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THE ECOLOGY AND SOCIAL BEHAVIOUR OF CHOWCHILLAS, *ORTHONYX SPALDINGII.*

Thesis submitted by

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for the degree of Doctor of Philosophy
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ABSTRACT

Chowchillas, *Orthonyx spaldingii*, are a common inhabitant of the World Heritage-listed Wet Tropics of North Queensland and are confined to the Australian tropical rainforests. They are sedentary and groups of two to five birds defend year-round all-purpose territories. They forage as a group and cooperate in territory defence but do not appear to breed cooperatively. The main focus of this study was to investigate what ecological and other factors could be involved in causing Chowchillas to live in groups but not breed cooperatively. I examined patterns of food availability, foraging strategies, territoriality, social behaviour and group structure in Chowchillas.

Food availability over time and between sites was measured by sampling the leaf litter fauna. Food availability varied seasonally and from year-to-year but the variation was small. Food availability in patches was predictable on the basis of readily observed characteristics of the leaf litter. Chowchillas ate most types of small animals occurring in the leaf litter. They were found not to search randomly when foraging, instead choosing patches which were likely to contain more food. This strategy probably involved learning the cues which indicated patch quality.

Several birds were fitted with radio-transmitters. Home ranges of two groups were mapped over several months and the home ranges of five neighbouring groups were mapped in one period. Home ranges were found to be stable over time and overlapped to some extent. Each group had a core area within their home range which was rarely encroached upon by other groups and this approximated the defended area. Home range size was larger in larger groups and the area per bird also increased with group size.

Groups were stable over time. The reproductive rate was estimated at 0.27 fledged young per group per year and the survival rate was estimated at 86% annually. As a result, few young were produced during the two and a half years of the study and only one dispersal event was witnessed.

Songs of groups on and near my site were recorded and analysed to examine differences between and within groups. Chowchillas were found to have

song dialects and the boundaries between these dialects were sharp. Thus there is a possibility that dispersal is restricted to within dialect areas and that individuals within the same dialect area are more closely related to each other than to those in other dialect areas.

I concluded that Chowchillas may not breed cooperatively because: (a) group members are unrelated so young birds would not increase their inclusive fitness by helping the breeders to raise offspring; and (b) young birds have the option of dispersing and possibly breeding on a nearby territory. However, group-territoriality can occur because: (a) young birds need to forage with experienced birds in order to find good food patches; and (b) older birds do not incur any costs by allowing them to do so and may also benefit by having help in defending the territory.

The role of Chowchillas in the rainforest was also investigated. Chowchillas were found to have a major impact on the forest floor litter fauna and to turn over large quantities of leaf litter. Their activities also provide other ground-foraging animals, particularly Musky Rat-Kangaroos, with a profitable foraging niche. Thus Chowchillas are an important component of the ecology of Australia's wet tropical rainforests.

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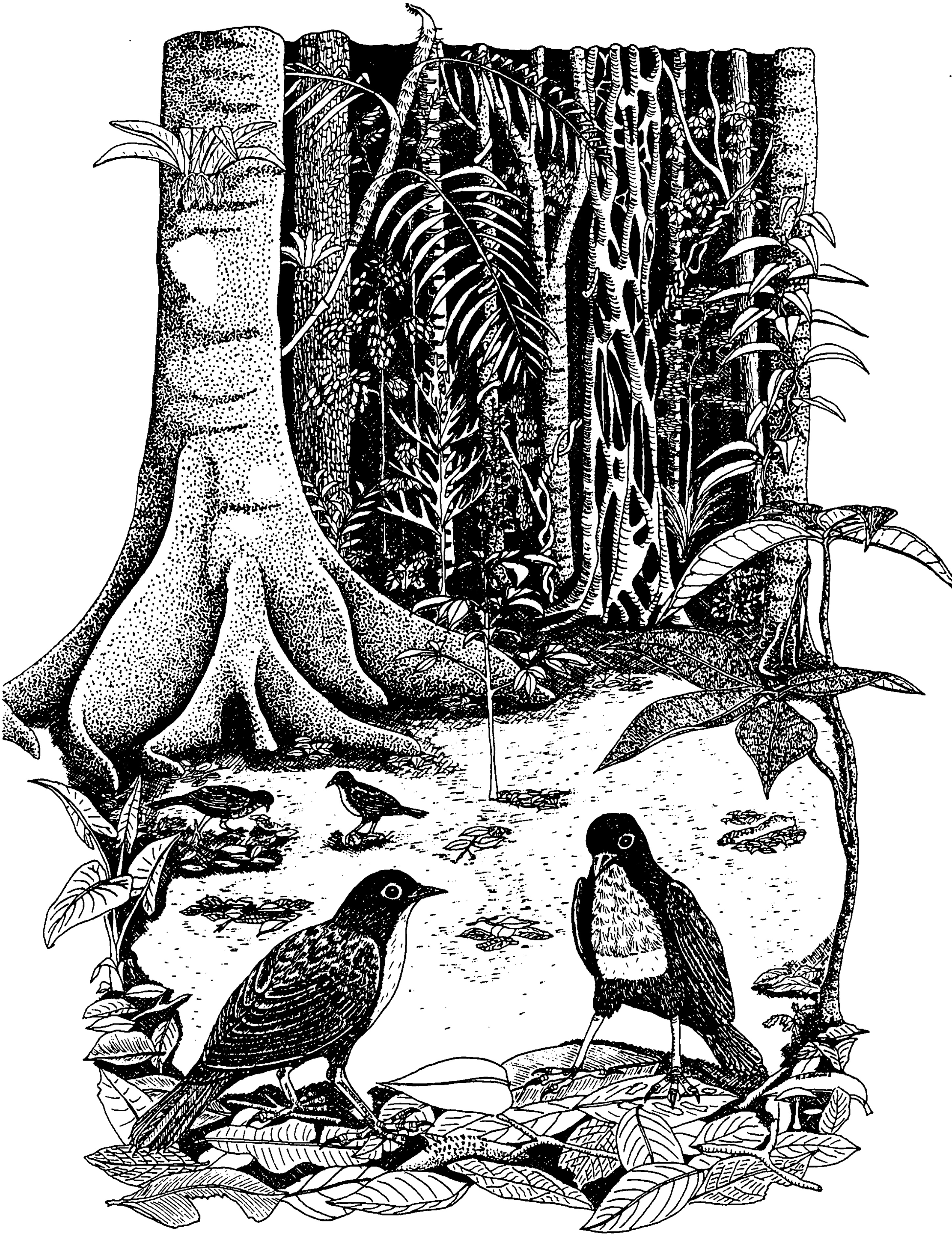

PREFACE

A group of four Chowchillas - small (25-30cm), mostly dark brown birds - scratch in the leaf litter on the forest floor. The light is dim, filtered through the continuous canopy overhead, but the forest floor is relatively open and covered with a layer of leaf litter and rotting twigs and branches. The birds scratch busily, pushing litter to either side with their strong legs and feet and pecking rapidly at minute animals exposed by their activity. Every so often, as one bird or another turns towards you, you see a glimpse of a female's bright orange breast or a male's white breast and the distinct blue ring around the eye. The birds move slowly over the forest floor, keeping to within a few metres of each other and making quiet "trilling" and "chirring" calls every so often.

Later, as you follow the group through the forest, they meet another group of Chowchillas and a loud bout of calling ensues. Some birds stay on the ground while others fly to low perches and several of them, both males and females, start calling; sometimes all at once and sometimes alternating between members of a group or between groups. The sounds are almost deafening, and incredibly complex - it's hard to believe that one bird can make such an wide range of sounds in such a short space of time. Eventually one group chases the other off and they all return to scratching quietly in the leaf litter.

ACKNOWLEDGEMENTS

I firstly wish to thank my supervisors, Professor Rhondda Jones and Doctor Richard Pearson, for their help and advice over the years, especially in the final stages of this project. They always managed to find time for me in my very brief visits to the University and provided invaluable assistance in the writing-up stage.

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Fellow postgraduate students helped me in the field: special thanks to Andrew Taplin, Murray Haseler, Jane Blackwood and Andrew Dennis. Doctor Colin Matthews helped in mapping my site, which involved wading up and down creeks and attempting to measure straight lines through seemingly impenetrable patches of wait-a-while and stinging trees. Working with the Townsville Bird Study Group, under the direction of Andrew Taplin, I was able to obtain my Bird Banding Licence shortly after starting this project.

The CSIRO Tropical Forest Research Centre in Atherton was very cooperative in providing laboratory space and the use of facilities. Les Moore and Tony Irvine from CSIRO were very helpful in identifying animals and plants, respectively, and provided much useful advice.

Cliff and Dawn Frith shared with me some of their observations of Chowchillas and were very helpful over the years. Stan Breeden helped in the field on occasion and Mike McGuire shared his observations on Chowchilla songs.

JSAT (James Cook University Students on the Atherton Tablelands) held regular meetings with invited guests and these provided moral support and generated many useful discussions during the course of the project. I particularly wish to thank Doctor John Winter, Andrew Dennis, Karl Vernes, Scott Burnett and Steve Williams for their support and advice.

As a fellow PhD student my mother, Loraine Jansen, was very supportive and we had many fruitful discussions about our respective projects.

I thank Ray Smith for helping me with some sound recordings and for making me appreciate Chowchilla songs from a different perspective (musical rather than scientific).

John Pandolfi and Cath Lovelock provided me with a place to stay in Townsville and always made me feel very welcome.

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I was supported by a Commonwealth Postgraduate Research Award during this project. Research funds were provided by James Cook University Research Grants. The Australian National Parks and Wildlife Service provided metal bands and Banding Licence. Permits to band birds were provided by the Queensland National Parks and Wildlife Service and permits to work on the site were provided by the Queensland Forest Service.

Finally, I wish to thank Andrew Dennis for all his help in so many ways. He took all of the photographs in this thesis, drew the delightful picture to complement the preface, and also prepared the other illustrations. Andrew was also my fellow PhD student, collaborator in sampling leaf litter fauna for our respective projects, my field assistant whenever I needed one (as I was his on occasion), and generally the person to whom I turned whenever I needed help of any kind.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Amy Jansen
31 March 1993

Plate 1. A female Chowchilla

CHAPTER 1
CHOWCHILLAS AND GROUP-TERRITORIALITY

1.1 Introduction

Chowchillas, *Orthonyx spaldingii*, belong to the family Orthonychidae in the order Passeriformes. According to DNA-DNA hybridization studies the only other member of this family may be the closely related Logrunner, *Orthonyx temminckii* (Sibley & Ahlquist 1985). Usually, however, the whipbirds, wedgebills and quail-thrushes (Simpson & Day 1984) and sometimes the Australian babblers and a few other New Guinean species (Boles 1988) are also included in the family. Certainly the only close relative of the Chowchilla is the Logrunner. Both are confined to the Australian region: the Chowchilla only occurs in tropical rainforests between Townsville and Cooktown in North Queensland while the Logrunner occurs in rainforests between Sydney and south-eastern Queensland and also in the highlands of New Guinea (Boles 1988).

The two species are similar in habits, being sedentary and foraging in pairs or small groups in the leaf litter on the forest floor. Both species are highly territorial and their songs are a distinctive feature of the rainforests in which they occur. In North Queensland Chowchillas are common in the tropical rainforest habitat and appear to inhabit all but the smallest fragments of rainforest.

Chowchillas are of interest for a number of reasons; both applied and theoretical. They are a common inhabitant of the World Heritage-listed Wet Tropics of North Queensland and are virtually confined to that region. Very little is known of the biology of any of the inhabitants of this region and it is important to find out more about both the rare species and the more common, representative species. Knowledge of these species will aid in developing strategies for managing this important area and for monitoring changes and impacts on the area.

In another respect Chowchillas are of interest too. They are sedentary and groups defend all-purpose territories year round (defined here as a group-territorial species). Group-territorial species of birds generally breed cooperatively and are particularly common in the tropics and Australia (Brown 1987a). Very few, however, at least of those studied, occur in rainforest. Chowchillas occur only in rainforest, are group-territorial and it was suggested to me that they may breed cooperatively (Cliff & Dawn Frith, pers. comm.). Their relatives, the Australian babblers also breed cooperatively and are group-territorial but they mostly live in open wooded and arid habitats (Simpson & Day 1984).

For these reasons Chowchillas are interesting and important birds to study. In observing them initially (see Preface) many questions about their social behaviour and ecology arose. What do they eat and how do they search for food? Do they do so systematically? How big an area do they search over? How territorial are they? Do the members of a group stay together all the time and, if so, why? Also, what happens in the longer term? How does seasonality affect their foraging behaviour and their home range size? When do they breed and do they cooperate in breeding as they appear to do in foraging and calling? When they call, do different individuals or different groups use different songs to enable recognition? What role do the Chowchillas have in the community ecology of the rainforests in the Wet Tropics of North Queensland?

In this thesis I attempt to answer these questions and others, based on two and a half years of research, from July 1990 to January 1993, in tropical rainforest on the Atherton Tablelands of Far North Queensland. The basic question was "Why do Chowchillas live in groups?" In other words, what selective advantage is there for Chowchillas to live in permanent groups when most birds live singly or in pairs for most of the year? Other studies of group-living birds have found that they may benefit through increased foraging success, improved predator detection and/or higher reproductive output (Brown 1987a). An investigation of how Chowchillas benefited by living in groups involved detailing food resource availability and dispersion, foraging strategies, home range use and defence, social behaviour, structure and composition of groups, breeding behaviour, and the extent of cooperation in various activities. The body of this thesis outlines this research and my conclusions. In the remainder of this chapter I review the literature relevant to this research. I first review the literature on the social behaviour and ecology of Chowchillas and their relatives the Logrunners. I then examine some of the ideas on why animals, especially birds, may live in groups and review information on the social behaviour and ecology of other group-living birds in the tropics. This review will set my research in the context of: (a) what is already known about Chowchillas; (b) why other birds may live in groups; and (c) other tropical birds with comparable social systems.

Chapter 2 outlines the basic methodology of the research: the site, how birds were trapped and marked for individual recognition in the field, how they were followed, and how basic data on locations and behaviour were recorded. Radio-transmitters were used for part of the work and here I describe the methodology specific to their use. Methods for particular sections of the research are outlined in the relevant chapters.

Chapter 3 gives a general description of the day-to-day behaviour of Chowchillas plus accounts of particular interesting behaviours. Aspects of breeding biology are also outlined here.

Chapter 4 deals with food resource availability; how this was sampled over time and between microhabitats, and the results of this investigation.

Chapter 5 looks at the diet of Chowchillas and relates this to the results on food availability from Chapter 4.

Chapter 6 investigates foraging strategies of Chowchillas in terms of how they decide where to forage, what cues they may use in the decision, and how foraging patterns change seasonally.

In Chapter 7 I bring together all the location data to look at home ranges and how they vary over time and between groups. Size and degree of overlap of home ranges are described and discussed.

Chapter 8 describes sociality in Chowchillas, including the structure and composition of groups and the extent of cooperation in foraging, defence of the home range, and breeding.

In Chapter 9 sonograms of the songs are used to look at the possibility of individual and/or group recognition and, on a broader scale, how the songs vary over distance and between isolated areas.

Chapter 10 describes and discusses the role of Chowchillas in the rainforest - especially their effect on leaf-litter turnover and their interactions with other rainforest inhabitants.

The final chapter compares my results to the literature reviewed here and draws conclusions as to why Chowchillas may live in groups.

1.2 Ecology and social behaviour of Chowchillas and Logrunners

Little work has been done on either member of the genus *Orthonyx*. A number of chance natural history observations contribute virtually all that is known of their ecology and behaviour. Both species are sexually dimorphic; the males being larger and having white breasts while the females have orange breasts. Both species are reported to be insectivorous, eating insects and other small invertebrates (Boles 1988) and, in the case of Chowchillas, perhaps berries too (North 1904). Both forage on the ground, in leaf litter (Cowles 1974, Zusi 1978, Boles 1988). In quantitative studies of rainforest bird foraging ecology, Frith (1984) found that Chowchillas foraged exclusively by scratching in leaf litter on the ground while Crome (1978) reported a few instances of searching leaves and tangles <1m above the ground as well as scratching in leaf litter on the ground.

Both species are highly territorial (Boles 1988) and Logrunners have been reported to attack a tape-recorder playing their calls (Beruldsen 1974). Chowchillas will also respond to a tape-recording of their calls by approaching and calling (pers. obs.). Before 1990, one Chowchilla had been marked for observations in the field (Lavery & Grimes 1978). Over a period of three years, with 24 observations, she was found (with her group) to occupy an area of 2.6ha. There are no reports of the size of the home range of Logrunners.

In defending the territory both sexes of both Logrunners (Hindwood 1934, Beruldsen 1974) and Chowchillas (Zusi 1978) sing and all birds in a group may become involved and take turns in singing (Beruldsen 1974, Zusi 1978). Logrunners are reported to occur in pairs or small family parties (Hindwood 1934, Boles 1988) while Chowchillas may occur in groups of two to six birds (North 1904, Cowles 1974, Zusi 1978). From their behaviour at nets, when birds have been caught, Boles (1977) suggested that a strong pair-bond exists in both species. Male Logrunners have been reported to feed females, even when not nesting (Hindwood 1934, Beruldsen 1974); presumably this strengthens the pair-bond. Cliff & Dawn Frith (pers. comm.) also observed a male Chowchilla feeding at least one female. In Chowchillas, groups may consist of varying numbers of males and females. Zusi (1978) reported one group of one male and two females and another group of four or five birds including two males.

Both species build large domed nests on or close to the ground (Boles 1988) and Logrunners normally lay two (sometimes three) eggs (North 1904, Hindwood 1934) while Chowchillas almost invariably lay one egg (North 1904, Campbell 1974). Both appear to breed mainly in winter although Logrunner nests have been found in January and every month from March to October (Campbell 1974, Hindwood 1934) and Chowchillas have been found breeding from May to December (North 1904, Campbell 1974, Lavery 1986). Only the female Logrunner incubates the eggs and feeds the nestlings although the male may give food to the female to take to the nest (Hindwood 1934, Beruldsen 1974). There are no reports of breeding behaviour in Chowchillas although Cliff & Dawn Frith (pers. comm.) observed only females attending nests. After fledging, Logrunner chicks may be fed by the female (Beruldsen 1974) or by the male (Boles & Shields 1980).

This summarizes virtually all that is known of the ecology and social behaviour of *Orthonyx* species, apart from the interesting fact that both Hindwood (1934) and Zusi (1978) reported foraging Logrunners being followed by Yellow-throated and White-browed Scrubwrens and Eastern Whipbirds (Latin names of all species mentioned in the text may be found in Appendix A.). These followers apparently took advantage of the Logrunners' foraging activities to find food for themselves. This has not been reported in Chowchillas.

1.3 Why live in groups?

Many animals live in permanent social groups and may cooperate in various activities such as foraging, territory defence, detection of predators and breeding. Three main types of hypotheses regarding the origin and maintenance of sociality have been proposed (Slobodchikoff & Shields 1988): (a) genetic; (b) ecological; and (c) phylogenetic. Phylogenetic hypotheses are usually invoked when neither of the first two types seem to explain the observed behaviour and suggest that sociality evolved in response to earlier conditions which no longer prevail. This class of hypotheses does not really explain anything and I will not consider them further here.

Genetic hypotheses propose that sociality can be explained by the high levels of kinship among group members (Slobodchikoff & Shields 1988) so that benefits to kin contribute to the inclusive fitness of individuals. Among related individuals, groups will form if the average benefit to all group members is higher than the average benefit to solitary individuals. Ecological hypotheses, on the other hand, propose that groups form and are maintained in response to environmental factors. Generally these hypotheses suggest that individuals within a group can exploit some resource more efficiently than solitary individuals (Slobodchikoff & Shields 1988). In fact, both genetic and ecological factors may be involved in the origin and maintenance of sociality in any species.

A cost-benefit analysis can be used to explore group-living and cooperative behaviour in a given species. Thus, for a species to exhibit sociality, the benefits of group-living and cooperative behaviour must outweigh the costs for each individual (Slobodchikoff & Shields 1988). Both genetic and ecological factors can be incorporated by examining both the direct (influencing the individual's survival and reproductive output) and indirect (influencing the individual's relative's survival and reproductive output) costs and benefits of sociality. The indirect costs and benefits are weighted according to the coefficient of relatedness between an individual and its kin (Hamilton 1964).

As well as separating genetic and ecological hypotheses for the evolution of sociality, it can also be useful to separate hypotheses concerning the origin of sociality from those relating to the maintenance of group-living. Here I will be considering mainly hypotheses relating to the origin of social groups. It is generally agreed that ecological and/or demographic factors are important in the formation of social groups of animals while kinship factors are of lesser importance (e.g. Emlen 1991, Brown 1987a,b, Myles 1988, Slobodchikoff & Schulz 1988).

Social groups can form *via* two main routes (Emlen 1991). Firstly, groups may form in response to inherent advantages of group-living, which may be in the form of increased protection from predators or more efficient utilization of some resource such as food. Alternatively, groups may form when offspring delay dispersal and remain on the parental territory, either because of a lack of opportunities for independent breeding or because they benefit in some way by remaining with their parents.

Although it is not the only way that groups could form, Brown (1987a) proposes that the main mechanism by which permanent group-territoriality and cooperative breeding arise is through delayed breeding and delayed dispersal of offspring. These offspring, forced to remain on the parental territory for whatever ecological reasons, are of course related to the parents and any future offspring produced by their parents. These conditions can be conducive to the development of cooperative breeding. In fact, Brown (1987a) states that all group-territorial species known are cooperative or communal breeders although in New Zealand, Australian Magpies are group-territorial but do not breed cooperatively (Veltman 1989). However, in this instance non-breeding birds have the option to disperse to non-territorial flocks (Veltman 1989) which is very unusual in group-territorial birds.

Here I will first consider the formation of groups as a result of the non-dispersal of offspring, which results in groups of related members, then go on to discuss more general reasons for the formation of groups, showing that groups of unrelated members may also form. The relationship between food dispersion patterns and group formation will be discussed. Some of the costs of group-living will then be considered. As noted earlier, groups will only form when the average benefits outweigh the average costs to the individuals within the group. This leads to a consideration of resulting group sizes. Presumably there will be an optimum group size depending on the interaction of costs and benefits.

Many reasons have been proposed for why young birds may choose to remain on their parental territories rather than disperse and breed independently. It has been suggested that group-territorial birds often occur in habitats which are saturated with territories and where there is no marginal habitat so young birds have neither the option of setting up a new territory in an unoccupied area nor of becoming a non-territorial bird (Brown 1987a). In Acorn Woodpeckers habitat saturation has been implicated in the formation of group-territories (Stacey 1979) and certainly intense competition occurs for breeding vacancies (Hannon *et al.* 1985). However, Stacey & Ligon (1987) suggested that habitat saturation may be a consequence rather than a cause of group-territoriality in this species and that other factors may have favoured cooperative breeding.

Another possibility is that young birds lack the skills necessary to set up a territory and breed independently (Brown 1987a). Foraging skill is thought to be most important here and it has been demonstrated in a number of species that young birds are less efficient foragers than adults. Older birds may be better able to locate good foraging patches (e.g. Brandt 1984), forage faster (e.g. Breitwisch *et al.* 1987) and be more successful at catching prey (e.g. Quinney & Smith 1980, Gochfeld & Burger 1984). Jansen (1990a) demonstrated that success at catching prey increased over at least two years in Heron Island Silvereyes. In the only study of foraging skills in a group-territorial species, Heinsohn *et al.* (1988) found that for White-winged Choughs foraging efficiency increased over a period of five years; the period for which breeding was delayed. Heinsohn *et al.* (1988) suggested that breeding was delayed because young birds lacked the foraging skills necessary to raise young.

Lack of seasonality may cause two difficulties for young birds attempting to disperse and breed independently. Ford *et al.* (1988) suggested that lack of seasonality may result in: (a) high survivorship and hence few breeding vacancies for young birds in a saturated habitat; and (b) difficulties for young birds in acquiring enough extra food to breed independently, especially when inexperienced.

Various other reasons for which young birds might prefer the option of staying on the parental territory rather than breeding independently have been proposed. These range from increased risk of predation after leaving the parental territory (Brown 1987a) although this has not been demonstrated in any species, to lack of mates or helpers with which to set up a territory. The lack of mates theory arose from the observation that in many group-territorial species the sex ratio is skewed in favour of males (e.g. Splendid Wrens (Rowley 1981), Pied Kingfishers (Reyer 1980)). Thus dispersing males may have difficulties finding a mate with which to breed (Brown 1987a). The other hypothesis, that lack of helpers may contribute to young birds not dispersing, arises from the observation that individuals in groups with helpers may raise significantly more offspring and survive better than paired individuals (Brown 1987a). In Stripe-backed Wrens, Wiley & Rabenold (1984) showed that by delaying dispersal males, and up to a certain age females, increased their inclusive fitness by delaying dispersal until they could form a group with helpers.

More general theories concerning the formation of groups suggest benefits such as more efficient exploitation of resources, improved detection of and defence against predators, or more successful defence of resources against conspecifics.

Improved detection of predators has often been cited as a possible reason for the formation of groups of birds (e.g. Pulliam & Caraco 1984), the theory being that with more birds available to detect predators, more time can be allocated to foraging and other activities. A number of group-territorial species apparently suffer high rates of predation (Brown 1987a) and Austad & Rabenold (1985) found that in Bicolored Wrens extra group members helped significantly in reducing predation on nestlings. Heinsohn (1987) found that vigilance in adult White-winged Choughs was reduced when the birds were members of large flocks, suggesting a possible reason for the formation of winter flocks in this cooperatively breeding species. Many species which are not group-territorial also form less permanent groupings, apparently in response to the risks of predation (Pulliam & Caraco 1984). Ford *et al.* (1988) suggested that group-territorial species may be particularly prone to predation since many of them forage on the ground in open habitats, in situations where living in groups could significantly increase the chances of detecting predators.

Defence against conspecifics may also play a role in the formation of groups (Gaston 1978). In territorial species living in a saturated habitat, the addition of more individuals to the territory could reduce defence costs (Brown 1987a).

Groups may also form in order to exploit food resources more efficiently. A number of mechanisms have been proposed for this. Morse (1980) suggests three: (a) a beating effect - where foraging birds flush prey which can then be captured; (b) minimizing duplication of effort - foraging birds could avoid areas where they have observed others foraging recently; and (c) facilitation - where group members observe other successful foragers and search in the same or similar patches. The facilitation effect has been demonstrated in two cage studies. Great Tits were found by Krebs *et al.* (1972) to be more likely to find food in groups than alone while Elgar & Catterall (1982) found a similar result in House Sparrows. Both suggested a facilitation mechanism for the greater food-finding success in groups. In the field, Krebs (1974) found that Great Blue Herons formed groups as a result of social facilitation rather than because larger groups increased the availability of prey or reduced the time spent in vigilance.

A simulation model of flocking in birds was used by Thompson *et al.* (1974) to examine advantages of flocking in different situations. Their conclusions were that flocking could reduce risk by minimizing variance in feeding rates and also that degree of clumping of the food resource had important effects on the benefits of flocking. Patchiness, predictability and abundance of the food supply can all affect the benefits of living in groups (Slobodchikoff & Shields 1988) and these factors are incorporated in the model of group-territoriality to be considered next.

An interesting model of group-territoriality has been developed by Bacon *et al.* (1991a, b). This model predicts that with particular types of food dispersion, territories defended by pairs can support extra members at no cost to the original occupants. This is most likely to occur when individual patches of food are of high quality and the variance between patches is large (Bacon *et al.* 1991b). This is because, if patches vary unpredictably in quality in space and time, the number of patches needed to provide the minimum requirements for a pair of birds may also support extra birds without affecting the original pair's intake.

Several studies have examined the relationship between food dispersion patterns and social organization in more detail. Bradbury & Vehrencamp (1976) suggested that in emballonurid bats territory size increased with the number of food patches needed per year and the distance between successively available food patches. Group size was then an increasing function of the quality of food patches. As a result, small groups with small territories would be associated with small, low quality food patches which were close together while large groups with large territories would form in response to large, rich food patches which were widely dispersed.

In a similar analysis of food dispersion and social organization in European Badgers, Kruuk (1978) and Kruuk & Parisk (1982) suggested similar relationships between group size, territory size and dispersion of food patches. Territory size increased in areas where food patches were more widely dispersed. Group size, on the other hand, increased as food patches increased in quality.

A very different suggestion was made by Rodman (1988), however, in explaining differences in group size among co-occurring primates. Grey Gibbons lived in small family groups and apparently experienced large, relatively rich food patches while Long-tailed Macaques foraged in larger groups and appeared to experience smaller, low quality patches which were closer together. Rodman (1988) suggested that the macaques may forage together to minimize repeated visits to small patches exhausted by other foragers.

Davies & Houston (1981) found that among territorial Pied Wagtails with a predictable food supply, on days when food availability was high, territory owners maximized their daily feeding rates by allowing a second bird on the territory. These extra birds were tolerated when food availability was high enough to provide for both occupants and they brought benefits in terms of help in defending the territory against intruders (and intruder pressure was greatest on days of high food availability.

In summary, these studies suggest that the relationship betwen food dispersion patterns and group size is complex. Important factors are the quality and size of food patches, their spacing, replenishment rates within patches, and the defensibility of food patches of varying quality. The definition of food patches is clearly important to this kind of analysis.

After noting all the benefits of group-living and reasons why young birds may prefer the option of remaining on the parental territory rather than dispersing to breed, it may seem surprising that all birds do not live in groups. However, there are a number of costs associated with group-living and these must be weighed up with the benefits for each species. Most birds do not form groups so clearly the costs must outweigh the benefits for these species. One of the obvious costs for young birds of remaining on the parental territory is that their options for breeding are restricted. Usually only a single pair breeds on a group-territory (Brown 1987a) although in the case of Groove-billed Anis two or more adult pairs may breed in one nest (Koford *et al.* 1990). Mostly, young birds do not have the option of breeding if they remain on the parental territory so cannot produce offspring immediately to increase their direct fitness.

Another potential cost of group-living is that larger groups may increase the risk of detection by predators or parasites (Gaston 1978, Pulliam & Caraco 1984). Also, in territorial animals occupying a restricted area, the addition of more individuals to a territory means that the same quantity of food must be shared between more foragers. Thus depletion of food resources could limit the number of individuals occupying an area (Brown 1987a).

Clearly all these costs and benefits of group-living affect different species in different ways depending on ecological constraints. Characteristics of the food supply and predation pressure are likely to be the most important factors influencing group size. Brown (1987a) developed a model of group-territoriality to predict the optimum group size based on territory quality, the pattern of depletion of resources as more individuals are added, and the change in defence costs with more defenders. This model enables prediction of the optimal group size for a given territory. However, the relationships become more complicated when factors such as dominant-subordinate interactions are considered. Dominants may be less susceptible to resource depletion, because they can usurp the food of subordinates, so they may have a different optimal group size to subordinates (Brown 1987a). A model of foraging group size developed by Giraldeau (1988) predicted that group sizes would rarely be optimal. This model predicts that stable groups will form which are often larger than optimal due to the relative sizes of the costs and benefits to group members and individuals attempting to join the group. However, the stable group size will approach the optimum group size under certain conditions: (a) when group members actively discourage invaders; (b) when dominance hierarchies exist; and (c) when group members and potential joiners are related (Giraldeau 1988).

This discussion has demonstrated the many costs and benefits associated with group-living. For any particular species, a variety of factors may influence the costs and benefits, and the weighing up of these results in the group sizes observed in that species. My research examines some of these costs and benefits for Chowchillas, to try to determine why they live in groups.

1.4 Group-territorial birds in the tropics

In this section I will review information on group-territorial birds living in the tropics relating to aspects of their ecology and life history strategies, ideas about why they may live in groups, and the extent of cooperation in groups. I have limited my definition of tropical birds to only those species which have been studied in the region between the Tropic of Capricorn and the Tropic of Cancer.

There is sufficient information on twenty species of tropical, group-territorial species to be included in this review, although not all information is available for all species. Table 1.1 summarizes data on group sizes, habitat and diet of the twenty species.

Table 1.1 Group sizes, habitat and diet characteristics of group-territorial birds in the tropics.

Species	Place	Group size Mean(range)	Habitat	Diet	References
Galapagos Hawk	Galapagos Islands	3.1 (2-6)	Dry, open woodland	Birds, reptiles, carrion	Faaborg & Bednarz (1990)
Red-throated Caracara	French Guiana	5.97 (3-9)	Rainforest	Mainly wasp & bee nests	Thiollay (1991)
Groove-billed Ani	Costa Rica	4.0 (2-8)	Open savannah	Arthropods	Koford *et al.* (1990)
Hoatzin	Venezuela	3.0 (2-8)	Forested creeks & swamps	Leaves, fruit & flowers	Strahl & Schmitz (1990)
Green Wood-hoopoe	Kenya	4.8 (2-15)	Open woodland	Arthropods	Ligon & Ligon (1990)
Acorn Wood-pecker	Costa Rica	(3-8)	Oak forest & pasture	Insects, nectar & fruit	Stanback (1989)
	Colombia	(5-10)	Mixed forest & farms	Insects, sap & fruit	Kattan (1988)
Grey-backed Fiscal Shrike	Kenya	5.3 (2-11)	*Acacia* woodland	Insects	Zack & Ligon (1985a) Zack (1986)
Yellow-billed Shrike	Ghana	12 (6-25)	Open savannah, parks & gardens	Invertebrates, lizards	Grimes (1980)
Stripe-backed Wren	Venezuela	4.6 (2-10)	Open savannah woodland	Arthropods	Rabenold (1990)
Bicolored Wren	Venezuela	2.2-3 (2-7)	Open savannah woodland	Arthropods	Rabenold (1990)
Galapagos Mockingbird	Galapagos Islands	4.2 (2-12)	Arid scrub woodland	Insects, nectar, fruit, etc.	Curry & Grant (1990)
Rufous Babbler	Papua New Guinea	4 (1-10)	Rainforest	Invertebrates	Bell (1982)
White-banded Tanager	Brazil	3.0 (2-4)	Savannah	?	Alves (1990)
White-browed Sparrow Weaver	Kenya	4.9 (3-7)	Open savannah	Seeds, insects	Collias & Collias (1978a)
	Zambia	4.4 (2-10)	Closed woodland	Seeds, insects	Lewis (1982)
Beechey Jay	Mexico	3.4 (2-5)	Low deciduous forest	Arthropods, fruit, lizards, grain	Raitt & Hardy (1979)
Bushy-crested Jay	Nicaragua	11 (1 group)	Disturbed cloud forest	Insects, fruit, seeds	Hardy (1976)
Nelson San Blas Jay	Mexico	(5-6)	Disturbed forest & palm groves	Insects, seeds, lizards	Hardy (1976)
Southern San Blas Jay	Mexico	(13-26)	Disturbed forest & crops	Insects, fruit, lizards	Hardy *et al.* (1981)
Brown Jay	Costa Rica	7.2 (6-10)	Disturbed forest pasture & crops	?	Lawton & Guindon (1981)
Green Jay	Colombia	6.1 (4-10)	Mixed crops & pasture	Invertebrates, fruit, lizards	Alvarez (1975)

Many of the group-territorial birds studied in the tropics live in relatively dry woodland or savannah habitats (this may reflect the preferences of ornithologists for working in these habitats!) while most of the remainder live in disturbed tropical forests mainly taken over by pasture and crop plantations. Two species, the Red-throated Caracara and the Rufous Babbler, live in rainforest.

Most species are generalist foragers, eating a range of insects, other invertebrates, small vertebrates and fruit and seeds. Exceptions are the Red-throated Caracara, a raptor which specializes on wasp and bee nests, eating the larvae, eggs and honey, and the Hoatzin, which is entirely herbivorous, eating mainly leaves. A number of species forage mainly on the ground (Groove-billed Ani, Grey-backed Fiscal Shrike, Yellow-billed Shrike, Galapagos Mockingbird and White-browed Sparrow Weaver). Two species forage mainly in the understorey (Rufous Babbler and Bushy-crested Jay) while the Galapagos Hawk forages from the air like a typical raptor. The remainder forage mainly in trees although most may also forage on the ground or in the understorey. Thus it appears that none of these are specialist foragers, restricted to a narrow foraging niche and diet.

The species studied range across central America, Africa and Papua New Guinea. The lack of species in Asia and tropical Australia probably reflects fewer studies in these areas rather than a lack of group-territorial species. Group-territorial species may occur in all tropical areas of the world (there are also many sub-tropical and some temperate species of group-territorial birds, particularly in Australia (Brown 1987a)).

Fourteen species of tropical group-territorial birds have been studied for long enough to estimate survival and reproductive rates. These estimates are summarized in Table 1.2. Tropical group-territorial species of birds have very low reproductive rates, many groups producing less than one offspring per year. They also tend to have high survival rates, particularly Galapagos Hawks, Groove-billed Anis and Hoatzins. Not surprisingly, those with the lowest reproductive rates tend to have the highest survival rates.

Table 1.2 Survival and reproductive rates of tropical group-territorial birds.

Species	Mean no. young/group/year	Annual adult survival	References
Galapagos Hawk	Pairs: 0.45 Groups: 0.89	Territorial birds: 90% Floaters: ~50%	Faaborg & Bednarz (1990)
Groove-billed Ani	0.6-1.1/female less in larger groups	80-100% higher in larger groups	Koford et al. (1990)
Hoatzin	0.3-1.2 more in larger groups	70% in first 3 years 87% when older	Strahl & Schmitz (1990)
Green Woodhoopoe	0-2.5 more in larger groups	Males: 60% Females: 70%	Ligon & Ligon (1990)
Grey-backed Fiscal Shrike	0.78-4.0 more in larger groups	66%	Zack & Ligon (1985a) Zack (1986)
Yellow-billed Shrike	0.88	~70%	Grimes (1980)
Stripe-backed Wren	Pairs & trios: 0.4 Larger groups: 2.4	62%	Rabenold (1990)
Bicolored Wren	Pairs: 0.4 Groups: 1.3	Breeders in pairs: 75% Breeders in groups: 90%	Rabenold (1990)
Galapagos Mockingbird	Pairs: 1.6 Groups: 1.9	60.5%	Curry & Grant (1990)
White-browed Sparrow Weaver	2-3 birds: 0.6 4-5 birds: 1.2 6-8 birds: 2.3	71%	Lewis (1982)
Beechey Jay	2-3	Adults: 70-80% 1-2yr olds: 48-60%	Raitt et al. (1984)
Southern San Blas Jay	4-8	50-77%	Hardy et al. (1981)
Brown Jay	3	?	Lawton & Guindon (1981)
Green Jay	3-4	?	Alvarez (1975)

In most species the number of young produced per year is greater in larger groups. In Galapagos Hawks and Groove-billed Anis the number of young produced per breeding bird decreases with increasing group size (Faaborg & Bednarz 1990, Koford *et al.* 1990, respectively) whereas in Stripe-backed Wrens and Bicolored Wrens the number of young produced per adult also increased with increasing group size, at least up to four adults in Stripe-backed Wrens and three adults in Bicolored Wrens (Rabenold 1990).

