Social Behaviour and Breeding Biology of the Yellow-Rumped Thornbill

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Declaration

The research presented in this thesis is my own original work and no part has been submitted for a previous degree.

Signed

Daniel Ebert
April 2004

Dedication

In memory of

Anjeli Catherine Nathan

18 March 1975 – 3 November 1999

Acknowledgements

This thesis was a work in progress, or not, for some years and many people made significant contributions of supervision, assistance or support.

My supervisor, Rob Magrath, and Andrew Cockburn and David Green were instrumental in promoting thornbill research as a worthwhile pursuit. I thank them for their contributions to the formulation of this project and their interest in my work. Rob Magrath's particular combination of insight, knowledge and patience was invaluable throughout this study. I am also grateful for the general advice and guidance of Rob Heinsohn and Sarah Legge.

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Minisatellite DNA fingerprinting is an error-prone and frustrating procedure usually requiring good fortune as well as good management for success. In my case neither was required due to the skilled supervision of Sarah Legge. Others who provided guidance and advice on DNA fingerprinting and molecular sexing were Angela Higgins, Mike Double, Simon Gilmore, Stephen Yezerinac and Ginny Sargent.

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Abstract

This study describes the breeding biology, mating and parental care systems and social organization of the yellow-rumped thornbill (*Acanthiza chrysorrhoa*, Pardalotidae) and the mating and parental care systems of the buff-rumped thornbill (*Acanthiza reguloides*). I studied populations of both species in a woodland reserve on the outskirts of Canberra, Australia between 1995 and 1998.

Yellow-rumped thornbills bred in pairs or small groups comprised of a single female and up to three males. Groups formed via the philopatry of the male offspring of a breeding pair. Over three years from 1995 to 1997 cooperative groups comprised 13.5% of breeding units. The breeding biology and demography of the yellow-rumped thornbill were typical of its family. Females laid from one to three clutches, usually of three eggs, over a breeding season of 3.6 months. Breeding success was low and most clutches failed before fledging. Overall, 60% of breeding units succeeded in fledging young in each season and the mean number of fledglings produced per female per year was 2.02. In comparison with a previous study of the species, the yellow-rumped thornbills studied here had a much shorter breeding season, and much lower reproductive success due to higher rates of nest predation. These disparities highlight the effects of multi-brooding and nest predation on productivity of species exhibiting the "long and slow" breeding biology characteristic of the Pardalotidae.

Nest predation was overwhelmingly the major cause of breeding failure in yellow-rumped thornbills accounting for at least 85% of clutches that failed to fledge. Changes in predation rates between incubation and nestling phases of the nesting cycle and over the breeding season indicated an important role for the pied currawong (*Strepera graculina*) in predation of yellow-rumped thornbill nests. Nest predation was more severe on broods of nestlings than on clutches of eggs and the rate of predation on nestlings peaked in November of each year. This peak corresponds with the period in late spring when pied currawongs take the nestlings of small birds to feed their own broods. The stage-specific patterns of predation on yellow-rumped thornbill nests provide an example of variable rates of nest predation that cannot be explained on the basis of characteristics of the prey species, such as nest concealment and the behaviour of parents and nestlings.

Assessment of parentage using minisatellite DNA fingerprinting revealed that both the yellow-rumped thornbill and the buff-rumped thornbill were overwhelmingly monogamous. Social sires, including dominant males in cooperatively breeding groups, were the genetic sires of 95.3% of yellow-rumped thornbill nestlings and 96.9% of buff-rumped thornbills. Such low rates of female infidelity indicate that helping behaviour in these species is not directly related to helpers gaining paternity in the brood. Genetic assessment of relatedness among members of cooperative groups confirmed that helpers of both species were usually the sons of the breeding pair they assisted. This result, in combination with the monogamous mating systems of both species, means that helpers almost always helped raise close relatives, sibs or half-sibs, thus promoting the potential for helpers of both species to gain indirect kin-selected benefits of helping.

Yellow-rumped thornbills and buff-rumped thornbills differed in their patterns of parental care. Parents did not change their individual provisioning rates when assisted by helpers in the yellow-rumped thornbill and provisioning was therefore additive in cooperative groups. In the buff-rumped thornbill, parents compensated for the contributions of helpers by reducing their individual feeding rates and total provisioning rates of pairs and cooperative groups were equal. This difference suggests that either the benefits of helping or the costs of provisioning differ between these two species despite the general similarity of their breeding biologies and mating systems.

A combination of field observation and genetic methods was used to describe the non-breeding social organisation of the yellow-rumped thornbill. Censusing over the non-breeding period confirmed that yellow-rumped thornbills overwintered in coherent flocks of stable membership which were largely continuous between years. Flocks formed through the affiliation of multiple breeding units (pairs or groups) and some of their juvenile offspring. Flocks occupied large home-ranges which generally overlapped substantially with those of neighbouring flocks. Genetic assessment of relatedness revealed that yellow-rumped thornbill flocks were mixtures of kin and non-kin and that kinship resulted from male natal philopatry. The combination of sex biased dispersal, the mixture of kin and non-kin and the lack of territoriality defines a highly unusual non-breeding social organisation. Together with studies of other Pardalotidae, these results highlight the diversity and complexity of social organisation in the non-breeding season, an aspect of avian social organisation that has been largely overlooked.

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CHAPTER 1

General introduction

This thesis describes the social organization, breeding biology and mating system of the yellow-rumped thornbill, *Acanthiza chrysorrhoa,* and the mating and parental care systems of the buff-rumped thornbill, *Acanthiza reguloides*. Four of the chapters are written as discrete units in a form suitable to submit for publication. As such, the pertinent literature is addressed in the introductions and discussions of each chapter. The purpose of this introduction, therefore, is to provide a general overview of the themes developed in the following chapters, introduce the study species and outline the structure of the thesis.

The original goal of this thesis was to provide a comprehensive comparison of the breeding systems and social organizations of two cooperatively breeding thornbill species. This objective was abandoned after the occurrence of a disease epidemic in the study population of buff-rumped thornbills. As this event effectively forced a change in the direction and emphasis of the research described in this thesis, some comment is warranted on the nature of the epidemic and its consequences.

The capture and banding of thornbills began at the start of the 1995 breeding season. At first, most effort was devoted to the yellow-rumped thornbill but during the 1996 breeding season a concerted effort was made to capture and band a study population of buff-rumped thornbills. All capture and banding techniques, including the bands used, were according to the guidelines of the Australian Bird And Bat Banding Scheme and were carried out under the necessary permits issued by the A.B.B.B.S. and local authorities. In the winter of 1997 a number of banded buff-rumped thornbills developed swollen lesions on their legs that were ultimately fatal. In light of the fact that yellow-rumped thornbills, which are slightly larger than buff-rumped thornbills, did not appear to suffer the same disease it was originally assumed that the problem arose from the size of the plastic colour bands. Intensive mist-netting was carried out and the colour bands on as many birds as possible were replaced with modified bands of a smaller diameter. This did not provide a long-term solution and in the winter of 1998 the problem recurred. Again, with the assistance of many volunteers, a concerted effort was made to recapture marked birds, this time to remove their bands. The A.B.B.B.S. was fully informed of the situation upon the first outbreak of disease, approved the attempt to solve the problem by modifying the diameter of colour bands, and established a moratorium on the colour banding of buff-rumped thornbills.

There were two major consequences of these events. First, the time and effort required to monitor and recapture banded buff-rumped thornbills was substantial and reduced the investment that could be made in the collection of data on both buff-rumped and yellow-rumped thornbills. Second, the data that was compiled on the demography and breeding biology of buff-rumped thornbills was compromised by the artificial increase in mortality. For these reasons this thesis is predominantly concerned with the biology of the yellow-rumped thornbill. However, a substantial amount of data was collected on the mating system and parental care behaviour of buff-rumped thornbills in the breeding seasons of 1996 and 1997. The first outbreak of the leg disease afflicting buff-rumped thornbills occurred in the winter between these two seasons, however, there were no significant changes in mating system and parental care variables between 1996 and 1997 (Chapter 4). For this reason, data pertaining to the mating system and parental care behaviour of the buff-rumped thornbill is included in this thesis.

The Pardalotidae

The yellow-rumped thornbill and the buff-rumped thornbill belong to the old endemic Australian family, Pardalotidae, which comprises a large group of small insectivorous passerines 49 of which are resident in Australia. In this thesis I follow the taxonomy of Christidis & Boles (1994). The family consists of three subfamilies: the speciose Acanthizinae includes the thornbills, gerygones, scrubwrens and allies; the Pardalotinae, the pardalotes; and the Dasyornithinae, the bristlebird and pilotbird. Compared with other Australian families, the social organisation and breeding biology of the group is relatively well described, although the majority of studies have focused on members of one subfamily, the Acanthizinae.

There is considerable variation in the social organization, parental behaviour and dispersal patterns among members of the Acanthizinae. Some species breed as simple pairs (e.g. the brown thornbill, A. pusilla, Bell and Ford 1986; Green and Cockburn 1999) while others breed cooperatively (e.g. white-browed scrubwren, Sericornis frontalis, Whittingham *et al.* 1997; Magrath 2001). However, the categorisation of species as "pair-breeders" and "cooperative breeders" appears to be simplistic in regard to the social organizations of members of the Acanthizinae. Behaviours that are usually associated with cooperative breeding are displayed by pair-breeding species and vice versa. For example, in the brown thornbill juvenile males often delay dispersal until the beginning of the following breeding season, behaviour that is more typical of cooperative breeders (Green and Cockburn 2001). However cooperative breeding never occurs in the brown thornbill and even philopatric males that do not find mates as yearlings do not become helpers at their parent's nests. Instead, they occupy vacant territories or small areas annexed from their parent's territories as solitary males (Green and Cockburn 1999). Speckled warblers, *Chthonicola sagittata,* breed as pairs or groups consisting of a female with two males (Bell 1984; Tzaros 1996; Gardner *et al.* 2004). However, as a group living and polyandrous species the speckled warbler is unusual in that subordinate males never help to raise offspring produced by the group, despite the fact that they sometimes gain paternity (Gardner *et al.* 2004). White-browed scrubwrens are frequent cooperative breeders with groups comprised of a dominant breeding pair and subordinate males. Subordinate males fall into two categories: those that do help at the nest of the dominant pair and those that do not (Magrath and Whittingham 1997). Subordinates are more likely to help if they are unrelated to the breeding female, indicating that, although groups form largely by natal philopatry and are therefore family based, helping by subordinate males is related to the pursuit of mating opportunities within the group rather than the opportunity to help raise collateral kin (Whittingham *et al.* 1997).

Despite relatively detailed knowledge of the breeding systems of these species, very little is known about social organization in the non-breeding season. Nevertheless, several species are known to form intraspecific flocks in winter including the speckled warbler, buff-rumped, yellow-rumped and striated thornbills, *Acanthiza lineata* (Bell and Ford 1986; Gardner 2004). There appear to be differences in the social composition and structure of winter flocks of buff-rumped thornbills and speckled warblers, which may indicate differences in the function of flocking behaviour. For example, speckled warblers form flocks of unrelated individuals while those of buff-rumped thornbills comprise clans of male and female relatives (Bell and Ford 1986; Gardner 2004), suggesting a role for both kin selection and individual fitness in flock formation in the Acanthizinae

Study species

Both the yellow-rumped thornbill and buff-rumped thornbill have been the subject of detailed study previously. Ford (1963) described some of the basic characteristics of breeding in the yellow-rumped thornbill, and Bell and Ford (1986) provided a description of both breeding biology and social organization in the buff-rumped thornbill. Both species are cooperative breeders; however, information on cooperative breeding in the yellow-rumped thornbill is limited to anecdote. The only observations of marked birds in the literature are those of Immelman (1960) and Ford (1963), neither of whom described the frequency of cooperative breeding or the composition of cooperative groups. In the better known buff-rumped thornbill, cooperative breeding is fairly common, with groups accounting for approximately 32% of breeding units in the study of Bell and Ford (1986), and appears to be kin-based. Groups are comprised of a breeding pair and one or two of their male offspring from previous breeding seasons (Bell and Ford 1986). At the end of the breeding season, neighbouring families coalesce into stable and winter flocks of up to 15 individuals that occupy flock territories encompassing the breeding territories of resident flock members (Bell and Ford 1986). The formation of winter flocks of stable membership via the merging of multiple breeding units is an unusual social structure, although it appears to be very similar to that of the well studied European long-tailed tit, *Aegithalos caudatus* (Hatchwell *et al.* 2001a), and may occur widely among the thornbills (Bell and Ford 1986; Nicholls *et al.* 2000). The winter social organization of the yellow-rumped thornbill is undescribed, although they are known to form flocks (Bell and Ford 1986).

Despite considerable knowledge of some characteristics of breeding biology and social organization in the thornbills, much remains to be understood. In particular, recent advances in molecular techniques now enable a much finer resolution of the genetic relationships of group members, as well as gender identification and assessment of parentage. Indeed, the use of such techniques has led to the recognition of the complexity and diversity of mating systems, and has refocused the debate on traits that shape social organization (Cockburn 1998).

The research described in this thesis combines the use of molecular techniques and behavioural observations to describe the mating system of buff-rumped and yellow-rumped thornbills, and the breeding and non-breeding social organization of yellow-rumped thornbills; areas where major gaps in our knowledge exist. The diversity of behaviours exhibited by closely related species within the Pardalotidae provide valuable comparative data and are informative in identifying traits that shape social organization.

Thesis structure

This thesis consists of four data chapters with a concluding chapter providing a summary of results and suggestions for future work. In Chapter 2 I describe the breeding biology of the yellow-rumped thornbill, providing data on breeding cycle and season, degree of multi brooding, dispersal and reproductive success. My results are compared with those of Ford (1963) and are discussed in the context of recent work on other Pardalotidae species.

Nest predation was the most important cause of reproductive failure for yellow-rumped thornbills and in Chapter 3 I explore patterns of predation in detail. I show that predation risk varies according to stage of the breeding cycle and over the breeding season and discuss the likely causes and consequences of this variation.

Chapter 4 examines the mating and helping systems of yellow-rumped and buff-rumped thornbills. I use DNA fingerprinting to classify the genetic relationships among members of cooperative groups, and to assess the parentage of young raised by pairs and groups. By observing provisioning behaviour at nests, I quantify the contributions to brood care made by different individuals, and relate this to the mating system as revealed by DNA fingerprinting.

The social organization of yellow-rumped thornbills in the non-breeding season is described in Chapter 5. I use census data to track the identity of flock members over three winters, and to describe the ranging behaviour and spatial relationships of each flock. The genetic structure of flocks is investigated using DNA fingerprinting. Comparisons with other winter-flocking species provide valuable insights into the function of flocking behaviour in yellow-rumped thornbills.

CHAPTER 2

The breeding biology of the yellow-rumped thornbill

INTRODUCTION

The majority of studies of avian life history and breeding biology have been carried out on northern hemisphere species (Martin 1996). In the case of the passerines this represents an important phylogenetic bias as the vast majority of northern hemisphere species are members of a single clade, the Passerida (Sibley and Ahlquist 1990; Barker *et al.* 2002), and are therefore unlikely to be representative of the passerines as a whole. The "old endemic" passerine families of Australia, for example, are thought to be characterised by life history and breeding biology traits which contrast markedly with those typical of Passerida species. They are longer lived and are thought to exhibit longer and slower reproduction characterised by small clutches, long breeding seasons and extended periods of juvenile development and post-fledging dependence (Woinarski 1985; Magrath *et al.* 2000; Russell 2000). They are also far more likely to breed cooperatively (Russell 1989; Cockburn 1996). Attempts to explain differences such as these in terms of environmental, ecological and phylogenetic factors have been hindered by a lack of quantitative information on the life histories and breeding biologies of southern hemisphere species (Martin 1996; Magrath *et al.* 2000; Russell 2000).

Recent comparative studies have highlighted the role that basic traits of life-history might play in the evolution of social aspects of avian breeding systems, such as cooperative breeding and mating strategies (Poiani and Jermiin 1994; Poiani and Pagel 1997; Arnold and Owens 1998; Arnold and Owens 2002). The analyses of Arnold and Owens (1998; 2002) in particular stress the importance of traits such as adult mortality and fecundity in the evolution of avian breeding and mating systems. Low rates of adult mortality are strongly associated with the frequency of cooperative breeding in avian families (Arnold and Owens 1998), while high rates of adult mortality and high fecundity are strongly associated with promiscuous mating systems and other forms of reproductive cheating such as intraspecific brood parasitism (Arnold and Owens 2002).

The Australian passerine family Pardalotidae is especially interesting in this light as its members have diverse social systems but very similar life-histories. The Pardalotidae is thought to be a typical old endemic Australian family in terms of life-history and breeding biology with its members characterised by high adult survival, low fecundity and "long and slow" breeding (Woinarski 1985; Ford 1989; Green and Cockburn 1999; Magrath *et al.* 2000). Furthermore, recent studies have highlighted the apparent uniformity of members of the family in terms of these life-history and breeding biology traits (Green and Cockburn 1999; Magrath *et al.* 2000). In spite of this relative uniformity, detailed study of breeding in a small number of Pardalotidae species has revealed diverse social systems. The brown thornbill, *Acanthiza pusilla*, is a strict pair-breeder with a monogamous mating system (Bell and Ford 1986; Green and Cockburn 1999; Green *et al.* 2002) while the white-browed scrubwren, *Sericornis frontalis*, and speckled warbler, *Chthonicola sagittata*, are group living species with variable parental care systems and complex polyandrous mating systems (Whittingham *et al.* 1997; Gardner 2004). The apparent dissociation of social characteristics from those of life-history and breeding biology is emerging as a feature of the Pardalotidae with important implications for social evolution within this speciose Australian family (Green and Cockburn 1999). However, very few members of the Pardalotidae have been studied in detail and apart from easily measured traits, such as clutch size, knowledge of demography, breeding biology and social behaviour is anecdotal or incomplete for the majority of species.

In this chapter I describe the basic reproductive biology, demography and social organisation of breeding in the yellow-rumped thornbill, *Acanthiza chrysorrhoa*. The genus *Acanthiza* is of particular interest in the context of the evolution of avian breeding systems as it includes species such as the brown thornbill, which is strictly pair breeding, although cooperative breeding is the ancestral condition in the genus and is thought to be exhibited by most thornbills (Nicholls *et al.* 2000). *Acanthiza* thus represents a case where pair-breeding species have evolved from a cooperatively breeding ancestor, an evolutionary scenario that is now thought to have occurred numerous times in the evolution of the passerines (Cockburn 2003; Heinsohn and Double 2004). The potential for the thornbills to elucidate processes of social evolution has been limited by the lack of comprehensive information on their breeding biology and behaviour and only one pair-breeding species, the brown thornbill, and one cooperatively breeding species, the buff-rumped thornbill, *Acanthiza reguloides*, have been studied in detail (Bell and Ford 1986; Green and

Cockburn 1999). In this chapter I aim to extend the observations of Ford (1963), who described some aspects of breeding in the yellow-rumped thornbill, and provide a comprehensive description of another cooperatively breeding member of the Pardalotidae.

METHODS

Species and study site

Yellow-rumped thornbills are small insectivorous passerines endemic to Australia. The species is the most widespread thornbill and is abundant in south-eastern and south-western continental Australia and Tasmania (Blakers *et al.* 1984; Christidis and Boles 1994).

I studied the population of yellow-rumped thornbills on the lower eastern slopes of the Mt Ainslie section of Canberra Nature Park ($35^0$16'S, $149^0$9'E), in the Australian Capital Territory (ACT), from 1995 to 1997. The study area was approximately 250ha of open eucalypt woodland dominated by *E. rossii*, *E. mannifera* and *E. macrorhyncha* with a sparse shrubby understorey interspersed with cleared grassy areas.

Field techniques

Adult birds were captured in mist nets and banded with a numbered aluminium band, supplied by the Australian Bird and Bat Banding Scheme, and a unique combination of three coloured plastic bands. The breeding population in the first year of the study, 1995, contained numerous unbanded birds. However, in 1996 and 1997, due to the survival of birds banded in earlier years and sustained mist netting during breeding and non-breeding periods, the vast majority of breeding individuals was banded. There was only one pair in 1996 and another in 1997 where neither bird was banded.

The social organisation of breeding units was assessed by observation throughout the breeding cycle. The classification of pairs and groups was generally straightforward in that supernumerary individuals were usually present from the start of the breeding season and were observed foraging with the breeding pair regularly during the nest-building and incubation stages of the breeding cycle.

