

**Ecological effects and social correlates of group living in
the Chestnut-crowned Babbler (*Pomatostomus ruficeps*)**



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This thesis is presented for the degree of Doctor of Philosophy

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This thesis represents a major part of the prescribed program of study.

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GENERAL ABSTRACT

Group-living represents a widespread feature of animal social organisation, which has implications for the evolution of cooperation and other complex behaviours. Yet, the factors selecting for animal aggregations, in particular stable groups forming through offspring philopatry, remain elusive. This thesis examines possible costs and benefits of group living in an Australian cooperatively-breeding bird species, the Chestnut-crowned Babbler (*Pomatostomus ruficeps*). The study was conducted at the UNSW Arid Zone Research Station at Fowlers Gap, in the far-west New South Wales, Australia, from October 2007 to March 2010. I found that ecology, mainly habitat characteristics and local predation pressure, has profound implications for babbler social organisation, as indicated by its effects on group size, space use, and behaviour, as well as patterns of dispersal within the study population. Specifically, predation risk appeared to vary with habitat-type and was associated with group behaviours consistent with adaptive risk reduction. Variation in local ecology was also a strong predictor of group ranging behaviour, was consistent with hypothesised local resource depletion, and seemed to interact with group size in determining movements of foraging groups on a daily basis. The importance of habitat features was confirmed by its effects on group home range size, which in turn, was a relevant predictor of group response to playback vocalisations simulating conspecific intrusion.

DECLARATION

I certify that the work in this thesis entitled '**Ecological effects and social correlates of group living in the Chestnut-crowned Babbler (*Pomatostomus ruficeps*)**' has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself has been appropriately acknowledged (see Preface). In addition, I certify that all information sources and literature used are indicated in the thesis.

The research presented in this thesis was approved by Macquarie University Animal Ethics Committee (No. 2010/032).

A handwritten signature in black ink, appearing to read 'Enrico Sorato'.

Enrico Sorato

September, 2011

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PREFACE

My supervisor, Simon Griffith, and co-supervisor Andy Russell, have assisted me with the conception, analysis and writing of all the chapters in this thesis.

I estimated my personal contribution to each chapter as follow:

Chapter 1: Conception 100%, writing 100%

Chapter 2: Conception 90%, data collection 100%, analyses 100%, writing 90%

Chapter 3: Conception 80%, data collection 90%, analyses 100%, writing 95%

Chapter 4: Conception 90%, data collection 100%, analyses 100%, writing 95%

Chapter 5: Conception 90%, data collection 100%, analyses 100%, writing 95%

Chapter 6: Conception 90%, data collection 50%, analyses 100%, writing 95%

Chapter 7: Conception 100%, writing 95%

All data on group movements, ranging behaviour, and playback experiments have been collected by myself with the help of field assistants. In chapter 3 and 6, I have also used capture-recapture data collected from AF Russell, Lucy Browning and field assistants

Chapter 1

General introduction

Evolution of group-living and sociality

Group-living is common in animals and is characterised by extensive variation in its form, ranging from fluid temporary aggregations of unrelated individuals to relatively stable long-term aggregations of kins forming family groups, or, in the most extreme cases, complex eusocial societies (Wilson 1975; Krause and Ruxton 2002). Yet, the mechanisms that select for group formation are still relatively poorly understood, particularly for social species, in which genetic structuring is conducive to complex cooperative strategies promoted by kin-selected indirect benefits (Hamilton 1964; Krause and Ruxton 2002). As a consequence, because group-living represents a prerequisite for the evolution of cooperative behaviour, the evolution of cooperation is still a largely unresolved question (Clutton-Brock 2009; Szekely et al. 2010). This point is illustrated by studies of cooperative breeding, where individuals within groups forego reproduction and cooperate in parental care of the offspring of the breeding pair (Brown 1987; Stacey and Koenig 1990; Koenig and Dickinson 2004; Bergmuller et al. 2007). Explaining the evolution of such social system requires an understanding of two phenomena, namely why stable-social groups form, typically through delayed dispersal of offspring leading to family-living, and what factors favour cooperation, in particular helping at the nest, once groups have formed (Ekman et al. 2004). In fact, the two questions are somehow independent of each other, because, while cooperative breeding generally implies group-living, the latter does not inevitably lead to reproductive skew within the group and alloparental care (Emlen 1995; Packer et al. 2001; Magrath et al 2004; Clutton-Brock et al. 2009). That cooperative breeding and group-living can be two independent phenomena is shown by some well-know model species. For example, Siberian Jays (*Perisoreus infaustus*) live in small family-groups that can include unrelated immigrants, and in which breeding is monopolised by the dominant pair, yet cooperative breeding is not observed (Ekman and Slepukovich 1994). On the other hand, in Long-tailed Tits (*Aegithalos caudatus*), following dissolution of winter groups, pairs breed independently, yet helping does also occur in the

form of redirected alloparental care of former breeders (Hatchwell and Russell 1996).

Whilst studies of cooperative breeding species have traditionally focused on reproductive cooperation (Brown 1987; Stacey and Koenig 1990; Cockburn 1998; Koenig and Dickinson 2004) and concentrated on indirect benefits of alloparental care (Clutton-Brock 2002; Griffin and West 2002, 2003; Dickinson and Hatchwell 2004), the fact that group-living can occur disjunct from cooperative breeding, coupled with the existence of considerable variation in genetic structure within groups, suggest that direct benefits of group-living may be a driving evolutionary force (Cockburn 1998; Kokko et al. 2001; Clutton-Brock 2009; Heg et al. 2010; Riehl 2010). For example, ecological conditions have been invoked as factors promoting family-living, either by constraining individual dispersal from natal groups (Emlen 1982; Koenig et al. 1992; Arnold and Owens 1999; Hatchwell and Komdeur 2000), or by promoting philopatry through benefits associated with resources present within the natal territory (Stacey and Ligon 1987; Baglione et al. 2006; Komdeur 1994; Pen and Weissing 2000). Other benefits of philopatry have been linked to the natal social environment, in particular with respect to extended parental care and nepotism (Ekman et al 2001; Kokko and Ekman 2002; Russell et al. 2004; Baglione et al. 2005; Covas and Griesser 2007; Dickinson et al. 2009).

Yet mechanisms of social group formation are not necessarily limited to philopatry, and more generalised benefits of group-living, such as protection from predators and increased foraging efficiency (Krause and Ruxton 2002; Caro 2005; Doerr and Doerr 2006), may also promote stable aggregations between non-relatives, and increase the social complexity of family groups by promoting dispersal and acceptance of immigrant individuals.

On the other hand, group living entails also costs, for example due to competition for limited resources, increased disease transmission, or conspicuousness to predators (Krause and Ruxton 2002). In fact, levels of cooperation versus conflict within groups reflect a complex balance between costs, and both direct and indirect fitness benefits of cooperative

behaviours. Accordingly, cooperation is context-dependant and individual-specific, and therefore variable both within and across societies. While synergy between individuals is expected to be favoured when individual interests converge, for example in the context of anti-predatory behaviour (Caro 2005), or during territorial intrusions of other groups (e.g. McComb et al. 1994), conflicts are more likely to surface when individuals are compelled to compete for limited resources (Cockburn 2004; Magrath et al. 2004). Clearly, an understanding of patterns and mechanisms of cooperation and competition across different contexts is necessary in order to partition benefits and costs of cooperative interactions among individuals, and reveal evolutionary pathways to group living (Cockburn 1998; Clutton-Brock 2009). While in cooperatively breeding societies cooperation in rearing and care of nestlings has been a major focus of research, other contexts for cooperative acts have been only marginally investigated (Heinsohn et al. 1990; Cockburn 1998). Foraging, for example, is likely to entail a balance of cooperation and competition shifting according to a range of factors, including individual condition, relatedness, and ecological conditions on the background. Increased detection of food patches and efficiency in their exploitation (Poetke and Liebig 2008), as well as reduction in individual allocation of time to vigilance against predators (Elgar 1989; Lima and Dill 1990), are likely to benefit all group members and favour cooperation. On the other hand, competition is also likely to be found in the same context, particularly within resource-poor habitats conducive to resource depletion (Milinski and Parker 1991).

The balance between cooperation and competition is perhaps most dramatically shifted towards the latter at the time of mating. In cooperatively breeding species, in which usually only a limited number of females per group are able to breed, and where sex ratios can be highly skewed, male intrasexual competition for mating opportunities can be particularly intense (Cockburn 2004; Magrath et al. 2004). Intrasexual competition for breeding can however be even more dramatic among females, particularly where a single female

monopolises reproduction in the group (Haydock and Koenig 2002; Vehrencamp and Quinn 2004). Accordingly, reproductive skew, and how it is originated and maintained, has also been an important focus of studies of cooperatively breeding systems (Magrath et al. 2004). Help from other non-reproducing group members, and limited nesting sites, may constitute some of the main resources females compete for, and, as a consequence, group size and territory quality may represent an important commodity evaluated by prospective immigrant females. Paradoxically, high competition between females for breeding could be one of the paths leading to cooperation during nestling care, if individuals precluded from independent reproduction opt for a best of a bad job strategy and allocate to group offspring production some of the resources that they would have otherwise invested into their own breeding. Levels of reproductive skew and competition may vary according to relatedness (kin benefits) and ecology, and have consequences for dispersal patterns and social organisation (Koenig and Haydock 2004).

Antipredator behaviour provides another testing ground for the investigation of cooperation and other benefits associated with group-living. Protection from predators constitutes a widely acknowledged benefit of group living, and may be the result of several non-exclusive mechanisms, including dilution effects (Cresswell and Quinn 2011), enhanced detection of predators (Elgar 1989), cooperative defence (Maklakov 2002; Graw and Manser 2007), and selfish herd effects (Hamilton 1971). At the same time though, large groups may also convey costs due to increased predation risk, for example if they can be more easily detected by predators (Vine 1973). Clearly, relative costs and benefits of group-living in the context of predation risk are likely to depend on local ecological features as well as prey and predator biology. Further, within family groups, kinship may represent an important force also for the evolution of antipredator tactics, as shown by some seemingly altruistic antipredator behaviours, such as sentinelling. In fact, there has been much debate about whether acting as a sentinel is a selfish or cooperative behaviour (Bednekoff 1997; Wright et al. 2001), and to

what extent this is directed to kin versus non-kin. Kinship has been suggested to be an important factor for the evolution of altruistic sentinel behaviour in mammals and birds (Blumstein 1999), but other cooperative mechanisms may also be involved (e.g. by-product mutualism, group augmentation benefits), or alternatively sentinelling may function primarily as a condition-dependent selfish strategy (Bednekoff 1997).

Finally, intergroup interactions may be another factor involved in the moulding of a species social organisation, such as group size, particularly in species with a high degree of territoriality (Brown 1982). In fact, once group living is selected for, competition between groups for limited resources may also be expected, and may concur with other factors in promoting large group size. This in turn, may lead to a game dynamic in which large local group size feeds into selection for increasing group size among neighbours, thereby pushing group size in the population further away from optima predicted in other contexts. Ultimately, local ecological conditions would set an upper limit to this process, and depending in particular to resource abundance and distribution, may largely dictate the degree of both intragroup and intergroup conflict.

Study system

The chestnut crowned babbler: group-living and cooperative breeding in an arid environment

The Chestnut-crowned Babbler (*Pomatostomus ruficeps*) is a 50 g passerine, endemic to arid and semi-arid regions of South East Australia (Figure 1, 2b, 3). Together with three other congeneric species occupying a range of habitats in Australia, and a fifth little-known species restricted to tropical forests in Papua New Guinea, it constitutes the family Pomatostomidae, one of a number of Corvoidea assemblages endemic to Australasia. *Pomatostomus* babblers are all cooperative breeders, generally living in rather large groups, and show considerable variation in details of their social organisation, both at an intraspecific and interspecific level, which parallels differences in local and regional ecological conditions.

Within its family, the Chestnut-crowned babbler is the least dependent on trees for foraging, consistent with its distribution across semi-arid habitat types in the Australian interior, and, accordingly, represents the most terrestrial species. Most foraging occurs on the ground, often in dry creek beds or in the proximity of smaller drainage lines. Babblers feed on a wide range of invertebrates, but small vertebrates like lizards are not uncommon prey items. Foraging techniques include mainly probing and digging in the ground, as well as substrate turning, and, less commonly, pecking and probing under the bark of trees (Sorato pers. obs.).

Chestnut-crowned Babblers breed in units of up to 15 adult members, while at other times of the year they can be found in groups of up to approximately 20 individuals, generally shortly after recruitment of offspring. Within large social groups, up to three different females may breed, leading to temporary dissolution of groups into distinct breeding units, constituted by a breeding pair and up to 13 helpers (Russell et al 2010). Social ties between units which are part of the same social group are however evident throughout breeding, as these frequently forage together, and occupy largely overlapping home-ranges (Portelli et al. 2009; Sorato pers. obs). Units fuse again shortly after the fledging of nestlings.

Helpers of both sexes are common, and can be either related or unrelated to the breeding pair. Unrelated helpers may be represented by immigrant, dispersing individuals, mainly females, or by local philopatric offspring of previous breeding individuals. Most helpers however are constituted by philopatric male offspring of breeding pairs, and the contribution of female birds to the rearing of nestlings, as measured by individual feeding rates at nest, is only marginal (Browning 2010). Helpers contribute a significant amount of total brood provisioning, and have a strong effect on group breeding success, with an extra nestling fledging for every three additional helpers in the group (Russell et al. 2010). In addition, helpers further increase group reproductive success by allowing earlier breeding and by reducing the time span between subsequent breeding attempts (Russell et. al 2010).

Breeding seems mainly seasonal, usually from July to November, but appears also to

respond to local ecological conditions, particularly rainfall. Breeding units can have up to three breeding attempt per season, though one or two successful attempts are most common. Average clutch size is four eggs, incubation is performed exclusively by the breeding female and lasts approximately 21 days, and nestlings typically fledge when they are 21-25 days old. Consistent with their resource-poor habitat, nestling starvation is not uncommon, and, coupled with a low frequency of nest-predation, is the leading cause of mortality of chicks. Post-fledging care is prolonged, as allofeeding can be observed for up to two months post-fledging (Browning 2010).



Figure 1. Chestnut-crowned Babblers feeding at a nest (Photo by E. Sorato)

Like their congeneric relatives, Chestnut-crowned Babblers build typical dome-shaped nests made of intertwined sticks, lined with feathers, and, locally, sheep wool (Figure 2). Several nests are built within a group's home range, either on tall-shrubs or trees, providing both breeding and roosting sites. Breeding females can be easily localised as they frequently utter loud distinctive peeping calls from the nest site, during both incubation and chick brooding. Roosting sites are selected by groups on a daily basis, and often several nests are prospected before a nest is finally selected. Group members may split between 2-3 different roosting nests, particularly when part of large groups, even though groups of up to 22 individuals have also been observed roosting in a single nest (Sorato, pers. obs). The same roost site may be selected over several consecutive nights, or different nests may be used.

As implied by their common name, babblers are highly vocal birds. Chattering of group members is commonly heard in several contexts, generally associated with excitement or arousal. Interestingly, loud chatter calls are uttered from roosts immediately preceding emergence at dawn, and these can be heard from a few hundred meters apart, suggesting a possible function in intergroup communication or advertisement (Sorato, pers. obs). Chatter vocalisations are also uttered in response to terrestrial predators, including humans. Besides by breeding females, high-pitch peeping calls are also used as contact vocalisation by other group members, particularly fledglings and juveniles, and a similar call type functions as an alarm for aerial predators.

Finally, the species appears characterised by a shy, risk-averse behavioural syndrome. Unlike other cooperative breeders, Chestnut-crowned Babblers do not mob potential predators, except when nests with eggs or chicks are under threat, and are not easily approached. Their overall shyness is particularly evident when their behaviour is compared with other babblers sharing their home range in areas of sympatry (E Sorato and AF Russell, pers. obs).



a)



b)

Figure 2. a) Chestnut-crowned Babbler nests on a red-gum tree (*Eucalyptus camaldulensis*), and
b) babblers inspecting a nest. (Photos by E. Sorato).

Study site and population

This study was conducted at Fowlers Gap Arid Zone Research station, Western New South Wales, Australia (31°05' S, 141°43' E; figure 3), from October 2007 to March 2010.

The total study area extended over more than 64 km², and encompassed four main habitat types, defined by a combination of different vegetation species, varying amount of vegetation cover and distribution, as well as differences in soil type and other landscape features, primarily distribution of ephemeral creeks and drainage lines (Figure 4).

Rainfall is generally low, with an average annual precipitation usually less than 200mm, and temperature shows a pronounced seasonal variation, with mean monthly minimums at their lowest in July with 5° C, and maximum averages at their top in January with 37 ° C.

As a consequence of the general aridity of the study area, the chenopod shrubland which dominated the site was typically sparse in its distribution. For example, in the 10km² central part of the field site, tree density (principally *Casuarina pauper*) was 0.5 trees per 100m², while the percentage of shrub ground-cover (principally bluebush: *Maireana* spp.; saltbush: *Rhagodia* and *Atriplex* spp; copperburs: *Sclerolaena* spp.) amounted to just 28%, the rest consisting largely of open gibber, clay, sand and exposed bedrock (Portelli et al. 2009). Trees and shrubs were more common in the narrow (1-5m) dry drainage lines descending from surrounding hills than they were in other areas, and invertebrate prey biomass was also heavier (Portelli et al. 2009). Much of the rest of the field site considered in this study was similar, but also included areas of floodplains in which creeks were more sparse and dominated by prickly wattle (*Acacia victoriae*), as well as a single large (generally dry) creek dominated by river red gum (*Eucalyptus camaldulensis*).

The most prevalent habitat type encompassed the hilly areas in the centre of the field site and was characterised by a medium density of *belah* and bluebush on thin clay soils with commonly exposed bedrock. A second habitat zone was distinguished as having low numbers of both trees and bluebush, but a deeper soil layer including sand/loam. A third type of habitat

could be identified as having overlapping soil and rock characters with the previous two, but differed because of a locally high tree density, coupled with a low amount of bluebush. A final habitat zone was characterised by a flood plain area, with a deep sandy soil layer, and was largely devoid of trees, with the exception of tall red gum trees bordering a large ephemeral creek, but had abundant tall shrubs, dominated by prickly wattle, as well as short shrubs in the form of both bluebush and saltbush.



Figure 3. Satellite image of the field site at Fowlers Gap, and its location within Australia. Blue dots in the main image show locations of breeding nests in the year 2007. In the inset image, the Chestnut-crowned Babbler range of distribution is shown in red.

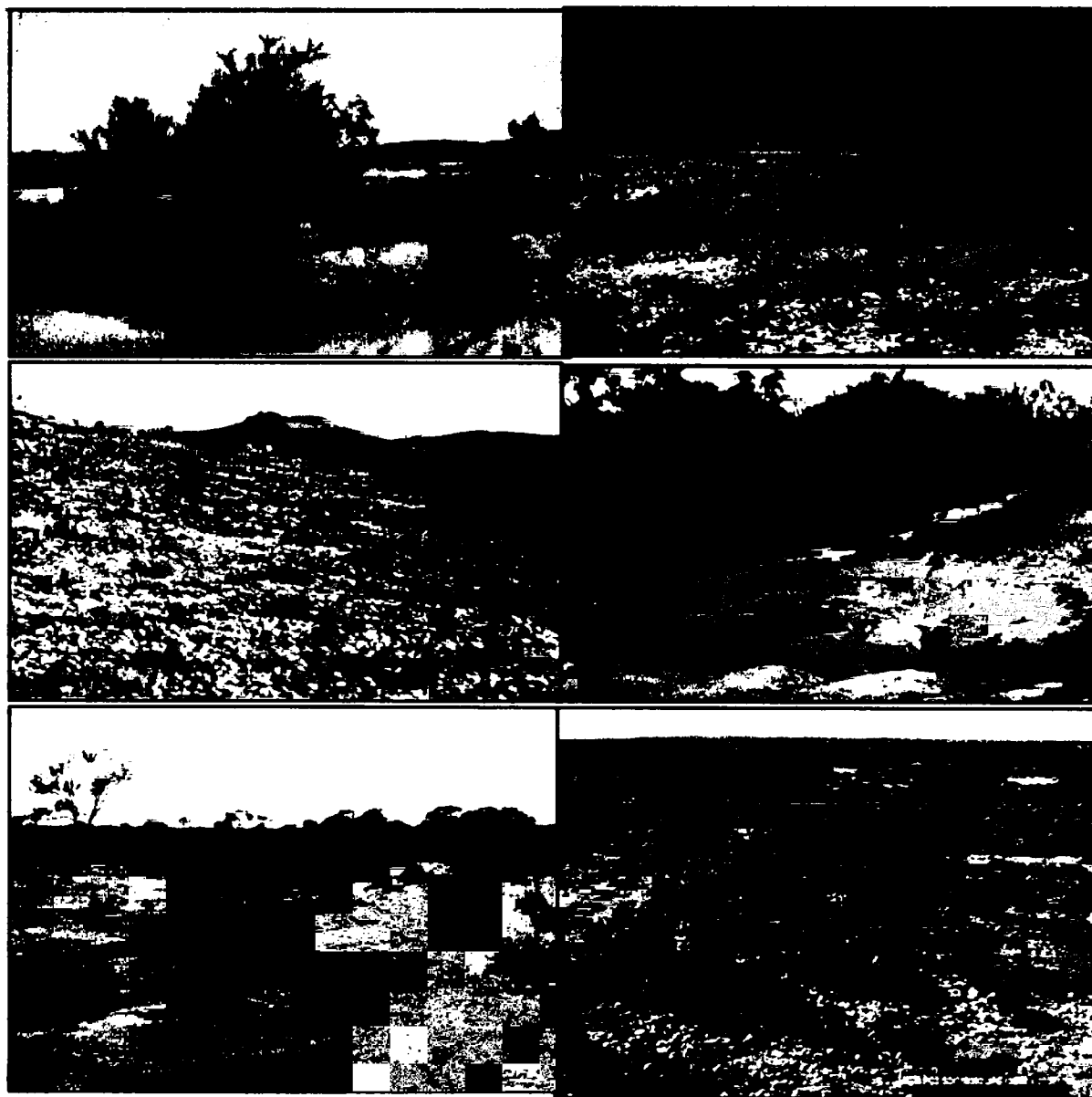


Figure 4. Examples of habitat variation within the field site at Fowlers Gap, showing the degree of variability in vegetation type, amount of cover, and soil type (Photos by E. Sorato).

It was perhaps inevitable for a study on a cooperatively breeding species to build on cooperation between a number of different people. The local babbler population had been under investigation since 2004 by Andy Russell, and this study has built and expanded on previous work to identify avenues and questions for research, as well as possible answers. Lucy Browning and James Savage have joined the study in 2007, and together with A. Russell have worked on cooperative breeding in the species. In particular, they have been monitoring breeding attempts, quantifying helper contributions at the nest, and have been in charge of catching and banding chicks and adult babblers. I joined the study in October 2007, and my work has focused on tracking groups while foraging away from the nest, and during the non-breeding season. I have also helped with searching for breeding nests, and followed groups to roost sites in order to record roost vocalisations on the following mornings. While tracking groups, I have noted group behaviours, and have performed playback experiments simulating encounters with other groups. Finally, over the years a number of field assistants have also contributed to the project by acting as helpers in all the aforementioned aspects of the study.

This thesis investigates effects of local ecology on group-living, as well as correlates and implications for sociality. While breeding and helping at the nest have been investigated since the establishment of the study system by the aforementioned investigators, my thesis focused on other aspects of group-living, studying in particular behaviour of groups while foraging away from the nest, and expanding the temporal scope of the investigation beyond breeding, to include different reproductive phases within years.

Thesis outline

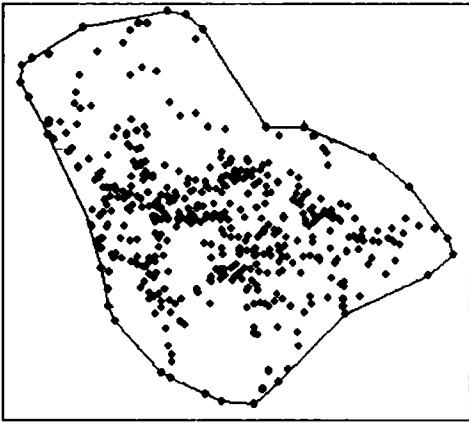
Among the several direct benefits that have been suggested to promote group-living, predator protection is one of the most widely invoked. In chapter 2, I investigated how risk of predation covaried with group size, and how it was affected by local ecological condition and reproductive phase.

Competition for finite resources imposes an upper limit to group size, which is largely determined by features of the local ecology that affect resource availability. Food abundance may represent the most limiting factor for group size, particularly in resource-poor habitats. Therefore, next (Chapter 3) I examined daily movements of babbler groups during foraging, and considered whether group movements showed any evidence of being affected by local resource depletion. Specifically, I analysed effects of group size and habitat type on group ranging behaviour.

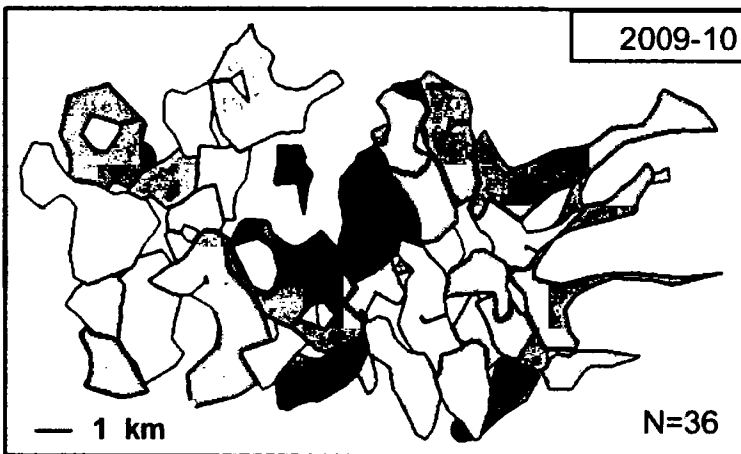
The temporal scope of the analysis is expanded in Chapter 4, to investigate how daily group movements combined over an extended time period to determine group home ranges (Figure 5). I examined how different measures of habitat quality and structure were related to group home ranging behaviour and group size, controlling for local social environments, as measured by focal group size and number of neighbours.

Whilst ecological conditions are likely to be the ultimate factors selecting for group-living, as well as prime determinants of group size, the local social environment may feedback and interact with ecology in further shaping species social systems. Therefore, in Chapter 5 I considered how babbler groups responded to simulated intergroup encounters using playbacks of group vocalisations. Specifically, I examined the effects of focal and playback group size, reproductive phase, home range size and features of local habitat previously considered.

At a proximate level, social groups are the outcome of the balance between group reproductive success, local mortality, and individual dispersal decisions. Delayed dispersal is the process that leads to family formation, while dispersal between groups affects genetic structuring within and between social units, which in turn have implications for cooperation. In Chapter 6, I investigated how dispersal was affected by individual phenotype, group size, and ecological factors. To this end, I used a large capture-recapture database, which allowed the detection of several dispersal events between groups in the study area.



a)



b)

Figure 5. a) Example of a post-breeding group home range; points represent relocations. b) Group home ranges for the study year 2009-10.

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Chapter 2

Predator encounter probability and behavioural responses in the cooperatively breeding Chestnut-crowned Babbler

ABSTRACT

There is a divergence between models examining the evolution of group living in species in which groups are based on families and those where it is based on aggregations between non-relatives. In the former, the onus has been on ecological and demographic factors that select for offspring philopatry, including high net costs of dispersal due to a lack of habitat or mates. In the latter, the importance of factors such as foraging success and predation risk are more typically emphasised. While the net constraints on dispersal have been identified in some family-living species, the factors that promote family-living in others are unclear. Here we examine the association between predator encounter rate and behaviour in the chestnut-crowned babbler (*Pomatostomus ruficeps*), a family-living bird species which does not appear to face classic ecological or demographic constraints on dispersal and breeding. We found that the probability of social groups encountering a predator varied with habitat type and increased with measures of group size and juvenile presence. Accordingly, high predator encounter rates were associated with a number of behaviours apparently aimed at reducing the risk of predation, including increased sentinel activity and reduced foraging on the ground. In addition, we calculate that the probability of an individual being caught by a predator is reduced in large groups compared with small ones, due to the dilution effect. We conclude that predation may constitute a significant force selecting for family living in this study system, and that variation in the risk of predation may help explain some of the differences in average group size and overall social organisation across cooperatively breeding species.

INTRODUCTION

Many animals live in social groups at some stage in their lives. While grouping can be costly, due for example to increased parasite transmission (Brown and Brown 1986), foraging competition (Milinski and Parker 1991) or increased probability of detection and attack by predators (Vine 1973; Lindstrom 1989; Cresswell 1994), it is also associated with numerous benefits (Krause and Ruxton 2002; Clutton-Brock 2009). For example, groups might be more adept at finding dispersed and highly clumped food resources (Jarwis et al. 1994), more efficient in foraging (Pulliam 1973; Shridar et al. 2009) and/or detecting or evading predators (Pulliam 1973; Neill and Cullen 1974; Elgar 1989; Roberts 1996; Caro 2005). Despite this, models on the evolution of cooperative breeding systems, where animals live in groups in which at least one member provides care to the offspring of others, seldom consider such generalised benefits of grouping (Emlen 1982, 1995; Poiani and Pagel 1997; Ekman et al. 2004; Doerr and Doerr 2006). Understanding the factors that govern group size in cooperative breeders is not only essential to the quest of providing a coherent theoretical framework for the evolution of cooperative breeding (Hatchwell and Komdeur 2000), but also for understanding the evolution of social complexity (Bourke 1999).

Group size in cooperative breeders is generally regarded as being a function of the costs and benefits of offspring dispersal (Emlen 1995; Hatchwell and Komdeur 2000). In birds in particular, wherein most of the research has been conducted (Ekman et al. 2004; Russell 2004), group size is predicted to increase when high variance in territory quality, coupled with high costs of dispersing to breed independently, lead to reduced offspring dispersal (Emlen 1982, 1995; Stacey and Ligon 1987; Koenig et al. 1992; Covas and Griesser 2007). In some cases, elegant experiments have upheld predictions of such models by showing that relaxation of a constraint led to offspring dispersal and reduced group sizes. For example, removal of territorial birds in superb-fairy wrens (*Malurus cyaneus*) caused dispersal of helpers from neighbouring groups as long as females were present to pair with (Pruett-Jones

and Lewis 1990). Similarly, experimental creation of limiting roosting (DuPlessis et al. 1992) or nesting (Walters et al. 1992) holes, led to increased dispersal in green woodhoopoes (*Phoeniculus purpureus*) and red-cockaded woodpeckers (*Picoides borealis*), respectively. Finally, translocation of families to previously unoccupied islands, lead to family dissolution in Seychelles warblers (*Acrocephalus sechellensis*) until habitat of equivalent quality to the natal one again became limiting (Komdeur 1992). While these examples provide compelling evidence to support the idea that constraints on dispersal promote family-living, in a number of other species the very existence and extent of such constraints are unclear.