Overall, group-territoriality in tropical birds appears to be correlated with high rates of survival and low reproductive rates. It has long been thought that tropical birds in general have higher survival rates than temperate birds (e.g. Lack 1966, Snow & Lill 1974). However, a recent analysis of adult survival rates of American forest birds suggests no difference between temperate and tropical species (Karr *et al.* 1990). The survival rates for tropical birds reported in this study (ranging from 33% to 73%), however, are lower than most of the values reported for group-territorial species (see Table 1.2). The estimates for group-territorial species are likely to be more accurate than most because they involve birds which have been marked for individual recognition in the field and have been followed intensively over long periods of time. Thus they should be comparable to the estimates presented in Karr *et al.* (1990), unlike earlier estimates for tropical birds.

In section 1.4 I discussed possible reasons for why animals may live in groups. There are many hypotheses and here I will summarize the reasons suggested for group-territorial species living in the tropics. Not all of the species listed in Table 1.1 have been studied well enough to suggest why they may live in groups so this summary will be limited to 17 species. In Table 1.3 I summarize the extent of habitat saturation in each species in the place studied, whether habitat saturation is thought to be important in causing group-territoriality, and other potential causes of group-living suggested by the authors. Habitat saturation, resulting in limited opportunities for young birds to disperse and breed independently, is thought to be an important factor in the origin of group-living in the Galapagos Hawk, Hoatzin, Grey-backed Fiscal Shrike and Galapagos Mockingbird.

Table 1.3 Causes of group-living in group-territorial birds in the tropics.

Species	Saturated habitat?	Habitat saturation thought to cause group-territoriality?	Other causes	References
Galapagos Hawk	Yes	Yes	Also high mortality of non-territorial birds	Faaborg (1986), Faaborg & Bednarz (1990)
Red-throated Caracara	Yes	Possibly	Foraging and predator detection advantages suggested too	Thiollay (1991)
Groove-billed Ani	Yes	One possible factor	Reduced mortality of breeders	Koford et al. (1990), Vehrencamp (1978)
Hoatzin	Yes	Yes	-	Strahl & Schmitz (1990), Strahl (1988)
Green Wood-hoopoe	Yes	Yes - a shortage of roosting cavities	Also high mortality of dispersing birds	Ligon et al. (1988), Ligon & Ligon (1990)
Acorn Wood-pecker	No	-	?	Kattan (1988)
Grey-backed Fiscal Shrike	Yes	Yes	Also high mortality and low breeding success in marginal habitat	Zack & Ligon (1985a,b)
Stripe-backed Wren	In some areas	No	Group defence against predators	Rabonold (1984, 1990)
Bicolored Wren	In some areas	May be a contributing factor	Group defence against predators	Austad & Rabenold (1985, 1986), Rabenold (1990)
Galapagos Mockingbird	Yes	Yes	Also biased sex ratios	Kinnaird & Grant (1982), Curry (1989), Curry & Grant (1990)
White-banded Tanager	Yes?	Yes?	Increased detection of predators	Alves (1990)
White-browed Sparrow Weaver	?	?	Foraging advantage to group-living	Collias & Collias (1978a,b)
Beechey Jay	Yes?	Yes?	Low probability of surviving & breeding for dispersing birds	Raitt et al. (1984)
Bushy-crested Jay	No?	No	?Improved detection of predators	Hardy (1976)
Nelson San Blas Jay	No?	No	?Improved detection of predators	Hardy (1976)
Brown Jay	No	-	Lack of breeding skill by young birds	Lawton & Guindon (1981) Lawton & Lawton (1985)
Green Jay	Yes?	?	Predator defence, foraging advantages	Alvarez (1975)

In the Galapagos Mockingbird there is a strong correlation between the degree of habitat saturation on an island and the occurrence of group-territoriality (Curry 1989), lending support to this hypothesis for the origin of group-territoriality. In other species the survival and/or breeding opportunities of young birds are limited in other ways: in Galapagos Hawks non-territorial birds suffer high mortality and young birds form groups to take over territories (Faaborg 1986); in Green Woodhoopoes mortality of dispersing birds is high and also roosting cavities, essential for survival in a species with poor thermoregulatory ability, are in short supply so young birds survive better by staying in a group with a roosting cavity (Ligon *et al.* 1988, Ligon & Ligon 1990); in Stripe-backed and Bicolored Wrens groups without helpers suffer high nest predation and young birds increase their inclusive fitness by staying on the parental territory rather than dispersing to breed independently (Rabenold 1984, Austad & Rabenold 1985, 1986, Rabenold 1990); in Beechey Jays dispersing birds may have a low probability of surviving and breeding (Raitt *et al.* 1984); while in Brown Jays young birds may lack the skills necessary to breed successfully (Lawton & Guindon 1981, Lawton & Lawton 1985).

Two studies suggest foraging-related advantages of group-living: Red-throated Caracara (Thiollay 1991) and White-browed Sparrow Weaver (Collias & Collias 1978a, b). However, no foraging advantage was found in Stripe-backed Wrens (Rabenold & Christensen 1979) and in fact it was suggested that group-foraging was detrimental to individual foraging success because of interference between foraging birds. Other species may also experience types and distributions of prey which are not conducive to group-foraging, e.g. Galapagos Hawks, Hoatzins, Green Woodhoopoes.

A few studies suggest predator detection as an advantage of group-living, e.g. White-banded Tanagers (Alves 1990), Bushy-crested and Nelson San Blas Jays (Hardy 1976) and Green Jays (Alvarez 1975) but none of these studies actually have any evidence for this hypothesis.

Defence of resources against conspecifics is a potential benefit of group-living in virtually all of the species considered. Since territory defence is nearly always a cooperative affair with all or most group members becoming involved, presumably more birds can more adequately defend a territory. However, the importance of this factor in the formation of groups is not known for any species.

This discussion suggests that the causes of group-living in group-territorial birds in the tropics are varied. No one ecological or demographic factor can explain group-living in all species. In fact, the factors involved are almost as wide-ranging as the species.

The final question concerns the activities in which cooperation occurs. Table 1.4 summarizes for each species whether members of the group cooperate in foraging, detection of and defence against predators, nestling care, fledgeling care and territory defence. In virtually all species group members cooperate in territory defence, except the Groove-billed Ani, in which only a few territorial interactions were observed and each involved a single male from each territory (Vehrencamp 1978). Cooperation in foraging is most highly developed in the Red-throated Caracara, where members of a group may share food (Thiollay 1991). In the other species which forage as a group there is cohesion between members of the group while foraging but little evidence of any actual cooperation between group members. However, this has been little studied in group-territorial birds except that in the Stripe-backed Wren it was found that foraging birds may actually have interfered with one another's foraging efforts if they foraged too close together (Rabenold & Christensen 1979).

In all species most or all members of a group cooperate in some aspects of breeding. Members of the group other than the parents at any nest help to feed the nestlings and probably the fledgelings in all species. In species such as the Galapagos Hawk (Faaborg & Bednarz 1990), Groove-billed Ani (Koford *et al.* 1990) and Hoatzin (Strahl & Schmitz 1990) incubation is also carried out by all members of a group. Predator detection and/or defence against predators is also commonly a group activity.

Table 1.4 Cooperation in various activities in group-territorial birds in the tropics.

Species	Foraging	Predator avoidance	Nestling care	Fledgeling care	Territory defence	References
Galapagos Hawk	No	-	Yes	Yes	Yes	Faaborg & Bednarz (1990)
Red-throated Caracara	Yes	Yes	Yes	?	Yes	Thiollay (1991)
Groove-billed Ani	No	?	Yes	Yes	No	Vehrencamp (1978), Koford *et al.* (1990)
Hoatzin	Yes	?	Yes	Yes	Yes	Strahl (1988), VanderWerf&Strahl(1990)
Green Wood-hoopoe	Yes	?	Yes	Yes	Yes	Ligon & Ligon (1978), Ligon & Ligon (1990)
Acorn Wood-pecker	Yes	?	Yes	Yes	Yes	Kattan (1988)
Grey-backed Fiscal Shrike	No	?	Yes	Yes	Yes	Zack (1986)
Yellow-billed Shrike	No	Yes	Yes	Yes	Yes	Grimes (1980)
Stripe-backed Wren	Yes	Yes	Yes	Yes	Yes	Rabenold & Christensen (1979), Rabenold (1984)
Bicolored Wren	?	Yes	Yes	Yes	Yes	Austad & Rabenold (1985, 1986)
Galapagos Mockingbird	No	No	Yes	Yes	Yes	Hatch (1966), Grant & Grant (1979), Curry (1988), Curry & Grant (1990)
Rufous Babbler	Yes	?	Yes	?	Yes	Bell (1982)
White-banded Tanager	Yes	Yes	Yes	Yes	Yes	Alves (1990)
White-browed Sparrow Weaver	Yes	Yes	Yes	Yes	Yes	Collias & Collias (1978a)
Beechey Jay	Yes	Yes	Yes	?Yes	Yes	Raitt & Hardy (1979), Raitt *et al.* (1984)
Bushy-crested Jay	Yes	Yes	Yes	?	Yes	Hardy (1976)
Nelson San Blas Jay	Yes	Yes	Yes	?	Yes	Hardy (1976)
Southern San Blas Jay	Yes	?	Yes	Yes	?	Hardy *et al.* (1981)
Brown Jay	Yes	?	Yes	Yes	?	Lawton & Guindon (1981)
Green Jay	Yes	Yes	Yes	Yes	Yes	Alvarez (1975)

Generally, cooperation in foraging, predator avoidance and territory defence is likely whether or not group members are related because of direct benefits to the individuals involved. Cooperation in breeding, however, is most likely to occur when group members are related so that helpers are related to the offspring being raised (Brown 1987b). An exception to this occurs in the Green Woodhoopoe where unrelated helpers are quite common in small groups. Because of high mortality in this species, helpers in small flocks are likely to inherit a group and territory within which they have helped, so helping can be explained as an investment in future direct fitness (Ligon & Ligon 1990).

This discussion has illustrated the range of ecological and demographic factors thought to influence group formation in tropical birds and the variations in their life history strategies and extent of cooperative behaviour. This will be compared to the behaviour of Chowchillas.

CHAPTER 2

GENERAL METHODS

2.1 Site description

2.1.1 Location

Figure 2.1 shows the location of the study site on the Atherton Tablelands in north Queensland (Latitude 145°42'58" East, Longitude 17°22'42" South). It is within sight of Bartle Frere, the highest mountain in Queensland (1611m) and is part of the Bellenden Ker National Park (formerly Gadgarra State Forest) in the Wet Tropics World Heritage Area. The elevation is between 800 and 840m above sea level and overall it slopes ENE, although on a smaller scale it slopes in every direction. It is situated at the head of the Mulgrave River catchment.

The study site is surrounded by rainforest on three sides. This rainforest is part of a continuous tract including the 94000 ha Bellenden Ker National Park. The boundary on the fourth side is a narrow dirt road on the other side of which is cleared pasture and a small rainforest patch (clear-felled in June 1992).

2.1.2 Climate

Maximum and minimum temperatures on the site were recorded whenever I visited the site. Daily rainfall records were kept on a nearby farm (≃0.8km from the study site) from mid-May 1988. Figure 2.2 shows the average maximum and minimum temperatures each month in the period when I visited the site regularly. Also shown are the mean monthly rainfall (averaged over the 4-5 years from June 1988 to December 1992), and the monthly rainfall during the period of this study. Average annual rainfall for the years 1989 to 1992 was 3390mm (range 2403 to 4147mm).

The highest temperature recorded on the site was 34°C in November 1990 while the lowest temperature recorded was 9°C in July 1991. Average maximum temperatures were highest in November 1990 (29.7°C) and January 1992 (27.9°C), before the rains started, and average minimum temperatures were lowest in July 1991 (11.7°C) and June 1992 (12.5°C), at the end of the wet season.

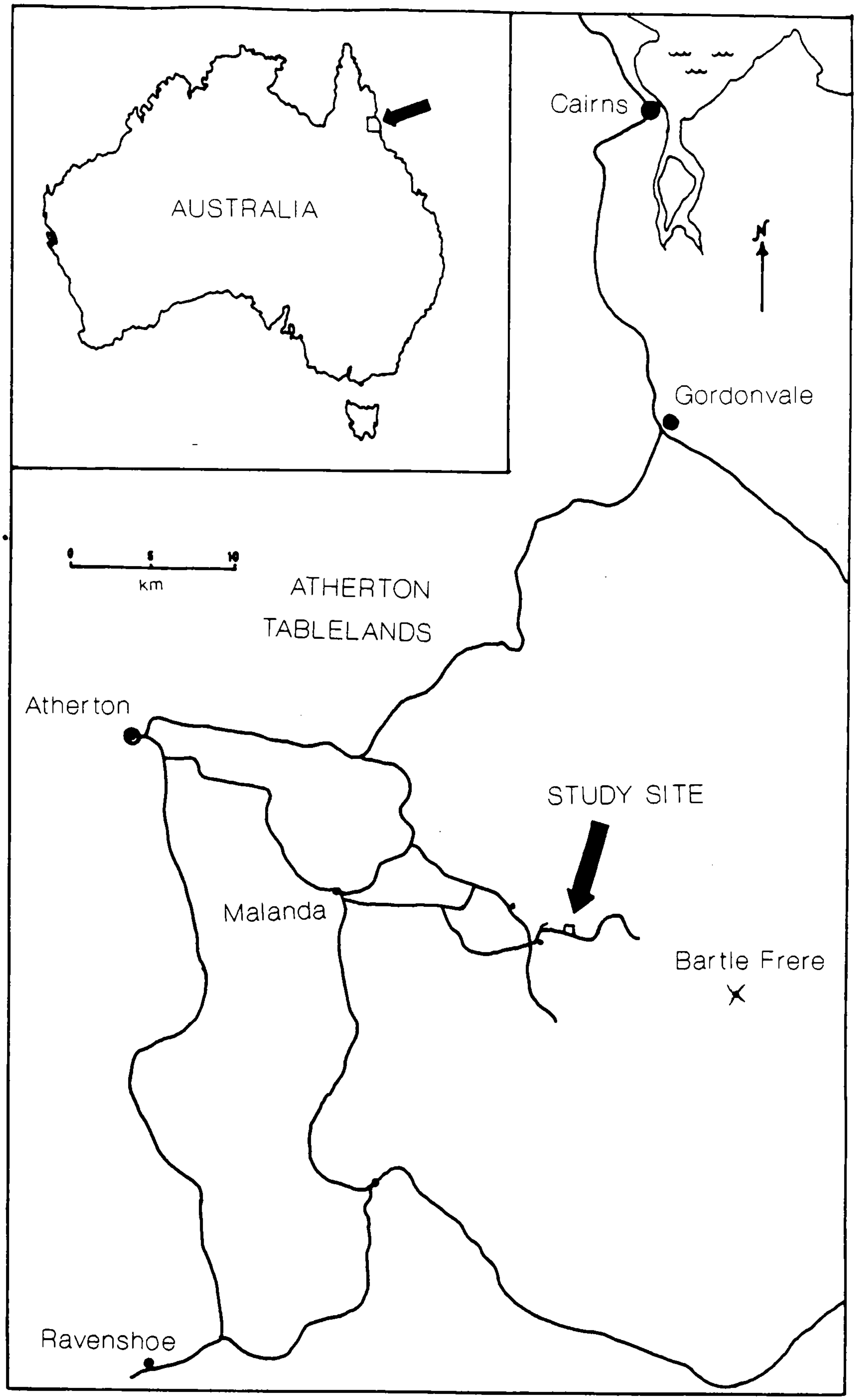


Figure 2.1 The location of the study site on the Atherton Tablelands in north Queensland.

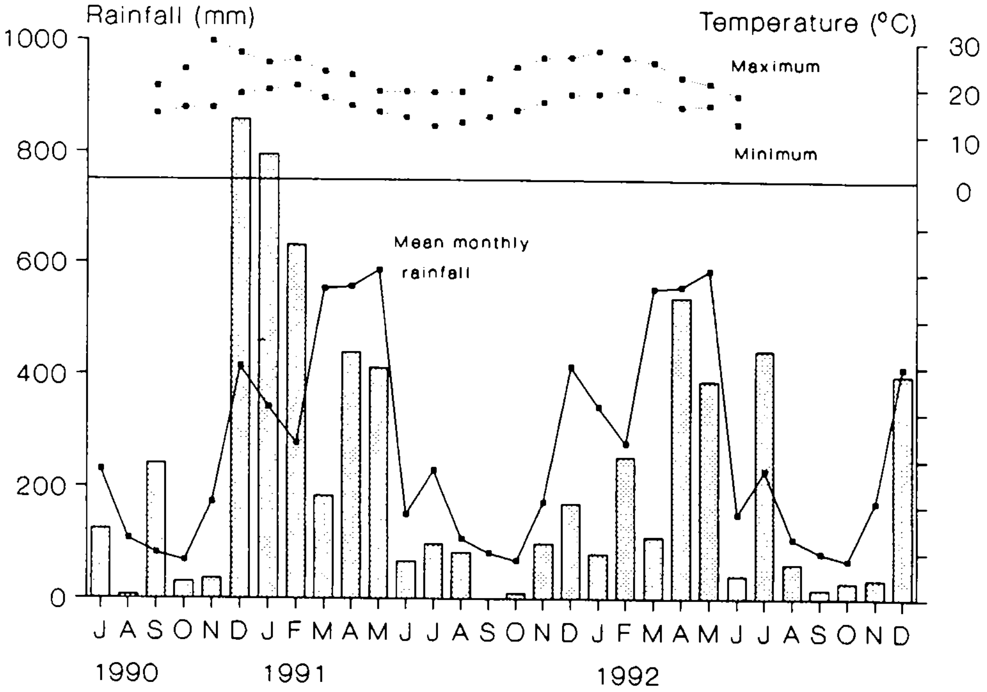


Figure 2.2 Mean monthly maximum and minimum temperatures (top) and total monthly rainfall (bars) recorded during the period of the study. Average monthly rainfall in the period June 1988 to December 1992 also shown.

Temperatures outside the forest were more extreme and frosts were sometimes experienced in June-July in nearby cleared areas. In the wet season of 1990-1991 higher than average rainfall was recorded in the early part of the season (due to the passage of Cyclone Joy at Christmas 1990) but lower than average for the rest of the season. In the 1991-1992 wet season below average rainfall was recorded although above average rainfall was finally recorded in July 1992.

Based on these changes in temperature and rainfall regimes, I divided the years into seasons: Wet season, starting in December when the rains started, and ending in April when temperatures started to drop; Winter, from May to July, when temperatures were low and rainfall lessened; Early Dry, from August to September, when temperatures started to rise again and there was little rain; and Late Dry, from October to November, when temperatures were high and very little rain fell.

2.1.3 Site characteristics

The site is intersected by a number of gullies, in one of which a creek flows year-round while in the others creeks flow intermittently in the wet season. Most of the site is sloping, either steeply or gently, and there are only a few small relatively flat areas. The steep slopes and the gullies are rocky, with many small to large granite boulders. The soil is red, basalt-derived, clayey, poorly drained and covered by a layer of leaf litter. This layer is thin (only scattered leaves) on ridges and open slopes, especially during the wet season, and thick (many layers of leaves) between buttresses and especially in gullies towards the end of the dry season.

Plate 2 shows a typical view of the site and Plate 3 shows a particularly open, flat gully area. The vegetation is Complex Mesophyll Vine Forest according to the classification of Tracey (1982). The main canopy is dense, uneven, and approximately 30-40m high with occasional emergents to at least 50m. There are no distinct understorey or ground-cover layers although a wide range of ground-cover, understorey plants and small to medium trees occur underneath the main canopy.

Plate 2. Typical vegetation on the study site

Plate 3. An open gully area on the study site

The trunks of the main canopy trees vary greatly in size and many have buttresses. Appendix B lists the common plant species on the site. There are at least 50 commonly occurring canopy species plus a range of understorey plants including at least 17 trees and shrubs, tree-ferns, tree-palms and other palms and pandans. On the ground a number of ferns, cycads, zingibers and aroids are common. There are also many lianes, epiphytes and strangler figs.

Light levels within the forest are low, with only occasional sun flecks reaching the ground. Cyclone damage has opened the canopy in a few places, and stinging trees (*Dendrocnide moroides*) are common in these openings. The site has been selectively logged: between 1970 and 1974 close to the road; and prior to 1954 in other areas.

2.2 Trapping and marking birds

Very few Chowchillas have been caught using standard mist-netting techniques (Townsville Bird Study Group records, Cliff & Dawn Frith, pers. comm.), mainly because they tend not to fly and if they do walk into a net, they rarely get tangled and can walk out again. I experimented with different trapping techniques and devised the following procedure: 12 m long large gauge (63 mm instead of the usual 31 mm) nets were set up in an area known to be used by a group of Chowchillas (from my observations). Either two nets were set, adjacent to one another and forming a wide angle or three nets were set, forming a 3-point star. The bottom string of each net was placed at ground level and staked down so the birds could not get under them. Gaps between the nets and between nets and poles were reduced by overlapping the nets and lashing them to the poles.

A small cassette player was then placed near the centre of the nets and used to play a tape of Chowchilla territorial calls. This recording was made at dawn on the site and was about 20 minutes long. One or two people manned the nets from strategic positions and the tape was played. If a Chowchilla group responded to the sounds and approached we attempted to direct them towards the nets. Any birds caught were removed as quickly as possible since they were very adept at getting out by themselves. In approximately 148h of mist-netting, the tape was played 133 times and 22 Chowchillas were captured. Three others were captured without the use of the tape - one by chasing it into the nets and the other two caught themselves.

Once caught, standard measurements and observations were made on the birds (see Appendix C) and ANPWS metal bands were fitted. For identification of individuals in the field, wing-tags were also fitted. It was decided that colour-bands would be too difficult to see in the forest so a method of wing-tagging was devised (after Claridge 1990). The wing-tags used were 6.5cm long and 3.5cm wide with a small flap to wrap over the front of the wing and were cut out of Tarpol - a heavy, tarpaulin-like material guaranteed not to fade or tear. The wing-tags were fastened using two thicknesses of nylon monofilament (strength 15 lbf), tiny glass beads and surgical knots. Figure 2.3 illustrates the attachment process and Plate 4 shows a wing-tagged bird. During wing-tagging, the bird was held in a sock with a hole cut in the side through which the wing could be drawn.

The wing-tags were made in four colours - red, white, orange and yellow - and were individually numbered with a cattle ear-tag marking pen. These colours could be easily distinguished in the field and the numbers could be read if I obtained a clear view of the bird. The wing-tags remained on the birds for three to at least 14 months.

Nestlings and a few adults were colour-banded rather than wing-tagged, using three size 7 colour-bands supplied by the Mist Net Service (Australian Bird Study Association).

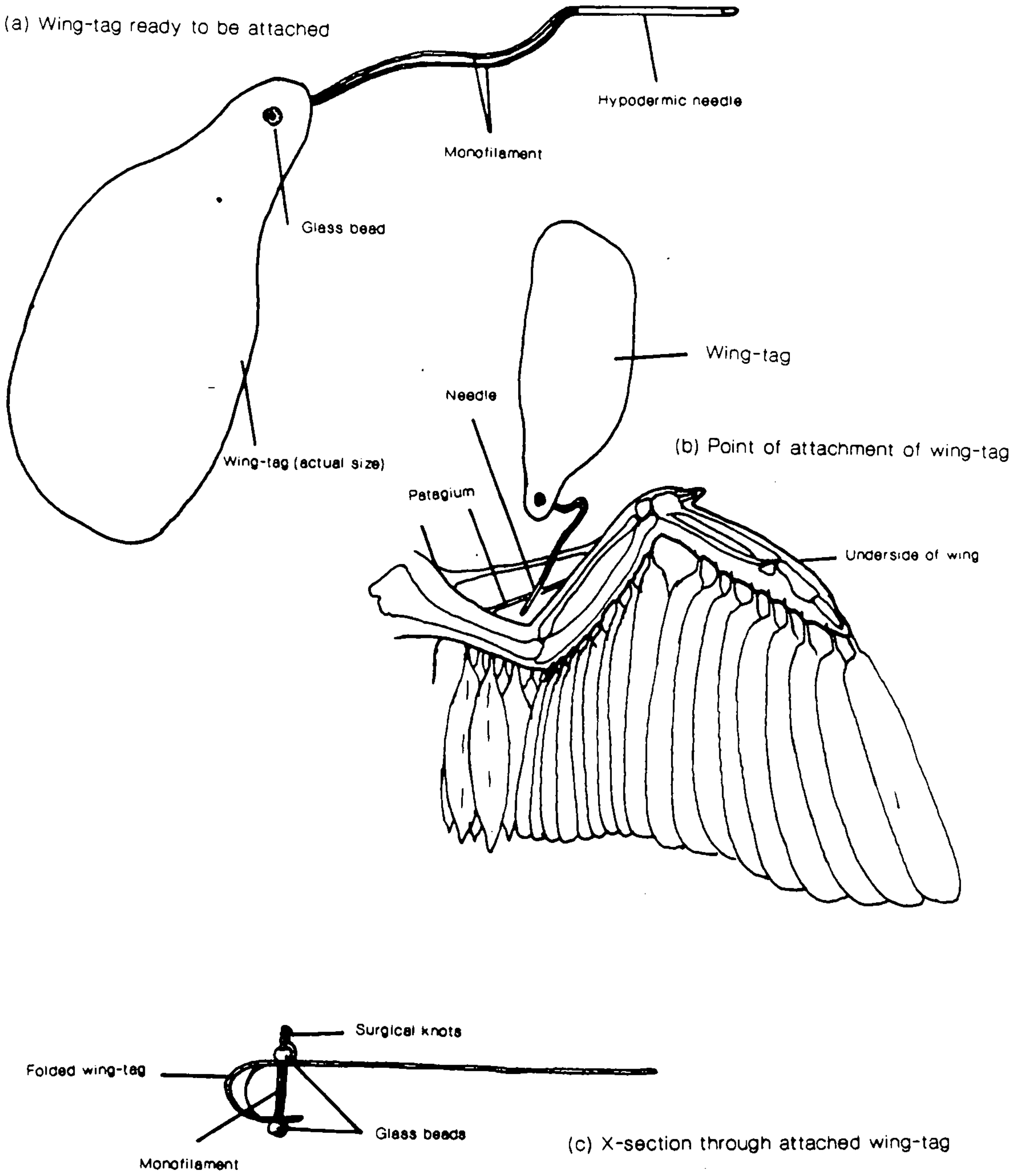


Figure 2.3 The wing-tag attachment process: (a) A glass bead was threaded onto a 20cm long piece of monofilament thread and both ends of the thread were forced into the blunt end of a sawn-off hypodermic needle (1.2x25mm). The needle was then threaded through the outer hole of the wing-tag; the monofilament forming a loop held in place by the bead. (b) The patagium was pierced from the underside with the needle. (c) the wing tag was folded over and the needle threaded through the inner hole. After removing the needle, a second glass bead was threaded onto one of the monofilament ends and the ends were tied using several surgical knots.

Plate 4. A wing-tagged Chowchilla

2.3 Locating and following birds

Location of birds fitted with radio-transmitters is discussed in section 2.5. This section deals with other methods of locating and following birds.

Methods of and success at locating birds depended largely on the moisture of the leaf litter. When the litter was dry the birds could often be located by the sounds they made scratching amid the dead leaves. When the litter was wet, these sounds were minimal and I relied more on walking close enough to the birds to see them or startle them, in which case they would give alarm calls and I could locate them. Occasionally the birds would call loudly, enabling me to locate them.

In the early part of the study I walked randomly around the study site to locate birds or sat in various places waiting for a sight or sound from them. As I became familiar with a group and its home range I started to search more systematically, trying to reduce bias in my home range estimates.

In heavy rain it was almost impossible to locate the birds either by sight or sound. The noise of the rain obscured any sounds the birds might make and visibility was severely restricted. Thus observations in the wet season were limited. Observations made during heavy rain, however, suggested that the birds were just as active as in drier conditions.

When a group of birds was located I followed them for periods of up to 2h, to identify all individuals in the group and to watch foraging and other behaviours. Birds were observed using Pentax 8X24 binoculars. Occasionally the birds appeared wary of my presence when I first began observing them, particularly if I accidently approached very close before they noticed me. However, after this initial period they usually appeared to take little further notice of me. Certainly they were aware of my presence and gave alarm calls if I came too close but usually they would resume foraging immediately and only look up to observe me occasionally.

2.4 Recording locations and behaviours

The study site was marked with flags at intervals along the gullies and trees were painted with numbers at strategic positions on the ridges and slopes. Part of the study site had been marked by CSIRO researchers from the Tropical Forest Research Centre, Atherton, with numbered stakes every 20m over 4ha. The flagged gullies and numbered trees were mapped in relation to the CSIRO grid, to produce a map of the site covering approximately 20ha.

When a group of birds was first located, the time and the distance and direction to the nearest flag, numbered tree or stake was recorded. Distances were estimated to the nearest metre between 0 and 10m, to the nearest 2m between 10 and 25m and to the nearest 5m above 25m to a maximum of 40m. Directions were estimated, using a compass, to the nearest 11.25°. Eastern Standard Time was used throughout.

Also noted when a group was first located were: activities of the birds - whether foraging, calling, preening or other; and site - whether ridge, slope or gully. Gullies were sites where water was present or had flowed previously and the relatively flat sites adjacent to these. Ridges were relatively flat sites with virtually no adjacent higher areas. Slopes were everywhere else. This classification of sites relates to sampling of food availability, as discussed in Chapter 4.

After a group was located it was observed for a time to determine the number and identity of group members, and behaviours were noted. If a calling session was observed, I tried to determine which individuals were involved, exactly where the interactions occurred, events during the session, and the outcome.

After the group moved on I usually checked the area for fresh faeces and collected any found. These could be assigned to the group and often to the individual which produced them. The faeces were dried and stored for later analysis.

2.5 Radio-transmitters

2.5.1 Design of the radio-transmitters

The radio-transmitters used in this study were supplied by Sirtrack Electronics, DSIR Land Resources New Zealand (now called Landcare Research New Zealand Ltd) and were designed specifically for this study, by consultation between Dave

Ward, Manager of Sirtrack Electronics and me. They were single-stage transmitters weighing approximately 1g, in the frequency range 150-151 MHz. Two battery sizes were used, a 2.6g mercury cell (V675HP) and a 4.6g cell (V625PX). These batteries run transmitters for 83 and 150 days respectively and, when made up, the transmitter packages weigh 5.6g and 8.0g respectively. The larger packages could only be used on male Chowchillas which are substantially heavier (average 185g versus 134g for females - see Appendix C). All transmitters were less than 4.6% of the relevant birds' body weights except one 8.0g transmitter accidently attached to a female which was 5.4% of her body weight. The recommended maximum is 5% of body weight for attachments (Aldridge & Brigham 1988). Caccamise & Hedin (1985) showed that birds of the weight of Chowchillas will experience a less than 5% reduction in the power surplus available for flight with transmitters of this size.

The transmitter and battery were packaged into a flat, roughly rectangular shape (≃28X12mm) with most of the weight (the battery) at the front end and a short whip antenna (≃85mm long) extending from the back. Two lengths of linen extended from each 'corner' of the transmitter package to attach it to the bird (see Figure 2.4). An epoxy resin was used to package the transmitter and battery.

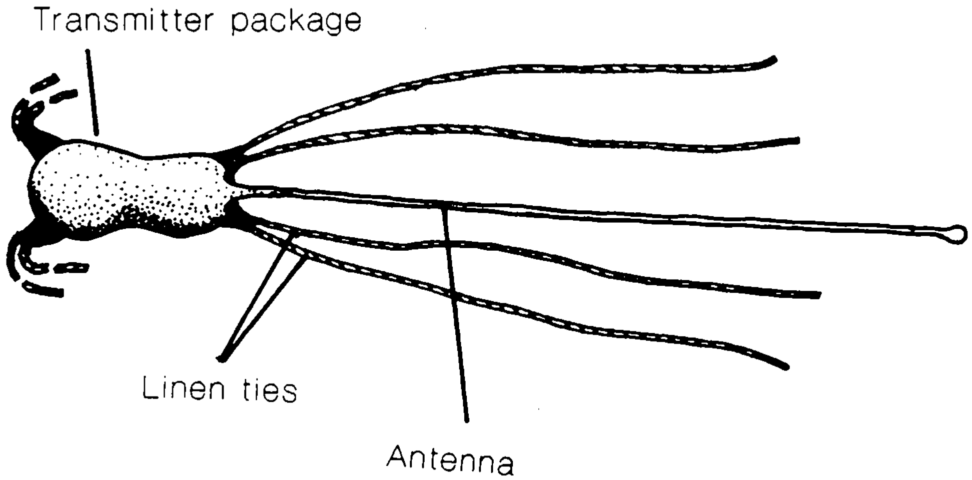


Figure 2.4 A packaged radio-transmitter ready for attachment (actual size).

2.5.2 Fitting transmitters to Chowchillas

While attaching transmitters, the birds were held, as for wing-tagging, in a sock with the tail exposed, although this was not necessary when a second pair of hands was available. The transmitter was attached to the top of the central two tail feathers, as close to the body as possible. The pairs of ties were tied around individual feather shafts with non-slip knots and secured with a dab of superglue on each knot. This was very effective for attaching the transmitter to the tail feathers - most transmitters were lost when the feathers became detached from the bird, either through a natural moult or when the extra weight became too great and the feathers were dropped. Chowchillas have very strong tail feathers which they use to lean on while foraging so they stood up quite well to having a transmitter attached. The position of the transmitter meant that the antenna hung down the length of the tail. The length of the antenna was limited by the length of the tail - any longer and it would be abraded against the ground. Plate 5 shows a transmitter attached to a wing-tagged bird.

2.5.3 Locating radio-tagged birds

Radio-transmitters were located using a receiver supplied by Custom Electronics of Urbana Inc., model no. CE12 and a hand-held, collapsible 3-element Yagi aerial supplied by Bio-telemetry Tracking (Australia) Ltd. Signals could be heard from up to about 100m away in the rainforest although the strength of the signal varied greatly depending on the bird's location and the position of the antenna in relation to the receiver and aerial. Generally I had to be within a bird's home range or fairly close by to receive a signal from that bird. When a signal was detected I tracked it down until the bird was in view. This could take anything from a few minutes to an hour depending on how far away I started and on the topography. The signals bounce very erratically in the rainforest, particularly in steep, rocky terrain, making location quite difficult at times.

Plate 5. A radio-tagged and wing-tagged Chowchilla

2.5.4 The effects and success of radio-transmitter attachments

A total of 17 transmitters were attached to nine different birds. Problems arose in the fitting of radio-transmitters to birds, in the functioning of the transmitters and one bird may have died as a result of a transmitter attachment. Three birds dropped their central tail feathers (plus the transmitter) within two weeks (one the same day) of attachment. Possibly either the extra weight or the stress incurred during handling was too great for these birds. However, seven other transmitters remained attached for 52 to at least 122 days with no obvious ill-effects on the birds. One bird carried a transmitter for 52-55 days and was weighed 1-4 days after losing it. It weighed 198g then, as opposed to 200g when the transmitter was attached.

One bird carried a transmitter for at least 60 days but was then found dead 14 days later with the transmitter still attached. The cause of death could not be determined - the bird was partly eaten but this could have happened before or after death. One possibility is that the stress of the transmitter attachment finally caused the bird's death and it was predated later. Two transmitters were faulty. One functioned intermittently for about 50 days before falling off while the other functioned perfectly for 23 days then the signal became faint and erratic for the remaining 80 days that it remained attached.

2.6 Analyses

Data were mostly analysed using the General Linear Models Procedure of SAS (SAS Institute Inc. 1985), except for Chi-square tests which were done by hand. Log-transformed data were used where necessary to make the data conform to the assumptions of normality. Log-transformations were of the form $lx=\ln(x+1)$ where ln is the natural logarithm and lx is the transformed variable. Rank-transformations were used when logarithmic transformations were not adequate and the resulting tests were equivalent to non-parametric tests. Significant differences or effects were accepted when alpha was <0.05.

CHAPTER 3

GENERAL BEHAVIOUR AND BREEDING BIOLOGY

3.1 Outline and methods

This chapter presents general descriptions of all behaviours observed in Chowchillas plus data on their breeding biology. These descriptions form a basic ethogram for the species. More intensive study of particular behaviours, and interpretations of them, will appear in later chapters.

Section 3.2 outlines the daily routine of a group of Chowchillas in the non-breeding season and gives frequency estimates for each main activity. Because many groups were located when they began calling, and because the birds were very inconspicuous when they preened, I used a subset of the observations for calculating these frequencies. I used only observations of groups which I had located by radio-tracking (so that the observations were independent of the behaviour of the birds), and only observations in which I saw all members of the group (to ensure that preening individuals were not missed). Each bird in every group observed under these criteria was scored separately. I scored the activity of each bird when it was first observed. If an individual was observed engaged in more than one activity in the first five minutes of observation, I gave it a half score for each activity. A total of 771 observations were scored.

Section 3.3 describes the foraging behaviour of individual birds. This deals only with the actual act of foraging; later I discuss what is eaten (Chapter 5), how foraging relates to food availability (Chapter 6), and foraging as a group (Chapter 8). Preening is described in section 3.4. Section 3.5 describes calling behaviour, the various calls identified and their contexts. Territorial calling is described in more detail in Chapter 8 and the songs are analysed in Chapter 9. Breeding biology and behaviour are described in section 3.6. This will be discussed in more detail in Chapter 8, in the context of the group.

All observations were made with either 8X24 binoculars or the naked eye, usually from within 10-20m of the birds. For nesting observations I used a small hide, constructed of bamboo poles and black shade cloth, placed 2-4m from the nest.

3.2 Daily routine

At night Chowchillas roost high in the canopy of the forest, probably in their groups since I have observed them ascending into the trees at dusk and coming down at dawn as a group. They start giving "territorial" and "flying" calls (described in section 3.5) at dawn while still in the trees and continue calling as they descend, in a series of short flights from branch to branch, eventually to the ground. Usually they then call as a group on the ground. This is often near an edge of their territory with another group calling nearby. This period of calling may last for a few minutes or up to an hour or more and its length may be related to weather conditions. On rainy or dark, cloudy days the birds may not call at all, or only briefly, while on bright sunny days they may call for a longer period.

After dawn, Chowchillas remain on the ground and are active for the rest of the day. In the main activity period (0700-1700 hours) shown in Figure 3.1, they spend most of their time foraging as a group (98.3%). They spend a very small amount of time preening (0.3%) and a small amount of time calling in territorial interactions (1.4%). Foraging consisted mainly of scratching in the leaf litter but also included periods of moving between patches and short periods of alert behaviour, apparently watching me or other disturbances. Instances of preening were short bouts of 1-3 minutes between foraging. "Territorial" calling could occur at any time of the day and ranged from a few minutes of calling exchanged with a neighbouring group to a half hour period of calling, physical attacks and chases when two groups met. Generally each individual in one of these interactions interspersed bouts of calling with foraging. As Figure 3.1 shows, Chowchillas spend a very large proportion of their time foraging.

At dusk Chowchillas start to fly up into the trees, usually giving frequent "flying" calls and occasionally brief bouts of "territorial" calling. They ascend in stages, flying from one branch to another, and settle gradually with occasional bouts of "flying" calls.