Adult survival was assessed for two years, 1995 and 1996, from the start of the breeding season, 1st of August, in the first year until the same date in the following year. Banded fledglings were monitored for survival until four weeks after fledging.

Nests were found by watching building birds, following females during incubation or following birds seen collecting prey to feed nestlings. Nests were visited regularly to determine the clutch initiation date for those found before laying, clutch size and hatching date for those found before hatching, and the fate of the nesting attempt, either fledging or failure. The incubation period, the number of days from the date of laying of the last egg to the date of hatching of the last nestling, was determined for a sample of clutches as was the nestling period, the number of days from the date of hatching to the date of fledging. Average incubation and nestling periods determined for these nesting attempts were used to back-date from hatching or fledging dates to estimate clutch initiation and hatching dates for those nesting attempts that were found at later stages. Nestlings were briefly removed from the nest for banding and blood sampling when they were between seven and 13 days old. The size and stage of feather development of nestlings of known age were used to estimate the ages of broods from nests that were found after hatching, and this estimate and the average incubation period was also used to estimate clutch initiation dates for these nesting attempts.

Nest predation was very high in the first two years of the study and in order to increase sample sizes for some datasets all accessible nests in 1997 were protected from larger predators by enclosure with wire or plastic mesh with a 5cm mesh size.

Sexing

Yellow-rumped thornbills are sexually monomorphic, and although only female birds were thought to incubate (Ford 1963), the sex of all banded birds was determined with a simple PCR based sexing technique (Griffiths *et al.* 1996; Griffiths *et al.* 1998). Briefly, a small blood sample was taken at the time of capture and DNA extracted according to standard protocols (Bruford *et al.* 1992). A small section of the sex linked CHD gene was amplified using primers P2 and P3 and standard PCR methods (Griffiths *et al.* 1996) and digested with the enzyme HaeIII. This enzyme does not cut the fragment amplified from the CHD-W gene, which only occurs in females, but does cut the equivalent fragment amplified from the CHD-Z gene. Digested PCR products were separated by electophoresis through 3% agarose in 1 X TBE buffer for one hour at 150V, stained with ethidium bromide and photographed. The sex-specific banding pattern was unambiguous and easily scored with males producing two bands (cleaved CHD-Z fragments) and females three (cleaved CHD-Z fragments and the uncleaved CHD-W fragment).

Data analysis

Reproductive success was assessed with three analyses, the probability of clutches that were initiated hatching, the probability of clutches that hatched fledging and the overall success rate of breeding pairs in each year in terms of success or failure to fledge any offspring and in terms of the number of offspring fledged. Only pairs that were known well enough to be sure that all nesting attempts were monitored were included in the analysis of overall yearly success rates. The independent variables tested for their effects on reproductive success were year, month of clutch initiation for probability of hatching, and month of hatching for probability of fledging.

Nest protection in 1997 was not random with regard to height and nests left unprotected may not have been representative in terms of their inherent risk of predation. Furthermore, predators may have modified their behaviour in response to the protection of a subset of nests. For these reasons apparent differences in reproductive success variables between 1995 and 1996 arising from analyses including 1997 data were verified by repeating the analysis excluding 1997 data. Wherever 1997 was included in analyses of reproductive success or the description of predation rates, protected nests were excluded and all breeding pairs that had one or more nest protected in 1997 were excluded from the analysis of overall success rate for the year.

Some datasets contained non-independent measurements, where breeding pairs were represented more than once within and between years. Analyses of reproductive success were performed on modified datasets where a single instance of each breeding pair in the initial dataset was randomly selected in order to achieve independence of data. The same modifications were not made for simple descriptive statistics, such as timing of the breeding season, clutch sizes and the durations of incubation and nestling periods.

Data were analysed using JMP ver. 3 (SAS Institute 1994). Categorical response variables, such as probability of hatching, were analysed using logistic regression and statistics presented below are likelihood ratio χ^2's. Continuous response variables, such as weight or incubation period, were analysed using standard least squares statistics. Sample sizes for many related analyses differ due to variation in the stage at which nests were found, and when they ended in the case of predated nests, and also due to variation in the details known of nests that were too high to access.

RESULTS

Breeding Biology

Nesting

Yellow-rumped thornbills built bulky domed nests comprised mostly of grass and spider's silk and lined with feathers in a variety of native tree and shrub species including *Eucalyptus* spp. (52%), the native cherry, *Exocarpus cupressiformis*, (12%), *Acacia* spp. (9%), mistletoes in eucalypts (9%) and Hakea spp. (6%) as well as the weed species briar rose, *Rosa rubiginosa*, and hawthorn, *Crataegus monogyna*, (11%, total for both weed species).

The heights at which nests were built varied greatly and ranged from 1m to approximately 20m from the ground (median nest height: 2.5m, n = 144). Of the 150 nests that were known to be active over the three years of the study 17% were unreachable as they were located high in the canopies of large eucalypts.

Both sexes participated in building and lining the nest. Subordinate birds in cooperatively breeding groups very rarely assisted with nest building and where subordinates were observed delivering nesting material their contributions were very minor in comparison with those of the breeding pair.

Birds started building nests in mid winter, June or July, although the earliest commencement of nest building was the 5th June 1996, more than two weeks before the winter solstice. The longest period between the start of nest building and clutch initiation was 62 days for the first pair to start building a nest in 1996. The shortest period between the start of nest building and clutch initiation was seven days for two pairs, both of which started building in September.

Old nests were re-used in 11% of nesting attempts (n = 150). The birds added a new nesting chamber to an old nest or relined the original nesting chamber.

Breeding Season

The first clutches of the breeding season were initiated in August in all three years and overall 97% of all first clutches were initiated in August or September (Figure 2.1). The timing of second clutches, laid after failure or fledging, was broadly spread throughout the season from late August to early December and the few third clutches were initiated from late October to late November (Figure 2.1). MacArthur's (1964) index of the length of the breeding season was 3.6 months. There was no difference among years in the timing of the last clutches of the season (ANOVA: $F = 1.25_{2,45}$, $p = 0.29$); however, there was a trend indicating that the synchrony of first clutches differed among years (Bartlett's test for homogeneity of variances: $F = 2.72_{2}$, $p = 0.06$) and a significant difference in the timing of first clutches among years (Welch's ANOVA: $F = 5.4_{2,28}$, $p = 0.01$). First clutches were initiated later in 1997 than in 1995 and 1996, and possibly more synchronously in 1995 than in 1996 and 1997 (Table 2.1).

Clutch Size and Laying Interval

The most common clutch size for yellow-rumped thornbills was three eggs (77% of 97 clutches) followed by clutches of four (17.5%). Smaller clutches of two eggs (3%) or one (2%) may have resulted from egg loss during the laying or incubation periods.

Eggs appeared to be consistently laid at two-day intervals. No clutches were checked daily throughout the laying period; however, of 21 nests that were checked on two consecutive days before the last egg was laid all were found to contain the same number of eggs on both days. The number of eggs in 11 nests that were checked three days apart early in the laying period increased by only one and not two as would be expected for a one day laying interval. A two-day laying interval was confirmed for four nests that were checked on three consecutive days during the laying period.

Incubation, Nestling and Fledgling Care Periods

Incubation began on the day the last egg was laid and lasted from 15 to 20 days with a mean of 17.1 ± 1.14 (s.d.) days (n = 38). There was a decrease in the length of the incubation period over the course of the season (linear regression: $F = 4.9_{1,36}$, $n = 38$, $p = 0.03$; Figure 2.2). Only the female incubated the clutch.

Clutches hatched roughly synchronously with all eggs in seven clutches that were checked on consecutive days hatching within 24 hours. The nestling period lasted from 17 to 21 days with a mean of 19.3 ± 1.4 (s.d.) days (n = 18). Females, alpha-males and subordinate males in cooperative groups all provisioned nestlings.

The period of fledgling care was at least four to five weeks. Seven broods were known to be fed by their parents for at least the first four weeks post-fledging and three were known to be fed for at least five weeks. It was likely that parental provisioning of fledglings extended beyond five weeks as no observations were made to determine the point at which fledglings became fully independent.

Multi-brooding

Yellow-rumped thornbills initiated up to three clutches per season, although the vast majority of pairs initiated one or two clutches and rarely fledged more than one brood (Table 2.1). Renesting was more common following nesting attempts that failed than after the successful fledging of a brood (62% of 37 failed attempts versus 26% of 39 successful attempts, logistic regression: $\chi^2 = 4.16$, df = 1, p = 0.04). Both for pairs that failed and for those that succeeded in fledging a brood there was a decline in the probability of initiating another clutch over the course of the breeding season (logistic regression: $\chi^2 = 32.4$, df = 3, $p < 0.0001$; Figure 2.3). When pairs did renest, the delay from the end of the first attempt to initiation of the second clutch was significantly shorter following a failed nesting attempt (means of 13.4 days for 14 failed attempts and 28.8 days for 7 successful attempts where the delay was known, t-test: t = 2.61, df = 19, p = 0.02).

Reproductive Success

Overall 67.6% of clutches initiated hatched (n=102 clutches). The main cause of failure was nest predation (Chapter 3). The only other cause of failure identified was damage to nests and clutches by high winds (n = 3) followed by abandonment. Clutches initiated later in the breeding season, in October or November, had a greater chance of hatching (logistic regression: $\chi^2 = 9.7$, df = 3, p = 0.02; Figure 2.4). There was no effect of year on the proportion of clutches hatching.

Of clutches that hatched, 53.6% fledged young (n = 69 broods). Again the main cause of failure was nest predation (Chapter 3). Other causes of failure included one brood parasitised by a Horsfield's bronze cuckoo and another abandoned after the disappearance of the breeding female. There was a strong effect of year on the probability of broods fledging: only 33% of broods successfully fledged in 1995 compared with 64% in 1996 and 91% in 1997 (Figure 2.5). The effect of year was significant in analyses including and excluding 1997 broods (logistic regressions, including 1997: $\chi^2 = 12.2$, df = 2, $p < 0.01$ and excluding 1997: $\chi^2 = 7.1$, df = 1, $p < 0.01$). There was a trend for fledging success to differ among months (logistic regression: $\chi^2 = 7.4$, df = 3, $p = 0.06$), and in all three years broods that hatched in November fared poorly. Overall only 33% of 12 broods hatched in November fledged young compared with a success rate of more than 50% for other months (Figure 2.6).

Despite variation among years in the probability of broods fledging there was no statistically significant variation among years in the proportion of pairs that fledged young, the number of broods fledged per pair or the number of fledglings per pair. However, there was some indication that 1995 was a poor year in terms of per pair productivity as it was the only year where no pair succeeded in fledging more than one brood and, therefore, was also the year with the lowest number of fledglings per pair (Table 2.1). Small sample sizes due to the small number of banded pairs in 1995 and the exclusion of pairs with protected nests in 1997 may have compromised statistical power in detecting an effect of low fledging success in 1995 on productivity. One effect of variation in fledging success among years was apparent in the extent of reproductive investment required in each year to achieve the virtually equal annual success rates. The proportions of pairs that succeeded in fledging young was almost exactly 0.6 in all three years (Table 2.1). This equality was achieved by a greater breeding effort per pair in 1995 with 77% of pairs initiating more than one clutch in 1995, when the fledging success of broods was lowest, compared with 52% in 1996 and 37.5% in 1997.

Over three years, 76 banded fledglings from 27 broods were monitored for survival to four weeks post fledging. The overall proportion surviving to four weeks was 0.62 and there was no significant variation among years (Table 2.1).

Social Organisation and Demography

Cooperative breeding

The vast majority of yellow-rumped thornbills bred in pairs (Table 2.1). Over the three breeding seasons the overall frequency of cooperatively breeding groups was only

13.5%, and ranged from 5% in 1996 to 15.8% in 1997. Cooperatively breeding groups consisted of a single female, an alpha-male and up to three subordinate male helpers (n = 9 subordinates sexed, one group of 5 in 1998). Helpers contributed to the provisioning of broods that hatched later in the same breeding season in which they themselves fledged (n = 2) or in subsequent seasons (n = 4 birds that became helpers as yearlings). Two individuals were known to be helpers for two consecutive seasons. Six helpers were of known origin as they were banded as nestlings. Five of these provisioned subsequent broods of their own parents while the sixth originally helped provision a brood of his parents before moving to become a helper at a neighbouring breeding attempt.

Juvenile Dispersal

Juvenile males were commonly philopatric whereas all females dispersed. Of 19 females that were banded as nestlings and were known to be alive four weeks after fledging none remained in the population at the start of the following breeding season. The latest a juvenile female was seen with her natal flock was mid January for two females which fledged late in the preceding breeding season and would have just been reaching independence at that time. In contrast, of 29 males which were banded as nestlings and were known to be alive four weeks after fledging 17 were still present in their natal flocks in July of the following year. Of these, five became breeding males and six became helpers in their first breeding season. The remaining individuals may have died, although it is more likely that some or all of them dispersed out of the study area early in their first breeding season.

Territoriality

Aggressive behaviour that might indicate territoriality, though not quantified in this study, was minor and although breeding pairs and groups were almost always found foraging in the vicinity of their nests, and were very rarely seen foraging with other birds, they apparently did not defend exclusive breeding territories. Birds that were not directly involved in a breeding attempt, in that they were not regularly associated with the breeding pair and did not build the nest or provision the nestlings, were observed in very close proximity to nests on numerous occasions. In these cases the owners of the nest often reacted aggressively by singing and displacing the "intruder"; however, they did not chase it a substantial distance in a manner consistent with the defence of a territorial area surrounding the nest. Based on cases where identification was possible, "intruders" were the juvenile male offspring of a neighbouring breeding pair (n = 4), a neighbouring breeding male (n = 3) and on one occasion a neighbouring breeding female. The juvenile males observed in these interactions often made repeated visits to nests containing nestlings to add small amounts of nesting material, rather than to feed the brood, and invoked very minor reactions from the owners of the nest. Two of the three "intruders" that were adult breeding males appeared to displace the original breeding male from a neighbouring breeding pair. In both of these cases one male appeared to replace another as the social mate of a female. However, in neither case did the apparently displaced male leave the general area of the nest: one continued to provision nestlings and the other continued to provision fledglings. One extra-pair copulation was observed. The extra-pair male appeared to stop provisioning his own nestlings for a period of several days in order to associate with a neighbouring female who was building a nest with her mate. The female's original male was present when the extra-pair copulation occurred and made no attempt to prevent it or repel the "intruding" male.

DISCUSSION

Breeding Biology

Clutch size

Yellow-rumped thornbills most commonly laid a clutch of three eggs, which is typical of the Pardalotidae (Woinarski 1985; Green and Cockburn 1999; Magrath *et al.* 2000; Gardner 2002). Small and relatively invariant clutch sizes are characteristic of Australian passerines (Woinarski 1985; Ford 1989; Rowley and Russell 1991; Magrath *et al.* 2000), but clutch size may be slightly more variable in the yellow-rumped thornbill than other Pardalotidae species. Three egg clutches accounted for only 77% of clutches in comparison with 90% or more for the white-browed scrubwren (*Sericornis frontalis*), speckled warbler (*Chthonicola sagittata*) and brown thornbill (Green and Cockburn 1999; Magrath *et al.* 2000; Gardner 2002). Unlike these species, clutches of four eggs were not especially rare in the yellow-rumped thornbill and accounted for 17.5% of all clutches laid in this study. Ford (1963) also found four egg clutches to be comparatively common, accounting for 24.2% of clutches laid.

Ford (1963) suggested that there was an increase in clutch size from early to later in the breeding season. Although there was no statistically unequivocal seasonal pattern in clutch size for the population described here, there was, if anything, a trend opposite to that proposed by Ford. Only two of the 24 clutches (8%) laid after September contained four eggs whereas 15 of 68 (22%) laid in August and September were four egg clutches. Studies of non-migratory multi-brooded northern hemisphere species have found that clutch size generally peaks in the middle of the breeding season (Lack 1968; Klomp 1970; Crick *et al.* 1993; Dhondt *et al.* 2002), a pattern generally thought to reflect variation in resource availability. The yellow-rumped thornbill may be unusual among the Pardalotidae in exhibiting a resource based pattern of seasonal clutch size variation, although there is evidence to suggest that the small insectivores breeding in the eucalypt forests of Australia do not experience the dramatic spring-summer peak in arthropod abundance that occurs in the northern hemisphere (Woinarski and Cullen 1984; Ford 1989). Larger sample sizes and more information on potential covariates such as resource availability and female age and breeding history will be required to fully describe and understand clutch size variation in the yellow-rumped thornbill.

Incubation and nestling periods

Long incubation periods are a feature of the Pardalotidae (Ricklefs 1993) and the mean period of 17.1 days for the yellow-rumped thornbills in this study is similar those reported for other members of the family (Woinarski 1985; Green and Cockburn 1999; Magrath *et al.* 2000; Gardner 2002). As reported for the brown thornbill (Green and Cockburn 1999) and the white-browed scrubwren (Magrath *et al.* 2000) the period for which yellow-rumped thornbill clutches were incubated decreased over the course of the breeding season. This was probably due to the seasonal increase in ambient temperature, from a mean daily maximum of 13^0C in August to 23^0C in November, assisting females in maintaining optimal incubation temperatures later in the season.

The mean nestling period of 19.3 days for the yellow-rumped thornbill is slightly longer than that reported for other non-cavity nesting Pardalotidae speces, which range from 15.1 days for the white-browed scrubwren (Magrath *et al.* 2000) to 16.5 days for the speckled warbler (Gardner 2002). The small sample size of accurately known nestling periods may have prevented the detection of a decrease in duration over the course of the breeding season as has been reported for the white-browed scrubwren (Magrath *et al.* 2000) and the brown thornbill (Green and Cockburn 1999).

Breeding season and multi brooding

The yellow-rumped thornbills described in this study had a breeding season of 3.6 months, which falls within the range reported for thornbills breeding in south eastern Australia; buff-rumped thornbills breed for approximately three months (Woinarski 1985; Bell and Ford 1986), while brown thornbills and striated thornbills both breed for approximately four months (Woinarski 1985; Bell and Ford 1986; Green and Cockburn 1999). Although members of the Pardalotidae are known for their long breeding seasons, thornbills appear to have comparatively short breeding seasons. The longest breeding season reported for a member of the Pardalotidae is 6.6 months for the speckled warbler breeding in the ACT (Gardner 2002). Seasons of more than five months have also been reported for the white-browed scrubwren (Magrath *et al.* 2000) and the spotted pardalote (*Pardalotus punctatus*) (Woinarski 1985).

MacArthur's index of the length of the breeding season for the yellow-rumped thornbill in Western Australia, as calculated from the data presented by Ford (1963), was 5.5 months. Climatic factors presumably underlie the substantial difference in the duration for which yellow-rumped thornbills bred at Ford's coastal study site and in the higher altitude and more seasonal environment of the Australian Capital Territory (ACT). The difference in the duration of breeding at the two locations was mainly due to when breeding began with first clutches initiated in early August toward the end of the comparatively severe winter of the ACT (mean July minimum temperature = $^{-}3^{0}$C), and in early July during the mild winter of the Perth region (mean July minimum temperature = 9^{0}C), where Ford's study was conducted.

Multi-brooding is a common trait in the Australian old endemic passerine families (Rowley and Russell 1991) and has been reported for most members of the Pardalotidae that have been studied. Thornbills breeding in the south-east of Australia, however, appear to be limited in their capacity for multiple breeding attempts by the relatively short duration of their breeding seasons. Both the white-browed scrubwren and speckled warbler breeding in the ACT can lay up to six clutches in their breeding seasons of 5.4 and 6.6 months respectively (Magrath *et al.* 2000; Gardner 2002) and the yellow-rumped thornbill breeding near Perth, Western Australia (WA). initiated up to five clutches over a breeding season of approximately 5.5 months (Ford 1963). In contrast, brown thornbills and yellow-rumped thornbills breeding in the ACT, which have breeding seasons of 4.0 and 3.6 months respectively, laid at most three clutches (Green and Cockburn 1999, Table 3.2). Variation in rates of nesting failure may have influenced the differences among species and populations in the absolute number of breeding attempts per season; however, the effect of breeding season duration on multiple breeding is also indicated by the behaviour of successful breeders. Near Perth, WA, 71% of yellow-rumped thornbill pairs that successfully fledged a brood on their first nesting attempt of the season initiated a second clutch (Ford 1963). In the ACT, where the breeding season was two months shorter, the frequency of renesting following a successful first breeding attempt was only 33% and was similar to the rate exhibited by brown thornbills breeding in the same region where 39% of successful first clutches were followed by a second breeding attempt (Green and Cockburn 1999).