More recently, the idea that group benefits can favour philopatry and lead to family living (Stacey and Ligon 1987) has been invoked in a number of species for which classic explanations of habitat saturation and mate limitation appeared unlikely (Ekman et al. 2004). For example, cooperation benefits in a foraging context have been suggested to account for the evolution of eusociality within mole-rats (Batherigidae, Jarvis et al. 1994), while thermodynamic benefits of huddling have been highlighted as a largely overlooked benefit of group-living in many cooperative birds (Du Plessis 2004). Nepotistic access to food resources and protection from predators provided by parents have also been suggested as mechanisms selecting for delayed dispersal in several family-living bird species (e.g. Griesser et al. 2006; Nystrand 2007; Dickinson et al. 2009). Predation risk in particular, has been invoked as the primary mechanism selecting for group-living in cooperative meerkats (*Suricata suricatta*, Clutton-Brock et al. 1999a), and has been experimentally shown to influence dispersal propensity of helpers in the cichlid *Neolamprologus pulcher* (Heg et al. 2004). That predation risk might constitute an important selection pressure on group living in cooperative species is further supported by the fact that some of these have evolved sentinel systems (McGowan and Woolfenden 1989; Clutton-Brock et al. 1999b; Wright et al. 2001a; Ridley and Raihani 2007). Sentinels are individuals standing guard from a prominent position scanning for predators while the rest of the group forages, presumably with increased

efficiency and safety (Bell et al. 2009). Despite this, the role of predation and other generalised group-living benefits are not commonly incorporated into models of group living in cooperative breeders.

The aim of this study is to examine the potential role of predation risk in moulding behavioural strategies, including group size, in a cooperatively breeding bird, the chestnut-crowned babbler (*Pomatostomus ruficeps*), a species that does not seem to be constrained by lack of potential breeding sites and mates. The chestnut-crowned babbler is a 50g bird endemic to arid and semi-arid regions of southeastern Australia. Previous analyses showed it to breed in groups of two to 15 adults (mean = 6.5) when some social groups break up into two to three breeding units (Portelli et al. 2009; Russell et al. 2010). During the non-breeding season, following re-amalgamation of breeding units, group sizes typically vary from seven to 16 adults (mean = 11), and can include up to ten juveniles (mean = 6). However, it is important to note that breeding units from the same social group commonly forage together, meaning that the sizes of foraging groups during breeding and non-breeding seasons are often similar (Portelli et al. 2009). Both pedigree and genetic data confirm that babblers live in extended family-groups formed through delayed dispersal of primarily male offspring (Chapter 6; SC Griffith & AF Russell unpubl. results). Chestnut-crowned babblers have no specific habitat requirement other than trees for nesting/roosting and the ground for foraging (Portelli et al. 2009; AF Russell unpubl. data). Evidence over the past eight years shows that habitat wherein successful breeding has occurred, commonly remains unoccupied (AF Russell unpubl. Data), and thorough analysis of the effects of known ecological correlates of breeding success (Portelli et al. 2009), has failed to identify any ecological or demographic factor which may account for vacant habitat patches apparently suitable for breeding (Russell et al. in prep). In short, the classic explanations for the evolution of family living based on the costs of dispersal, a lack of habitat or mates of sufficient quality for breeding, and high variance in territory quality, do not appear to fully explain family-living in this species.

By contrast, the role of predation remains a distinct, but seldom considered, possibility, because the openness of the arid habitat, and frequent digging in the ground during foraging (Portelli et al. 2009), might make chestnut-crowned babbler particularly vulnerable to aerial predators (Ford et al. 1988; Clutton-Brock et al. 1999a,b).

The specific aims of this study are thus three-fold. First, we quantify predation risk, measured by the encounter rate of babbler groups with known or likely aerial predators, and investigate the effects of habitat characteristics, group size (total and number of adults) and reproductive stage on the probability of encountering a predator. Second, we examine the behavioural responses to increased predation risk, including choice of foraging substrate (ground, tall shrubs, trees) and sentinel activity. Finally, we discuss the likelihood that group size (number of adults) may be selected, in part, by the risk of predation. Based on previous evidence relating predation risk, habitat, foraging technique or substrate, sentinel activity and group size (Lima and Dill 1990; Nystrand 2006, 2007; Bell et al. 2009; Griesser and Nystrand 2009), we predict that predation risk will drive behaviours aimed at reducing such threat, including foraging in safer areas, employment of a sentinel, and increasing group size.

MATERIALS AND METHODS

Study site

The study was conducted from October 2007 to March 2010 in an area of 64 km² at the University of New South Wales (UNSW) Arid Zone Research Station at Fowlers Gap, in the far-west New South Wales (31°05' S, 141°43' E), Australia. Details of the climate and a representative central area of the present study site are presented elsewhere (Portelli et al. 2009). Briefly, for the purposes of our investigation here, rainfall is generally low, on average ranging from 200-2500 mm, and the chenopod shrubland which dominated the site was accordingly typically sparse in its distribution. For example, in the 10km² central part of the fieldsite, tree density (principally *Casuarina pauper*) was 0.5 trees per 100m², while the

percentage of shrub ground cover (principally bluebush: *Maireana* spp.; saltbush: *Rhagodia* and *Atriplex* spp; and copperburs: *Sclerolaena* spp.) amounted at just 28%, the rest consisting largely of open gibber, clay, sand and exposed bedrock (Portelli et al. 2009). Trees and shrubs, which can offer protection from predators, were more common in the narrow (1-5m) dry drainage lines descending from surrounding hills, than they were in other areas, and invertebrate prey biomass was also heavier (Portelli et al. 2009). Much of the rest of the fieldsite considered in this study was similar, but also included areas of floodplains in which creeks were more sparse and dominated by prickly wattle (*Acacia victoriae*) as well as a single large (generally dry) creek dominated by river red gum (*Eucalyptus camaldulensis*).

We categorised habitat throughout the field site into four types based on the amount and species of the dominant trees and shrubs, as well as underlying soil type, depth and geology. The most prevalent habitat encompassed the hilly areas in the centre of the field site and was characterised by a medium density of *belah* and bluebush on thin clay soils with commonly exposed bedrock ('Zone 1'). The second habitat zone was distinguished as having low numbers of both trees and bluebush, but a deeper soil layer including sand/loam ('Zone 2'). The third type of habitat ('Zone 3') had overlapping soil and rock characters as Zone 1 and 2, but differed because of a locally high tree density, coupled with a low amount of bluebush. Finally, Zone 4 was characterised by a flood plain area, with a deep sandy soil layer, and was largely devoid of trees, with the exception of tall river red gum trees bordering a large ephemeral creek, but had abundant tall shrubs, dominated by prickly wattle, as well as short shrubs in the form of both bluebush and saltbush. Habitat type was assigned to babbler groups on the basis of overlap between zones and group home ranges (see below).

The primary predators of independent babblers are likely to be aerial. Red foxes (*Vulpes vulpes*), present within the study site, are unlikely to have the capacity to catch highly mobile babblers, while feral cats (*Felis catus*) are uncommon and tend to hunt at night when babblers are roosting inside inaccessible dome-shaped nests. Further, snakes may be able to capture

babblers, for example at roosts, but they are rarely seen and their importance as predators cannot be quantified. Aerial predators, by contrast, can be spotted on a daily basis throughout most of the study site, and are likely to pose a considerable threat to babblers, as testified by our witnessing of two successful predation events and several attempts. Among falcons, nankeen kestrel (*Falco cenchroides*) is abundant, brown falcon (*F. berigora*) is common, peregrine falcon (*F. peregrinus*) and Australian hobby (*F. longipennis*) are seen occasionally, while black falcon (*F. subniger*) is rarely seen. Among accipiter hawks, both brown goshawk (*Accipiter fasciatus*) and collared sparrowhawk (*A. cirrocephalus*) are common. All species are known to hunt birds of babbler size and all elicit pronounced aerial alarm calls and evasive actions from babblers when flying in obvious proximity (E. Sorato and AF Russell pers. obs).

Data collection

Data were collected during five distinct time periods: October 2007-January 2008, May-July 2008, August-October 2008, July-October 2009, and January-March 2010. These time-windows not only reflected distinct periods, but also variable reproductive stages of the birds. In 2007 and 2008, breeding began in all groups between late July and late August and continued until late October, while in 2009, most likely as a consequence of prolonged drought conditions, breeding started in late August and was limited to about 40% of groups within the study site. Following heavy and prolonged rains beginning at the end of November in 2009, some breeding was also observed in February and March, but again involved only a minority of babbler groups. Thus, the first observation period was largely post-breeding, with fledglings and juveniles common, the second period encompassed a pre-breeding phase, the third was marked by extensive breeding, while the last two periods simultaneously encompassed non-breeding, and, to a minor extent, breeding phases.

Babbler groups were located by extensively searching throughout the study site, aided by

their loud and distinctive calls (group chatter calls and individual long-distance contact calls), or by visiting known roost nests pre-dawn. Groups were identified in the field using unique colour-band combinations and typically followed for up to 4 hours (range = 0.25 – 4 hours; mean = 2.4 hours, follows of < 1h were omitted from analysis). We tracked a total of 48 groups, mainly during early-mid mornings (6-11 h, n = 198 group follows), and, to a lesser extent, in late afternoon (16-19 h, n = 26 group follows) and between late morning and mid-day (11-16 h, n = 32) when babblers were generally less active and tended to spend the majority of their time resting and preening on trees or within favourite thickets of vegetation. Scan sampling (Martin and Bateson 2007) was adopted for five minutes every five minutes throughout the tracking, since the often cryptic and flighty nature of the birds precluded instantaneous sampling. For the same reasons, behaviour was generally recorded at the group, rather than individual, level. For each five-minute period, the general behaviour of the birds (e.g. foraging, resting) and the location in which they were doing so were noted. The location was categorised as: ground, if they were foraging on the ground or in a small shrub under 50cm high; tall shrubs, if they were foraging in vegetation between 50cm and 2m high; and trees, if they were foraging in vegetation over 2m high.

Data on predator encounters and sentinel behaviour were collected on an *ad libitum* basis every time either was observed. Usually, predators were spotted by the observer following aerial alarm calls, and more rarely when flying distantly or perched nearby in trees, neither of which appeared to elicit alarm calls, presumably because they were of little immediate threat (Griesser 2008). Predator encounters were categorised in terms of whether or not they reflected a predation attempt, the latter representing active targeting of the focal group by the predator. Sentinel behaviour was defined as a single bird perching and being vigilant on an exposed prominent position, usually a tall shrub (1-2 m height), while the rest of the group was typically intent on foraging activity on the ground (see Wright et al. 2001a; Clutton-Brock et al. 1999b for similar definitions). Sentinel bouts were recorded qualitatively

and were not timed, as they were generally short, none lasting more than a five-minute period, presumably due to the rapid pace at which babblers moved through their habitat.

Finally, for each track, the following information was also recorded: a) start and end-times, b) location on a Garmin GPS, c) group size and number of juveniles when present, and d) reproductive phase. Time was collected to control for potential seasonal and diurnal variation. GPS location was used to determine the primary zone over which babblers foraged. Fledglings and juveniles were defined as offspring up to one month and between one and three months, post-fledging, respectively. Reproductive phase was categorised as: *breeding* if the groups were in the incubation or nestling phase of reproduction; *young-with-group* if fledglings or juveniles were present; and *non-breeding* for all other times.

Statistical analysis

All statistical analysis was performed in R version 2.11.1 (R Development Core Team, 2010). Statistical modelling was conducted running Generalized Linear Mixed Models (GLMM) using the R package lme4 (Bates and Maechler 2010).

Group identity was fitted as a random intercept in all analyses to account for hierarchical data structure due to statistical non-independence of multiple observations sessions on focal groups, and to appropriately model the random sampling of social groups from the study population.

To facilitate interpretation and comparison of estimates of effect sizes within and between models, all model predictors were centred by subtraction of mean values, and continuous variables were further standardised by dividing them by their sample standard deviation (Schieffelin 2010). Scatterplots of residuals and predicted values were generated to check model assumptions. We then used an information-theoretic approach to select best explanatory models from candidate model sets, based on the Akaike information criterion (AIC. Burnham and Andersson 2002) with the Hurvich and Tsay correction for finite sample

size (AICc). Sets of candidate models were defined on the basis of biologically plausible hypothesis, and included combinations of the track-specific confounding terms and the aforementioned group-specific and ecological predictors. Model selection was performed with the R package AICcmodavg (Mazerolle, 2011), which yielded relative weights for candidate set models based on AICc scores. The best model was defined as the one with the lowest AIC score, whilst models with $\Delta AICc > 5$ were deemed as unlikely and excluded from final candidate model sets (Burnham and Anderson, 2002). Inference was based on the single top-ranking model if this yielded a relative Akaike weight > 0.9 , otherwise lower-ranking models, with $\Delta AICc \leq 5$, were also considered as relatively plausible, in proportion to their relative weights.

The factors affecting the probability of encountering a predator and proportion of time groups spent on the ground, were both analysed using binomial error structures and logit link functions. In the former, predator met (0, 1) was fitted as the response term and 1 was fitted as the binomial denominator, while in the latter, the number of 5-min observations in which the focal group was located mainly on the ground was fitted as the binomial numerator and the total number of 5-min scans was fitted as the binomial denominator. Habitat type, group size (either total group size or number of adults in the group) and reproductive stage were fitted as primary explanatory terms of interest, while track duration and time of the day were fitted as covariates. Whether or not a predator was met in the course of a tracking session, was entered as a further explanatory term of interest in the foraging substrate analysis. Factors associated with sentinelling behavior were analysed using a GLMM with Poisson error structure and logarithm link function. Whether or not sentinel behavior was observed during each group-follow constituted the dependent binary dependent variable in the analysis.

Habitat zone, group size, reproductive phase, percentage of time foraging on the ground, and whether or not a predator was encountered, were entered as primary fixed effects of interest, while track duration and start time were again entered as potentially confounding covariates.

Finally, a one-tailed binomial test was run to test whether sentinelling was more likely to be observed after a predator was encountered rather than in the preceding period during which the group was followed.

RESULTS

Predator encounters

Predators were encountered on a total of 63 tracking sessions, out of a total of 211 (30%). Further, of these 63 encounters, 13 resulted in a predator attack (20%), and two had fatal outcomes (3%). Falcons (*Falco* spp.) were encountered in the course of 57 tracking sessions (90.5%), and accipiterine hawks (*Accipiter* spp.) were met during 6 sessions (9.5%). Predator attacks were observed during 10 encounters with falcons (17% of encounters), and three encounters with accipiterine hawks (50%). Finally, of the two attacks that produced fatalities, one involved a peregrine falcon (*Falco peregrinus*) and the other a brown goshawk (*Accipiter fasciatus*).

Groups appeared to differ substantially in their probability of encountering a predator: at one extreme of the range of variation, one group never met a predator in the course of a total of 15 hours of observation spread on a total of 7 days, while at the other extreme, another group met predators on 5 out of 6 tracking sessions, covering a total of 13 hours. After accounting for the effects of track duration, predator encounter probability varied systematically with habitat zone, group size and reproductive phase (Table A1a in Appendix, Table 1). Models featuring either total group size or number of adult birds in the group indicated that the latter was a better predictor, though differences in AICc scores were not pronounced ($\Delta\text{AICc} < 2$).

According to best model predictions, the probability that a group encountered a predator was almost three times higher when young were present in the group as compared to breeding (incubation and nestling phases. Figure 2a). In addition, there was an almost twofold increase

in encounter risk from zone 4 to zone 2 (Figure 3a). Finally, the probability of encountering a predator also increased with number of adults in the group (Figure 1).

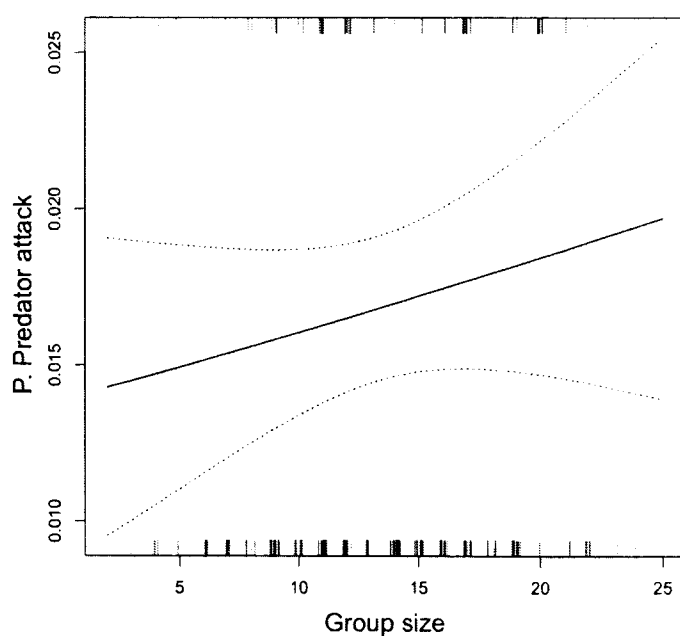


Figure 1. Relationship between predation risk and group size. The continuous line represents probability estimates from the best model with total group size substituted to number of adults in the group. Dotted lines show errors of estimates (SE). Rugs indicate distribution of raw observations of group encounters with predators.

Table 1. Best model estimates of random and fixed effects on probability of predator encounter.

BEST MODEL				
Random effects:				
	Variance	Std.Dev		
Group ID (Intercept)	0.25	0.50		
Number of obs: 210				
Groups: 48				
Fixed effects:				
	Estimate	Std. Error	z-value	P
(Intercept)	-0.97	0.19	-5.13	<0.01
Duration	0.19	0.17	1.15	0.25
Breeding	-0.24	0.65	-0.36	0.71
Young	1.16	0.37	3.11	<0.01
Zone 2	0.35	0.46	0.75	0.45
Zone 3	-0.55	0.54	-1.01	0.31
Zone 4	-0.65	0.66	-0.98	0.33
N. adults	0.09	0.18	0.51	0.61

All fixed effects estimates are from standardised centred predictors (Schieelzeth 2010).

Behavioural Responses

Babblers spent between 41% and 100% (mean = 41%) of their time foraging on the ground or in small shrubs, between 0 and 83% (mean = 24%) foraging in tall shrubs, and 0 to 95% (mean = 35%) of their time foraging in trees. The proportion of time that babblers spent foraging on the ground was influenced by time of day, habitat zone, reproductive phase, whether or not they encountered a predator, and only weakly by group size (Table A1c, 3). Babblers spent more time foraging on the ground in early morning and late afternoon, their peak foraging periods and spent almost twice as much time foraging on the ground in habitats where tall shrubs or trees were least common (Figure 3c). In addition, the ground foraging strategy became less common when young (fledglings and juveniles) were present in the group (Figure 2c) and when predators were encountered. Predicted amount of time spent on the ground decreased from 40% for tracking sessions with no predator encounter, to 30% when a predator was met.

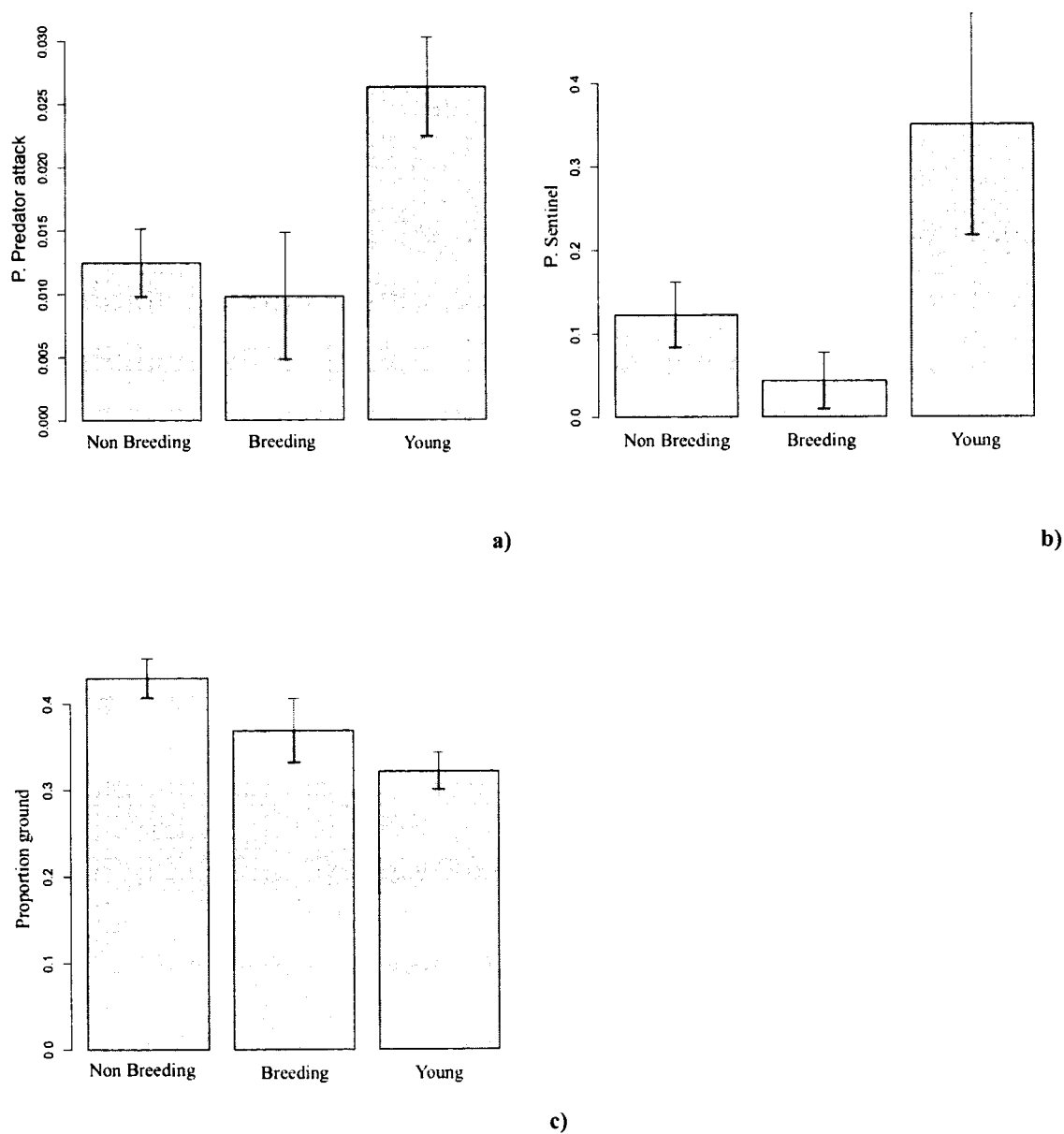


Figure 2. a) Predation risk, b) probability of occurrence of sentinel behaviour, and c) proportion of ground-substrate use during different reproductive phases. Bars show estimated marginal means \pm SE.

Table 2. Best model estimates of random and fixed effects on probability of sentinel occurrence.

BEST MODEL				
Random effects:				
	Variance	Std.Dev		
Group ID (Intercept)	0.82	0.91		
Number of obs: 164				
Groups: 46				
Fixed effects:				
	Estimate	Std. Error	z-value	P
(Intercept)	-1.90	0.30	-6.25	<0.01
Start time	-0.43	0.33	-1.33	0.18
Start time ^2	0.05	0.15	0.34	0.73
Start time ^3	0.24	0.13	1.88	0.06
Duration	0.73	0.20	3.65	<0.01
Breeding	-1.03	0.77	-1.33	0.18
Young	1.04	0.30	3.48	<0.01
Zone 2	0.00	0.52	0	0.99
Zone 3	-1.19	0.75	-1.57	0.11
Zone 4	-1.84	0.88	-2.09	0.04
Ground substrate use	0.63	0.20	3.13	<0.01

All fixed effects estimates are from standardised centred predictors (Schielezeth 2010).

Sentinel behaviour was observed during 44 out of 166 tracking sessions (26%). Mean number of sentinel bouts per average tracking period= 0.5). According to the best model, sentinel behaviour was influenced by track duration, time of day, substrate use, reproductive phase, and habitat type (Table A1b, 2). The frequency of sentinelling increased from early to late morning, decreased slightly during midday and early afternoon, and increased again in late afternoon. Predicted sentinelling frequency showed a 3-fold decrease between non-breeding and breeding phases, and a 7-fold increase when fledglings or juveniles were present in the group (Figure 2b). Further, amount of sentinel activity in different habitats appeared to match local predation risk, with more than a five-fold increase in sentinel behaviour from zone 4 to zone 1 & 2 (Figure 3b). Finally, although overall, there seemed to be no effect of predator encounter on probability of observing sentinelling, within those tracking sessions during which a predator was met and sentinel activity was also observed, sentinelling was more likely to be observed after the encounter with the predator rather than before (one-tailed binomial test, $P=0.01$).

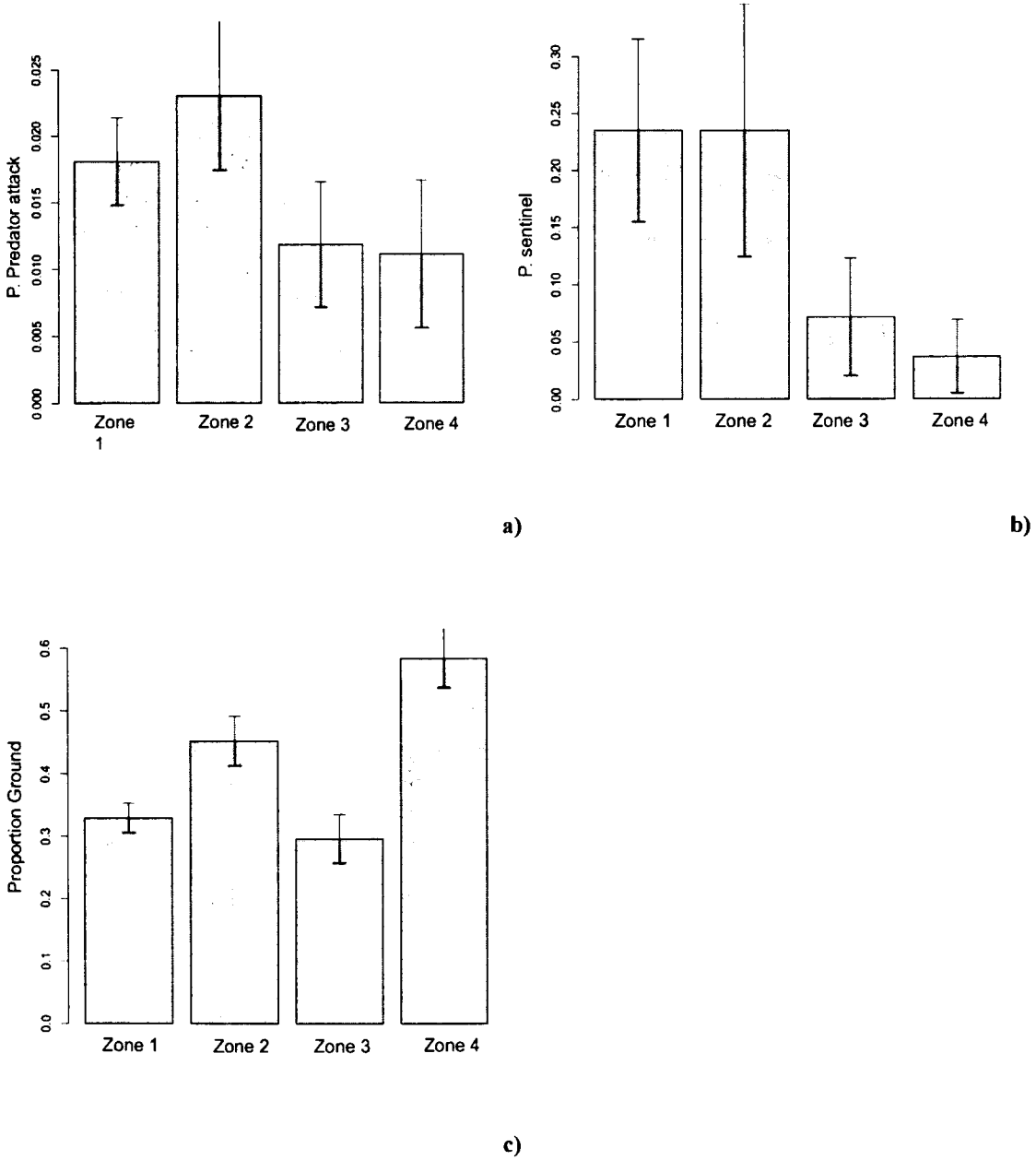


Figure 3. a) Predation risk, b) probability of occurrence of sentinel behaviour, and c) proportion of ground-substrate use in different habitat zones. Bars show estimated marginal means \pm SE.

Table 3. Best model estimates of random and fixed effects on amount of ground-substrate use.

BEST MODEL				
Random effects:				
	Variance	Std.Dev		
Group ID (Intercept)	0.13	0.37		
Number of obs: 204				
Groups: 48				
Fixed effects:				
	Estimate	Std. Error	z-value	P
(Intercept)	-0.50	0.08	-6.16	<0.01
Start time	-0.42	0.08	-5.36	<0.01
Start time ^2	0.08	0.04	1.93	0.05
Start time ^3	0.10	0.03	3.82	<0.01
Breeding	-0.25	0.16	-1.61	0.10
Young	-0.46	0.10	-4.73	<0.01
Zone 2	0.51	0.18	2.80	<0.01
Zone 3	-0.16	0.21	-0.76	0.49
Zone 4	1.04	0.21	4.88	<0.01
Predator met	-0.34	0.10	-3.47	<0.01
Group size	0.09	0.05	1.84	0.07

All fixed effects estimates are from standardised centred predictors (Schielezeth 2010).

DISCUSSION

Chestnut-crowned Babbler groups encountered aerial predators on 30% of 211 tracking sessions with an average duration of 2.4 hours. The probability that predators were encountered varied significantly between habitat types and increased with measures of group size and with the presence of young in the group. At the same time, babblers showed a number of behaviours that were presumably employed in response to the perceived risk of predation. Most notably, groups were least likely to forage on the ground when young were present, and when a predator had been met. In addition, babbler groups were more likely to have a sentinel when they were foraging on the ground, when they included young birds, in habitats where predators were more commonly encountered, and after encountering a predator. Taken together, these results suggest that the perceived threat of predation can influence individual and group strategies on a behavioural time-scale.