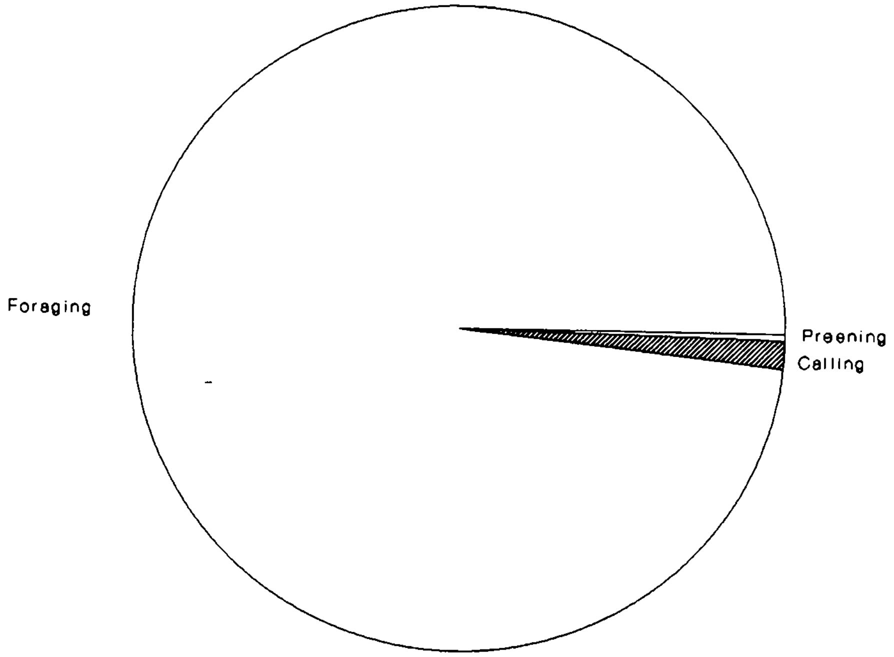


Figure 3.1 Proportions of time spent in different activities between 0700 and 1700h by 16 individuals in five groups over 122 days between June 1991 and August 1992 (771 observations).

3.3 Foraging

Chowchillas forage in the leaf litter, mainly on the forest floor, but also on top of dead logs, stumps and large boulders. They push aside layers of leaf litter with one leg while supporting themselves on the other leg and their strong tail. They use a sideways raking movement and alternate legs to clear an area around and in front of themselves. When the litter is relatively thin they clear it to the soil layer then peck at food items exposed. With thicker litter they alternate between clearing litter and pecking at food items, found both in the exposed area and escaping from the disturbed litter. Sometimes with very thick litter amid buttresses a bird will almost bury itself in litter as it scratches around in a small area.

When a Chowchilla has finished in one spot it moves from a few centimetres to several metres away before starting to scratch again. Chowchillas forage as a group although usually not closely enough to interfere with each other's foraging efforts. Generally group members remain at least 50cm and up to 10m apart while foraging. In a particularly good foraging area a group may spend up to 20-30 minutes continuously scratching and pecking without moving more than a few centimetres at a time. When they do move to a new area, they move as a group, walking or half-running. Quiet contact calls are used during foraging (see section 3.5)

3.4 Preening

In the few instances of preening that I have observed, the bird has stopped foraging, hopped onto a rock or stick just above the ground and spent a few minutes (less than 5 minutes on each occasion) preening wings and tail with the beak. Although I have seen groups near water on many occasions, I have not seen a Chowchilla bathing. Some groups do not have any water to bathe in within their home ranges for several months of the year.

3.5 Calling

Chowchillas have a large vocabulary of calls, some of which are very complex. There were four main calls which I could distinguish readily and for which I could identify the context.

"Territorial" calling is a loud, complex song used during territorial interactions. A single song lasts about 5-8 seconds and seems to be unique to a small number of groups in one area (see later analysis of songs in Chapter 9). This song has a distinct rhythm, pitch and sequence of notes and all members of a group may sing it during territorial interactions. Each individual sings the entire song although different individuals may sing together, usually starting at different times. This song is used at dawn, presumably to proclaim the territory, and at intervals throughout the day during encounters between groups. Sometimes during these encounters, a bird from each group will stand on the ground facing each other 20 to 30cm apart and sing alternately until one or both give up and separate. In all of these interactions that I observed the two birds were of like sex, either male or female.

Another loud call, that I named the "flying" call, is a series of "chucks", given when the birds appear to be agitated in some way. They gave it when I disturbed them abruptly into flying away and while chasing and being chased during territorial interactions. They also gave it, or something very similar, while flying to and from their roosts at dusk and dawn. Hence the name "flying" call as it usually seemed to be given when the birds were flying or running fast towards or away from something.

Two quiet calls are used between members of a group, seemingly as contact calls. The first is a "chirring" call, used when members of a group are foraging close together. The birds were often out of sight of each other (and me!) because of the numerous trees, rocks and other obstacles on the ground and this call presumably helped them remain in contact. It is also used by the female as she approaches her nest with food for the nestling and by both members of a pair when the male brings food to a breeding female.

The other call is a very quiet version of the "territorial" song, apparently given when members of a group become widely separated (by more than a few metres) and cannot hear or see each other. Often I would hear this quiet song after I had disturbed a group and they had become separated. It would often be followed by "flying" calls as the group members ran or flew back together. However, it also seemed to be used when individuals had become widely separated while foraging in different directions and then apparently noticed that they were alone.

3.6 Breeding behaviour and biology

Eight nests in which eggs were laid were observed between February 1991 and February 1993 on and near my site. One egg was laid in each nest. Incubation occurred in the months of January, February, May, July, September and December. Of the eight eggs, four were presumably predated in the egg stage, the egg disappearing before hatching. At two nests the egg hatched successfully and the chick was reared but disappeared at about the time it was due to fledge. At another nest the chick fledged successfully but disappeared soon afterwards (only a few weeks after fledging) (Andrew Dennis, pers. comm.). One nest successfully produced a fledgeling which was still with two adults over a month after fledging (Andrew Dennis, pers. comm.).

I observed incubation at one nest and the nestling stage at three nests. Rates of growth of nestlings were estimated at these nests by measuring tarsal length. Another chick, whose nest I did not discover, was observed shortly after fledging.

3.6.1 Nests

The Chowchilla nest is a large domed structure placed on or near the ground (2m above ground was the highest observed). It is a sturdy structure with a framework of sticks filled with moss, fern fronds and other fibrous material and lined with fibres and moss. It can be built against a fallen log, stump or rock if on the ground, while above the ground it may be built in a tangle of fallen logs, amid *Calamus* vines, at the base of the fronds of an *Oraniopsis* palm or on top of a Bird's nest Fern (*Asplenium*). Plate 6 shows a nest.

Plate 6. A typical Chowchilla nest

A typical nest was measured and found to be 335mm wide, 375mm deep and 310mm high. The nest chamber was 170mm wide, 150mm deep and 205mm high. Many incomplete nests were found - some were just small conglomerations of sticks while many had a complete framework of sticks except for the dome but were not filled in. A few appeared virtually complete but were never used.

3.6.2 Incubation

At the nest observed during incubation, the incubation period was at least 25 days, the period between discovery of the nest and hatching of the egg. The nest was observed for four periods of between 120 and 160 minutes in the last half of the incubation period. In 550 minutes of observations during this period, the female spent 45% of her time in the nest. Figure 3.2 shows how the proportion of time spent incubating decreased as the hatching date approached. For five periods in which I observed the female entering then leaving the nest, her average sitting time was 29 minutes (range 20-36 minutes).

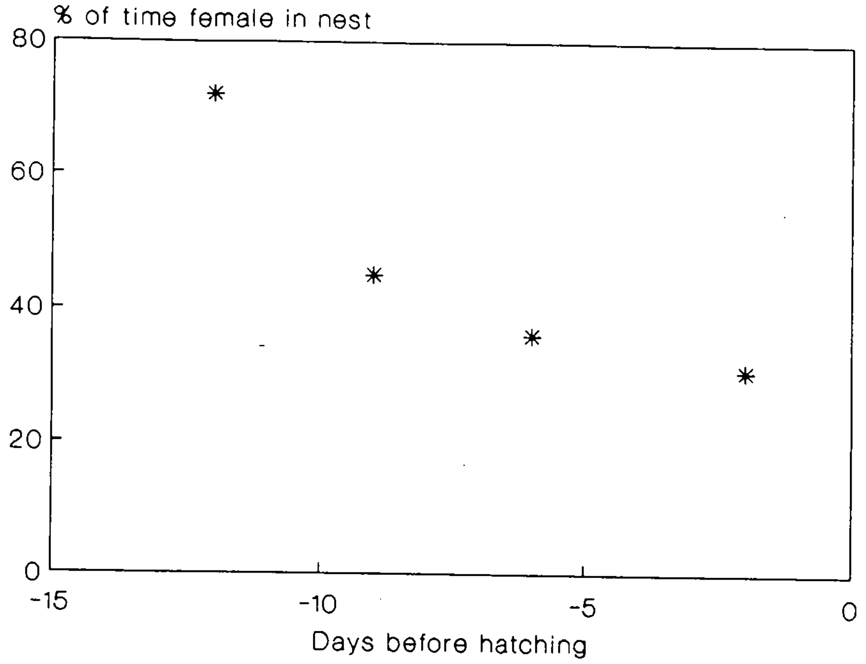


Figure 3.2 Incubation at a Chowchilla nest in September-October 1991.

3.6.3 Nestling stage

Three nests were observed during the nestling stage. Table 3.1 shows the timing of events at these nests.

Table 3.1 Events at three nests during the nestling stage.

	Nest 1		Nest 2		Nest 3	
Age (days)	Date	Events	Date	Events	Date	Events
1		Hatching	5.10.91	Hatching		Hatching
2-3	6.8.91	Recently hatched			22.12.92	Recently hatched
4-5	8.8.91	Chick in nest				
6			11.10.91	Observed (0900-1100h)		
8-9					28.12.92	Chick in nest
9			14.10.91	Observed (1100-1405h)		
11-12					31.12.92	Observed (190 mins)
12			17.10.91	Observed (1000-1230h)		
15-16					4.1.93	Observed (130 mins)
16			21.10 91	Chick in nest		
17			22.10.91	Chick in nest		
19-20	23.8.91	Observed (1330-1600h)			8.1.93	Chick in nest
20			25.10.91	Chick in nest		
21-22					10.1.93	Observed (155 mins)
22-23	26.8.91	Observed (1400-1630h)			11.1.93	Chick in nest
23			28.10.91	Chick in nest		
23-24	27.8.91	Observed (1111-1411h)				
25-26					14.1.93	Chick gone
26			31.10.91	Chick gone		
26-27					15.1.93	Adults seen without chick
29-30	2.9.91	Chick gone				
31			4.11 91	Adults seen without chick		
40-41	13.9.91	Chick near nest with adults				
65-66	8.10.91	Chick near nest with adults				

Nest 1 was followed through to successful fledging while at Nests 2 and 3 the chicks disappeared between 23 and 26 days after hatching and were presumed dead since the females attending those nests were seen shortly afterwards with their groups but without the chicks. It can be seen from the table that the nestling period lasted at least 23 days and possibly up to 29 days.

Nests 1 and 2 were observed for a total of 455 minutes each while Nest 3 was observed for a total of 475 minutes. I recorded all visits to the nest during each observation period. Figure 3.3 shows provisioning rates and rates of removal of faecal sacs during these observations. Both rates increased during the nestling period.

Only a single female appeared to attend each nest. At Nest 1 the appearance and behaviour of the female attending the nest suggested that it was always the same bird. At Nest 2 the female could be identified by a distinctive white fleck on her right wing, while at Nest 3 the female was colour-banded and radio-tagged. A male was seen near two of the nests, sometimes foraging less than 1m away from the nest. Males were never observed to enter the nest although they were observed feeding the females away from the nest. Nest 2 was checked one night and only the identifiable female was brooding the chick.

Figure 3.4 shows the tarsus measurements for the three chicks followed through the nestling stage. For comparison, the mean tarsus lengths of adult males and females are also shown. The larger chick was apparently a male while the smaller one was probably a female. The other could have been of either sex but was more probably a female too. Chowchillas do not moult into adult plumage until at least one year old (Les Moore, pers. comm.)

3.6.4 After fledging

I observed one family group, consisting of a male, a female and a very recently fledged chick (probably 1-2 days out of the nest), on 2.9.91. The chick sat on the ground between the buttresses of a tree while the adults foraged nearby. From time to time the female brought a beak full of food to the chick. When I came too close the female came to the chick then it followed her to a new sitting place between buttresses. The male stayed close by and occasionally fed the female but never approached the chick. The chick moved slowly and clumsily and apparently could not fly.

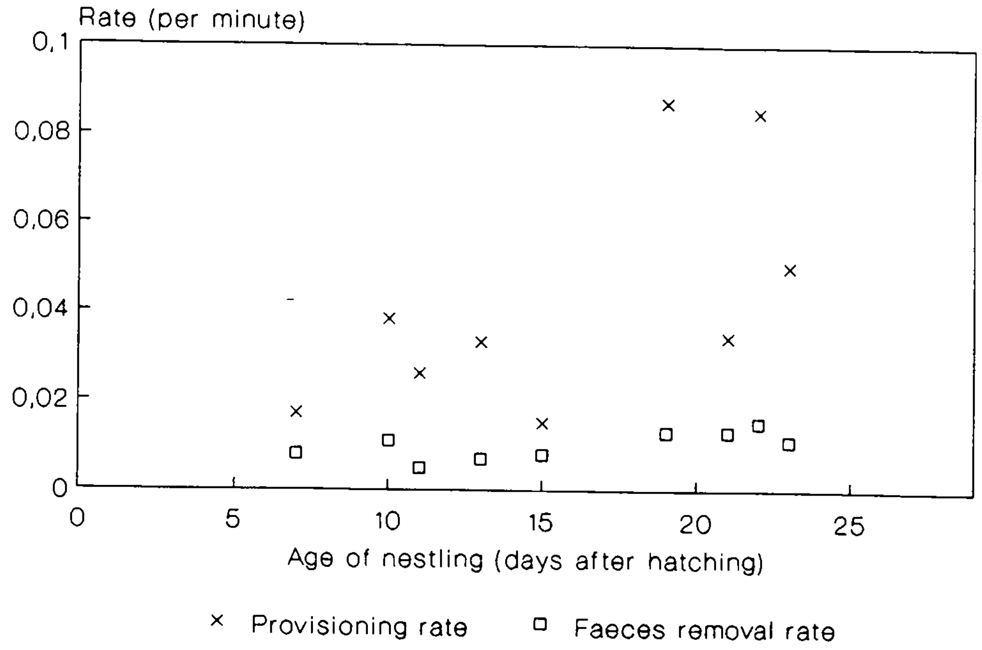


Figure 3.3 Attendance rates at three Chowchilla nests during different stages of the nestling period. Periods of observation for each point are shown in Table 3.1.

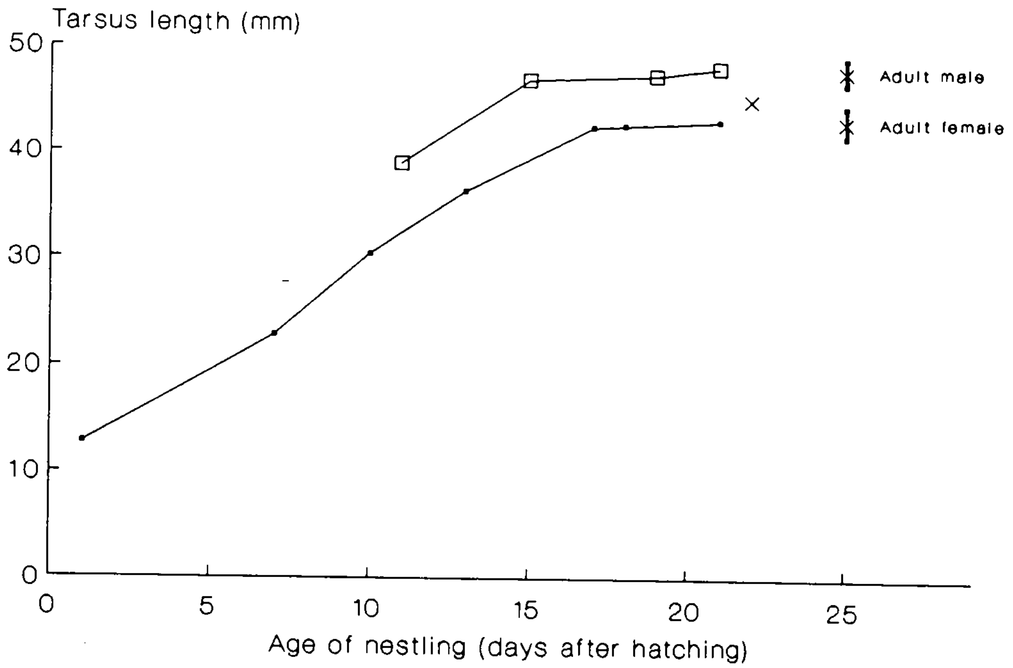


Figure 3.4 Tarsus lengths of three nestling Chowchillas. Mean (±1 standard deviation) tarsus lengths of adults also shown (data in Appendix C).

3.6.5 Summary of breeding biology

Nesting occurs throughout the year and only one egg is laid in a nest. Incubation takes at least 25 days and is probably performed by a single female. The nestling period is about 25-30 days and the nestling is attended by a single female. After fledging, the chick continues to be fed by the female for at least a few days. Few nesting attempts are successful; most nests being predated either in the egg stage or around the time of fledging.

CHAPTER 4

FOOD RESOURCE AVAILABILITY

4.1 Introduction

Chowchillas forage entirely in the litter and mainly on the ground (Frith 1984, Crome 1978) although I have also seen them foraging in litter on top of fallen logs and on large boulders. They eat only animal life found in the litter, ignoring fruit, fungi, roots, etc. (personal observation, Andrew Dennis, pers. comm.). Thus to sample their food resources I sampled the litter fauna. In this chapter I examine patterns of abundance of the litter fauna. In Chapter 5 I will relate food availability to what the Chowchillas actually eat.

Very little is known about the litter fauna in tropical rainforests, particularly in Australia. Only two published studies have examined the litter fauna of Australian tropical rainforests. Frith & Frith (1990) sampled invertebrate litter faunas monthly in ridge and gully areas over 19 months at Paluma, North Queensland. They reported results for all major invertebrate groups, excluding those <1mm in length. Holt (1985) sampled arthropods in litter and soil from three sites (two upland, one lowland tropical rainforest) on six occasions at 3-monthly intervals. This study only reported the results for Acari and Collembola and samples were divided according to depth - leaf litter, top soil (0-4cm depth) and lower soil layer (4-8cm depth). Neither study looked at characteristics of the litter such as quantity or moisture content although both stated that these are likely to influence arthropod litter populations.

These two Australian studies, and two other studies of tropical leaf litter faunas (on Barro Colorado Island (Levings & Windsor 1982, 1985) and in Peru (Pearson & Derr 1986)) found significant seasonal fluctuations in invertebrate numbers. All found a marked increase in numbers with the onset of the wet season. There was also significant variation between years (Levings & Windsor 1982, 1985, Pearson & Derr 1986, Frith & Frith 1990), corresponding to variations in the wet season rains and severity of the dry season.

Frith & Frith (1990) suggested that there may be a relationship between litter invertebrate numbers and rainfall, litter moisture content and quantity of leaf litter on the forest floor. Levings & Windsor (1982) found low but significant correlations between numbers of arthropods and both litter dry weight and litter moisture content. In an experimental study on Barro Colorado Island, Panama, where plots were cleared of arthropods and watered regularly, numbers of arthropods increased significantly compared to unwatered plots (Levings & Windsor 1984). Thus litter moisture content significantly influenced arthropod numbers.

I quantified food availability over time and between sites so that patterns of abundance could be related to Chowchilla foraging behaviour and to seasonal events such as breeding. The litter fauna was sampled over a two-year period from a range of microhabitats, and characteristics of the litter were measured for each sample. Food availability was related to time of year, temperature and rainfall, microhabitat, litter quantity and litter moisture content.

4.2 Methods

Samples were collected on the study site every two months from November 1990 to November 1992, usually near the beginning of the month. A stratified sampling design was used so that 12 samples were collected, equally divided between randomly chosen ridge, slope and gully sites on each occasion. Sampling points were chosen by walking 10 paces along the length of the area and tossing the quadrat into the air. Where it landed defined the sample. This was done four times for each site.

A 0.25m^2 quadrat was used and all litter within the quadrat was scraped up by hand into a large plastic bag which was then sealed, labelled and weighed. There were usually distinct soil and litter layers; only the litter layer was collected, except for a little loose soil which could not easily be separated.

The samples were placed in Berlese funnels (MacFadyen 1961) within about two hours of collection. The extraction set-up was as follows: a rack of 30 40-watt globes was placed so that the lights were within 5-10cm of the litter samples. Each funnel consisted of a 700ml round plastic container filled to $\simeq$1cm depth with 70% ethanol and a plastic funnel (25cm top width, 8cm bottom width) with a piece of wire mesh across the bottom to prevent the litter falling through into the ethanol. The samples were divided between the funnels so that no funnel contained too much leaf litter. This was especially important when the samples were very wet. Each funnel was covered with a piece of mosquito netting weighted down at the corners to prevent insects flying into or out of the samples. A few animals escaped during this procedure but most were recaptured and placed in the ethanol while the order and size of the rest were noted.

The samples were left under the lights for two days. After this time what remained in the leaf litter was usually dead. The litter was then removed from the funnels and oven-dried at $\simeq$40°C until no change in weight was recorded between weighings (usually about one week) to obtain dry litter weights and calculate moisture contents from the known wet weights recorded earlier (this was not done in November 1990). Any invertebrates trapped dead or alive in condensation on the sides of the funnels were removed into the ethanol and the extracted samples were stored in glass jars until they could be sorted.

On a few occasions there was too much litter to extract all 12 samples at once. Then samples were collected from two of the sites on the first day and from the remaining site two days later when the first set had been extracted. On these occasions the weather and dampness of the leaf litter did not change noticeably between the two sets of samples.

The extracted samples were sorted using a binocular microscope and the animals found were classified according to size (<1mm, 1-2mm, 2-5mm and >5mm), sorted into groups (insect, crustacean, myriapod and arachnid orders, snails, leeches, worms, etc.) and counted. Insect larvae of all holometabolous orders were lumped together as "unidentified larvae".

The extraction method used is known to be more efficient for some groups of animals than others (Macfadyen 1961). No assessment of this was made in this study so all numbers of animals reported here are relative - sufficient for comparisons between samples but not for estimating populations.

The data were analysed using General Linear Models (PROC GLM of SAS). The analyses examined the effects of time of year, site, dry litter weight and water content on total numbers of invertebrates and numbers of invertebrates >2mm (thought to be significant food for Chowchillas). The analyses were done on log-transformed numbers since the counts were not normally distributed. Taking ln(L+1) where L is the number of invertebrates resulted in a normal distribution.

Numbers of invertebrates >2mm (large invertebrates) rather than biomass was used as an estimate of food availability for three main reasons: (a) biomass seemed to be reflected quite well in numbers of large invertebrates; (b) biomass could not be measured directly without destroying the samples which was undesirable because of the importance of the collection: and (c) biomass could not be estimated accurately from length-weight relationships because of the lack of published relationships for Australian tropical invertebrates and the lack of any published relationships for some of the groups collected.

Patterns of abundance of significant groups of invertebrates were also examined.

4.3 Results

Figure 4.1 shows the rainfall and average temperatures in the 30 days prior to each collection of leaf litter. The pattern of rainfall varied markedly between years. In December 1990 a cyclone resulted in 1300mm of rain falling in the 30 days before the January 1991 collection date. In 1992, however, the wet season did not start until much later and most rain fell in the 30 days preceding the May collection date, when temperatures were much lower. Temperatures were higher in January 1992 than in January 1991 and lower in July 1992 than in July 1991.

Figure 4.2 shows the mean percent water content and dry litter weight of the litter samples. Changes in percent water content closely followed the rainfall pattern at all sites although the gully sites retained the highest water content in the driest period (July 1991 to January 1992). Patterns in the dry litter weight are not as consistent. On gully sites mean dry litter weight was highest at the beginning of the wet season (January 1991 and March 1992) and decreased to its lowest level by the next collection period. This was probably due to the combined effects of: (a) water in the gullies washing away accumulated leaf litter; and (b) more rapid decomposition in the moister conditions.

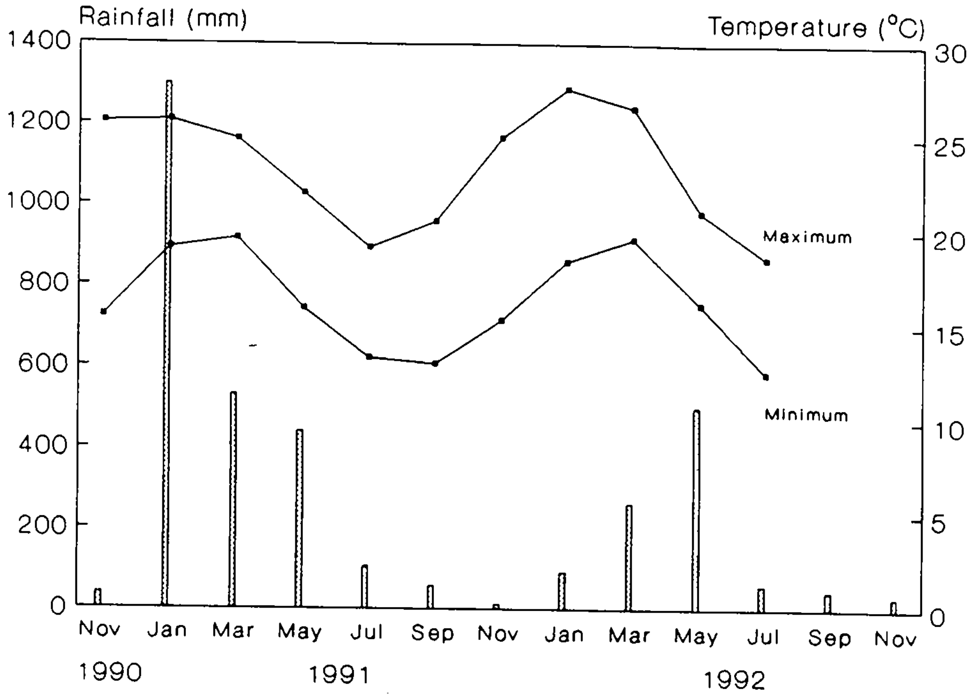


Figure 4.1 Mean maximum and minimum temperatures (lines) and total rainfall (bars) in the 30 days preceding each collection of leaf litter.

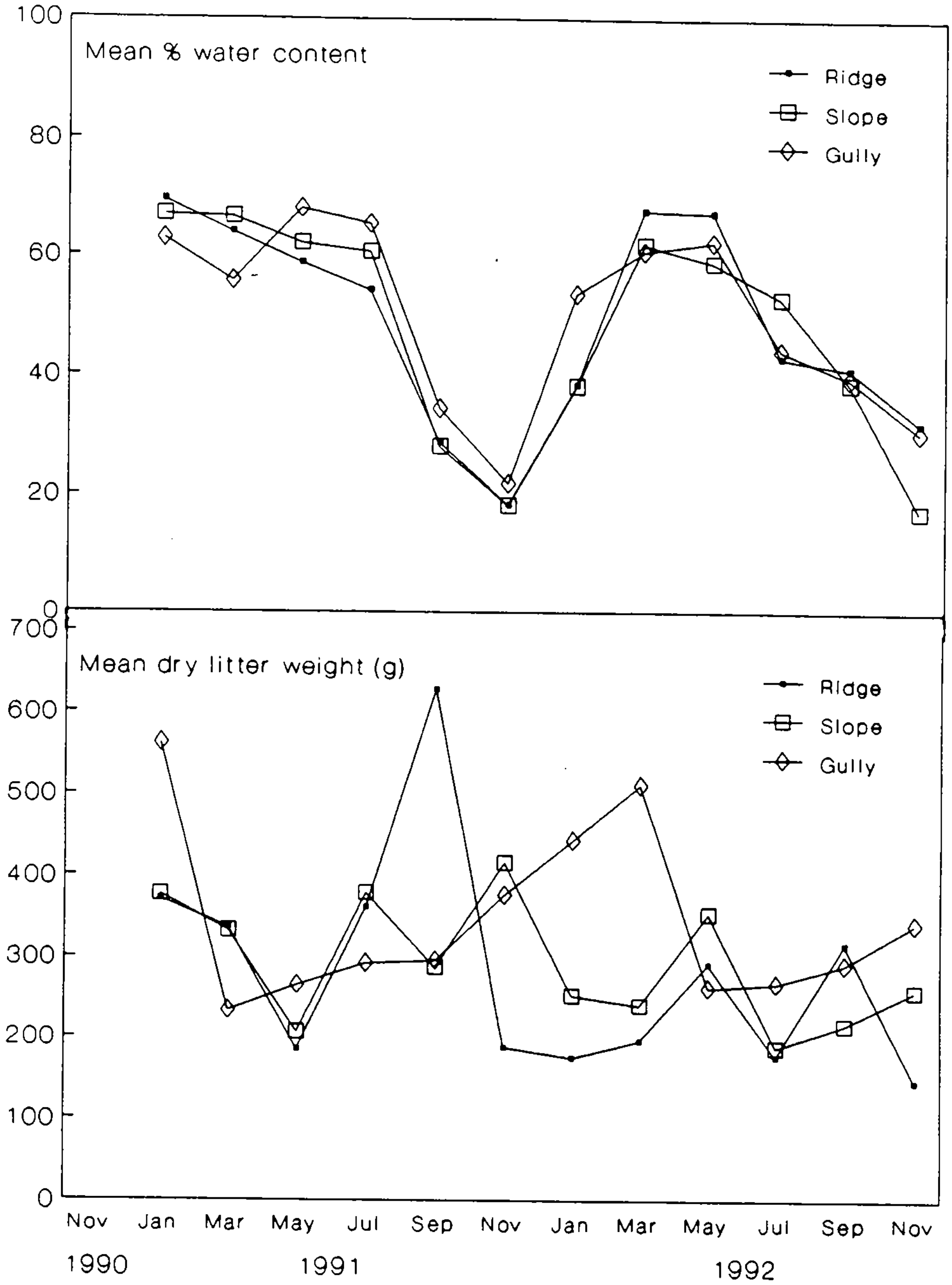


Figure 4.2 Mean water content and dry litter weight of leaf litter samples collected at different times of the year from different sites (N=4 for each mean).

Dry litter weights then increased on the gully sites throughout the dry season as litter fall increased and decomposition rates probably slowed in the drier conditions. On ridge sites dry litter weights were low in the wet seasons and very high in September 1991 when litter fall was very high and decomposition rates were probably at their lowest due to the relatively low temperatures and very dry conditions. On slope sites dry litter weight was variable throughout the year.

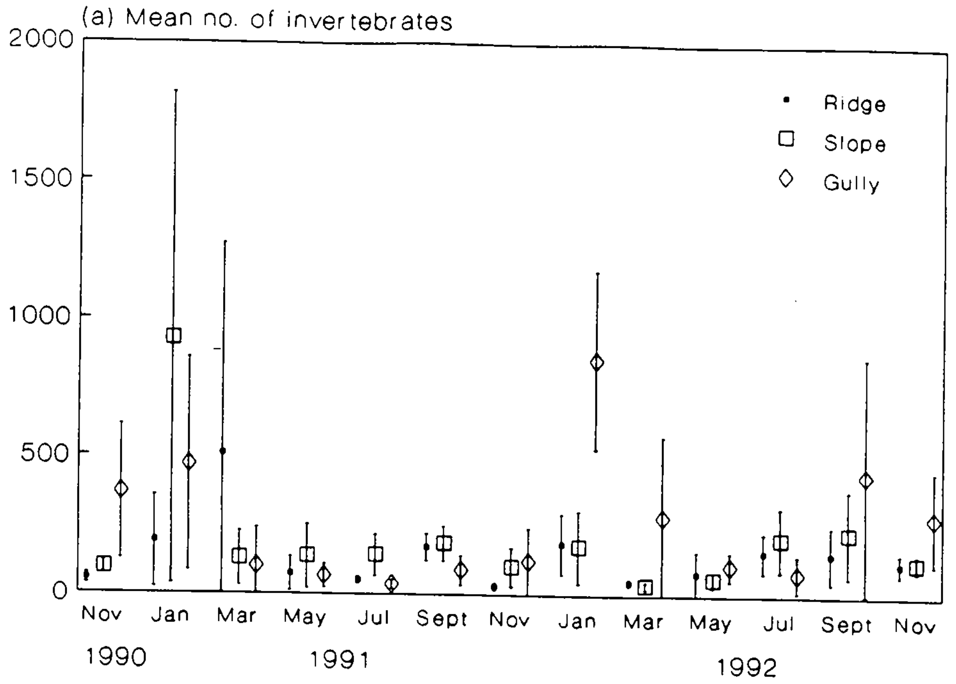
A total of 30,458 invertebrates, of which 4,944 were large, were collected. Figures 4.3 (a) and (b) show the mean number of invertebrates and mean number of large invertebrates respectively for each month and site. These two measures of food availability are highly correlated (on the log-transformed data Pearson's Rho=0.802, N=156, $p<0.0001$). Thus even if invertebrates smaller than 2mm form an important part of the diet of Chowchillas, the number of large invertebrates is still a good index of food availability. Mean total and large invertebrates were highest in January 1991 corresponding to the wettest collection period. Mean numbers of large invertebrates were generally lowest on ridge sites, except after the beginning of the wet season each year, when gully sites had low numbers, corresponding to low dry litter weights in these periods.

Variation in the numbers of large invertebrates was analysed with respect to time, site, leaf litter water content and dry weight of the leaf litter. Table 4.1 shows the relevant analysis of variance.

Table 4.1 Analysis of Variance table for the log-transformed numbers of large invertebrates.

Source	d.f.	Type I SS	F	p	Type III SS	F	p
Y	1	0.42	0.66	0.4195	2.42	6.66	0.0110
M	5	22.69	12.49	<0.0001	20.24	11.14	<0.0001
Y*M	5	10.17	5.60	<0.0001	14.82	8.16	<0.0001
S	2	2.14	2.95	0.056	4.38	6.03	0.003
WC	1	7.12	19.59	<0.0001	7.65	21.07	<0.0001
DLW	1	27.84	76.64	<0.0001	18.65	51.35	<0.0001
DLW*S	2	3.47	4.78	0.01	3.47	4.78	0.01
Model	17	73.67	11.93	<0.0001			

Y=year, M=month, S=site, WC=%water content, DLW=dry litter weight.



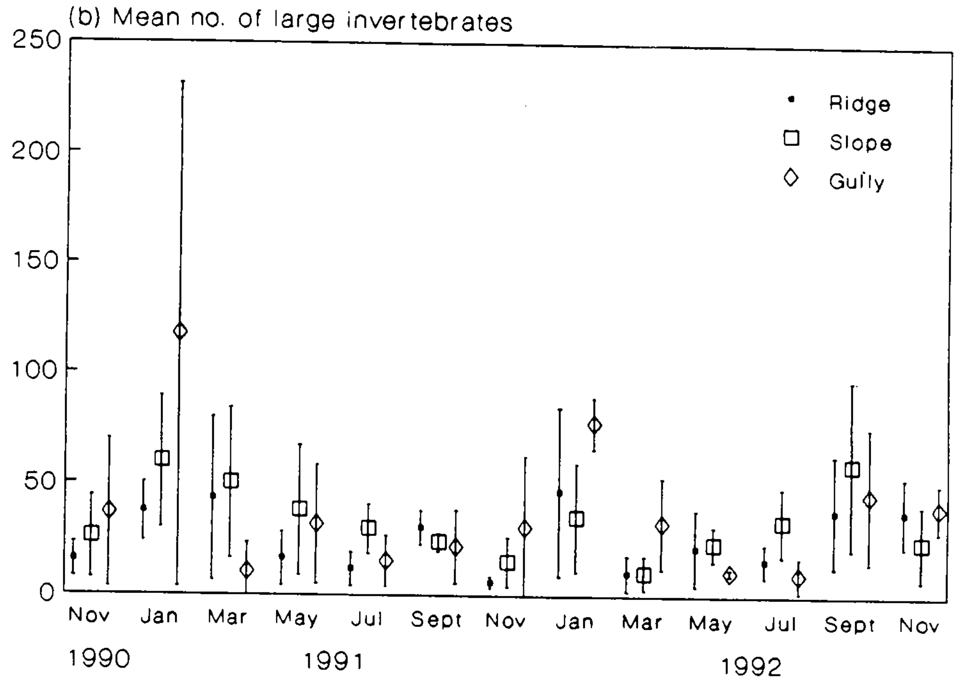
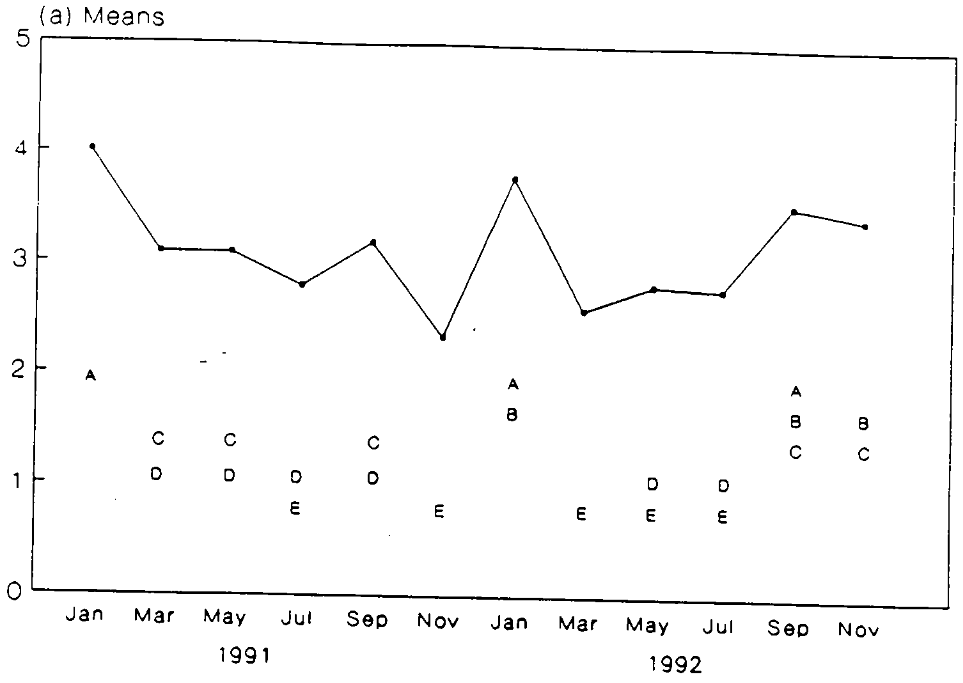


Figure 4.3 Mean numbers (±1 standard deviation) of (a) invertebrates and (b) large invertebrates in the leaf litter samples (N=4 for each mean).

This model explained 61.7% of the variance in the log-transformed numbers of large invertebrates. No other interactions were significant and there was no significant curvature in the effects of either water content or dry litter weight.

The numbers of large invertebrates varied between months and the significant Y*M interaction shows that this pattern was different for 1991 and 1992. Figure 4.4(a) shows the means for each month and which means are not significantly different from each other. Food availability was highest in January of both years and September 1992 and lowest in July and November 1991 and March to July 1992. In 1991 food availability generally decreased throughout the year, apart from a slight peak in September, and this follows the pattern of rainfall that year. The peak in September was probably due to the high levels of dry litter weight at that time (see Figure 4.2). In 1992, however, food availability again peaked in January, probably in response to rising temperatures more than rainfall since little rain fell in January (see Figure 4.1). Food availability dropped to low levels in March, possibly because the litter was completely saturated, then rose for the rest of the year. High food availability in the period September to November was probably a result of the constant, slightly moist conditions from the frequent showers in this period.