Reproductive success

Annual rates of reproductive success for yellow-rumped thornbills observed in this study were substantially lower than those observed by Ford (1963). Over the three years of this study approximately 60% of pairs breeding in each year succeeded in fledging at least one brood and on average each pair produced 2.02 fledglings per year. As calculated from two years of data presented by Ford (1963), approximately 96% of yellow-rumped thornbill pairs breeding near Perth, WA, fledged at least one brood in each year and, on average, pairs produced 3.6 fledglings per year. The discrepancy in reproductive success between these two populations appears to be due to the unusually high success of the population observed by Ford (1963) rather than unusual failure by the population described here. The productivity of yellow-rumped thornbills breeding in the ACT falls within the range achieved by other members of the Pardalotidae breeding in the south-east of Australia. White-browed scrubwrens are the most successful breeders in the south-east producing 2.8 fledglings/pair/year (Magrath and Yezerinac 1997), followed by the yellow-rumped thornbill (2.02), the brown thornbill (1.57) (Green and Cockburn 1999), the buff-rumped thornbill (1.1) (Bell and Ford 1986) and the speckled warbler (approx. 1) (Gardner 2002). At the population level, reproductive success is ultimately determined by the extent of reproductive investment by breeding individuals and the success rate of individual breeding attempts. It is likely that variation in both of these factors explains the discrepancy in reproductive success between yellow-rumped thornbill populations breeding near Perth, WA, and in the ACT.

Rowley and Russell (1991) proposed that unlike the passerines of the northern hemisphere, where multi-brooding is less common, variation in seasonal reproductive effort within populations of Australian passerines arises from variation in the number of breeding attempts per season rather than variation in clutch size per attempt. For members of the Pardalotidae this is also likely to apply to comparisons at the population and species level as variation in clutch size within and among species is minor (Woinarski 1989) and is unlikely to greatly influence annual productivity at the population level. However, a major determinant of the extent of multi-brooding, the duration of the breeding season, varies substantially between species and populations. In the south-east of Australia, 23% of white-browed scrubwren pairs and 18% of speckled warbler pairs fledged more than one brood per season (Magrath *et al.* 2000; Gardner 2002). These two species have very long breeding seasons. By comparison three thornbill species breeding in the same region had comparatively short breeding seasons (shorter by at least 1.5 months) and the frequencies with which pairs fledged multiple broods were 10% for the yellow-rumped thornbill (this study), 3% for the brown thornbill (Green and Cockburn 1999) and 0% for the buff-rumped thornbill (Bell and Ford 1986). The comparison of yellow-rumped thornbill populations breeding near Perth, WA, and in the ACT also indicates a role for reproductive effort expressed via multi-brooding in determining seasonal reproductive success. The two populations had almost identical mean clutch sizes of 3.2 (W.A., Ford 1963) and 3.1 (ACT, this study); however, yellow-rumped thornbills breeding near Perth had a longer breeding season and higher frequency of attempted multi-brooding than those breeding in the ACT. The West Australian population was correspondingly more productive, with 40% of pairs breeding near Perth fledging more than one brood in a season (Ford 1963).

Differences in predation rates between the population described here and that studied by Ford (1963) may also explain the variation in reproductive success of the two populations. As is commonly the case in birds (Ricklefs 1969; Martin 1992) nest predation is the major cause of breeding failure for thornbill species in the south east of Australia. The majority of breeding attempts fail due to predation of eggs or nestlings in the yellow-rumped thornbill (Chapter 3), the brown thornbill (Bell and Ford 1986; Green and Cockburn 1999), the buff-rumped thornbill and the striated thornbill (Bell and Ford 1986) breeding in south eastern Australia. In contrast, only 22% of the 111 yellow-rumped thornbill clutches observed near Perth by Ford (1963) were lost to predators before fledging, which is less than half the 54% predation rate for the same species breeding in the ACT (Chapter 3). One contributing factor to this marked difference may be differences in the complement of nest predators in the two regions. A major nest predator in the ACT, and elsewhere in south eastern Australia, is the pied currawong (*Strepera graculina*) (Major *et al.* 1996; Prawiradiliga 1996; Gardner 1998; Fulton and Ford 2001), which does not occur in West Australia but which appears to have a significant impact on yellow-rumped thornbills breeding in the ACT (Chapter 3).

Annual and seasonal variation in reproductive success of yellow-rumped thornbills breeding in the ACT reflected changes in rates of nest predation between years and over the breeding season. The probability of clutches hatching improved over the course of the breeding season. This may have been due to a reduction in the exposure of clutches to nest predators as incubation periods declined by approximately two days over the breeding season. The trend for decreased fledging success of broods in November corresponds with a dramatic increase in predation pressure, specifically affecting nestlings rather than eggs, in November due to the impact of pied currawongs hunting to feed their own nestlings in late spring (Chapter 3). Annual variation in breeding success also corresponds with variation in predation pressure. Predation of nestlings was particularly high in 1995 (Chapter 3) and the success rate per breeding attempt in 1995 was virtually half that of 1996 when nest predation was more moderate (Chapter 3). Nonetheless, variation in per breeding attempt success rates between years did not affect the proportion of pairs that succeeded in each year as renesting following failed breeding attempts compensated for variation in per breeding attempt success rates. The proportion of pairs that fledged young was almost exactly 0.6 in all three years which is the same rate of success as for brown thornbills breeding in the ACT (0.57, Green and Cockburn 1999).

In this study the survival of fledglings was monitored for only four weeks, which was shorter than the total period of dependence, although by four weeks fledglings were mostly foraging for themselves. The survival rate to four weeks after fledging for yellow-rumped thornbills (Table 2.1) was very similar to the 63–64% survival rates to independence for brown thornbills (Green and Cockburn 1999), white-browed scrubwrens (Magrath and Yezerinac 1997) and speckled warblers (Gardner 2002) breeding in the ACT, suggesting that survival to four weeks was an accurate measure of the probability of yellow-rumped thornbill fledglings reaching independence.

Social Organisation and Demography

Survival

High adult survival and longevity are characteristic of Australian passerines (Fry 1980; Yom-Tov 1980; Rowley and Russell 1991) and the oldest recorded yellow-rumped thornbill was at least 9.5 years old when last captured (Grace 1979). Annual survival of adult yellow-rumped thornbills in the ACT was at the lower end of the range reported for other members of the Pardalotidae (Green and Cockburn 1999) but similar to that reported for buff-rumped thornbills near Armidale by Bell and Ford (1986).

Juvenile dispersal

Yellow-rumped thornbills had a sex biased dispersal pattern with all juvenile females dispersing during or soon after the breeding season in which they fledged while males commonly remained within the natal flock over winter and then either dispersed, mated and bred within the flock home-range (Chapter 5), or helped in the breeding attempts of their parents. Several dispersal patterns have been described for members of the Pardalotidae. Bell and Ford (1986) found that both male and female buff-rumped thornbills did not necessarily disperse from their natal flocks and that female yearlings could assume the breeding position left vacant upon the death of their mothers. In contrast Gardner (2002) found that juvenile dispersal was universal in the speckled warbler and both males and females always left the natal territory soon after reaching independence. Delayed dispersal is characteristic of species which breed cooperatively (Emlen 1995) although among the Pardalotidae it is not only exhibited by cooperatively breeding species such as the yellow-rumped thornbill and white-browed scrubwren (Magrath and Whittingham 1997) but also by the strictly pair breeding brown thornbill (Green and Cockburn 2001).

Territoriality and Cooperative Breeding

Breeding pairs and groups of yellow-rumped thornbills did not appear to establish breeding territories from which other birds were excluded. This is in contrast with all well known members of the family which do breed on exclusive territories (brown thornbill, Bell and Ford (1986), Green and Cockburn (1999); buff-rumped thornbill, Bell and Ford (1986); white-browed scrubwren, Magrath *et. al.* (2000); speckled warbler, Gardner (2002)). Male yellow-rumped thornbills in particular were occasionally observed in association with more than one nest or more than one breeding female. In most cases this appeared to entail the toleration of the juvenile offspring of other flock members, for example when juvenile males began adding nesting material to nests that were already fully constructed and contained nestlings. However, there were also two cases where helper males provisioned nestlings of neighbouring breeding groups and several instances of the domination of one adult breeding male by another that appeared to be related to access to breeding females. These incidental observations suggest that flock level social affiliations (Chapter 5) may play a role in the social organisation of breeding particularly in regard to helping behaviour by male birds.

Cooperatively breeding groups of yellow-rumped thornbills were similar in size and composition to those of the buff-rumped thornbill described by Bell and Ford (1986). Helpers in buff-rumped thornbill groups are the male offspring of the breeding pair, and with the exception of one individual who helped at the nests of two different pairs all yellow-rumped thornbill helpers of known origin were the offspring of the pair they assisted. As reported by Immelman (1960) and Ford (1963) juvenile males could become helpers later in the breeding season in which they themselves fledged, although most helpers were yearlings when they first provisioned at the nest.

The frequency of cooperative breeding by yellow-rumped thornbills was low, only 13.5% overall, and varied among years. In comparison, the frequency of cooperatively breeding groups in the populations of buff-rumped and striated thornbills studied by Bell and Ford near Armidale, New South Wales (NSW) were approximately 32% and 43% respectively (Bell and Ford 1986). There was some indication that the occurrence of cooperative breeding by yellow-rumped thornbills was influenced by annual reproductive success and adult survival. Given that helpers were almost always the offspring of the breeding pair they assisted, two prerequisites for the formation of cooperative groups are, firstly, the presence of male offspring from the current or previous breeding season and, secondly, the continuation of the breeding relationships that produced them. Annual reproductive success determines at least the potential number of yearling males that may be available to become helpers in the following year and the number of helpers in the population increased from one in 1996 to six in 1997 following the comparatively successful 1996 breeding season. From 1995 to 1998 there were 42 instances where it was possible to detect the persistence of a breeding pair from one season to the next and in only eight cases did a male and female form the same breeding pair in consecutive seasons. Of these, six were assisted by helpers in the second year in which they bred together. The low rate of continuity in breeding relationships was mostly due to the death of one or both birds although there were four known cases of divorce (where both members of a pair were alive in the subsequent breeding season but were mated to other birds). The affect of inter-annual persistence of breeding pairs on cooperative breeding is also indicated by the transition between the 1995 and 1996 breeding seasons. Corresponding with the relatively low adult survival between these two breeding seasons none of the 11 fully identifiable pairs breeding in 1995 persisted in 1996. Helpers were especially rare in 1996 and the only helper identified was assisting a pair of unknown history that may have bred together in the previous year.

CONCLUSION

The breeding biology and demography the yellow-rumped thornbill is typical of its family (see Green and Cockburn 1999; Magrath *et al.* 2000 for reviews of Pardalotidae). It is long lived, lays a small clutch with a two day laying interval, has long incubation and nestling periods and a long period of post fledging dependence, and can display a high rate of multi-brooding over a long breeding season. These results support the view of Green and Cockburn (1999) that factors other than variation in life-history and breeding biology traits must underlie the evolution of diverse social systems in the Pardalotidae.

The comparison of the yellow-rumped thornbill population described here and that described by Ford (1963) reveals substantial within species variation in some reproductive characteristics. As noted by Magrath *et al.* (2000), few species of the Pardalotidae have been studied in detail and although there may be sufficient quantitative information to characterise easily measured traits such as clutch size at a species or family level, the characterisation of other, potentially more variable traits, on the basis of a single population may be misleading. Regional differences in breeding season duration and predation rates between Ford's West Australian population and the population described here underlie major differences in rates of multi-brooding, reproductive success and productivity and would lead to very different characterisations of these aspects of yellow-rumped thornbill breeding biology should either population alone be considered representative of the species. Considered together, the two populations demonstrate the capacity of a typical member of the Pardalotidae, exhibiting the syndrome of long and slow reproduction, to achieve remarkable reproductive success in favourable conditions and the importance of nest predation in limiting that success.

Table 2.1. Annual patterns of social organization, timing of breeding and breeding success in the yellow-rumped thornbill. Eleven pairs breeding in 1997 were excluded from calculations of breeding success as their nests were protected from predators.

	1995	1996	1997	Years combined
Male survival (n)	0.45 (11)	0.61 (18)	0.64 (20)	0.59 (51)
Female survival (n)	0.39 (13)	0.60 (20)	0.43 (22)	0.49 (53)
n for social organisation	13	20	19	52
Number of cooperative groups (n trios, n quartets)	2 (2, 0)	1 (1, 0)	4 (1, 3)	7 (4, 3)
Frequency of cooperative groups	15.4%	5%	21%	13.5%
Number of males per breeding female	1.15	1.05	1.34	1.1
n for timing	12	18	15	45
First clutch initiated ± s.d.	27 Aug ± 9 days	2 Sep ± 17 days	10 Sep ± 12 days	4 Sep ± 14 days
Last clutch initiated ± s.d.	15 Oct ± 36 days	2 Oct ± 21 days	1 Oct ± 24 days	5 Oct ± 27 days
Clutches initiated – 1	3	10	5	17
2	10	8	3	21
3	0	2	0	2
Broods fledged – 0	6	8	3	17
1	8	9	4	21
2	0	3	1	4
Proportion of pairs that fledge young	0.61	0.60	0.62	0.61
Fledglings per pair ± s.d.	1.61 ± 1.39	2.15 ± 1.93	2.37 ± 2.06	2.02 ± 1.78
Fledgling survival to 4 weeks (n fledglings, n broods)	0.56 (16, 6)	0.62 (29, 10)	0.64 (31, 20)	0.62 (76,27)

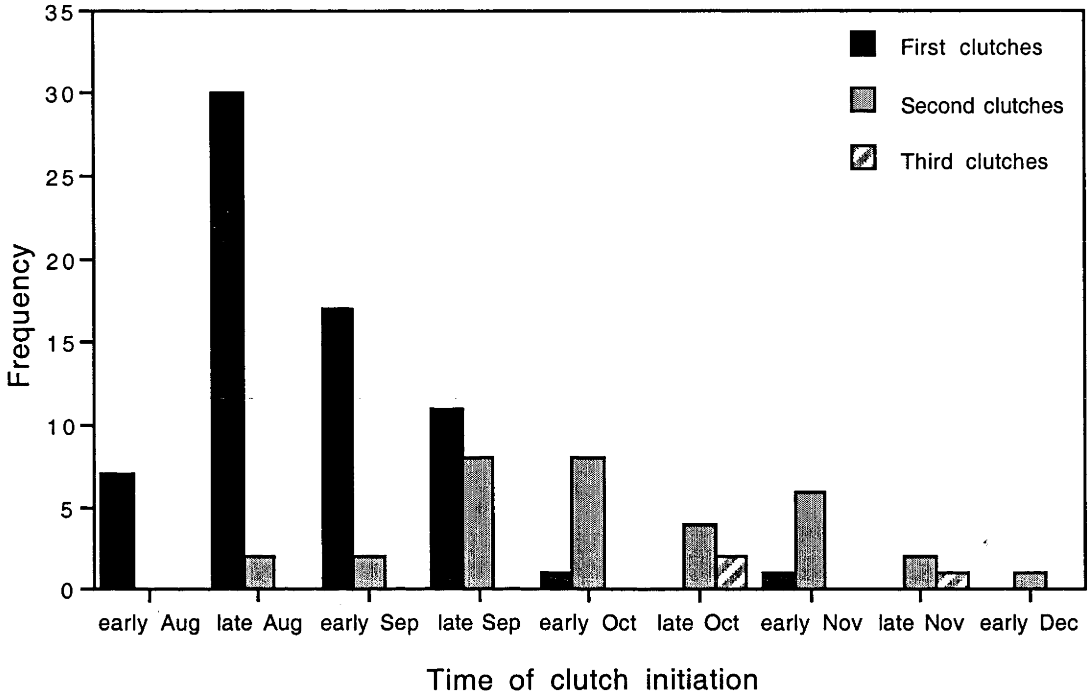

Figure 2.1. Timing of clutch initiation in yellow-rumped thornbills. "Early" and "late" in each month refers to the periods from the1st to the 15th and the 16th to the end of the month, respectively.

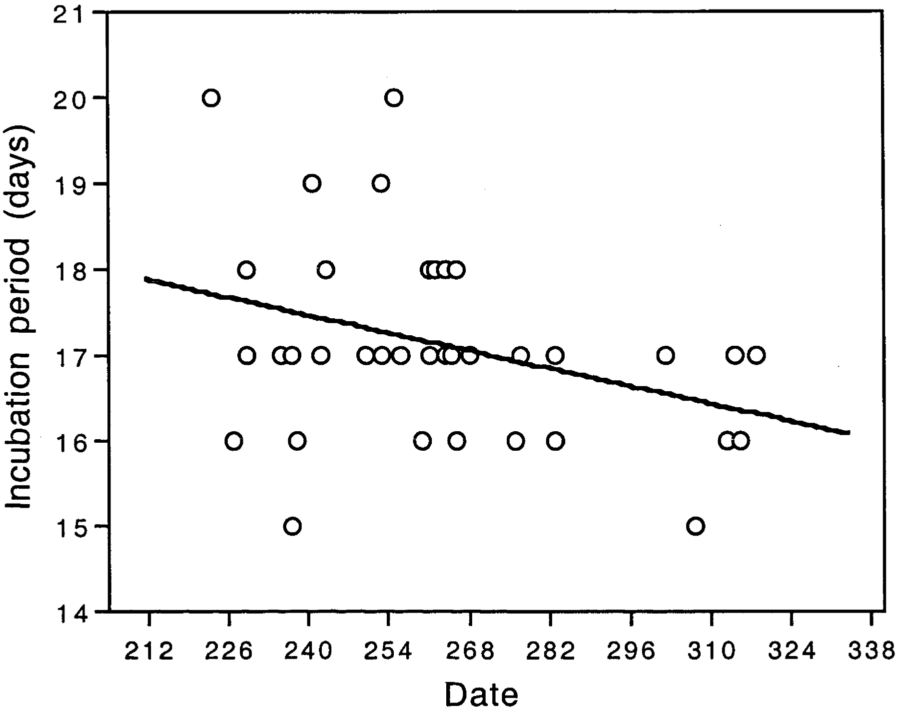

Figure 2.2. The decrease in incubation period over the course of a breeding season for yellow-rumped thornbills. Points are observed incubation periods and the line represents the regression of incubation period on clutch initiation date. Date used is the Julian date, where 1 = January 1st.

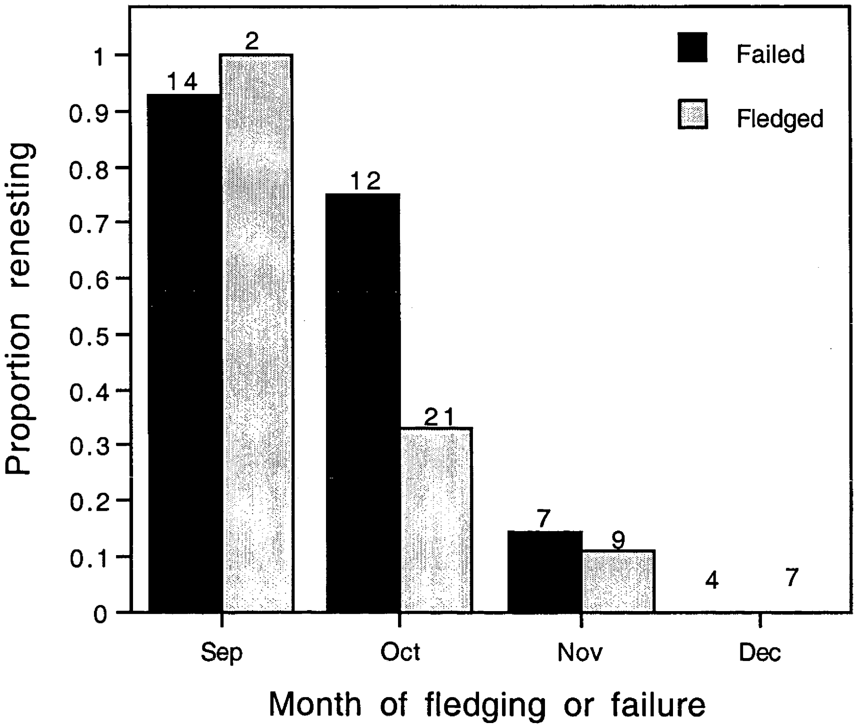

Figure 2.3. Proportion of yellow-rumped thornbills renesting after failed or successful nesting attempts by the month in which the previous attempt ended. Numbers above bars are sample sizes.

