prawiradilaga 1994).

Historically, in south-eastern Australia Currawongs were seasonal altitudinal migrants (Wimbush 1969; Rowley 1975; Pizzey 1986). They would flock and move to lower altitudes or towns and settlements during autumn and winter (Hobbs 1961; Lamm & Wilson 1966; Readshaw 1968; Bass 1990) and return to the mountain forests for breeding in spring (Hobbs 1961; Walsh 1965; Readshaw 1968; Lenz 1990). However, in the last few decades a substantial number of breeding pairs have not returned to the mountains but have stayed around human settlements and bred there (Lenz 1990).

Currawongs are territorial and both sexes expel intruders. During the breeding season, the foraging area is confined to the territory which is about 8 ha. Nest building commences in August and only the female builds the nest and incubates eggs. Incubation takes about 21 days and the nestling period is approximately 30 days. Both males and females feed nestlings and fledglings. They raise one brood every year. After the young reach independence, they join large flocks.

Study area and population

Observations of the behaviour of young Currawongs were conducted at the Australian National Botanic Gardens (ANBG) and the Australian National University campus (ANU), Australian Capital Territory (149º 15'E 05'S) during two breeding and post-breeding seasons from September until December 1993 and 1994. The vegetation at the ANBG is a mixture of plantations of Australian plant species, and with native vegetation comprising woodland dominated by *Eucalyptus macrorhyncha* and *E. rossii* and with a mixed *Stipa/Danthonia/Poa* grassland understorey. The vegetation at the ANU campus is open parkland where *Eucalyptus* spp. are mixed with introduced tree and shrub species.

Behavioural data were collected each year from eight banded families of Pied Currawongs which could be reliably located. Most fledglings (70%) were unbanded, because nests were inaccessible and fledglings were sensitive to the disturbance of banding. Although pied currawongs often lay clutches of three eggs, nestling and fledgling mortality was high.

Data collection

After fledging I attempted to find the study families every two days. However, after the young fledged, families became locally nomadic and it was not always possible to locate them. Thus, observations were not always made at regular intervals. Observations continued until seven weeks after fledging. Although the young were not entirely independent by this stage, they were very mobile and were not always associated with their parents.

When a Currawong family was located, I observed the young for 1 hour. From broods of two or three I selected one young for observation. This focal young was followed and its behaviour during the one hour observation period was recorded. There were six behavioural categories: (1) begging for food from parents; including any activity that involved loud and frequent screams directed towards the parents; (2) pecking any objects nearby without swallowing them; (3) foraging actively for self (this category usually involved swallowing); (4) comfort movements (stretching and preening); (5) hopping or flying to follow parents or siblings; and (6) others (resting, sleeping, contact calls and indeterminate activities). The number of food items given by parents to the focal individual during observation was also recorded. Data collection ceased when the young moved out of sight or hid because of becoming alarmed. Data collected from periods of less than one hour were discarded.

Foraging effort was categorised into feeding attempts, proportion of all feeds obtained by self foraging and the proportion of feeding attempts that led to capture of prey. Feeding attempts were measured by counting the number of pecks at food or other objects and the number of food items swallowed in each hour of observation.

Juveniles of some families were sampled more often than those of others, because data collection relied on locating families with large ranges. The minimum number of 1-hour samples per individual over the transition period was 2, and the maximum was 12. In total, data sets were obtained from 16 juveniles.

Data analysis

Data collected from individual (focal) observations involved repeated measurements. These data had the form of a mixed model containing factors of interest (fixed effects: age of young; brood size and study area) and factors which had no biological meaning (random effects: the identity of individual young) (Bennington & Thayne 1994). Age of young was determined as the number of days after fledging. Brood size was the number of young per brood. Study areas were the Australian National Botanic Gardens (ANBG) and the Australian National University (ANU) campus.

Data on the number of begging calls, parental feeds and feeding attempts per hour were obtained in the form of counts. Because these data did not have a normal distribution, they were normalised by square root transformation. Proportions (self feeds and successful feeds) were normalised by square-root arcsin transformation. These transformations allow fitting at restricted maximum likelihood (REML) models (Dempster *et al.* 1984) which were calculated using the REML procedure in Genstat v 5.3 (Genstat 5 Committee 1993).