Both water content and dry weight of the leaf litter had significant linear effects on food availability. The Type I sums of squares show that even when the temporal effects of these factors were taken into account (in the Y and M effects), they still accounted for a large proportion of the spatial variation in numbers of large invertebrates within sites. Table 4.2 shows the slopes of the lines relating numbers of large invertebrates to water content and to dry litter weight for each site (since there was a significant interaction between site and dry litter weight). The y-intercept for each site is also shown.



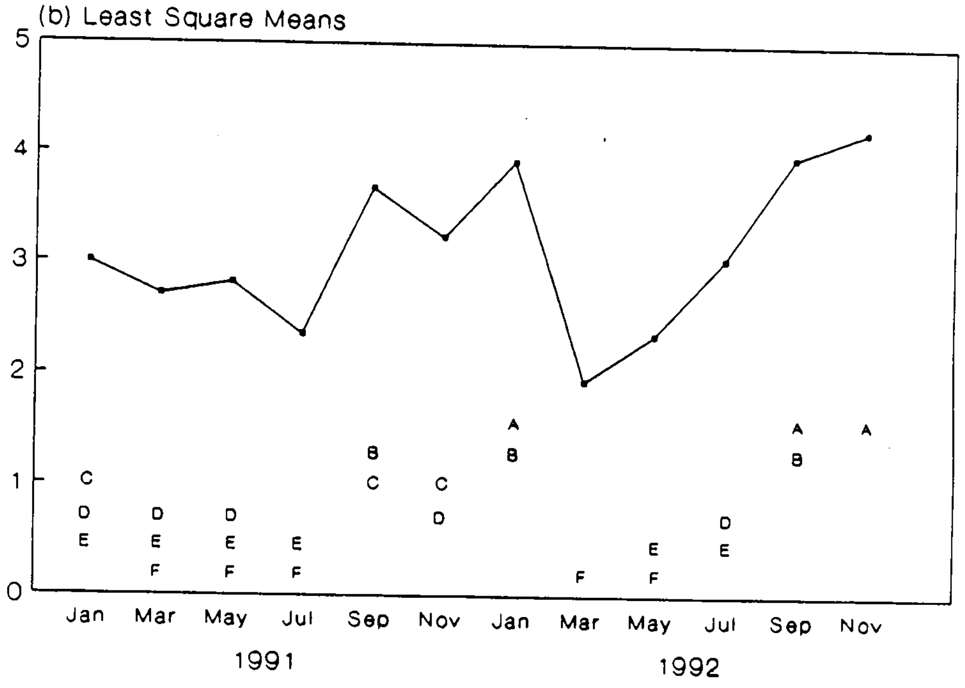


Figure 4.4 (a) Mean and (b) Least Square Mean (corrected for differences in water content and dry litter weight) log-transformed numbers of large invertebrates at different times of the year (N=12 for each mean). Means with the same letter are not significantly different.

Table 4.2 Relationships of water content and dry litter weight to the log-transformed numbers of large invertebrates.

Factor		Slope estimate	Intercept	T for Ho: slope=0	p
WC		0.0340		4.59	<0.0001
DLW	Ridge	0.0016	0.8903	2.65	0.0090
	Slope	0.0024	0.9452	3.10	0.0024
	Gully	0.0039	0.0804	8.35	<0.0001

Thus food availability increased with both water content and dry litter weight. The effect of site depended on dry litter weights. In sparse litter (up to 350g of litter per sample), food availability was highest on slope sites and lowest on gully sites. At intermediate dry litter weights (between 350 and 575g) food availability on gully sites was between that on slope and ridge sites. In deep litter (over 575g) food availability was highest on gully sites and lowest on ridge sites. The effect of water content was the same for all sites. From Figure 4.2 it can be seen that dry litter weights were usually in the range where slope sites had the highest food availability.

Figure 4.4(b) shows the mean log-transformed number of large invertebrates for each month when variations in water content and dry litter weight were removed. This demonstrates that when food availability on average was low, such as in September to November 1991, patches with high water content and dry litter weight would have had high food availability. In March 1992, however, when food availability on average was also low, the least square mean food availability was also low so there were likely to be few patches with high enough water content and dry litter weight to provide high numbers of large invertebrates. This analysis demonstrates that in good patches (with high water content and dry litter weight) food availability is likely to be higher in the dry season than in the wet season.

Food availability was highly patchy in distribution, not only over time and between sites, as can be seen from Figure 4.3(b), but also within sites at any given time. The average variance/mean ratio for large invertebrates from the sets of four replicates for each site in each month was 14.39, indicating an aggregated distribution of large invertebrates. In only two sets of samples (out of 39) was the variance/mean ratio less than one, indicating a random or more uniform distribution.

Figure 4.5 shows the patterns of abundance of the five most common groups of large invertebrates found in the leaf litter. Coleoptera were most abundant in September 1992, particularly on slope sites. Another peak occurred from November 1991 to January 1992 on gully sites. There was no obvious seasonal or year-to-year pattern. Amphipoda were more abundant in 1991 than in 1992 and virtually absent in November of each year. Numbers tended to increase with the beginning of the wet season each year and stay relatively high until September. Araneae were persistent throughout both years with little change in abundance. Hymenopteran numbers were variable, showing little pattern. The high peak on the ridge in January 1992 was due to one sample containing 81 ants. This demonstrates the patchiness of ant distributions. Larvae were most abundant in January of each year, particularly on gully sites and were more abundant in the first half of 1991 than 1992.

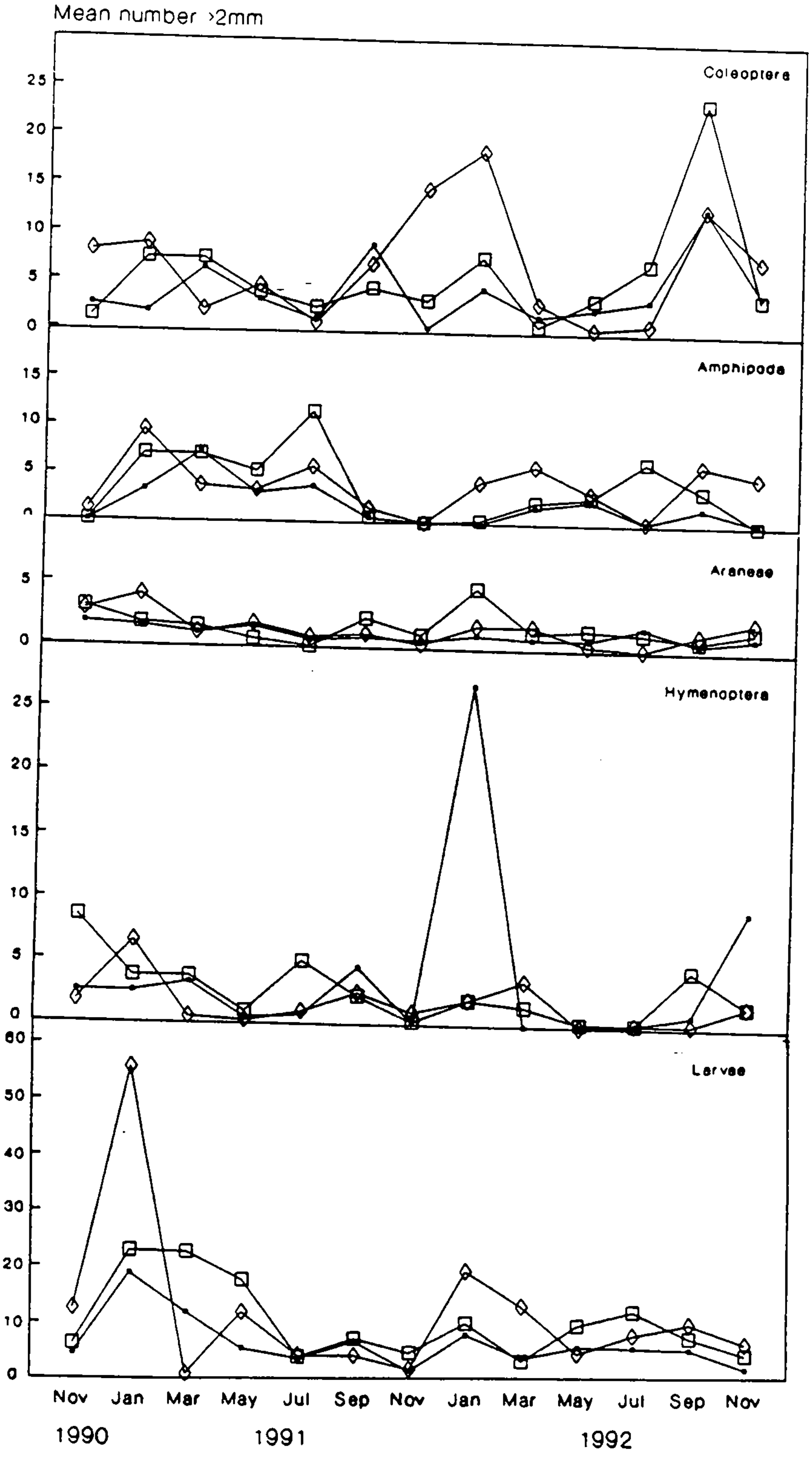


Figure 4.5 Mean numbers of large invertebrates of five groups in the leaf litter (N=4 for each mean). Dots represent ridge sites, squares slope sites, and diamonds gully sites.

4.4 Discussion

Food availability was patchily distributed in both space and time. However, numbers of large invertebrates at any time could be predicted quite well from site, moisture content and quantity of leaf litter. Some of the seasonal variation in food availability could be related to seasonal fluctuations in moisture content and quantity of leaf litter. However, there was also a seasonal effect independent of these fluctuations, suggesting that other factors such as temperature, light or the life cycles of the invertebrates also played a role.

Ford *et al.* (1990) suggested that lack of seasonality in food availability may be correlated with the incidence of cooperative breeding, and group-territoriality. They measured seasonality as the ratio of peak to lowest abundance of food and they found that cooperatively breeding birds were more common in eucalypt forests, with seasonality indices of about 3:1 to 13:1, than in rainforests (temperate and sub-tropical) which had seasonality indices of 10:1 to 20:1. These indices are all for aerial and foliage-living invertebrates.

I estimated seasonality indices from four studies of forest-floor invertebrates. For tropical rainforests these were 5:1 in southeastern Peru (Pearson & Derr 1986), 12:1 in upland northeastern Queensland (Frith & Frith 1990) and 27:1 on Barro Colorado Island, Panama (Levings & Windsor 1985). An estimate for sub-tropical rainforest, in southeastern Queensland, was 6:1 (Plowman 1979). For my study, the seasonality index was 7:1 for all invertebrates but only 4:1 for large invertebrates. Thus food availability in this study was probably less seasonal than in other tropical and Australian rainforests. Seasonality was comparable to that estimated for eucalypt forests by Ford *et al.* (1990).

The seasonality in food availability that did occur could also have been offset by selective foraging. Examination of the Least Square Means showed that when average food availability was at its lowest, good patches often contained more food than at other times of the year. Thus, assuming that Chowchillas always had access to good patches to forage in (as I will show that they did in Chapter 7) and that they can forage selectively (which I will demonstrate in Chapter 6), they probably experienced very little seasonality in food availability.

Different groups of invertebrates showed widely different patterns of abundance with time and between sites. The groupings used here lump together groups with widely different ecologies (e.g. herbivorous and carnivorous beetles, ants and wasps). This probably masks patterns which would be evident if functional groupings were used. The large number of undescribed taxa (species, genera and possibly families) in the collection means that more detailed analysis of individual groups will have to wait until the collection is examined by entomological experts.

CHAPTER 5

DIET

5.1 Introduction

Most tropical group-territorial birds are generalist foragers (see Chapter 1), as are most Australian group-territorial birds (Ford *et al.* 1988). However, few studies of group-territorial birds have examined diet in any detail. If diet is mentioned, they simply give a list of items eaten. Optimal foraging theory predicts that with a range of food types varying in energy value and handling time, the number of food types included in the diet will increase as the overall abundance of food decreases (Pyke *et al.* 1977).

In this chapter I investigate the diet of Chowchillas and relate what is eaten to the availability of different food types.

5.2 Methods

Chowchilla faeces were collected each month from August 1991 to July 1992. Most of these were collected by following foraging birds, as noted in Chapter 2. A few were also collected from birds captured during banding operations. They were dried and later sorted under a microscope after teasing them apart in a small amount of 70% alcohol. Any identifiable fragments were removed, compared to my invertebrate collections for identification, and counted. Much of the faecal matter consisted of tiny unidentifiable fragments and particles. Occasional pieces of a number of different invertebrate groups would pass through in a relatively undigested state and could be identified to order. Ants and Amphipoda could be identified reliably enough to count the fragments and obtain some idea of their relative abundance in the diet at different times of the year.

For ants I counted the minimum number of bodies to which the various body parts could have belonged while for amphipods I counted the number of fragments (these were very small and could not be related to numbers of amphipod bodies but gave an index of numbers). I counted these parts in the faeces collected in each bi-monthly period from August 1991 to July 1992, and compared these numbers to the numbers collected at each site in the leaf litter samples for the corresponding dates.

For ants I included only those >2mm since virtually all those found in the faeces were of this size class. For amphipods I included all size classes (very few were <2mm anyway). For the comparisons I used the numbers found in each faecal sample or site as a proportion of the total number of body parts of that group found in either the faeces or the leaf litter. These proportions were transformed using an arcsin-square root transformation before analysis. The proportions were compared with 2-way ANOVAs on the transformed data using Type III Sums of Squares since there were unequal numbers of faecal samples in each time period.

For other identifiable fragments in the faeces I simply noted when they occurred in the diet.

Food items brought to nests could sometimes be identified. From the nests observed in August 1991, October 1991 and December 1992 - January 1993, I recorded all items that I could identify in the female's bill from my hide. These were added to the list of groups identified in the diet.

Prey items taken by foraging birds could occasionally be identified and these were also added to the list.

5.3 Results

5.3.1 Diet

Table 5.1 shows the groups of animals identified in the diet using the different methods. No plant material was found in any of the faeces and Chowchillas were never observed to eat fruit or other vegetable matter.

Table 5.1 Animal groups identified in the diet of Chowchillas and other groups found in the leaf litter but not identified in the diet.

Identified in diet:

	In faeces	At nests	Foraging
Acarina	X		
Amphipoda	X	X	
Araneae	X	X	
Blattodea	X	X	
Chilopoda	X	X	
Coleoptera	X	X	
Diplopoda	X		
Gastropoda	X		
Hemiptera	X		
Hirudinea		X	
Hymenoptera	X		
Microhylidae	X	X	
Oligochaeta		X	X
Orthoptera	X	X	
Pseudoscorpiones	X		
Scincidae		X	
Unidentified insect larvae	X	X	

In leaf litter but not in diet:

Collembola #
Dermaptera *
Diplura *
Diptera #
Isopoda #
Isoptera *
Lepidoptera #
Odonata (nymphs) *
Opiliones *
Psocoptera #
Symphyla *
Thysanoptera #
Turbellaria *

* rare groups, # soft-bodied and/or small

Andrew Dennis (pers. comm.) observed Chowchillas feeding in areas of fruit falls favoured by Musky Rat-Kangaroos and never saw the Chowchillas eat any fruit. In fact, they often kicked aside fruit in their searches for animals in the litter. Thus Chowchillas eat a wide range of animal material - mainly invertebrates, but also small frogs (probably microhylids) and small skinks.

The sizes of items brought to nests appeared no different from those eaten by adult Chowchillas; nor were there any obvious differences in the types. Some of the items seen brought to nests would not have been identifiable in faeces (e.g. leeches), and conversely, some of the items found in faeces would not have been seen in observations at nests (e.g. Diplopoda, snails, Acarina). These differences in digestibility and sightability account for all of the observed differences between items found in faeces and those identified at nests.

I classified the groups found in the leaf litter but not identified in the diet of Chowchillas according to rarity and digestibility (see Table 5.1). All of these groups may have been eaten by Chowchillas but were probably undetectable in the faeces.

5.3.2 Diet and prey availability

I compared the proportions of ants and amphipods found in the faecal samples to their relative abundances on the site at different times of the year. Table 5.2 shows the Analysis of Variance tables for these comparisons.

Table 5.2 Analysis of Variance tables for arcsin-square root-transformed proportions of (a) ants and (b) amphipods in Chowchilla faeces and in the leaf litter at different times of the year.

(a) Ants

Source*	d.f.	Type III SS	F value	p
M	5	0.2516	2.55	0.0442
T	1	0.0051	0.26	0.6157
MxT	5	0.2309	2.34	0.0606
Model	11	0.4281	1.97	0.0607

(b) Amphipods

Source*	d.f.	Type III SS	F Value	p
M	5	0.1334	2.69	0.0361
T	1	0.0102	1.03	0.3169
MxT	5	0.1534	3.09	0.0198
Model	11	0.2463	2.25	0.0321

*M=bi-monthly period, T=type - whether faecal or leaf litter sample

For both ants and amphipods the interaction term was substantial (borderline significance for ants). Figure 5.1 shows the mean proportions in the diet and available in the leaf litter for each group. Within each bi-monthly period, least square means were used to test for significant differences between proportions available and proportions eaten. For ants, the only (barely) significant difference was in December-January when Chowchillas appeared to avoid them. Amphipods were significantly more abundant in the diet than in the leaf litter in October-November, and significantly less abundant in the diet in February-March. Thus ants were avoided when food was most abundant (see Figure 4.4(a) in the previous chapter) while amphipods were preferred when food was least abundant but avoided when food was slightly more abundant. The numbers of amphipods in the faeces in October-November was particularly significant given that I collected no amphipods in the leaf litter in November.

Chowchillas clearly did not forage at random with respect to prey type, at least for ants and amphipods. This selectivity could have been achieved at least in part by foraging in sites where these prey types were most or least likely to occur (Figure 4.5 in the previous chapter shows that the availability of ants varied from site to site depending on the time of year, while amphipods were generally more abundant on gully and slope sites than ridge sites). To investigate this I weighted the proportions of ants and amphipods found in the leaf litter at each site by the proportions of time Chowchillas were observed foraging at these sites at different times of the year (Table 6.6 in the next chapter shows these site usage frequencies). Table 5.3 shows the Analysis of Variance tables for the comparisons of observed proportions eaten and expected proportions encountered.

Neither of these analyses of variances are significant. This shows that when Chowchilla preferences for different sites at different times of the year are removed, there is no longer any evidence of selectivity for ants or amphipods at different times of the year.

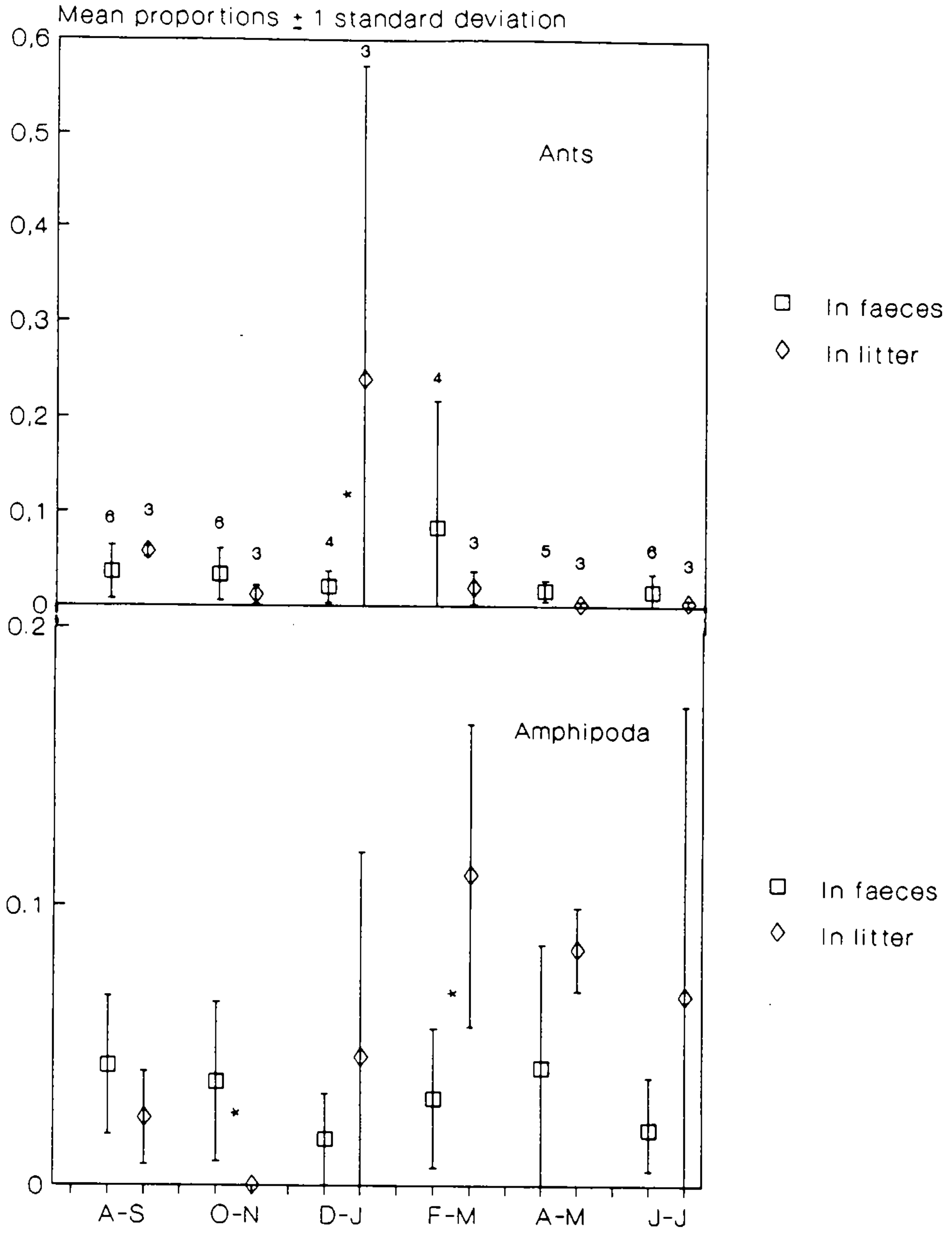


Figure 5.1 Mean proportions of ants and amphipods found in the leaf litter and in Chowchilla faeces. Significant differences between proportions eaten and proportions available are shown with an asterisk. N values are the same for ants and amphipods and are shown above each set of samples.

Table 5.3 Analysis of Variance tables for arcsin-square root-transformed proportions of (a) ants and (b) amphipods in Chowchilla faeces and expected to be encountered in the leaf litter at different times of the year.

(a) Ants

Source*	d.f.	Type III SS	F value	p
M	5	0.0635	1.16	0.3492
T	1	0.0406	3.69	0.0623
M*T	5	0.0388	0.71	0.6230
Model	11	0.1417	1.17	0.3386

(b) Amphipods

Source*	d.f.	Type III SS	F Value	p
M	5	0.0356	0.82	0.5415
T	1	0.0338	3.90	0.0557
M*T	5	0.0564	1.30	0.2843
Model	11	0.1188	1.25	0.2928

*M=bi-monthly period, T=type - whether faecal or leaf litter sample

5.3.3 Diet and food availability

I compared the numbers of groups of animals identified in the diet from the faecal samples at different times of the year to see if this could be correlated with the availability of food at different times of the year. The comparison is crude since invertebrates were only identified to order. Table 5.4 shows the number of groups identified in the diet in each bi-monthly period and food availability ranked from lowest to highest for the corresponding periods (from Figure 4.4(a) in the previous chapter).

There was no correlation between food availability and number of groups of animals identified in the diet (Spearman's Rho= -0.088, $p>0.05$).

Table 5.4 Numbers of groups of animals identified in faecal samples of Chowchillas during periods of differing food availability.

Period	A-S	O-N	D-J	F-M	A-M	J-J
No. of groups	8	9	10	10	6	9
Rank of food availability	5	1	6	2	4	3

5.4 Discussion

These results show that Chowchillas are generalist foragers, eating virtually any small animals in the leaf litter. They do not appear to forage selectively for particular types of prey, except insofar as they may forage in sites more likely to contain these types of prey (e.g. amphipods when food availability is at its lowest). I detected no sign of increasing dietary specialization as food availability increased. This may reflect the crudity of my measure of dietary specialization. Another possibility is that food availability was never low or high enough to make changes in dietary specialization profitable. A third possibility is that food types vary so little in energy value and handling times that there is no advantage in foraging selectively for different food types.

Thus patterns of abundance of the invertebrates in the leaf litter reflect well what is available as food for Chowchillas. The vertebrate prey in the leaf litter were not sampled but they were very rare compared to the invertebrate prey and their abundances could not be readily estimated.

CHAPTER 6

FORAGING STRATEGIES

6.1 Introduction

In the previous two chapters I examined the food available to Chowchillas and their diet. In this chapter I investigate how Chowchillas exploit that food supply. Optimal foraging theory deals with the decisions that animals must make to exploit their food supplies efficiently. It is generally assumed that animals have evolved to be efficient foragers and the role of optimal foraging theory is to determine how the animals make foraging decisions: what constraints they operate within; what currency is to be optimized; and what variables are taken into account in the decisions (Schoener 1971, Pyke *et al.* 1977). Foraging strategies fall into four main types of decisions: (a) what size group to forage in; (b) when and how long to forage for; (c) where to forage; and (d) what to eat (Schoener 1971). Most theory and tests have dealt with the last two categories and they can be subdivided further into the decisions of: (a) choice of patches to search; (b) choice of prey items to eat; (c) how long to spend in a patch; and (d) movement within and between patches (Pyke 1984).

In examining foraging strategies of Chowchillas, I concentrated mainly on the first decision - that of where to forage. In deciding where to forage, animals could use information on patch quality from three main sources: information on the quality of patches could be provided in external cues; the quality of patches could be learnt from previous experience; and, where patches are renewed predictably, animals could pattern their foraging so that areas are not revisited until they have had time to be replenished. Few studies have examined situations in which patch quality can be assessed before searching. Particularly for insectivorous birds, the prey tend to be cryptic and there are rarely obvious cues to suggest the quality of patches.

In an elegant study of Checker-throated Antwrens, Gradwohl & Greenberg (1984) found that long, highly curled dead leaves contained the most arthropods and that the antwrens were quite successful at exploiting this resource. However the birds did not specialize on these types of leaves, instead foraging at random with respect to leaf size and degree of curl. In a cost-benefit analysis, taking into account the time required to search these apparently profitable leaves, it was found that the capture rate was quite similar for these leaves as for the average of all dead leaves and thus there was no advantage in specializing on what seemed to be the most profitable leaves.

Two other studies have looked at similarly small scale patches: Greenberg & Gradwohl (1980) compared the prey densities on the upper and lower surfaces of leaves for foliage-gleaning birds while Greenberg (1987) compared live and dead leaves in both the tropics and the temperate zone for the migratory Worm-eating Warbler. Both found some tendency for the birds to concentrate on the more profitable surfaces or leaf types. In the case of the Worm-eating Warbler, the profitability of live *versus* dead leaves increased from the tropics to the temperate zone and there appeared to be a period of learning when the birds first arrived in the tropics when they had not yet started to specialize on dead leaves which were more profitable in that region.

Two studies have looked at large scale patches - tree species and strata within the trees. Both looked at ten species of foliage-foraging insectivorous birds and found that they tended to show preferences for those tree species and strata which had higher prey abundances (Holmes & Robinson 1981, Holmes & Schultz 1988). In a study of Ovenbirds, Zach & Falls (1979) compared areas along the foraging paths of the birds with random, unsearched areas of territories and found significantly more biomass and numbers of invertebrates in searched areas. This suggests that the birds had either learnt the location of high quality patches on their territories or there were cues to patch quality which they used in deciding where to forage.

Some experimental studies, on Ovenbirds (Zach & Falls 1976a,b), Great Tits (Smith & Dawkins 1971, Smith & Sweatman 1974), and Black-capped Chickadees (Heinrich & Collins 1983) found that the birds learnt where good quality patches were and, after a learning period, foraged mainly in these patches. In these experiments there were no external cues to the quality of patches so the birds could only select good quality patches after learning their locations. It has been suggested that they did not forage only in the highest quality patches because they needed to check other patches occasionally in case of changes in patch quality (Pyke 1984). When patch locations were shifted the birds gradually relearnt to forage in the higher quality patches (Zach & Falls 1976a,b, Smith & Dawkins 1971, Smith & Sweatman 1974).

Another way in which birds can concentrate on high quality patches, when resources renew in a predictable fashion, is to forage systematically so that patches are not revisited until they have had time to be replenished. This type of foraging strategy has been demonstrated in Pied Wagtails (Davies & Houston 1981) as well as in some nectarivorous birds such as sunbirds (Gill & Wolf 1977) and Amakihi (Kamil 1978).

In Chapter 4 I showed that food is patchily distributed and that the quality of a patch (i.e. how much food it contains) could be predicted quite well from its location, depth of leaf litter and litter moisture content. In this chapter I define the area sampled in the investigation of food availability (i.e $0.25m^2$) as equivalent to a 'patch'. The forest floor is relatively homogeneous so the definition of patches is somewhat arbitrary. However, patches of $0.25m^2$ seem relevant to the foraging behaviour of Chowchillas in that: (a) food availability is patchy on this scale; and (b) they appeared to pattern their movements so that they searched within small areas of $<0.25m^2$ and moved at least 0.5m away before searching in a new spot. Important to this definition of patches is that adjacent patches were not necessarily of similar quality because of variations in litter moisture content and depth which resulted from small-scale topographical and vegetation cover differences.

I hypothesized that Chowchillas could assess the quality of patches from site, dry litter weight and water content and choose those patches which were likely to contain more food to forage in. I investigated this hypothesis by comparing patches chosen by foraging Chowchillas to random patches within the study area.

6.2 Methods

Foraging strategies of Chowchillas were investigated in two ways, examining two different scales of patch use. On the small scale, an experiment was undertaken at two different times of the year to compare points where Chowchillas were observed foraging to random points on the forest floor. On a larger scale, the observational data on Chowchilla foraging sites over a period of 14 months was examined for indications of site preferences.

6.2.1 The experiment

The experiment was conducted in March 1991, in the middle of the wet season, and again in September 1991, at the driest time of year. Patterns of insect abundance were different at these two times of the year (see Chapter 4) so foraging strategies were examined at both times. To carry out the experiment, I located foraging birds (either by searching or by radio-tracking for radio-tagged birds - see Chapter 2) and marked points where I saw birds foraging. When a group of birds was located, I was sometimes able to obtain two or more points where different individuals foraged. Sometimes the same group was located again later. To increase the independence of samples, I ensured that if I obtained two points for the same individual, they were at least 0.5h apart.

After marking the points, I returned to each one within about 2h and sampled the area around the marked point with a 0.25m^2 quadrat centred on the point. For each point I recorded: the individual observed foraging there (if tagged); the site (whether ridge, slope or gully); and the weight of the leaf litter enclosed by the quadrat (the litter was scraped up and put in a bag to be weighed in the same way as litter was collected for sampling food availability - see Chapter 4). A subsample of the leaf litter (usually 100-200g) was placed in a paper bag, weighed, labelled and then taken to be oven-dried until its weight remained constant. For each foraging point sampled in this way I also sampled an additional point on the study area chosen by moving a random number of paces (between 1 and 200) on a randomly chosen compass bearing (E, W, N or S) from the last sampled point to a new point. These additional points will be referred to as `random points`.

From the weights of the oven-dried litter samples I calculated the percent water content of each original sample (the change in weight of the subsample after drying divided by the wet weight of the subsample multiplied by 100) and the dry weight of each original sample (percent water content multiplied by the wet weight of each original sample, subtracted from the wet weight of each original sample). Thus for each foraging point, and for an equivalent number of random points, site, water content and dry litter weight could be compared to the food availability data. In March 1991 I sampled 21 foraging points and 21 random points while in September 1991 I sampled 30 foraging points and 30 random points. Data collection was spread over six days in March and three days in September (locating birds was more efficient in September because I had some radio-tagged birds).

In analysing the data I first developed a model for predicting food availability from measurements of site, dry litter weight and water content for the 1991 food availability data for large invertebrates. I used only the data for large invertebrates because: (a) a larger proportion of the variance was explained by the model for large invertebrates; and (b) large invertebrates are probably more relevant to the birds' foraging strategies. Chowchillas do eat items smaller than 2mm but they probably do not contribute significantly to energy intake. I used only the 1991 data because year-to-year variation in weather and food availability patterns was substantial and the 1992 data would not have been relevant to this experiment (see Chapter 4). General Linear Models were used to find a model to predict food availability from site, dry litter weight and water content. To analyse the experimental data the foraging and random samples were compared in terms of: (a) site usage; (b) water content; (c) dry litter weight; and (d) predicted number of invertebrates >2mm from the model. Chi-square tests were used to compare site usage frequencies while t-tests were used for the remaining comparisons; the data were rank-transformed where necessary.

6.2.2 Observational data

The food availability data showed some predictable differences in invertebrate numbers between sites (i.e. ridge, slope or gully), at least at certain times of the year. I investigated whether Chowchillas were tracking these large-scale differences by showing preferences for the more profitable sites at different times of the year. To do this I collated the observational data on foraging sites of all groups of birds into two-monthly periods and compared site usage frequencies to those expected if the birds were foraging at random on their territories. The proportions of different sites expected if the birds were foraging at random was estimated by recording the site type at each of the 120 CSIRO pegs on their 4ha grid which covered part of my study area. These pegs were distributed among all site types and gave good estimate of the proportions of different site types available to the birds.

Site preferences were examined using Chi-square tests and any preferences found were correlated to differences in food availability between sites for that period. I again used only the data for large invertebrates and only the data for the period May 1991 to July 1992, corresponding to the period covered by the observational data.

6.3 Results

6.3.1 Analysis of the 1991 food availability data

The best-fitting model for predicting availability of large invertebrates involved all four factors measured (time, site, dry litter weight and water content) and explained 72% of the variation in the log-transformed data on numbers of large invertebrates. Table 6.1 shows the General Linear Models analysis of variance table with the Type III Sums of Squares (which are independent of the order of the terms entered into the model).

Table 6.1 Analysis of Variance table with Type III Sums of Squares for the availability of large invertebrates in 1991 Total number of samples was 72.

Factor	d.f.	SS	F	p
Time	5	8.17	1.63	0.0005
Site	2	4.55	2.28	0.0016
Water content	1	6.90	6.90	<0.0001
Dry litter weight	1	13.12	13.12	<0.0001
DLW*Site	2	3.69	1.85	0.0049
Model	11	48.87	14.02	<0.0001

Although it is difficult to say anything definite about the effect of site on food availability because of the interaction term, it is clear in examining a plot of numbers of large invertebrates over time (see Figure 4.3b) that in March gully sites had fewer large invertebrates than ridge or slope sites and that slope sites had more than ridge sites. In September, however, there was very little difference between sites.

Table 6.2 shows the slopes of the lines relating water content and dry litter weight to the log-transformed food availability data. The slopes for dry litter weight were estimated separately for each site because of the interaction term.

Table 6.2 Relationships of water content and dry litter weight to the log-transformed numbers of large invertebrates in 1991.

Factor	Slope estimate	T for Ho: slope=0	p
Water content	0.052	4.67	<0.0001
Dry litter weight			
Ridge	0.0016	2.36	0.0215
Slope	0.0020	2.35	0.0218
Gully	0.0043	8.06	<0.0001

This shows that sites with higher both water contents and dry litter weights had higher food availability. Although the effects appear small, this is because the food availability data were log-transformed.

6.3.2 Comparing foraging and random samples from the experiment

Site usage frequencies, water contents, dry litter weights, and the predicted number of large invertebrates were compared in both March and September. Table 6.3 shows the site usage frequencies for each month and the analysis using Chi-square tests.

Table 6.3 The proportions of different sites in foraging and random samples in both March and September.

Month	Site	Foraging	Random	Chi-square	d.f.	p
March	Ridge	2	5			
	Slope	19	10			
	Gully	0	6			
	Total	21	21	10.08	2	<0.01
September	Ridge	3	7			
	Slope	22	22			
	Gully	5	1			
	Total	30	30	4.27	2	>0.1

This shows that in March there was a significant difference between the proportions of sites available to and used by foraging Chowchillas. They showed a preference for slope sites and an avoidance of gully sites. This matches the food availability data - slope sites contained the most invertebrates >2mm while gully sites contained the least. In September the birds showed no preferences for particular sites and again this matches the food availability data - there was little difference between sites in September.

Table 6.4 compares the water content and dry litter weight of foraging and random samples in each month.

Table 6.4 Mean water content and dry litter weight (±1 standard deviation) of foraging and random samples in March and September.

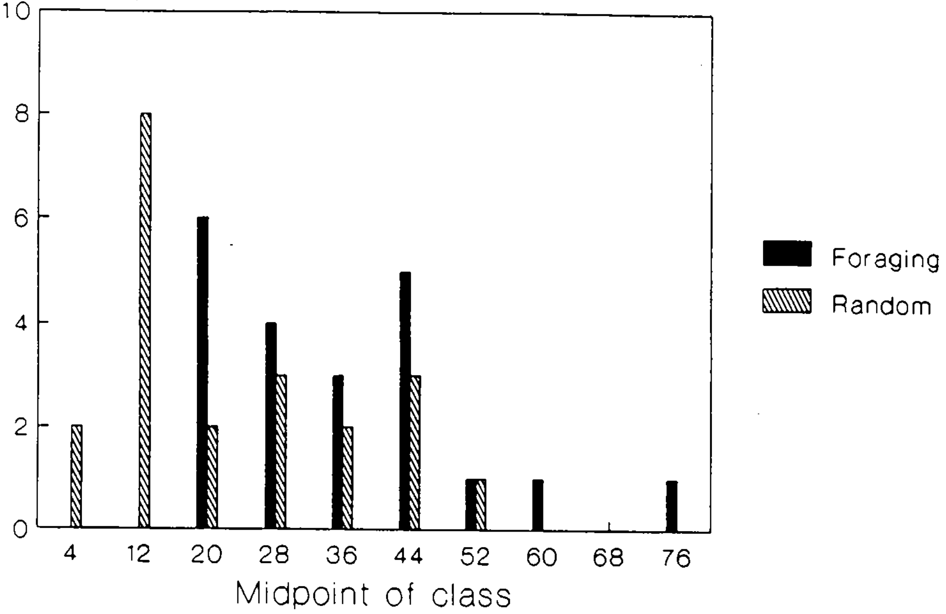
	Foraging	Random	T	d.f.	p
March					
Water content	63.8±5.2	60.1±11.6	0.31*	40	0.31
Dry litter weight	296.8±106.7	224.3±115.0	2.12	40	0.04
September					
Water content	42.5±11.9	37.0±10.0	1.96	58	0.055
Dry litter weight	274.1±98.2	175.0±86.2	4.15	58	<0.0001

* t-test done on ranked values because of unequal variances

The mean values of dry litter weight were significantly higher for foraging than random samples in both months while for water content there was no difference in March but a borderline significant difference in September. Thus Chowchillas tended to forage in sites which had higher average dry litter weight and, at least in September, somewhat higher average water content than random sites. From the earlier analyses it will be recalled that higher numbers of large invertebrates were found in wetter sites with more leaf litter.