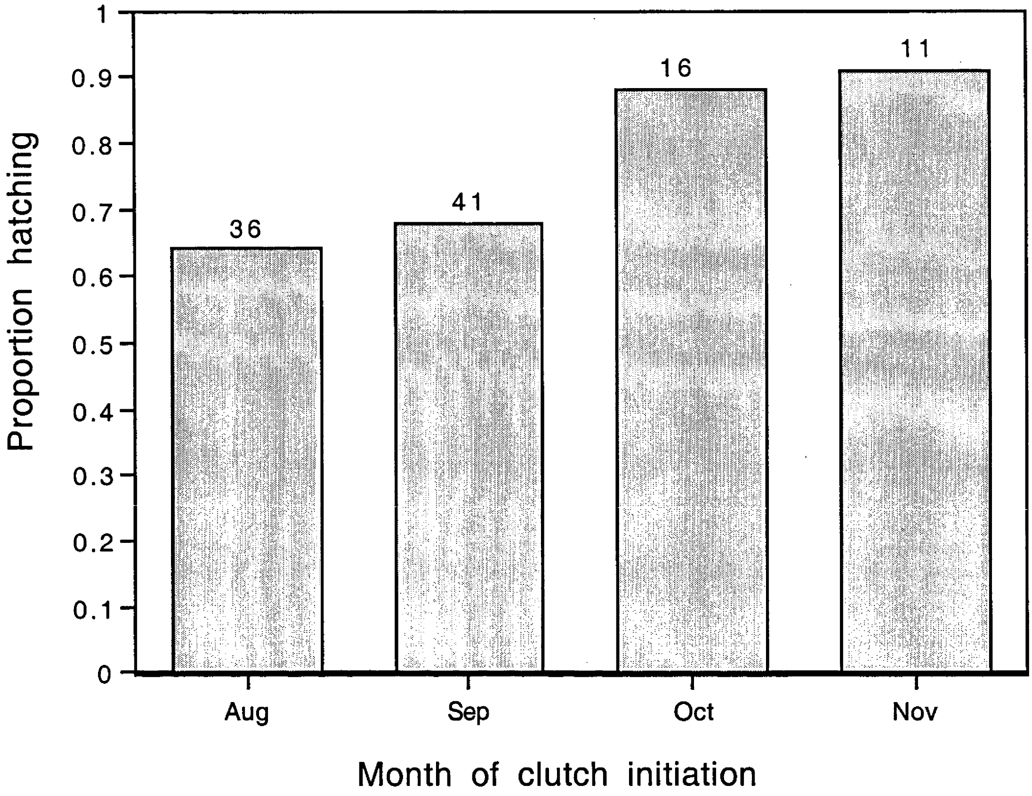

Figure 2.4. Observed proportions of yellow-rumped thornbill clutches hatching according to month of initiation. Samples sizes above bars.

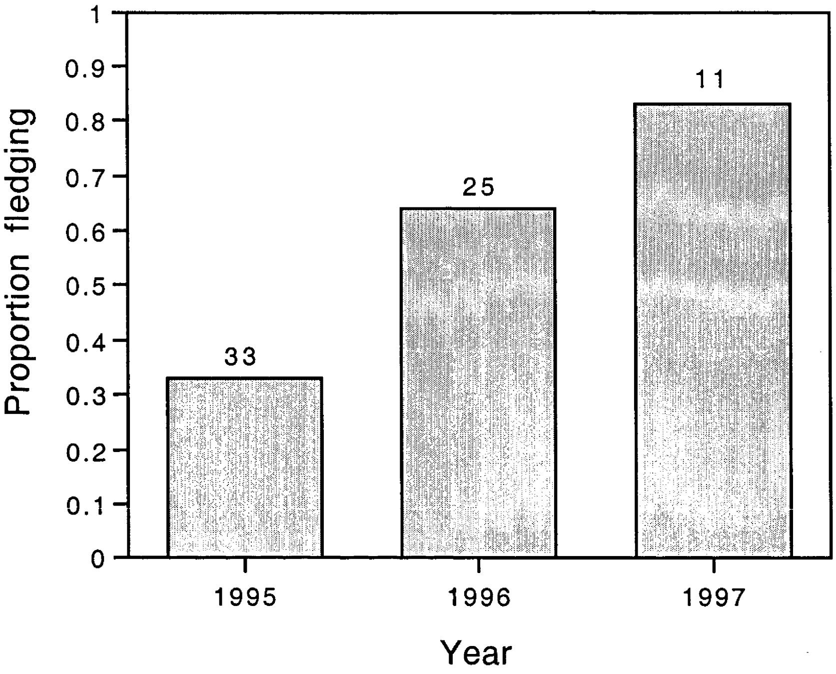

Figure 2.5. Proportion of yellow-rumped thornbill broods fledging by year. Sample sizes are shown above bars.

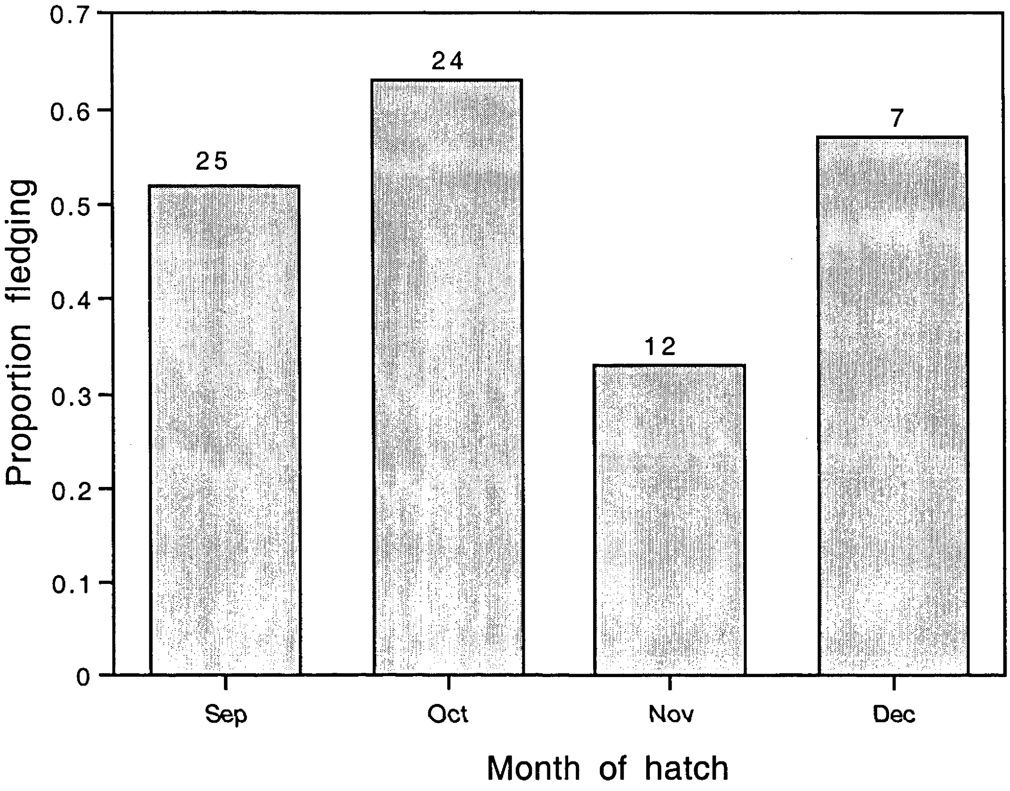

Figure 2.6. The proportion of yellow-rumped thornbill broods fledging by month of hatch, combining data from 3 years. Sample sizes are shown above the bars.

CHAPTER 3

Nest predation in the yellow-rumped thornbill

INTRODUCTION

Predation of eggs and nestlings is commonly the major source of juvenile mortality and the main constraint on reproductive success in birds (Ricklefs 1969; Martin 1992). As such, nest predation is an important issue in the study of avian life history evolution (Skutch 1949; Slagsvold 1984; Skutch 1985; Martin 1992; Martin *et al.* 2000a), behaviour (e.g. Poiani and Pagel 1997; Briskie *et al.* 1999; Haskell 1999; Ghalambor and Martin 2001), ecology (e.g. Martin 1988), and the conservation of declining bird populations (see Ford *et al.* 2001; Chalfoun *et al.* 2002 for recent reviews). The widespread importance of nest predation in avian biology has inspired a substantial body of theoretical and empirical work seeking to understand variation in rates of nest predation. Most of this work has focused on ecological factors, such as habitat fragmentation and edge effects (e.g. Stephens *et al.* 2003; Batary and Baldi 2004), or traits of life-history and breeding biology, such as nesting habits (e.g. Martin and Li 1992; Martin 1995), that might influence rates of nest predation at the landscape or species level. Less attention has been devoted to variation in rates of nest predation within species and populations. For example, variation in rates of nest predation between incubation and nestling phases of the breeding cycle remains poorly described and understood despite its relevance to evolutionary questions, such as the evolution of clutch size (Skutch 1949; Martin 1996; Martin *et al.* 2000a). Variation at this level also has potentially important implications in the interpretation of artificial nest experiments, which, although they provide much of the data on nest predation, provide no information on predation during the nestling phase of the breeding cycle.

Rates of nest predation are expected to increase after hatching for at least two general reasons. An increase in the rate at which parents visit the nest when they are feeding nestlings and audible begging by nestlings are both factors that may increase the detection of nests by predators during the nestling period (Skutch 1949). However, despite empirical support for increased parental visitation rates after hatching (Roper and Goldstein

1997; Martin *et al.* 2000b), and positive effects of both parental visitation and nestling begging calls on risk of nest predation (Redondo and Castro 1992; Haskell 1994; Martin *et al.* 2000a), evidence for a general increase in predation risk after hatching is lacking. Patterns of predation over the course of the nesting cycle have rarely been described quantitatively. However, several studies have found that predation rates on open nesting species do not increase after hatching (western slaty antshrike, *Thamnophilus atrinucha*, Roper and Goldstein (1997); wood thrush, *Hylocichla mustelina*, Farnsworth and Simons (1999); Eastern yellow robin, *Eopsaltria australis*, Zanette and Jenkins (2000), Berry and Lill (2003)). Furthermore, Martin *et al.* (2000b) quantified stage-specific predation rates for ten forest-dwelling North American species and found that predation rates actually decreased after hatching in most species. Decreased rates of nest predation after hatching were also reported for five of seven non-cavity nesting species included in the review of Clark and Wilson (1981). These surprising results may be explained by other variables affecting rates of nest predation in incubation and nestling phases of the breeding cycle.

Martin *et al.* (2000b) also assessed the effect of nest site on risk of predation and found evidence of fine scale temporal variation. Nests that were inherently easier for predators to find, due to characteristics of nest placement, were likely to be preyed upon earlier in the nesting cycle, during incubation, than later, after hatching. At the population level this effect may counteract the influences of parental visitation rates and nestling begging and reduce or reverse the expected increase in predation rate after hatching.

A recent study of the interactions of parents and nestlings in the white-browed scrubwren (*Sericornis frontalis*) found that parents were able to suppress the vocalization behaviour of their nestlings by alarm calling (Platzen and Magrath in press). This largely unexplored parental strategy may reduce the effects of nestling begging on nest predation and therefore negate the expectation that predation should increase after hatching due to audible begging by nestlings.

In light of the work of Martin *et al.* (2000b) and Platzen and Magrath (in press) variation in rates of nest predation between incubation and nestling phases of the breeding cycle, or the lack thereof, might be seen solely as the result of factors acting on the detectability of nests to predators. Increased parental activity at the nest after hatching and audible begging by nestlings may make nests more detectable, and therefore more likely to be preyed upon in the nestling period, while the inherent detectability of nests, due to characteristics of nest placement or concealment, biases risk of predation to the early stages of nesting attempts. However, by focusing on variation in nest detectability, this view neglects other potential influences on stage-specific nest predation such as variation in the behaviour of predators.

In this chapter I describe variation in rates of predation on nests of the yellow-rumped thornbill (*Acanthiza chrysorrhoa*) at different stages of the breeding cycle, over the course of the breeding season and between years. I aim to demonstrate that temporal and stage-specific patterns of predation on yellow-rumped thornbill nests cannot be explained by factors acting on nest detectability alone and indicate a more active role for predators themselves than is normally assumed. The potential practical consequences of fine scale variation in predation rates for the study of nest predation, particularly in a conservation context, are also briefly discussed.

METHODS

Species and study site

The yellow-rumped thornbill, *Acanthiza chrysorrhoa*, is a small insectivorous passerine endemic to Australia. The species is widely distributed and abundant in the temperate regions of the south-east and south-west of continental Australia and in Tasmania (Blakers *et al.* 1984; Christidis and Boles 1994). During the breeding season, which extends from late winter to early summer, both sexes build bulky, domed nests in shrubs and trees at heights ranging from 1 to 20 metres from the ground. Only the female incubates the clutch, but nestlings are fed by both parents and occasionally also by one to three male helpers.

I studied the population of yellow-rumped thornbills on the lower eastern slopes of the Mt Ainslie section of Canberra Nature Park ($35^0$16'S, $149^0$9'E), Australian Capital Territory (ACT), from 1995 to 1997. The study area was approximately 250ha of open eucalyptus woodland, dominated by *E. rossii*, *E. mannifera* and *E. macrorhyncha*, with a sparse shrubby understorey interspersed with cleared grassy areas.

Monitoring nesting attempts

Nests were found by watching building birds, following females during incubation or following birds seen collecting prey to feed nestlings. Nests were visited regularly, generally daily or every second day, to determine the clutch initiation date for those found before laying, the hatching date for those found before hatching, and the date of fledging or failure. Average incubation and nestling periods determined from a sample of nesting attempts were used to back-date from hatching or fledging dates to estimate clutch initiation and hatching dates for those nesting attempts that were found at later stages. Nestlings were briefly removed from the nest for banding, blood sampling and measurement between the ages of 7 and 13 days, where the day of hatching was age 0. The size and stage of feather development of nestlings of known age were used to estimate the ages of broods from nests that were found after hatching. A small number of nests was unreachable due to height, in which cases the timing of the stages of the breeding cycle and the fates of these nests were inferred from the behaviour of the parent birds.

Nesting failure and predation

All nesting attempts were monitored until fledging or failure. When nests that had contained mature nestlings were found empty and undamaged the brood was assumed to have fledged. In almost all such cases fledging was confirmed by the sighting of at least one fledgling. Predation was inferred as the cause of failure when a nest was abandoned after the disappearance of some or all of the eggs or nestlings. In the vast majority of such cases the whole clutch or brood was missing and the nest was substantially damaged.

The fate of nesting attempts and the role of predation in nesting failure was assessed for each year in terms of the proportion of clutches initiated that failed to fledge. Stage-specific failure was assessed as the proportion of clutches initiated that failed to hatch and the proportion of broods that failed to fledge.

Daily predation rates were calculated following the method of Mayfield (1975). Problems of bias in Mayfield estimates arising from error in dating the fledging or failure of nesting attempts (Manolis *et al.* 2000) were minimized in this study by very frequent censusing. Daily predation rate was calculated as the number of predation events on a particular class of nest during a month of the breeding season or over the entire season divided by the number of exposure-days for the same class of nest over the same period. Only predation events that terminated a breeding attempt were included in the calculations. Daily predation rates were calculated for three stages of the nesting cycle: nests with eggs, nests with broods younger than seven days old, and nests with broods seven days old or older. The seven day old threshold in this analysis was intended to separate very young broods, which were more or less silent (pers. obs.), from those old enough to make begging calls audible from a distance. Rates were calculated for each month of the breeding season and for each year.

The population of yellow-rumped thornbills used in this study was under observation for a larger breeding biology project and, in order to increase sample sizes for datasets not directly related to nest predation and breeding success, all accessible nests in 1997 were protected from larger predators by enclosure with wire or plastic mesh. Nest protection was not random with regard to height, and nests left unprotected may not have been representative in terms of their inherent risk of predation. Furthermore, predators may have modified their behaviour in response to the protection of nests resulting in an artificial change in predation risk for those left unprotected. For these reasons, protected nests were excluded from calculations of nesting failure and predation rates and the discussion of annual rates of predation below focuses on differences between 1995 and 1996.

RESULTS

Nest Predators

Nest predators were not identified in this study; however, an artificial nest experiment was conducted in nearby and similar habitat in the ACT by Gardner (1998) in the 1994-1995 nesting season. Gardner (1998) found that birds were responsible for almost all attacks on artificial nests (96%) where the predator could be identified to class and of 15 attacks where the predator was photographed five were committed by pied currawongs (*Strepera graculina*). Pied currawongs have been repeatedly identified as a major predator of the nests of small birds in Eastern Australia (Major *et al.* 1996; Prawiradiliga 1996; Wood 1998; Fulton and Ford 2001). They were common in the Campbell Park study site and were observed taking the contents of yellow-rumped thornbill nests on five occasions. It was very likely that pied currawongs were responsible for much of the predation on yellow-rumped thornbill nests; however, other predators may also have taken eggs and nestlings. Other avian nest predators present in the study site were grey shrike-thrushes (*Colluricincla harmonica*), Australian magpies (*Gymnorhina tibicen*), grey currawongs (*Strepera versicolor*) and ravens (*Corvus spp.*). Reptiles and small mammals may also have contributed to nest predation.

Nest Predation and Breeding Failure

More than half of clutches initiated failed to produce fledglings and predation was overwhelmingly the major cause of breeding failure at both the incubation and nestling stages (Table 3.1). Over the three years of the study nest predation was inferred as the cause of failure of 85% of clutches initiated that failed to produce fledglings (Table 3.1).

Breeding attempts were more likely to fail at the nestling stage than at the incubation stage and, over three years, 46% of nesting attempts which hatched failed to produce fledglings, whereas 32% of clutches initiated failed to hatch (Table 3.1). The daily predation rate for nests with eggs was 1.9% whereas that for nests containing nestlings was 3.1% (Table 3.2). The daily predation rate on nests containing young broods was 1.6%, similar to that for nests with eggs, whereas the daily predation rate on older broods was 4.0%, (Table 3.2).

Nest Predation Over The Breeding Season

The daily risk of nest predation was not constant over the breeding season and was clearly influenced by the contents of the nest (Figure 3.1). The daily predation risk for broods at least seven days old was almost five times greater in November (17%) than in any other month (0% - 3.6%). The November peak in daily predation risk for broods at least seven days old was also more than five times greater then the highest daily predation risk of any month for clutches or broods less than seven days old (0% - 3.3%). The pattern of daily predation risk on older broods over the season, characterised by a peak in November, was similar in all three years.

Nest Predation Over Three Years

There was a decline in daily predation risks over the three years of this study, specifically for old broods (Figure 3.2). The daily risk of predation for clutches and younger broods declined only slightly, however, the daily predation risk for older broods declined substantially from 1995 to 1996 and again between 1996 and 1997. The greatest decline in predation risk occurred from 1995 to 1996 when no nests were protected from predators.

Year to year variation in daily predation rates was reflected in rates of failure of breeding attempts. In 1995, the year with the highest daily predation rates, 79% of clutches initiated failed to produce fledglings (Table 3.1). The overall failure rates for 1996 and 1997 were substantially lower at 56% and 23% respectively (Table 3.1). The impact of predation specifically on nestlings in creating this variation between years was clear. Focusing on 1995 and 1996, the two years where nests were not protected, the decline in daily predation rate was substantial for nests containing older broods and negligible for nests containing clutches or younger broods. The change in the failure rate for older broods was similarly large, from 67% in 1995 to 36% in 1996, and similarly slight for clutches and younger broods, from 38% in 1995 to 31% in 1996 (Table 3.1).

DISCUSSION

Most yellow-rumped thornbill breeding attempts failed and nest predation was overwhelmingly the major cause of failure, accounting for at least 85% of clutches that did not produce fledglings. Overall stage-specific failure rates indicated that predation was more severe after hatching with 68% of clutches initiated hatching but only 54% of broods successfully fledging (Table 3.1). The comparison of daily rates of predation during incubation and nestling stages also reflected an increase in risk of predation after hatching. Brood age also had an important effect on predation rates. Daily predation rates for broods younger than seven days old (1.6%) were similar to those for clutches (1.9%) whereas the daily predation rate for broods older than seven days was twice as high (4%). Daily rates of predation on old broods also varied among years and within the breeding season. Predation on old broods was more severe in 1995 than in later years and was particularly severe in November in all three years.