RESULTS

Initial modelling

In initial models of foraging skill in pied currawongs, brood size, study area, interaction between age and brood size, and interaction between age and study area did not affect begging calls, parental feeds, feeding attempts, self feeding or feeding success (Tables 1 and 2), except for a marginal effect of area which suggested that birds in the ANBG had a higher rate of self feeding than in the ANU campus. This result is not obviously explicable. I suspect that this is a Type I error and it will not be discussed further.

Age factor

By contrast, there was a consistent effect of age on all aspects of foraging performance.

Begging calls

Begging increased slightly with age in young Currawongs (Figure 1, $\chi^2 = 6.6$; df = 2; $p \simeq 0.01$).

Parental feeds

Feeds from parents increased significantly as the young grew older (Figure 2, $\chi^2 = 5.2$; df = 2; $p < 0.05$).

Feeding attempts

Although young tried to feed as soon as they fledged (Figure 3), feeding attempts increased strongly with age (Figure 3, $\chi^2 = 21.7$; df = 2; $p < 0.001$).

Self feeding

The young began to recognise food and feed by themselves 10 days after fledging (Figure 4). The proportion of feeds obtained by the young themselves increased dramatically with age (Figure 4, $\chi^2 = 54.7$; df = 2; $p < 0.001$).

Feeding success

The proportion of successful attempts at foraging increased significantly with age (Figure 5, $\chi^2 = 63.8$; df = 2; $p < 0.0001$).

Observation from foraging with parents

During the transition to foraging independence, there are other behavioural aspects which may be important in the development of foraging which have not been studied in depth here including learning of foraging skills and of handling prey from the parents. The young followed their parents and observed them feeding. Later, the young imitated their parents and fed by themselves.

DISCUSSION

Interactions between parents and offspring

As young Currawongs grew older, they begged more often (Figure 1). This increase probably reflects greater acitivity and mobility, allowing young to follow their parents more and harass them for food. Similar patterns have been reported in young Spotted Flycatchers (Davies 1976) and Northern Wheatears (*Oenanthe oenanthe*) (Moreno 1984).

Young Pied Currawongs receive virtually all of their food from begging for about 10 days after fledging (Figures 2, 4 and 5). Parental feeding rates increased slightly with age of young (Figure 2), which was also likely to reflect a greater proximity to young and a slight increase in begging rates.

Young Pied Currawongs seem to have prolonged parental care. At fifty days after fledging, they were still being fed by their parents (Figure 2). This prolonged parental care may correspond to the difficulties performing highly skilled feeding techniques (Ashmole and Tovar 1968). Most of the animal prey of pied currawongs is toxic (pentatomid bugs), difficult to catch or handle (e.g. *Myrmecia* sp., birds), or requires skill to find (e.g. eggs and nestlings).

Development of foraging skills in Pied Currawongs

Young Pied Currawongs started to peck at a variety of objects as soon as they fledged (Figure 3). Such exploratory feeding represents the early development of prey capture techniques (Barraud 1961, Wunderle 1991) and has been observed in several other passerines (Barraud 1961; Smith 1973; Davies 1976; Davies and Green 1976; Moreno 1984). As they grew older, they became more experienced.

Ten days after fledging, the young appeared to recognise food and were able to obtain food by themselves (Figure 4, 5). They followed their parents and foraged from the ground. The parents seemed to train them in simple foraging techniques. When the young were about 20 days after fledging, both parents led them to glean on foliage or in the canopy and seemed to show them how to search for foliage insects. If it was possible, after feeding their young both parents also showed them how to cache the remaining food. In addition, the male parents seemed to demonstrate bird prey capture, killing and handling in front of their young (Chapter 4).

In this study, the evidence for improved foraging performance because of developmental maturation or of learning is marked by the increase in obtaining food by themselves (Figure 4) and feeding success (Figure 5) with age. At the end of the observation period which was 50 days after fledging, the young obtained 80% of feeds by self foraging (Figure 4).