The analysis comparing predicted numbers of large invertebrates gave similar results. Figure 6.1 shows the frequency distribution of predicted numbers of large invertebrates for foraging and random samples in each month. The March data (see Figure 6.1a) fit the assumptions of normality and the mean (± standard deviation) predicted number of large invertebrates is 35.4±15.3 for foraging samples and 22.2±14.3 for random samples. A t-test on this data gives T=2.89, d.f.=40, p=0.006. The September data, however, were not normal (see Figure 6.1b) and had to be rank-transformed before analysis. The mean (± standard deviation) predicted number of large invertebrates is 58.9±53.2 for foraging samples and 30.2±15.0 for random samples. A t-test on the ranked data gives T=2.31, d.f.=58, p=0.024. In both months Chowchillas were clearly foraging in sites with higher predicted numbers of large invertebrates than the average available sites.

(a) Frequencies in March



(b) Frequencies in September

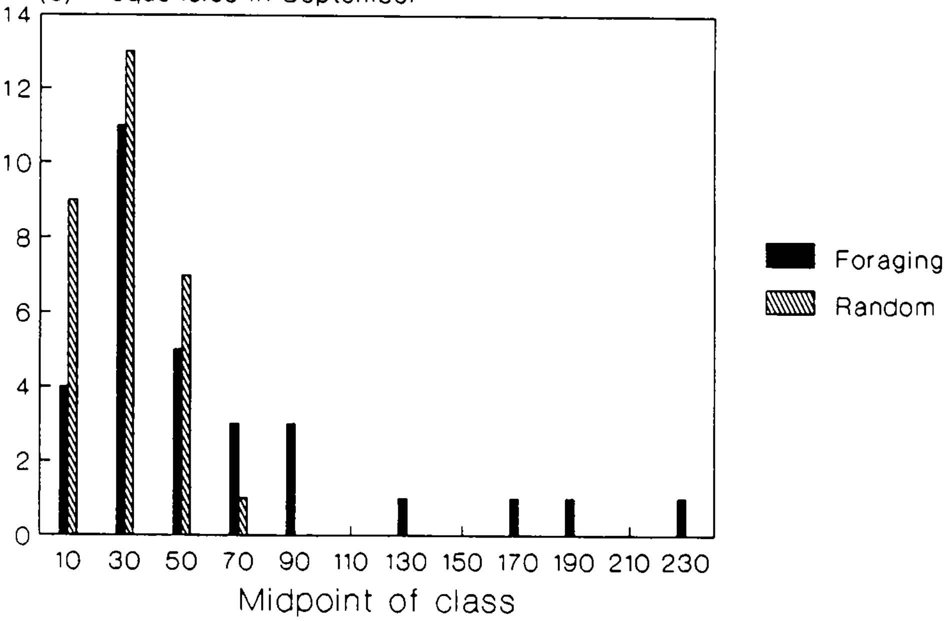


Figure 6.1 Frequency distributions of predicted numbers of large invertebrates for foraging and random samples in (a) March and (b) September.

6.3.3 Observational data on site usage patterns

The data on food availability in the period May 1991 to July 1992 was used to examine the effects of time and site. Using only these two factors the model explained only 45% of the variation in the log-transformed number of large invertebrates. Table 6.5 shows the analysis of variance table.

Table 6.5 Analysis of Variance table for the availability of large invertebrates from May 1991 to July 1992. Total number of samples was 96.

Factor	d.f.	SS	F	p
Time	7	16.40	4.41	0.0004
Site	2	2.25	2.12	0.1277
Time*Site	14	12.80	1.72	0.0698
Model	13	31.45	2.57	0.0012

The interaction term was of borderline significance and pair-wise comparisons showed that in two months, March 1992 and July 1992, there were significant differences between sites. Figure 4.3b shows how food availability varied between sites in each month. The fact that sites vary significantly in food availability, at least in some months (though this model only explained 45% of the variation in invertebrate numbers) suggested that Chowchillas might improve their foraging success by discriminating among sites.

I divided the observational data on the foraging sites of all Chowchilla groups observed into bi-monthly periods corresponding to the food availability data. Table 6.6 presents the frequency data and Chi-square tests are used to compare the observed proportions of site usage to those expected if the birds were foraging at random, based on the 21 Ridge, 85 Slope and 14 Gully sites recorded at the CSIRO grid pegs.

Table 6.6 Observed frequencies of site usage by all Chowchilla groups in bi-monthly periods compared to frequencies expected if the birds were foraging at random. D.f.=2 for each Chi-square test.

Period	Frequencies Ridge	 Slope	 Gully	Chi-square	p
J-J 1991	6	38	13	4.473	0.107
A-S 1991	11	46	16	3.639	0.162
O-N 1991	8	65	28	11.613	0.003
D-J 1992	7	45	22	10.785	0.005
F-M 1992	0	12	6	sample size too small	
A-M 1992	5	35	16	8.689	0.013
J-J 1992	37	108	27	2.082	0.353

In all the periods for which significant site preferences were evident there was a preference for gully sites, avoidance of ridge sites and use of slope sites approximately in proportion to their availability. In November 1991 through to March 1992 gully sites had more invertebrates >2mm than slope or ridge sites and this corresponds to the period when Chowchillas showed significant preferences for gully sites. In May 1992 there was little difference in numbers of invertebrates >2mm between sites although the birds still showed a significant preference for gully sites in the period April-May 1992. This, and the fact that no preferences for particular sites were shown in some periods, even when food availability clearly varied between sites (for example July 1992), may be explained by the fact that the factor site only explains some of the variation in numbers of invertebrates >2mm and that Chowchillas use other cues (such as dry litter weight and water content - as shown in section 6.3.2) in patch choice.

6.4 Discussion

The results show that numbers of large invertebrates are quite predictable on the basis of site type, dry litter weight and water content and that Chowchillas may use any or all of these as cues in deciding which patches to forage in. Site on its own was not always a useful predictor of food availability. Chowchillas showed preferences between sites only at times when food availability differed between sites. At other times they foraged at random with respect to site but were more likely to forage in patches with a higher water content and high dry litter weight.

Variations in dry litter weight explained the most variance in food availability (see Table 6.1) and certainly in September, when site gave no prediction of food availability, patch choice was most strongly correlated with dry litter weight. Thus Chowchillas had a flexible foraging strategy, using those cues which best indicated food availability at any time of the year.

Patch choice at this level could come about either through learning or through assessment of patches. I have implied throughout this chapter that Chowchillas could assess patches in terms of site, dry litter weight and water content to decide whether to forage in them but it could also be the case that familiarity with their territories allows them to know where good patches are at different times of the year. Probably both factors are involved here; certainly experience would have shown the birds where the good patches are located but it is likely that assessment of patches at the time of foraging also occurs. It is relatively easy (even for me who has done far less sampling of the leaf litter than the average Chowchilla) to assess patches for food availability by examining the site, quantity of leaf litter and how moist it appears. This assessment could be made as the birds move across the forest floor and it seems most likely that this occurs. Learning is probably involved at the larger scale; in deciding which part of the territory to forage in and in avoiding recently searched areas. Chowchillas search areas quite thoroughly when they forage and it would probably not be profitable to return to areas already searched until they have had time to be replenished.

As noted earlier in this chapter, several studies have demonstrated that birds can learn the quality of patches and eventually concentrate their foraging on those patches known to be of higher quality (e.g. Zach & Falls 1976a, b, Smith & Dawkins 1971). In these studies the patches could not be assessed before they were sampled so learning was clearly involved in patch choice. I know of no studies on birds in which only assessment of patches, rather than learning, has been demonstrated. However a study on two species of *Eurema* butterflies (Mackay & Jones 1989) examined host-finding behaviour and found that the butterflies tended to search patches more likely to contain host plants and to alight on plants resembling their host plants in terms of leaf shape and size more often than would be expected if they were searching and alighting at random. The fact that they often alighted on non-host plants resembling the host plant indicated that they had not learnt the location of their host plants (good quality patches to them) but assessed patches on the basis of cues - leaf shape and size in this case.

Much of the foraging theory in relation to patch choice deals with the situation in which patches are of unknown quality and must be sampled first. This is thought to be the more common situation for insectivorous birds - where it is thought that there are relatively few external cues to the availability of food in different patches. A number of strategies have been proposed for how the birds may sample patches efficiently (Krebs 1973): (a) hunting by expectation; (b) area-restricted searching; and (c) optimal giving-up times. The idea of hunting by expectation was first proposed by Gibb (1962) to explain the behaviour of tits foraging for larvae in pine cones. However, his data do not convincingly support the hypothesis that the birds expected a certain number of larvae per cone in a given area and stopped searching a cone after obtaining that number of larvae (Krebs 1973). The idea of area-restricted searching relates to clumped distributions of prey and suggests that after one prey item is found the predator will modify its searching behaviour so that it searches nearby areas which are also likely to yield prey. This has been demonstrated in European Blackbirds and Song Thrushes by Smith (1974). This hypothesis does not seem applicable to Chowchillas because good patches (as I defined them) were not necessarily clumped in distribution. Thus the birds may not have benefited by area-restricted searching.

The idea of optimal giving-up times is that a predator should leave a patch once its capture rate drops below the average for the area. The Marginal Value Theorem (Charnov 1976) deals with this situation and allows prediction of the time animals should spend foraging in patches depending on their quality, the rate of depletion in patches, and the time taken to travel between patches. I did not investigate this possibility at all; I only examined initial patch choice, not how long was spent in each patch. Given that the factors I measured to predict food availability - site, dry litter weight and water content - did not explain all of the variability in numbers of large invertebrates (R^2 for the model was 72%), there is some potential for sampling of patches after patch choice. This potential may explain the large variance in predicted numbers of large invertebrates found in foraging samples (see Figure 6.1) - some of the foraging samples had as low predicted food availability as some of the random samples.

In some places it may have been worthwhile for the birds to sample patches which appeared less profitable on the basis of site, dry litter weight and water content in case they were of higher quality due to the unexplained variation. In this case there is the potential for Chowchillas to exhibit patch choice not only before searching but also to adjust their search times within patches, according to their sampling of food availability in the patches, as predicted by the Marginal Value Theorem. This could be examined by investigating not only patch choice but also allocation of time to patches of differing quality. Another possibility of course is that Chowchillas also used other cues besides the three I examined, and that these allowed even more accurate assessment of patches.

CHAPTER 7

HOME RANGES AND TERRITORIALITY

7.1 Introduction

Many studies of group-territorial birds give estimates of territory size and generally relate this to group size. Territory size is often used as an indicator of territory quality. It is hypothesized that either larger groups are more able to defend higher quality territories than smaller groups or that a higher quality territory is needed to support a larger group. Brown (1987a) suggested that there is an optimum group size which is related to defence costs for a particular population density and territory quality, and to the pattern of resource depletion as more birds are added to a group's territory. At least up to a point, the optimum group size should be larger for higher quality territories. Where territory size indicates quality, this point will be reached when the area becomes too large for one group of birds to defend. Studies such as those of Ligon & Ligon (1990) on Green Woodhoopoes, Rabenold (1990) on *Campylorhynchus* wrens and Curry & Grant (1990) on Galapagos Mockingbirds found a positive relationship between territory size and group size while Vehrencamp (1978) found a negative relationship in Groove-billed Anis and Strahl & Schmitz (1990) found no relationship in Hoatzins. Territory size may not always be the best indicator of territory quality, especially if the habitat is heterogeneous. However, in relatively homogeneous habitats it can be difficult to know exactly what determines the quality of a territory and size may be the best available indicator.

Most studies define territory boundaries from observed interactions between different groups and, without saying how, estimate the size of the area defended (e.g. Galapagos Mockingbirds (Curry 1988), Hoatzins (Strahl 1988), Stripe-backed Wrens (Rabenold 1990), Green Woodhoopoes (Ligon & Ligon 1990), Yellow-billed Shrikes (Grimes 1980)). Some other studies use all observations of a group and draw a minimum convex polygon around the outer fixes (e.g. Groove-billed Anis (Koford *et al.* 1990), White-banded Tanagers (Alves 1990)) or divide the area into a grid and define the home range as the boundary around all the grid cells used (e.g. Red-throated Caracaras (Thiollay 1991)).

Other studies give territory sizes without stating how or what data were obtained and without stating how the sizes were estimated (e.g. Bushy-crested Jays (Hardy 1976), Southern San Blas Jays (Hardy *et al.* 1981), Brown Jays (Lawton & Guindon 1981)). All of these studies give vague estimates of territory or home range size but none relate the territory or defended area to the area actually used by each group (the home range) and very few attempt to estimate the home range area. Only the study of Red-throated Caracaras (Thiollay 1991) examined the pattern of usage of the home range.

Sophisticated methods have been developed for estimating home range size and usage patterns, mainly using radio-tracking data (Worton 1987, Harris *et al.* 1990). These have rarely been used in studies on birds and certainly not in any published studies of group-territorial birds. It is important in studies of group-territorial birds to determine the area actually used for all activities by a group and the pattern of usage, particularly when comparing groups of differing size and reproductive output.

I used radio-tracking to obtain data on movements of Chowchillas to examine home range size, core areas and usage patterns of two groups over 10 to 13 months and of five neighbouring groups in one short period. Because all members of a group usually stay together throughout the day, I was able to radio-tag one member of each group and locate each group with reasonable reliability. Radio-tracking allowed me to locate each group in such a way that fixes were independent both of the behaviour of the birds in the group and of the difficulties of observation in particular areas of the site.

7.2 Methods

In section 2.5.3 I described how I radio-tracked birds to obtain fixes. When using radio-tracking data in analyses of home range size and usage patterns it is important to ensure that successive fixes are independent. If fixes are too close together in time and the animals move little between fixes, autocorrelated data will result, giving poor estimates of usage patterns (Harris *et al.* 1990). I determined the appropriate time interval to obtain independent fixes by locating a radio-tagged bird every half hour one day, in the period 0730 to 1530, then selecting the fixes separated by different time intervals to determine which time interval gave independent fixes (Swihart &

Slade 1985). This involved calculating, for each time interval, the ratio of the mean squared distance between successive observations to the mean squared distance from the centre of activity, then comparing this ratio (t^2/r^2) to critical values given in Swihart & Slade (1985). Since acceptance of the null hypothesis is required to find the appropriate time interval, and since several tests must be done to find it, Swihart & Slade (1985) recommend using the critical value corresponding to alpha=0.25 for these tests. I assumed an eccentricity of e=1 since the lengths of the major and minor axes of the home range of Group 1 were virtually equal. The time interval which gave independent fixes was then used as the minimum time interval for all fixes used in analysing home ranges.

I also determined the minimum number of fixes necessary to give an accurate representation of the home range, initially by compiling cumulative plots of area enclosed by a minimum convex polygon around the fixes *versus* number of fixes (Harris *et al.* 1990) and determining where the curve started to level off. This gave a working estimate of about 30 fixes necessary to define a home range. After radio-tracking one group for a year and obtaining approximately 240 independent fixes, I used the method suggested by Harris *et al.* (1990) to calculate a home range asymptote. From the 240 independent fixes I selected 60 at random and calculated the size of the minimum convex polygon as each fix was added then plotted area *versus* number of fixes. Where the slope levelled off was selected as the minimum number of fixes necessary to estimate home range size and usage patterns.

I was able to radio-track five groups of birds for varying intervals in the period June 1991 to July 1992. Group 1 was tracked over the entire interval, Group 3 from October 1991 to July 1992 and groups 4, 5 and 6 from June to July 1992. I attempted to obtain at least 25, preferably 30 fixes each month for each group, distributed evenly throughout the day between 0700 and 1700 hours. Although it was often light for at least an hour outside these times, it was dim in the forest, making observations very difficult. The time period used encompassed the main activity period of the Chowchillas. Because of limitations due to transmitters not working or falling off I was not always able to obtain the required number of fixes per month or a completely even distribution over the time period. Chowchillas were equally active throughout the day, however, and time of day appeared to have little effect on the data collected. With a combination of radio-tracking and searching when transmitters were non-functional, I was able to obtain sufficient fixes to divide the data for Groups 1 and 3 into subsets to look at seasonal changes in home ranges size and usage patterns. In June-July 1992 I obtained sufficient data on all five groups to compare their home ranges and usage patterns for that period.

I investigated a variety of methods of analysing home ranges. These are reviewed in Worton (1987), Harris *et al.* (1990) and in the Ranges IV manual (Kenward 1990). The Ranges IV program was used for most of the analyses. All of the methods reviewed have positive and negative aspects; there is no "best" method. I chose the methods which appeared to have the fewest negative aspects and which best displayed the data. I used minimum convex polygons as one estimate of home range size. This is in some ways a poor estimate because it is based on outliers of the range and can include large areas never used, but it is the only method which really allows comparison with other studies. This is because most other studies of group-territorial birds, where they have indicated the method of estimating the home range or territory size, have used only this method. The other estimate of home range size that I used was the 95% isopleth of the utilization distribution from kernel analysis.

Kernel analysis gives a non-parametric estimation of the utilization distribution from a set of fixes (Worton 1989). The utilization distribution is a probability density function so, for example, the 95% isopleth from a utilization distribution represents where the animal was estimated to spend 95% of its time in the period of fix collection. The 95% isopleth was chosen as best representing home range size, rather than the 100% isopleth which tended to include large areas never visited by the birds. I estimated territory size as the area of the minimum convex polygon around all the fixes where I had observed the group giving territorial songs. This gave the best estimate of territory size as there were too few fixes to generate a utilization distribution using kernel analysis. I was only able to estimate territory size for Groups 1 and 3, although I also obtained some observations of locations of singing for other groups.

To investigate "core areas", or areas of concentrated use within home ranges, I used two different methods. From the utilization distributions produced by kernel analysis I examined plots of the increment in area *versus* isopleth value and determined the inflexion point of the curve. The isopleth value corresponding to this point gives a good representation of the core area of the home range (Harris *et al.* 1990). The second method involved examining the utilization distribution from a multinuclear clustering analysis. Multinuclear clustering starts with the two closest fixes and forms clusters based on nearest neighbour distances. Polygons are drawn to include increasing percentages of fixes as clusters are formed (Kenward 1990). Thus in the same way as for kernel analysis, a plot of the increment in area *versus* percentage of fixes included can be examined for the inflexion point (Kenward 1990).

7.3 Results

7.3.1 Determining home range size and core areas

To determine the time interval necessary to obtain independent fixes, I calculated t^2/r^2 for the time intervals 1 hour, 1.5 hours and 2 hours using the 17 fixes obtained at half-hourly intervals on the 26.6.91. These values were compared to the critical values given in Swihart & Slade (1985). Table 7.1 shows the results of these tests.

Table 7.1 Determination of the time interval for independence of fixes.

Time interval	No. of fixes	t^2/r^2	Critical value @ alpha=0.25	Conclusions
1 hour	9	1.3796	1.695	Not independent
1.5 hours	6	1.7284	1.640	Independent
2 hours	5	2.0951	1.614	Independent

Clearly fixes only one hour apart were not independent while those at least 1.5 hours apart were. All fixes used in subsequent analyses were at least 1.5 hours apart. Table 7.2 shows the number of independent fixes obtained for each group in the time periods used in the analyses.

Table 7.2 Number of independent fixes for each group.

Time period	(season)	Group 1	3	4	5	6
May '91 - July '91	(winter)	57	-	-	-	-
Aug '91 - Sept '91	(early dry)	59	-	-	-	-
Oct '91 - Nov '91	(late dry)	39	53	-	-	-
Dec '91 - April '92	(wet)	47	51	-	-	-
May '92 - July '92	(winter)	41	56	-	-	-
22.6.92 - 9.7.92		28	28	28	28	28

The seasonal divisions used are based on changes in temperature and rainfall as well as patterns of food availability (see Chapters 2 and 4). The wet season could not be subdivided because of insufficient data.

To determine the number of fixes necessary to define a home range I plotted area of a minimum convex polygon *versus* number of fixes (Figure 7.1). It is clear that about 30 fixes are needed to obtain a good idea of home range size.

To find core areas I plotted the increment in area *versus* isopleth value from both kernel analysis and multinuclear clustering (Figures 7.2 (a) and (b) respectively). These plots are of the mean values from the five home ranges determined in June-July 1992. From these graphs the 60% isopleths were chosen to represent the core areas of a home range.

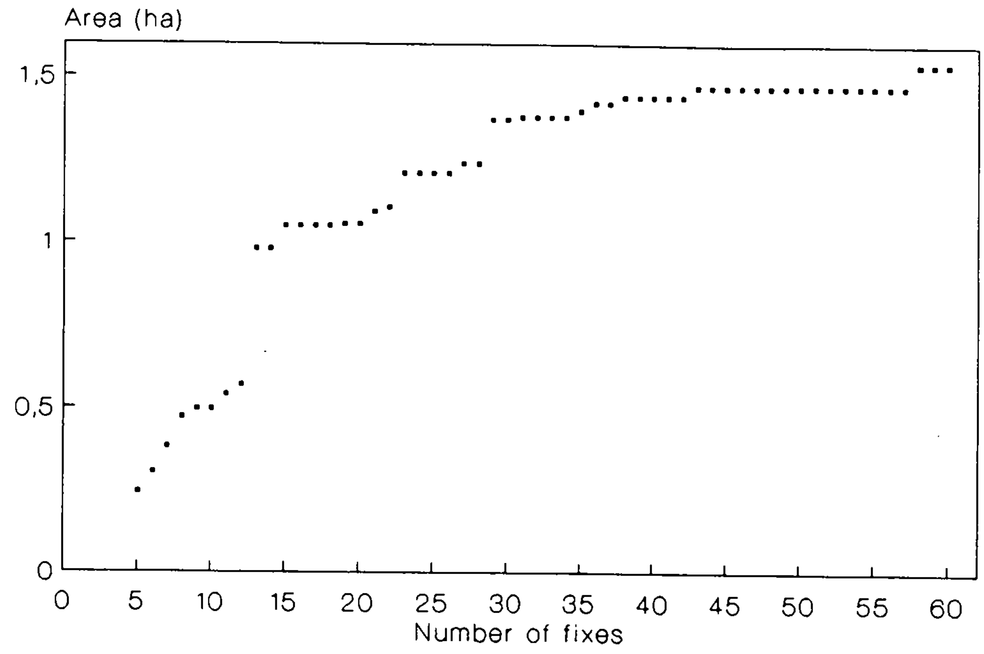


Figure 7.1 The increase in the area of the home range outlined by a minimum convex polygon around increasing numbers of randomly selected fixes of Group 1.

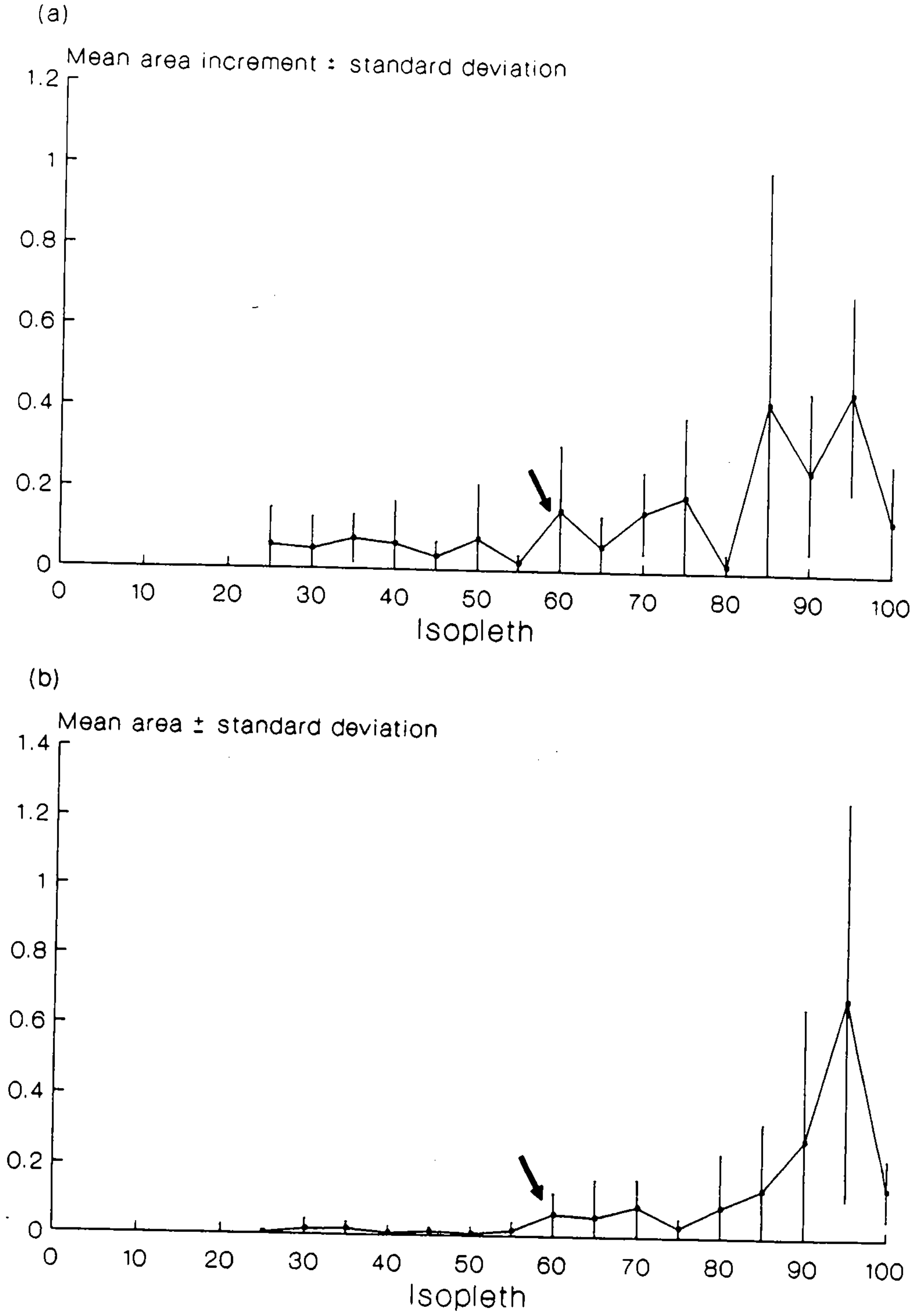


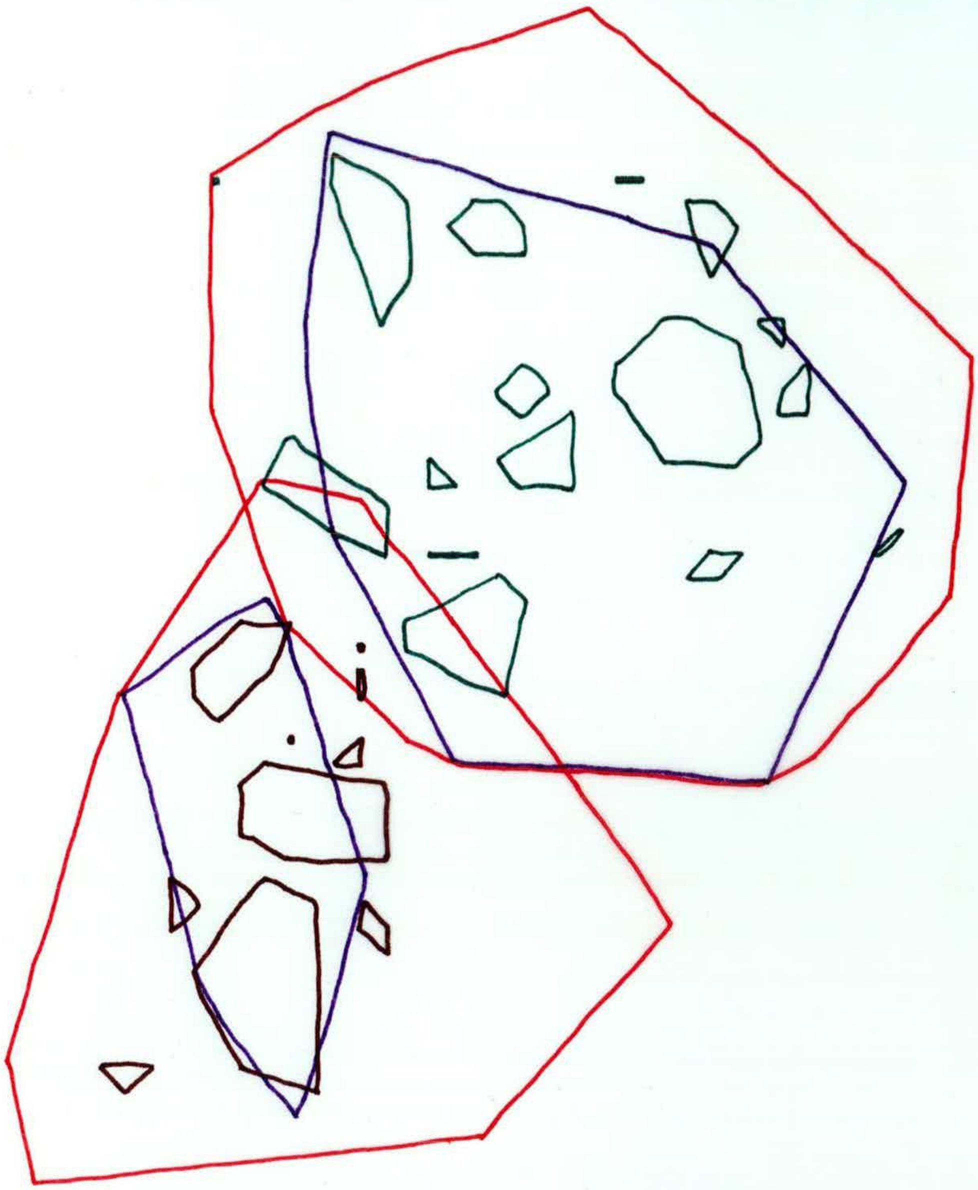
Figure 7.2 Mean (± standard deviation) increment in area corresponding to each isopleth value from (a) kernel analysis and (b) multinuclear clustering of five groups' fixes in June-July 1992.

In Figure 7.3 I have depicted the home range and core area from kernel analysis of all independent fixes for Groups 1 and 3. Overlayed are the minimum convex polygon around all the fixes, the territory, and the core areas from multinuclear clustering for both groups. The sizes of each of these areas are given in Table 7.3.

Table 7.3 Sizes of home ranges and core areas of two groups.

Area	Size (ha) Group 1	 Group 3
Kernel analysis home range	1.75	1.07
MCP home range	1.97	1.33
Territory	1.24	0.33
Kernel analysis core area	0.78	0.40
Multinuclear clustering core area	0.25	0.18

For Group 1, which consisted of three birds, I obtained 262 independent fixes and 20 observations of territorial calling (to determine territory size) while for Group 3, which consisted of a pair of birds, I obtained 160 independent fixes and 15 observations of territorial calling.



Overlay. Minimum convex polygon home ranges (red) and territories (blue) of Groups 1 and 3. Multinuclear clustering core areas of Group 1 (green) and Group 3 (black).

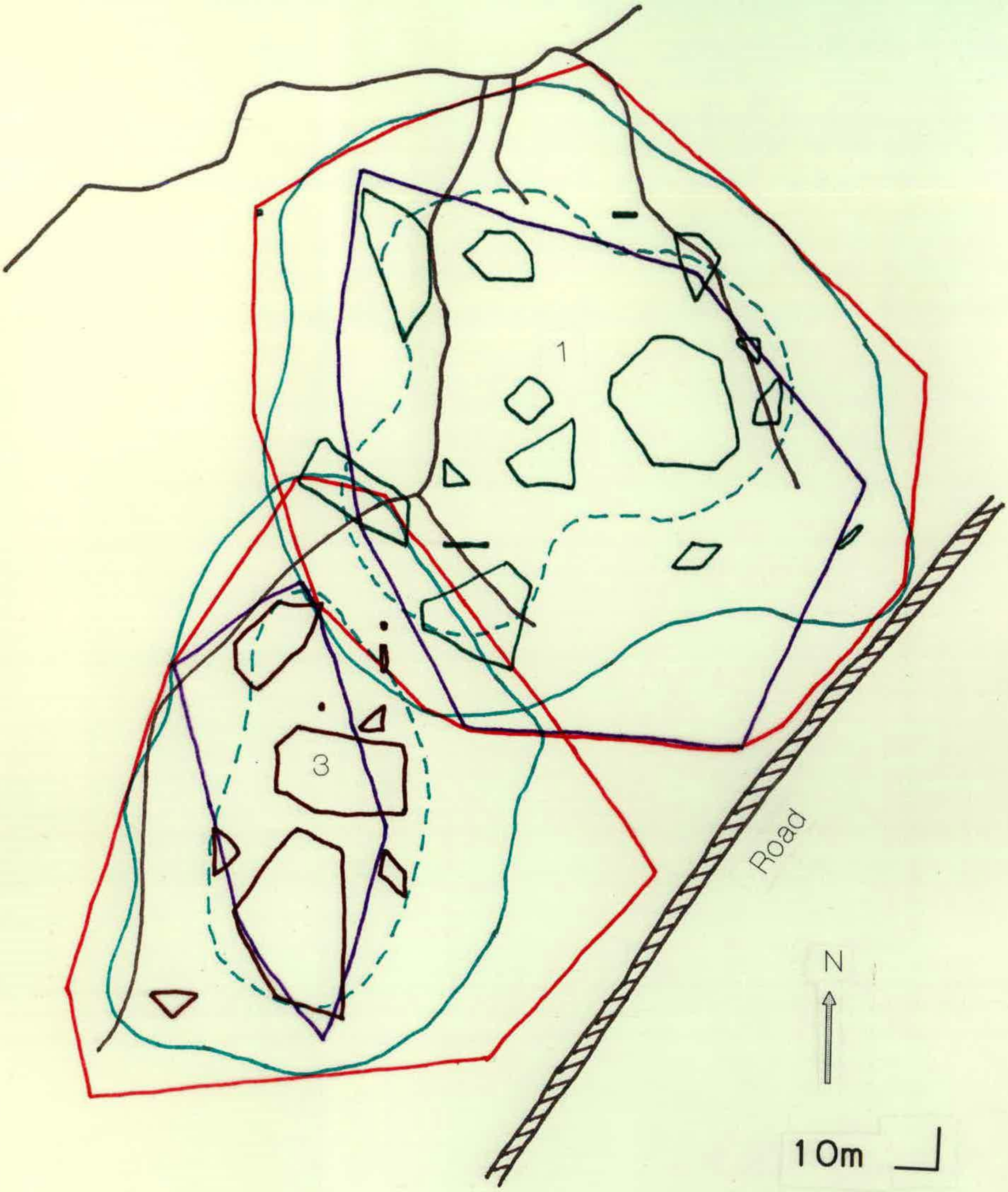


Figure 7.3 Kernel analysis home ranges (continuous green lines) and core areas (dashed green lines) of Groups 1 and 3. Black lines show gullies on the site.

Overlay. Minimum convex polygon home ranges (red) and territories (blue) of Groups 1 and 3. Multinuclear clustering core areas of Group 1 (green) and Group 3 (black).

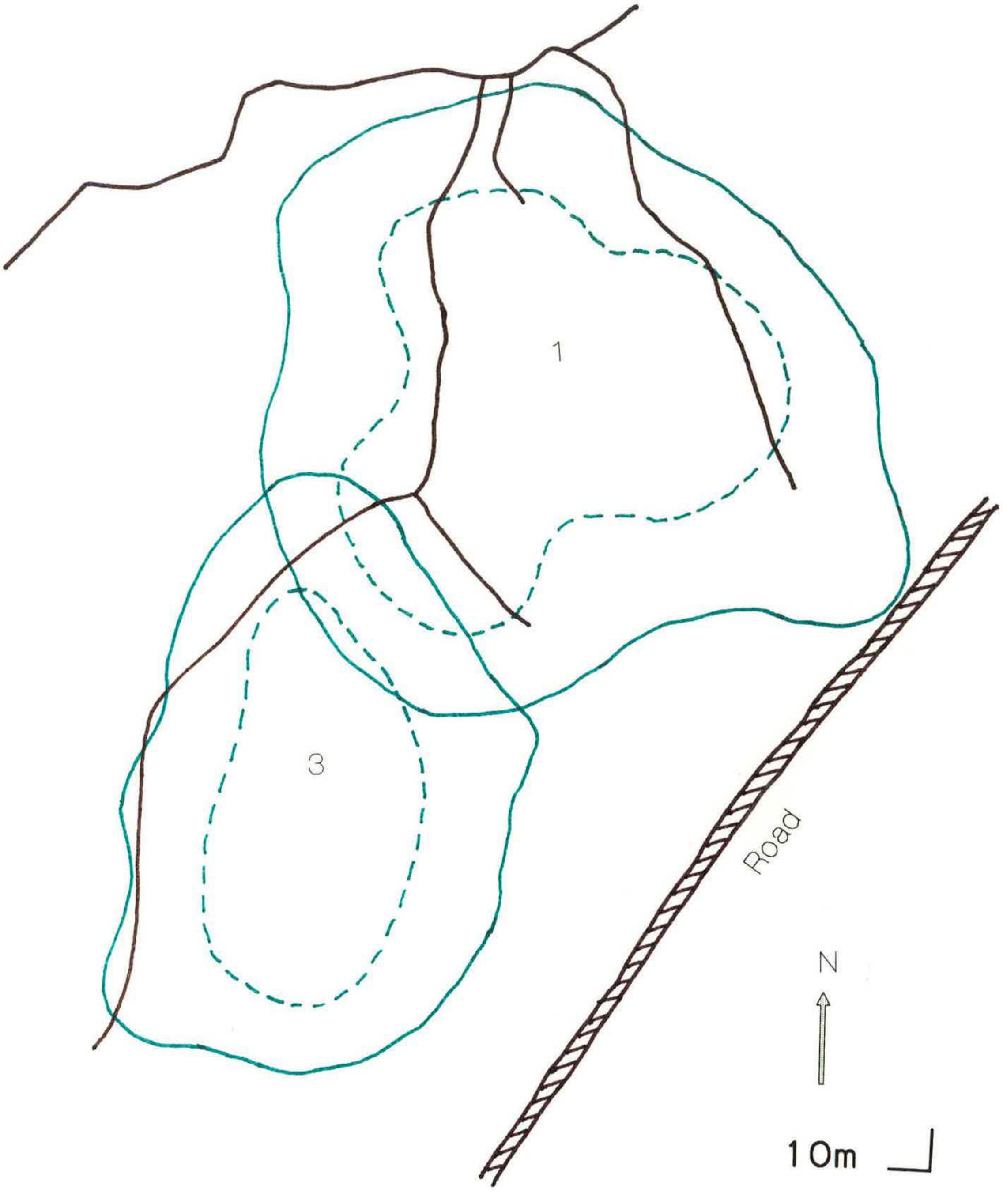


Figure 7.3 Kernel analysis home ranges (continuous green lines) and core areas (dashed green lines) of Groups 1 and 3. Black lines show gullies on the site.