Variation in predation risk within years

The risk of predation for yellow-rumped thornbill nests varied according to the contents of the nest. For a single day of exposure, nests containing nestlings at least one week old were approximately twice as likely to be predated than nests containing eggs or younger nestlings. Such a substantial increase in daily rates of predation after hatching appears to be unusual. Of twelve open nesting species studied in central and North America by Roper and Goldstein (1997), Farnsworth and Simons (1999) and Martin et al. (2000b) only three were found to suffer increased predation after hatching, and in all three cases the increase was slight (Martin *et al.* 2000b). In Australia, daily rates of nest predation have been quantified for the eastern yellow-robin (*Eopsaltria australis*) in New South Wales, by Zanette and Jenkins (2000), and in Victoria, by Berry and Lill (2003), and both studies found no difference in predation between incubation and nestling stages. In contrast with these results, however, recent studies of three species breeding in the ACT have found substantially increased rates of nest predation after hatching. Daily rates of nest predation more than doubled after hatching in the brown thornbill, *Acanthiza pusilla*, (Green and Cockburn 1999), the speckled warbler, *Chthonicola sagittata*, (Gardner 2002) and the white-browed scrubwren, *Sericornis frontalis*, (R. Magrath pers. comm.) breeding in the ACT. Recent work by Martin *et al.* (2000b) on the effects of nest placement on temporal changes in predation rates suggest that, in the absence of other influences, predation rates at the population level should decrease over the course of the breeding cycle. In this light the large increases in predation rates after hatching in the yellow-rumped thornbill, and three other species breeding in the same region, require explanation.

Two factors that may contribute to an increase in predation risk after hatching are parental activity at the nest and audible begging by nestlings. The general pattern of an increase in provisioning rates with brood age described for many species (e.g. Dunn and Cockburn 1996; Hatchwell and Russell 1996; Hall 1999; Green 2002), including the yellow-rumped thornbill (Chapter 4), suggests that parents, and other adults in the case of cooperative breeders, are likely to visit their nests at a higher frequency when feeding nestlings than during incubation. Comparisons of parental activity at the nest between incubation and nestling phases of the breeding cycle are rare but available information for a small number of species confirms the expected increase in visitation rates after hatching (Roper and Goldstein 1997; Martin *et al.* 2000b). That provisioning trips to the nest by adult birds might aid predators in detecting nests and therefore influence rates of nest predation during the nestling period was first proposed by Alexander Skutch in 1949 but has only recently been confirmed empirically. A comparative and experimental study of ten North American species by Martin *et al.* (2000b) found that, after controlling for the effects of nest site on predation risk, rates of nest predation were positively related to the rate at which parents visited their nests to feed nestlings. Parental activity at the nest during incubation was not quantified in my study; however, it is highly likely that the switch from incubation, performed only by the female, to the nestling stage where both parents, and occasionally helpers, provision the brood entails an increase in the rate of visits to the nest.

As such, provisioning behaviour by parents and helpers may have contributed to the increased predation of yellow-rumped thornbill nests after hatching.

Audible begging by nestlings represents a characteristic of the nestling phase of the breeding cycle that does not apply during incubation and that may enhance the detection of nests by predators. A recent comparative study of 25 North American species found that the structure of nestling begging calls was related to species level rates of nest predation (Briskie *et al.* 1999). Species subject to higher rates of nest predation made quieter begging calls of higher frequency than those subject to lower rates of nest predation. As both of these acoustic features are related to the "locatability" of the source of sound, the species level pattern described by Briskie *et al.* (1999) implies that nest predation is a selective force acting on nestling vocalisations and that begging incurs a predation cost (Briskie *et al.* 1999). At a proximate level, studies of the effects of begging behaviour on nest predation have been hampered by technical and methodological problems (Haskell 2002); however, there is some evidence that begging entails a predation cost. Nestling vocalisations have been shown to attract nest predators in artificial nest experiments using recorded begging calls (Haskell 1994; Leech and Leonard 1997); however, the relevance of these results to natural nests may be compromised by the neglect of parental effects on begging behaviour (e.g. Platzen and Magrath in press). A positive relationship between begging intensity and risk of predation has been demonstrated in natural broods of the magpie, *Pica pica* (Redondo and Castro 1992). Older yellow-rumped thornbill nestlings make begging calls, usually associated with a provisioning visit by an adult, that can be heard meters from the nest (pers. obs.) and as such nestling begging may have contributed to the increase in predation rate after hatching.

Stage-specific rates of nest predation in the yellow-rumped thornbill are consistent with the expected effects of parental activity at the nest and audible begging by nestlings. In the yellow-rumped thornbill, predation rates increase after the first week of the nestling period. This change corresponds with increased provisioning rates (Chapter 4) and is also likely to coincide to some extent with the development of nestlings to the stage where they are capable of loud vocalization. However, parental activity at the nest and audible begging by nestlings do not explain variation in rates of predation on older broods of nestlings over the course of the breeding season.

Parental activity at the nest and nestling begging are expected to influence predation rates in a similar manner. Both factors pertain to the detectability of nests to predators such that nests containing older nestlings are likely to be more detectable, and therefore more vulnerable to predation, than those containing eggs or younger nestlings. A third, generally unacknowledged, factor that may contribute to an increase in predation risk after hatching is the value of the contents of the nest to predators. The energetic value of the contents of a nest presumably increases after hatching as the nestlings enter a phase of rapid growth (O'Connor 1984). If nestlings are more valuable to nest predators than eggs some nest predators may actively "hunt" nests containing nestlings. Parental activity and nestling begging are both potential cues as to the contents of nests and the age of nestlings and may therefore influence predation risk beyond their effects on nest detectability. A nest predator attuned to adult birds carrying food items, or to the begging calls of nestlings, might effectively target nests containing nestlings and contribute to an increase in predation risk after hatching. Patterns of predation on yellow-rumped thornbill nests over the breeding season suggest that predation risk is not simply determined by detectability, but is heavily influenced by the behaviour of nest predators themselves.

If detectability of the nest were the only influence on predation risk the number of predation events on nests of a particular class, those containing older nestlings for example, should be roughly correlated with the exposure of that class of nest to predators. Such a correlation would result in a more or less constant daily rate of predation over the course of the breeding season. This was not the case for broods of yellow-rumped thornbill nestlings. Nests containing broods that were at least one week old were far more likely to be predated in November than any other month. This temporal variation in predation rate contrasts markedly with the pattern for nests containing eggs or younger nestlings. Despite substantial variation in exposure of nests containing eggs or younger nestlings among months of the breeding season the predation rate for these nests was virtually constant. This pattern is what would be expected if the predation rate was effectively determined by the rate at which predators encounter nests – in months where nests with eggs or younger nestlings were more common more of them were predated – and suggests a more or less constant hunting effort by predators. On the other hand the November peak in predation risk for nests containing older nestlings suggests that predators targeted older broods of yellow-rumped thornbill nestlings in November. This possibility is supported by what is known of the diet of one of Eastern Australia's main nest predators, the pied currawong (*Strepera graculina*).

The pied currawong is an omnivore subsisting largely on fruit and arthropods for most of the year but switching to the eggs and especially the nestlings of other birds when feeding their own dependent young in late spring and early summer (Prawiradiliga 1996; Wood 1998). Prawiradiliga (1996) observed 19 pied currawong nests in Canberra for two breeding seasons and estimated that a pair of pied currawongs killed approximately 40 broods of small passerines in order to raise a single brood of their own. The same study found that the frequency of egg remains in the pellets of pied currawong collected over three years peaked from September to October while the frequency of nestling remains in pellets peaked in November when currawongs were feeding their own nestlings (Prawiradiliga 1996). This seasonal change of diet by pied currawongs is consistent with the patterns of predation on yellow-rumped thornbill nests over the breeding season with a peak in predation of nests with eggs when they are most common in September and October and a peak in predation of nests containing nestlings not when they are most common, in October, but when pied currawongs have nestlings of their own to feed in November.

Variation in predation risk between years

There was a marked difference between years in the rates of predation on yellow-rumped thornbill nests. The largest difference was between 1995 and the two subsequent years but due to the manipulation of some nests in 1997 I will focus on the changes between 1995 and 1996. A reduction in nest predation was apparent in the overall failure rates for breeding attempts in the two years with 79% of clutches initiated in 1995 failing to produce fledglings compared with a failure rate of 56% in 1996. An obvious potential influence on annual levels of nest predation is the interaction between the abundance and breeding patterns of nest predators such as pied currawongs and the abundance and breeding patterns of yellow-rumped thornbills and other prey species. Unfortunately the data required to assess these factors were beyond the scope of this study. However, the analysis of the provisioning behaviour of yellow-rumped thornbills presented in Chapter 4 suggests another potential influence on annual levels of predation: variation in parental activity at the nest.

The rate, in terms of nest visits per hour, at which yellow-rumped thornbills provisioned broods of nestlings was assessed for four years from 1995 to 1998 (Chapter 4). A surprising finding to emerge from the these data was that yellow-rumped thornbills visited their nests much more frequently in the 1995 breeding season than in any other. The cause of the elevated feeding rate in 1995 was not clear but may have been influenced by annual variation in rainfall and its effect on invertebrate prey populations, as 1995 was a year of above average rainfall in the ACT following a year of drought. A potential consequence of increased nest visitation rates is increased nest predation (Martin *et al.* 2000b) and the predation rate on older broods of yellow-rumped thornbill nestlings was approximately three times greater in 1995 than in 1996 (Figure 3.2). There was indirect evidence to suggest that predation pressure in general, as influenced by the abundance of predators for example, was not substantially different between these two years. Firstly, the daily predation risk for nests containing eggs or younger nestlings was virtually identical in 1995 and 1996 (Figure 3.2), and secondly, the extent of the November peak in daily predation risk for older broods of nestlings was also similar in both years (1995: 0.21, 1996: 0.25). The cause of the elevated rate of predation on older broods of nestlings in 1995 remains unclear; however, one possibility is that nests containing older nestlings were preyed upon to a greater extent in 1995 because they were made more detectable to predators by unusually high parental activity at the nest.

Implications of variable predation rates

A feature of predation on yellow-rumped thornbill nests is that predation risk increases dramatically after hatching and that this increase appears to be due, at least in part, to the targeted predation of older nestlings by nest predators. The coincidence of the quantitative switch to avian prey by pied currawongs when they are feeding broods of their own (Prawiradiliga 1996; Wood 1998) and the peak in predation risk for yellow-rumped thornbill nestlings strongly suggests that pied currawongs are a major contributor to the increase in predation after hatching. Pied currawongs have also been implicated as a major nest predator of the brown thornbill, the speckled warbler and the white-browed scrubwren breeding in the ACT (Green and Cockburn 1999; Gardner 2002; Maurer *et al.* 2003) and these species also exhibit substantial increases in rates of nest predation after hatching. Daily predation rates for brown thornbill, speckled warbler and white-browed scrubwren nests are 1.2%, 1.3% and 0.9% respectively during incubation and increase to 4%, 5.8% and 4.4% respectively after hatching (Green and Cockburn 1999; Gardner 2002 and R. Magrath pers. comm.).

Variation in predation rates among and within species is of interest in relation to the evolution of various traits of avian breeding biology and life history. However, the factors generally assumed to underlie variable predation rates in this context tend to be heavily focused on the behaviour and strategies of the prey species such as nesting habit, nest site selection, and the roles of parental activity and nestling begging that collectively pertain to the vulnerability of nests to predators. The pattern of predation on yellow-rumped thornbill nests constitutes a strong circumstantial case that the behaviour of predators can also be an important source of fine scale variation. This may have important implications for the interpretation of stage-specific variation in rates of nest predation. For example, differences in predation rates for nests containing eggs and those containing nestlings has been viewed as a potential test of the importance of parental activity on predation risk (e.g. Roper and Goldstein 1997). Although parental activity certainly may be an important factor in such variation, the targeted predation of nestlings by predators may confound the vulnerability effect of parental activity in some cases.

Many bird species native to the woodlands of southern Australia have suffered substantial population declines largely due to habitat loss (Ford *et al.* 2001) and the possibility of increased nest predation due to the fragmentation or degradation of remaining habitat has been a subject of concern for the conservation of residual populations (Ford *et al.* 2001). The pied currawong is of particular interest in this context as it appears to have increased in abundance and expanded its breeding range in some areas as a result of urban development and the proliferation of fruit bearing weeds (Ford 1993; Prawiradiliga 1996).

Two recent studies have attempted to assess the role of the pied currawong in nest predation using artificial nests (Major *et al.* 1996; Fulton and Ford 2001). Although both concluded that pied currawongs were important nest predators, data from artificial nest experiments are unlikely to accurately reflect the impact of pied currawong predation on the success of real nesting attempts. The many limitations of artificial nest experiments are well documented (reviewed by Major and Kendal 1996) and include the potential to overestimate real predation rates (e.g. Zanette 2002; Burke *et al.* 2004). On this basis Bayly and Blumstein (2001) argued that the role of the pied currawong in nest predation, as estimated by artificial nest experiments, may be overstated. Direct observation of the prey of breeding pied currawongs by Prawiradiliga (1996) and Wood (1998), and the increase in rates of predation after hatching for four species subject to pied currawong predation in the ACT, suggests that much of the impact of pied currawong predation occurs after hatching.

Daily rates of nest predation doubled after hatching for yellow-rumped thornbills (this study), more than tripled for brown thornbills (Green and Cockburn 1999), and increased more than fourfold for speckled warblers (Gardner 2002) and white-browed scrubwrens (R. Magrath pers. comm.) breeding in the ACT. The magnitude of these increases suggests that the impact of pied currawong predation on the nesting success of prey species is far more likely to be underestimated by artificial nest experiments, which by their nature neglect predation on nestlings, than overestimated, as suggested by Bayly and Blumstein (2001).

CONCLUSION

Stage specific variation in rates of nest predation has important theoretical implications in the context of avian life-history evolution and behaviour, as well as practical consequences for the study of predation with artificial nests. The factors usually considered to underlie such variation, such as nest placement and the behaviour of parents and nestlings, focus on characteristics of the prey species that might influence the detection of nests by predators. In the yellow-rumped thornbill population studied here daily rates of nest predation increased substantially after the first week of the nestling period as might be expected according to hypotheses related to nest detectability. Annual variation in the rate of predation on broods that were at least one week old was also consistent with the effect of parental visitation on nest detectability and likelihood of predation. However, variation in rates of predation over the course of the breeding season suggests that stage-specific changes in nest detectability were not wholly responsible for stage-specific variation in rates of nest predation. Predation of eggs and young broods showed little variation over the five months of the breeding season whereas predation of older broods of nestlings jumped dramatically in November, the peak month of brood rearing in the pied currawong. These patterns, combined with information on the diet of pied currawongs, are consistent with the targeted predation of older broods of nestlings by pied currawongs when they are feeding their own nestlings.

The capacity of nest predators to specifically target nestlings has implications for the study of nest predation. On one hand, predator behaviour potentially confounds the vulnerability effects of nest placement and parental and nestling behaviour in comparisons of nest predation during incubation and nestling phases of the breeding cycle. On the other hand, however, targeted predation of nestlings highlights the potential importance of factors likely to influence the vulnerability of nests during the nestling phase of the breeding cycle in particular. Variation in the behavioural adaptations of parents and nestlings during this critical period may be an important influence on variation in predation rates within and among species. Finally, an important practical implication of targeted predation of nestlings is that artificial nest experiments, a predominant source of information on nest predation, cannot account for what, in some cases, might be a major determinant of breeding success in prey species and need to be interpreted accordingly.

Table 3.1. The role of nest predation in the failure of yellow-rumped thornbill breeding attempts during incubation and nestling stages. Clutches and broods in nests protected from predators in 1997 were excluded.

	1995	**1996**	**1997**	**Years combined**
Clutches failing to hatch				
n clutches	53	36	13	102
Proportion failed before hatching	0.38	0.31	0.15	0.32
Proportion of failed clutches depredated[1]	0.85	1.0	1.0	0.91
Broods failing to fledge				
n broods	33	25	11	69
Proportion failed before fledging	0.67	0.36	0.09	0.46
Proportion of failed broods depredated[1]	0.77	0.77	1.0	0.78
Overall – clutches failing to fledge				
n clutches	53	36	13	102
Proportion failed before fledging	0.79	0.56	0.23	0.64
Proportion of failed clutches depredated[1]	0.81	0.90	1.0	0.85

[1] This is the proportion of failed breeding attempts that were known to have failed due to predation and is a minimum estimate of the contribution of predation to failure of breeding attempts, as some attempts that failed for reasons unknown may have been preyed upon.

Table 3.2. Predation events and daily predation rates on yellow-rumped thornbill nests at various stages of the nesting cycle, data pooled over three years, 1995 – 1997.

Nest Contents	**n**	**Exposure Days**	**Predation Events**	**Daily Predation Rate**
Clutches	84	1344	26	1.9%
Broods	50	647	20	3.1%
Clutches and young broods[1]	85	1648	31	1.9%
Young broods[1]	50	304	5	1.6%
Old broods[2]	50	343	15	4.0%

[1] Young broods = broods of nestlings younger than 7 days old.

[2] Old broods = broods of nestlings 7 days old or older.

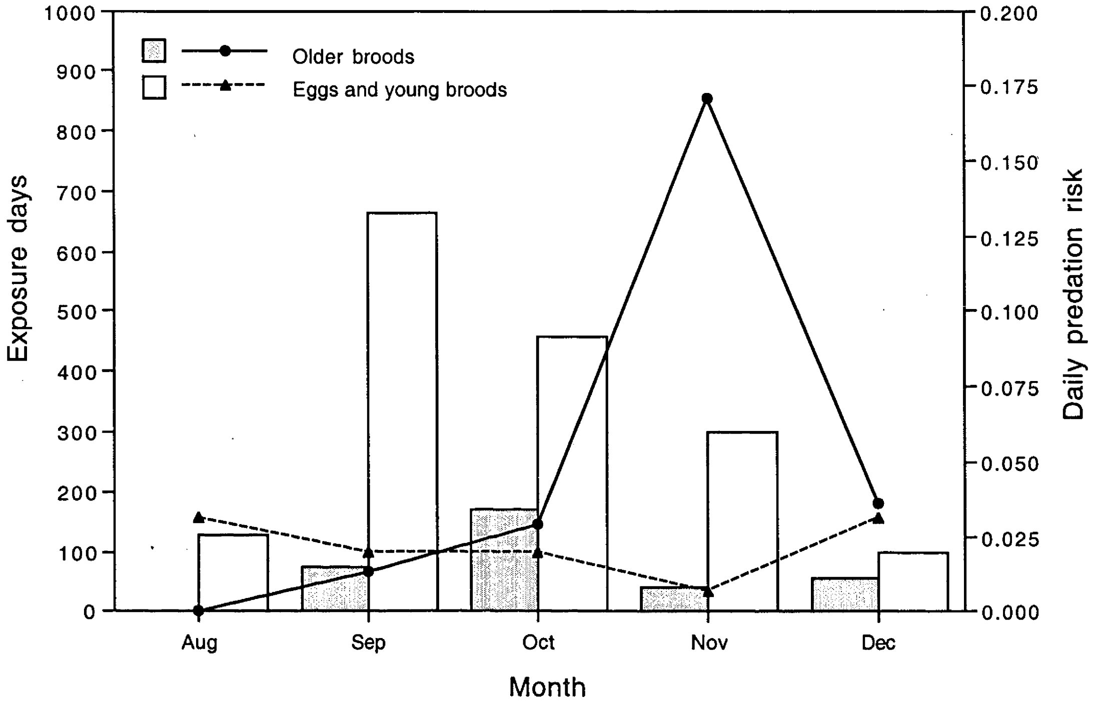

Figure 3.1. Seasonal pattern of daily predation risk (lines) and number of exposure days (bars) for yellow-rumped thornbill clutches and broods less than 7 days old (triangles and white bars), and broods 7 days old or older (circles and grey bars). Data was combined over three years.