For predation risk to exercise an important selection pressure on group living, individuals must experience a decreasing risk of predation with increasing group size (Krause and Ruxton 2001). That large groups more commonly encountered a predator would seem inconsistent with this hypothesis and be more supportive of a cost of group living in the form of increased visibility to predators (Cresswell and Quinn 2011). However, an alternative interpretation of our results is that group size increases with predation, rather than the other way around, as a way of reducing individual predation risk. A number of findings are more consistent with this latter hypothesis. First, given that large groups were more frequently attacked by predators, we might expect them to forage on substrates providing cover from predators (i.e. tall shrubs and trees) and to employ a sentinel more often (Bell et al. 2009; Ridley et al. 2010). However, we failed to find evidence of either: group size was not associated with sentinel frequency and showed a weak positive relation with ground foraging. It is noteworthy that this absence of predicted group size effects on foraging substrate or sentinel activity was found despite the findings that groups were less likely to forage on the

ground and more likely to employ a sentinel when predators were encountered (Bell et al. 2009; Ridley et al. 2010). That group members would appear to have the capacity to modify their behaviour in response to predation risk but do not do so in groups of varying size, suggests that individuals in large groups do not suffer higher predation despite the increased predator encounter rate. Second, if predators targeted larger groups per se, we would expect total group size (adults + non-adults) to be a superior predictor of predator encounter rate than the number of adults. On the contrary, we found that the number of adults was the best predictor. Together, these results suggest that the association between group size and predator encounter rate may have been driven by an adjustment of group size to perceived (or actual) local predation risk (van Schaik and Hörstermann 1994; Hill and Lee 1998; Krause and Ruxton 2002; Crasswell and Quinn 2011).

Assuming the above interpretation leaves as an open question what might have been the antipredator benefits of group living in chestnut-crowned babblers. Predator deterrence can be ruled out, since babblers never mob predators and always flee to cover when attacked. Nepotistic benefits represent another unlikely possibility. For example, while in Siberian jays, in which groups generally comprise three to four birds, which include the breeding pair and philopatric offspring or dispersed young birds, breeders are more likely to utter alarm calls when predators threaten their offspring (Griesser and Ekman 2004), in chestnut-crowned babblers groups are larger and more complex, often containing extended families of varying kinship and immigrant females (Chapter 6), and always appear to utter alarm calls when predators approach (E. Sorato & AF Russell pers. obs.). Accordingly, more likely explanations may be that larger groups are more efficient in detecting predators early (Elgar 1989; Krause and Ruxton 2001), while at the same time individuals within large groups are less likely to be predated should predators not be detected in time, either because of confusion (Landeau and Terborgh 1986), selfish herd mechanisms (Hamilton 1971), or dilution effects (Cresswell and Quinn 2011).

While we could not quantify selfish herd mechanisms, and how detection latency varied with group size, we estimated dilution effect by using the estimates of individual predation risk derived from model predictions of probability of predator- encountering as a function of group size, multiplied by the probability of the predator engaging in an attack, and then dividing this product by group size. This calculation shows that despite the higher probability of predation encounters associated with an increasing number of adults in groups, estimated individual risk of predation showed a roughly exponential decrease with increasing group size. Therefore, all else being equal, birds were increasingly less likely to be the target of an attack until group sizes reached approximately 10 individuals, after which the probability declined only slightly. In this study the average group size was 13.5 (range 2 – 25), consistent with predictions of optimal trade offs between dilution benefits and costs of large group size. While we do not imply that predation is the only force involved in selection for group living in babblers, and other factors are in fact likely to promote family living and kin association, we suggest that predation risk may affect optimal group size and be implicated in the relatively high level of dispersal, predominantly from smaller into larger groups, that seems to characterize the study population (Chapter 6).

An analogous calculation can also be used to estimate the habitat-specific benefits of group size. In this case, larger groups appear to benefit more from dilution effects in habitats with higher risk of predation, and differences in average group sizes across different habitat types were consistent with the predicted increased benefits of living in larger groups in areas with higher predator densities (Figure 4a).

A further result of interest regarding dilution effects and consequences of group-living more generally is that predation encounter rate increased in the presence of fledglings and juveniles. In contrast with the interpretation of the effect of the number of adults above, this result is likely to be driven by the increased visibility and vulnerability of juveniles in groups. For example, the reduced mobility of such age classes of birds often lead to them trailing the

group while frequently uttering long-distance contact calls (E Sorato & AF Russell pers. obs.). Another non mutually exclusive explanation for this pattern, that higher frequency of predator encounters in the presence of young in the group may have been a consequence of increased predator activity, for example if breeding of local raptors coincided with the fledging period of babblers, seems unlikely in the light of the temporal spread of breeding and the between year variation in breeding success that characterised our study population. Even though the presence of young appeared costly in terms of increased predation, larger group size partially compensated these costs through an increased dilution effect (Figure 4b). Indeed, it is conceivable that adult group members benefit from the presence of juveniles, since juveniles are likely to be a preferred target for predators. This potential benefit would be most reaped by those which are distantly related to the offspring, such as immigrant females, increasing the potential selective advantage for such females to join groups with juveniles. Further work is required in this area, however, to test the potential costs and benefits of group living for individuals of varying degrees of relatedness.

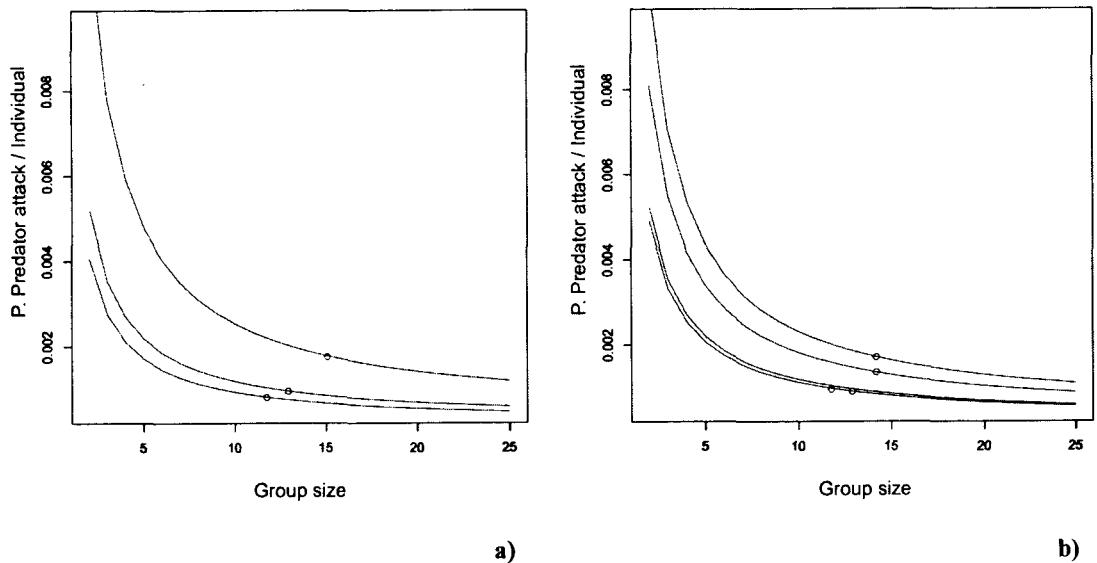


Figure 4. Estimated individual risk of predation as a function of group size.

- a)** Separate lines represent estimates for different reproductive phases. From top to bottom curve: i) probability when groups have young, ii) probability when groups are not breeding and do not include young, iii) probability during breeding (incubation and nestling phases). For each reproductive phase, open circles show estimated individual predation risk in correspondence of mean observed group size values.
- b)** Separate lines represent estimates for different habitat zones. From top to bottom curve: i) probability in zone 2, ii) probability in zone 1, iii) probability in zone 4, and iv) probability in zone 3. For each habitat zone, open circles show estimated individual predation risk in correspondence of mean observed group size values.

Finally, although our aim was not to test the various models of sentinelling behaviour, primarily due to the difficulty with consistently identifying individuals in the field, some findings are of note. The function of sentinels and the factors that affect their prevalence are contentious (Bednekoff 1997, 2003; Clutton-Brock et al. 1999b; Wright et al. 2001b; Russell 2004; Bell et al. 2009; Ridley et al. 2010). For example, while sentinelling has been suggested to be a selfish, condition-dependent strategy promoting self-survival (Bednekoff 1997) and some studies uphold this idea (Clutton-Brock et al. 1999b; Wright et al. 1999), others have suggested that it might constitute a costly cooperative activity (Russell 2004; Hollen et al.

2008). In our study, overall, patterns of sentinel activity appeared to match spatio-temporal variation in the probability of encountering a predator (Bell et al. 2009, Ridley et al. 2010) because it was more likely in areas and at times when predators were more commonly encountered. These results suggest that sentinelling is, at least in part, a behaviour that occurs in response to predation pressure. Nevertheless, it would appear to be less common in chestnut-crowned babblers than has been reported in other species (Wright et al. 2001a; Ridley and Raihani 2007; Clutton-Brock et al. 1999), possibly due to the relatively higher density of ground-shrubs providing protective cover from predators (Whitfield 2003; Portelli et al. 2009). Whether or not this behaviour is selfish or cooperative, however, is less clear. That sentinelling increased throughout early morning suggests that it may be condition-dependent (see also Bednekoff and Woolfenden 2003; Clutton-Brock et al. 1999b; Wright et al. 2001c). Alternatively, increased sentinelling may have matched increased predator activity, but countering this hypothesis is the lack of effect of time of the day on probability of encountering a predator. Further, the fact that individuals were more likely to go on sentinel when offspring were travelling with the group, might suggest that sentinel behavior is a condition-dependent cooperative strategy, as is the case with all cooperative activities (Boland et al. 1997; Clutton-Brock et al. 2002). Disentangling whether or not the primary force selecting for sentinelling is selfish and any benefits to the rest of the group are incidental, or whether it is a costly cooperative activity, cannot be verified at this time.

In conclusion, we suggest that group living in chestnut-crowned babblers is a behavioural mechanism that, at least in part, has evolved to reduce the risks of predation. Given that babblers live in extended family-groups generated, in part, through the retention of offspring, suggests that predation pressure might help to explain variation in group size and social complexity within this species and among some others (Griesser; Heg et al. 2004; Clutton-Brock et al. 1999a). Nevertheless, group sizes of both below and above the mean number expected given predation risk were observed. Other potentially explanatory factors

include poor breeding success in the previous season, or competition for food and breeding opportunities (Emlen 1982; Brouwer et al. 2006; Krause and Ruxton 2002). Given that group size is suggested to be the most important determinant of social complexity in cooperatively breeding species (Bourke 1999), future work in this and other species into the determinants of group size is likely to shed light on the evolution, maintenance and complexity of cooperative breeding systems. While specific ecological constraints are likely to play an important role, we suggest that more classic generalised group-living benefits also need to be considered both theoretically and empirically in research of family-living species if we are to understand the variation within and among species, and to arrive at a single all-encompassing theoretical framework for understanding the evolution of sociality.

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Chapter 3

Ranging behaviour in the cooperatively breeding Chestnut-crowned Babbler is consistent with local resource depletion affecting daily group movements

ABSTRACT

Models and empirical studies examining the evolution of group living have focused on benefits of social aggregation and philopatry, or have considered constraints to individual dispersal as factors promoting family living. In contrast, costs of group living have received comparatively less attention, or have been relatively narrow in their scope. In particular, studies of cooperative breeding species, and more generally group-living species, while focusing on cooperation have largely overlooked costs of competition for limited food resources. This may have hampered progress in our understanding of social evolution, because resource limitation is likely to have implications for social living, primarily by constraining maximum group size and counterbalancing group augmentation benefits, particularly in resource-poor environments. In this study we examine daily movements of foraging groups in the cooperatively breeding chestnut-crowned babbler, a bird species inhabiting semiarid and arid habitats in the Australian interior. We consider whether group movements during foraging showed evidence of being affected by local resource depletion, particularly during breeding, when resource demand is at its highest and birds are constrained in their movements due to parental and alloparental care at the nest, and whether group ranging behaviour was related to group size, and habitat type. We found that an index of local revisitation, and the average distance from the nest during breeding, co-varied with group size, reproductive phase, and habitat in ways consistent with predictions of local resource depletion. We conclude that studies of cooperative breeding should expand their scope beyond behaviour in close proximity of the breeding nest, and should incorporate implications of costs and constraints to resource acquisition for individual investment in parental care.

INTRODUCTION

Reproduction represents a central event in animal life history, and because of its energetic requirements and related constraints, can lead to major reorganisation in animal behaviour, physiology and social organisation. Not surprisingly, cooperative breeding has been an important focus in studies of group-living social organisms, but it has been somehow limited in its scope by revolving mainly around group and individual behaviour at the nest, or in close proximity to it (Heinsohn et al. 1990; Cockburn 1998).

In fact, while foraging behaviour in relation to the needs of offspring provisioning has been investigated in many species of birds with biparental care, leading to the development of a distinctive field of investigation within optimal foraging theory (central place foraging, Houston and McNamara 1985; Stephens et al 2007; Olsson et al 2008), the development of similar studies for group living social birds has largely lagged behind (Hegner 1982; Krebs and Avery 1985; Sauter et al 2006). This is understandable in the light of the logistic and practical difficulties of following highly mobile organisms like birds, nevertheless a comprehension of group behavioural dynamics away from the nest may prove crucial for a full appreciation of the costs and benefits to individuals, that underpin cooperative systems. The foraging ecology of groups and individuals away from the nest may have important implications for studies of cooperatively breeding species, given that ecological factors have been routinely invoked to explain variation in vertebrate social organisation (eg Emlen and Oring 1977), and have in particular been deemed as central for understanding avian cooperative breeding (Emlen 1982; Stacey and Ligon 1987; Koenig et al 1992; Hatchwell and Komdeur 2000). However, while several studies have addressed the importance of habitat quality for individual dispersal decisions (Hatchwell and Komdeur 2000; Ekman et al 2004), few have considered the effects of ecology on group foraging dynamics and parental care (Baglione et al. 2006; Canestrari et al. 2008; Portelli et al 2009; Buintjes et al 2010; Wright and Radford 2010).

This is unfortunate, as considering resource availability within a framework provided by the optimal foraging theory (Stephens and Krebs 1986; Wright et al. 1998), may also be relevant for studies of relative individual contributions to cooperation within social groups (Wright and Radford 2010). Adaptive explanations routinely invoked in this context, focus on kinship benefits and individual conflicts over optimal amount of care, whereas the variance in individual costs of provisioning arising from differential individual access to resources, and effects of group size on the latter, have not received the same amount of attention (Legge 2000; Radford and Du Plessis 2000; Dickinson and Hatchwell 2004; Heinsohn 2004). In this study, we investigate whether movements of foraging social groups in an avian cooperative breeder were consistent with costs and constraints of local depletion of food resources. In particular, we analyse how the ranging behaviour of groups was affected by reproductive phase, group size, and habitat type, and further discuss implications for patterns of individual investment in (allo-)parental care, and for reproductive benefits of group living, relevant for studies of cooperative breeding. We hypothesised that benefits of increased brood care associated with large groups, may be counterbalanced by costs due to higher local resource depletion, in particular in resource-poor habitat types and at times when food demands for offspring provisioning peak, potentially leading to specific group size optima for group reproduction. We tested these predictions in an Australian cooperative breeder, the chestnut-crowned babbler (*Pomatostomus ruficeps*), a species typical of open, semiarid habitats providing the opportunity to visually track foraging groups for extended periods of time.

MATERIALS AND METHODS

Study species and site

Chestnut-crowned Babblers are typical of the semi-arid interior of South East Australia, where they can be found in groups ranging from two up to more than 20 birds, the latter following recruitment of offspring in the group. The species can be regarded as a plural breeder, since within large groups, up to three different females may independently reproduce. Consequently, groups can temporary split into distinct units during breeding, constituted by a breeding pair and up to 13 helpers. Yet breeding units belonging to the same social groups frequently forage together and do not appear to use exclusive territories. Further details on the species social organisation, habitat preferences and reproduction are provided elsewhere (Portelli et al 2009; Russell et al 2010).

The study was conducted at the University of New South Wales (UNSW) Arid Zone Research Station at Fowlers Gap, in the far-west New South Wales (31°05' S, 141°43' E), Australia, from October 2007 to March 2010. Within this period, data were collected during the following time windows, defined by a combination of time period and dominant reproductive phase: October 2007- January 2008, May-July and August-October 2008, July-October 2009, and January-March 2010.

Babblers bred between July and October in the first two study years (2007, 2008) while in 2009, most likely as a consequence of prolonged dry conditions, breeding started later in August and was limited to only about 40% of groups within the study site. Following rains in November-March, another breeding bout was observed starting in February 2011, but again involving only a minority of babbler groups.

Within the study site, vegetation consisted of an open chenopod shrubland which present a substantial degree of spatial heterogeneity reflecting variation in local geology and hydrology. Noticeably, creeks, and smaller drainage channels descending from surrounding hills, are important landscape features because of their positive impact on vegetation: red-gum trees

(*Eucalyptus camaldulensis*) are restricted to rims of major creek systems, while in close proximity of smaller channels, *belah* (*Casuarina pauper*), prickly wattle (*Acacia victoriae*), and, to a lesser extent dead finish (*Acacia tetragonophylla*) and rosewood (*Heterodendrum holeifolium*) predominate. Similar positive effects on vegetation biomass are also evident for shrubs, mainly bluebushes (*Maireana* spp.), saltbushes (*Rhagodia* and *Atriplex* spp.) and copperburrs (*Sclerolaena* spp.). Far from creeks, land is characterised by extensive areas with scarce or no arboreal cover, and patchy variable shrub cover which alternates with bare ground patches, the latter including gibber, clay, sand along main creeks, and bedrocks on hills.

Data collection

A total of 40 Babbler groups were studied during the 2007-2008 field season, 23 groups were followed in the breeding phase in 2008, and 32 groups between 2009 and 2011, within a study area that extended over approximately 64 square kilometres. Birds were captured at the nest as nestlings, as well as mist-netted post-fledging, and were ringed with unique colour-bands combinations, to allow individual and group identification. Morphometric measures were also taken, including tarsus length and body weight. Groups were almost exclusively captured during breeding seasons, mostly between August and November of each study year.

In order to collect behavioural data and record movement paths, groups were located throughout the study site with the aid of acoustic cues (group chatter calls and individual contact calls) and followed for a maximum of 4 hours, shorter track durations being usually the consequence of the loss of the focal group. Groups were mainly tracked during early-late mornings (6:00-11:00 hours; n. tracks=259), and to a lesser extent between late morning and mid-afternoon (11:00 -16:00; n. tracks=41) and in late afternoon-evening (16:00-19:00; n. tracks=44). Average distance of the observer from the focal group was to some extent dependant on group approachability (range 10 – 50+ m, approx. average ca 30 m). A GPS

location was automatically recorded every 50 m, using a Garmin eTrex or Geko 301 global positioning system (GPS). As each GPS fix actually represented the position of the observer, care was put into replicating as close as possible the path followed by the tracked group (accuracy ca 10m). A group was regarded as lost, and the tracking session ended, once it could not be located for more than 10-15 minutes, while, for shorter time periods of temporary disappearance, the GPS device was switched off as soon as the group location could not be determined, and switched on again once the group was relocated. Focal groups were scan-sampled whenever individual birds could be sighted, and individual colour-band combinations, group size and the number of juveniles were noted whenever possible.

Finally, for each track, the following information was noted: a) date, b) start and end-time, c) group size and number of juveniles when present, and d) reproductive phase. Based on estimated laying, hatch and fledging dates (see Russell et al 2010 for details), the latter was categorised as: i) 'incubating, ii) 'nestling', iii) 'young', if fledglings or juveniles (up to 120 days post-hatching) were present in a non-breeding focal group, and vi) 'non-breeding' for the remaining.

Movement analysis

Group movement trajectories were quantitatively described by the following basic path descriptives: i) average speed of movement, ii) area covered by the moving focal group, and iii) an index of patch revisitation during each tracking session.

Average speed was obtained by dividing total path length by total track duration, while area was estimated from movement trajectories by applying a 10 m buffer on each side of the steps defined by two consecutive relocations. Buffer size was chosen to account for spread of individual birds within the focal group, and uncertainty in measures of group position.

Thereby, areas correlated with total path length, but deviated from the latter in proportion to the extent of overlap in the trajectory.

To derive the revisitation index, trajectory areas were subtracted from the area of the rectangular polygon of base L , where L is the total path length, and height 20 (=total buffer width), corresponding to the path area expected under the hypothesis of no patch revisitation, and the resulting value was then divided by the latter. This yielded an index of revisitation with a lower bound of 0 for non-overlapping trajectories, and a value of 1 as an upper asymptotic limit for highly overlapping paths.

Finally, for tracks collected during the breeding phase, we also characterised group movement in relation to position of the breeding nest. To this end, linear distances between the nest and trajectory fixes were used for calculating median, mean and maximum path distances from the group breeding nest. Because these three measures turned out to be highly correlated (pairwise correlations: $r > 0.9$, $P < 0.01$), only the median of the distances from the nest was retained as an index of central tendency in subsequent analysis.

All movement analysis was performed using R software version 2.11.1 (R Development Core Team 2010.)

Habitat categorization

We categorised habitat type for each focal group based on the amount and type of average tree and shrub cover, as well as the local geology of the site. In this way, four different habitat zones were defined within the whole study site: the most prevalent habitat encompassed the hilly areas in the centre of the fieldsite and was characterised by a medium density of *belah* and *bluebush* on thin clay soils with commonly exposed bedrock ('Zone 1'). The second habitat zone was distinguished as having low numbers of both trees and *bluebush*, but a deeper soil layer including sand/loam ('Zone 2'). The third type of habitat ('Zone 3') had overlapping soil and rock characters as zones 1 and 2, but differed because of a locally high tree density, coupled with a low amount of *bluebush*. Finally, Zone 4 was characterised by a flood plain area, with a deep sandy soil layer, and was largely devoid of trees, with the

exception of tall red gum trees bordering a large ephemeral creek, but had abundant tall shrubs, dominated by prickly wattle, as well as short shrubs in the form of both bluebush and saltbush. Habitat type was assigned to babbler groups on the basis of overlap between zones and group home ranges.

Main Statistical analysis

Statistical analysis was performed using PASW Statistics v.18 (SPSS, Chicago, IL, USA). Tracks of a duration too short to provide meaningful information on group movements, were removed from subsequent analysis: we used as a threshold value a minimum tracking duration time of 60 min, as this seemed to yield a satisfactory signal to noise ratio, and appeared to provide a sufficient amount of data points for meaningful inference.

Before proceeding to statistical modelling, we assessed correlations between movement variables (two-tailed Pearson correlation) on a data subset obtained by randomly selecting a single track for each group in order to avoid violation of independence assumptions.

Statistical modelling

We used General linear mixed models (LMMs, MIXED Procedure implemented in PASW Statistics v.18) to assess the effects of relevant explanatory terms on group movement parameters and individual condition, estimated by body weight. All model predictors were centred by subtraction of mean values, and continuous variables were further standardised by dividing them by their sample standard deviation (Schiele 2010), as this procedure allows to compare estimates of effect sizes within models and eases interpretation of interactions. Models were checked to confirm to assumptions; correlated predictors were fitted in separate models only, and final models were inspected for normality of residuals and homogeneity of variance. Non-normal dependent variables were transformed to meet LMM normality preconditions.

For group ranging behaviour, we ran two separate analyses on two different time

scales: the first analysis included data from all the four reproductive phases previously defined ('full dataset analysis'), whereas the second was limited to breeding tracks ('breeding-only analysis'). To control for repeated observations and associated non-independence of error-structure, group identity was fitted as a random intercept in the full dataset analysis, but not in the breeding-only analysis, due to small sample size and limited numbers of groups with repeated measures.

Besides 'Group ID' as a random term, predictors for the full dataset models included 'reproductive phase' and 'habitat type' as 4-levels factors. Variables consisted of 'total group size', 'number of adult birds', and 'track duration' and 'start time' as confounding explanatory independents. For each variable, quadratic terms were also considered in conjunction with correspondent linear predictors, to reveal potential non-linear effects. Biologically plausible two-way interactions between the above predictors were also included in relevant candidate models. In the breeding only analysis, 'phase' was substituted by 'brood-age' as finer scale continuous temporal variable, while 'group size' was essentially synonymous with 'number of adults'. Habitat type was coded as a 3-level factor because of low sample size. 'Breeding attempt' number (first or second attempt) was also considered as an additional predictor, and track duration and start time were fitted to models like for the full dataset analysis. Interactions were not considered, as here limited sample size was likely to give rise to spurious effects and lead to model overfitting. For models of individual body weight, we also entered 'Group ID' as a random intercept term, together with 'individual ID' to properly model multiple individual captures. We controlled for time of capture, and for body size by entering tarsus length as a covariate in all models. Predictors of interest were represented by year, brood age, measured as number of days from laying of the last clutch by the breeding female of the group/unit, brood number, group size, and habitat zone. We implemented an information-theoretic approach to model selection based on the Akaike information criterion (AIC), with the Hurvich and Tsay correction for finite sample size

(AICc). Candidate set of models were defined based on biologically plausible hypothesis. AICc scores were then calculated for each model, and compared with the best model score (lowest AICc value). We removed all the models which were a more complex version (featuring more parameters) of simpler models with a lower AICc value. The remaining models with a $\Delta AICc \leq 5$ ($\Delta AICc = \text{focal model AICc} - \text{best model AICc}$) were retained as plausible, and featured in the reduced final candidate model sets (Burnham and Anderson 2002).

RESULTS

Ranging behaviour

Across the entire study period, our sample consisted of 345 tracks with duration ≥ 60 minutes, from a total of 54 social groups (mean value \pm SD: 137.5 ± 47.5 min.).

Typically, group members moved together in a coordinated and cohesive way, with distances between foraging individuals rarely in excess of 10m. Occasionally, one or more individuals, particularly inexperienced young birds, temporally lost contact with the rest of the group, for example when they were moving at a fast pace. Separation however was generally brief, as birds strived to regroup with the aid of loud contact calls. Single birds could be encountered more often during breeding, but these were mostly breeding females attending their nest, and their mates, while the rest of the group appeared to move as a cohesive unit also during brood provisioning.

Average group speed ranged between 0.2 and 1.6 m/s (mean= 0.6 m/s), area covered, obviously related to track duration, was comprised between 2.1 and 66.6 ha (mean= 8.9 ha), while revisitation index ranged between 0 and 0.54 (mean= 0.12).

Within the whole sample, speed was significantly positively correlated with area covered by the focal group, and, to a lesser extent, with revisitation index, while the latter was largely independent from area (Table 1a). For the breeding sample, median distance from the nest

was positively associated with area and speed, whereas revisitation index did not correlated with any other movement parameter (Table 1b).

Thereby, our set of movement parameters provides information on different aspects of ranging behaviour with a limited amount of internal redundancy.

Table 1. Correlations between variables describing group ranging behaviour

	area	median dist. from nest	speed	revisitation index	
area			x r=0.632, P<0.001	r=0.188, P=0.177	
median distance from nest	r=0.657, P<0.001			x	A) whole dataset (n=54 groups)
speed	r=0.779, P<0.001	r=0.806, P<0.001		r=0.416, P=0.002	
revisitation index	r=0.050, P=0.813	r=0.131, P=0.534	r=0.028, P=0.896		
	B) breeding only (n= 26 groups)				

Top right side: correlations from the full dataset; bottom left side: breeding-only sample

Table 2. Best model estimates of fixed effects on descriptives of group movements:

a) full-dataset analysis, b) breeding-only analysis.

Response variable	Fixed effects		Estimate	Std. Error	t	P
Area	Intercept		0.02	0.06	0.30	0.76
	duration		0.60	0.04	15.12	<0.01
	start time		-0.07	0.04	-1.88	.06
	Reproductive phase	Incubating	-0.01	0.13	-0.05	.96
		Nestlings	-0.74	0.13	-5.59	<0.01
		Young	-0.64	0.08	-7.60	<0.01
	Habitat	Zone2	0.26	0.16	1.57	.12
		Zone3	0.35	0.19	1.87	.07
		Zone4	0.48	0.16	2.99	<0.01
Speed	Intercept		0.02	0.07	-0.31	.76
	duration		-0.20	0.05	3.96	<0.01
	start time		-0.04	0.05	0.88	.38
	Reproductive phase	Incubating	0.14	0.16	-0.86	.39
		Nestlings	-0.76	0.17	4.62	<0.01
		Young	-0.76	0.11	7.00	<0.01
	Group size		-0.10	0.05	1.86	0.06
	Habitat	Zone2	0.30	0.19	-1.57	0.12
		Zone3	0.51	0.21	-2.36	0.02
		Zone4	0.62	0.19	-3.35	<0.01
Revisitation index	Intercept		-0.09	0.09	-0.92	0.36
	duration		0.25	0.06	4.54	<0.01
	start time	start time	0.02	0.09	0.20	.84
		start time ^2	0.11	0.07	1.69	.09
	Reproductive phase	Incubating	0.65	0.17	3.77	<0.01
		Nestlings	0.48	0.18	2.72	<0.01
		Young	-0.15	0.12	-1.25	.21
	Group size		-0.27	0.06	-4.94	<0.01
	Habitat	Zone2	-0.21	0.18	-1.15	.26
		Zone3	0.30	0.21	1.48	.15
		Zone4	0.16	0.18	0.85	.40

a)

Response variable	Fixed Effect	Estimate	Std. Error	t	P
Median dist. nest	Intercept	-0.18	0.12	1.46	0.15
	duration	0.07	0.14	-0.48	0.63
	start time	-0.23	0.13	1.81	0.08
	brood age	-0.45	0.13	3.59	<0.01
	N adults	0.30	0.13	-2.29	0.03
	habitat zone 2	0.41	0.27	-1.48	0.15
	habitat zone 3	0.28	0.31	-0.87	0.39
Speed	Intercept	-12.30	5.31	2.32	0.03
	breeding attempt	-0.71	0.31	2.31	0.03
	brood age	-0.50	0.14	3.61	<0.01
	habitat zone 2	0.24	0.29	-0.83	0.41
	habitat zone 3	1.11	0.36	-3.07	<0.01
Revisitation Index	Intercept	0.01	0.15	0.05	0.96
	duration	0.23	0.14	1.59	0.12
	brood age	-0.15	0.15	-1.00	0.33
	N adults	-0.27	0.16	-1.71	0.10
	habitat zone 2	-0.60	0.33	-1.78	0.08
	habitat zone 3	0.13	0.38	0.34	0.73

b)

Speed and revisitation index feature as dependant variables in both analyses, while area covered is substituted by median distance from the nest in the breeding-only analysis. All predictors have been standardised through centring (Schielzeth 2010). The full-dataset analysis includes Group ID as a random term.

Table 3. Factors affecting adult body weight.

Fixed effect	Estimate	Std. Error	t	P
Intercept	0.04	0.07	0.55	0.59
time	0.17	0.04	3.85	<0.01
tarsus	0.28	0.04	6.39	<0.01
year 2009	-0.75	0.17	-4.49	<0.01
brood age	-0.24	0.08	-3.14	<0.01
brood age ^2	0.07	0.03	2.39	0.02
Secondary brood	0.06	0.10	0.56	0.57
Unit size	-0.12	0.05	-2.16	0.03

All predictors have been standardised through centring (Schielzeth 2010). Group and individual ID are included as random factors

Models

Track area and median distance from the nest.