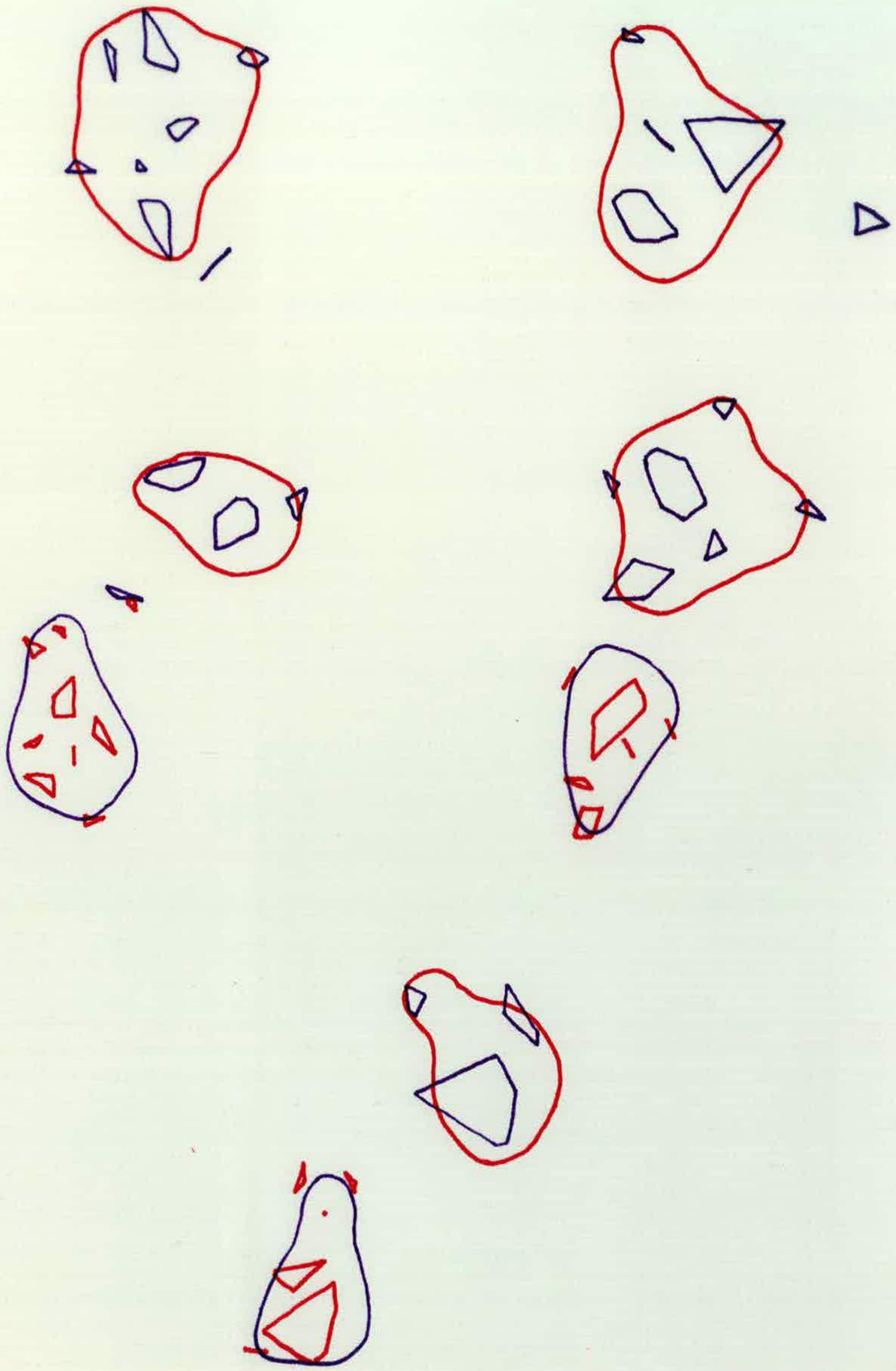
7.3.2 Seasonal changes in home range size and structure.

In examining seasonal changes I looked at home range size and location as well as size and location of core areas within the home range. Figure 7.4 shows the 95% isopleths from kernel analysis of the home ranges of Groups 1 and 3 during the different seasons. The overlay shows the core areas from the two different methods of analysis used. Table 7.4 gives the sizes of these areas.

Table 7.4 Home range and core area sizes (ha) for two groups in different seasons.

Season	Group	N	Home range (kernel)	Core area (kernel)	Core area (MNC*)
Winter '91	1	57	2.10	0.83	0.09
Early Dry '91	1	59	1.56	0.77	0.17
Late Dry '91	1	39	1.30	0.39	0.08
	3	53	1.03	0.46	0.05
Wet '91-'92	1	47	1.45	0.78	0.14
	3	51	0.79	0.38	0.08
Winter '92	1	41	1.34	0.50	0.16
	3	56	1.03	0.38	0.10

* MNC=Multinuclear clustering



Overlay. Kernel analysis core areas (red for Group 1 and blue for Group 3) and multinuclear clustering core areas (blue for Group 1 and red for Group 3) in different seasons.

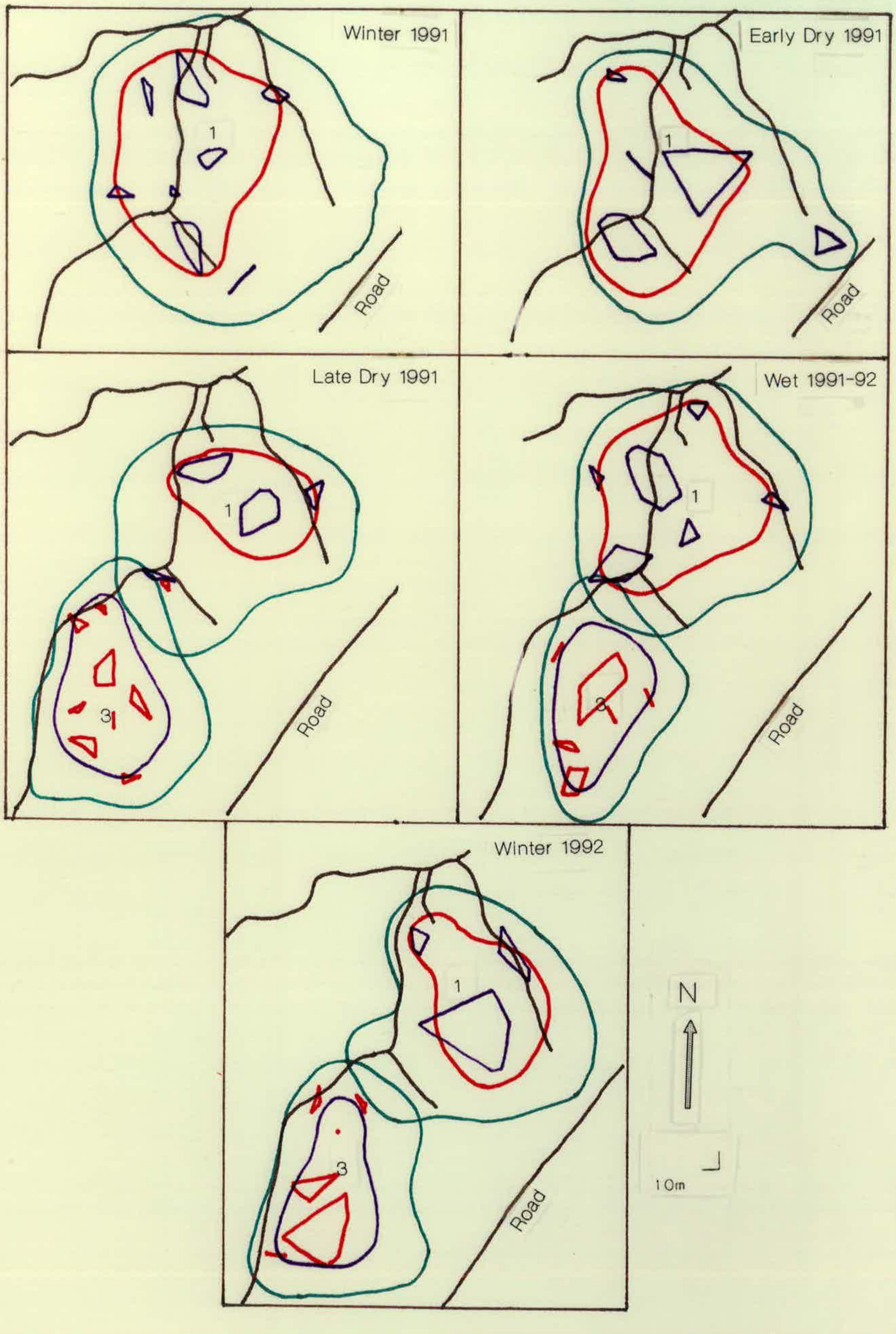


Figure 7.4 Kernel analysis home ranges (green) of Groups 1 and 3 in different seasons. Black lines show gullies on the site.

Overlay. Kernel analysis core areas (red for Group 1 and blue for Group 3) and multinuclear clustering core areas (blue for Group 1 and red for Group 3) in different seasons.

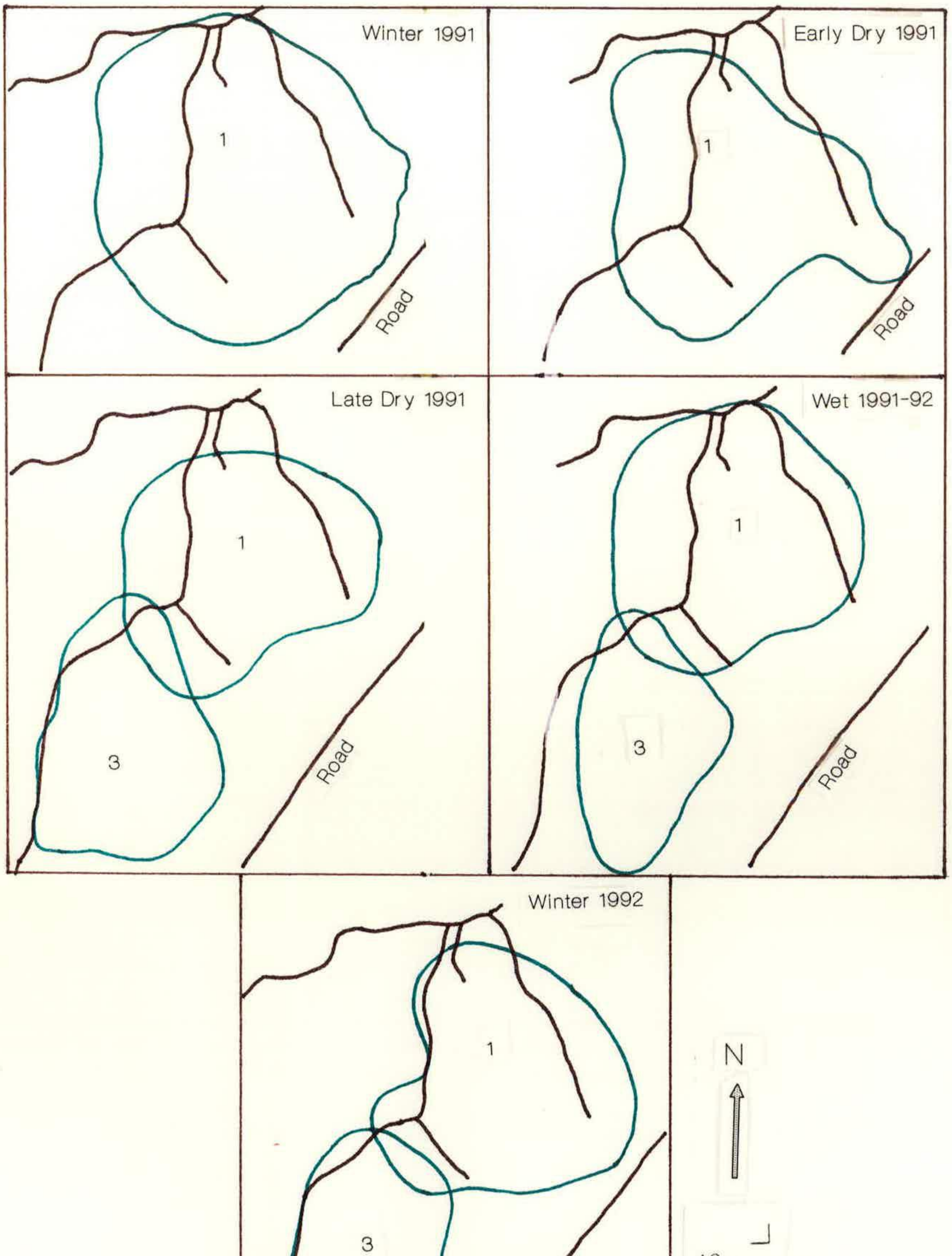


Figure 7.4 Kernel analysis home ranges (green) of Groups 1 and 3 in different seasons. Black lines show gullies on the site.

The two core area size estimates are quite different but the Figure 7.4 Overlay shows that they correspond quite well in location. The core areas of the two groups did not overlap at all; nor did the home ranges of either group encroach on the core areas of the other group (except very slightly in the wet season). Over the period studied there was little change in the location of each group's home range and only minor changes in the boundaries. These changes were at least partly attributable to sampling error. Significant shifts, however, occurred in the location of the multinuclear clustering core areas.

To examine these shifts in more detail, I estimated the amount of overlap in core areas over successive seasons and compared this to what would be expected by chance if the birds used core areas independent in location of those in the previous season. To obtain the areas expected to overlap by chance, I calculated CA1/THRA X CA2/THRA X THRA where CA1 and CA2 are the core areas in successive seasons and THRA is the total home range area (1.97ha for Group 1, 1.33ha for Group 3). This gave an expected area of overlap in hectares for each pair of seasons. Ranges IV provided estimates of the actual areas of overlap. Table 7.5 gives the observed and expected areas of overlap in core areas in successive seasons.

Table 7.5 Observed and (expected) areas (ha) of overlap in multinuclear clustering core areas in successive seasons for two groups of birds.

Successive seasons	Group 1				Group 3	
	Season				Season	
	Winter 91	Early Dry 91	Late Dry 91	Wet 91-92	Late Dry 91	Wet 91-92
Early Dry 91	**0.01 (0.008)**	-	-	-	-	-
Late Dry 91	0.002 (0.004)	**0.024 (0.007)**	-	-	-	-
Wet 91-92	0.004 (0.006)	0.02 (0.012)	**0.011 (0.006)**	-	**0.008 (0.003)**	-
Winter 92	0.01 (0.007)	0.052 (0.014)	0.02 (0.007)	**0.009 (0.011)**	0.012 (0.004)	**0.017 (0.011)**

Figure 7.5 shows the difference between the observed and expected values of overlap for successive seasons and seasons further apart in time.

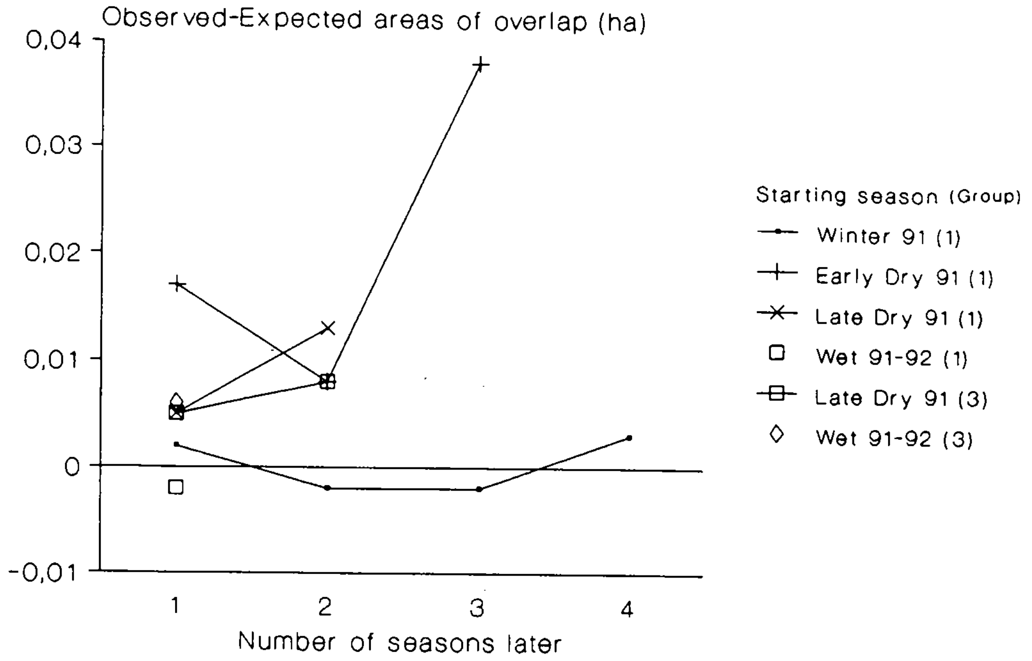


Figure 7.5 The difference between observed and expected areas of overlap in multinuclear clustering core areas in successive seasons for Groups 1 and 3. For example, the first '+' shows the observed minus expected area of overlap between the core areas of Group 1 in the Early Dry 1991 and the Late Dry 1991 while the second '+' shows the same overlap between the Early Dry 1991 and the Wet 1991-1992.

Apart from the interval Early Dry '91 to Late Dry '91 for Group 1, the overlap in core areas in successive seasons is little different from that expected by chance. Also, there is a slight tendency for the overlap to increase above that expected by chance as more time separates the seasons. This suggests that, generally, the birds tend to move away from the core areas used in previous seasons to concentrate more on less utilized areas, but that they may begin to return to the old core areas after three or four seasons (nearly a year later). The major exception was the interval Early to Late Dry '91 when Group 1 clearly continued to utilize much of the core area in the Late Dry that they had in the Early Dry.

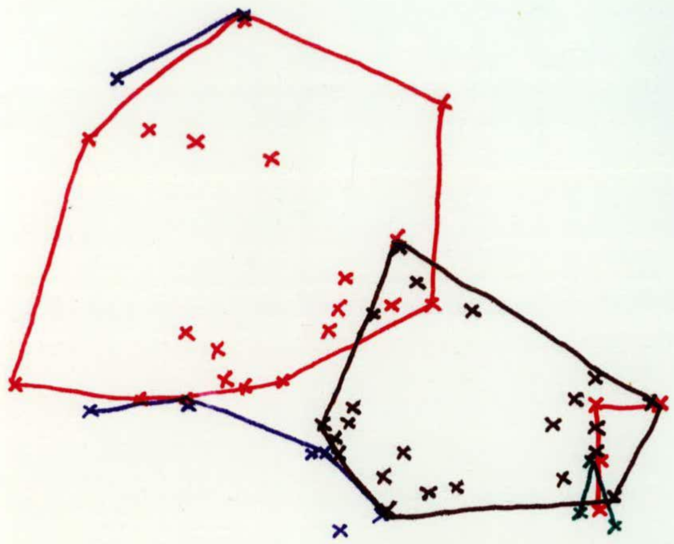
7.3.3 Home ranges and core areas of five neighbouring groups.

Figure 7.6 shows the home ranges estimated using kernel analysis of five neighbouring groups in June-July 1992. The first overlay (1) shows the core areas estimated using the two different methods. The second overlay (2) shows the minimum convex polygon home range of each group. A total of 28 fixes were obtained for each group in this period. Table 7.6 gives the sizes of each of these areas.

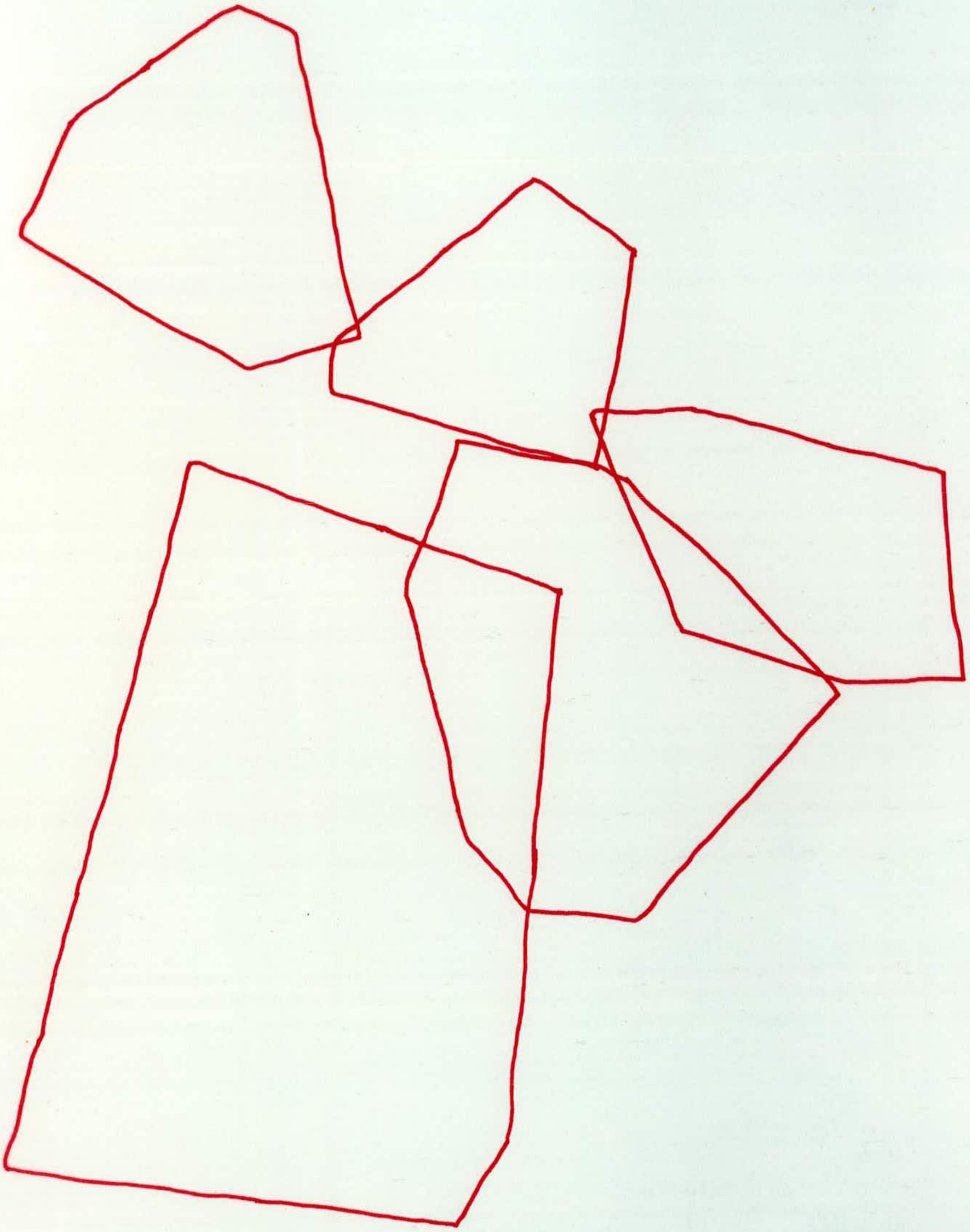
Table 7.6 Sizes (ha) of home ranges and core areas of five groups.

Group	No. of birds	MCP* (ha)	95% isopleth (ha)	Core area (kernel)	Core area (MNC#)
1	3	0.99	1.35	0.33	0.16
3	2	0.71	0.93	0.30	0.02
4	3	0.94	1.30	0.37	0.05
5	3	1.75	2.58	0.76	0.26
6	5	3.95	5.49	2.19	0.25

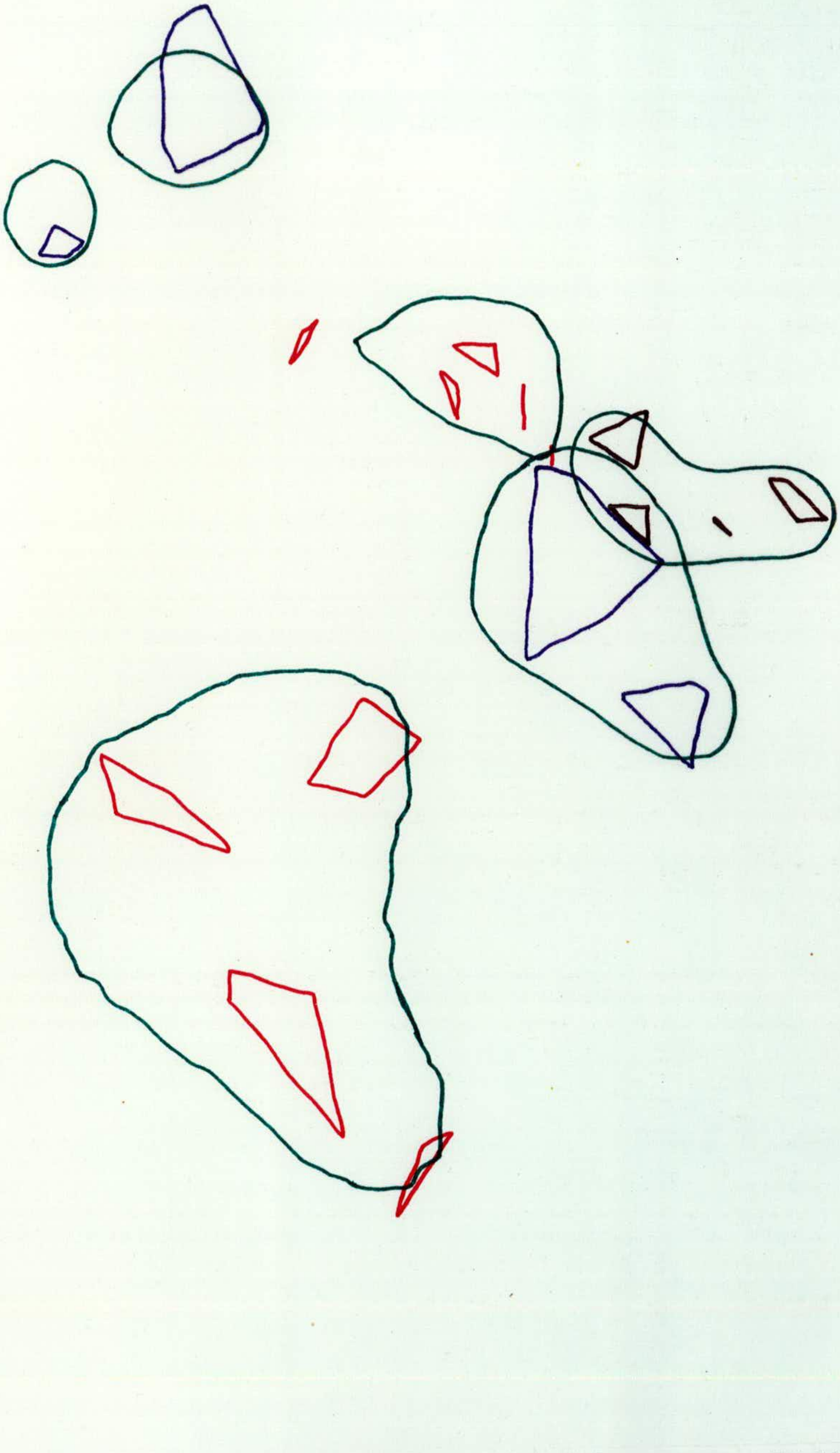
* MCP = Minimum Convex Polygon
\# MNC = Multinuclear clustering



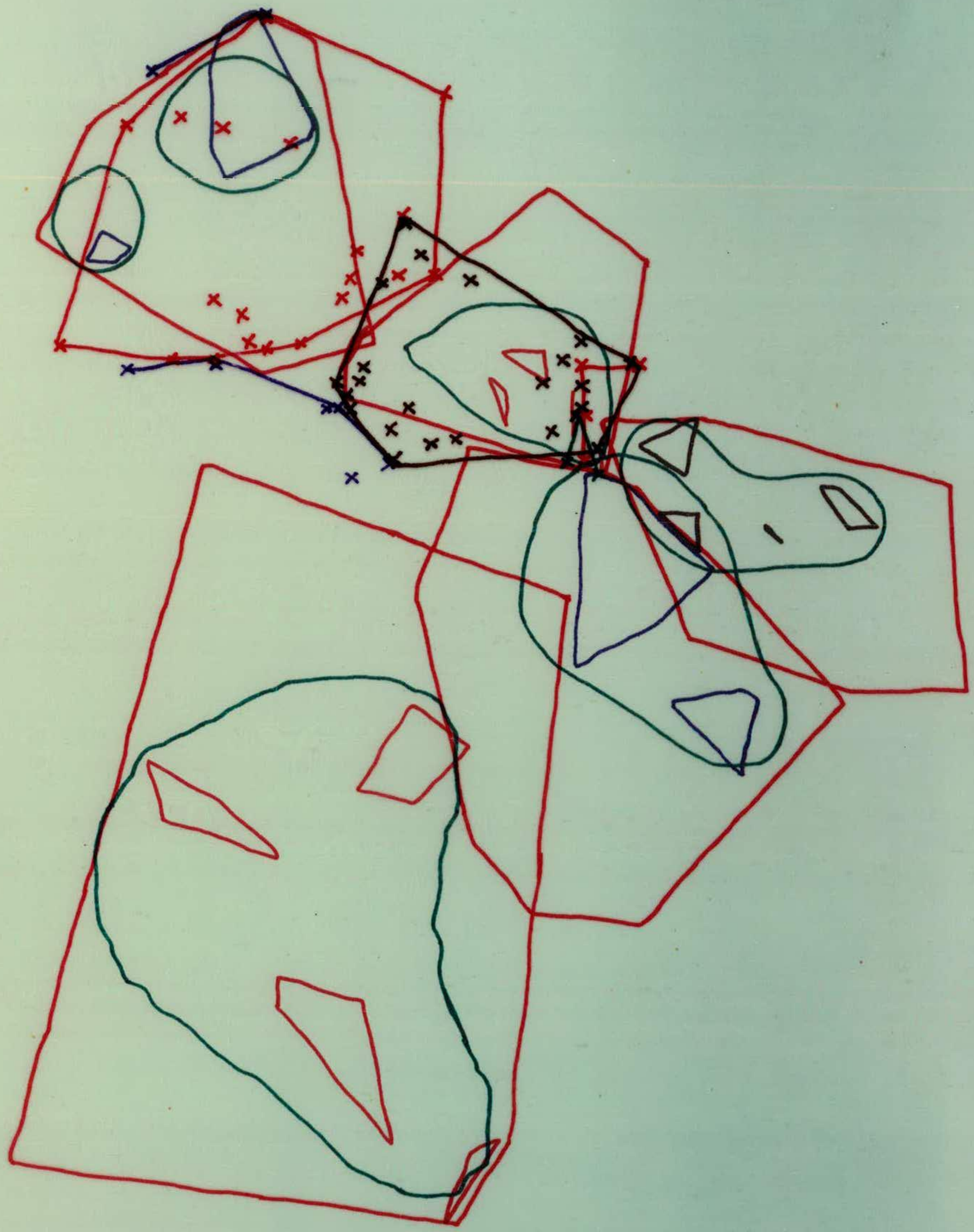
Overlay (3) Sites of territorial calling of six groups. Groups 1 and 4 (red), Group 3 (black), Group 5 (green), Groups 2 and 7 (blue).



Overlay (2) Minimum convex polygon home ranges of five groups.



Overlay (1) Kernel analysis core areas (green) of five groups. Multinuclear clustering core areas of Groups 1 and 5 (blue), Groups 3 and 6 (red) and Group 4 (black).



Overlay (1) Kernel analysis core areas (green) of five groups. Multinuclear clustering core areas of Groups 1 and 5 (blue), Groups 3 and 6 (red) and Group 4 (black).

Overlay (2) Minimum convex polygon home ranges of five groups.

Overlay (3) Sites of territorial calling of six groups. Groups 1 and 4 (red), Group 3 (black), Group 5 (green), Groups 2 and 7 (blue).

Figure 7.6 Kernel analysis home ranges (green) of five groups. Black lines show gullies on the site.

Overlay (1) Kernel analysis core areas (green) of five groups. Multinuclear clustering core areas of Groups 1 and 5 (blue), Groups 3 and 6 (red) and Group 4 (black).

Overlay (2) Minimum convex polygon home ranges of five groups.

Overlay (3) Sites of territorial calling of six groups. Groups 1 and 4 (red), Group 3 (black), Group 5 (green), Groups 2 and 7 (blue).

There is a significant positive relationship between group size and home range size estimated using either method (Spearman's Rho=0.9, N=5, p=0.05). Using the kernel estimate the mean home range size for groups of three birds was 1.23ha (N=3).

In Figure 7.6, Overlay (3) shows the sites of all instances of territorial calling for which accurate locations were determined. To each location I have assigned the group or two groups thought or known to be involved (not all occurred between marked groups of birds). Thus for Groups 1 and 3 I was able to draw territory boundaries while for Groups 2, 4, 5 and 7 I could only draw those boundaries bordering on the central groups. No instances of calling by Group 6 were observed.

In Figure 7.6, a large degree of overlap in the home ranges of neighbouring groups is evident. The only gap is between Groups 1, 3 and 6. This area was actually occupied by another group of four birds (Group 7) which I was unable to catch to radio-tag so I could not estimate their home range. Overlay (1) shows that there was some overlap in the kernel analysis core areas of neighbouring groups but none in the multinuclear clustering core areas. Between Groups 3, 4 and 5 there was some overlap of home ranges onto the core areas of neighbouring groups. The main area of overlap corresponded to a wide, flat gully area which remained damp but not wet throughout the year. Overlay (2) shows the close packing of the groups with the one apparent gap actually occupied by Group 7. The gaps along the edges of the home ranges of Groups 1, 3 and 4 were dry ridge areas along the edge of the road. Overlay (3) shows how the territories of adjacent groups overlapped very little but were closely packed.

7.4 Discussion

Radio-tracking proved to be a very useful tool in this study. It enabled me to find target birds, and the groups to which they belonged, far more often than was possible simply by searching for such inconspicuous birds in the rainforest habitat. It also provided sufficient data for some quite sophisticated methods of analysing home ranges and usage patterns. Previous studies of group-territorial birds have generally only mapped territories, rather than attempting to determine the space actually used by a group of birds. This data set could be used to compare territory estimates with other estimates of space use, and to demonstrate how different analyses may show different aspects of space use patterns.

The minimum convex polygon home range represents the extremes of each group's range while the kernel analysis home range represents the area within which each group spends virtually all of its time. The territories represent the areas defended from other groups and show little overlap. The kernel analysis core area represents the central part of a group's home range, within which it spends 60% of its time, and which overlaps very little onto the home ranges of neighbouring groups. There was some correspondence between the kernel analysis core areas and the defended territories, suggesting that the birds may have mainly defended that part of their home range which only they used. The multinuclear clustering core areas seem to represent quite well those areas favoured for foraging. Most of these lie within the kernel analysis core area. Each group has its own favoured foraging areas which are rarely encroached upon by other groups. The only area in which encroachments were observed was a gully which appeared to be particularly good for foraging.

The analysis of seasonal changes in the home ranges and usage patterns of two groups showed that home ranges were quite stable in location over time. Minor shifts in boundaries probably reflect differing foraging needs at different times of the year. Earlier (Chapter 6) it was demonstrated that Chowchillas select places to forage based on food availability and that sites vary in food availability over time (Chapter 4). Thus it is necessary for the birds to shift their foraging efforts to track these shifts in food availability.

It might also be expected that depletion of invertebrates would occur with excessive utilization of particular areas. From the analysis of seasonal changes in core areas it appears that Chowchillas tended to shift their favoured foraging areas from season to season, perhaps in response to this depletion effect. The exception was in the early to late dry season when Group 1 tended to keep concentrating on the same favoured foraging areas. This may have been because at this time of year food availability was low and these core areas, which were mainly on gullies and slopes which retained some moisture, were the best areas for foraging, despite the effect of depletion.

The fact that there was always some overlap of core areas from season to season suggests that there were some parts of the home range which were always good foraging spots and could be relied upon by the birds at any time of the year. Possibly the time scale on which the seasons were divided was longer than the life cycles of many of the invertebrates eaten so depletion might not be a big factor over these time intervals. My observations suggested that on a shorter time scale Chowchillas tended to avoid areas in which they had recently foraged, apart from particularly rich areas, with deep, moist leaf litter. The fact that the birds had favoured patches to which they returned at any time of the year indicates that they did learn the location of patches, as suggested in the previous chapter. Presumably these favoured patches were areas of high food availability; certainly they had the attributes of good quality patches - in terms of location, quantity and moisture content of the leaf litter. These favoured foraging areas were not sampled to compare food availability in these and other, less favoured areas, mainly because I only determined the location of these core areas after finishing data collection for each season. By then it was too late to sample food availability since food availability patterns varied over time (Chapter 4).

Home range size was positively correlated with group size in this study. This is a common finding in studies of group-territorial birds. An exception is the Groove-billed Ani in which Vehrencamp (1978) found a negative relationship between group size and territory size across habitats ranging from pasture to swamp. However, within the pasture habitat, Koford *et al.* (1986) found a significant positive relationship between group size and territory size as well as other measures of territory quality. Thus it is apparent that within relatively homogeneous habitats territory size usually increases with group size.

Home ranges of Chowchilla groups were estimated from the minimum convex polygon method to be 0.7 to 4.0ha in size. This estimate is probably the one most comparable to estimates of home range/territory size from other studies of group-territorial birds in the tropics which I have summarized in Table 7.7. I have also noted how the estimates were made.

Table 7.7 Home range estimates of group-territorial birds in the tropics.

Species	Group size Mean (range)	Home range size (ha) Mean (range)	Determined how?*	References
Galapagos Hawk	3.1 (2-6)	Not given	Territorial interactions	Faaborg & Bednarz (1990)
Red-throated Caracara	5.97 (3-9)	396 (One 450 group)	Grid cells used MCP (all obs.)	Thiollay (1991)
Groove-billed Ani	4.0 (2-8)	3.3 (1-10)	MCP (all obs.)	Vehrencamp (1978), Koford et al. (1990)
Hoatzin	3.0 (2-8)	(0.1-0.3)	Territorial interactions	Strahl & Schmitz (1990), Strahl (1988)
Green Woodhoopoe	4.8 (2-15)	80 (26-133)	Territorial interactions	Ligon & Ligon (1990)
Grey-backed Fiscal Shrike	5.3 (2-11)	Not given	Territorial interactions?	Zack (1986)
Yellow-billed Shrike	12 (6-25)	16.6 (10.6-27.1)	Territorial interactions	Grimes (1980)
Stripe-backed Wren	4.6 (2-10)	(0.3-3.6)	Territorial interactions	Rabenold (1990)
Bicolored Wren	2.2-3 (2-7)	1.3-4.3	Territorial interactions	Rabenold (1990)
Galapagos Mockingbird	4.2 (2-12)	0.94 (0.1-3.5)	Territorial interactions	Curry & Grant (1990)
Rufous Babbler	4 (1-10)	4 (One group)	All obs.	Bell (1982)
White-banded Tanager	3.0 (2-4)	4.3 (One group)	MCP (all obs.)	Alves (1990)
White-browed Sparrow Weaver	4.9 (3-7)	(0.36-0.43)	Total area occupied/ no. of groups	Collias & Collias (1978a)
Beechey Jay	3.4 (2-5)	25 (1 group) (18-43)	All obs. Area occupied/no. of groups	Raitt & Hardy (1979)
Bushy-crested Jay	11 (1 group)	3.9 (2.5-7.1)	Not stated	Hardy (1976)
Nelson San Blas Jay	(5-6)	3.1 (One group)	All obs.	Hardy (1976)
Southern San Blas Jay	(13-26)	Not given	All obs.?	Hardy et al. (1981)
Brown Jay	7.2 (6-10)	10-20	Not stated	Lawton & Guindon (1981)
Green Jay	6.1 (4-10	(42-67)	All obs. and territorial interactions	Alvarez (1975)

* MCP = Minimum Convex Polygon estimate

It can be seen that territory size estimates range from < 1ha for Hoatzins and Galapagos Mockingbirds to 80ha for Green Woodhoopoes and 450ha for Red-throated Caracaras. My estimates for Chowchillas fall within this range.