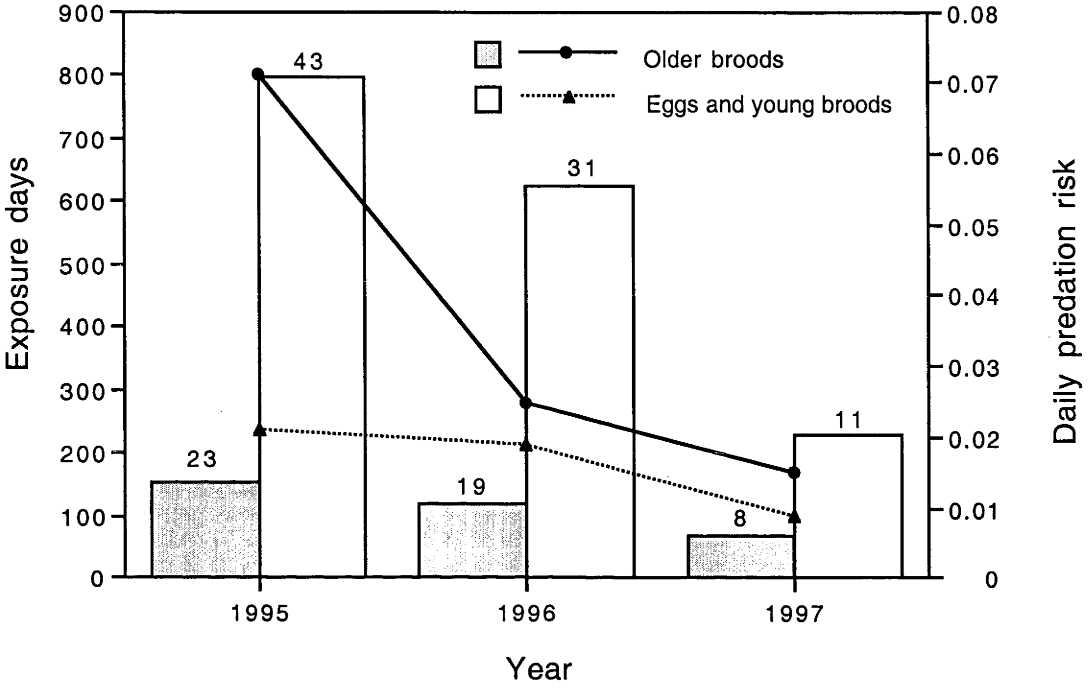

Figure 3.2. Daily predation risk (lines) and number of exposure days (bars) by year for clutches and broods younger than 7 days old (triangles and white bars), and for broods at least 7 days old (circles and grey bars). Sample sizes shown above bars.

CHAPTER 4

Mating systems, social organisation and helping

INTRODUCTION

Avian cooperative breeding systems, in which some individuals apparently forego or delay breeding themselves and assist in the breeding attempts of others, present a fundamental evolutionary problem. By caring for offspring that are not their own, the behaviour of "helpers" appears to flout the most basic tenets of natural selection and has prompted a vast amount of theoretical and empirical work seeking to describe the occurrence and explain the evolution of cooperative breeding. A major finding of this empirical effort has been the diversity of social and genetic systems within which cooperative breeding occurs (Brown 1987; see Cockburn 1998 for recent review). The application of genetic methods has been instrumental in describing and understanding this diversity by allowing the direct assessment of two critical factors, relatedness among members of cooperative groups and the individual reproductive success of those members. Patterns of relatedness and mating system characteristics are major determinants of the benefits of helping and are fundamental in understanding the occurrence of cooperative breeding in any species.

In many cooperatively breeding birds, helpers are related to the breeding pair they assist, commonly as their offspring, and therefore may gain indirect inclusive fitness benefits by contributing to the production of non-descendent kin (Brown 1987; Emlen 1997). In other species the cooperative care of young is directly related to parentage such that "helpers" are actually co-breeders that stand to gain direct fitness benefits by providing care to descendent kin (Davies 1992; Hartley and Davies 1994). These two modes of cooperation are not mutually exclusive and in some species subordinate group members may accrue indirect kin-selected benefits by helping to raise non-descendent kin or pursue opportunities for individual reproduction depending on, among other factors, their relatedness to the dominant breeders in their group and their offspring and their access to mating opportunities within and outside the group (Emlen 1995; Richardson *et al.* 2002).

In most cooperatively breeding birds, groups form when the offspring of a socially dominant breeding pair delay dispersal and assist with the production of later broods (Brown 1987). In such systems the potential benefits of helping, particularly with respect to individual reproductive opportunities, are likely to be constrained by the social and genetic structure of the family. Incest avoidance generally precludes the possibility of helpers gaining parentage within family groups (Emlen 1997), severely restricting the potential for direct reproductive benefits; however, the close kinship between helpers and the young they help raise promotes the potential for indirect inclusive fitness benefits of helping through enhancing the production of non-descendent kin. Even within the constraints imposed by family based cooperative breeding, relatedness among group members and the reproductive options open to subordinates may vary. The replacement of deceased breeders with individuals from outside the group can produce groups where helpers are no longer closely related to both members of the dominant pair. This scenario not only reduces the helper's kinship with subsequent offspring of the dominant pair but also, where the replacement breeder is of the opposite sex, may allow helpers to pursue mating opportunities within the group (Emlen 1995; Magrath and Whittingham 1997). Promiscuous mating systems can also dramatically affect patterns of relatedness and the reproductive opportunities available to subordinate group members. Genetic assessments of parentage in cooperatively breeding birds have revealed high rates of promiscuity even in species that appear to be monogamous. Among the fairy-wrens (*Malurus* spp.), for example, groups are comprised of a socially monogamous breeding pair and their philopatric offspring, but the majority of young are sired by males from outside the social group (Brooker *et al.* 1990; Mulder *et al.* 1994). Extreme promiscuity has multiple effects on the nature of cooperative breeding in this genus. It reduces the incidence of genetically incestuous matings despite the frequent occurrence of socially incestuous pairings in the splendid fairy-wren (M. splendens, Brooker *et al.* 1990) while in the superb fairy-wren (*M. cyaneus*) it has a double effect. On one hand it reduces the relatedness of helpers to the offspring they care for, thus reducing their potential to gain inclusive fitness benefits by helping, but on the other hand it provides the opportunity for helpers to achieve individual reproductive success as extra-group sires (Mulder *et al.* 1994; Dunn and Cockburn 1999).

In cooperative breeding systems the relationship between the genetic mating system and the relatedness between helpers and the recipients of their care is both potentially complex and crucial to understanding the behaviour of helpers. In this chapter I use multi-locus DNA fingerprinting to describe the mating systems and patterns of relatedness within groups in two cooperatively breeding thornbill species, the buff-rumped thornbill (*Acanthiza reguloides*) and the yellow-rumped thornbill (*A. chrysorrhoa*). I also describe the provisioning of nestlings by pairs and groups in both species with the aim of exploring the potential benefits of helping behaviour in each species within the genetic context established by the fingerprinting results. The genus *Acanthiza* is of particular interest in the context of the evolution of avian breeding systems as cooperative breeding is exhibited by most but not all of the 13 species and is the ancestral breeding system in the genus (Nicholls *et al.* 2000). As such it represents a clade where pair-breeding species have evolved from a cooperatively breeding ancestor, an evolutionary scenario that is now thought to have occurred on a much larger scale in the evolution of the modern passerines (Cockburn 2003). However, despite their potential informativeness very little is known of the breeding systems of thornbill species and this study is the first to describe the mating and provisioning systems of cooperatively breeding thornbills.

METHODS

Species and study site

The genus *Acanthiza* comprises 13 small (<10g) insectivorous species, 12 of which are Australian residents, and is one of the three main genera, with *Sericornis* and *Gerygone*, in the old endemic Australian passerine family Pardalotidae (Christidis and Boles 1994). The buff-rumped thornbill inhabits the eucalypt woodlands and open forests of the south-east of continental Australia and co-occurs with the yellow-rumped thornbill over much of this area, although the yellow-rumped thornbill's range also extends to the interior of the continent, southern Western Australia and Tasmania (Blakers *et al.* 1984). The breeding seasons of both species extend from late winter to early summer; females may lay several clutches in one season. The usual clutch size is three, and the clutch is incubated by female members of breeding pairs and groups. Nestlings are fed by both members of the breeding pair and sometimes also by one or more helpers (Immelmann 1960; Ford 1963; Brown and Brown 1982; Bell and Ford 1986).

Both the buff-rumped thornbill and the yellow-rumped thornbill have an unusual two-phase social structure where breeding pairs and groups affiliate in larger groups throughout the non-breeding period of each year (Bell and Ford 1986, Chapter 5). In the yellow-rumped thornbill non-breeding flocks are stable groups of up to 15 individuals usually including the members of more than one breeding pair or group, some male offspring from the preceding breeding season, immigrant birds and occasional transients (Chapter 5). As some males are natally philopatric, adult male flock-mates are often but not always relatives (see Chapter 5 for details). The composition of non-breeding flocks in the buff-rumped thornbill is less well documented. Bell and Ford's study (1986) suggests that flock composition is broadly similar to that of the yellow-rumped thornbill, with some differences in the timing of the dispersal of young.

The role of flock level sociality, if any, in the breeding season social organisation is unclear for both species. Bell and Ford (1986) described discrete breeding units, pairs or groups, in the buff-rumped thornbill that actively defended exclusive breeding territories against members of the same flock although they also observed the cooperative care of fledglings by members of more than one breeding unit. The yellow-rumped thornbill also forms discrete breeding units where pairs and groups occupy an area within the flock home-range surrounding their nest and almost always forage separately from other breeding units. However, the territorial behaviour of this species may not extend to the active exclusion of other flock members from a clearly defined breeding territory (pers obs).

I studied the populations of yellow-rumped thornbills and buff-rumped thornbills on the lower eastern slopes of the Mt Ainslie section of Canberra Nature Park ($35^0$16'S, $149^0$9'E), Australian Capital Territory, from 1995 to 1997. The study area was approximately 250ha of open eucalypt woodland dominated by *E. rossii*, *E. mannifera, E. meliodora* and *E. macrorhyncha* with a sparse shrubby understorey interspersed with cleared grassy areas.

Field Methods

Adult birds were captured in mist nets and were each banded with a numbered aluminium band supplied by the Australian Bird and Bat Banding Scheme and a unique combination of three coloured plastic bands to allow individual identification. A small blood sample, less than 100ul, was collected from the brachial vein as a source of DNA.

Breeding was monitored for three full seasons from 1995 to 1997 and for the first broods raised in the 1998 breeding season. The social organisation of breeding units was assessed by regular observation of breeding pairs and groups throughout the breeding season. The classification of a breeding unit as a group rather than a pair was generally straightforward for both species in that supernumerary individuals were present from the beginning of the breeding season and were seen in the company of the primary pair in almost all observations during the nest building and incubation phases of the breeding cycle. The identification of the breeding pair in cooperative groups was similarly straightforward in that one male (defined as the alpha-male) was clearly more closely associated with the breeding female throughout the breeding season in all cases.

Nests were found at varying stages of the breeding cycle by watching building birds, following females during incubation or following birds seen collecting prey to feed nestlings. Most nests were found before hatching and were visited regularly in order to determine clutch size and the date of hatching. Clutches of both species hatched roughly synchronously, with all eggs hatching within 24 hours, and the date of hatch was regarded as age zero for the purpose of ageing broods. Nestlings were briefly removed from the nest for banding and blood sampling between the ages of seven and 13 days and at this point brood size was confirmed and the ages of broods that were found after hatching were estimated by comparing nestling size and feather development with those of known age. Two yellow-rumped thornbill and eight buff-rumped thornbill broods that were included in provisioning observations were taken by predators before they were handled and the number of chicks in these broods was assumed to be equal to the number of eggs in the clutch as this was true for the majority of broods that were handled for both species.

Provisioning at the nest was observed through binoculars from a distance of approximately 25m from most nests. Where nests were not visible from a distance a hide was used to enable a closer point of observation. Observations were made between 8:00 and 16:00 and lasted 30 or 60 minutes. During each observation the identity of the bird visiting the nest was recorded for every visit to the nest. Nests that were found before hatching were observed every two to four days, from the day after hatching (i.e. brood age of one day) until the brood either fledged or was taken by a predator. As some nests were not found until after hatching, and many broods were taken by predators before fledging, the distribution of provisioning observations with regard to brood age varied among nests.

Due to nest predation the dataset for the genetic analysis of parentage and social organisation and that for the analysis of nestling provisioning were overlapping but not equivalent in terms of the breeding units and breeding attempts they included.

Sexing

Both species of thornbill are sexually monomorphic and although only female buff-rumped thornbills build the nest (Bell and Ford 1986) and only the females of both species incubate (Ford 1963; Bell and Ford 1986) the sex of all banded birds was determined with a simple PCR based sexing technique (see Griffith *et al.* 1999 for method).

Fingerprinting Methods

DNA was isolated from blood following standard procedures (Bruford *et al.* 1992). Ten to 20ug of DNA was digested overnight with HaeIII, and 5ug of digested DNA was then electrophoresed at 3.5V/cm through a 40cm 0.8% agarose gel with 7.5ng of in-lane size standard (λ/EcoR1+HindIII Marker, 3 (MBI Fermentas)). Gels were run in 1 X TBE buffer for 72 hours at 4^0C. The running buffer was replaced after 36 hours. Gels were depurinated in 0.25M HCL for 10 minutes then denatured in 0.4M NaOH, 1.5M NaCl for 30 minutes and neutralised in 0.5M Tris, 1.5M NaCl for 30 minutes. DNA was then transferred to Hybond-Nfp membranes (Amersham) by capillary transfer and fixed by UV crosslinking at the energy level recommended by the membrane manufacturer. Membranes were separately hybridised to 33.15 and 33.6 (Jeffreys *et al.* 1985; Shin *et al.* 1985) minisatellite probes followed by the in-lane size standard labeled with α-[^{32}P]-dCTP at 65^0C for a minimum of 6.5 hours. Unbound probe was removed from membranes by washing at least four times with 6XSSC at 65^0C or by washing three times with (Piper and Rabenold 1992) 2XSSC, 0.1% SDS at 65^0C followed by two washes with room temperature 1XSSC. Sealed membranes were exposed to X-ray film for one to 14 days with or without an intensifying screen at $^-70^0$C.

Scoring Fingerprints

Individuals were arranged on gels in family units. Families varied in size from three to 17 individuals and where families shared a member they were run on the same gel and scored together. The largest group scored as a unit consisted of 21 individuals. Distance between lanes has been shown to bias fingerprint scoring (Piper and Rabenold 1992). In order to minimise this potential scoring error, putative parents in large families were duplicated on gels such that almost all offspring were within four lanes of their putative parents. The largest separation of offspring and putative parent was six lanes. The banding patterns of duplicated samples and in lane size standards were used to account for uneven migration of fragments across large families.

Autoradiographs were scored by eye by marking the position of bands from 2kb to 21kb on acetate overlays. Bands that differed in position by less than 1mm and in intensity by less than two-fold were scored as shared. Bands that may have been obscured by more strongly hybridizing fragments of similar mobility were excluded as were weakly hybridizing bands that may not have been discernible in fainter lanes of an autoradiograph.

The independence of probes was assessed for each species by scoring the three autoradiographs for one fingerprint onto a single acetate overlay. A small degree of overlap was found in fragments detected by the three probes for both species. The largest overlap was for the probes 33.15 and 33.6, where 10% and 9% of all bands scored for buff-rumped thornbills and yellow-rumped thornbills, respectively, were detected by both probes. The smallest overlap was for the probes 33.6 and per where, for both species, 2% of all bands scored were detected by both probes. In light of the capacity for the probes to detect the same fragments the scoring of all novel fragments was checked between autoradiographs to ensure none was scored more than once. Otherwise the scores for the three probes were treated as independent and all statistics presented here are derived from the accumulated scores across probes.

The average number of bands scored per individual was 50.2 ± 10.9 (SD) for buff-rumped thornbills and 48.1 ± 9.2 (SD) for yellow-rumped thornbills. Mutation rates, estimated from nestlings with 0-2 novel fragments (see Burke and Bruford 1987 for method), were used to calculate the probability of a given number of novel fragments in an offspring's fingerprint arising from mutation alone (e.g. Whittingham *et al.* 1997). Fingerprint similarity coefficients, the proportion of bands shared by a pair of individuals, were calculated following Wetton *et al.* (1987) using a computer program written specifically for this purpose.

Parentage

Putative parents were identified for each brood based on repeated observation of the breeding attempt. In no case was more than one female observed to be associated with a nest and hence the classification of putative mothers was based simply on identification of the female that built the nest, incubated the clutch and provisioned the brood. The identification of putative sires was similarly straightforward for breeding pairs where a single male was observed in close association with each nesting female and provisioned her brood. In the case of breeding groups the male most closely associated with each female throughout the breeding attempt, the alpha-male, was classified as the putative sire of her brood, other males in the group were regarded as potential sires and were also included in parentage analyses. Most broods included in the analysis of parentage were from completely sampled families, where all associated adults were captured, but a small number of broods of both species were produced by partially sampled families, where at least one adult associated with the brood was not captured and could not be fingerprinted.

Parentage exclusion and assignment was based on a two step analysis of novel fragments and pairwise similarity coefficients very similar to that of Lifjeld *et al.* (1993) and as follows:

1. Novel fragments, nestlings from complete families only - Putative parents were accepted as the actual parents of any offspring with zero or one novel fragment, (the probability of one novel fragment occurring by mutation was 0.12 for buff-rumped thornbills and 0.14 for yellow-rumped thornbills). The occurrence of three or more novel fragments in an offspring's fingerprint was taken to indicate that one or both of the putative parents were not the genetic parents of that individual, (the probability of three novel fragments arising by mutation was less than 0.001 for both species). Offspring with two novel fragments were considered ambiguous cases based solely on novel fragment analysis, (the probability of two novel fragments arising by mutation was 0.008 for buff-rumped thornbills and 0.01 for yellow-rumped thornbills). For nestlings produced by breeding groups novel fragments were scored for all combinations of the female and each of the males in the group, including the alpha-male.

2. Similarity coefficients - Dyads of known relatedness were used to create reference distributions of similarity coefficients for unrelated birds, second order relatives and first order relatives of both species. Members of breeding pairs provided the samples of unrelated dyads; n = 29 for buff-rumped thornbills and n = 32 for yellow-rumped thornbills. The samples of first order relatives were comprised of all parent-offspring dyads assigned according to the occurrence of novel fragments and all full-sib dyads inferred from assigned parentage; n = 323 for buff-rumped thornbills and n = 434 for yellow-rumped thornbills. Similarly the samples of second order relatives were comprised of all half-sib dyads that could be inferred from assigned parentage, n = 51 for buff-rumped thornbills and n = 142 for yellow-rumped thornbills.

The sample of unrelated dyads was limited by the arrangement of individuals on gels and was necessarily based on assumption, as it was not possible to know with certainty which individuals in the population were "truly" unrelated. Due to the likelihood of a kin-based social structure in both species, particularly among males, and the likelihood that juvenile females disperse to find breeding positions, dyads comprised of breeding pairs were used to create reference distributions for "unrelated" dyads. The use of breeding pairs as a reference for unrelated dyads assumed that the mating of close relatives did not occur. A somewhat circular test of this assumption was possible and the highest coefficients of similarity between the members of a breeding pair were 0.246 and 0.220 for the buff-rumped thornbill and the yellow-rumped thornbill, respectively. These values are considerably lower than the similarity expected of first order and second order relatives according to the rules of inheritance and the nature of multi-locus minisatellite markers (Lynch 1988).

Confidence intervals derived from reference distributions of similarity coefficients were used to classify the relationships of offspring and putative parents in cases where novel fragment data indicated a misassignment of one or both parents and in cases where novel fragment data were ambiguous (i.e. offspring from complete families with two novel fragments), or where novel fragment data were not available (i.e. offspring from partial families).

The similarity index thresholds most commonly used in previous studies to classify the relationship between two individuals are a one-tailed upper confidence limit from a distribution of known unrelated dyads and/or a lower one-tailed confidence limit from a distribution of known first order relatives. However, in species where natal philopatry is known or suspected, the crucial threshold in deciding parental relationships, assuming no incest, is that between second and first order relatives. This is due to the likelihood of putative parents of the philopatric sex having relatives as neighbours during the breeding season or indeed as members of their breeding groups in the case of cooperatively breeding species. Both species in this study show male philopatry; it was therefore assumed that at least some putative sires were likely to have close male relatives at neighbouring nests, or as helpers at their own nests. Hence, judgements of paternity based on fingerprint similarity should encompass the possibility that a misassigned putative sire might be related to a nestling at a second order level as an uncle or grandfather.