After controlling for track duration and start time, the area covered by babbler groups ('whole dataset') was best predicted by reproductive phase and habitat type: reproductive phase was the most relevant biological predictor, as it featured in all final candidate models and showed the highest standardised effect size in the best model, while habitat effects, ranked as second best predictor of area (Appendix, Table A2a, 2a). Track area was smallest during the 'Nestling' and 'Young' phases, compared to 'Non breeding' and 'Incubation', with a predicted average 38% increase between the former and the latter two phases. Habitat effects on the other hand, were associated with a 25% average difference in predicted area between the two extremes of habitat type. (Table 2a).

Results from the analysis of movements of breeding groups relative to nest location ('median distance from the nest'), pointed to 'brood age' as the most important predictor (Table A2b, 2b), with an almost twofold reduction in group median distance from the nest as breeding progressed from laying to fledging (Figure 2a). Further, median distance from the nest increased with group size (Figure 1b), while the trend for habitat was in brood agreement with results from area models (full dataset), and consistent with a general increase in average distance from the nest as vegetation cover decreased (see Appendix, Table A2; Table 2b).

Speed

Average group speed was predicted by reproductive phase and habitat type (Appendix, Table A2a; Table 2a). Therefore, the average speed of babbler groups decreased when nestlings or young were present, and increased in parallel with decreasing vegetation cover (Table 2a). Moreover, group size was also supported as a relevant predictor in the final best model, even though it appeared a weaker predictor of speed compared to reproductive phase and habitat type (Appendix, Table A2a; Table 2a). Similarly, breeding stage ('brood-age') and habitat type were the most relevant predictors of speed in the breeding analysis (Table A2b). Speed at the

end of the nestling phase was about half the value during the first week of incubation, and decreased also from first to second breeding attempts. Moreover, it increased by 40% between the habitat type with highest vegetation cover and the zone most devoid of vegetation (Table 2b).

Revisitation

The index of revisitation covaried with reproductive phase, group size, and to a minor extent, with habitat type (Table A2a).

Effects size estimates for reproductive phases (Table 2a), predicted an approximate 50% increase in expected average revisitation from the non-breeding phase to incubation, followed by a comparable post-breeding decrease from incubation to young-in-the-group phase. Group size effects were also supported, with the best model predicting more than a 50% reduction in revisitation from smallest to largest groups (Table 2a, Figure 1a).

Effects revealed by the analysis of the breeding only dataset were in general agreement with the above (Table A2b; Table 2b).

Finally, after controlling for effects of time of the day and tarsus length, weight of adult birds was significantly lower in the year 2009 than in 2007-08, and further decreased with both brood age and group size (Table A2c, 3, Figure 3).

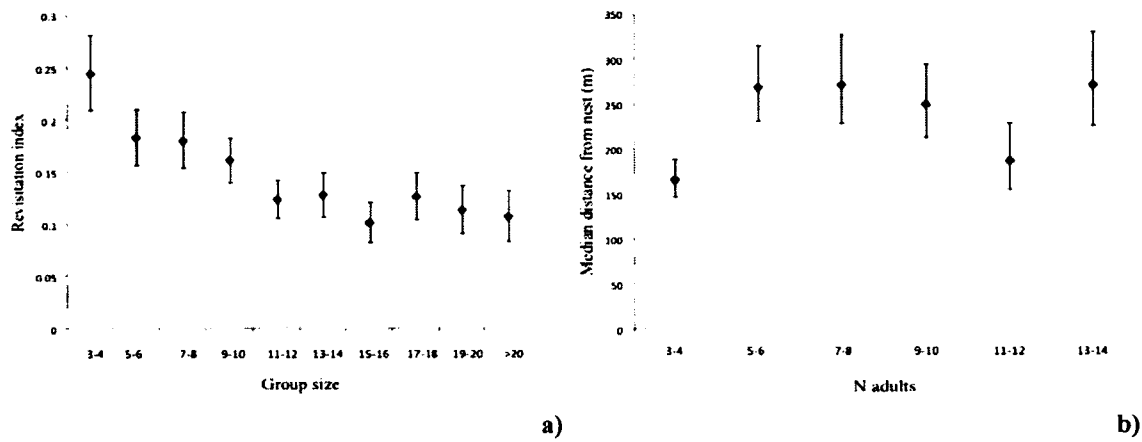


Figure 1. Relationship between group size and: a) revisitation index (full-dataset analysis), b) median distance from the nest (breeding-only dataset). Points represent marginal means predicted by best models, bars indicate SE.

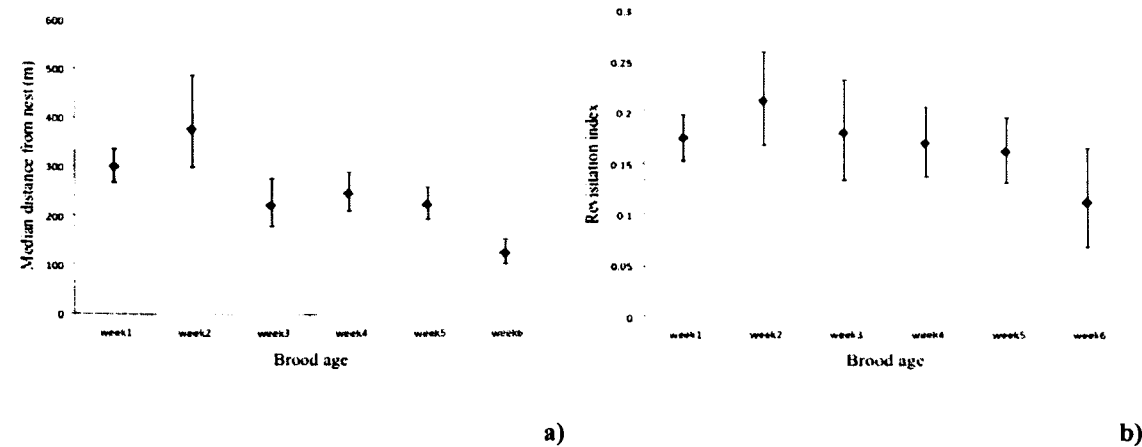


Figure 2. Relationship between brood age and: a) median distance from the nest (breeding-only analysis), b) revisitation index (full-dataset analysis). Points represent marginal means predicted by best models, bars indicate SE. Weeks are counted starting from hatching date.

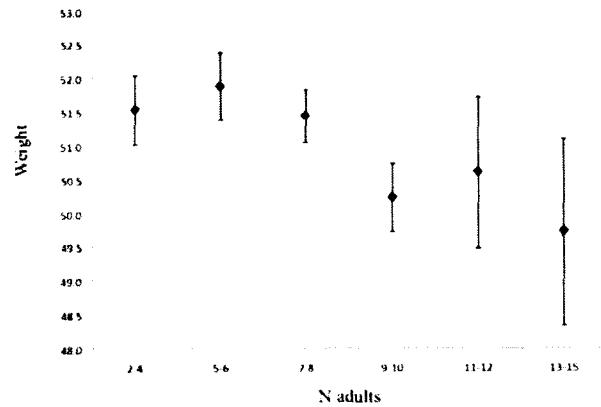


Figure 3. Relationship between individual weight of adult birds and group size, measured as number of adults in the group. Points represent marginal means predicted by the best model, bars show SE

DISCUSSION

In this study we have found that short-term ranging behaviour of Chestnut-crowned Babbler groups varied in parallel with reproductive phase, group size, and habitat type, in ways consistent with hypothesised local depletion of food resources. Costs of group living due to competition for limited food resources were further supported by a negative effect of group size on weight of adult group members. Reproductive phase appeared to be the main biological determinant of ranging behaviour in babbler groups. The range of group movements, as estimated by track area, showed a marked decline during the nestling phase, which persisted into the subsequent period during which social groups move with their newly fledged offspring. Given that this decrease in the area covered was closely matched by a concomitant reduction in the average speed of group movement, such a trend could probably be ascribed to reduced group mobility. During the nestling phase the group may be constrained by the need to regularly attend the nest during provisioning visits and later by the limited mobility of non-fully independent young. This seems to be a more likely explanation than the alternative, that increased seasonal habitat productivity may have lead to a decrease

in the extent of group movements through higher resource availability. We feel this second alternative is unlikely as the main explanation for our results, since seasonality was not pronounced, and because, due to variance in laying dates and multiple breeding attempts, breeding stages were poorly matched to calendar date. Instead, actual timing and extent of changes in group movements may have primarily responded to social needs and constraints associated with different reproductive phases. Among these, parental and alloparental care during reproduction feature prominently, and has been shown to affect spatio-temporal patterns of animal movements through the economics of commuting between foraging patches and the nest (Hegner 1982; Lessels and Stephens 1983; Houston and McNamara 1985; Naef-Daenzer 2000). Classical central place foraging theory predicts that provisioners should maximise offspring feeding rates (Stephens and Krebs 1986). Reducing the average distance from the nest at which adults forage as the food requirements of nestlings rise, may be one possible way of doing this in an energetically constrained species like the Chestnut-crowned babbler (Stephens et al. 2007).

Inevitably, a restricted range of movement implies a higher average proportion of time spent per area unit, and this may lead to local resource depletion through increased foraging pressure (Bonal and Aparicio 2008; Elliott et al. 2009; Santema et al. 2009) in the area around the nest. As local food resources become exhausted, the amount of time spent on habitat patches and the probability of subsequent revisitation are predicted to decrease. Our findings are in agreement with these predictions. The index of revisitation showed a steady decline between the incubation and young phase, as well as within the breeding phase, which is consistent with local resource depletion associated with reduced group mobility and increased local foraging pressure during offspring provisioning. These changes in revisitation appeared largely independent of concomitant changes in area and speed of movements, as indicated by relative temporal trends and the overall lack of correlation between the index of revisitation and other movement parameters. Accordingly, an intriguing possible explanation for the

decrease in average distance of groups from active nests as breeding progressed, may be that groups strategically chose their foraging locations in order to defer the exploitation of food patches in closer proximity to the nest, and match it to brood demands. Although, our data are consistent with such an explanation, a proper test of this hypothesis would require temporal and spatial quantification of local resources, and possibly experimental manipulations involving food abundance and brood size.

Group size effects on revisitation provide further support for the relevance of resource depletion. All else being equal, the rate of resource exhaustion within patches is likely to increase as a linear function of the number of individuals exploiting it (Brown and Brown 1996; Bonal and Aparicio 2008), and the strong linear effect of group size fulfilled this prediction. Further, the increase in average distance from the breeding nest with increasing group size, was also in agreement with a resource depletion scenario. Although, large group size in cooperatively breeding species is commonly considered to have a positive effect on breeding success, through increased total provisioning, or on breeders, due to load-lightening (Hatchwell 1999), limited local resource availability may constrain such benefits, and lead to context-dependant optimal group size (Komdeur 1994; Legge 2000; Luck 2002). Therefore a helper working in a large group may actually have to pay a proportionally higher cost in delivering a prey item to the nest than a helper in a small group, because the local area would be more depleted and consequently helpers would have to move further from the nest to forage efficiently. Supporting this, we have found that condition of adult birds, during and immediately after breeding, appeared to be negatively affected by group size, and worsened as breeding progressed. Moreover, another study on the same population found that average nestling weight peaked at intermediate group sizes (Russell et al 2010), consistent with non-linear effects of helpers number on reproduction. This study has also shown a clear effect of habitat type on area covered by groups and average speed of movement, in that groups inhabiting more open areas with less arboreal vegetation, covered larger areas and moved at a

faster pace. This area effect can be reconciled with predictions from optimal foraging theory models (Stephens et al. 2007; Olsson et al. 2008), because lower habitat quality and increasing distances between profitable vegetation patches are expected to enhance the scale of movement and lead to higher average speed by substantially increasing the proportion of travel time between habitat patches (Pulido and Diaz 2000; Stauss et al. 2005; Trembley et al. 2005). Predation risk may also contribute to this pattern. In fact, by being more vulnerable to attacks from aerial predators as consequence of increased conspicuousness and lack of shelter, groups may be expected to minimise the amount of time spent in open areas, which could be achieved by increasing movement speed (Vasquez et al 2002; Fischhoff et al 2007).

Low habitat quality and increasing average inter-patch distance, may also be expected to exacerbate local resource depletion, and thus translate into a reduction of patch revisitation (Vedder 1984; Watts 1998). However, we did not find a clear relationship between habitat openness and our index of revisitation, possible as a consequence of variation in landscape structure between habitat types. For example, in areas with little arboreal cover, trees and shrubs were mainly restricted along isolated creeks, and because babbler groups exhibit a clear preference for these drainage zones, probably due to higher prey biomass and protection from aerial predators compared to surroundings (Portelli et al 2009; Chapter 1), group movements tended to be spatially constrained and funnelled along these relatively narrow corridors. (Sorato pers. obs)

In conclusion, in this study we have investigated the spatial ecology of the chestnut-crowned babbler groups by tracking foraging group and recording their movement trajectories with GPS devices at different times of the year. Although this methodology has limitations, mainly related to difficulties in following animals as they move, and possible effects on behaviour associated with observer disturbance that need to be taken into account, recent technological advances, such as miniaturised GPS loggers, have the potential to overcome these problems and allow fine-scale, continuous remote quantification of behaviour of small-

sized animals (Cagnacci et al. 2010). We believe that by expanding their spatio-temporal scope and not just focusing on behaviour in close proximity of the nest during breeding, studies of cooperative breeders will benefit by gaining new insights into evolutionary forces at work in shaping such a fascinating, yet still elusive, social system.

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Chapter 4

Habitat effects on home-ranging behaviour and group size in cooperatively breeding Chestnut-crowned Babblers

ABSTRACT

Ecological factors have been suggested as prime determinants of group living and animal social organisation, as exemplified by classical studies of avian cooperative breeding. More recently however, the role of ecology in the formation of stable group aggregations has been downplayed, in the light of a strong phylogenetic signals of evolutionary history, and due to difficulties in finding common and consistent ecological themes underlying variation in social organisation across taxonomic levels. Here we examined how different measures of habitat quality and structure were related to group home ranging and group size in an Australian cooperatively-breeding social species, the chestnut-crowned babbler (*Pomatostomus ruficeps*), a bird endemic of semiarid habitats in the Australian interior. By studying this species in a site with a considerable degree of habitat heterogeneity, we showed that different components of habitat ecology, essentially related to different aspects of vegetation type and abundance, explained a large amount of variation in both home-range and group size, whereas contributions of local social environment were mostly marginal. Mechanisms that were likely to mediate these habitat effects, and implications for studies of cooperative breeding and sociality in general, are discussed. We suggest that habitat structure, and specifically spatial dispersion of resources, may have represented a crucial feature of local ecology conducive to group living, through its effects on space use. We conclude by implying that these findings may be of general relevance for studies of social organisation, and that spatio-temporal variation in ecological conditions should be a more stringent focus of future research.

INTRODUCTION

In order to explain the evolution of animal societies, it is essential to understand what are the factors selecting for stable aggregations of individuals (Emlen and Oring 1977; Krause and Ruxton 2002). As the main pathway leading to sociality, family-living has been the focus of a number of theoretical and empirical studies (Ekman et al. 2004). While ecological effects, such as costs and constraints to dispersal, have been widely invoked to explain the occurrence and prevalence of philopatry within species (Emlen 1982; Hatchwell and Komdeur 2000), more recently, the general failure of ecological explanations in accounting for patterns of variation in group-living at higher taxonomic levels, has prompted a shift of focus towards evolutionary history (Arnold and Owens 1998; Ligon and Burt 2004) and social benefits, accrued for example through prolonged associations with parents (Ekman et al. 2001), as the main factors at play. Accordingly, in the light of a strong phylogenetic signal in interspecific patterns of sociality, life history has been suggested as the main predisposing factor to group living in avian lineages, and ecological conditions have been considered of secondary, accessory importance only (Arnold and Owens 1998, Ligon and Burt 2004).

Yet such a dichotomy is probably unwarranted, and the two factors may in reality exert a complementary synergetic effect onto the evolution of sociality (Hatchwell and Komdeur 2000; Jetz and Rubenstein 2010). In fact, as ecology interacts with life history and other aspects of biology in shaping species, ecological niche, ecological and life-history effects may be reconciled, and together contribute to the balance of relative costs and benefits of group living. Such a dual interaction, may account for the difficulty in finding consistent effects of ecology across taxa, as the same ecological conditions may have different implications depending on the biology of the species under study. Related to this point, the precise set of ecological conditions involved in the shaping of social organisation may also be contingent to the evolutionary history of the organism. It may therefore prove crucial to consider a wide set of ecological factors, guided by knowledge of the study systems' biology, if one is expected to

reveal effects of ecology on social system variation (Jetz and Rubenstein 2011). For example, while local abundance of critical limited resources, such as food, nesting sites and mates, have been routinely considered in studies of cooperative breeding birds (Emlen 1982; Brown 1987; Stacey and Ligon 1987; Komdeur 1992; Hatchwell and Komdeur 2000), the effects of spatial and temporal dispersion of resources have received only marginal attention (Noske 1991; Langen and Vehrencamp 1998; Rubenstein and Lovette 2007; Jetz and Rubenstein 2011). Habitat structure, as reflected by resource patchiness, has been suggested to be an important determinant of spacing behavior, particularly in mammals (Carr and Macdonald 1986; Maher and Burger 2011; Johnson et al. 2002), and the effect of resource dispersion in promoting spatial aggregations of individuals has been supported in several studies of carnivores' home-ranges (Johnson et al 2002). Yet such a narrow taxonomic focus is probably not justified, and may underscore a more general relevance of this mechanism for the evolution of sociality (Davies et al. 1995; Langen and Vehrencamp 1998; Johnson et al. 2002).

The aim of the present study was therefore to investigate the effects of local ecological features on group size and ranging behavior in a social, cooperatively-breeding bird, living in a spatially heterogeneous and temporally variable habitat. The chestnut-crowned babbler (*Pomatostomus ruficeps*) is a medium-sized passerine endemic to the semi-arid interior of South-East Australia, where it lives in family groups ranging in size from two up to about 16 adult members (Russell et al. 2010). Within groups, up to three females may breed, leading to a transient fragmentation of groups into distinct breeding units, consisting of a breeding pair and up to 13 helpers (Russell et al 2010). Breeding units re-amalgamate at the end of the nesting phase of the reproductive cycle, as soon as nestlings have fledged (Sorato, pers. obs), and groups remain together until the onset of the following breeding season. The chestnut-crowned babbler is the least arboreal of the five closely related Australasian babbler species (family Pomatostimidae), and is most typically found in semiarid chenopod shrubland habitat, where there is only limited, patchy tree cover (Higgins and Peter 2002). It appears to have

no specific habitat requirements, apart from the availability of trees or tall shrubs for building of breeding and roosting nests, and the presence of suitable patches for ground-foraging and possibly predator protection (Portelli et al. 2009; Chapter 2,3).

In this study, we address three related questions. First, how different habitat features affected home ranging of babbler groups, controlling for group size effects, local social environment, and other confounding factors. Second, how habitat in turn affected group size, and lastly, how habitat effects on group and home range size combined to determine local babbler density.

MATERIALS AND METHODS

Study site

This study was conducted at the University of New South Wales Arid Zone Research Station at Fowlers Gap, in far-west New South Wales (31°05' S, 141°43' E), Australia, from October 2007 to March 2010. The site is characterised by a dry climate with low unpredictable rainfall, and a rather pronounced seasonality, with minimum monthly temperature averaging 5 °C in July and maximum mean temperature reaching 37 °C in January.

The main vegetation type within the study site consisted of an open chenopod shrubland. Patches of trees were predominantly found in close proximity to creeks and smaller drainage channels: large red gum trees (*Eucalyptus camaldulensis*) were restricted to margins of major creek systems, whereas smaller *belah* trees (*Casuarina pauper*) predominated in proximity of drainage channels. Other, less common trees were, in relative order of abundance, mulga (*Acacia anaeura*), rosewood (*Heterodendrum oleifolium*), and native apricot (*Pittosporum phylliraeoides*). Dominant tall shrubs included prickly wattle (*Acacia victoriae*) and dead finish (*Acacia tetragonaphylla*), while short shrubs consisted of bluebushes (*Maireana* spp.), saltbushes (*Rhagodia* and *Atriplex* spp.) and copperburrs (*Sclerolaena* spp.). Overall, besides creeks and drainage channels, vegetation type, structure

and distribution was determined by local soil type, elevation and past land-use, which together contributed to the substantial degree of spatial heterogeneity that characterised the local landscape.

Data collection

Data were collected in the course of five continuous time windows: October 2007- January 2008, May-June 2008, August- October 2008, July-October 2009, and January-March 2010. For the purpose of home range estimation and statistical analysis, we lumped these time intervals based on a combination of temporal occurrence and dominant life-history stage. Thereby, we defined three study periods, the first, from October 2007 till begin of July 2008 (referred to as '2007-08 Non-breeding'), marked the non-reproductive phase that preceded the 2008 breeding season (August-October), which in turn constituted the second study period ('2008 Breeding'). The remaining study period, July-October 2009 and January-March 2010 combined ('2009-10'), saw only limited breeding that involved a marginal number of groups, and was characterised by widespread failure as a consequence of prolonged drought conditions.

The study area extended over more than 64 square kilometres, holding approximately 50 babbler family groups. A total of 35 babbler groups were followed in the course of the first study period, 18 during the breeding phase in 2008, and 33 groups between 2009 and 2010. Because most groups were sampled during each of the three study periods, and the remaining either during two or a single study season, a total of 50 family groups were studied in the course of the entire study duration. As a part of an ongoing long-term research project (see introduction), within each social group most individual birds had been banded with individual colour-ring combinations, which allowed individual and group identification.

To obtain home range estimates and information on group size and composition, babbler groups were located by extensively searching throughout the study site, aided by group

vocalisations and individual contact calls. Once found, we tried to follow groups for 3-4 groups were usually followed for 3-4 hours, though this was not always achievable as a consequence of loss of contact and failure in relocating the group. Therefore average track duration was 2.4 hours (min=0.25, max=4 hrs), whereas mean number of tracking sessions per group-period was 3.5 (range: 3-15) and total amount of group tracking per study period averaged at 11 hours (min=4, max=29 hours). Generally, tracking sessions involved entire family groups, with the exception of the 2008 reproductive season when plurally breeding family groups temporally split into distinct breeding units with partially overlapping ranges (Portelli et al 2009). However, since the focus of this investigation was on ranging behaviour and attributes of family groups, which represents the fundamental unit of social organisation in the species, for the purpose of subsequent analysis tracks from different breeding units were merged according to social group membership. Groups were mainly tracked during early mornings, late afternoon, and, to a minor extent, between late morning and mid-day, as at this time of the day groups were generally less active and tended to spend the majority of their time resting and preening on trees or within favourite thickets of vegetation. A GPS location was automatically recorded every 50 m, using a Garmin eTrex or Geko 301 global positioning systems (GPS). Since each GPS fix actually represented the position of the observer, care was put into replicating as close as possible the path followed by the tracked group (accuracy ca 10m). A group was regarded as lost, and the tracking session ended, once it could not be located for more than 10-15 minutes, while, for shorter time periods of temporary disappearance, the GPS device was switched off as soon as the group location could not be determined, and switched on again once the group was relocated. Tracked groups were scan-sampled whenever individual birds could be sighted, and individual colour-band combinations, group size and number of juveniles were noted whenever possible. On the basis of these observations, total group sizes and number of adult in the groups were estimated for each of the three study periods. Given that some groups were sampled over a time window of

several months, if group composition changed during the sampling period we used average estimates weighted by the relative amount of sampling. Based on group observations and mist-netting, we have only scant evidence of individuals temporarily visiting other social groups. We are therefore confident that our estimates of group size are unlikely to be confounded by temporary forays of individuals into other territories.

Home range analysis

Group home ranges for each of the three study periods were estimated from pooled track-points using the local convex hull method (LoCoH, Getz et al 2007). The LoCoH method can be seen as a generalisation of the traditional minimum convex polygon technique (MCP), and allows a non-parametric estimation of utilisation distributions which is free from limitations and statistical assumptions of probabilistic kernel home range models (Getz et al 2007). Because it does not require independence of fixes, the LoCoH procedure is suitable for analysing temporally autocorrelated spatial locations (De Solla et al 1999), and it further provides accurate border detection and area estimation that is relatively robust with respect to extreme locations (Downs and Horner 2008). We used the adaptive local convex hull algorithm (a-LoCoH, Getz et al 2007; implemented in the R package Adehabitat, Calenge 2006), which provides home range estimates by merging MCP polygons calculated for each relocation by selecting a local set of neighbour points based on the condition that the sum of their distances from the focal point is less or equal to the specified parameter 'a'. Because the size of each polygon is inversely related to its associated local density of points, by merging the single polygons from the smallest to the largest until a specified percentage of points is included, it is possible to obtain estimates of space use within the total home range in the form of X% isopleths of the utilisation distribution. More specifically, by taking the deciles as cutting points, the algorithm produces the 10-100% isoplethes of the point distribution. We selected a single a-parameter value to be used in the analysis by plotting, for each group-year,

100%-isopleth areas against a range of corresponding a -values, and selecting the smallest parameter value in correspondence of which the area-parameter curve levelled off. The use of such a procedure was justified by the fact that small values of the a -parameter resulted in isopleths that matched local density of fixes at a rather fine spatial resolution, but presented also several 'holes', implying unused patches within the home range. Holes within home ranges however were most likely a consequence of limited sample size, and therefore spurious, as also suggested by the absence of clear habitat boundaries or other physical barriers. By selecting a higher a -values, holes are progressively filled, but at a price of decreased precision of local area use. In other words, with increasing a -values the spatial resolution decrease, as does the probability of type I errors. Conversely, lower a -values increase the spatial resolution and decrease the probability of type II errors (Getz et al 2007). Our parameter selection was therefore aimed at minimising type I error over type II, as the former was in all likelihood more probable because of incomplete sampling. We used 100% isoplethes as estimates of total group home ranges, while 50% isoplethes were selected as estimates of core home range areas (Borger et al. 2006). Accuracies of home ranges estimates were evaluated by analysing percentage cumulative home-ranges as a function of cumulative number of fixes. To this end, bouts of ten fixes were subsequently added to previous locations, and 100% LoCoH isopleths areas were calculated for each subsample of points. The resulting percent increase in area of the 100% isopleth was then calculated. Inspections of the resulting plots of area increase versus number of points showed a general trend of exponential decrease towards zero when total amount of group tracking approached 10 hours.

Habitat analysis

To quantify variation in habitat, we used a regular grid design to frame the whole study area and sampled across this at a total of 268 locations spaced at 400 m intervals. We visually assessed habitat within hypothetical quadrants of approximately 400 m length centred in

correspondence of each sampling point, and semi-quantitatively scored the following variables: i) amount of cover (scores 0-4) for each of the main tree /tall shrubs species, and for all trees/tall shrubs combined, ii) cover of dominant short shrub genres and for all short shrubs combined, iii) average height of tree/tall shrubs, iv) average height of short shrubs, and v) amount of surface cover for categorised soil types ('silt/clay', 'sands', 'gibber', and 'rocks'). A categorical principal component analysis (PASW statistics 18.0) was run on these variables and used to characterise the main dimensions of variation in habitat type within home ranges. This was done by calculating weighted average principal component scores of habitat quadrants overlapping with each 100% isopleth and core home range polygon, wherein weights were represented by the proportion of home range surface covered by each habitat quadrant.

Since there is evidence that babblers show a preference for ephemeral creek and drainage lines (Portelli et al 2009), and thereby the availability of these temporary water channels may affect space use of babbler social groups, we also estimated areas and spatial distribution of creeks, using the GIS software Arcmap (Arcgis vers 9.2, Esri) to draw creek lines in a geo-referenced aerial image of the study site. Creek lines were then buffered 10 m on each side, and the resulting polygons used to quantify the amount of overlap of home ranges with drainage zones. Surface areas of creeks within each focal home range were then divided by home range areas (100% isoplethes and cores) to provide a measure of the proportion of home range surface covered by drainage channels.

Main Statistical analysis

All statistical analysis was done in R version 2.11.1 (R Development Core Team, 2010). Linear mixed models (LMMs) were fitted using the package lme4 (Bates and Maechler 2010), wherein 'group identity' was set as a random intercept effect, to account for partial population sampling and repeated group measures over the entire study duration. All model predictors

were centred by subtraction of mean values, and continuous variables were further standardised by dividing them by their sample standard deviation (Schielzeth 2010), in order to allow direct comparison of estimates of effect sizes within and between models. Response terms were transformed to achieve normality whenever needed. Scatterplots of residuals and predicted values were generated to check model assumptions. Given the spatial component of most of the variables under analysis, spatial bubbleplots of model residuals were also created, using the R package *gstat*, and inspected to ascertain lack of spatial autocorrelation (Zuur et al 2009). The effects of habitat and social factors on home range size (cores and 100% areas) were investigated by fitting LMMs featuring combinations of the following terms as predictors: i) total tracking time, ii) period, iii) habitat principal components, iv) creek cover, v) number of adult birds in the social group, vi) total group size, vii) number of neighbour groups, and viii) average number of adults in the neighbouring groups. To analyse effects of habitat and local social environment on group size, expressed as number of adult birds, we fitted models that included period, habitat principal components, creek cover, number of neighbours, and average adult numbers in neighbour groups. Finally, LMMs were also fitted on group density, calculated as number of adults in the group divided by total home range size, and included the following as candidate predictors: total tracking time, period, habitat principal components, creek cover, number of neighbour groups, and average number of adult birds in the neighbouring groups.

We defined candidate model sets on the basis of biologically plausible hypothesis and used an information-theoretic approach to select best explanatory models, based on the Akaike information criterion (AIC Burnham and Andersson 2002) with the Hurvich and Tsay correction for finite sample size (AICc). Model selection was performed with the R package *AICcmodavg* (Mazerolle, 2011), which calculates AICc scores and relative weights for candidate model sets. Inference was based on the single top-ranking model if this yielded a relative Akaike weight >0.9 , otherwise lower-ranking models with a $\Delta AICc \leq 5$, were also

considered as plausible, in proportion to their relative AICc scores and associated weights (Burnham and Anderson, 2002). To facilitate comparisons, we present effects estimates for both the best models (defined within each candidate model set as the models with the lowest AICc score) and the full nested models featuring the entire set of potential predictors.

Finally, we compared habitat features of cores and full home ranges using paired t-tests for principal component scores and proportion of creek cover. Separate analyses were run for each of the three study periods.