The foraging techniques performed by young Currawongs during the transition to independence include walking and foraging, sallying and gleaning in the foliage (personal observation) which are possibly the simplest techniques used by this species. Similar evidence on other bird species also showed that the simpler foraging techniques appear first (Davies 1976; Davies and Green 1976; Moreno 1984; Wunderle 1991). Other difficult foraging techniques such aerial hawking to hunt vertebrate prey may develop later (Muller 1974; Wunderle 1991). Also, the young Currawongs have demonstrated early caching behaviour during the transition to foraging independence (Prawiradilaga 1994).

In summary, young Pied Currawongs are completely dependent on parental feeds until 10 days after fledging. Their foraging techniques begin with pecking inanimate objects and their skills improve with age as shown by their increasing success rate.

In the early development stage, the young seemed to learn food recognition and simple foraging techniques from their parents. Parents appeared to train their young by leading them to foraging sites and accompanying them while foraging. They acquire simple foraging techniques in the period of the transition to independence. Young Currawongs can forage by themselves 50 days after fledging.

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Table 1. Summary of statistical analysis (χ^2) for brood size, age and interaction between brood size and age effects from restricted maximum likelihood (REML) models.

Analysis	No. of 1-hour samples	Effect of		
		Age vs brood interaction df = 2	Brood df = 2	Age df = 2
Begging calls	110	0.9, ns	0.6, ns	6.6, p=0.01
Parental feeds	110	2.8, ns	4.8, ns	5.2, p<0.05
Feeding attempts	106	2.5, ns	0.9, ns	21.7, p<0.001
Proportion of feeds from self foraging	101	0.2, ns	0.04, ns	54.7, p<0.001
Proportion of success	106	2.5, ns	0.2, ns	63.8, p<0.0001

Table 2. Summary of statistical analysis (χ^2) for area and interaction between area and age effects from restricted maximum likelihood (REML) models.

Variable	Total No. of 1-hour samples	Age vs Area df = 1	Area df = 1
Begging	110	0.2, ns	2.4, ns
Parental feeding	110	1.5, ns	0.6, ns
Feeding attempts	106	0.5, ns	0.6, ns
Proportion of feeds from self feeding	101	0.2, ns	5.1, $p < 0.05$
Proportion of successes	106	1.4, ns	0.9, ns

Figure 1. The number of begging calls per hour in relation to age of 16 juvenile Currawongs. For analysis, number of begging call was normalized by a square-root transformation. The back transformed regression line is presented.