Consequently, the upper one-tailed 99% confidence interval for second order relatives and the lower one-tailed 99% confidence interval for first order relatives were used as thresholds for parentage classification. If a putative sire/offspring similarity coefficient fell below both thresholds the putative sire was rejected as the genetic sire of that nestling. If a putative sire/offspring similarity coefficient exceeded both limits the putative sire was accepted as the genetic sire of that nestling. For both species the upper one-tailed confidence limit for second order relatives exceeded the lower one-tailed confidence limit for first order relatives, creating a zone of overlap where a simple classification of relationships was not possible. Putative sire/offspring dyads with similarity coefficients in the zone of overlap were assessed as individual cases; where possible a conservative judgement of the relationship was made (see below).

In breeding groups, reference distributions of fingerprint similarity coefficients were also used to classify the relationships of helpers to the female and the alpha-male, and to the brood to which they contributed care.

Analysis of provisioning rates

The rate of feeding was analysed in two ways for both species. For each observation period at a nest the total number of feeds to the brood delivered per hour and the number of feeds to the brood per hour for each individual in the pair or group were calculated. Two datasets were thus created for each species, one for the analysis of total feeding rate and another for the analysis of the feeding rates of individual adults.

Provisioning data contained many non-independent observations due to the repeated observation of broods and the observation of multiple broods for some breeding pairs and groups. The data were also unbalanced with regard to most explanatory variables. To cope with repeated sampling and an unbalanced design, linear mixed models were used. Random effects (brood and pair/group identity) were estimated using the restricted maximum likelihood procedure in Genstat 5.4.1 for Windows (Genstat 5 Committee 1997), and fixed effects were estimated from weighted least squares. The significance of fixed effects was assessed using the Wald statistic, which approximates to a Chi-squared distribution.

The explanatory variables, year, brood age, brood size and whether the breeding unit was a pair or a cooperative group, were tested for their effects on the total feeding rate to broods. The same variables plus individual status (breeding female, alpha-male or helper male) were tested for their effects on the feeding rates of individual adults. Broods were classified into five age categories: age one to four days, five to eight days, nine to 12 days, 13 to 16 days and older than 16 days. Although broods of three chicks were most common, brood size ranged from one to four in both species. For analysis, broods were classified as small (one or two chicks) or large (three or four chicks). Broods fed by more than three adults were rare and breeding units were therefore classified as pairs or groups. Two yellow-rumped thornbill breeding units were unusual in that their memberships appeared to change while they were provisioning a brood. In the first case two males fed at the nest during the first observation period, but this was followed by a further six observation periods in which only one male provisioned the brood. This breeding unit was classed as a group for the first observation and as a pair thereafter. In the second case, one male fed at the nest for the first two observations and then, after an observation where only the female fed, a different male provisioned the brood in the final four observations. This breeding unit was classed as a pair for every observation since no more than one male fed at the nest in any single observation.

For each analysis an initial model including all main effects and two-way interactions was fitted and a final model was selected by iteratively dropping non-significant interaction terms and then non-significant main effects from the model. Effects that were dropped from models in early iterations were re-entered into final models to confirm their lack of significance. Residual plots were examined for all models to check for deviations from normality. Wald's statistics for significant ($p < 0.05$) effects as well as those for non-significant effects of biological interest are reported below. The influence of statistically significant effects on feeding rates are presented graphically using the predicted mean for each level of the effect calculated with the final model controlling for the other significant effects. Sample sizes in terms of the number of broods, the number of pairs and the number of observations are presented in Table 4.1.

RESULTS

Social organization

In both species the most common breeding unit was the unassisted pair (Table 4.1). Over three breeding seasons 86.5% of all yellow-rumped breeding units were pairs (Chapter 2). Over two breeding seasons 80% of 64 buff-rumped thornbill breeding units were pairs (1996: 71%, n = 31; 1997: 88%, n = 33). Trios were the most common cooperative group with three adults provisioning 13 of 15 buff-rumped thornbill and four of seven yellow-rumped thornbill broods that were fed by groups. The largest number of adults to provision a brood was five (one group of five for each species). All of the 13 buff-rumped thornbill and seven yellow-rumped thornbill helpers that were sexed were male.

Helpers generally, but not always, assisted their social parents and could become helpers in the same breeding season in which they fledged. Only one buff-rumped thornbill helper was banded as a nestling and this individual became a helper at the nest of his parents later in the same breeding season in which he fledged. Six yellow-rumped thornbill helpers were banded as nestlings and four of these helped at nests of their social parents one year after they fledged while the remaining two became helpers in the same breeding season in which they fledged. In both species helpers were not always the offspring of the breeding pair they assisted. One yellow-rumped thornbill helper assisted his social parents for one week before abandoning them to provision a similarly aged brood of a neighbouring breeding pair. One buff-rumped thornbill helper fed two broods belonging to a single female; however, the alpha-male from the first breeding attempt disappeared and was replaced before the second attempt. Another buff-rumped thornbill helper provisioned the broods of two different breeding pairs.

Relatedness in cooperative groups

Nine buff-rumped thornbills included in the genetic analysis were helper males in cooperative groups, with one of these participating in two breeding attempts with different breeding pairs (Figure 4.1). The occurrence of novel fragments indicated that five of these individuals, including one helper that was banded as a nestling, were the offspring of both the female and the alpha-male in their groups. The relatedness of three of the remaining buff-rumped thornbill helpers to the dominant pair in their groups was clearly indicated by their genetic similarity coefficients. Two were close relatives (most likely first order relatives) of the breeding female but unrelated to the alpha-male, while one was closely related to the alpha-male but unrelated to the breeding female. The latter individual helped at the nests of two different breeding pairs. This helper was unrelated to both of the females he was associated with and was a close relative (most likely a first order relative) of the first male he assisted. His relatedness to the second male was ambiguous because their genetic similarity index (0.267) fell within the distributions of both unrelated dyads (upper

99% C.I. = 0.295) and second order relatives (lower 99% C.I. = 0.183). One buff-rumped thornbill male became a helper at the nest of a pair late in the breeding season after attempting to breed independently as a member of a pair. This individual was also clearly unrelated to the female of the pair he assisted but was a first or second order relative of the breeding male. Their coefficient of genetic similarity, 0.4, was within the reference distribution for second order relatives (upper 99% C.I. = 0.47), and at the lower end of the distribution for first order relatives (lower 99% C.I. = 0.41).

The varying levels of relatedness between helper buff-rumped thornbills and the breeding pairs they assisted led to a range of relationships among helpers and the offspring they helped raise. Five helper males helped raise full siblings, three helped raise half siblings and, by virtue of being related at a second order level to one parental bird and unrelated to the other, three helped raise third order relatives.

Nine yellow-rumped thornbill males were involved in breeding attempts as helpers (Figure 4.2). Novel fragment analysis confirmed that all nine were the genetic offspring of both the female and the alpha- male they initially assisted. However, due to the movement of one helper between the breeding attempts of two neighbouring pairs and the replacement of the breeding female in one trio there were two cases where a helper male was not the offspring of one or both of the dominant individuals in his group. Both cases relate to the same helper and occurred in consecutive years. In the first year this helper abandoned the nest of his parents after provisioning his siblings for one week and became a helper at the nest of two birds to which he was probably unrelated. This individual's coefficients of genetic similarity with the breeders at the second nest were both below the lower 99% confidence interval for second order relatives and well within the distribution for unrelated birds. In the second year the same male was "reunited" with his parents as a helper in a trio until his mother disappeared, and presumably died, early in the breeding season, and was replaced by a new female.

Therefore, most helper males in yellow-rumped thornbill cooperative groups helped raise nestlings to which they were related as full siblings, but occasionally they helped unrelated young.

Parentage

The vast majority of offspring from complete families of both species could be classified as the genetic offspring of their putative parents simply on the basis of the occurrence of novel fragments. The fingerprints of 91 buff-rumped thornbill nestlings (94.8%) and 97 yellow-rumped thornbill nestlings (91.5%) had zero or one novel fragments when compared with their putative parents (Figures 4.3 and 4.4, respectively).

The relationships of a small number of nestlings to their putative parents could not be classified without ambiguity on the basis of novel fragments. The fingerprints of two buff-rumped thornbill and four yellow-rumped thornbill nestlings displayed two novel fragments (Figures 4.3 and 4.4). There was no evidence of misassigned maternity for any of these nestlings as all of them had fingerprint similarity coefficients with their putative mothers that were greater than the lower one-tailed 99% CI for first order relatives. Both buff-rumped thornbill nestlings and two of the yellow-rumped thornbill nestlings were also classified as the genetic offspring of their putative sires with similarity coefficients in excess of the upper one-tailed 99% CI for second order relatives. The two remaining yellow-rumped thornbill nestlings had similarity coefficients that fell between the two threshold confidence limits. Both of these nestlings were more likely first order relatives to their putative sire than second order relatives: both similarity coefficients exceeded the upper one-tailed 95% CI for second order relatives and the lower one-tailed 95% CI for first order relatives. On this basis both were classified as legitimate offspring of their putative parents.

Based on fingerprint similarity coefficients almost all nestlings from partially sampled families could also be classified as legitimate with respect to the putative parent that had been sampled. Of 16 buff-rumped thornbill nestlings from partial families that could be compared against their putative mothers, 15 had coefficients exceeding the lower one-tailed 99% confidence interval for first order relatives. Of the ten buff-rumped thornbill nestlings from partial families that could be compared against a putative sire eight could be classified as first order relatives. All yellow-rumped thornbill nestlings from partial families (ten compared against a putative mother and six against a putative sire) also could be classified as legitimate, with respect to the sampled parent, on the basis of genetic similarity.

Extra-pair paternity

A small number of nestlings from completely sampled families were clearly the result of extra-pair paternity. The fingerprints of two buff-rumped thornbill nestlings (both from groups) and four yellow-rumped thornbill nestlings (two from groups, two from unassisted pairs) contained numerous novel fragments when compared against their putative parents and displayed high genetic similarity with their putative mothers but low genetic similarity with their putative sires (Figures 4.3 and 4.4).

In addition, one nestling of each species had an anomalous combination of novel fragments and putative parent/offspring genetic similarities. The fingerprints of one buff-rumped thornbill nestling and one yellow-rumped thornbill nestling contained three and four novel fragments respectively when compared against those of their putative parents, numbers unlikely to result from mutation. However they both also had high genetic similarities with both of their putative parents. The most likely explanation of these data is extra-pair parentage where the extra-pair parent is a close relative of one of the putative parents. The buff-rumped thornbill nestling in question displayed a level of genetic similarity with its putative mother typical of a nestling of legitimate parentage while its genetic similarity with its putative sire was lower than all other such comparisons involving legitimate nestlings (Figure 4.3). The yellow-rumped thornbill nestling in question displayed very similar levels of genetic similarity with both its putative parents (Figure 4.4), however on the basis of female-biased dispersal and male philopatry in this species (Chapter 5) extra-pair paternity involving a male closely related to its putative sire was far more likely than extra-pair maternity (e.g. via egg dumping) involving a close relative of its putative mother. Therefore both nestlings were most likely the result of the cuckoldry of the putative sire by a close relative. The buff-rumped thornbill nestling was one of a brood of four raised by a trio. Treating the helper male as the putative sire of this nestling resulted in a count of five novel fragments indicating that he also was extremely unlikely to be its genetic sire.

In summary, rates of extra-pair paternity, based on nestlings from complete families, were 4.7% of yellow-rumped thornbill nestlings in 12.8% of broods, and 3.1% of buff-rumped thornbill nestlings in 10% of broods (Table 4.2).

Paternity in cooperative groups

The alpha-male in a cooperative group was excluded as the genetic sire of only two nestlings in each species (Table 4.2). The two buff-rumped thornbill nestlings were produced by different breeding groups and in both cases the helper male was also excluded as the sire of the extra-pair offspring on the basis of novel fragment analysis. The two cases of extra-pair paternity in the yellow-rumped thornbill involved the cuckoldry of the same alpha-male in consecutive years. In the first year the breeding group was a trio consisting of a breeding pair and a helper male who was the offspring of both the female and the alpha-male. Both males were excluded as the sire of one nestling in a brood of three on the basis of novel fragment analysis. However, when the alpha-male from the nearest neighbouring group was considered as the putative sire the number of novel fragments in the nestling's fingerprint was zero, indicating that he was the extra-pair sire. In the second year the female member of the trio disappeared early in the breeding season and was replaced by a new female. The nesting attempt that ensued was notable for the sustained aggressive interaction of the two males and resulted in a brood of only one chick which, according to the occurrence of novel fragments, was sired by the helper male.

Provisioning at the nest

Total feeding rates of pairs and groups

Age of the brood was a strong influence on the total number of feeds per hour delivered to the nest by both species (Tables 4.3 and 4.4; Figures 4.5 and 4.6). Both species increased their total feeding rates substantially after the brood reached five days old, but yellow-rumped thornbills showed a decline in feeding rate to broods in the older age classes.

Brood age was the only significant effect in the final model for total feeding rate of buff-rumped thornbills. Brood size, breeding unit, and brood age had no significant effect (Table 4.3).

In contrast to buff-rumped thornbills, total feeding rate in yellow-rumped thornbills was affected by year, brood size, and the type of breeding unit, in addition to brood age (Table 4.3). The year effect was due largely to an unusually high feeding rate in 1995 (Figure 4.7). Yellow-rumped thornbills also provisioned broods of three or four chicks significantly more than smaller broods of one or two chicks (Figure 4.8), and groups also provisioned their broods at a significantly greater rate than pairs (Figure 4.9).

Individual feeding rates

The rate at which individuals of both species provisioned at the nest depended on their status and the age of the brood (Table 4.4). Females of both species fed broods in the youngest age class, one to four days old, at very low rates (Figures 4.10 and 4.11). Females of both species brood young nestlings for approximately the first week after hatching (pers. obs.) and their feeding rates increased to broods in the second two age classes as their time spent brooding declined. In both species females eventually fed at the highest rates (Figures 4.10 and 4.11). Yellow-rumped thornbill alpha-males and helpers showed similar patterns of increasing feeding rates over the first three brood age classes before decreasing their feeding rates to older broods, although helper males consistently fed less often than alpha-males (Figure 4.10). In contrast, buff-rumped thornbill continued to increase their feeding rates as the chicks aged. Also unlike yellow-rumped thornbills, buff-rumped thornbill alpha-males and subordinates fed at similar rates (Figure 4.11).

Individual feeding rates of yellow-rumped thornbills were affected by year with feeding rates substantially higher in 1995 than any other year, and by brood size, with individuals feeding broods of three or four chicks at almost twice the rate at which they fed broods of one or two chicks (Table 4.4). There was no significant effect of breeding unit on the feeding rates of individual yellow-rumped thornbills (Table 4.4) and the lack of a response to breeding unit did not depend on status (pair vs group * status interaction: $\chi^2_2 = 2.7$, $p = 0.3$) indicating that neither females nor alpha-males adjusted their feeding rates when they were assisted by helper males.

Unlike yellow-rumped thornbills, individual buff-rumped thornbills modified their feeding rates with brood age in different ways, depending on their breeding unit (Table 4.4). Individuals in groups did not increase their feeding rates as broods got older, whereas those in pairs did (Figure 4.12). The effect of breeding unit on individual feeding rates did not depend on status (pair vs group*status interaction: $\chi^2_1 = 0.55$, $p = 0.5$), indicating that both females and alpha-males responded to the assistance of helpers by failing to increase their feeding rates as broods got older. In contrast with yellow-rumped thornbills, individual buff-rumped thornbill feeding rates were not affected by year or by the size of the brood (Table 4.4).

DISCUSSION

This study represents the first application of genetic methods to elucidate the breeding systems of cooperative thornbill species. Despite the small sample of cooperative groups, two important breeding system characteristics were confirmed for both yellow- and buff-rumped thornbills. First, helper males are generally close relatives of one or both members of the breeding pair in their group. Second, the mating systems of both species are overwhelmingly monogamous. These two characteristics define the genetic context of cooperative breeding in yellow-rumped and buff-rumped thornbills and have important implications for the potential benefits that helpers might accrue via natal philopatry and helping. This study also includes the first quantitative description of nestling provisioning in both species. When considered in the light of the genetic results these data provide further insight into the means by which helpers in cooperative thornbills might benefit from their helping behaviour.

Social organisation and mating systems

Observations of marked birds by Ford (1963), Bell and Ford (1986) and in this study suggest that cooperative groups are formed by the natal philopatry of male offspring in both the yellow-rumped and the buff-rumped thornbills; the genetic analysis presented here confirms that most helpers of both species are the male offspring of both the female and the alpha-male in their groups. The formation of family based breeding groups through natal philopatry is common among cooperatively breeding birds (Brown 1987; Emlen 1995; Emlen 1997).

Cooperative breeding based on the nuclear family implies certain constraints on the benefits of helping particularly with regard to the reproductive opportunities available to helpers. The within-group reproductive opportunities available to helper/subordinate males are likely to be limited by incest avoidance (Emlen 1997). However, a promiscuous mating system may provide the opportunity to obtain individual reproductive success outside the group. For example, in the highly promiscuous superb fairy-wren, which also forms kin-based breeding groups via the natal philopatry of male offspring, helpers very rarely gain paternity within the group but can be highly successful extra-group sires (Mulder *et al.* 1994; Dunn and Cockburn 1999). In contrast to the promiscuity displayed by *Malurus* species (Brooker *et al.* 1990; Mulder *et al.* 1994) the mating systems of the two thornbills studied here are characterised by the fidelity of females to their social mates. The rates of extra-pair paternity (3.1% of nestlings for buff-rumped thornbills, and 4.7% of nestlings for yellow-rumped thornbills) are lower than the average for socially monogamous birds (11% of nestlings, Griffith *et al.* 2002) and are the lowest rates of extra-pair paternity yet described for members of the Pardalotidae (*Acanthiza pusilla*: 6.2% of nestlings (Green *et al.* 2002); *Sericornis frontalis*: 24% of nestlings (Whittingham *et al.* 1997); *Chthonicola* *sagittata*: 10.7% of nestlings (Gardner *et al.* 2004)). Such low rates of female infidelity suggest that subordinate males of both species are extremely unlikely to derive any benefit from natal philopatry or helping via the achievement of individual reproductive success as extra-group sires.

Changes in group composition can provide within-group reproductive opportunities to helpers in family based cooperative breeders (Emlen 1995; Emlen 1997). Although most helpers in both thornbill species were the sons of the breeding female in their group, there was one instance in each species where this was not the case. The disappearance, presumably due to death, of a female from one yellow-rumped thornbill trio led to the replacement of the helper's mother with an unrelated female. Although the histories of the individuals involved were not known, a similar replacement may also have given rise to the only buff-rumped thornbill trio where the subordinate was unrelated to the female. The single brood produced by each trio represent the only situations where incest avoidance did not preclude helpers from gaining paternity within their groups. The sample size of one brood for each species provides no information regarding the frequency with which helpers gain paternity in such groups. However, the fact that the single nestling produced by the yellow-rumped thornbill trio was sired by the helper rather than the alpha-male indicates that, at least in that species, there are occasional opportunities for helpers to gain direct reproductive benefits from delayed dispersal. Since direct reproductive benefits for helpers are probably uncommon within their group, they are unlikely to be an important factor in the evolution of helping behaviour in yellow-rumped or buff-rumped thornbills.

Although the combination of a family-based social grouping and monogamy severely restrict one of the major routes by which helpers might gain direct benefits from helping, it is likely to have the opposite effect on their potential to accrue indirect benefits. An important corollary of the monogamous mating systems of both species is that males that delay dispersal and help one or both of their social parents raise later broods will almost always be contributing care to close relatives (full or half siblings). The mating systems and social organisation of breeding in yellow-rumped and buff-rumped thornbills therefore provide the potential for helpers to gain inclusive fitness benefits from their contributions to breeding.