Table 1. Factor loadings for categorical principal component analysis on habitat variables

Component Loadings					
PC1		PC2		PC3	
saltbush	0.51	trees_height_score	0.73	shrubs_percent_cover	0.61
Prickly wattler	0.44	trees_percent_cover	0.68	saltbush	0.43
sand_cover_score	0.35	Prickly wattle	0.62	copperburr	0.41
Other shrubs	0.16	sand_cover_score	0.59	Other trees	0.39
shrubs_height_score	0.11	Wild apricot	0.46	gibber_cover_score	0.32
copperburr	0.06	bluebush	0.25	Wild apricot	0.31
nelja	-0.17	earths_cover_score	0.20	sand_cover_score	0.29
rocks_cover_score	-0.26	shrubs_height_score	0.19	bluebush	0.22
gibber_cover_score	-0.26	rocks_cover_score	0.11	Prickly wattle	0.20
trees_height_score	-0.26	Other trees	0.11	belah	0.11
shrubs_percent_cover	-0.41	Other shrubs	0.11	trees_percent_cover	0.06
Other trees	-0.51	belah	0.07	trees_height_score	0.05
trees_percent_cover	-0.55	shrubs_percent_cover	0.04	rosewood	-0.03
rosewood	-0.60	nelja	0.02	Dead finish	-0.05
Dead finish	-0.64	rosewood	-0.06	shrubs_height_score	-0.15
earths_cover_score	0.17	Dead finish	-0.07	Other shrubs	-0.18
Wild apricot	0.31	mulga	-0.10	mulga	-0.25
bluebush	-0.68	saltbush	-0.17	nelja	-0.35
mulga	-0.70	copperburr	-0.46	rocks_cover_score	-0.47
belah	-0.75	gibber_cover_score	-0.61	earths_cover_score	-0.52

RESULTS

Principal component analysis on habitat variables extracted three main factors, which altogether explained 50% of sample variance (Table 1). The first component (PC1) was characterised by high absolute values of factor loadings for amount of cover of tree and shrub species, and was thereby interpreted as an index of vegetation type in terms of species composition. The second component, showing the highest loadings for tree height and total amount of tree surface-cover, and low negative scores for amount of gibber and copperburr-shrub cover, was deemed as an index of arboreal biomass, thereby differentiating sites along a vertical dimension. Finally, the third principal component, being strongly positively correlated with total amount of short-shrubs cover, was interpreted as an index of non-arboreal vegetation abundance, identifying sites dominated by chenopod shrubland with little or no tree cover.

Total and core home range size averaged 104 and 22 ha respectively for the first study period (2007-08 Non Breeding), 53 and 11 ha for the 2008 breeding period, and 127 and 24 ha during the 2009-10 season. Total home range size during the first study period, 2007-08 NB, was significantly correlated with size during 2009-10 ($r=0.62$, $n=24$, $P<0.01$).

Pairwise comparisons of habitat type between core and 100% isopleth home ranges, revealed significantly higher average scores within core home ranges for both the habitat second principal component ('tree cover') and for creek cover during each study period, whereas differences in the first and third habitat components were equivocal and specific to different study periods (Table 2).

Table 2. Pairwise comparisons of habitat principal components and creek cover between core home range areas (50% isopleth) and full home range area (100% isopleth).

Habitat variable	Study-year	t-value	d.f.	P
PC1	2007-08NB	1.05	31	0.30
	2008 Breeding	-0.21	13	0.84
	2009-10	2.54	31	0.02*
PC2	2007-08NB	-2.73	31	0.01**
	2008 Breeding	-1.98	13	0.07
	2009-10	-3.92	31	<0.01**
PC3	2007-08NB	-2.05	31	0.05*
	2008 Breeding	-0.05	13	0.96
	2009-10	-0.76	31	0.45
Creek cover	2007-08NB	-4.02	31	<0.01**
	2008 Breeding	-1.77	13	0.10
	2009-10	-5.02	31	<0.01**

Positive t-values are indicative of lower variable values in the core home-range. Significant results are marked (*': $0.01 < P \leq 0.05$; ***: $P \leq 0.01$)

Total home range size was strongly predicted by study-year (Table A3a, 3a), with the expected average home range area being 40% smaller for the 2008 breeding season as compared to the other two study seasons. Habitat type was the next strongest predictor of home range area, as indicated by the fact that all three habitat principal components, as well as creek cover, featured in the two top ranking models (Table A3a). More specifically, home range area increased in parallel with change of vegetation type (PC1) from an open woodland dominated by *belah* to a tall prickly wattle shrubland interspersed by red gum creeks, while ‘tree’ (PC2) and creek cover, and to a lesser extent, ‘shrub cover’ (PC3) had a negative effect on home range size (Table 3a, Figure 1). Group size and local social environment on the other hand appeared to be only marginally associated with home range size (Table A3a, 3a): home range area was predicted to increase in parallel with group size, in particular with number of adults in the group, whereas number of neighbours had a negative effect. Analogous results were found for core home range areas, with the exceptions that total sampling duration was not featuring as a relevant predictor, the habitat second principal component only (‘tree cover’) was supported by top ranking models, and number of neighbour groups had a positive effect on area (Table A3b, 3b).

Table 3. Factors affecting: a) total, and b) core home range area.

BEST MODEL				FULL MODEL			
Random effects:				Random effects:			
	Variance	Std.Dev.			Variance	Std.Dev.	
ID (Intercept)	14827	121.76		ID (Intercept)	14199	119.16	
Residual	14164	119.01		Residual	13764	117.32	
Number of obs: 78, Groups: 45				Number of obs: 78, Groups: 45			
Fixed effects:				Fixed effects:			
	Estimate	Std. Error	t-value		Estimate	Std. Error	t-value
(Intercept)	982.78	23.20	42.36	(Intercept)	983.75	22.83	43.09
Duration.tot	90.27	20.19	4.47	Duration.tot	92.41	21.14	4.37
Breeding 2008	-210.44	46.68	-4.51	Breeding.08	-207.60	48.30	-4.30
NB 2009-10	13.61	37.65	0.36	NB 09-10	10.60	38.17	0.28
PC1	55.45	26.69	2.08	PC1	54.16	26.95	2.01
PC2	-61.56	30.50	-2.02	PC2	-64.78	30.59	-2.12
PC3	-32.22	23.40	-1.38	PC3	-32.97	23.43	-1.41
Creeks.cover	-63.47	28.01	-2.27	Creeks.cover	-61.00	28.77	-2.12
				N.adults	25.75	18.52	1.39
				N.neighbours	-18.58	19.33	-0.96
				N.adults.neighbours	-1.93	19.59	-0.10

a)

BEST MODEL				FULL MODEL			
Random effects:				Random effects:			
	Variance	Std.Dev			Variance	Std.Dev.	
ID (Intercept)	6689.80	81.79		ID (Intercept)	5687.60	75.42	
Residual	3407.40	58.37		Residual	3582.10	59.85	
Number of obs: 78, Groups: 45				Number of obs: 78, Groups: 45			
Fixed effects:				Fixed effects:			
	Estimate	Std. Error	t value		Estimate	Std. Error	t-value
(Intercept)	436.67	14.12	30.92	(Intercept)	437.99	13.49	32.46
Breeding 2008	-138.55	21.56	-6.43	Breeding 2008	-127.87	23.94	-5.34
NB 2009-10	6.10	17.07	0.36	NB 2009-10	10.20	18.13	0.56
PC2	-36.24	14.07	-2.58	PC2	-36.95	15.09	-2.45
Creeks.cover	-30.97	13.11	-2.36	PC1	6.15	14.95	0.41
				PC3	-4.35	12.63	-0.34
				Creeks.cover	-27.44	13.59	-2.02
				N.adults	12.53	9.93	1.26
				N.neighbours	4.95	9.91	0.50
				N.adults.neighbours	5.75	10.47	0.55

b)

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

Table 4. Factors affecting group size, as measured by number of adults within the group.

BEST MODEL				FULL MODEL			
Random effects:				Random effects:			
	Variance	Std.Dev.			Variance	Std.Dev.	
ID (Intercept)	0	0		ID (Intercept)	0	0	
Residual	8.468	2.91		Residual	8.065	2.840	
Number of obs: 77, Groups: 44				Number of obs: 77 Groups: 44			
Fixed effects:				Fixed effects:			
	Estimate	Std. Error	t-value		Estimate	Std. Error	t-value
(Intercept)	10.60	0.33	31.96	(Intercept)	10.60	0.32	32.74
PC2	0.64	0.34	1.89	Breeding 2008	0.63	1.00	0.63
N.neighbours	0.55	0.35	1.58	NB 2009-10	0.08	0.75	0.11
N.adults.neighbours	0.98	0.34	2.84	PC2	1.37	0.52	2.64
				PC1	0.55	0.42	1.29
				PC3	0.36	0.36	1.01
				Creeks cover	-0.70	0.45	-1.56
				N.neighbours	0.49	0.35	1.40
				N. adults neighbours	0.83	0.37	2.23

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

Table 5. Factors affecting group density, calculated as number of adult members in the group divided by total home range area.

BEST MODEL				FULL MODEL			
Random effects:				Random effects:			
	Variance	Std.Dev.			Variance	Std.Dev.	
ID (Intercept)	0.12	0.34		ID (Intercept)	0.10	0.31	
Residual	0.10	0.32		Residual	0.10	0.32	
Number of obs: 77; Groups: 44				Number of obs: 77, Groups: 44			
Fixed effects:				Fixed effects:			
	Estimate	Std. Error	t-value		Estimate	Std. Error	t value
(Intercept)	-11.43	0.06	-177.91	(Intercept)	-11.42	0.06	-186.63
Duration.tot	-0.14	0.06	-2.49	Duration.tot	-0.16	0.06	-2.88
Breeding 2008	0.54	0.12	4.47	Breeding 2008	0.57	0.13	4.38
NB 2009-10	-0.07	0.09	-0.78	NB 2009-10	-0.02	0.10	-0.20
PC2	0.28	0.06	4.27	PC2	0.19	0.09	2.25
PC3	0.12	0.06	1.98	PC1	-0.10	0.07	-1.39
				PC3	0.09	0.06	1.43
				Creeks.cover	0.08	0.08	0.97
				N. neighbours	0.05	0.05	1.03
				N. adults.neighbours	0.07	0.05	1.29

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

The number of adult birds within social groups ranged between two and 20 (2007-08 non-breeding: mean=10.6, n=35; 2008 Breeding: mean=10.5, n=18; 2009-10: mean=10.4, n=33), and was best predicted by local social environment (number of neighbour group and average N. of adults in neighbour groups), followed by, in order of relative importance, the habitat second principal component and creek cover (Table A3c, 4). Therefore, group size increased with number of neighbour groups and average neighbour group size, as well as with amount of arboreal cover in the home range (Table 4, Figure 2).

Finally, driven by changes in home range size, average group density was highest for the 2008 reproductive season (mean=0.27 individuals/ha, min=0.06, max=0.69, n=35), and lowest during the other two period ('2007-08NB': mean=0.12, min=0.03, max=0.39, n=18; '2009-10': mean=0.11, min=0.02, max=0.53, n=33). Accordingly, density was predicted by year, with the expected group density for the 2008 breeding season being 80% higher than for the other two, essentially non-breeding, periods. Habitat effects were also evident in terms of a positive effect on the density of PC2 ('tree cover') and, secondarily, PC3 ('shrub cover'), while local social environment, either as number of neighbour groups or average neighbour adult number, appeared a less relevant predictor (Table A3d, 5).

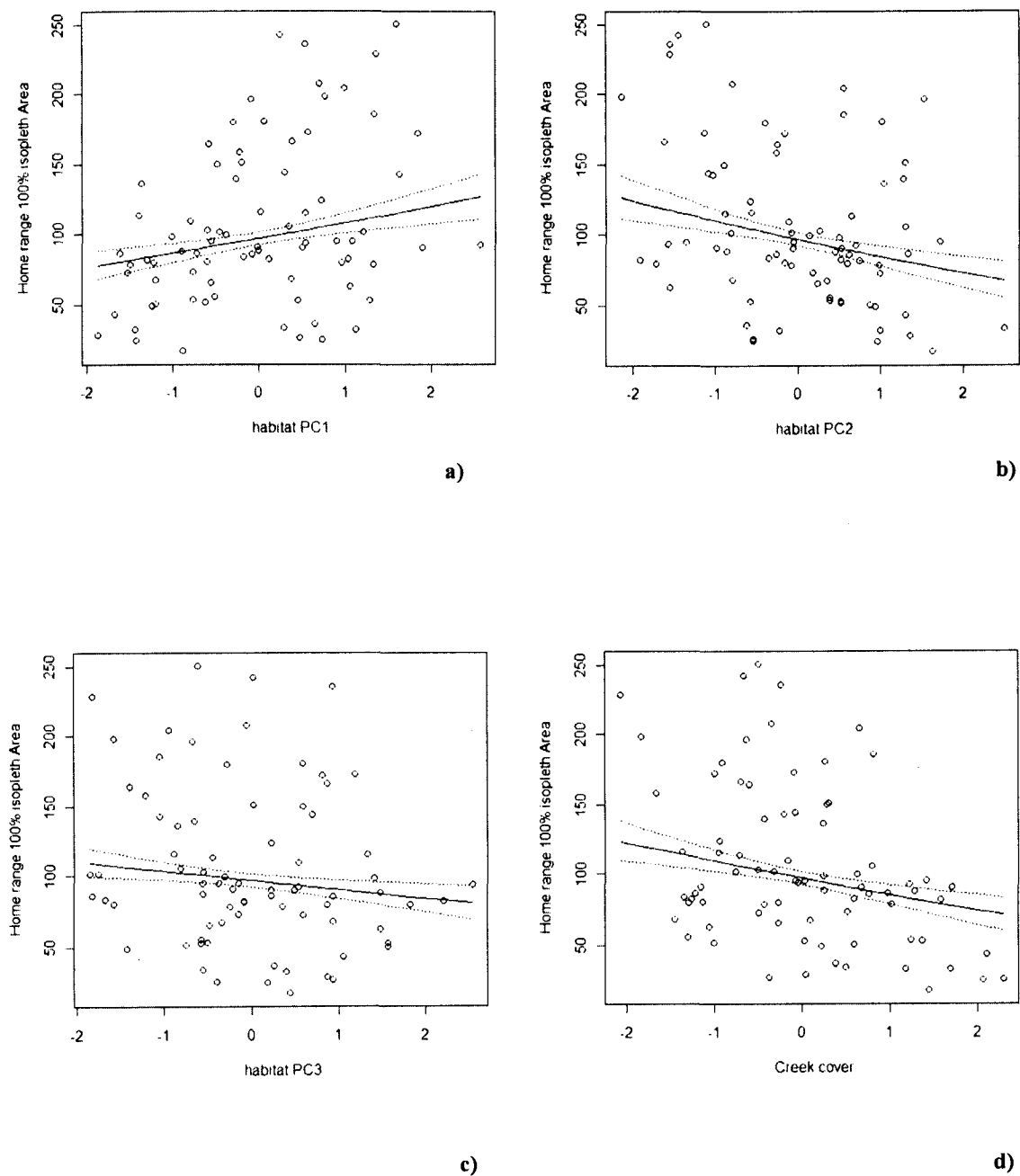
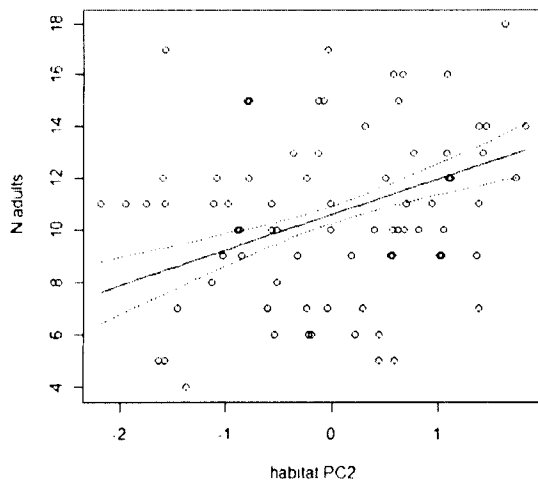
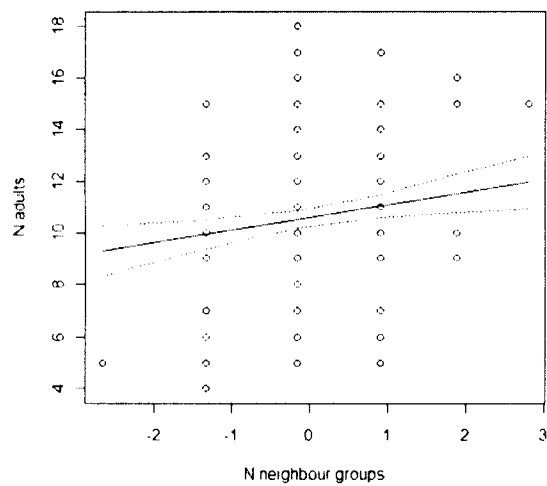


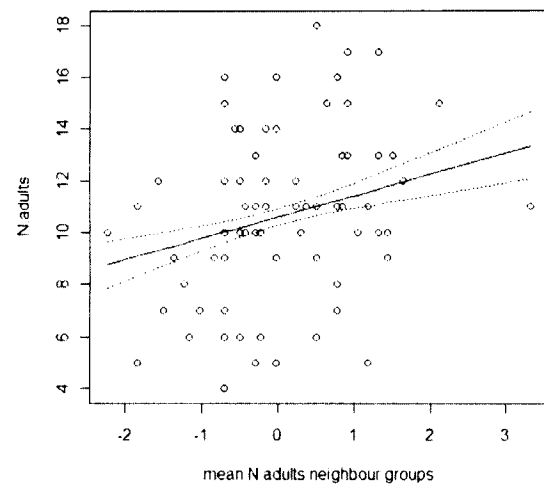
Figure 1. Relationship between total home range area and: a) habitat PC1, b) habitat PC2, c) habitat PC3, d) creek cover. Continuous lines represent best model estimates, dotted lines delimit estimate errors. Points show observed values.



a)



b)



c)

Figure 2. Relationship between group size (N. adults) and: a) habitat PC2, b) number of neighbour groups, c) average size of neighbour groups. Continuous lines represent best model estimates, dotted lines delimit estimate errors. Points show observed values.

DISCUSSION

We found that local ecology, as measured by habitat type, was an important determinant of space use by babbler groups within our study population. More specifically, total home range area appeared to be affected by local vegetation type (PC1), while at the same time, the amount of trees, and to a lesser extent, shrub cover (PC2 and PC3 respectively) were negatively associated with both total and core home range size.

A potential explanation for our finding is that home ranges of babbler groups may be adjusted to local habitat quality, and thereby vary in size depending on the presence of preferred vegetation and substrate type, as well as the total amount of food resources, which, depending on primary productivity, may be predicted by tree and shrub cover (Brown 1982; Balshine et al. 2001). In addition, because suitable trees for nesting and roosting are likely to represent a critical, limited resource, home range boundaries may also reflect the need to include enough trees providing sites for nest construction, similarly to what has been suggested for other cooperatively breeding bird species (Ligon and Ligon 1990). Consistent with this hypothesis, babbler groups cooperatively build and routinely maintain several dome-shaped nests that are widely distributed within their home ranges and serve both as breeding sites and group roosts. Trees therefore represent an important commodity as they provide sites for construction of nests, which in turns are associated with energetic benefits during roosting and at the same time may conceal and protect both roosting groups and breeding females from potential predators (Ligon and Ligon 1990).

Number of trees and the total amount of vegetation cover, however, may not represent either the sole, nor the most relevant factor responsible for our findings, as spatial distribution of tree and shrub patches is likely to represent another important attribute of local habitat affecting group space use (Langen and Vehrencamp 1998; Johnson et al. 2002; Cale 2003). Supporting this, is the observation that babblers do not appear to constrain their nest sites within a single area in close proximity of each other, irrespective of the fact that suitable

building sites may be available, but rather, seem to prefer to widely distribute their nests over a large area, possible as an anti-predator adaptation aimed at reducing predictability and detectability of both roosting and nesting sites. Such a requirement, has in the turn the implication that, average size of vegetation patches, together with their relative spatial positioning, may largely dictate nest distribution and translate into specific patterns of home range use and territoriality. The spatial availability of vegetation patches providing profitable food resources and cover from predators (Portelli et al. 2009), may also lead to a positive association between home range extension and local spatial dispersion of critical resources (Carr and Macdonald 1986; Noske 1991; Langen and Verhencamp 1998; Johnson et al. 2002; Doerr and Doerr 2006). This mechanism is exemplified by classical studies on dunnocks and alpine accentors (family Prunellidae. Davies 1995; Nakamura 1995; Davies and Hartley 1996), which showed, through a combination of observations and experimental manipulations, that food distribution as measured by its patchiness, was a causal factor explaining home range overlap and association between individuals. Among other group-living and cooperatively-breeding bird species, home range size in green woodhoopoes (*Phoeniculus purpureus*) appeared affected by the need of multiple roosting cavities offering protection from predators, whereas food amount was not a limiting resource (Radford and Du Plessis 2004). In white-throated magpie-jays (*Calocitta formosa*) the spatial dispersion of woodland and pasture patches was identified as the main factor constraining size and spatial features of group territories (Langen and Vehrencamp 1998). Such findings lend support to the hypothesis that clumped distribution and spatio-temporal unpredictability of resources may lead to large home ranges, which in turn would favour group-living through the negative costs-benefits balance of exclusive individual territoriality (Carr and Macdonald 1986, Johnson et al. 2002). While this model does not imply resource dispersion as the sole or most important mechanism driving the evolution of group living (Johnson et al. 2002), certainly it may represent a relevant contributing factor in many systems, and be especially important in

explaining variation in group size across taxonomic levels. The habitat effects we have found in this study, are consistent with this hypothesis, because habitat patchiness increased as one moved from *belah* open woodland to areas largely devoid of vegetation, except for patches dominated by prickly wattle and red gum tress (PC1), and appeared also negatively associated with amount of tree cover as measured by the second habitat principal component. The idea that landscape features may be prime determinants of group ranging behaviour, is further supported by the observations that, despite changes in group size and occasional group turnover, home range size and boundaries appeared relatively stable between years (Russell A.F. and Sorato E., pers.obs), while at the same time the spatial distribution of creeks and tree patches appeared to largely dictate group movement paths (Chapter 3). Therefore, habitat quality *per se*, and more specifically local average abundance of food resources, may have a more marginal role for group home ranging, with the possible exception of reproductive periods, when seasonally increased habitat productivity may be critical in allowing groups to be spatially constrained within proximity of breeding nests without depleting local resources to a level detrimental for their survival (Chapter 3).

The weak positive association between home range and group size in babblers is also consistent with habitat characteristics and landscape structure as the primary determinants of home range features. Previous research investigating the relationship between group and territory size among other cooperatively-breeding bird species, has produced mixed results in this respect. Some studies have found a positive relationship between territory size and group size (Rabenold 1990; Langen and Vehrencamp 1998; Jansen 1999), whereas others have shown no association between the two (Seddon et al. 2003; Radford 2004; Radford and Du Plessis 2004), or even a negative relationship (Vehrencamp 1978). Moreover, patterns of association between the two variables appear to vary among different populations of the same species (e.g. green woodhoopoes: Ligon and Ligon 1990; Radford and Du Plessis 2004), as well as between closely related sympatric species (Chan and Augusteyn 2003). Taken

together, these findings suggest that a combination of local ecology, species niche and demography, may be responsible for the variation in the pattern of association between group and home range size (Radford and DuPlessis 2004). In particular, a positive effect of group size on territory size may be predicted when local population density is high and intergroup competition becomes a significant force (Schradin et al 2010). In the chestnut-crowned babbler however, local social environment did not seem to be a prime factor in the moulding of group ranging behaviour, consistent with the large home range size, and the relatively low level of territoriality, which appeared typical for the species.

While group size was not strongly associated with home-range size, the number of adult birds within social groups was also associated with habitat, in particular by the amount of tree cover (PC2). At the same time, local social environment, as reflected by number of neighbouring groups and average neighbour group size, was another strong predictor of group size, possibly a spurious effect of spatial autocorrelation of other ecological variables not included in the analysis. Thus, the same habitat aspect (PC2) had two divergent effects on home-range size, in that higher tree-cover predicted smaller home-range areas, but also had a more marginal positive indirect effect on home-range size mediated by its positive association with group size. As a consequence of the combined effects of habitat on group size and home range size, tree cover was also the second strongest predictor of group density, preceded only by the effect of breeding. These findings are in agreement with resource dispersion models for group-living (Carr and Macdonald 1986; Johnson et al. 2001, 2002; Verdolin 2009), which predict that, while spatio-temporal dispersion of critical resources is the main factor determining group home-ranging, group size is mainly affected by habitat quality and total resource availability. Analogous conclusions were reached in studies of white-throated magpie-jays (Langen and Vehrencamp 1998), wherein group size was determined by the total amount of acacia food resources; mexican jays in northern Mexico (*Aphelocoma ultramarina*, Bhagabati and Horvath 2006), in which group size increased with productivity of oak and

pine trees; and for congeneric Australian babbler species, namely Hall's babbler (*Pomatostomus halli*, Brown and Balda 1977) and grey-crowned babbler (*Pomatostomus temporalis*, Brown et al. 1983). The latter two studies are of particular relevance here, given the close taxonomic affinity of grey-crowned and Hall's babblers in particular, to chestnut-crowned babblers. Specifically, in their study of Hall's babblers, Brown and Balda (1977) found positive correlations between group size and both tree and herbaceous cover, which were speculated to indicate availability of refuge from predators, and habitat foraging potential respectively. While we could not determine the exact causal mechanism responsible for the effect of habitat on group size, it is likely that, as suggested for Hall's babblers, trees provided protection from predators for adult birds (Chapter 2), and possibly, by increasing number and decreasing conspicuousness of nests, also for eggs and nestlings. At the same time, we cannot rule out an effect of food resources, because, even though babbler prefer to forage on ground, tree cover may correlate with total local prey biomass.

In conclusion, we have found that habitat effects on group ranging and group size, are consistent with the hypothesis that resource dispersion may represent an ecological feature favouring group-living in the chestnut-crowned babbler. We suggest that spatio-temporal dispersion of resources may be a factor of general relevance for a complete understanding of the evolution of cooperative-breeding, and more generally sociality. Consistent with this contention, most cooperatively-breeding, group-living species, are found in habitats characterised by a high degree of spatial heterogeneity and/or temporal unpredictability of resources (Ford et al. 1988; Du Plessis et al. 1995; Rubenstein and Lovette 2007; Jetz and Rubenstein 2010). We believe that future research on the evolution of group-living should explicitly incorporate spatial and temporal ecological variation, as a thorough examination of different aspects of ecology may prove crucial for an in-depth complete understanding of sociality across taxonomic levels.

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Chapter 5

**Interacting effects of local ecology and group size predict group
approach to playback vocalisations in Chestnut-crowned
Babblers**

ABSTRACT

The costs of dispersal and benefits of philopatry have been invoked as key mechanisms selecting for the formation of social groups in cooperatively breeding species. Against this background, intergroup conflict for local resources has received only marginal consideration as another potential factor contributing to optimal group size. In order to study the effects of group size and local ecological conditions on intergroup contests, we acoustically simulated inter-group encounters in chestnut-crowned babbblers, a group-living bird species of the Australian arid zone. Specifically, we investigated the effects of focal and playback group size, study-year, reproductive phase, home-range size, and local habitat, on the probability that groups initiated an approach to playbacks, and the degree to which they closely approached the source of playback. We found that local ecology was an important predictor of the likelihood of approach, while size of focal groups, but not of playback groups, had opposite effects in the two study-years. Our findings highlight the importance of local habitat on response to simulated group intrusions, and suggest that benefits of group size in the context of intergroup encounters may be contingent on local ecological conditions and have a high degree of temporal variation.

INTRODUCTION

Group-living, and in particular the evolution of stable aggregations as typified by extended family groups, has attracted considerable attention in recent years (Krause and Ruxton 2002; Griesser and Barnaby 2010). Nevertheless, the main factors selecting for this kind of sociality is still a matter of debate. Traditionally, explanations for the occurrence of family groups have concentrated on ecological explanations, such as constraints to individual dispersal (Emlen 1982; Hatchwell and Komdeur 2000), and more recently on benefits of philopatry, for example in terms of resources available in the natal territory and extended parental care by nepotistic parents (Stacey and Ligon 1987; Covas and Griesser 2007). Still, other, more generalised benefits of group-living, like protection from predators, may also be involved and contribute to optimal group size (Ford et al. 1988; Clutton-Brock et al. 1999; Krause and Ruxton 2002; Doerr and Doerr 2006; Clutton-Brock 2009; Mosser and Packer 2009).

Besides cooperation, conflict is another evolutionary force that shapes interactions among social animals (Krause and Ruxton 2002). The role of conflict has been recognised in studies of cooperatively breeding species, where for example reproductive skew within groups has been the subject of both theoretical and empirical investigation (Magrath et al. 2004). Yet, conflict often extends beyond the realm of single groups, and involves higher levels of social organisation, as shown by intergroup contests in territorial species. While there is a rather extensive literature on conflicts between territorial groups of social carnivores and primates (e.g. McComb 1994; Wilson et al. 2001, 2002; Hale et al. 2003; Spong and Creel 2004), less is known about intergroup interactions in group-living bird species, despite the fact that group territorial displays and contests are a common feature of many avian cooperative breeders (Radford 2003; Seddon and Tobias 2003; Theuerkauf et al. 2009). The relative neglect of intergroup competitive dynamics is likely to have hindered our understanding of variation in social organisation of cooperatively-breeding birds (Cockburn 1998), because it has the potential to interact with local ecological conditions and affect

optimal group size and composition (Brown 1982). For example, contests for food resources may select for larger group size, or change optimal group sex ratio in sexually dimorphic species, whilst benefits of having helpers may extend beyond alloparental care (Heinsohn et al. 1990; Cockburn 1998). Costs and benefits of intergroup territoriality in turn, are predicted to vary as a function of species niche as well as local ecological condition, such as abundance, spatio-temporal dispersion, and defensibility of resources (Riechert 1979; Enquist and Leimar 1987; Seddon and Tobias 2003; Radford and Du Plessis 2004; Crofoot et al. 2008). As contests may entail significant costs, in terms of injury risk, energy expenditure and increased stress levels (Briffa and Sneddon 2007), groups and individuals within, are also expected to adjust their behaviour according to their resource-holding potential and the perceived asymmetries with opponents (Hammerstein 1981; Parker and Rubenstein 1981; Petrie 1984; Putland and Goldizen 1998; Radford 2003). While differences in body size and condition have been shown to be major factors for outcome of conflicts between individuals, group size of the opponents may be a key trait for group-living, social animals (McComb 1994; Seddon and Tobias 2003; Radford and Du Plessis 2004; Furrer et al. 2011). Yet, individual phenotypes within groups, may still be important in a number of social species, and could at times overcome group-size asymmetries (Heinsohn and Packer 1995; Seddon and Tobias 2003; Harris 2010).

In this study, we used acoustic playback experiments to investigate how local ecological conditions and group attributes affected responses to simulated intergroup encounters in cooperatively-breeding chestnut-crowned babbler (*Pomatostomus ruficeps*).