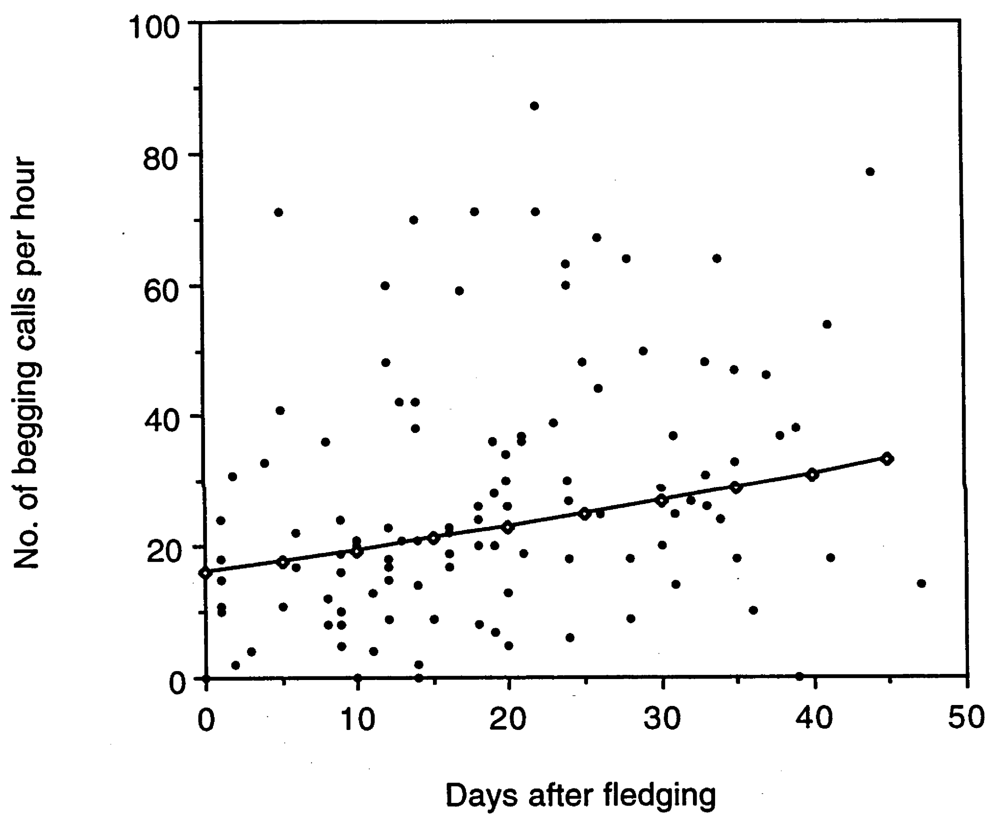


Figure 2. The number of parental feeds per hour in relation to age for 16 juvenile of Currawongs. For analysis, the number of parental feeds was normalized by a square-root transformation. The back transformed regression line is presented.

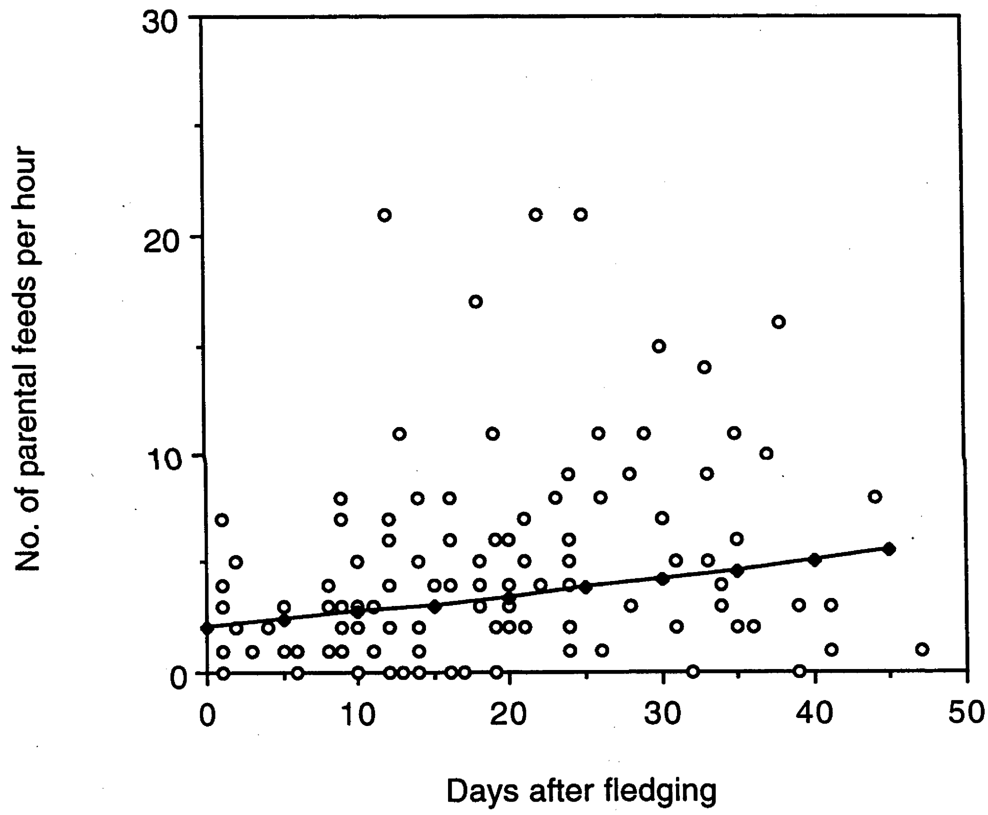


Figure 3. The number of feeding attempts per hour by 16 juvenile Currawongs. For analysis, the number of feeding attempts were normalized by a square-root transformation. The back transformed regression line is presented.