I found a high degree of overlap in the home ranges of neighbouring groups of Chowchillas. The territories were virtually non-overlapping, consistent with other studies of group-territorial birds, but the space actually used included significant overlap. This probably reflects the way in which I collected that data on space use. Most of the studies summarized in Table 7.7 used territorial interactions to define territory boundaries so they could not estimate the space used by each group if this was different from the defended area. Two studies estimated territory size by dividing the total area occupied by all groups by the number of groups. Clearly, using this estimate, it is impossible to ascertain how much space is actually used by each group. Only the studies on Red-throated Caracaras, Groove-billed Anis and White-banded Tanagers stated how the boundaries were drawn around observations to define the home range. In all the other studies the boundaries may or may not have included or excluded areas that the birds used.

Ovenbirds, which are similar to Chowchillas in that they are forest-dwelling and forage on the ground but differ in being solitary and setting up territories only in the breeding season, defend territories which are only exclusive with respect to singing. Foraging occurs outside the territories and foraging areas of neighbouring birds overlap (Zach & Falls 1979). It is not surprising that in habitats such as rainforest, with low visibility, and particularly with small groups of birds which cannot always be patrolling the boundaries, that some overlap can occur. Certainly I have seen a group of birds encroaching on a neighbouring group's territory when I (and probably the birds) knew that the resident group was across the other side of the home range, out of sight. If the encroaching group was detected, however, the resident birds would chase them out from within the territory area but might then let them forage nearby in the area of overlap between the home ranges.

The degree of habitat saturation shown in this study for Chowchillas is consistent with most other studies of group-territorial birds. In fact, habitat saturation plus high survivorship may be important factors resulting in the formation of group-defended territories (Brown 1987a). If the habitat is fully occupied and young birds cannot find vacant territories left by dead birds, they could be forced to stay on their parents' territories or join other birds to form groups.

CHAPTER 8
SOCIALITY

8.1 Introduction

In this chapter I discuss group structure and dynamics, and the extent of cooperation in various activities by Chowchillas.

Group composition in group-territorial species of birds in the tropics varies widely. In a number of species most groups consist of a behaviourally monogamous pair plus a variable number of non-reproductive helpers (e.g. White-banded Tanagers (Alves 1990), Green Woodhoopoes (Ligon & Ligon 1990), Grey-backed Fiscal Shrikes (Zack 1986), Yellow-billed Shrikes (Grimes 1980), Stripe-backed and Bicolored Wrens (Rabenold 1990), White-browed Sparrow Weavers (Collias & Collias 1978a, Lewis 1982a), Beechey Jays (Raitt & Hardy 1979), and Green Jays (Alvarez 1975)). In the Galapagos Hawk groups are polyandrous, consisting of a single female and 1-5 males (Faaborg & Bednarz 1990) whereas in Groove-billed Anis up to four mainly monogamous pairs may occur in one group and all use the same nest with a variable number of non-reproductive helpers (Koford *et al.* 1990). Galapagos Mockingbirds have variable group compositions. Groups contained up to four breeding females and these were usually behaviourally monogamous and nested separately. However, some males had more than one mate and these females often nested jointly. Some individuals were breeders at one nest and helpers at another, others helped at one or more nests and some were neither breeders nor helpers (Curry & Grant 1990).

Groups tend to be stable over time in most tropical group-territorial species. High survival rates, low reproductive rates and low rates of emigration and immigration all contribute to this. An example of this is seen in the Galapagos Hawk. Once a group formed in this species, the only changes that occurred were due to the deaths of individual members. Only when all males or the female died were replacements added to the group. Young birds were expelled a few months after fledging (Faaborg & Bednarz 1990). Green Woodhoopoes, in contrast, have much less stable groups. This is probably due mainly to the relatively high mortality in this species (Ligon & Ligon 1990).

Green Woodhoopoes frequently moved between groups, usually after the death of one or both of the breeders or when a vacancy occurred in a nearby high-quality territory (Ligon & Ligon 1990).

I have already discussed the extent of cooperative behaviour in tropical group-territorial species in Chapter 1. Most importantly, it was seen that all of them cooperated in breeding. All other group-territorial species also breed cooperatively (Brown 1987), except possibly the Australian Magpie (Veltman 1989).

8.2 Methods

Data on the group structure and dynamics of five Chowchilla groups come from 284 observations of marked individuals in Group 1, 164 similar observations of Group 3, 35 of Group 4, 35 of Group 5 and 28 of Group 6. Two other unmarked groups were observed occasionally. Observations of Group 1 extended from August 1990 to August 1992 while observations of Group 3 extended from October 1991 to August 1992. The other three groups were only observed in June-July 1992 so I have little information on group dynamics in these groups.

Marked individuals and known groups were checked occasionally until February 1993, to obtain estimates of survival and reproductive output.

Data on the extent of cooperation in various activities come from all the observations of groups plus observations at and near three nests which hatched young.

8.3 Results

8.3.1 Group structure and dynamics

Table 8.1 shows the composition of seven groups in July 1992.

Table 8.1 Group composition of seven groups of Chowchillas.

Groups	Number of females	Number of males	Group size
3	1	1	2
1,4,5	2	1	3
2,7	2	2	4
6	3	2	5

One of the females in Group 6 had only just moulted into adult plumage (and was therefore approximately one year old - Les Moore, pers. comm.). All of the other birds were adults. The most common group sizes in the area surrounding my site were three and four adults.

Groups 1 and 3, for which I have the longest records, were relatively stable during the study. Figure 8.1 shows the changes in Group 1 over the two year period of observations.

```
Date:  Aug   Oct   Jan   May   Jun   Nov   Aug
       1990        1991                    1992
YM1    *-------------------T
OF2    *-------------------------------------+
WF3    *-------T
RM12                           *-------------+
UBF    +     +     +           +------?
YF8                                  *-------+
```

Figure 8.1 Changes in the composition of Group 1 between August 1990 and August 1992. *=First banded, T=Disappeared, +=seen.

OF2 was a member of the group throughout the period. YM1 was the first bird banded in the group. He was last seen on 22/5/91. RM12 was banded 12 days later and had apparently taken over the position of YM1 who disappeared. RM12 then remained with the group for at least 14 months. WF3 was only seen with the group for two months before disappearing in early October 1990. An unbanded female was seen with the group occasionally in the months August 1990 to January 1991. From June 1991 to November 1991, an unbanded female, possibly the same one, was always seen with the group. She was banded as YF8 in November 1991 and remained with the group for the rest of the period. Until June 1991 she may have been a wandering bird, looking for a position since I also saw an unbanded female in neighbouring Group 2's home range which was most likely the same bird. I suspect that the female which became YF8 did not join Group 1 full-time until after WF3 disappeared. Thus Group 1 consisted of three birds virtually throughout the two year period, and disappearing birds were replaced by others of the same sex. At least RM12 and OF2 were still part of Group 1 in February 1993. Group 1 did not appear to attempt nesting in the period August 1990 to July 1992 and did not successfully fledge any young in the period July 1990 to February 1993.

In Group 3, two unbanded birds were first seen in August 1991. They were banded, as YM13 and WF14, in early October 1991 and were seen as a pair right through to August 1992. This pair were still Group 3 in February 1993 and they fledged a chick in early 1993. In Groups 4 and 5 the birds were first counted in November 1991 and each had one identifiable female. In each group the other two birds were a male and a female. The compositions of these groups stayed the same right through to August 1992, the other members of each group being banded in June 1992. The only other change in group composition that I observed was between Groups 6 and 7. From October 1991 I observed that Group 7 consisted of four adults plus a juvenile. In June 1992 I banded a female with traces of juvenile plumage in Group 7's home range (presumably the juvenile I had observed earlier). Immediately after this she moved to neighbouring Group 6 and stayed with them through July.

In the year to June 1991 observations of Groups 1, 2 and 7 suggested that only Group 7 successfully fledged a chick. In the year to June 1992 no chicks were fledged in Groups 1, 3, 4, 5 or 7 although Group 4 nested unsuccessfully. Between July 1992 and late February 1993 Groups 2 and 3 but not Group 1 successfully fledged chicks. Thus reproductive rates were very low (~0.27 fledged young/group/year or ~0.09/individual/year). Adult survival rates, however, were high. Two marked birds disappeared and were presumed dead in the first year after they were banded. Eight other birds survived at least a year after banding and two of these survived at least two years after banding. The annual adult survival rate from these data is ~86%.

8.3.2 Cooperative behaviour

(a) Cooperation in foraging

Generally all members of a group foraged together throughout the day. Of 284 records of Group 1, at least 161 included all birds in the group. Similarly for Group 3, 161 of the 164 records included both members of the group. On most occasions when I did not record all of the group the bird(s) were probably out of sight rather than absent. However, on a few occasions the groups definitely did split up.

In Group 1 I observed YM1 foraging by himself once and the unbanded female was seen by herself twice, rejoining the group later in the day. In Group 3 I once observed YM13 foraging by himself. A few minutes after I found him, he called quietly and a response was heard from nearby. WF14 was foraging 20-25m away and YM13 then rejoined her and they continued foraging together. In the larger groups I sometimes observed a pair of birds (male and female) foraging together, apparently apart from the rest of the group.

As noted in Chapter 3, foraging birds use quiet contact calls and stay close together but do not interfere with each others' foraging efforts. Because they stay close together, young birds have the opportunity to find good patches to forage in by foraging in the same area as more experienced birds. Their diet and foraging methods are not conducive to cooperation in catching prey or sharing prey items.

(b) Cooperation in territory defence

In all territorial interactions that I observed, all birds in each group became involved. These interactions generally began when two or three foraging groups encountered each other near the common boundary of their home ranges. On the

18/12/91 I observed an interaction between Groups 3, 4 and 5 in the area where their three home ranges overlapped. Both birds in Group 3 were seen calling, as well as at least two birds from each of the other groups. At one stage YM13 and the male from Group 4 stood on the ground about 20cm apart, facing each other, and took turns calling loudly while other birds from each group called from further back. This face-to-face calling was also observed on other occasions between two males and between two females but not between a male and a female. On the 11/12/91 when I observed an interaction between Groups 1 and 7, two females called face-to-face and the encounter ended when the females flew at each other then separated. On a few other occasions I also observed physical attacks and heard scufflings of birds fighting on the ground.

Briefer interactions with little territorial calling also occurred. Often when one group was discovered by another within its home range the intruding group was chased a few metres away with a few bursts of territorial calling and a lot of "flying" calls. Both groups then returned to foraging, often only about 20m apart.

During most territorial interactions members of a group took turns in calling. Usually only one or two members of a group were calling at any one time, while the other members foraged and gave occasional "flying' calls.

Territorial calling also occurred at dawn but did not always involve interactions between groups. On the 4/10/90 I observed Group 1 at dawn. I first saw the group calling together on the edge of the road which formed one boundary of their home range. No other groups were calling nearby. About 15 minutes later I saw one of the females of the group, apparently by herself, calling $\simeq$40m further up the road at a 'corner' of the home range, again without any other groups nearby. Thirty minutes later this female was again foraging with the group. It appears that at dawn the groups may sometimes split up and different birds go to different parts of the boundary to declare the territory.

(c) Cooperation in breeding

As noted in Chapter 3, only single females were seen attending each of the three nests observed during the incubation and nestling stages. Also, only a single female was observed feeding the recently fledged chick that I watched for 2.5h in

September 1991. Unfortunately I was unable to obtain any other observations of fledged chicks because they all disappeared. Thus no cooperation in breeding was observed up to the time of fledging, and may not have occurred after fledging.

One of the nests observed belonged to Group 4, consisting of three birds, while the other two nests belonged to groups of four birds off my site. During the nestling stage the male of Group 4 and one of the males at one of the other nests were often seen near the nests and fed the breeding females on occasion. The other members of the groups were never seen at the nest or with the breeding females. At the third nest the breeding female was found on five occasions away from the nest; each time she was foraging by herself. The other members of the group were seen twice foraging near the nest without the breeding female but did not visit the nest.

In one of the groups of four birds off my site I suspect that both pairs in the group bred independently. I banded the chick in the nest under observation and a few days after it fledged I saw another unbanded chick with an adult pair within $\simeq$10m of the nest site. The banded chick was caught with an adult male a few days later beyond where the unbanded chick was seen (Andrew Dennis, pers. comm.) so apparently both pairs of adults and both chicks occupied the same home range. I was unable to track the group down again to determine when (and if) the two pairs reunited later.

8.5 Discussion

Chowchilla groups were stable in size and composition. Of course, this study was much shorter than most studies of group-territorial birds and several more years of data would be needed for comparisons with these studies. Reproductive rates were very low. It is possible that birds on my site did not attempt nesting because of my presence and my activities in catching and locating them regularly. Some birds in groups off my site did nest successfully in this period. However, others did not, so interference effects are unlikely to be wholly responsible for this low reproductive rate. Survival rates were high, and comparable to survival rates of other group-territorial birds in the tropics (see Table 1.2 in Chapter 1). My survival rate estimate is likely to be biased in several ways. The two birds that disappeared early on may have been predated because of their wing-tags which made them highly visible. Several birds were banded and not seen again more than a few months later. These were not counted as they could have been still alive but not seen (they were in groups I was not very familiar with for long periods of time). They could, however, have died. I also did not count one bird which died about three months after banding because the radio-transmitter may have been involved (see Section 2.5.4). Also, a number of birds were alive for at least several months more than the one or two years assigned to them. The net result of all these biases was probably that I underestimated survival rates.

A few instances of movements between groups were observed, in one case by a bird which was just one year old. Thus young birds do not necessarily stay with their parents, helping them to raise more young, until they can inherit the territory or find a breeding vacancy elsewhere, as occurs in most other group-territorial birds. Cooperation in foraging may benefit young and inexperienced birds while cooperation in territory defence should benefit all group members. The benefits of cooperation in breeding experienced by most other group-territorial birds must be outweighed by the costs in Chowchillas.

CHAPTER 9

SONGS

9.1 Introduction

Chowchillas sing at dawn and sometimes at dusk on their territories and also during the day in territorial interactions with neighbouring groups. Singing occurs daily year-round although it appears to occur less frequently and in shorter bouts during the wet season. Singing is likely to function more in territorial defence than as a mate attracting mechanism (Catchpole 1982), especially given that Chowchillas appear to form permanent pair-bonds and both sexes sing.

All members of a group sing during dawn sessions and in territorial interactions. I cannot say whether or not they can be considered as a duetting species, however. Farabaugh (1982) suggested that overlapping bouts of song be considered as a duet if: (a) overlap of songs between individuals is high; and (b) song bouts of different individuals are highly organized with respect to each other. Chowchilla songs are very complex and singing individuals remain close together so I was never able to separate song bouts when more than one individual was singing to see if they were coordinated. My impression is that they are not a duetting species. However, more study of this is needed and certainly Chowchillas fit all the other common characteristics of duetting species - having prolonged and probably monogamous pair-bonds, year-round territoriality, and occurring in the tropics (Farabaugh 1982). The fact that members of a group sing together at dawn when they are not involved in territorial interactions, suggests that the group-singing may play a role in maintaining group cohesion (Farabaugh 1982).

Chowchilla songs vary from place to place, both on a small scale (Cliff & Dawn Frith, pers. comm., Mike McGuire, pers. comm.) and on a larger scale (pers. obs.). Many bird species show both micro- and macro-geographic variation in their songs (Mundinger 1982). Microgeographic variation is often in the form of song dialects which are learned song traditions shared by a local population of birds (Mundinger 1982). Most birds with song dialects probably learn them early in life although they may have a genetic template to direct what is learnt

(Kroodsma 1982).

Song dialects can have important consequences for population genetic structure (Baker 1982). These consequences depend on several factors (Baker 1982):

(a) Dispersal - Baker & Mewaldt (1978) found less dispersal of White-crowned Sparrows across dialect boundaries than would be expected by chance, while Jenkins (1977) found that dispersing male Saddlebacks usually moved away from their natal dialect area and learned the dialect of the area to which they moved. Thus song dialects may influence dispersal to either promote or lessen gene flow between areas.

(b) Female mate choice - Baker *et al.* (1982) found that female White-crowned Sparrows responded to their natal dialect but not to an alien dialect. On the other hand, McGregor *et al.* (1988) found that female Corn Buntings did not necessarily mate with males singing their natal dialect. Thus assortative mating could result from female choice of specific song dialects.

(c) Territorial interactions - territory owners may respond differentially to songs from their own dialect, neighbouring dialects, and more distant dialects (Baker 1982). This could influence the ease with which dispersing birds may set up territories in areas with their natal dialect or more distant areas.

Song dialects have rarely been studied in group-territorial birds. Characteristics of group-territorial birds such as low rates and distances of dispersal (Brown 1987) as well as high survival rates and permanent occupancy of territories (see Chapter 1) could result in the development of song dialects and these could reflect the genetic structure of the population. I investigated songs of Chowchilla groups on my site and in nearby areas to examine the possibility of song dialects in this species.

9.2 Methods

Recordings were made mainly at dawn, using a National Panasonic mini cassette recorder, Model RQ-356, with an inbuilt microphone. Most recordings were made within $\simeq$20m of the birds. They were easily approached when singing and were so loud that a more sensitive microphone was not necessary. I obtained samples of songs from most groups on my site as well as from nearby sites (see Figure 9.1). For comparison, I also recorded songs from a completely isolated patch of ≃100ha of rainforest ≃12km WSW of my site (at Tarzali). Birds were recorded on my site in October 1990, and January, September and October 1992. Near my site, birds were recorded at Mingara in August 1989, adjacent to my site in October 1990 (Group 2), across the road from my site in October 1990 and February 1993 (Group 8), and at the Midway site and Andrew's site in February 1993 (see Figure 9.1). Birds were recorded at Tarzali in August 1990.

Songs were analysed using the software SoundEdit and AudioGraph on a Macintosh computer. Sounds were sampled in the frequency range 0-11.13kHz with a vertical resolution of 43.5Hz/point and a horizontal resolution of 0.01s/point. Sonograms were produced from all of the usable song recordings. Representative sonograms are shown in the results. All of the sonograms shown of songs recorded on my site were recorded on 6.10.92 except that of Group 5, recorded on 21.9.92. Those of Groups 2 and 8 were recorded on 4.10.90 while the remainder of those of Group 8, the Midway site bird and the Andrew's site bird were recorded on 24.2.93. That of the Tarzali bird was recorded in August 1990 while that of the Mingara bird was recorded in August 1989.

9.3 Results

Figure 9.1 shows the location of all groups recorded on and near my site. The sonograms are presented in Figures 9.2(a)-(e), 9.3(a)-(e) and 9.4(a)-(e).

Chowchilla songs consisted of a number of sharp bursts of sound connected by warbling notes. Each song was very stereotyped and lasted about 5-9s. An individual appeared to sing only one song type and this was repeated precisely many times during a singing bout (compare Figures 9.3(c) and (d) and Figures 9.4(b) and (c) for pairs of songs recorded from the same bird in the same session). I detected no individual or within-group variation in songs. However, when two birds in a group sang, one sometimes had a more resonant and louder song than the other. I was able to record few analysable songs to enable comparisons within groups because it was rare for a bird to sing alone, which was necessary to obtain a recording which could be analysed. Generally birds sang together and I could not analyse these recordings. I believe that the songs I recorded were representative of the songs of the groups to which they belonged.

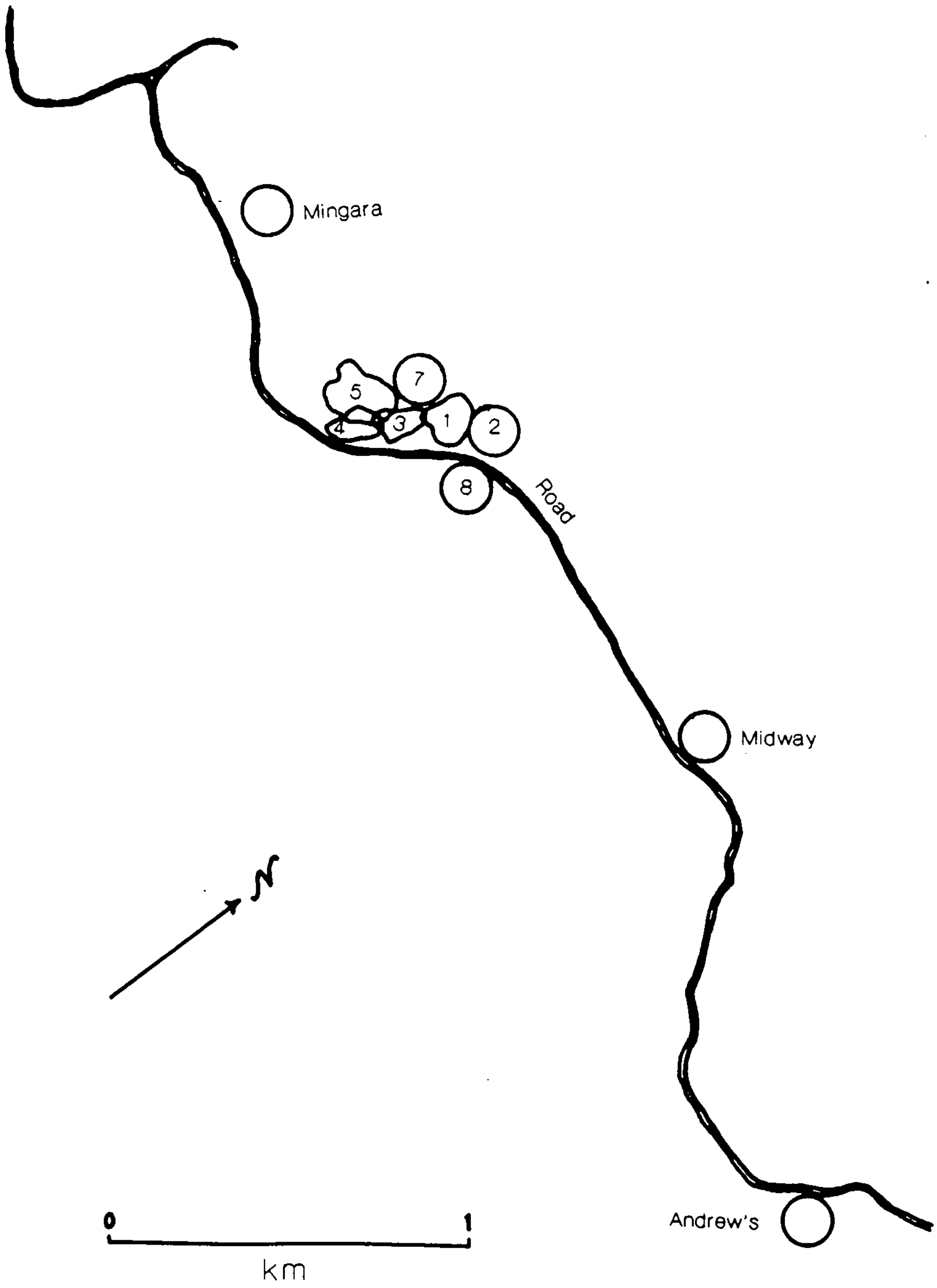


Figure 9.1 The location of groups recorded on tape along the road passing my site. The numbered home ranges are those of the groups on my site.

Figures 9.2(a)-(d) and 9.3(a)-(b) show the songs of five neighbouring groups on my site whose territories are shown in Figure 9.1. Groups 3, 4, 5 and 7 appeared to have identical songs although that of Group 5 was truncated in this recording. There was a slight difference between the song of Group 1 and the other groups, in the number of peaks at the beginning of the song. Another slight variant, shown in Figure 9.2(c), had an extra peak near the beginning and lacked a peak halfway through the song. This song was produced by a male who could have belonged to either Group 1 or Group 7: at dawn when both groups were calling together this was impossible to determine. It was certainly a different individual from the ones that produced the songs shown in Figures 9.2(a) and (b). Thus there may be slight intra- and inter-group variants on songs in one area. Extending this further, the sonogram in Figure 9.2(e) was recorded $\simeq$0.75km from my site (see Figure 9.1) and, although truncated and a poor recording, shows only a slight variant (lacking one peak in the middle) on the songs recorded on my site.

Completely different songs were recorded from birds on the other side of my site. Figures 9.3(c) and (d) show two songs recorded from one bird in Group 8 on 24.2.93 while Figure 9.3(e) shows a song recorded from the same place on 4.10.90. These songs are almost identical and could have been produced by the same bird although I have no way of confirming this. Interestingly, between these two recordings the patch of forest in which Group 8 lived was entirely cleared except for a clump of about six spindly trees on the edge of the road. The recordings made in February 1993 were made when the birds were in the trees at dawn, prior to their descent to the ground. Immediately after the patch of forest was cleared, in June 1992, a new group of birds (probably Group 8) were observed foraging on the road edge of the home range of Group 1. Thus despite total destruction of their foraging range, Group 8 apparently still roosted in their original home range, in the few remaining trees, and retained the same song.

On the opposite side of the road to Group 8, and adjacent to Group 1, a third song type was recorded. Figure 9.4(a) shows that Group 2 had a different song from either of its neighbours on the western and southern sides. However, Figures 9.4(b) and (c) show that the bird recorded at the Midway site had the same song as Group 2. The Group 2 bird and the Midway site bird were $\simeq$1km apart.

Two further song types are shown in Figures 9.4(d) and (e). The Andrew's site bird, $\simeq$1.4km from the Midway site and $\simeq$2.4km from my site, had a song showing some resemblance to the Midway site songs but still distinctly different. Birds from Tarzali had a very different song.

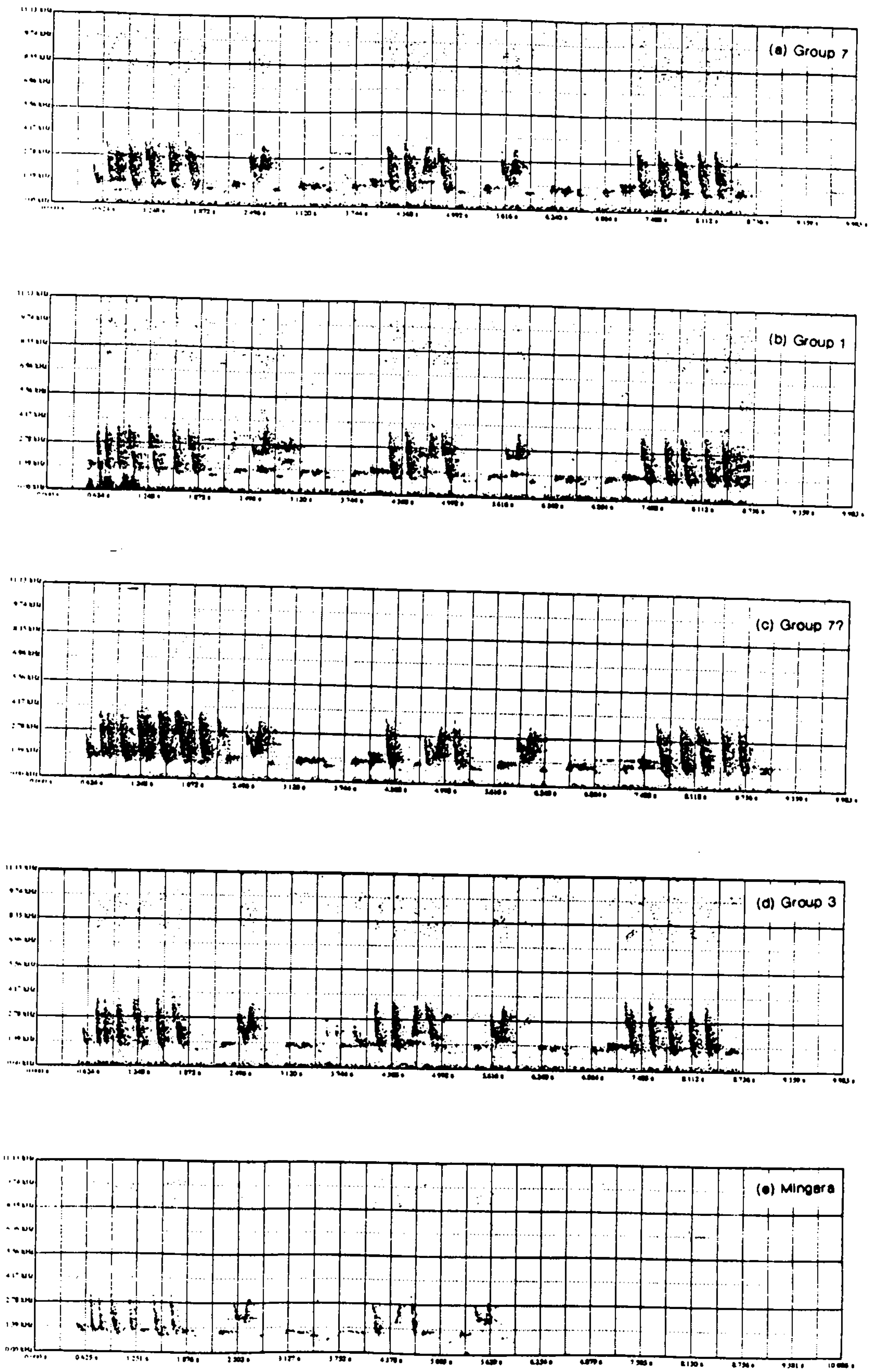


Figure 9.2 Sonograms of Chowchilla songs recorded from groups on and near my site (locations shown in Figure 9.1).

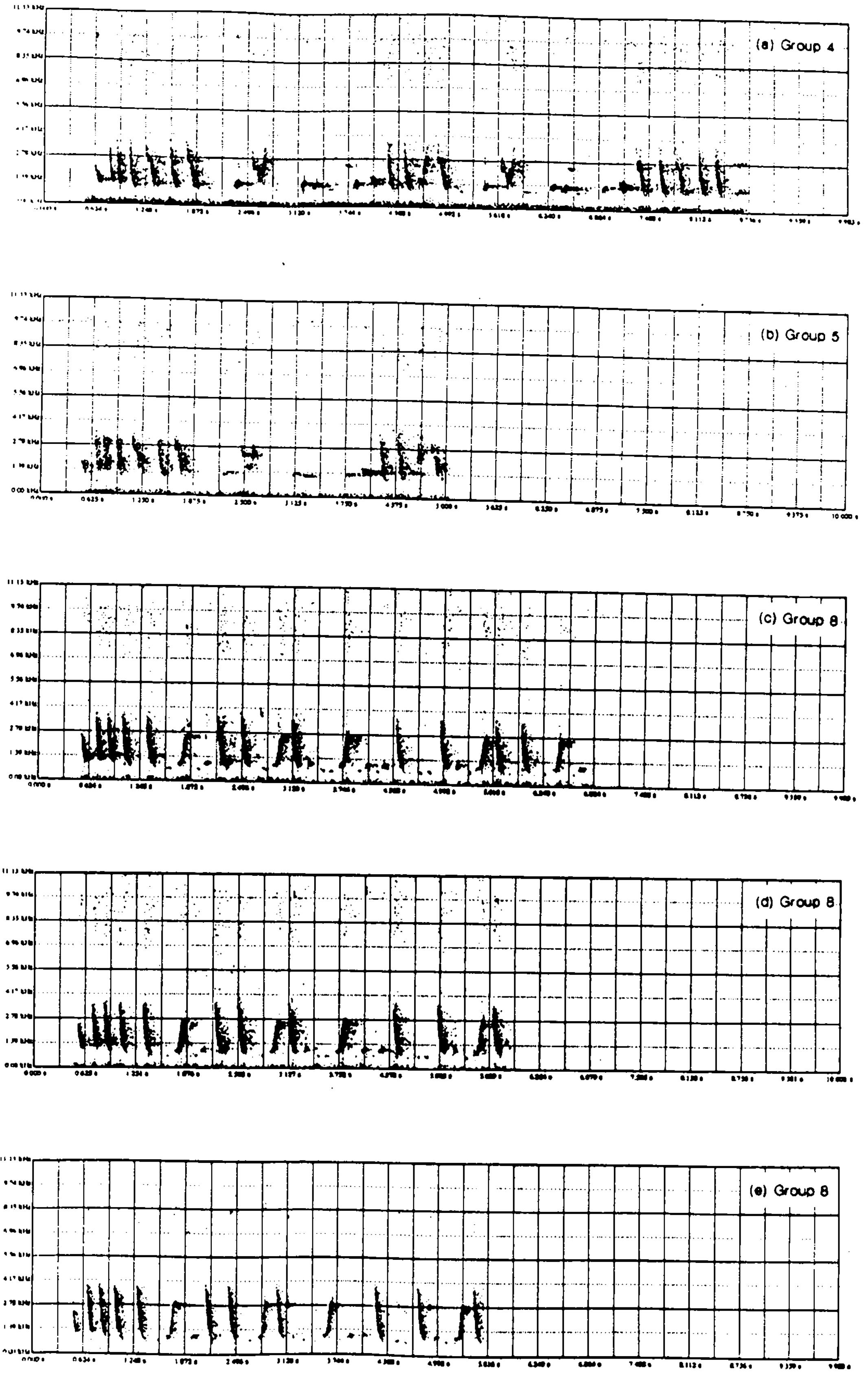


Figure 9.3 Sonograms of Chowchilla songs recorded from groups on and near my site (locations shown in Figure 9.1).

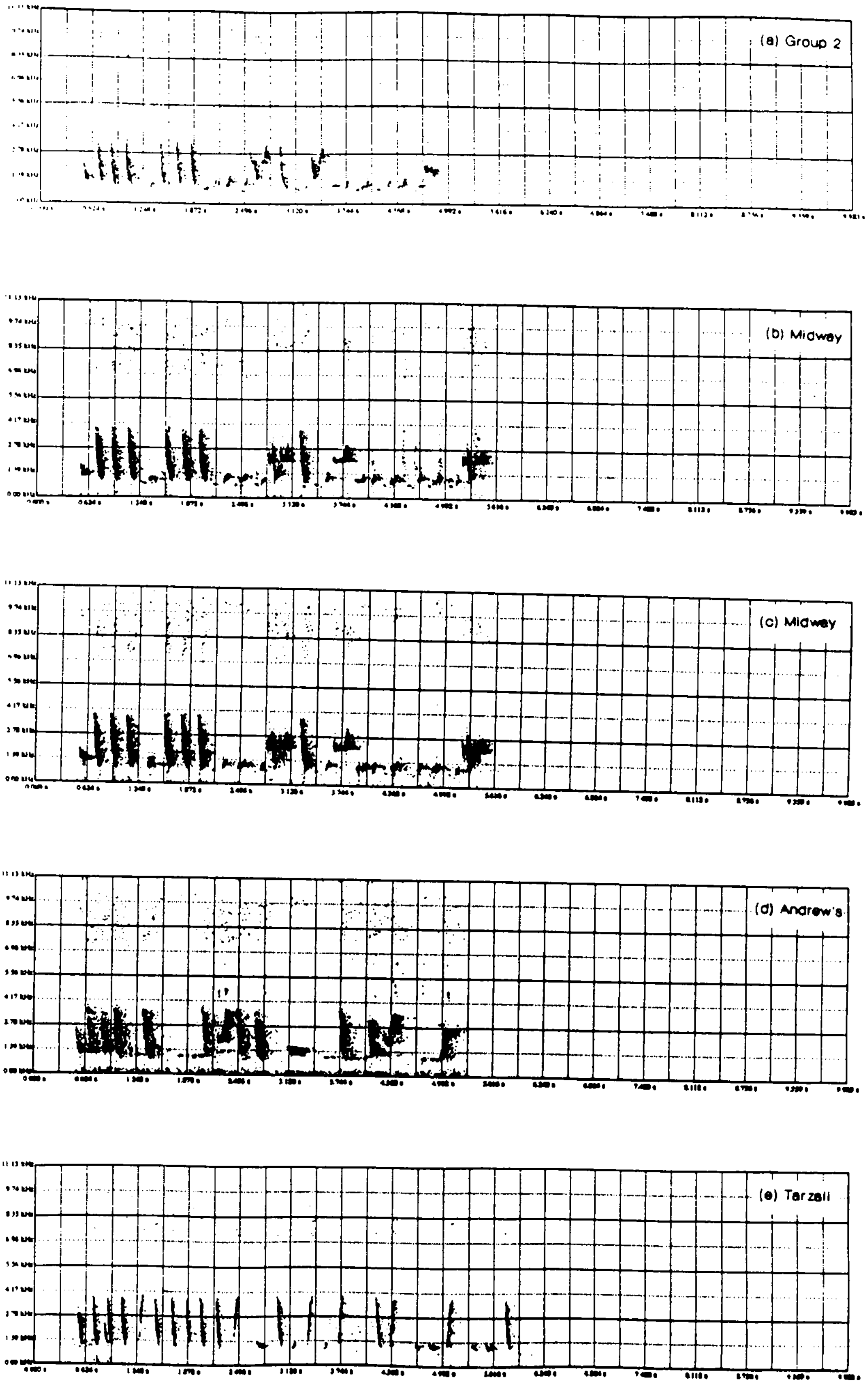


Figure 9.4 Sonograms of Chowchilla songs recorded from groups near my site (locations shown in Figure 9.1) and at Tarzali (≃12km from my site).

9.4 Discussion

Chowchillas appear to have song dialects. Within a dialect group, all birds appear to sing the same song, with very minor variations, and these songs are conserved over long periods of time. Between dialects, songs are very different and these differences increase with distance. Although I did not record birds from further afield, songs of birds separated by greater distances appeared to differ even more markedly. Leo Joseph (pers. comm.) noted that Chowchillas on the Windsor Tableland ($\simeq$140km north of my site) had a very different song from those on the Atherton Tableland and that this was correlated with morphological and genetic differences.

These results are very suggestive but at this stage it is difficult to say what influence the song dialects may have on the structure of the population. More data are required on how far birds disperse, whether they disperse only within dialect areas or outside them, and when the song is learned in relation to when dispersal occurs. It is interesting that boundaries between dialects appear very abrupt and that songs on each side of the boundary are so different. This makes it seem unlikely that birds could disperse across the boundaries easily and learn the new song, especially since they apparently stay within their natal territory for at least a year (which is the period during which most birds learn their songs (Kroodsma 1982)). It seems likely that dispersal occurs mainly within dialect areas (given my one observation of a very short dispersal distance) and that birds with the same dialect are more closely related than birds with different dialects. It seems possible that within a dialect area, consisting of maybe 15-30 groups of birds (estimated by filling in the gap between Mingara and my site, which form two edges of that dialect area), individuals are somewhat more related than would be expected if mating occurred at random, and that these birds could be considered as a discrete sub-population.

CHAPTER 10

THE ROLE OF CHOWCHILLAS IN THE RAINFOREST

10.1 Introduction

Chowchillas prey upon much of the leaf litter fauna (see Chapter 5) and may be preyed upon by a number of rainforest animals. They are also one member of a guild of ground-foraging animals which often forage together (pers. obs.).