Chestnut-crowned babblers are medium-sized passerines endemic to the semi-arid interior of south-east Australia, where they live in family groups that range in size from 2 up to 16 adult members (Russell et al. 2010). Groups have large home ranges that usually overlap to a degree with those of their neighbours' although core areas, wherein babblers spend the majority of their time and build their typical doomed-shaped nests for breeding and roosting,

appear largely exclusive (Chapter 4). Inter-group interactions are commonly observed, particularly in proximity of home range borders, and generally involve displaying, chasing and loud vocalisations (Sorato pers.obs). There seems to be a certain amount of variation in both the quality and quantity of behaviours observed during group encounters. At one extreme, neighbours may tolerate each other or even forage together without overt aggression, though more often some degree of escalation in aggressiveness is observed (Sorato pers. obs.). Chasing and counter chasing is commonly seen, in the form of individuals hopping and running on the ground. As the behaviour escalates, so does the amount and intensity of vocalisations. When conflict escalation is more extreme, birds can be seen flight-chasing, and at times fierce fighting between pairs of birds can also be observed (Sorato pers.obs).

We simulated group encounters by using playbacks of group vocalisation recorded at dawn in proximity of roost sites (McComb 1992; McGregor 2000). Roost calls are commonly uttered by chestnut crowned babbler groups, starting with first light when birds are still inside the nest and usually continuing for a few seconds after the group has left the roost. Roost vocalisations last for about 30 seconds, and take the form of a loud intense chattering, with several birds calling at the same time. To the human ear, they appear indistinguishable from chatter vocalisation heard during group contests, and visual qualitative comparisons of sonograms seem to confirm the lack of obvious features separating the two calls. In fact, because of their loudness, roost calls can be heard from up to a few hundred meters apart, meaning that vocalisations of neighbour groups can at times be heard from roost-sites. This in turn suggests that roost calls might have a territorial function, and be involved in between group advertisement, as found for other avian cooperative breeders (e.g. Reyer and Schmidl 1988), and provides further justification for the use of roost vocalisations in playback experiments.

We therefore used group calls recorded at roost-sites, to create playback loops and investigate factors affecting both group general approach to loudspeakers, irrespective of

nearest distance reached, and close approach to playbacks, defined as groups closely approaching loudspeakers (closest distance $\leq 5\text{m}$). We predicted that home-range characteristics and local habitat features would affect probability of approach, and that group response would also vary according to measures of group size.

MATERIALS AND METHODS

Study site and population

The study was conducted between October 2007 and March 2010, on a population of chestnut-crowned babbler at the University of New South Wales Arid Zone Research Station, Fowlers Gap. The site is located in the far-west New South Wales, Australia, and is characterised by a dry, arid climate, with low annual rainfall that is unpredictable and not seasonal. The predominant vegetation type is constituted by an open semi-arid chenopod shrubland, with a high degree of spatial heterogeneity. Trees are scarce, and occur mostly in patches in close proximity to creeks and small drainage channels. Further details on habitat and climate are given elsewhere (Chapter 1).

We studied a total of 43 babbler groups, in the course of five continuous time periods within the total study duration: October 2007-January 2008, May-June 2008, August-October 2008, July-October 2009, and January-March 2010. During the first two study-years, 2007 and 2008, babblers bred between July and October. In contrast, breeding was limited during the last two study periods, between 2009 and 2010, because of prolonged drought conditions: in August 2009 less than 50% of groups started to breed, although there was a second breeding bout initiated in February 2010 following abundant rainfall in November and December 2009.

For the purpose of home range estimation, we lumped continuous time intervals, based on a combination of temporal occurrence and dominant life-history stage, and defined in this way three study-periods: the first, from October 2007 till begin of July 2008 (referred to as ‘2007-08 Non-breeding’), marked the non-reproductive phase that preceded the 2008

breeding season (August-October), which in turn constituted the second study period ('2008 Breeding'). The remaining study period included July-October 2009 and January-March 2010 ('2009-10') and saw only limited successful breeding. As playback experiments began in May 2008, the number of playback trials was too small for using the same three study periods (as used I home range estimation as above) in playback analysis, and therefore models of response to playbacks featured two study-years: '2008', including playbacks experiments carried on between May and October 2008, and '2009-10', as previously defined.

All birds were banded with individual color-ring combinations to allow visual individual and group identification. Groups of babblers were located throughout the study site by extensive searching, or listening for group vocalisations and individual contact calls, or by waiting at known roost sites before sunrise. Focal groups were followed for an average of 2.4 hours (min=0.25, max=4 hrs) in order to estimate home range area, group size, and to perform playback experiments.

Habitat analysis and home range estimation

We estimated group home range areas to investigate effects of home range size on playback response of babbler groups. During each tracking session a GPS coordinate was automatically recorded every 50 m using a Garmin eTrex or a Geko 301 GPS device. Group-specific track coordinates were subsequently pooled according to their temporal occurrence with respect to three broad time periods, defined through a combination of year and life-history stage. Thereby, we estimated group home ranges based on tracks collected between October 2007 and June 2008, when groups were not reproducing ('2007-08 Non-breeding'), during the 2008 breeding season, between August and October ('2008 Breeding'), and between July 2009-March 2010, when only a limited number of groups managed to breed ('2009-10'). We calculated home range areas using the local convex hull algorithm (Getz et al. 2007), a non-parametric method that is suitable for analysis of temporally autocorrelated coordinates and

relatively robust to extreme locations. Home range areas were estimated as 100% isoplethes using the R package Adehabitat (Calenge 2006). Further details on the algorithm and the home range validation procedure are provided elsewhere (Chapter 4).

We quantified variation in habitat by using a regular grid design to frame the whole study area and sampling across this at a total of 268 locations spaced at 400 m intervals. We visually assessed habitat within hypothetical quadrants of approximately 400 m length centred in correspondence of each sampling point, and semi-quantitatively scored the following variables: i) amount of cover (scores 0-4) for each of the main tree /tall shrubs species, and for all trees/tall shrubs combined, ii) cover of dominant short shrub genres and for all short shrubs combined, iii) average height of tree/tall shrubs, iv) average height of short shrubs ,and v) amount of surface cover for categorised soil types ('silt/clay', 'sands', 'gibber', and 'rocks'). To characterise the main dimensions of variation in habitat type within home ranges, a categorical principal component analysis (PASW statistics 18.0) was run on these variables, and weighted average principal component scores were calculated for habitat quadrants overlapping with each home range polygon, wherein weights represented the proportion of home range surface covered by each habitat quadrant.

Recording of roost vocalisations

We recorded group vocalisations at known roost nests, using a Marantz PMD660 solid-state recorder (sampling rate of 44 100 Hz at 16-bit precision), connected to a Sennheiser ME 66/K6 directional microphone. Roosting nest-trees were quietly approached before sunrise and the recording apparatus set at a distance of 5-10 m from the target nest. After starting the recording, we moved away from the roost nest, and waited at a distance of about 50 m to avoid any disturbance or interference with group vocal behaviour. Typically, groups started their loud calls at first light from inside the roosting nest, and briefly continued upon leaving the nest. Most vocalisations lasted for a total of 15-40 seconds.

Between May 2008 and October 2009, we recorded a total of 72 roost calls from 35 social groups within the study site. Poor quality recordings were discarded, and the rest were used to create playback recording for use in field experiments (n. playbacks=50).

Playback experiments

Using Wavepad sound editor (NCH software, 2008), we created playback loops from group roost vocalisations, by selecting from each recording the 10-15 second section in which group calling was most intense, and repeating it to create a 30 second vocalisation bout. Background noise was removed by using a cut-off filter of 300 Hz, and a further 30 seconds of silence was added at the end of the vocalisation. Sound intensity was standardised so that different playbacks were of similar loudness. The entire 60 second track was then looped 9 times to give a 10 min playback, and a further 60 seconds of silence was added at the beginning of loop. The total playback duration and structure were devised to mimic the typical pattern and duration of vocalisation observed during natural intergroup encounters.

Vocalisations of both familiar neighbour groups and unfamiliar non-neighbours were used as playback stimuli for focal groups. Given that a preliminary analysis did not reveal any effect of familiarity on response to playbacks, and because the focus of the study was on a different set of questions, we did not include this factor in the analysis and discussion presented here.

Playback trials were conducted either by roost sites soon after group emergence, or during group tracking, from 6:00 am to 11:00 am, and from 3:00 pm to 5 pm. Playbacks were initiated when the group was relatively quiet and mostly intent in foraging, using an ipod connected to a Logitech im207 loudspeaker. The playback apparatus was set opposite to the direction of the last movement of the group, for playback experiments performed during group tracking, or in a position suitable for observation, within about 30 m from the roost location, in the case of dawn playbacks run at roost sites.

To avoid interfering with group responses, once the playback was started we used the 60 seconds of initial silence of the playback track, to move away from the playback location. Generally, the observer moved sideways with respect to the hypothetical line connecting the group with the playback location, and sat down at an approximate distance of 50 m from both the group and the playback. Although we tried to standardise the initial distance of the playback from the focal group, start distances ranged between 20 to about 100 m, mainly due to groups moving during the 60 s period preceding the playback vocalisation.

Once the playback started, the following response variables were recorded: 1) if the group approached, 2) the closest approach distance from the speaker, and 3) the initial distance of the group, both estimated with respect to the individual closest to the loudspeaker.

Statistical analysis

All statistical analysis was done in R version 2.11.1 (R Development Core Team, 2010). We fitted generalised linear mixed models (GLMMs) using the package lme4 (Bates and Maechler 2010). To account for random sampling and repeated measures, group and playback identity were both entered as random intercept factors in all models. All model predictors were centred by subtraction of mean values, and continuous variables were further standardised by dividing them by their sample standard deviation (Schielzeth 2010), in order to allow direct comparison of estimates of effect sizes within and between models. Scatterplots of residuals and predicted values were generated to check model assumptions.

We investigated which factors affected the probability that a group moved towards the speaker ('Approach'), and the probability that a group closely approached the speaker (distance of closest bird <5 m: 'Approach close'). Both variables were set as binary response terms in GLMM models with binomial error structure and logit-link function. Although we estimated closest approach distance as a continuous variable, we have chosen to recode it as a binary factor ('Approach close') on the basis of the observation that the nearest distance of

groups that did not closely approach the loudspeaker may have been largely dictated by local habitat features. In particular, as approaching groups often appeared to use tall shrubs or trees as vantage points, it is likely that the local distribution of these was the main determinant of approach distance. In contrast, groups that closely approached the playback speakers, generally did it in a rather straight, directed way, covering the distance to the speaker through a combination of short flights and running on the ground.

We analysed the effects of habitat, space-use, social factors, study-period, and life-history phase, by fitting GLMMs with combinations of the following predictor terms: i) start playback distance, ii) period, iii) group life-history stage, iv) home range area, v) average habitat principal components within the home range, vi) number of adult birds in the social group, vii) number of adult birds in the playback group, at the time of recording, viii) size difference, and ix) size ratio, between focal and playback groups. Finally, plausible two-way interactions were also considered.

We used an information-theoretic approach to select best explanatory models from an initial candidate model set, based on the Akaike information criterion (AIC. Burnham and Andersson 2002) with the Hurvich and Tsay correction for finite sample size (AICc). Model selection was performed with the R package AICcmodavg (Mazerolle 2011), which calculates AICc scores and relative weights for candidate model sets. Inference was based on the single top-ranking model if this yielded a relative Akaike weight >0.9 , otherwise lower-ranking models with a $\Delta AICc \leq 5$, were also considered as plausible, in proportion to their relative AICc scores and associated weights (Burnham and Anderson 2002). To facilitate comparisons, we present effects estimates for both the best models (defined within each candidate model set as the models with the lowest AICc score) and the full nested models featuring the entire set of potential predictors.

RESULTS

Response to playback vocalisations

We performed a total of 159 playback experiments between May 2008 and March 2010. Of these, 86 (54%) elicited an approach response, and 43(27%) a close approach (within 5m from the loudspeaker) to the playback by focal groups. Typically, individuals within groups appeared to pay attention, or to actively react to playback vocalisations by changing their behaviour. When not approaching, birds usually reacted to playbacks by stopping their previous activity, and either by vocalising back towards the playback, or by otherwise keeping silent while paying attention to broadcasted calls. In the latter case, individual birds were often seen on top of tall shrubs and trees, facing in the direction of the loudspeakers in a vigilant position. Alternatively, the entire group seemed to hide under the cover of shrubs and trees while holding their spatial position usually for the entire playback duration. Only in a minority of cases, did the focal group continue in its previous activity without showing any obvious sign of response, or appeared to respond by quietly withdrawing.

For playbacks that provoked an approach, typically all or part of the group members responded by vocalising back and by moving towards the speaker following a leading bird. When approaching closely birds were commonly seen hopping and running around the speaker showing obvious excitement. This behaviour usually continued for the duration of each single playback loop, pausing during the silent portions of the playback and resuming once playback vocalisation started again. Almost invariably, groups left the playback site within a few minutes from the end of the playback experiment. Generally, groups that did not approach closely, seemed to use vantage points to patrol the surroundings of the playback and vocalise back.

Habitat

Principal component analysis of habitat variables extracted three components, which together explained 50% of total sample variance. The first component, (PC1) was characterised by high absolute factor loadings for amount of cover of tree and shrub species, and was thereby interpreted as an index of vegetation type in terms of species composition. The second component (PC2), showing the highest loadings for tree height and total amount of tree surface-cover, and low negative scores for amount of gibber and copperburr-shrub cover, was deemed as an index of arboreal biomass, thereby differentiating sites along a vertical dimension. Finally, the third principal component (PC3), being strongly positively correlated with total amount of short-shrubs cover, was interpreted as an index of non-arboreal vegetation abundance, identifying sites dominated by shrubland with little or no tree cover.

Table 1. Factors affecting: a) probability of approach to playbacks, and b) probability of close approach (min. distance $\leq 5m$).

BEST MODEL					FULL MODEL				
Random effects:					Random effects:				
	Variance	Std.Dev				Variance	Std.Dev.		
Group ID (Intercept)	0.46	0.68			Group ID (Intercept)	0.29	0.54		
Playback ID (Intercept)	0.21	0.45			Playback ID (Intercept)	0.27	0.52		
Number of obs: 151					Number of obs: 149				
Groups: 43					Groups: 41				
Playbacks: 37					Playbacks: 37				
Fixed effects:					Fixed effects:				
	Estimate	Std. Error	z-value	P		Estimate	Std. Error	z-value	P
(Intercept)	-0.24	0.24	-1.01	0.31	(Intercept)	-0.30	0.24	-1.25	0.21
Start distance	-0.63	0.23	-2.73	<0.01	Start distance	-0.55	0.23	-2.38	0.02
Year2009-10	-1.25	0.50	-2.50	0.01	Year2009-10	-1.20	0.53	-2.28	0.02
Breeding	0.77	0.51	1.52	0.13	Breeding	0.76	0.55	1.38	0.17
Young	0.45	0.59	0.76	0.45	Young	0.42	0.63	0.66	0.51
Home range area	-0.61	0.25	-2.49	0.01	Home range area	-0.44	0.28	-1.60	0.11
N.adults*year2009-10	-0.94	0.44	0.44	0.03	N.adults*year2009-10	-1.14	0.50	-2.30	0.02
					PC1	0.10	0.26	0.38	0.71
					PC2	0.12	0.26	0.46	0.64
					PC3	0.31	0.25	1.25	0.21
					N adults	-0.18	0.24	-0.73	0.47
					N adults playback	0.01	0.26	0.03	0.97
					Home-range area* year2009-10	0.23	0.53	0.44	0.66

a)

Random effects:				Random effects:					
	Variance	Std.Dev			Variance	Std.Dev.			
Group ID (Intercept)	0.37	0.61		Group ID (Intercept)	0.29	0.54			
Playback ID (Intercept)	0.52	0.71		Playback ID (Intercept)	0.43	0.66			
Number of obs: 149				Number of obs: 149					
Groups: 41				Groups: 41					
Playbacks: 37				Playbacks: 37					
Fixed effects:				Fixed effects:					
	Estimate	Std. Error	z-value	P		Estimate	Std. Error	z-value	P
(Intercept)	-1.32	0.28	-4.67	<0.01	(Intercept)	-1.36	0.29	-4.68	<0.01
Start distance	-0.47	0.24	-1.92	0.05	Start distance	-0.40	0.25	-1.64	0.10
Year2009-10	-0.87	0.51	-1.70	0.09	Year2009-10	-0.71	0.59	-1.21	0.22
Breeding	0.79	0.56	1.40	0.16	Breeding	0.78	0.59	1.32	0.19
Young	0.76	0.65	1.16	0.24	Young	0.70	0.69	1.02	0.31
PC2	0.44	0.27	1.60	0.11	PC2	0.43	0.30	1.43	0.15
N.adults*year2009-10	-1.29	0.49	-2.61	<0.01	N.adults*year2009-10	-1.35	0.54	-2.52	0.01
					PC1	0.11	0.27	0.40	0.60
					PC3	0.10	0.28	0.37	0.71
					Home-range area	-0.17	0.29	-0.59	0.56
					N.adults	-0.23	0.27	-0.85	0.40
					N.adults playback	0.27	0.32	0.84	0.40
					Home-range area* year2009-10	0.21	0.55	0.38	0.70

b)

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

Environmental and social effects on playback response

The probability of the focal group approaching the playback was affected by study- year, life history phase, home-range size, initial distance of the group from the playback, and by the interaction between study-year and the number of adults in the focal group. Models featuring habitat principal components or playback group size were not supported (Table A4a, 1a).

Groups were more likely to approach in 2008 than in 2009-10, and when breeding. The probability of approach decreased with increasing home range size and the distance of the group from the loudspeaker at the beginning of the playback. There was a strong interaction between study-year and the number of adults in the group, with large groups more likely to approach in 2008, and small groups more likely to approach in 2009-10 (Table 1a, Figure 1).

Similar results were observed for the probability of approaching the playback closely ('Approach close'), with the exception that the second principal habitat component, and not home range area, featured in the best model (Table A4b, Figure 2). Thereby, the probability of a focal group moving to close proximity of the loudspeaker increased with average tree-cover within the focal group home-range.

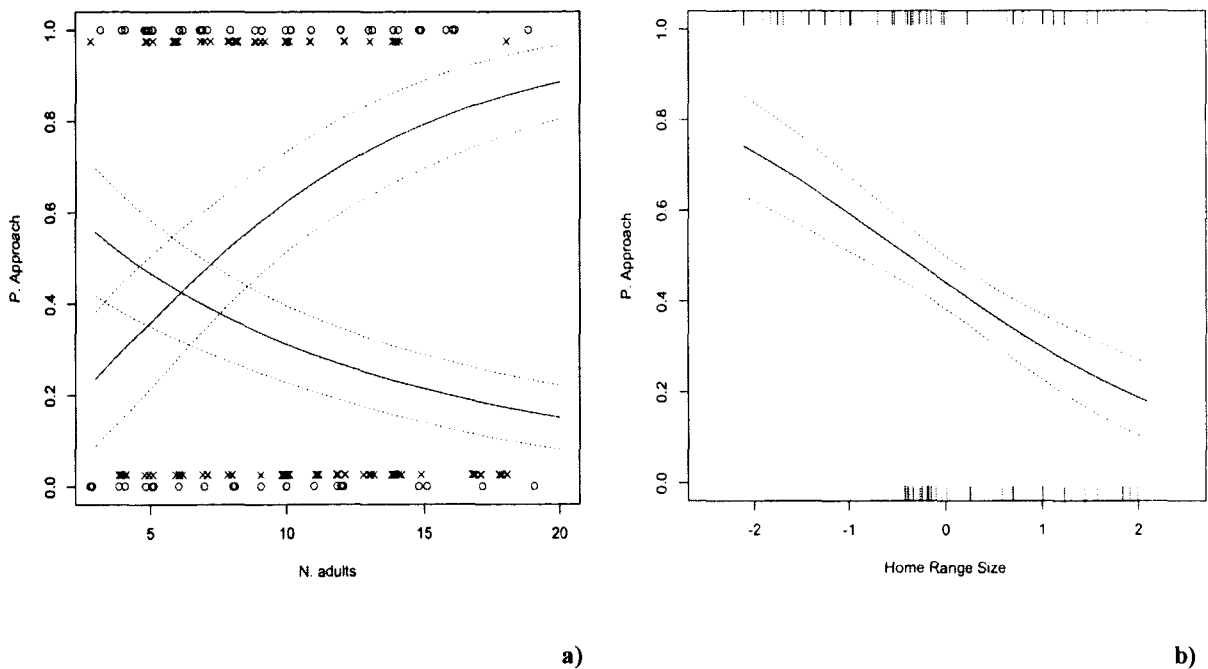


Figure 1. Relationship between probability of approach to playback and: a) number of adults in the focal group, b) home range size. Continuous lines represent best model estimates, dotted lines show errors. In a) the effect of group size is shown separately for the two study-years, 2008 (top increasing curve) and 2009-10 (bottom decreasing curve). Open circles and crosses represent observed responses observed, respectively, in the year 2008 and 2009-10.

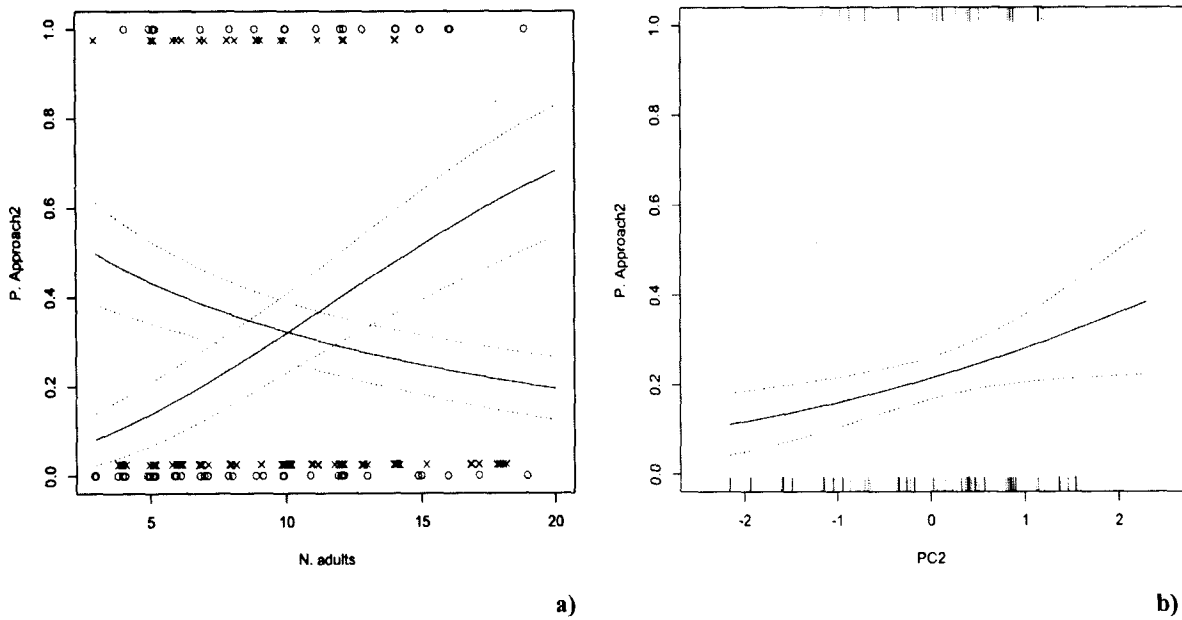


Figure 2. Relationship between probability of close approach to loudspeaker (min. distance $\leq 5\text{m}$) and: a) number of adults in the group, b) habitat PC2.

Continuous lines represent best model estimates, dotted lines error intervals. In a) the effect of group size is shown separately for the two study-years, 2008 (top increasing curve) and 2009-10 (bottom decreasing curve). Open circles and crosses represent observed responses observed, respectively, in the year 2008 and 2009-10.

DISCUSSION

The propensity of chestnut-crowned babbler groups to approach playback vocalisations was strongly affected by study-year, by the interaction of number of adults in the group with study-year, and by home range size. Groups were also more likely to approach when breeding, and, approach more closely when the average tree cover in their home range was high. Therefore, group reactions to playback stimuli appeared mainly predicted by local ecological conditions (that varied across years) and by their interactions with group size.

The effect of home range size and habitat variation on group response to playback is consistent with intergroup variation in payoffs of territorial behaviour, both in relation to differences in habitat quality (Riechert 1979; Enquist and Leimar 1987; Johnsson et al 2000) and economic defensibility of resources (Davies and Houston 1984; Goldberg et al 2001). We have shown elsewhere (Chapter 4) that within the study population, home range size was predicted by habitat, both in term of vegetation type and biomass: home range areas increased in sites where the dominant vegetation appeared suboptimal in the light of known babbler preferences for tree and shrub species, as well as with decreasing average tree and shrub cover. The association between home range size and habitat, suggests that resources may have been less valuable for groups with large home ranges because of their poorer average quality, and thereby the cost of a sharing a part of their area with another group would have been lower, both in absolute and relative terms, compared to groups with smaller home ranges (Grant 1993; Davies et al.1996). Related to this point, the higher habitat patchiness that characterised groups with large home ranges (Chapter 4) may have also meant an increased probability of the playback experiment being performed in a location of marginal value, leading to an average lower propensity to approach in such areas. On a proximate level, the actual frequency and outcome of encounters with neighbouring groups may also have differently primed groups to approach, either through learning mechanism or by changing the hormonal status of individuals (Wingfield et al. 1990; Silverin 1998). Ultimately however,

variation in intergroup interactions would have still been likely to depend on habitat, because both local group density and extent of home range overlap between groups seemed positively associated with habitat quality (Sorato pers. obs.). That habitat quality was influencing the response to simulated group intrusions is further supported by the comparison between approach and close approach to playbacks. The two variables measured the same type of response, approach to speakers playing vocalisations of a conspecific group, but at different quantitative levels. In other words, within approaching groups, those that reached the playback site were likely to represent a subsample with higher motivation to respond to group intrusions. The fact that the second habitat principal component, a measure of habitat quality which, by predicting both home range size and group size is likely to represent an index of resource value within the group home range, was a predictor of the probability of closely approaching the loudspeaker, suggests that the intensity of group responses may have been affected by the value of local resources at stake (Johnsson et al. 2000; Gherardi 2005; Harris 2010). The value of defended resources, may have also contributed to stronger responses during breeding, since the need of nest provisioning, by constraining home range size and increasing group foraging, may have exacerbated local depletion of food resources (Chapter 3).

The strong effect of study-year on group approach is also consistent with group responses to territorial intrusions being affected by ecological conditions, while habituation to playback stimuli can be ruled out in the light of the considerable temporal separation between the two study-years. The substantial decrease between the years 2008 and 2009-10 in both measures of approach, matched an evident deterioration in local ecological conditions as a consequence of persistent drought. Accordingly, for the first time since the establishment of the study system in 2004, only a minority of groups within the study site managed to breed and successful fledge young in the year 2009. A decrease in both group size and number of groups was also evident towards the end of the study period, particularly in areas where

vegetation had been hit more severely by prolonged lack of rainfall (Sorato pers. obs.). Moreover, the average weight of birds showed a significant decrease during the same time period (Chapter 3), and it is possible that changes in individual condition may have also played a role in the decreased responsiveness to playback vocalisations (Petrie 1984; Marden and Waage 1990; Jennings et al. 2004). In fact, besides resource value, relative resource holding potential of contestants is predicted by game-theoretical models to be a prime determinant of conflict escalation and final outcome (Parker 1974; Parker and Rubenstein 1981). A number of empirical studies, mainly on disputes between single individuals, have confirmed this prediction (Petrie 1984; Schradin 2004; Gherardi 2005; Lindstrom and Pampoulie 2005; Harris 2010). Evidence for group-living animals seems also to support the importance of group resource holding potential in the context of intergroup conflicts (McComb et al. 1994; Radford 2003; Radford and Du Plessis 2004), though in this case the identification of key factors explaining group asymmetries in fighting ability is less straightforward, and confounded by the presence of multiple interacting individuals with different phenotypes (Franks and Partridge 1993; Wilson et al 2001; Harris 2010). Therefore, whilst individual body size and condition have been identified as prime actors in dyadic contests (Maynard Smith and Parker 1976; Jennings et al. 2004; Briffa and Sneddon 2007), other group traits, such as the number of individuals, group sex ratio, and age distribution, may also represent critical factors affecting resource holding potential of contesting groups. Supporting this group size has been shown to be positively associated with approach to playback vocalisations in several group-living species, including lions (*Panthera leo*, McComb et al. 1994), Chimpanzees (*Pan paniscus*; Wilson et al. 2001), and green woodhoopoes (*Phoeniculus purpureus*, Radford and Du Plessis 2004), while group sex ratio affected response to simulated encounters in subdesert mesites (*Monias benschi*, Seddon and Tobias 2003). Nevertheless, it can be difficult to determine the relative importance of different factors due to correlations between traits. Experimental manipulations of group phenotypes

could represent a potential way to circumvent this problem, or alternatively, natural variation between population and temporal variability in associations between traits following changes in local biotic and physical environments, may provide other windows of opportunity. In this light, our finding of a diverging year-specific effect of group size on response to playback experiments is noteworthy. The predicted positive association between number of adults in the group and probability of approach was found only for the first study year, whereas bigger groups were significantly less likely to approach during the second study year. A possible explanation for this result is that, against a background of a general decline in individual condition over the study duration, individuals in larger groups suffered a disproportionately higher cost of deteriorating ecological conditions, because of higher local resource depletion. Supporting this hypothesis, besides the aforementioned year effect, individual body weight was also found to be negatively associated with group size (Chapter 3), implying that, on average, individuals in large groups may have been less likely to approach because of reduced fighting ability and lower energy reserves available for a potential contest (Harris 2010). Interestingly, another study has found year-specific effects on amount of intergroup interactions in a group-living bird species: during natural encounters, in Tasmanian native hens (*Gallinula mortierii*), smaller groups were more likely to start interactions with other groups limited to one of three consecutive breeding seasons (Putland and Goldizen 1998). Yet, we are not aware of any other experimental study that suggests opposite, year-specific effects of group size on group territorial behavior. An important implication of this finding is that the balance between costs and benefits of living in groups of different size may show cyclical or stochastic temporal variability, which, on the face of the dangers of basing conclusions on short-term research, further highlights the need for longer-term studies, that can better account for variable ecological conditions (Griffith et al. 2003).

Besides resource value, self-condition, and fighting ability, animals involved in contests are also predicted to base their strategic decisions onto the resource holding potential of their

opponents (Maynard Smith and Price 1973; Parker 1974; Radford 2003). Accordingly, in social species groups may be expected to assess phenotypes of rivals, and relate them to self-perceived fighting potential, in order to match their response to the level of asymmetry with the opponents (Radford 2003). In this respect, group vocalisations may represent an important cue, as they may provide integrated information about size, composition, and possibly condition of the group. For example, in lions, roaring has been shown to provide reliable information on pride size (McComb et al. 1994), in green woodhoopoes, group members tuned their response to the size of both actual and simulated intruding groups (Radford 2003), and in subdesert mesites groups were less likely to approach playbacks with a large number of vocalising individuals (Seddon and Tobias 2003). On the other hand, Bradley and Mennil (2009) failed to find any effect of number of simulated intruding individuals on the response of cooperatively breeding rufous-naped wrens (*Campylorhynchus rufinucha*) to playback experiments. Similar to the latter study, we did not find any effect of playback size on the probability that chestnut-crowned babbler groups approached playbacks. This may imply that babblers did not based their decisions, about whether to approach the playback source or not, based on perceived size of simulated intruding groups. Another possibility is that rather than group size, groups sex ratio or other aspects of group phenotype may have represented more important traits (Seddon and Tobias 2003). Still, a more simple explanation may be that playback calls simply lacked the relevant information about group size. Discriminating between these alternatives, is beyond the scope of the present study, and would require sound analyses of playback calls to reveal any correlates of vocalisation features with group size and composition. We just note that a lack of information may be a plausible explanations, because there appeared to be a certain amount of variability in roost vocalisations within repeatedly sampled groups, and occasionally groups left their roosting sites without uttering any call (Sorato pers. obs.).