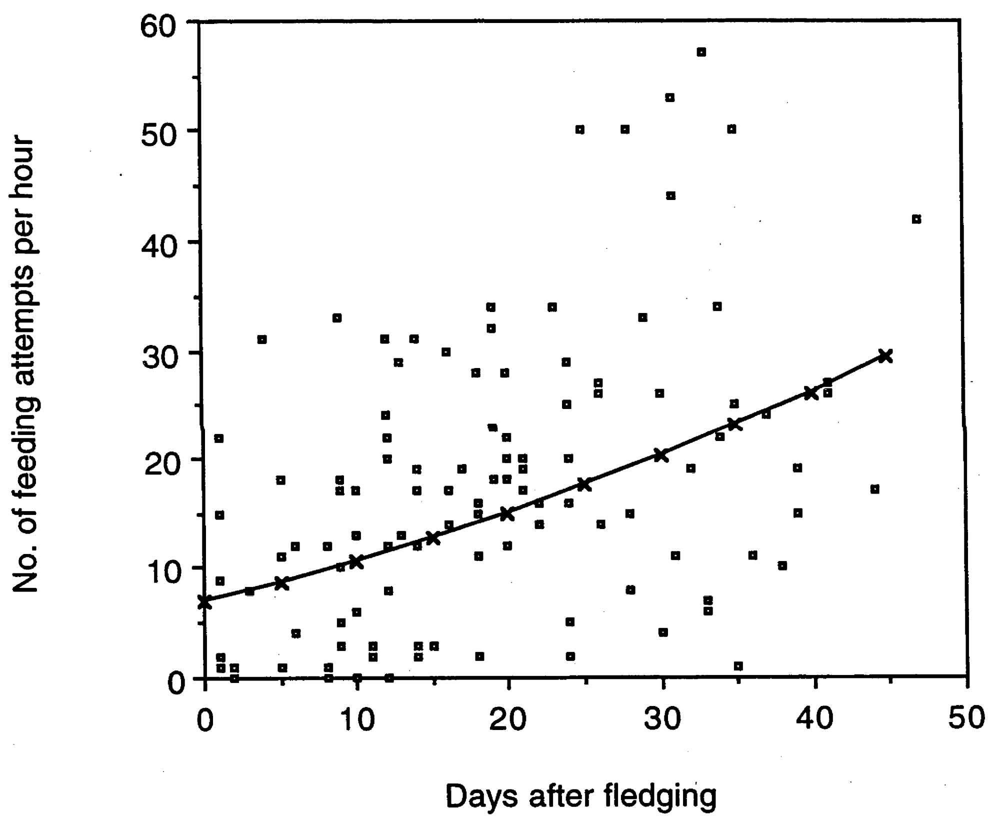


Figure 4. The proportion of feeds obtained by self foraging by 16 juvenile. For analysis, the proportion of feeds was normalized by a square root arcsin transformation. The back transformed regression line is presented.