Mixed-species foraging flocks of birds are common, particularly among insectivorous birds (Morse 1971). At least two other group-territorial birds in the tropics join mixed-species foraging flocks (Rufous Babbler - Bell 1982, and White-banded Tanager - Alves 1990) as do a number of Australian group-territorial species, e.g. Superb Fairy-wren, White-browed Scrubwren, Buff-rumped Thornbill (Bell 1980). In a particular area there are often a few species, termed 'nucleus' species (Greig-Smith 1978) which occur regularly in mixed-species flocks and which the other species appear to follow and organize their activities around. In the Australian Capital Territory and near Monteverde in Costa Rica these nucleus species are generally ones which form small family parties or flock intraspecifically (Bell 1980 and Buskirk 1976, respectively).

The occurrence of intra- and inter-specific flocking in birds in Costa Rica was correlated with patterns of food dispersion and vulnerability to predation by Buskirk (1976). He suggested that species which experienced dispersed foods (so that intra-specific flocking was not advantageous) but were vulnerable to predation would be those most likely to join mixed-species flocks. Thus insectivorous birds with dispersed food resources which were intra-specifically solitary or occurred only in small groups and which foraged in the more open forest strata were those which tended to join mixed-species flocks (Buskirk 1976).

Here I will examine the role of Chowchillas in the formation of groups of ground-foraging animals as well as their possible effects on their food supply and their vulnerability to predation.

10.2 Methods

Between June 1991 and July 1992 I noted animals associated with Chowchilla groups. The most common associate was the Musky Rat-Kangaroo. During searches for Chowchillas I also noted the occurrence of other Musky Rat-Kangaroos not associated with Chowchillas. This provided an index of association between Chowchillas and Musky Rat-Kangaroos. Thus I could determine what proportion of all Musky Rat-Kangaroos seen were with Chowchillas and what proportion of Chowchilla groups seen also contained a Musky Rat-Kangaroo. These measures were probably biased in that I was more likely to see a Musky Rat-Kangaroo associated with a group of Chowchillas than one on its own. In counting the number of Chowchilla groups, I did not include single birds or birds seen in the few areas with very dense undergrowth where I was unlikely to have observed a Musky Rat-Kangaroo if it was present.

10.3 Results

10.3.1 Chowchillas and the leaf litter fauna

Chowchillas turn over large quantities of leaf litter during their foraging activities and probably have important effects on it. Regular turning of the litter would be expected to increase its rate of decomposition, as well as its rate of movement down slopes and its moisture content. Moisture content and quantity of leaf litter influenced the numbers of invertebrates found in it (see Chapter 4). Thus the foraging activities of Chowchillas may influence invertebrate numbers by both direct consumption and habitat modification.

Their tendency towards systematic foraging, such that recently searched areas are avoided for a while (see Chapter 7), may be related to both rates of renewal of depleted invertebrates and to minimizing the effects of frequent disturbance of the leaf litter which could be detrimental to the litter fauna.

To obtain some idea of the impact of Chowchilla foraging on invertebrate litter populations, I made a very crude estimate of the food supply available to and required by a group of Chowchillas on their home range. I made the following assumptions using data on Group 1 as an average group: (1) they foraged over an area of 1.35ha (see Chapter 7); (2) there was an average of 32.2 large invertebrates per $0.25m^2$ overall (see Chapter 4); (3) large invertebrates had an average length of 3.5mm and conformed to the length-weight relationship $W=0.0305L^{2.62}$ with weight (W) measured in mg and length (L) measured in mm (Rogers *et al.* 1976); (4) Chowchillas required $\simeq$15% of their body weight in food per day (an estimate derived from Welty 1979); and (5) Group 1 consisted of two females weighing 134g each and one male weighing 185g (see Appendix C). Using these assumptions, I calculated that the home range of Group 1 contained on average $\simeq$1411g of food in the form of large invertebrates at any time and that the group required $\simeq$70g per day. Thus the available food would last $\simeq$20 days. This is without taking into account consumption by other animals.

Presumably a Chowchilla home range is large enough to ensure an adequate food supply for its inhabitants. Even if invertebrate litter numbers were renewed every 2-3 weeks, Chowchillas would have had to forage over their entire home range at least every month in order to obtain enough food to survive, and thus probably utilized most of the available food. This is consistent with my observations suggesting that most of the leaf litter in a group's home range was turned over at least every month.

10.3.2 Predation on Chowchillas

I have no direct evidence of predation on Chowchillas. I think it unlikely that adult birds would have been predated upon during the day. However, two wing-tagged birds and a number of eggs and chicks in the nest did disappear and these may have been predated. Eggs and chicks were very vulnerable to predation since the nests were on or close to the ground and only a single female attended the nest both at night and during the day. Potential nest predators that I observed on my site included White-tailed Rats, Spotted Tree Monitors, Amethystine Pythons and Carpet Pythons. All of these could also have taken roosting birds at night. A possible diurnal predator, which could have taken the wing-tagged birds, was the Grey Goshawk.

10.3.3 Interactions with other ground-foraging animals

Other birds often associated with Chowchillas included Yellow-throated Scrubwrens, Fernwrens, Eastern Whipbirds, Spotted Catbirds and Grey-headed Robins. The most common associate, however, was a marsupial - the Musky Rat-Kangaroo. It was always clear that these associates were following the Chowchilla groups and not *vice versa*. Figure 10.1 shows the proportion of foraging Chowchilla groups which included a Musky Rat-Kangaroo and the proportion of Musky Rat-Kangaroos seen with Chowchillas at different times of the year. A relatively large proportion of Chowchilla groups included a Musky Rat-Kangaroo in June-August 1991 and April-July 1992. Few Musky Rat-Kangaroos were seen with Chowchilla groups in the period September 1991 to February 1992.

Looking from the other perspective, nearly half of all Musky Rat-Kangaroos seen were with Chowchilla groups in the periods June-October 1991 and April-July 1992. Few Musky Rat-Kangaroos were seen in September-October 1991 and in the period November 1991 to February 1992 only a small proportion were seen with Chowchilla groups. The period October 1991 to January 1992 corresponded to the peak in fruit availability for the year (Andrew Dennis, pers. comm.). Musky Rat-Kangaroos eat fruit and leaf litter invertebrates (Andrew Dennis, pers. comm.). These data suggest that Musky Rat-Kangaroos adjust their foraging strategies so that when fruit is abundant they forage mainly by themselves (spending most of their time moving from fruit fall to fruit fall) while when fruit is less abundant they spend a large proportion of their time following Chowchilla groups.

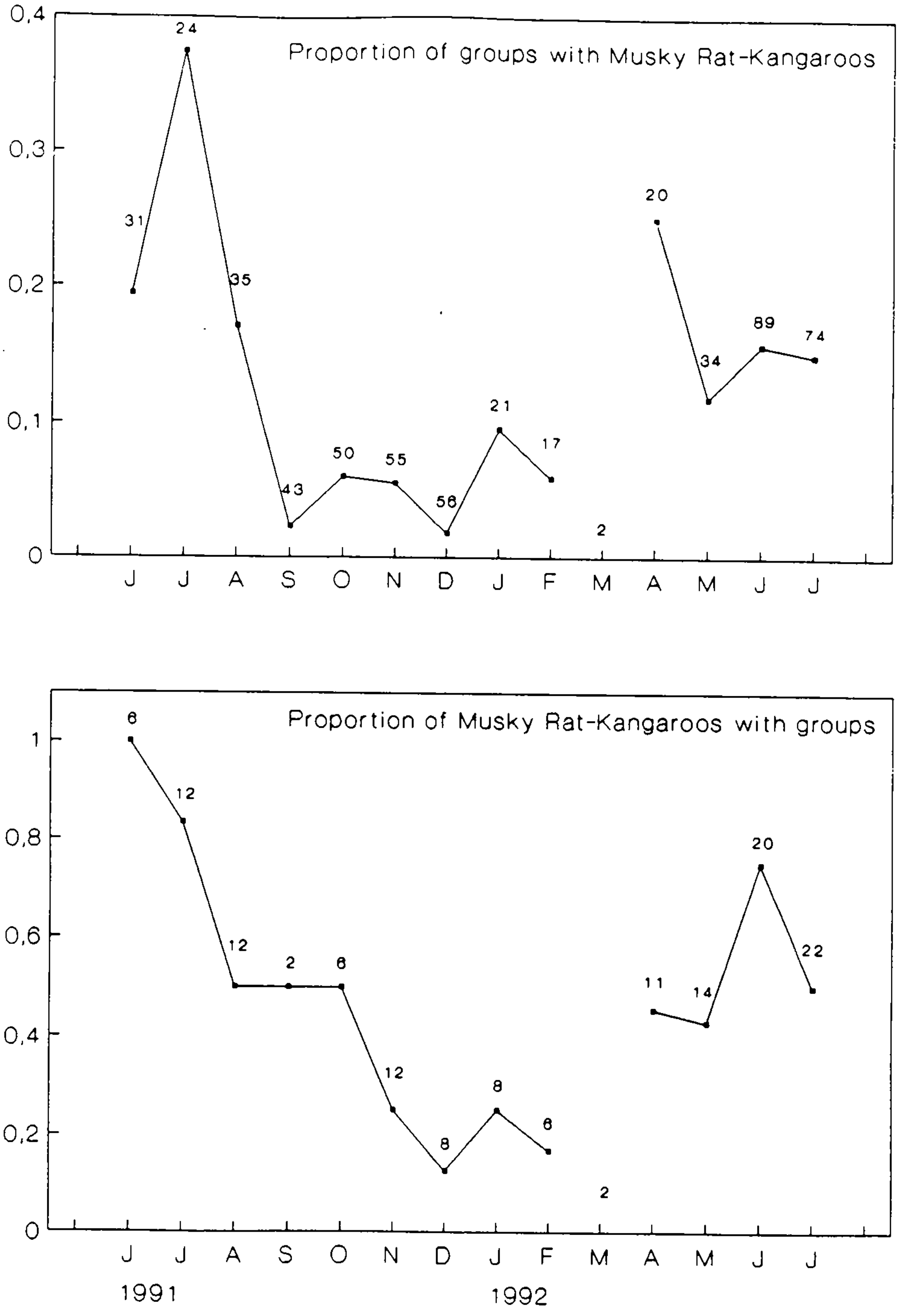


Figure 10.1 The proportion of Chowchilla groups which included Musky Rat-Kangaroos (numbers of groups seen given above points) and the proportion of Musky Rat-Kangaroos seen with Chowchilla groups (numbers of Musky Rat-Kangaroos seen given above points).

The other species which associate with Chowchillas showed no clear pattern of seasonality. All except the Spotted Catbird are insectivorous and probably experience the same fluctuations in food availability as Chowchillas. Catbirds are mainly frugivorous and were only seen occasionally (five of 551 observations of Chowchilla groups included a catbird). Yellow-throated Scrubwrens were the second-most common associate of Chowchillas, seen in 21 of the 551 observations of Chowchilla groups. They were seen with Chowchillas occasionally throughout the year, most commonly as pairs. They were also almost invariably seen in pairs when not foraging with Chowchillas. The other associates were only very occasional (two observations of Fernwrens, six of Eastern Whipbirds and one of a Grey-headed Robin).

In all the cases of association seen, Chowchillas were clearly the nucleus species. They were always at the front of the group, appeared to ignore the other species, and did not adjust their foraging behaviour in any way when associated with other species. The other species were clearly taking advantage of the Chowchilla's foraging activities but did not interfere with them at all. Musky Rat-Kangaroos, Yellow-throated Scrubwrens and Fernwrens were all often seen foraging in areas where Chowchillas had just turned over the leaf litter. The Spotted Catbirds were observed perching a few metres above foraging groups of Chowchillas and swooped down to the ground after watching the group for a while, presumably when the Chowchillas uncovered something that the catbirds could eat. The Grey-headed Robin was observed perching $\simeq$1m above a foraging pair of Chowchillas and swooped several times to catch flying insects disturbed by the foraging activities of the Chowchillas.

10.4 Discussion

Chowchillas are clearly a very important component of the ecology of the forest floor. They appear to turn over the leaf litter within their home ranges approximately every month and to consume a large proportion of the invertebrate fauna available at any one time. A number of other animals in the rainforest also turn over the leaf litter: the Orange-footed Scrubfowl and the Australian Brush-turkey both scrape up the leaf litter into piles to create their incubation mounds;

both Fernwrens and Eastern Whipbirds lift leaves with their beaks in their searches for food; and the Yellow-footed Antechinus burrows into the leaf litter in its searches for prey (all pers. obs.). All of these, however, have a very minor impact compared to Chowchillas.

Chowchillas experience a food supply which is patchy and clumped on a small scale (see Chapter 4). However, in comparison to the food supply of a frugivore, their food supply is relatively dispersed. Chowchillas do not appear to be particularly vulnerable to predation while foraging. In this respect they are comparable to the ground-foraging insectivorous birds in Costa Rica described by Buskirk (1976) which are generally solitary when foraging. As noted earlier, the fact that Chowchillas forage in groups may be related to the greater food-finding ability of more experienced birds so that younger birds can take advantage of this by foraging with them. In terms of interspecific flocking, however, Chowchillas would not be expected to gain any advantage by joining mixed-species flocks. My observations suggest that Chowchillas do not 'join' mixed-species flocks. However, they do not attempt to discourage other species from following them when foraging.

The main species which I observed following Chowchillas fitted the category of Buskirk's (1976) which tended to form mixed-species flocks in that they experienced dispersed food resources and may have been more vulnerable to predation. Certainly Musky Rat-Kangaroos are taken by Grey Goshawks (Andrew Dennis, pers. comm.), the only active diurnal predator, and because of their poor sight (pers. obs.) may be more vulnerable to predation. Thus foraging with a group of Chowchillas could incur advantages in terms of early warning of predators. However, the fact that Musky Rat-Kangaroos mainly associated with Chowchillas when fruit (a clumped food resource) was less abundant, suggests that the pattern of food dispersion was the main factor influencing their tendency to join groups.

Thus all of the species observed to forage with Chowchillas probably did so for reasons related to food availability rather than for any predator avoidance-related advantage. This differs from Buskirk's (1976) conclusion that predation was the main factor influencing the formation of mixed-species flocks in Costa Rica.

CHAPTER 11

GENERAL DISCUSSION AND CONCLUSIONS

Chowchillas are one of the few group-territorial birds studied in the tropics which live in rainforest. A little is known about two other rainforest-dwelling species: the Red-throated Caracara in French Guiana (Thiollay 1991) and the Rufous Babbler in Papua New Guinea (Bell 1982). Both of these species breed cooperatively. One other rainforest-dwelling Australian tropical species, the Large-billed Scrubwren, about which very little is known, also breeds cooperatively (Jansen 1990b). This paucity of information about rainforest-dwelling group-territorial birds probably reflects the difficulties of working in rainforest more than anything else. Most studies of group-territorial birds have been conducted in open savannah habitats where birds are easy to find and observe, territories are easy to map, and nests are easily found. None of these are easy in rainforest, so I was able to study relatively few groups compared to other work on group-territorial birds.

Chowchillas, unlike other group-territorial birds studied so far, do not appear to breed cooperatively, although they do forage as a group and cooperate in territory defence. Thus the main focus of this study was to investigate what ecological and other factors could be involved in causing Chowchillas to live in groups but not breed cooperatively. In most well-studied group-territorial birds group-territoriality and cooperative breeding are principally a result of delayed juvenile dispersal, which may be the result of ecological and/or demographic constraints (Smith 1990). An important ecological factor which may promote permanent group-territoriality is an adequate food supply on the territory to support the group during the period of lowest food availability (Smith 1990). I examined patterns of food availability, foraging strategies, territoriality, social behaviour and group structure in Chowchillas. The main conclusions of this study were as follows:

(1) Food availability in patches was predictable on the basis of readily observed characteristics of the leaf litter;

(2) Average food availability varied seasonally and from year to year but the seasonality was low compared to that found in some other tropical rainforests and probably very low compared to that found in insect populations in most temperate areas. Also, food availability in good patches was high even when average food availability was at its lowest level;

(3) Chowchillas were generalist foragers. Thus patterns of food availability in the field accurately reflected what was utilized by the Chowchillas;

(4) Chowchillas did not search randomly when foraging, instead choosing patches which were likely to contain more food. This strategy would have reduced the effects of seasonality because of the presence of good patches even when average food availability was low. The strategy probably involved learning the cues which indicated the quality of patches;

(5) Home ranges were stable over time and overlapped to some extent. However, each group had a core area which was rarely encroached upon by other groups. The defended territories, roughly corresponding to these core areas, were exclusive;

(6) there was a positive correlation between group size and home range size but this appeared non-linear. Larger groups had disproportionately large home ranges;

(7) Groups were stable over time and reproductive and mortality rates were very low;

(8) One dispersal event was of a year-old female moving to a neighbouring group;

(9) Cooperation occurred in territory defence and members of a group foraged together. However, no cooperation was observed in breeding up to the time of fledging;

(10) Chowchillas had song dialects and this may be related to dispersal distances and levels of relatedness between groups.

I will first discuss the merit of these conclusions and place them in the context of other findings. Then I will use them to deal with the question of why Chowchillas may live in groups but not breed cooperatively.

Patterns of food dispersion have not been studied in such detail for any other group-territorial bird in the tropics, nor for most temperate ones, with the exception of the Acorn Woodpecker (Koenig & Mumme 1987). As subjects for studies of this kind, Chowchillas have the advantage of a very well-defined and narrow foraging niche (only leaf litter on the ground) which is relatively easily sampled.

Many studies of group-territorial birds in the tropics have noted that the birds are generalist foragers but none of them have related patterns of food availability to diet. I showed that Chowchillas exhibited little selectivity for particular prey types at different times of the year, except to the extent that they may have foraged in those patches most likely to contain those prey types. Also, the range of prey types taken did not appear to vary with changes in food availability. This was possibly because of the small seasonal variation in food availability or because there was little difference in the energy values and catchability of different prey items so there was no advantage in selective foraging for particular prey types.

I studied the foraging behaviour of Chowchillas, in order to relate foraging strategies to food availability, and also to examine age-related differences in foraging behaviour. Few studies, and none of group-territorial birds, have assessed in detail the relationship between food availability and foraging strategies. In Chowchillas the strategy of choosing good patches to forage in was probably dependent on learning the cues associated with good patches. Thus young birds could be expected to take some time to learn how to forage successfully.

Only Heinsohn's (1991) study of White-winged Choughs has examined age-related effects on foraging skill in a group-territorial species. I could not examine the foraging behaviour of juvenile birds since there was only one, whose range I was not very familiar with, on my study site during the two years of this study. Age-related effects on both success at finding good patches to forage in and success at capturing prey were found in European Blackbirds, which forage on the ground like Chowchillas (Desrochers 1992). I predict that young Chowchillas would have been less successful at finding good patches to forage in than adult birds. They may also have been less adept at catching prey, as demonstrated in other insectivorous birds such as Heron Island Silvereyes (Jansen 1990a), American Robins (Gochfeld & Burger 1984) and Northern Mockingbirds (Breitwisch *et al.* 1987). Young Chowchillas could have overcome the first difficulty by foraging with older birds which were better at finding good patches, providing that they were tolerated by the older birds. The second difficulty, that of capturing prey, may be less important for Chowchillas since their prey are relatively slow moving compared to flying insects.

Most studies of group-territorial birds have found home ranges to be virtually exclusive. Two factors may explain the fact that I found overlapping home ranges in Chowchillas. I used radio-tracking to locate birds so that my observations of their positions were independent of biases related to where I might have expected the birds to be and of any difficulties related to locatability in different parts of the site. Thus I was more likely to obtain observations of birds outside their territories than most workers who either did not state how they mapped home ranges or used randomly collected observations of locations to plot home ranges (see Table 7.7 in Chapter 7). The other factor is that all of the other studies which mapped home ranges of more than one group were conducted in open habitats where birds were more visible not only to human observers but also to other groups of birds. Thus it might be expected that overlap in open habitats would be less because intruding birds would be more often seen by the occupants of a territory and chased off. Intruding groups of Chowchillas were chased off by the occupants of a territory when detected but they could often intrude without being detected.

In other respects home ranges of Chowchillas were similar to those of other group-territorial birds in the tropics. They were permanently defended by all members of a group and were stable over long periods of time. Size comparisons are difficult to make because of the range of habitat types, bird sizes and group sizes exhibited by other group-territorial birds. However, the sizes of

Chowchilla home ranges were quite comparable to those of other small passerines living in small groups in relatively wet habitats (see Table 7.7 in Chapter 7), e.g. Bicolored Wrens (Rabenold 1990), Rufous Babblers (Bell 1982) and Bushy-crested and Nelson San Blas Jays (Hardy 1976), and also Galapagos Mockingbirds which live in an arid habitat (Curry & Grant 1990).

Chowchilla home ranges were probably large enough to ensure an adequate food supply, even during the period of lowest availability. This is reflected in the fact that home range size increased with group size, although the increase was disproportionate to the increase in group size (see Table 7.6 in Chapter 7). The sample size for this correlation was small and I have no way of assessing the accuracy of my home range estimates. However, it is interesting to note that the larger home ranges also had greater overlap with neighbouring home ranges. It is possible that the area within which each group had exclusive access was porportional to the number of birds in each group. I could not calculate the area of exclusive use for any group because all of them had neighbours whose home ranges I did not measure. Given slow rates of replenishment of the litter fauna (which needs experimental confirmation), and the (probably) limited number of good foraging patches available in poor seasons, it is likely that each bird required exclusive access to a certain number of good patches to ensure survival through poor seasons. Given the difficulty of defending the territory in this low visibility habitat (which is reflected in the high degree of overlap in large home ranges), larger groups may have to use much larger home ranges in order to ensure this access.

The composition of Chowchilla groups was quite stable over time and birds that did disappear were quickly replaced by others of like sex. Contributing to this stability were the high survival (at least 86% annually) and low reproductive rates (0.27 fledged young per group per year). Using this estimate I calculated the expectation of further life for an adult bird (after Lack 1954) at 6.6 years. However, I suspect that annual adult survival is likely to be closer to 90 or 95% and that Chowchillas may live for up to about 20 years. This is supported by the observed very low reproductive rate. If the population is stable (as it appears to be), the annual survival rate must be at least 91% to match the reproductive rate of 0.09 fledged young/individual/year. This survival rate is comparable to the highest values recorded for other group-territorial birds in the tropics (see Table 1.2 in Chapter 1). Because of their low reproductive rate, I was unable to determine how groups form in Chowchillas, to see if young birds generally stayed on their parental territory to form groups of related individuals.

Only one dispersal event was observed. There is a slight possibility that this young bird dispersed because of my actions in catching, wing-tagging and radio-tagging it. However, my later observations indicated that the bird was well established in the group to which it moved so this dispersal event was probably not unusual.

I could not rule out the possibility that group members other than the parents help feed the young once they have fledged, because so few young left the nest that I was unable to observe more that one fledged chick. Even if Chowchillas do feed other birds' young once they have left the nest, this would still be very unusual. In all other cooperative breeders helpers feed chicks both in the nest and out of it, after they have fledged.

My data on the songs supports the idea that dispersal most likely occurs over short distances and possibly only within a defined number of groups, all with a similar song. However, a great deal more work needs to be done on the songs to ascertain the relationships between song learning, the timing of dispersal, and how dispersal is affected by the dialects.

The combination of high adult survival rates and the close packing of home ranges observed on my site suggests habitat saturation in Chowchillas. This is supported by my observation that most areas of habitat which could support Chowchillas did so, and that there was very little marginal habitat for Chowchillas. Thus young Chowchillas which have reached independence have few options. Most will either have to remain on the parental territory or join another group which is likely to already contain at least two or three birds. This is a common situation in group-territorial birds and generally it is found that young birds remain on the parental territory until either they can inherit a breeding vacancy there or a vacancy occurs in a nearby territory which they can occupy (reviewed in Brown 1987). In many of these species there is the constraint of only one breeding pair per territory, and generally the result is that young birds unable to disperse remain and help their parents raise further young (Brown 1987).

Habitat saturation has often been suggested to be a cause of group-territoriality and cooperative breeding in birds (e.g. Stacey 1979, Koenig & Pitelka 1981). However, a more careful analysis of the data on Acorn Woodpeckers suggested that young birds often did not disperse and breed independently even when they had the option to do so (Stacey & Ligon 1987). They suggested that young birds tended to stay on the parental territory because of benefits related to remaining, such as direct benefits of group-living or the enhancement of present or future access to some limiting resource, rather than because of costs of dispersal. In the case of Acorn Woodpeckers, young born on high quality territories (with many stored acorns) were likely to remain there and help rather than disperse to vacant, low quality territories. Conversely, young born on low quality territories were more likely to disperse with the chance of finding a good quality territory to occupy. Stacey & Ligon (1987) concluded that these decisions made sense based on the expected lifetime inclusive fitness of the birds on territories of differing quality. They also noted that in a number of species direct benefits of group-living have been identified or suggested and that sociality, resulting in more efficient utilization of some resource or higher survival rates, may cause habitat saturation rather than *vice versa*.

In Chowchillas a number of factors, mainly relating to the pattern of food dispersion and availability, may result in group-territoriality. Food is patchily distributed on a small scale but quite predictable, particularly for birds familiar with the area. Thus territoriality is likely to be the best strategy for utilizing the food supply since it enables familiarization with a small area and food is not so abundant in patches that intruder pressure would make territories indefensible. However, food availability in patches varies sufficiently in both space and time that a number of patches must be defended to provide the minimum requirements for a pair of birds and, as predicted in the model of Bacon *et al.* (1991b), the territories thus defended may also be large enough to support one or more extra birds. Thus a pair of Chowchillas may not incur any cost by allowing an extra bird to remain or join them on their territory according to this hypothesis. The extra bird could also bring benefits in the form of help in defending the territory.

A second factor related to the pattern of food availability which may promote group-territoriality in Chowchillas, is the possible lack of skill in foraging of young birds. As I noted earlier, food is patchily distributed and young birds are likely to take some time to learn how to assess the quality of patches and hence forage successfully. During this learning phase their best option would be to forage with adult birds which were experienced at finding good patches to forage in. Provided that older birds incur no costs in allowing young birds to forage with them, they should allow them to do so, particularly if they are previous offspring so that inclusive fitness is increased by increasing the probability of survival of the offspring. The fact that birds usually foraged far enough apart not to interfere with one another's foraging efforts suggests that birds did not incur any costs by allowing others to forage with them.

My observations of the one juvenile on my site moving to a new group when she was one year old, and of missing birds being replaced by (presumably unrelated) adults suggests that, at least in some cases, groups consist of unrelated birds. The factors which may promote group-territoriality in this species will generally hold whether or nor group members are related. There is also a possibility that young birds are able to breed if they disperse to a new group, even if the group already contains a breeding pair. This possibility is suggested by the fact that in one group of four birds near my site both pairs appeared to breed at the same time and independently. Young birds would be unlikely to be able to breed if they remained on the parental territory, because of a lack of potential mates who were not too closely related. However, by dispersing they may be able to do so.

These tentative ideas suggest that: (1) Chowchillas do not breed cooperatively because: (a) group members are unrelated so young birds would not increase their inclusive fitness by helping the breeders to raise offspring; and (b) young birds have the option of dispersing and possibly even of breeding in a nearby territory. (2) Group-territoriality can occur because: (a) young birds need to forage with experienced birds in order to find good food patches; and (b) older birds do not incur any costs by allowing them to do so and may also benefit by having help in defending the territory.

Chowchillas play an important role in the tropical rainforests in Australia. They are common in virtually all of the well-developed rainforests between Townsville and Cooktown. These rainforests have recently been placed on the World Heritage list and Chowchillas are one of their more conspicuous inhabitants. Chowchillas play an important role in turning over leaf litter on the forest floor, and probably consume a large proportion of the invertebrates found in the leaf litter, as well as some small vertebrates. They also appear to be important to a number of other ground-foraging animals in the rainforest, particularly Musky Rat-Kangaroos, because their foraging activities provide these animals with a profitable foraging niche.

In this study I have shown that Chowchillas are of interest for both theoretical and practical reasons. Their social system is unusual among group-territorial birds and this raises questions about some of the hypotheses used to explain cooperative breeding in other species. At this stage a great deal more data is needed on the relatedness between group members, the origin of groups, and the extent of dispersal by young birds before firmer conclusions on why group-territoriality but not cooperative breeding occur in this species.

In practical terms, Chowchillas clearly have an important role in the turnover of leaf litter on the forest floor, and hence affect nutrient cycling, the leaf litter fauna and other ground-dwelling animals in the rainforest. It would be of great interest to determine what proportion of the leaf litter is turned over by Chowchillas, the level of their impact on the leaf litter fauna and rates of recovery from this impact, and the importance of Chowchillas to other animals foraging on the forest floor.

APPENDIX A

SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Birds

Acorn Woodpecker	*Melanerpes formicivorus*
Amakihi	*Loxops virens*
American Robin	*Turdus migratorius*
Australian Brush-turkey	*Alectura lathami*
Australian Magpie	*Gymnorhina tibicen*
Beechey Jay	*Cyanocorax beecheii*
Bicolored Wren	*Campylorhynchus griseus*
Black-capped Chickadee	*Parus atricapillus*
Brown Jay	*Psilorhinus morio*
Buff-rumped Thornbill	*Acanthiza reguloides*
Bushy-crested Jay	*Cyanocorax melanocyanea*
Checker-throated Antwren	*Myrmotherula fulviventris*
Chowchilla	*Orthonyx spaldingii*
Corn Bunting	*Miliaria calandra*
Dunnock	*Prunella modularis*
Eastern Whipbird	*Psophodes olivaceus*
European Blackbird	*Turdus merula*
Fernwren	*Crateroscelis gutteralis*
Galapagos Hawk	*Buteo galapagoensis*
Galapagos Mockingbird	*Nesomimus parvulus*
Great Blue Heron	*Ardea herodias*
Great Tit	*Parus major*
Green Jay	*Cyanocorax yncas*
Green Woodhoopoe	*Phoeniculus purpureus*
Grey-backed Fiscal Shrike	*Lanius excubitorius*
Grey Goshawk	*Accipiter novaehollandiae*
Grey-headed Robin	*Poecilodryas albispecularis*
Groove-billed Ani	*Crotophaga sulcirostris*
Heron Island Silvereye	*Zosterops lateralis chlorocephala*
Hoatzin	*Opisthocomus hoazin*
House Sparrow	*Passer domesticus*
Large-billed Scrubwren	*Sericornis magnirostris*
Logrunner	*Orthonyx temminckii*
Nelson San Blas Jay	*Cyanocorax sanblasiana nelsoni*
Northern Mockingbird	*Mimus polyglottos*
Orange-footed Scrubfowl	*Megapodius reinwardt*
Ovenbird	*Seiurus aurocapillus*
Pied Kingfisher	*Ceryle rudis*
Pied Wagtail	*Motacilla alba*

Birds (continued)

Red-throated Caracara	*Daptrius americanus*
Rufous Babbler	*Pomatostomus isidori*
Saddleback	*Philesturnus carunculatus*
Song Thrush	*Turdus philomenos*
Southern San Blas Jay	*Cyanocorax sanblasianus sanblasianus*
Splendid Wren	*Malurus splendens*
Spotted Catbird	*Ailuroedus melanotis*
Stripe-backed Wren	*Campylorhynchus nuchalis*
Superb Fairy-wren	*Malurus cyaneus*
White-banded Tanager	*Neothraupis fasciata*
White-browed Scrubwren	*Sericornis frontalis*
White-browed Sparrow Weaver	*Plocepasser mahali*
White-crowned Sparrow	*Zonotrichia leucophrys*
White-winged Chough	*Corcorax melanorhamphos*
Worm-eating Warbler	*Helmitheros vermivorus*
Yellow-billed Shrike	*Corvinella corvina*
Yellow-throated Scrubwren	*Sericornis citreogularis*

Mammals & Marsupials

European Badger	*Meles meles*
Grey Gibbon	*Hylobates muelleri*
Long-tailed Macaque	*Macaca fascicularis*
Musky Rat-Kangaroo	*Hypsiprymnodon moschatus*
White-tailed Rat	*Uromys caudimaculatus*
Yellow-footed Antechinus	*Antechinus flavipes*

Reptiles

Amethystine Python	*Morelia amethistina*
Carpet Python	*Morelia spilota*
Spotted Tree Monitor	*Varanus timorensis*

APPENDIX B

COMMON PLANT SPECIES OCCURRING ON THE STUDY SITE.

Canopy trees

- *Acronychia vestita*
- *Alphitonia whitei*
- *Apodytes brachystylis*
- *Argyrodendron peralatum*
- *Argyrodendron trifoliolatum*
- *Athertonia diversifolia*
- *Beilschmiedia bancroftii*
- *Beilschmiedia brunnea*
- *Beilschmiedia recurva*
- *Beilschmiedia tooram*
- *Cardwellia sublimis*
- *Castanospora alphandii*
- *Cinnamomum laubatii*
- *Corynocarpus cribbeanus*
- *Cryptocarya angulata*
- *Cryptocarya corrugata*
- *Cryptocarya mackinnoniana*
- *Cryptocarya murrayi*
- *Cryptocarya oblata*
- *Daphnandra repandula*
- *Darlingia ferruginea*
- *Doryphora aromatica*
- *Elaeocarpus angustifolius*
- *Elaeocarpus arnhemicus*
- *Elaeocarpus largiflorens*
- *Elaeocarpus ruminatus*
- *Endiandra insignis*
- *Endiandra monothyra*
- *Endiandra palmerstoni*
- *Endiandra sankeyana*
- *Endiandra sideroxylon*
- *Endiandra xanthocarpa*
- *Ficus spp.*
- *Franciscodendron laurifolium*
- *Geissois biagiana*
- *Gillbeea adenopetala*
- *Litsea leefeana*
- *Myristica insipida*
- *Opisthiolepis heterophylla*
- *Pouteria castanosperma*
- *Prunus turneriana*

Canopy trees (continued)

- *Syzygium boonjie*
- *Syzygium cormiflorum*
- *Syzygium cryptophebium*
- *Syzygium gustavioides*
- *Syzygium kuranda*
- *Syzygium papyraceum*
- *Syzygium trachyphloirum*
- *Sloanea australis*
- *Sloanea macbrydei*
- *Tetrasynandra laxiflora*

Understorey

Trees and shrubs

- *Citronella smythii*
- *Cupaniopsis flagelliformis*
- *Fontainea picrosperma*
- *Garcinia gibbsiae*
- *Goniothalamus australis*
- *Lepiderema largiflorens*
- *Macaranga subdentata*
- *Neolitsea dealbata*
- *Niemeyera prunifera*
- *Pollia macrophylla*
- *Polyscias elegans*
- *Polyscias murrayi*
- *Polyosma rhytophloia*
- *Randia hirta*
- *Solanum dallachyi*
- *Synima macrophylla*
- *Triunia erythrocarpa*

Others

- *Cyathea cooperi*
- *Linospadix microcarea*
- *Oraniopsis apendiculata*
- *Pandanus monticola*

Ground layer

- *Alpinia arctiflora*
- *Alpinia modesta*
- *Alocasia macrorrhiza*
- *Bowenia spectabilis*
- *Diplasium conjugatum*
- *Nephrolepis hirsutula*
- *Pleuranthodium racemigerum*

Lianes and epiphytes

- *Arthropteris beckleri*
- *Arthropteris palisotii*
- *Asplenium simplicifrons*
- *Austrosteenisia blackii*
- *Caesalpinia scortechini*
- *Calamus australis*
- *Calamus moti*
- *Faradaya splendida*
- *Freycinetia excelsor*
- *Jasminum simplicifolium*
- *Maesa muelleri*
- *Omphalea queenslandia*
- *Pothos longipes*
- *Rhipogonum album*
- *Rhipogonum elseyanum*
- *Salacia disepala*
- *Smilax calophylla*

APPENDIX C

TABLE C.1 BANDING DATA FOR CHOWCHILLAS TRAPPED IN THE STUDY

ID	ANPWS Band no.	Status	Age	Date	Time	W	HB	WL	TR	TA
YM1	07200354	New	1+	100890	1034	167	54.5	132	47.7	100
OF2	07200355	New	1+	130890	1530	139	52.5	127	43.0	104
WF3	07200356	New	1+	130890	1530	123	50.5	118	41.0	93
YF4	07200357	New	1+	081090	1220	141	51.0	128	45.9	103
RF6	07200358	New	1+	101090	1125	143	52.5	127	42.3	88
WF1	07200359	New	1+	180191	0735	133	52.6	124	49.0?	90
OM9	07200360	New	1+	200591	1150	180	53.0	139	47.2	112
YF10	07200361	New	1+	200591	1150	133	51.1	122	41.9	96
RM12	07200362	New	1+	030691	1430	208	54.3	136	50.2	112
OF2	07200355	Retrap	1+	030691	1430	148	51.1	129	44.3	102
YF10	07200361	Retrap	1+	050891	1215	138	50.8	130	42.3	96
RF17	07200363	New	1+	160891	1030	141	51.1	121	42.5	96
OJ	07200364	New	≃22d	260891	1610	107	44.6	87	45.1	12
WF14	07200365	New	1+	031091	1020	132	49.5	120	43.5	94
YM13	07200366	New	1+	031091	1020	184	54.5	135	47.0	109
RM12	07200362	Retrap	1+	111091	0820	200	54.0	135	48.8	107
YJ	07200267	New	21d	251091	1612	88	44.9	84	43.1	0
YF8	07200368	New	1+	251191	1200	133	51.6	119	43.6	96
OF2	07200355	Retrap	2+	061291	1000	138	51.6	127	43.3	100
RM12	07200362	Retrap	1+	061291	1000	198	55.3	134	48.4	109
YM13	07200366	Retrap	1+	110592	1205	177	54.6	137	45.6	112
YF8	07200368	Retrap	1+	150692	0835	134	51.5	125	43.3	94
OF18	07200369	New	1+	160692	0910	141	51.0	129	42.4	100
WM21	07200370	New	1+	160692	0910	182	55.4	135	47.7	112
OM11	07200371	New	1+	180692	0840	188	54.2	137	47.3	115
RF17	07200363	Retrap	1+	180692	0855	137	50.4	120	41.9	97
WF15	07200372	New	1+	180692	0855	127	48.1	117	42.0	94
RF23	07200373	New	1	190692	0915	123	49.4	118	40.6	97
WF1	07200359	Retrap	2+	281292	1045	131	52.0	123	42.7	91
GJ	07200374	New	≃19d	080193	1100	129	48.9	89	47.4	16

ID=Colour code + sex (M=male, F=female, J=juvenile of unknown sex) + identifying number
ANPWS=bands supplied by Australian National Parks & Wildlife Service
Age=in years for adults, in days after hatching for juveniles
Date=day, month, year
W=weight (g)
HB=head+bill length (mm)
WL=wing length (mm)
TR=tarsus length (mm)
TA=tail length

TABLE C.2 ADULT MORPHOMETRICS (MEAN±STANDARD DEVIATION)

Sex	W	HB	WL	TR	TA	N
Adult Males	184.8 ±13.4	54.3 ±0.8	135.7 ±2.3	47.9 ±1.2	110.0 ±5.3	6
Adult Females	134.1 ±7.1	50.9 ±1.4	122.5 ±4.3	42.6 ±1.4	95.9 ±4.7	12

Note: Measurements from first captures used except TR for WF1 which was probably incorrect.

Codes as in Table 1.

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