In conclusion, we have found that responses of chestnut-crowned babbler groups to simulated group territorial intrusions were affected by spatio-temporal variation in ecological conditions, and that these seemed to interact with focal, but not playback, group size in predicting probabilities of response.

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Chapter 6

**Interacting effects of sex, individual phenotype, group size, and
habitat on dispersal in the cooperatively breeding Chestnut-
crowned Babbler**

ABSTRACT

Dispersal has been the focus of studies of cooperative breeding due to its role in family formation and its consequences for the genetic structure of social groups.

Ecological conditions have been acknowledged as prime factors promoting delayed dispersal, and recently local social environment has also come under scrutiny as a factor promoting philopatry. In this study, we investigated individual, social and environmental factors affecting individual probability of dispersal, and compared features of groups that were source of dispersers with characteristics of destination groups. We show that dispersal was strongly female-biased, seemed to decrease with age, and with habitat features likely to be important for individual fitness. Moreover, we also found that dispersal patterns were sex-specific, in that dispersing females were on average lighter than non-dispersing ones, while the opposite applied to males. Similarly, group size had also diverging effects in males and females, as females dispersed more often from small groups, and seemed to target large ones as destination, whereas males appeared to emigrate mainly from large groups and move into small ones.

INTRODUCTION

Dispersal represents a crucial stage in the life cycle of mobile animals, because of its far-reaching consequences for species ecology, genetic structure and evolutionary dynamics (Clobert et al 2001). The implications of dispersal are particularly evident in the context of social evolution, as exemplified by studies of cooperatively breeding species, wherein a leading pathway involved in the formation of stable social groups is represented by offspring philopatry (Brown 1987; Ekman 2006). In fact, dispersal can exert profound effects on social organisation, due to its consequences on population density and local genetic structure, and in turn may be conducive to cooperation promoted by kin selection mechanisms (Hamilton 1964; Sharp et al. 2006; Cornwallis et al. 2009). Thereby, understanding the factors that are involved in individual dispersal behaviour within populations, as well as in variation at interspecific and higher taxonomic levels, is essential in order to explain differences in animal social organisation. Nevertheless, dispersal still represents a relatively poorly understood behavioural trait. Ecological conditions have been routinely invoked in classical studies of cooperative breeding as prime factors promoting delayed dispersal (Emlen 1982; Hatchwell and Komdeur 2000; Russell 2001; Kokko and Ekman 2002). For example, ecological constraints, such as shortages of vacant breeding territories (Emlen 1982; Koenig et al 1992), and benefits of philopatry, promoted by variance in quality of local habitat (Stacey and Koenig 1987; Dickinson and McGowan 2005; Baglione et al. 2006), have been hypothesised to be prime mechanisms conducive to family formation in cooperatively breeding avian species (Hatchwell and Komdeur 2000; Dickinson and Hatchwell 2004). More recently, partly as a consequence of difficulties of ecological explanations in accounting for variation in dispersal between species, social factors, in particular benefits of extended parental care provided to independent offspring by nepotistic parents (Ekman and Griesser 2002; Ekman 2006), have come under scrutiny, and have been linked to life history traits favouring extended social bond between relatives (Covas and Griesser 2007; Eikenaar et al. 2007).

Still, social factors may exert their influence through a multitude of pathways, and nepotistic benefits may coexist with socially mediated competition (Ekman et al. 2002). Ultimately, the net balance between costs and benefits of staying in the natal group versus leaving, is likely to be affected by the interaction between local ecological conditions, group size and genetic structure, as well as individual genotypes and phenotypes (Daniels and Walters 2000a). Accordingly, social dominance may promote dispersal of subordinates due to competition for local resources (Christian 1970; Dobson et al. 1998; Pasinelli and Walters 2002), or on the contrary, may favour philopatry through the advantages of holding position within age-dependant social queues for breeding (Zack and Rabenold 1989; Yaber and Rabenold 2002). At the same time, sex-biased dispersal may arise, due to modes of reproductive competition specific to different mating systems (Greenwood 1980; Dobson 1982), or linked to inbreeding avoidance (Clutton-Brock 1989; Daniels and Walters 2000b; Szulkin and Sheldon 2008).

In this paper, we describe dispersal, with respect to sex and age categories, and further evaluate ecological and social factors affecting individual propensity to disperse within a population of group-living chestnut-crowned babbblers (*Pomatostomus ruficeps*), using recapture data from a banding dataset gathered over five years. Specifically, we investigated how the probability that babblers were recorded in the same group, as opposed to a different one, in the course of consecutive recapture events, was affected by individual phenotypes, in terms of sex, age, weight, habitat type within the home range of the group to which they belonged to, and group size, measured as the number of adults in the group. We evaluated in particular if effects of social and environmental factors showed evidence of being specific to individual phenotypes by considering interactions with individual age and sex. Finally, in order to assess whether dispersal events were associated with changes in individual weight, and if dispersing individuals might have targeted specific group sizes and local habitat features for their dispersal destinations, we compared effects of relevant individual, social and

ecological predictors of dispersal, when measured either at initial capture or following subsequent recapture.

MATERIALS AND METHODS

Study species and population

Chestnut-crowned babblers can be found in groups ranging from two up to more than 20 birds, the latter usually following breeding and consequent recruitment of philopatric offspring in the group. They are endemic to the semiarid interior of South East Australia, where they can be found across a range of different habitats, though the species seems to occur predominantly in semiarid chenopod shrublands and avoids areas with extensive tree cover. Chestnut-crowned babblers represent the least arboreal species within their family, showing a preference for ground-foraging, while trees or tall shrubs seem required mainly for construction of breeding and roosting nests. Within social groups, up to three different females may reproduce, leading to temporary dissolution of groups into smaller breeding units, constituted by a breeding pair and up to 13 helpers (Russell et al. 2010). Group home ranges are typically large (Chapter 4), and accordingly the species does not seem to show strong territoriality. In turn, there is no obvious evidence of habitat saturation, and vacant breeding patches which appear suitable for breeding pairs are not uncommon (Russell pers. Comm.). Based on capture-recapture data and demographic observations, adult survival does not appear particularly high (Russell pers. Comm.), as would be typical for cooperatively breeding species, possibly a consequence of general food scarcity combined with high predation pressure which appear to characterise the species (Chapter 2). Breeding females seem to commonly originate from other groups (Russell and Sorato pers. obs.) and preliminary genetic investigation is consistent with substantial gene flow within the study population and female-biased dispersal (Rollins & Griffith Pers. Comm.).

For this study, we used data collected between 2004 and 2008, on a total of 51 babbler social groups, at the University of New South Wales Arid Zone Research Station, Fowlers Gap, in the far-west New South Wales, Australia. The study site is characterised by a dry, arid climate, with low unpredictable rainfall, and the predominant vegetation type is constituted by an open semiarid chenopod shrubland, wherein trees are scarce and mostly restricted to patches in close proximity of creeks and small drainage channels. Further details on habitat and climate are given elsewhere (Chapter 1).

Babblers were mist-netted or caught in the nest before fledging, and were individually marked with metal rings and unique color-band combinations. Following capture, blood samples for genetic sexing were also taken, as well as morphometric measures. A total of 481 individuals were recaptured at least once over the course of the entire study period, and this sample constituted our dataset for dispersal analysis. Recaptures came from a total of 14 groups in 2005, 33 and 39 groups in 2006 and 2007 respectively, and 42 groups in 2008. An individual was considered to have dispersed when caught in a different social group from the one of previous capture. Subsequent group observations and recaptures generally confirmed putative dispersal events as genuine, and not the result of misinterpreted temporary individual forays into social groups. Based on precise knowledge of age from extensive banding of nestlings, birds were aged as young or immatures if they were born in the same year of capture or in the preceding year, else they were categorised as mature adults, if more than one calendar year old. Because chestnut-crowned babblers cannot be reliably sexed based on phenotypic characters, sex was determined through molecular analysis (Holleley, Rollins & Griffith unpublished data). Group sizes were assessed based on capture data as well as following observations of groups in the field.

Between the years 2007-2010, groups were also tracked in order to estimate home range size, and several habitat variables within home ranges were also measured by scoring. We estimated total home range size of focal groups using the local convex hull method (LoCoH,

Getz et al 2007), while habitat measures included indexes of total vegetation cover for trees and shrubs, as well as cover of dominant tree species and substrate type, which, following principal component analysis, were reduced to three composite factors summarising the main variance in habitat characteristics. Furthermore, area of the home range covered by creeks and small drainage channels was also estimated in ESRI Arcgis 9.2, using geo-referenced aerial photographs of the field site. Details on home-range measures and sampling procedures for habitat features are provided elsewhere (Chapter 4). As estimates of average habitat features within group home ranges, we calculated mean values of the first three principal habitat components. Mean estimates were based on home ranges assessed during the year 2007-08, supplemented by estimates from the period 2009-10 for groups that had not been tracked earlier. Therefore, there was a time mismatch with dispersal data, which may have introduced a certain degree of inaccuracy in estimates of group habitat quality relative to the years 2004-2006. However, the amount of noise introduced in this way is likely to be only minimal, because overall, group home ranges appeared remarkably consistent across years (Russell, Sorato pers.obs). A high correlation between non-breeding home range areas in 2007-08 and 2009-10 further support the general long-term stability of home ranges (Sorato unpublished data).

Statistical analysis

All statistical analysis was done in R version 2.11.1 (R Development Core Team, 2010). We fitted generalised linear mixed models (GLMMs) using the package lme4 (Bates and Maechler 2010). To account for repeated sampling of individuals within groups, group identity was entered as a random intercept factor in all models. All model predictors were centred by subtraction of mean values, and continuous variables were further standardised by dividing them by their sample standard deviation (Schielezeth 2010), in order to allow direct

comparison of estimates of effect sizes within and between models. Scatterplots of residuals and predicted values were generated to check model assumptions.

We investigated the effects of individual attributes, group size, and local habitat features, on the probability that individuals had dispersed between consecutive capture events, by fitting GLMMs with binomial error structure and logit-link function. Predictors featuring in candidate model sets included number of days between subsequent captures, to control for the effect of time available to disperse, individual sex, age, weight and number of adults in the group at first capture, and finally, habitat variables, again relative to the group at first capture, including creek cover, and the three habitat principal components.

We used an information-theoretic approach to select best explanatory models from an initial candidate model set, based on the Akaike information criterion (AIC. Burnham and Andersson 2002) with the Hurvich and Tsay correction for finite sample size (AICc). Model selection was performed with the R package AICcmodavg (Mazerolle, 2011), which calculates AICc scores and relative weights for candidate model sets. Inference was based on the single top-ranking model if this yielded a relative Akaike weight >0.9 , otherwise lower-ranking models with a $\Delta AICc \leq 5$, were also considered as plausible, in proportion to their relative AICc scores and associated weights (Burnham and Anderson, 2002). To facilitate comparisons, we present effects estimates for both the best models (defined within each candidate model set as the models with the lowest AICc score) and the full nested models featuring the entire set of potential predictors.

Finally, in order to contrast relevant individual, group and habitat variables before and after dispersal, we compared the final best model, featuring variables measured at first capture, with an analogous model that included variables measured at recapture, controlling for time between captures, sex, and age at first capture. In this way we wanted to assess if predictors of dispersal probabilities were still discriminating between individuals that dispersed versus individuals that did not, once variables were measured at recapture in the

group of dispersal rather than in the group of origin, or in other words, if traits measured in groups that were source of dispersing individuals differed on average from those in destination groups, and in groups not interested by dispersal.

RESULTS

From 2004 to 2008, we detected a total of 78 dispersal events between groups in the study area. Out of a total of 51 groups sampled, dispersers were detected as originating from 32 groups, and immigrants were recaptured in 34 groups. Further, 21 groups were both source and destination of dispersers, 10 were only source, and 12 destination only for dispersers. Of the 56 dispersing individuals that were genetically sexed, 13 (23%) were males and 43 (77%) females, whereas within birds that did not disperse, 209 (57%) individuals were sexed as males and 152 (43%) as females. With respect to age, 37 individuals were captured as immatures before dispersal, and 41 as adults (47% and 53 % respectively). Among individuals that did not disperse, 243 (48%) were immatures and 260 mature adults (52%).

Table 1. Factors affecting individual probability of dispersal.

BEST MODEL					FULL MODEL				
Random effects:					Random effects:				
	Variance	Std.Dev.				Variance	Std.Dev.		
ID (Intercept)	1.59	1.26			ID (Intercept)	1.42	1.19		
Number of obs: 447, Groups: 32					Number of obs: 421, Groups: 30				
Fixed effects:					Fixed effects:				
	Estimate	Std. Error	z-value	P		Estimate	Std. Error	z-value	P
(Intercept)	-3.75	0.46	-8.11	<0.001	(Intercept)	-3.68	0.46	-7.91	<0.001
N.days	1.19	0.29	4.06	<0.001	N.days	1.22	0.30	4.06	<0.001
Sex	2.13	0.55	3.89	<0.001	Sex	1.97	0.56	3.51	<0.001
Age	-0.98	0.55	-1.78	0.076	Weight	-0.31	0.37	-0.83	0.40
Creek.cover	-1.05	0.46	-2.27	0.023	N.adults	-0.20	0.38	-0.53	0.60
Sex*N.adults	-1.10	0.48	-2.28	0.022	Age	-0.72	0.71	-1.01	0.31
Sex*weight	-0.95	0.43	-2.20	0.028	Creek.cover	-1.02	0.52	-1.96	0.05
					PC1	0.31	0.45	0.68	0.49
					PC2	0.24	0.39	0.63	0.53
					PC3	-0.10	0.37	-0.26	0.80
					Sex*N.adults	-1.05	0.56	-1.87	0.06
					Sex*Weight	-0.66	0.63	-1.04	0.29
					Sex*Age	-0.16	1.29	-0.12	0.90
					Age*N.adults	-0.13	0.50	-0.26	0.80

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

Table 2. Comparison between best model estimates for individual probability of dispersal, and estimates from the analogous model, with the same kind of predictors, but relating to values at recapture.

FIRST CAPTURE					RECAPTURE				
Random effects:					Random effects:				
	Variance	Std. Dev.				Variance	Std. Dev.		
ID (Intercept)	1.59	1.26			ID (Intercept)				
Number of obs: 447, Groups: 32					Number of obs: 419, Groups: 37				
Fixed effects:					Fixed effects:				
	Estimate	Std. Error	z-value	P		Estimate	Std. Error	z-value	P
(Intercept)	-3.75	0.46	-8.11	<0.001	(Intercept)	-3.24	0.51	-6.37	<0.001
N.days	1.19	0.29	4.06	<0.001	N.days	0.89	0.28	3.21	0.001
Sex	2.13	0.55	3.89	<0.001	Sex	1.95	0.53	3.66	<0.001
Age1	-0.98	0.55	-1.78	0.076	Age2	0.41	0.55	0.75	0.45
Creek.cover1	-1.05	0.46	-2.27	0.023	Creek.cover2	-0.07	0.34	-0.22	0.83
Sex*N.adults1	-1.10	0.48	-2.28	0.022	Sex*N.adults2	0.89	0.44	2.01	0.04
Sex*weight1	-0.95	0.43	-2.20	0.028	Sex*weight2	0.08	0.43	0.19	0.84

For comparison, estimates from both the best model and the full model are provided. All predictors are centred and continuous variables are further standardised through scaling (Schielezeth 2010).

Habitat

Principal component analysis on habitat variables extracted three main factors which altogether explained 50% of sample variance. The first component (PC1) was characterised by high absolute factor loadings for amount of cover of tree and shrub species, and was thereby interpreted as an index of vegetation type in terms of species composition. The second component, showing the highest loadings for tree height and total amount of tree surface-cover, and low negative scores for amount of gibber and copperburr-shrub cover, was deemed as an index of arboreal biomass, thereby differentiating sites along a vertical dimension. Finally, the third principal component, being strongly positively correlated with total amount of short-shrubs cover, was interpreted as an index of non-arboreal vegetation abundance, identifying sites dominated by chenopod shrubland with little or no tree cover.

Phenotypic, social and environmental effects on dispersal

The probability that an individual had dispersed between successive captures was strongly predicted by sex, number of days between capture dates, age, amount of creek cover in the natal home range, and by the interactions between sex and weight, and sex and number of adults in the group of first capture (Table A5, 1). Models featuring habitat principal components were not supported as relevant. According to the best model, predicted marginal mean probabilities of dispersal were $1 \pm 0.6\%$ for males, and $8 \pm 3\%$ for females (average time interval between captures: 297 days). With respect to age, predicted dispersal probabilities were $4 \pm 2\%$, and $1 \pm 0.8\%$, for young and adult birds respectively. Probability of dispersal was also predicted to decrease with weight at first capture in females, but to increase with weight in males, though here the effect appeared much weaker (Table 1; Figure 2). Accordingly, between the two extremes of weight variation, probability of dispersal was predicted to decrease from $36 \pm 18\%$ to $2 \pm 2\%$ in females, and to increase from $0.3 \pm 0.3\%$ to $3 \pm 2\%$ in males. Number of adults in the group of first capture had analogous effects on

dispersal probabilities (Figure 2): mean marginal probabilities predicted by the best model, decreased with group size, from $35 \pm 18\%$ to $2 \pm 2\%$, in females, and increased from $0.3 \pm 0.3\%$ to $3 \pm 2\%$ in males. Finally, dispersal probability was negatively associated with area covered by creeks in the home territory (Table 1, Figure 3). Predicted mean marginal probability of dispersal decreased from $9 \pm 5\%$ for the group with minimum creek area, to $0.2 \pm 0.2\%$ for maximum creek area in the home territory.

Comparison between the best model, featuring variables measured at first capture, before potential dispersal events, and the analogous model with predictor values relative to recapture, indicated that following recapture, average weight of dispersing individuals was no longer different from the weight of non-dispersers (Table 2, Figure 1b). Similarly, creek cover within home ranges of groups into which dispersers had moved, did not differ from cover associated with philopatric individuals (Table 3, Figure 3b). On the other hand, female dispersal appeared biased towards large destination groups, while males seemed to disperse mainly into small groups (table 2, Figure 2b).

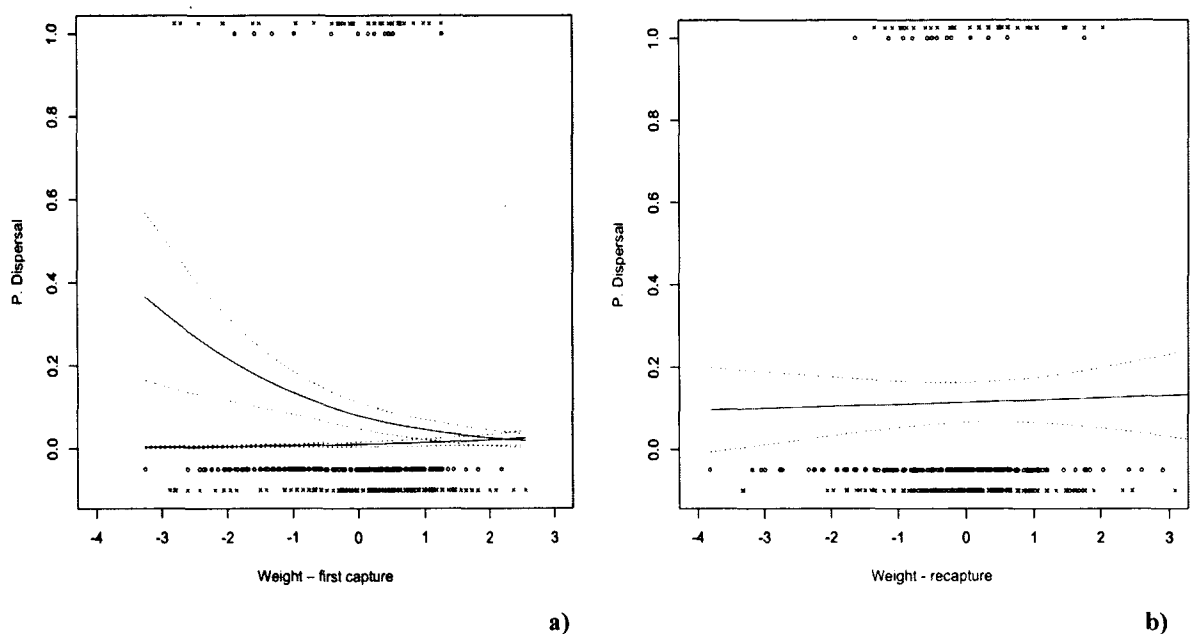


Figure 1. Probability of dispersal as a function of: a) weight at initial capture, b) weight at subsequent recapture. Continuous lines represent respectively best model estimates (a), and “recapture” model estimates (b). Dotted lines show error intervals. Open circles show observed dispersal values (0= no dispersal, 1=dispersal) for males, crosses indicate values for females. In a), separate curves show dispersal probabilities for females (top decreasing curve), and for males (bottom increasing curve).

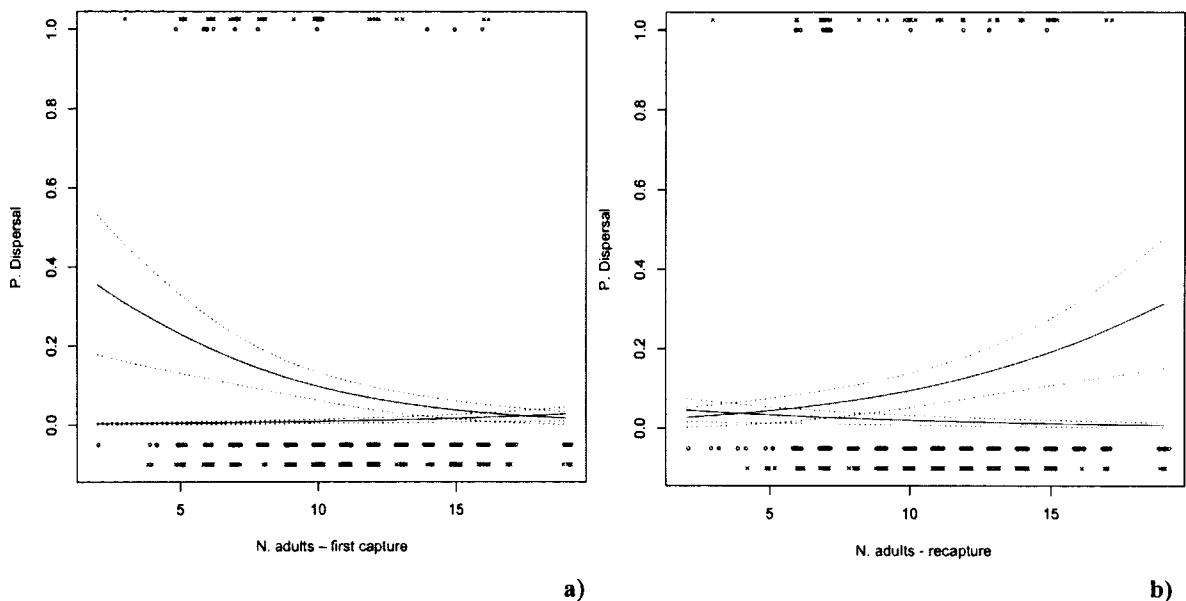


Figure 2. Probability of dispersal as a function of: a) number of adults in the group at initial capture
b) number of adults in the group following recapture. Continuous lines represent respectively best model estimates (a), and “recapture” model estimates (b). Dotted lines show error intervals. Open circles show observed dispersal values (0=no dispersal, 1=dispersal) for males, crosses indicate values for females. In a) the top decreasing curve represent predicted dispersal probabilities for females, while the bottom increasing curve shows predicted probabilities of dispersal for males.
In b) predicted dispersal probabilities in females are represented by the top increasing curve, while probabilities for males are shown by the bottom decreasing curve.

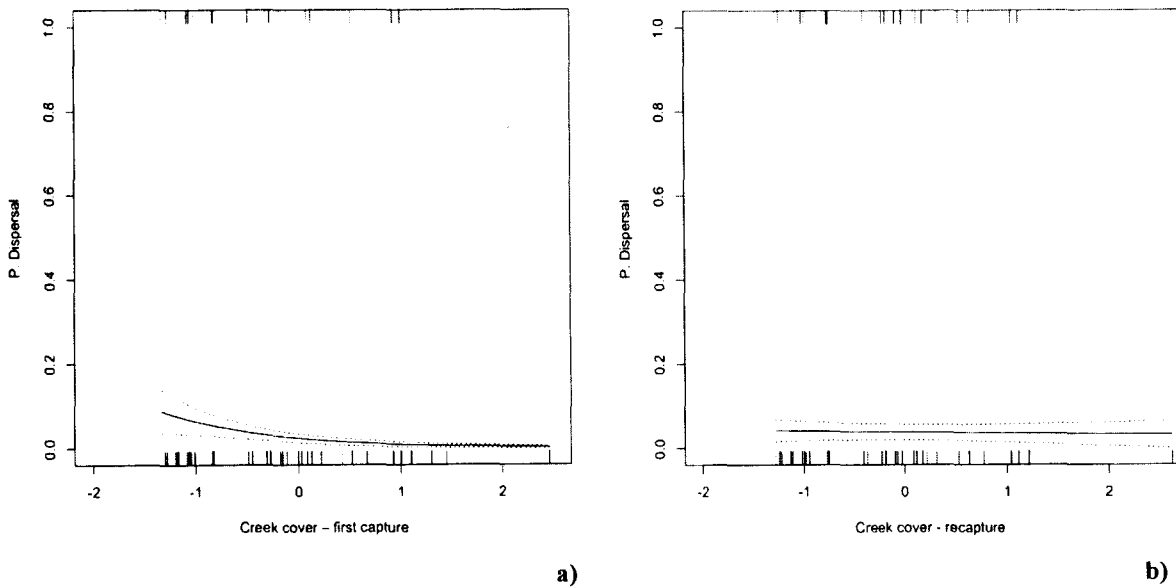


Figure 3. Probability of dispersal as a function of: a) creek cover at initial capture site, b) creek cover at subsequent recapture. Continuous lines represent respectively best model estimates (a), and ‘recapture’ model estimates (b). Dotted lines show error intervals. Rugs represent observed values.

DISCUSSION

As typical for birds (Greenwood 1980), dispersal within our study population was strongly biased towards females. Male-biased philopatry coupled with female-biased dispersal, constitutes also the general pattern found in group living, cooperatively breeding species, even though a few notable exceptions exist. For example, male dispersal is found in Seychelles warblers (*Acrocephalus sechellensis*, Richardson et al. 2002), white-throated magpie-jays (*Calocitta formosa*, Berg et al. 2009), and brown jays (*Cyanocorax morio*, Williams and Rabenold 2005), while a lack of sex bias has been detected in some of the most extreme Australian cooperative breeders: the white-winged chough (*Corcorax melanorhamphos*, Beck et al. 2008), the apostlebird (*Struthidea cinerea*, Woxvold 2005), and the aforementioned grey-crowned babbler (Eguchi et al. 2007; Blackmore et al. 2011). The

absence of sex-biased dispersal in grey-crowned babbler is particularly interesting, in the light of the contrasting results found for our study population of chestnut-crowned babblers, despite the close phylogenetic affinity of the two species, and the similarities in their social organisation (Higgins and Peter 2002; Blackmore and Heinsohn 2008). In fact, while Greenwood's (1980) mating system hypothesis is generally invoked to explain the predominance of female-biased dispersal in birds, our findings concur with previous studies of cooperatively breeding species in suggesting that Greenwood's explanation appears to fail to account for the diversity of dispersal modes within this type of social organisation. Instead, dispersal patterns in group-living, social species, may be largely an outcome of the relative availability of breeding opportunities in the natal versus non-natal groups (Russell and Rowley 1993; Yaber and Rabenold 2002; Arlt and Paart 2008; Berg et al. 2009; Raihani et al. 2010), and inbreeding avoidance may in turn be an important mechanism constraining reproduction within kin-structured groups (Dobson and Walters 2000b; but see Eikenaar et al. 2008). In particular, because in cooperatively breeding species reproductive opportunities often arise following death of dominant breeders, whereas at the same time incest-avoidance commonly prevents inheritance of breeding positions by philopatric offspring (Cockburn et al. 2003, 2008), sex-specific mortality rates might lead to sex-biased patterns of dispersal (Williams and Rabenold 2005; Berg et al. 2009). For example, in grey-crowned babblers, helpers have been shown to inherit their natal territory only if not related to the opposite-sex breeder (Blackmore and Heinsohn 2008), whilst higher mortality of male breeders (relative to female breeders) leads to more frequent breeding vacancies for males, and consequently, seemed to promote male dispersal (Blackmore and Heinsohn 2011). Similarly, in white-throated magpie-jays (Berg et al. 2009) and brown jays (Williams and Rabenold 2005), higher breeder turnover for males was identified as the principal cause of female philopatry and male-biased dispersal that characterised the two species. On the other hand, chestnut-crowned babblers are likely to suffer a relatively high mortality rate compared to other cooperatively-

breeding species, and disappearance of breeding females in particular, presumably due to death, is not uncommon (Russell and Browning, Pers. Comm.). Taken together, these findings suggest that inter-specific differences in the association between sex and individual dispersal, may be a consequence of diverging sex-specific mortality rates, and in turn, ultimately depend on local ecological conditions. Supporting an effect of local ecology, predation of adult birds is likely to be a relevant selective force in our study system (Chapter 2). Breeding females in particular, may be at risk while solitarily attending their nest, due to the conspicuousness of their breeding site, their frequent loud vocalisations, and the protracted lack of protection from the rest of the group foraging away from the nest (Sorato pers.obs.).