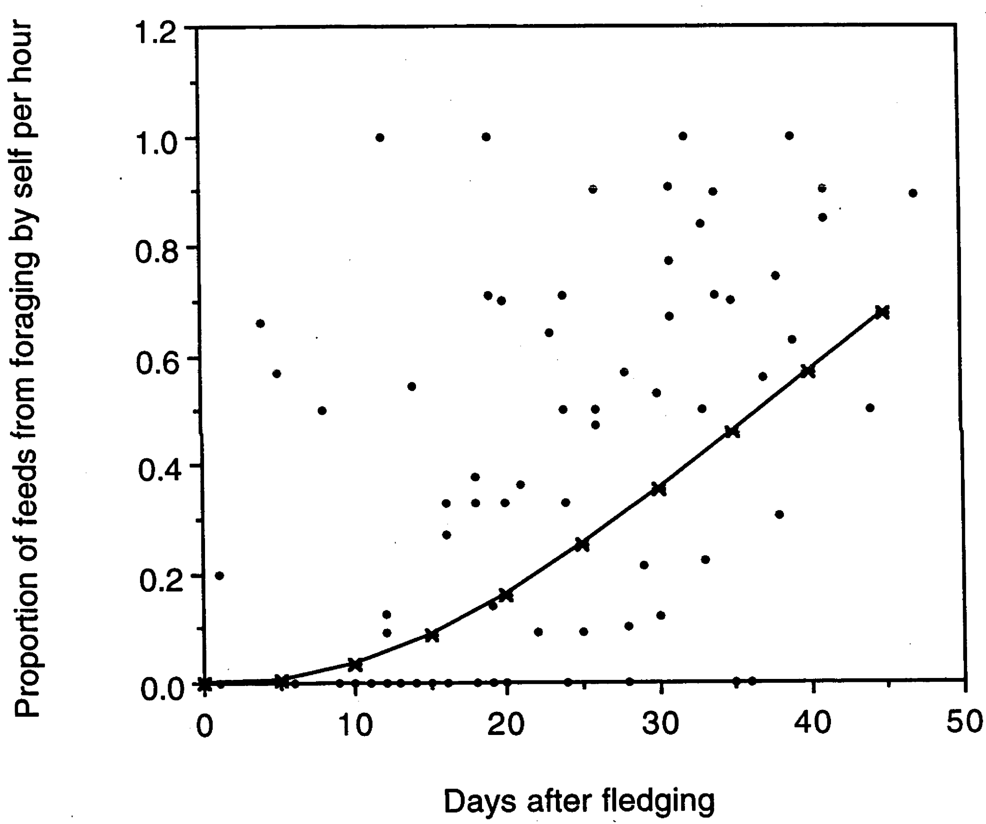
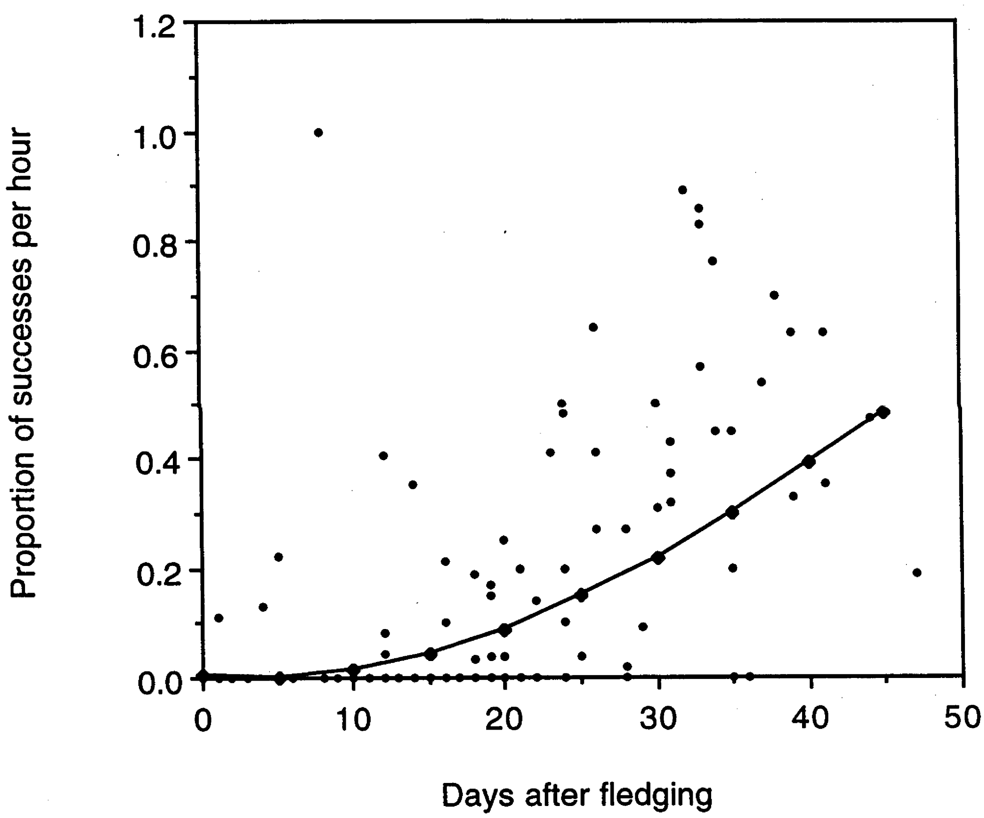


Figure 5. The proportion of succesful attempts per hour out of all foraging attempt during the transition to foraging independence of 16 juvenile Currawongs. For analysis, the proportion of successes was normalized by a square root arcsin transformation. The back transformed regression line is presented.



Chapter 6

General discussion and future prospects

General Discussion

The diet of pied currawongs is diverse and varies seasonally (Chapter 2). Fruit dominated the autumn and winter diet, and arthropods, particularly insects dominated the spring and summer diet. Vertebrate prey were common during spring and summer when the pied currawongs were rearing their young.

Identification of fruit species in the diet confirms suggestions (Recher and Lim 1990) and previous study in Armidale, New South Wales (Bass 1995) that introduced fruit species, notably from the Family Rosaceae contribute to increased survival of pied currawongs during winter. This study also confirms suggestions that pied currawongs are important seed dispersers of weed species (Hatton 1989, Bass 1990, 1995).

Identification of insect species in the diet indicates that pied currawongs prey upon aggressive insects such as bulldog ants (*Myrmecia* spp.) and species that are often presumed to be toxic (Pentatomidae and Chrysomelidae). High predation on folivorous insects such Christmas beetles (*Anoplognathus* spp.) during summer supports previous observations on the role of pied currawongs in controlling stick insect populations (Readshaw 1965, 1968).

It is not surprising that this study confirms the role of pied currawongs as predators of birds, eggs and nestlings (Gardner 1995, Priddel and Carlile 1995, Major *et al.* in preparation). They are important predators of the two well-studied species (*Malurus cyaneus* and *Sericornis frontalis*) at the ANBG (Chapter 3). This predation is deleterious, causing between 45% and 89% of brood losses of those prey species when the pied currawongs were rearing their young (between September and December).

The presence of aggressive or toxic insects in the diet (Chapter 2) and observations on the development of foraging skills (Chapter 5) suggest that the pied currawongs have a difficult foraging niche, and require time to learn how to acquire their prey. However, the pied currawongs were adept and bred successfully in their recently colonised areas.

Future prospects

Several lines of investigation are suggested by the results of this study.

What do pied currawongs eat in their original range?

This study has documented seasonal variation in the diet of pied currawongs (Chapter 2) and predation on two prey species (*Malurus cyaneus* and *Sericornis frontalis*) during the breeding season (Chapter 3) in recently colonised areas of their range. It would be of great interest to examine the diet of pied currawongs in their original habitat using comparable methods.

How and when juveniles acquire proficient hunting skills ?

My investigation in early development of foraging skills suggests that the transition to foraging independence in pied currawongs is slow (Chapter 5). The most important skills which need to be acquired are hunting and handling large prey. These skills have to be acquired before the birds start breeding, because they need to feed their offspring with vertebrate prey. Possibly, hunting skills develop when juveniles congregate in large flocks either flocks of juveniles or mixed flocks between adults and juveniles. Further research to investigate the ontogeny of hunting behaviour and how relates this to the sexual maturity of the birds would be valuable.

Sexual difference in foraging behaviour

In particular, my descriptive data support Recher's (1979) suggestion that there are sexual differences in foraging behaviour of pied currawongs, and suggest additionally that males do most hunting of bird prey (Chapter 3). The ontogeny of this difference would be of considerable interest.

Is it necessary to control pied currawong population ?