Further, the existence of a causal relation between local social environment and individual dispersal, was supported by the effects of individual age, weight and group size, on the probability of recapture in a different group. That young individuals were predicted to be more likely to disperse is in agreement with predictions of social dominance hypotheses (Walters et al. 1992; Pasinelli and Walters 2002), as typically, young are subordinate to older individuals, and are therefore expected to suffer most from intragroup resource competition (Covas et al. 2011). If dispersal was promoted by competition for food resources and mates, we would have also expected an association between individual probability of dispersal and phenotypic traits that are usually involved in social dominance. Among the latter, body size and condition are prime determinants of individual resource holding potential and competitive asymmetries (Parker and Rubenstein 1981). Interestingly, the sex-specific effect of body weight on dispersal probability reported here, suggests different modes and consequences of social competition in males and females, though the low number of dispersing males means the result should be treated with a bit of caution. A possible explanation for intersexual differences in the effect of individual weight on dispersal, may lay in the hypothesised higher breeding turnover for females, which may have promoted dispersal of low-ranking females into groups with breeding vacancies (Cockburn et al. 2003). On the other hand, the opposite

effect of body weight on dispersal probability for males, may be explained by higher competition within this sex, as would be implied by the seemingly lower male mortality and related male-skewed sex ratio at the population level. Therefore, higher competition for comparatively rarer breeding vacancies and possibly indirect fitness benefits, may have favoured philopatry and queueing within natal groups for future breeding opportunities as the main strategy for males, while limiting at the same time dispersal options to individuals capable of successful competition with philopatric males in the group of destination (Griesser et al 2007). Another result worth of note, is that following immigration into a new group, weight of dispersing individuals was no longer different from average weight within the population. In particular, an improvement in body condition was evident for female dispersers, which suggests that dispersing females may not have left their group because forced to do so, but may have instead 'decided' to immigrate into a new social unit on the basis of future benefits as opposed to a best of a bad job strategy.

Since individuals in bigger groups are expected to suffer more competition, for both mates and food resources, large group size may also be expected to promote dispersal (Greenwood 1980; Kim et al. 2009; Vanderwaal et al 2009; Gienapp and Merila 2011). Whilst the positive association between group size and male dispersal in our study population was in agreement with this expectation, for females we found the opposite pattern of decreased dispersal probability with increasing group size. Moreover, males seemed also to preferentially disperse into small groups, further supporting competition as a significant force involved in individual dispersal decisions within males, but females showed again an opposite pattern, and seemed more likely to immigrate into large groups. These associations between dispersal in females, and size of groups of origin and destination, counter predictions of models of dispersal based on social dominance, since both local resource depletion and competition for breeding opportunities may be expected to increase with group size. Rather, our findings seem to imply benefits of living in large groups as a central force involved in

dispersal decisions of females (Zack and Rabenold 1989; Dobson et al. 1998; Cockburn et al. 2003; Heg et al. 2008). Several features of the species social organisation and breeding ecology are consistent with this possibility. First, because chestnut-crowned babbler are plural breeders, large groups may actually offer more opportunities for independent breeding to females, particularly when group sex ratios are skewed towards males. Second, thanks to additive helper effects on parental care, breeding success in the study population has been shown to be significantly enhanced by large group size (Browning 2010), which, in the light of higher reproductive investment by females, would in turn select for preferential breeding in large groups by this sex (Cockburn et al 2003). Third, large group size may also provide other more general benefits, such as increased protection from predators for vulnerable nesting females, and mobbing of predators threatening broods in the nest (Browning 2010).

Finally, we also found evidence of a direct effect of local habitat features on individual dispersal probabilities (Cockburn et al. 2003). Babblers appeared less likely to disperse from groups occupying high quality areas, as indicated by the negative association between probabilities of dispersal and local amount of surface cover by creeks and smaller drainage channels. This effect is consistent with the clear preference shown by babbler groups for drainage zones as a foraging substrate, due to the higher prey biomass found within creeks (Portelli et al 2009), and the protection from aerial predators offered by vegetation within these zones (Chapter 2; Portelli et al. 2009).

In summary, our results point to the importance of benefits of philopatry for individual permanence in natal groups, as shown by the lower propensity to disperse for birds living in areas holding valuable resources, and, limited to females, by the negative effect of groups size on probability of dispersal. At the same time, intragroup competition for local resources and mates appears another important factor affecting individual dispersal, particularly for males, while inbreeding avoidance and higher availability of breeding openings may have promoted female-biased dispersal. In conclusion, we have found that dispersal was affected by

individual sex, age, condition and group size. Condition and group size had contrasting effects in males and females, suggesting different causes and benefits of dispersal for the two sexes.

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Chapter 7

General discussion

In each component of my work, ecological factors had far-reaching implications for group living in the chestnut-crowned babbler. In particular, variability in habitat quality and structure, and consequently the availability of key resources, such as food, nest sites and shelter from predators, largely determined space use, behaviour, and phenotype of babbler groups.

This study confirmed the importance of predation pressure as a force moulding a range of aspects of behaviour and social organisation (Caro 2005). Large group size in chestnut-crowned babbler matched with a relatively high local abundance of predators that combined with habit openness and features of the foraging ecology contributes to the species vulnerability to predation (Chapter 2). In particular, spatio-temporal variation in average size of babbler groups was consistent with a passive mechanism of predator-protection through a dilution effect on predation risk to individuals (Krause and Ruxton 2002; Cresswell and Quinn 2011). Other benefits of large group size may have been present, such as more efficient predator-detection, though testing and quantifying this possibility was beyond the reach of this study. Other active mechanisms of predator protection, such as mobbing (Krause and Ruxton 2002; Grause and Manser 2007), appeared less important for adult and juvenile survival. Although the species is known to mob potential nest predators (Browning 2010), and this may have contributed to low rates of nest predation in the local population (Russell et al. 2010), I have never observed mobbing away from breeding nests, despite hundreds of hours of observations of foraging groups. Rather, I showed that babblers reduced their predation risk by adjusting substrate use to different rates of encounter with predators associated with reproductive phases and habitat types. Sentinelling was another behavioral strategy that appeared to be expressed in response to variation in risk of predation (Ridley et al. 2010), though the overall frequency of such activity was low, particularly when compared to other cooperatively breeding species (Clutton-Brock et al. 1999; Wright et al. 2001; Bell et al. 2009). Since the rarity of sentinelling did not seem to be matched by a low predation risk, and

in fact encounters with predators were more frequent than observation of sentinel behaviour, a possible explanation for the low frequency of sentinel behaviour may lie in local habitat structure: compared with other cooperative breeders occupying arid habitats, short shrubs were relatively common throughout the study site, particularly in close proximity to creeks and drainage lines, to which babbler groups showed a clear preference, and offered shelter from predator attack. On a proximate level, another non-mutually exclusive explanation for the rarity of sentinel behaviour, may be found in the general behavioural syndrome of the species, seemingly characterised by risk aversion, neophobia (Browning, pers comm), and a lack of interspecific aggression (Sorato, pers. obs), which may have favoured passive strategies as a way of reducing predation risk.

At the same time, while local habitat features seemed to enhance antipredator benefits of group-living, resource scarcity typical of a semi-arid environment with low productivity, appeared to be associated with group-living costs due to the local depletion of shared food resources (Brown and Brown 1996; Bonal and Aparicio 2008). Consistent with a resource-depletion scenario, I found that the area covered by foraging groups increased in low quality habitat, both on the short time-scale of daily group movements (Chapter 3), and on the longer period as reflected by larger home range size (Chapter 4). As individual weight did not appear to covary with habitat (Chapter 3), increased movement across a larger home range seemed to compensate for a lower density of resource availability.

Although competition for limited food in a resource-poor environment may be expected to select against group living, this is not necessarily the case (Johnson et al. 2002). In fact, other features typical of habitats with low-productivity, primarily dispersion and spatio-temporal unpredictability of food resources, have been hypothesised to promote sociality (Davies 1995; Johnson et al. 2002). This possibility is supported by theoretical models, which show that unfavourable economics of exclusive territorial defence may favour individual aggregations (Carr and Macdonald 1986). Moreover, when food is patchily

distributed or otherwise unpredictable in its occurrence, group living may have a positive effect on resource detection (Giralda and Caraco 2000), and/or allow a more efficient exploitation of food patches, for example through decreased individual vigilance and cooperative hunting (Elgar 1989; Beauchamp 1998). Accordingly, the cost of resource sharing within groups of babbler, supported by lower average body weight in large groups, may have been counterbalanced by a reduction in the risk of starvation (Ekman and Hake 1988). A prediction of this hypothesis, which could be tested in the future, is that variance in condition would be lower across large groups compared to small ones.

In Chapter 4, I showed that independent measures of habitat quality and structure predicted home range and group size. In particular, patchiness and spatial dispersion of resources seemed paralleled by larger home-range areas, while increased tree cover was associated with smaller home ranges. The effect of arboreal vegetation on group home ranges is noteworthy, as it matches differences between babbler species occupying a wide range of habitat types (Higgins and Peter 2002). Given that chestnut-crowned babblers are preferentially ground-foragers, the reason behind the negative association between tree cover and home-range area is not evident. Possibly, tree abundance may co-vary with local prey abundance, and/or it may have been associated with the availability of vegetation patches providing shelter from predators and sites for nest construction.

Home range size decreased also with the surface area covered by creeks and smaller drainage lines, which was consistent with the preference shown by babbler groups for such zones (Portelli et al. 2010). Accordingly, creek zones have been shown to harbour greater prey biomass than surrounding areas (Portelli et al. 2009), and particularly in more open habitat zones, they may have provided patches with trees and tall shrubs in an otherwise barren landscape. On the other hand, home range area appeared largely independent of group size, consistent with the relatively weak territoriality in the species (Chapter 5), whilst group size was positively associated with variation in habitat quality within the home-range (Johnson et

al. 2002; Langen and Vehrencamp 1998).

Quality and the distribution of resources are also expected to have implications for group territorial behaviour (Brown 1982; Johnson et al. 2002). As patchiness and temporal unpredictability of food resources may favour the transition from individual aggregations into stable social groups, they may also be conducive to intergroup interactions, and in turn lead to complex social organisation extending above the group level (Griesser et al. 2009). Therefore, both the frequency and quality of group encounters may vary according to features of local ecology. For example, low habitat quality, by increasing group home-range size while reducing local population density, may be expected to reduce the frequency of intergroup encounters, and at the same time promote tolerance between groups because of reduced territoriality (Johnson et al. 2002). On the other hand, weak territorial behaviour may allow extensive overlap between home-ranges, and long-distance movements during foraging may translate into complex networks of interactions involving several groups (e.g. Griesser et al 2009). In agreement with these predictions, in Chapter 5, I showed that responses of babbler groups to simulated intergroup encounters were predicted by both habitat quality and home range size. Thereby, groups occupying smaller home-ranges and higher quality habitat (indicated by tree cover), were more likely to approach playbacks, consistent with an effect of quality of resources at stake on group territorial behaviour (Jennings et al. 2004; Harris 2010). Beside spatial habitat variability, temporal changes in ecological conditions, due to fluctuating yearly rainfall patterns, appeared also to affect intergroup interactions, as shown by the striking decrease in probability of approach to playbacks during the last study-year (2009-10). A possible explanation for such between-year variation is that decreased resource quality devalued the benefit of territorial defence, or, as a non-mutually exclusive explanation, it may have negatively affected resource holding potential of groups (Putland and Goldinzen 1998; Hale et al. 2003; Radford 2003). That individual condition, as measured by body weight, was significantly worse in 2009 than in the previous two study-years, is consistent with the latter

hypothesis, and suggests that, at a proximate level, low habitat productivity may have reduced territorial behaviour by limiting fighting ability and the amount of energy available for allocation to contest.

Ecological factors can be conducive to social group formation by delaying dispersal and promoting offspring philopatry (Emlen 1982; Stacey and Ligon 1987; Hatchwell and Komdeur 2000). Accordingly, most cooperatively breeding species are characterised by small family groups, generally dominated by a breeding pair and their offspring (Stacey and Ligon 1990; Koenig and Dickinson 2004). More complex group structures arise when dispersal is delayed for several years and mortality is low, leading to multiple generations of kin within the group, and when local ecological conditions are conducive to a certain amount of gene-flow between groups by promoting intergroup dispersal (Cockburn 1998). Limited dispersal options due to saturation of habitat suitable for independent breeding, shortage of mates, or costs associated with dispersal, like increased predation risk, have all been hypothesised to promote family living by constraining dispersal options (Emlen 1982; Hatchwell and Komdeur 2000). On the other hand, variance in territory quality has also been invoked as a factor promoting philopatry in high quality territories, irrespective of habitat saturation (Stacey and Ligon 1987; Covas and Griesser 2007). Patterns of dispersal in chestnut-crowned babblers are consistent with predictions of the benefit of philopatry hypothesis, while habitat saturation seems unlikely in the light of the availability of areas that appeared suitable for breeding (Chapter 6). The probability that individuals dispersed from the natal group was negatively associated with an index of habitat quality, measuring the availability of creeks and drainage lines within the natal home range. Such finding is in agreement with the obvious preference of babblers for creeks as a foraging substrate, and suggests that philopatry may have been promoted by resources critical for survival (prey abundance, cover from predators, roost sites) and reproduction (prey abundance, breeding sites) which in the study were mainly associated with ephemeral creeks.

Group size effects

Once group living is selected for and moulded by local ecological conditions, group size and other aspects of local social environment can have cascade effects on individual and group behaviour (Krause and Ruxton 2002; Koenig and Dickinson 2004). In turn, in synergy with ecology, local social environment may be an important determinant of the balance between individual benefits and costs of group living.

I have previously mentioned that an important benefit of group size in the study system seemed to be a reduction of individual predation risk through dilution effects (Chapter 2). Interestingly, however, contrary to expectations, group size did not predict the frequency of active antipredator behavioural strategies, like substrate preference for foraging, or the frequency of sentinel behaviour. With respect to sentinelling in particular, group size has been shown to have a positive effect on sentinel occurrence in cooperative breeders (Bell et al. 2009; Ridley et al. 2010). The absence of such an effect in chestnut-crowned babblers, may perhaps be reconciled with the relative rarity of sentinel behaviour and with the reliance on other mechanisms of predator protection, like preference for areas providing protective cover. It is also possible that only dominant individuals engaged in sentinel activity (Wright et al. 2001), though the low frequency of the behaviour and the difficulties in closely observing individual babblers without interfering with their activity, precluded a quantitative test of this possibility.

Group size also affected movements and local space use by social units on a short temporal scale (Chapter 3), in a way consistent with the local depletion of food patches, as shown by the decrease in local revisitation with group size. Yet, area covered by foraging groups did not appear to be affected by group size, and, on a wider time scale, size of social units had only a marginal effect on total home-range area. Therefore, large groups appeared to respond to higher depletion of prey items, as suggested by lower individual weights, by

adjusting their ranging behaviour on a small spatial scale, by diversifying their use of space for foraging, rather than on a large scale, by increasing the range of their movements. Accordingly, group size was a weaker predictor than habitat for home-range size, and the direction of causality was probably a reversed one, in which habitat within home-ranges may have set an upper limit for total group size (Johnson et al. 2002).

Studies of social species have also shown group size to be an important determinant of the outcome of contests between groups for local resources (McComb et al. 1994; Radford and DuPlessis 2004). Thereby, group size was anticipated to affect the probability of approach of babbler groups to playback vocalisations simulating encounters with another group. However, this effect was found during the first study-year only, while, unexpectedly, the opposite relationship was found during the following year. To my knowledge, no previous study has found such temporal shifts in the effect of group size on response to playback experiments in group-living, social species. An important implication of this finding is that group size benefits may have been contingent on variation in ecological conditions, possibly mediated by the synergetic effect of availability of food resources and group size on individual condition. Supporting this, a pronounced decrease in individual weight matched a decline in habitat condition as a consequence of prolonged drought, and in turn, was associated with the aforementioned decrease in group responsiveness to playback vocalisations.

Finally, in the study-population, group size appeared to affect also individual dispersal, in a sex-specific way (Chapter 6). In females, dispersal seemed promoted by small natal group size, and dispersing individuals seemed to target large groups as their final destination. The opposite pattern was found for males, which, as typical for birds (Greenwood 1980; Clarke et al. 1997), dispersed much less than females. While dispersal has been shown in other studies to be affected by the size and sex ratio of both natal and destination groups (Yaber and Rabenold 2002; Cockburn et al. 2003; Williams and Rabenold 2005; Berg et al. 2009), I am

unaware of any other study of dispersal in a cooperative breeding species that has detected an analogous sex-specific effect of group size, suggesting sex-specific costs and benefits of large group size. Specifically, that probability of male dispersal increased with natal group size, and they preferentially joined small groups, suggesting an effect of social dominance within groups (Pasinelli and Walters 2002). Supporting this hypothesis, dispersing males were heavier than philopatric ones, while again the opposite pattern was found in females. Therefore, males in good condition seemed to emigrate from large groups into smaller ones, where they may have had an edge on competition with local males. On the other hand, females would appear to benefit more in large groups, possibly through a local resource enhancement effects of cooperative breeding (Perrin and Lehmann 2001). In agreement with this possibility, helper effects are largely additive in this species, and accordingly reproductive success increases considerably with group size (Browning 2010; Russell et al 2010), as predicted for species occupying resource-poor environments (Hatchwell 2009). Moreover, group size may also have had positive effects on the survival of breeding females, as during incubation females depend on mates and helpers for feeding, and may be less vulnerable to predation in large groups (Chapter 2). Therefore, the number of group members within social units may have been a crucial attribute of both natal and prospective groups, on which females may have based their dispersal decisions.

Future directions

Genetic relatedness

Having considered the effect of ecological variation on aspects of group phenotype and behaviour, future work will extend into interplays with the local population genetic structure. Although not a focus of this thesis, at the individual level, patterns of genetic relatedness within groups are expected to be important determinants of individual investment in cooperative activities, such as helping at the nest and other aspects of individual fitness

(Browning 2010). At the group and population level, it would be desirable to integrate observational data on dispersal with indirect estimates of individual movements between groups, and associated gene flow. Further, with respect to group ranging behaviour, intergroup interactions could be contrasted with intergroup relatedness, as measured for example by genetic networks linking individuals according to pairwise relatedness values. For example, there were obvious differences in the amount of home-range overlap between neighbours, which may have been due at least in part to differences in genetic relatedness, particularly in the light of the fact that neighbour units may originate through a variety of processes, including budding and local immigration of foreign groups (AF Russell, E Sorato pers obs). In relation to this point, I observed consistent variation in both the frequency and type of interactions between neighbouring groups. As discussed in Chapter 5, this may have been in part an effect of variation in local habitat quality and group size, but it is conceivable that differences in genetic relatedness between neighbours may have also contributed to the variation in inter-group aggression. Thereby, it would be also interesting to incorporate genetic data into the analysis of group responses to playbacks, given that vocalisations typical of the species seem to be characterised by considerable distinctiveness at both the individual (J Crane pers. comm.), and population level (E Sorato pers. obs). This would be particularly desirable in the light of patterns of dispersal within the population, as gene-flow does not appear to be constrained to neighbouring units, and consequently intergroup relatedness may be largely disjunct from the amount of spatial separation between groups.

Interpopulation comparisons

Within a single population of an avian cooperative breeder, this study has highlighted significant effects of ecological factors, despite the limited amount of variation in ecological conditions that can be found within a single site. By extending the range of variation available for research, and by providing independent samples, interpopulation comparisons have the

potential to further improve our understanding of the factors promoting variation in social organisation, and can provide a bridge between intraspecific and interspecific investigations. Within species, comparative studies are especially important in the light of the confounding interplays between phylogeny and ecology, and may allow testing of the predictive power of ecological models in accounting for variation in sociality across taxonomic levels (Safran et al. 2007).

The chestnut-crowned babbler constitutes an ideal model system in this respect, because of the variety of habitats occupied by the species within its distributional range. While habitat typologies within the study population seem representative of habitat preferences of the species (Higgins and Peter 2002), populations at the North Western limit of the species distribution can be found in habitats characterised by more extreme ecological conditions. For example, we have already identified a number of candidate populations for future field work, including those which occupy sand-dune habitat devoid of trees, wherein the only nest sites are provided by isolated patches of tall shrubs, and at the other extreme of the range of regional variation in ecological conditions, chestnut-crowned babbler populations at their Southern distributional limit, in the state of Victoria, can be found in mallee habitat types, where tree-cover is substantial, rainfall is higher, and climate is characterised by a more pronounced seasonality. Further habitat types include mulga (*Acacia aneura*) woodlands and other eucalyptus woodlands in eastern limit of the species distribution. In addition, besides differences in vegetation type and structure, sites may also differ with respect to other key ecological factors, such as local predation pressure, rainfall, and seasonality. Therefore, by allowing one to decouple associations between ecological variables, a comparative study of different populations could dissect relative contributions of different feature of local ecology to details of social organisation.

Finally, as locally chestnut-crowned babblers can occur in sympatry with up to two other *Pomatostomus* species, interspecific comparisons within some of the same sites may

have the potential for teasing apart relative contributions to social organisation of local ecology, as opposed to species life-history traits, biology and ecological niche.

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Appendix

Table A1.

Model selection (Chapter 2) for: a) probability of predator encounter by focal group, b) probability of observing sentinel behaviour, c) amount of ground-substrate use.

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group + duration + Repr. Phase + N. adults + Zone	10	318.9	0	0.80	0.80	298.0
Group + duration + Repr. Phase + N. adults	7	323.7	4.8	0.07	0.87	309.3

A)

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group + start time + start time ² + start time ³ + duration + Repr. phase + zone + ground	12	168.3	0.0	0.47	0.47	142.3
Group + start time + start time ² + start time ³ + duration + Repr. phase + zone + ground + predator met	13	169.8	1.5	0.23	0.70	141.4
Group + start time + start time ² + start time ³ + duration + Repr. phase + zone + trees	12	170.5	2.2	0.16	0.86	144.5
Group + start time + start time ² + start time ³ + duration + Repr. phase + ground + predator met	10	171.0	2.6	0.13	0.98	149.5

B)

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group + stat timetart time ² + start time ³ + Repr. phase + zone + predator met + group size tot	12	353.8	0.0	0.63	0.63	328.2
Group + stat timetart time ² + start time ³ + Repr. phase + zone + predator met	11	354.9	1.1	0.37	1.00	331.5

C)

'K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; Δ AICc is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measure the relative probability of each model within the full candidate model set; 'Deviance' is calculates as $-2\log$ likelihood of the model. Only models with Δ AICc ≤ 5 are shown.

Table A2.

Model selection (Chapter 3) for: a) group movement descriptives during the whole study period ('full-dataset analysis'); b) group movement descriptives during reproduction ('breeding-only' analysis); c) body weight of adult birds.

Model	K	AICc	ΔAICc	weight	Cum. Weight	Deviance
Area track:						
Group + duration+ start time + Repr. phase + habitat	10	704.5	0.0	0.90	0.90	684.5
Group + duration + start time + Repr. phase	6	709.0	4.5	0.10	1.00	697.0
Speed :						
Group + duration + start time + Repr. phase + habitat + Group size	11	848.0	0.0	0.62	0.62	826.0
Group + duration+ start time + Repr. phase + habitat	10	849.0	1.0	0.38	1.00	829.0
Revisitation index:						
Group + duration + start time + start time^2+ Repr. phase + Group size + habitat	12	877.0	0.0	0.60	0.60	853.0
Group + duration + start time + start time^2+ Repr. phase + Group size	8	878.0	1.0	0.36	0.96	862.0
A)						
Model	K	AICc	ΔAICc	weight	Cum. Weight	Deviance
Median distance from nest:						
duration+ start time + age + habitat + N adults	7	87.5	0.0	0.51	0.51	73.5
duration+ start time + age + N adults	4	88.5	1.0	0.31	0.82	80.5
duration+ start time + age + habitat	6	90.0	2.5	0.15	0.97	78.0
Speed:						
age +habitat + breeding attempt	5	90.0	0.0	0.91	0.91	80.0
age + habitat	4	94.7	4.7	0.09	1.00	86.7
Revisitaion index:						
duration + age + N adults + habitat	6	99.0	0.0	0.84	0.84	87.0
duration + age + N adults	3	102.7	3.7	0.13	0.97	96.7
B)						
Model	K	AICc	AICc	weight	Cum. Weight	Deviance
Individual weight:						
Unit + indivual + tarsus+ time+year + brood age + brood age ^2 + breeding attempt + unit size	11	1233. 0	0.0	0.52	0.52	1211.3
Unit + indivual + tarsus+ time+year + brood age + brood age ^2 + breeding attempt	10	1234. 0	0.6	0.38	0.90	1213.9
Unit + indivual + tarsus+ time+year + brood age + brood age ^2 + breeding attempt + unit size+ habitat	15	1237. 0	3.2	0.10	1.00	1206.5
C)						

'K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; ΔAICc is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measure the relative probability of each model within the full candidate model set; 'Deviance' is calculates as -2log likelihood of the model. Only models with ΔAICc ≤ 5 are shown.

Table A3.

Model selection (Chapter 4) for: a) total home-range area (100% isopleth); b) core home-range area (50% isopleth); c) group size (number of adults in the group); d) group density.

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group + time + year + pc1+ pc2+pc3+ creeks	10	1035.2	0.0	0.36	0.36	1012.0
Group + time + year + pc1+ pc2+pc3+ creeks+ N.adults	11	1036.3	1.0	0.22	0.58	1010.2
Group + time + year + pc1+ pc2+pc3	9	1037.5	2.3	0.11	0.69	1016.8
Group + time + year+ pc2+pc3	8	1037.8	2.6	0.10	0.79	1019.6
Group + time + year + pc1+ pc2+pc3+ creeks+N.adults+ N.neighbour groups	12	1038.1	2.9	0.09	0.88	1009.4
Group+time+year+creeks	7	1039.9	4.7	0.03	0.91	1024.4
Group +time+year+pc2	7	1040.0	4.8	0.03	0.95	1024.4
Group+ time +year+ pc1+pc2	8	1040.1	4.9	0.03	0.98	1022.0

A)

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group + year+ pc2 + creeks	7	935.8	0.0	0.36	0.36	920.2
Group + year+ pc2 + creeks+ N.adults	8	936.2	0.4	0.30	0.66	918.2
Group + year+ pc2 + creeks+ N.adults+ N. neighbour groups	9	938.5	2.6	0.10	0.76	917.8
Group+year+pc2	6	938.8	2.9	0.08	0.85	925.6
Group + year + creeks	6	939.7	3.9	0.05	0.90	926.6
Group + year+ pc2 + creeks+ N.adults+ N. neighbour groups+ N.adults.neighbours	10	940.7	4.9	0.03	0.93	916.2
Group + year + pc2 + p c3	7	940.8	5.0	0.03	0.96	925.2

B)

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group+pc2+N.neighbour.groups+N.ad.neighbours	6	396.2	0.0	0.29	0.29	383.0
Group+pc2+N.ad.neighbours	5	396.3	0.1	0.27	0.56	385.4
Group+pc2+creeks+N.ad.neighbours	6	397.4	1.2	0.16	0.72	384.2
Group+pc2+creeks+N.neighbour.groups+ N.ad.neighbours	7	397.8	1.6	0.13	0.84	382.2
Group+N.ad.neighbours	4	398.5	2.3	0.09	0.93	390.0

C)

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group+duration+year+pc2+pc3	8	106.7	0.0	0.25	0.25	88.6
Group+duration+year+pc2	7	108.0	1.3	0.13	0.39	92.4
Group+duration+year+pc2+pc3+N.neighbour.groups	9	108.0	1.4	0.13	0.52	87.4
Group+duration+year+pc2+pc3+N.ad.neighbours	9	108.2	1.5	0.12	0.64	87.4
Group+duration+year+pc1+pc2+pc3	9	108.4	1.7	0.11	0.75	87.6
group+duration+year+pc2+pc3+creeks	9	109.2	2.5	0.07	0.82	88.4
Group+duration+year+pc1+pc2	8	109.7	3.0	0.06	0.88	91.6
Group+duration+year+pc2+pc3+N.neighbour.groups+ N.ad.neighbours	10	110.0	3.3	0.05	0.93	86.6
Group+duration+year+pc2+pc3+creeks+N.ad.neighbours	10	110.6	3.9	0.04	0.96	87.2

D)

K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; Δ AICc is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measure the relative probability of each model within the full candidate model set; 'Deviance' is calculates as $-2\log$ likelihood of the model. Only models with Δ AICc ≤ 5 are shown.

Table A4.

Model selection (Chapter 5) for: a) probability of focal group approach to playback; b) probability of close group approach (min. distance ≤ 5 m) to playback.

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + N.adults*year	9	194.7	0.0	0.30	0.30	175.4
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + N.adults*year + PC2	10	195.5	0.9	0.19	0.49	174.0
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + N. adults + N.adults*year	10	196.6	1.9	0.12	0.61	175.0
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range	8	197.8	3.1	0.06	0.68	180.8
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + PC3	9	198.3	3.6	0.05	0.73	179.0
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + PC2	9	198.8	4.2	0.04	0.76	179.5
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + N. adults	9	199.0	4.3	0.03	0.80	179.7
Group ID + playback ID + start dist. + Year + Breeding + Young+ Home-range area + PC1	9	199.0	4.3	0.03	0.83	179.7
A)						
Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group ID + playback ID + start dist. + Year + Breeding + Young+ N.adults*year + PC2	10	173.3	0.0	0.39	0.39	151.7
Group ID + playback ID + start dist. + Year + Breeding + Young+ N.adults*year + Home-range area	9	173.8	0.6	0.29	0.69	154.6
Group ID + playback ID + start dist. + Year + Breeding + Young+ N.adults*year + Home-range area + N.adults	10	176.0	2.8	0.10	0.79	154.4
Group ID + playback ID + start dist. + Year + Breeding + Young+ PC2	9	177.2	3.9	0.06	0.85	160.1
B)						

K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; Δ AICc is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measure the relative probability of each model within the full candidate model set; 'Deviance' is calculates as $-2\log$ likelihood of the model. Only models with Δ AICc ≤ 5 are shown.

Table A5.

Model selection (Chapter 6) for individual dispersal probability.

Model	K	AICc	Δ AICc	Weight	Cum.Weight	Deviance
Group+N.days+sex+age+creek.cover+sex*weight+sex*N.adults	8	189.7	0.0	0.27	0.27	-86.7
Group+N.days+sex+age+weight+creek.cover+sex*N.adults+sex*weight	9	191.0	1.3	0.14	0.42	-86.3
Group+N.days+sex+age+weight+creek.cover+sex*N.adults	8	191.0	1.4	0.14	0.56	-87.3
Group+N.days+sex+age+creek.cover+sex*N.adults+sex*weight+age*N.adults	9	191.7	2.1	0.10	0.65	-86.7
Group+N.days+sex+age+creek.cover+sex*age+sex*N.adults+sex*weight	9	191.7	2.1	0.10	0.75	-86.7
Group+N.days+sex+age+creek.cover+sex*N.adults+sex*weight+age*weight	9	191.8	2.1	0.10	0.85	-86.7
Group+N.days+sex+age+weight+N.adults+creek.cover+sex*N.adults	9	192.7	3.1	0.06	0.91	-87.2
Group+N.days+sex+weight+N.adults+creek.cover	7	192.8	3.2	0.06	0.96	-89.3
Group+N.days+sex+age+weight+N.adults+creek.cover	8	193.8	4.2	0.03	1.00	-88.8

K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; Δ AICc is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measure the relative probability of each model within the full candidate model set; 'Deviance' is calculates as $-2\log$ likelihood of the model. Only models with Δ AICc ≤ 5 are shown.