Pied currawongs breed successfully in their recently colonised areas (Chapter 4), though populations in some areas may now have stabilised (Chapter 1). Although pied currawongs are likely to exert significant negative pressure on on other populations of birds, control by killing or poisoning may prove ineffective. Killing large numbers of other pest birds has usually failed to reduce the population size, because rapid immigration into areas where birds had been killed and compensatory changes in production, survival and recruitment took place (Feare 1993). Instead, education programs which promote the destruction of winter fruiting species like *Pyracantha* spp. and encourage the growth of native plant species whose spines provide protection for bird nests (e.g. *Hakea* spp.) may prove a superior management plan.

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Appendix A

and in particular Eastern Whipbird *Psophodes olivaceus* and White-browed Scrubwren *Sericornis frontalis*) were significantly commoner in Broom-infested vegetation. Of these, only the Eastern Whipbird seems likely to compete for food with Blackbirds, both feeding on invertebrates under leaf litter on ground beneath dense shrub canopies. White's Thrush *Zoothera dauma*, closely related to the Blackbird and another possible competitor, is less common in the area. Bell (1990) recorded densities of c. 0.34 and 0.06 per hectare for Eastern Whipbird and White's Thrush respectively in Broom-infested sites in the area.

It might be expected that in their newly found, nearly vacant ecological niche at Barrington Tops, Blackbirds in the short term will increase further in numbers and local range, especially in areas over-run by Broom. Longer-term changes in the environment, and their effects upon the avifauna, are difficult to foresee but will be of great interest. They may involve Broom-induced deterioration of the eucalypt overstorey or, conversely, a thinning of the Broom thickets as a result of a biological control program currently under way.

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Caching Behaviour of Breeding Pied Currawongs *Strepera graculina*

Although Pied Currawongs *Strepera graculina* have been seen caching food, this behaviour has not been clearly understood. Reynolds (1969), Williamson (1975), Cooper & Cooper (1981) and Hastwell (1985) observed the storing of given food and food scraps, but none of them explained how the stored food was recovered. Bell (1983) observed only the recovery of stored food, and did not watch the storing process. This paper describes caching behaviour in Pied Currawongs based on observations during the 1992 breeding season (September to December) at the Australian National Botanic Gardens, the Australian National University campus and a Canberra suburb (Turner). On each occasion that I observed caching, I recorded the sex of the caching bird, types of cached food, location of cache, time of recovery if applicable and use of cached food. Male and female Currawong were distinguished by plumage intensity and brood patch (in females only).

Pied Currawongs usually ate some of the food item before attempting to cache it and they often hid when eating. Fourteen instances of caching behaviour were observed: 11 from adult males, two from adult females and one from a young bird. The food cached by the males comprised nestlings of Superb Fairy-wren *Malurus cyaneus* and White-winged Chough *Corcorax melanorhamphos*, pieces of adult Blackbird *Turdus merula*, Red Wattlebird *Anthochaera carunculata* and Common Starling *Sturnus vulgaris*, the skin of a Black Rat *Rattus rattus*, and also bread provided by the observer. The females and the young bird were observed only to cache the bread provided.

Pied Currawongs are seasonal migrants and maintain a territory during breeding (Wimbush 1969, Recher 1976). In this study the adult birds cached food within their breeding territories and the young bird cached it in its parents' territory. The storage sites varied from on the ground or in open grass to a fork or branch (0.6-1.0 m above the ground) of a bush such as Fiery Bottlebrush *Callistemon phoeniceus*, to the top branch of a large tree (10 m high). Caching sites were 2-50 m from the nest tree.

Pied Currawongs can be said to be short-term cachers (Smith & Reichman 1984, Stanback 1991). During my observations, the recovery of the cached food occurred between half an hour and one day later. When the cached food was recovered, part of it was eaten by the cachers. Then, if the cachers were the males, the remains were given to the females, nestlings or fledglings. However, the females sometimes helped themselves by following the males to the storage sites and collecting the cached food from there.

Thus, in Pied Currawongs there are two reasons to cache food during the breeding season: first, to provide for the cachers later on because the food is abundant at the time of caching or cannot all be eaten at once; and second, for provisioning of the breeding female and her young. Males are the predominant cachers, using stored food to feed their mates as well as nestlings and fledglings. However, females are the predominant incubators and brooders of nestlings (unpublished data).

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