Redirected helping

In the populations studied here most cooperative breeding occurred in the social and genetic context of the nuclear family. However there were indications in both species that social organisation at the flock level may also influence helping behaviour. Two buff-rumped thornbill males and one yellow-rumped thornbill male moved from their original breeding units and become helpers at nearby nests. These movements were temporary, occurred during the nestling phase, and lasted only as long as the breeding attempt. With so few observations it is not possible to discern the significance of this behaviour, but similar "redirected helping" occurs in other cooperatively breeding birds including the long-tailed tit (*Aegithalos caudatus*), a species with a similar two-tiered social organisation to the cooperative thornbills. Long-tailed tits form stable kin-based flocks over winter that break down into monogamous pairs at the start of the breeding season (Hatchwell *et al.* 2001a; Russell and Hatchwell 2001). All birds attempt to breed independently but some individuals become helpers at the nests of flock-mates after the failure of their own breeding attempts (Gaston 1973). Helpers are usually male. Their contributions to provisioning nestlings and fledglings are strongly biased toward close kin and are not related to paternity (Russell and Hatchwell 2001; Hatchwell *et al.* 2002).

As in the long-tailed tit, both yellow-rumped and buff-rumped thornbills may have close relatives as neighbours during the breeding season. Both thornbill species form kin-based non-breeding flocks (Chapter 5). When breeding begins the flocks break down into pairs and small groups that nest within the flock home range (Chapter 5, Bell and Ford 1986). The two instances of redirected helping in the buff-rumped thornbill were similar to the behaviour of long-tailed tits in two important respects. First, both males moved immediately after the failure of their own breeding attempt, in one case due to nest predation and in the other due to the disappearance (presumably death) of the breeding female. Second, both males moved to become helpers at the nests of male relatives and neither sired any of the nestlings they provisioned. The single instance of redirected helping in the yellow-rumped thornbill differed. The helper in a trio abandoned the ongoing breeding attempt of his parents after provisioning their nestlings for one week and instead became the second helper provisioning the nestlings, none of which he sired, of a neighbouring but unrelated breeding pair. More observations are required to determine the frequency and significance of redirected helping in thornbills, however my observations suggest that, at least in the buff-rumped thornbill, the behaviour may be a means of making the best of a bad situation by investing in the breeding attempts of related flock mates following breeding failure. The yellow-rumped thornbill observation remains anomalous but may indicate that factors other than relatedness influence helping in that species.

Provisioning at the nest

The response of parents to the provisioning contributions of helpers differed for yellow-rumped and buff-rumped thornbills. Buff-rumped thornbill parents compensated by reducing their own provisioning rates when assisted by helpers, whereas yellow-rumped thornbill parents did not. Thus, buff-rumped thornbill broods raised by pairs and groups were fed at the same overall rate, but yellow-rumped thornbill broods raised by groups received more food than those raised by pairs. This difference is surprising as it suggests that despite similar life-histories and social organizations, buff-rumped and yellow-rumped thornbill helpers may derive different benefits from helping.

Yellow-rumped thornbill

Reviews of provisioning patterns among avian species where helping is kin-based, rather than directly related to parentage, have identified a dichotomy in the occurrence of feeding compensation related to the frequency of nestling starvation (Hatchwell *et al.* 1999; Legge 2000). In species where nestling starvation is an important limitation on reproductive success, the provisioning contributions of helpers tend to be additive and compensation by parents (and other helpers) is rare. Conversely, compensation by parents is common among species where nestling starvation has little or no impact on reproductive success (Hatchwell *et al.* 1999; Legge 2000).

Additive provisioning in yellow-rumped thornbills seems anomalous because nestling starvation was very rare (only one of 156 nestlings that were marked in this study was found dead in its nest), allowing limited potential for helpers to enhance the reproductive success of their groups. Alternatively, additive provisioning may be beneficial if it results in increased fledging weights, and this translates into enhanced post-fledging survival and recruitment. For example, a study of long-tailed tits, which also experience very little nestling starvation, showed that although helpers have no immediate effect on the success of breeding attempts, there is a highly significant relationship between the number of helpers provisioning a brood and the subsequent survival and recruitment of those juveniles into the breeding population (Hatchwell 1999). This effect was due to the improved condition of juveniles caused by the higher provisioning rates of groups, resulting in heavier fledglings (MacColl and Hatchwell 2003; Hatchwell *et al.* 2004).

Although the data required to test this possibility in yellow-rumped thornbills were not collected in this study, there was a weak indication from data available on nestling weight that male nestlings provisioned by groups (n = 15) were heavier than those provisioned by pairs (n = 56) (t-test using residuals from regression of nestling weight on age: t = 1.627, d.f. = 69, p = 0.10). Female nestlings did not show this trend (n = 8 for groups, n = 57 for pairs, t = 0.572, d.f. = 63, p = 0.57). However, male yellow-rumped thornbills are larger than females (4.5% heavier on average, D. Ebert unpublished data) and may have higher nutritional demands and therefore benefit more from increased provisioning. More data on nestling condition, juvenile survival and analyses controlling for possible confounding variables such as parental quality, brood size and territory quality would be required to explore the potential benefits of additive provisioning in yellow-rumped thornbill groups.

Buff-rumped thornbill

Unlike yellow-rumped thornbills, buff-rumped thornbill parents compensated in response to the contributions of helpers. This is the usual pattern among kin-based cooperative breeders, especially when nestling starvation is rare (Hatchwell *et al.* 1999; Legge 2000). However, despite the widespread occurrence of the behaviour, conclusive demonstrations of the benefits of such compensation, or 'load-lightening' have been lacking, partly due to two practical difficulties. First, the effects of load-lightening are commonly confounded by group size and territory quality effects (Cockburn 1998) and, second, the hypothesised benefits of load-lightening may be subtle and difficult to measure in short term studies. Nevertheless, three potential benefits of load-lightening do have empirical support, and each is briefly discussed below with regard to the provisioning behaviour of buff-rumped thornbill groups.

First, in the superb fairy-wren dominant males benefit from load-lightening through an increase in their opportunity to pursue extra-group matings (Green *et al.* 1995). This model does not apply to the buff-rumped thornbill, where strong monogamy precludes a mating system explanation for load-lightening. Second, load-lightening may reduce nest predation, if breeders can invest more in nest defence when helpers take on some of their provisioning duties. For example, in the stripe-backed wren (*Campylorhynchus nuchalis*) both breeders, but especially the male, reduce their provisioning rates when assisted by helpers (Rabenold 1984). Male breeders are far more active in nest defence than either female breeders or helpers, and groups of stripe-backed wrens have much higher reproductive success than pairs largely due to reduced nest predation (Rabenold 1984). In buff-rumped thornbills, nest predation was the major cause of breeding failure, responsible for 72% of all failed broods (n = 32). However, the relative frequencies of predation for pairs versus groups was similar: 35.3% of broods fed by groups (n = 17) and 40.5% of broods fed by pairs (n = 42) failed from predation ($\chi^2 = 0.14$, p = 0.71). Thus nest defence does not appear to be a benefit of load-lightening in the buff-rumped thornbill.

The third, and most widely cited, potential benefit of load-lightening is an increase in the survival or the future fecundity of breeders due to the amelioration of reproductive costs (Brown 1978; Brown 1987; Crick 1992). Where helpers are related to the breeders they gain inclusive fitness benefits. Khan and Walters (2002) reviewed the correlative evidence for this hypothesis and found that load-lightening was associated with increased survival of breeders in a number of species: red-cockaded woodpecker, *Picoides borealis* (Khan and Walters 2002); white-browed sparrow weaver, *Plocepasser mahali* (Lewis 1992); splendid fairy-wren, Malurus splendens (Rowley *et al.* 1989); bicolored wren, *Campylorhynchus griseus* (Austad and Rabenold 1985); pied kingfisher, *Ceryle rudis* (Reyer 1984); and the rifleman, *Acanthisitta chloris* (Sherley 1990). However, other studies have failed to find positive correlations between load-lightening and breeder survival (e.g. western bluebird *Sialia mexicana* (Dickinson *et al.* 1996); stripe-backed wren, *Campylorhynchus nuchalis* (Rabenold 1984); long-tailed tit, *Aegithalos caudatus* (McGowan *et al.* 2003)). Cooperatively breeding species are often very long-lived and small effects on adult survival may be difficult to detect (Hatchwell *et al.* 2004), may occur only under poor conditions, or apply only to certain categories of breeder (Magrath 2001). This study was too brief to assess the potential survival benefits of load-lightening in the buff-rumped thornbill, and cannot be ruled out as a potential benefit of helping in this species.

CONCLUSION

Both the buff-rumped thornbill and the yellow-rumped thornbill usually bred in pairs, but cooperative groups occurred at a low frequency. Both species were genetically monogamous; the vast majority of nestlings were legitimate. These species therefore present a case where the social and mating systems are largely congruous.

Where cooperative groups did exist, helpers were always males, and usually related to at least one member of the breeding pair. Although helpers may often be unable to gain within-group paternity because of incest taboos, they are potentially able to seek extra-pair copulations with neighbouring females. However, even this occurred rarely, indicating that it is probably not because of direct reproductive benefits to helpers that cooperative breeding is maintained. The helpers contributed substantial amounts of care to young. Since they were usually closely related to the breeders and their young, helpers may be gaining inclusive fitness benefits. In this study, helpers had no discernable effect on the success of each breeding attempt, mainly because the incidence of predation was so high (Chapter 3). However, predation may have been artificially inflated due to the proximity of the study site to suburban gardens, which foster large populations of predatory birds like pied currawongs; in less disturbed situations helpers may have positive effects on breeding success.

Buff-rumped thornbill breeders responded to the provisioning of helpers by reducing their own feeding rates. Yellow-rumped thornbills showed no such compensation. This is an intriguing difference between two species that are apparently so similar in terms of general ecology, social and mating systems. The two species may have diets that are critically different so that foraging costs for yellow-rumped thornbills are much less than for buff-rumped thornbills. If so, load-lightening might provide no substantial energetic benefits. Alternatively, the benefits of extra provisioning to nestlings (in terms of post-fledging survival) may be more important for yellow-rumped thornbills compared with buff-rumped thornbills. Whatever the reason, the different patterns of provisioning behaviours imply subtly different benefits of cooperative breeding in the two species.

Table 4.1. Sample sizes for nestling provisioning observations for both species. If more than one brood for a single pair was observed, for example in more than one year, the pair was included only once in this count. Pairs were classified on the basis of the identities of both birds in breeding pairs and the female and alpha-male in breeding groups.

	Yellow-rumped thornbill			**Buff-rumped thornbill**		
	Breeding unit			Breeding unit		
	Pair	Group	Total	Pair	Group	Total
Broods	24	7	30	25	15	40
Breeding pairs	22	4	24	23	13	33
Observations	84	35	119	81	49	130
Hours	61.5	31	92.5	67	37	104

Table 4.2. Extra-pair paternity in broods raised by groups and pairs of yellow-rumped and buff-rumped thornbills. Total numbers of nestlings and broods are shown in parentheses.

	Yellow-rumped thornbills		**Buff-rumped thornbills**	
	Nestlings	Broods	Nestlings	Broods
Complete families				
Pairs	3 (86)	3 (31)	1 (58)	1 (17)
Groups	2 (21)	2 (8)	2 (38)	2 (13)
Total	5 (107)	5 (39)	3 (96)	3 (30)
% extra-pair paternity	4.7%	12.8%	3.1%	10%
Partial families[1]				
Pairs	0 (10)	0 (6)	0 (17)	0 (5)
Groups	0 (7)	0 (2)	1 (6)	1 (2)
Total	0 (17)	0 (8)	0 (23)	0 (7)

[1] Inferred paternity for partially sampled families was based on genetic similarity between offspring and sampled putative sires.

Table 4.3. Factors tested for their effect on the total number of feeds per hour to broods of yellow-rumped thornbills and buff-rumped thornbills. Statistics derived from linear mixed models using the REML procedures of Genstat 5 (Genstat 5 Committee 1997). Only main effects are included as no two-way interactions were significant for either species. Probabilities below 0.05 are in bold type.

	Yellow-rumped thornbill			**Buff-rumped thornbill**		
	Wald statistic	d.f.	p	Wald statistic	d.f.	p
Brood age	13.32	4	**0.010**	42.96	4	**<0.001**
Number of chicks	8.8	1	**0.003**	1.30	1	0.330
Breeding unit	12.89	1	**<0.001**	0.51	1	0.474
Year	13.18	3	**0.004**	0.44	1	0.440

[1] Breeding unit (pair or group).

[2] There were four year classes, from 1995 to 1998, for the yellow-rumped thornbill and two year classes, 1996 and 1997, for the buff-rumped thornbill.

Table 4.4. Factors tested for their effect on the feeding rates of individual adults to broods of yellow-rumped thornbills and buff-rumped thornbills. Statistics derived from linear mixed models using the REML procedures of Genstat 5 (Genstat 5 Committee 1997). Only main effects not involved in significant interactions are shown. Probabilities below 0.05 are in bold type.

	Yellow-rumped thornbill			**Buff-rumped thornbill**		
	Wald statistic	d.f.	p	Wald statistic	d.f.	p
Brood age	-			-		
Status[1]	-			-		
Breeding unit[2]	0.66	1	0.415	-		
Number of chicks	22.96	1	**<0.001**	1.00	1	0.930
Year[3]	9.66	3	**0.022**	0.53	1	0.466
Brood age * status	22.4	8	**0.004**	22.71	8	**0.004**
Brood age * br. unit[2]	-			10.56	4	**0.032**

[1] Status in breeding unit (female, alpha-male or subordinate)

[2] Breeding unit (pair or group).

[3] There were four year classes, from 1995 to 1998, for the yellow-rumped thornbill and two year classes, 1996 and 1997, for the buff-rumped thornbill.

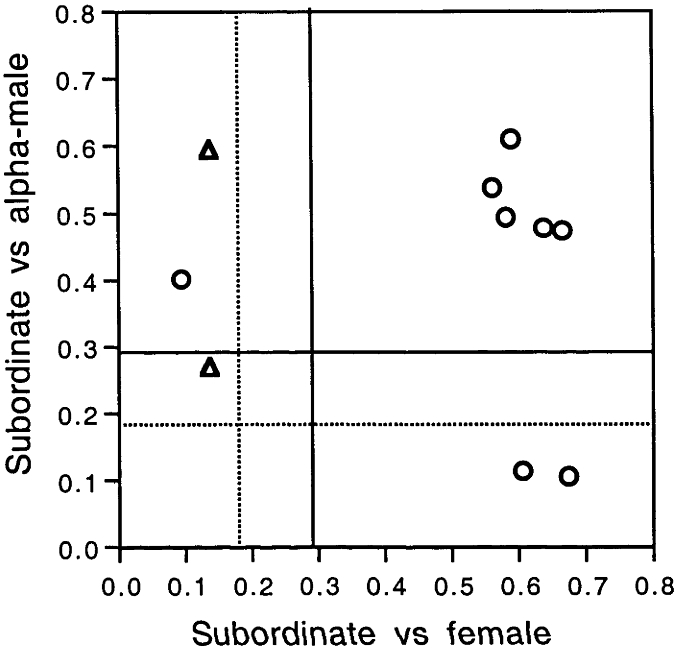

Figure 4.1. The genetic similarity of buff-rumped thornbill subordinate males to the female and alpha-male of their group. The broken line marks the lower 99% confidence interval of the distribution of genetic similarity for second order relatives (0.18); the solid line marks the upper 99% confidence interval of the distribution of genetic similarity for unrelated birds (breeding pairs; 0.29). Triangles represent a single subordinate that was a member of two different breeding groups.

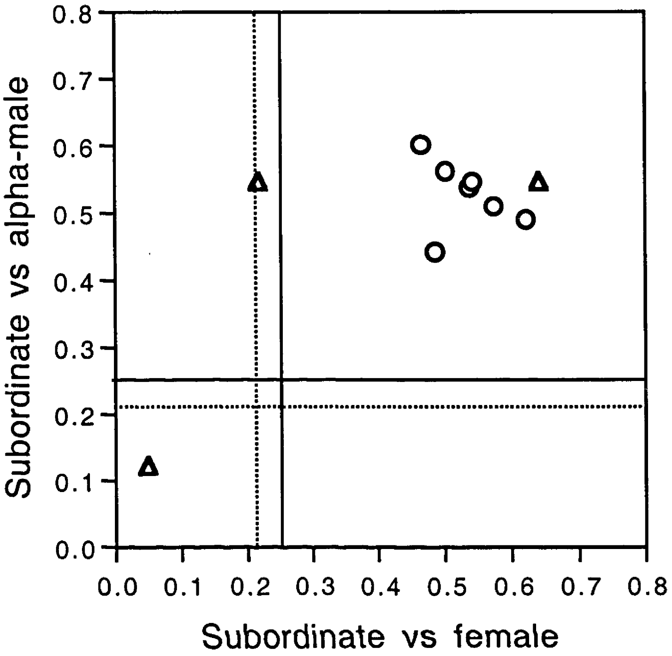

Figure 4.2. The genetic similarity of yellow-rumped thornbill subordinate males to the female and alpha-male of their group. The broken line marks the lower 99% confidence interval of the distribution of genetic similarity for second order relatives (0.21); the solid line marks the upper 99% confidence interval of the distribution of genetic similarity for unrelated birds (breeding pairs; 0.25). Triangles represent a single subordinate that was a member of three different breeding groups.

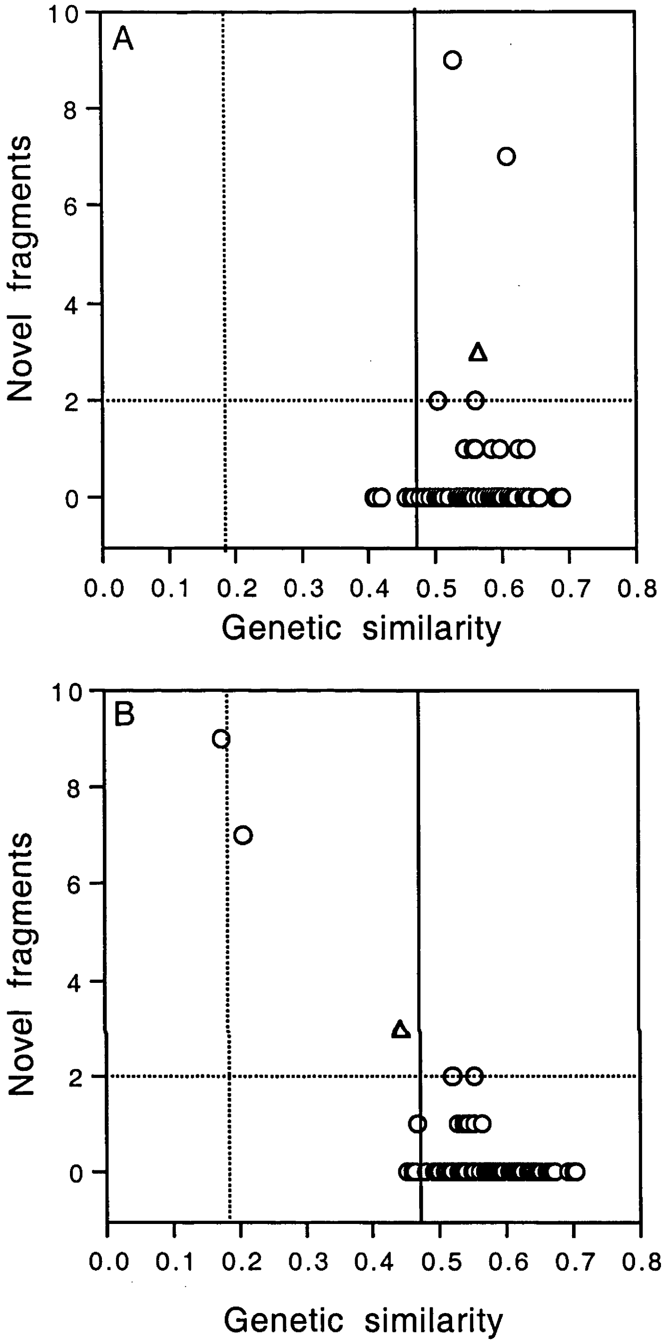

Figure 4.3. The number of novel fragments and the genetic similarity of buff-rumped thornbill nestlings to their putative mothers (A) and fathers (B). Vertical lines depict lower (broken) and upper (solid) 99% confidence intervals for the distribution of genetic similarity of second order relatives (lower, 0.18; upper, 0.47). The lower 99% confidence limit for first order relatives was 0.41 (not shown). The horizontal line shows the threshold of 2 novel fragments, above which one or both of the putative parents were not the genetic parents of an individual. The triangle depicts a nestling of ambiguous parentage.

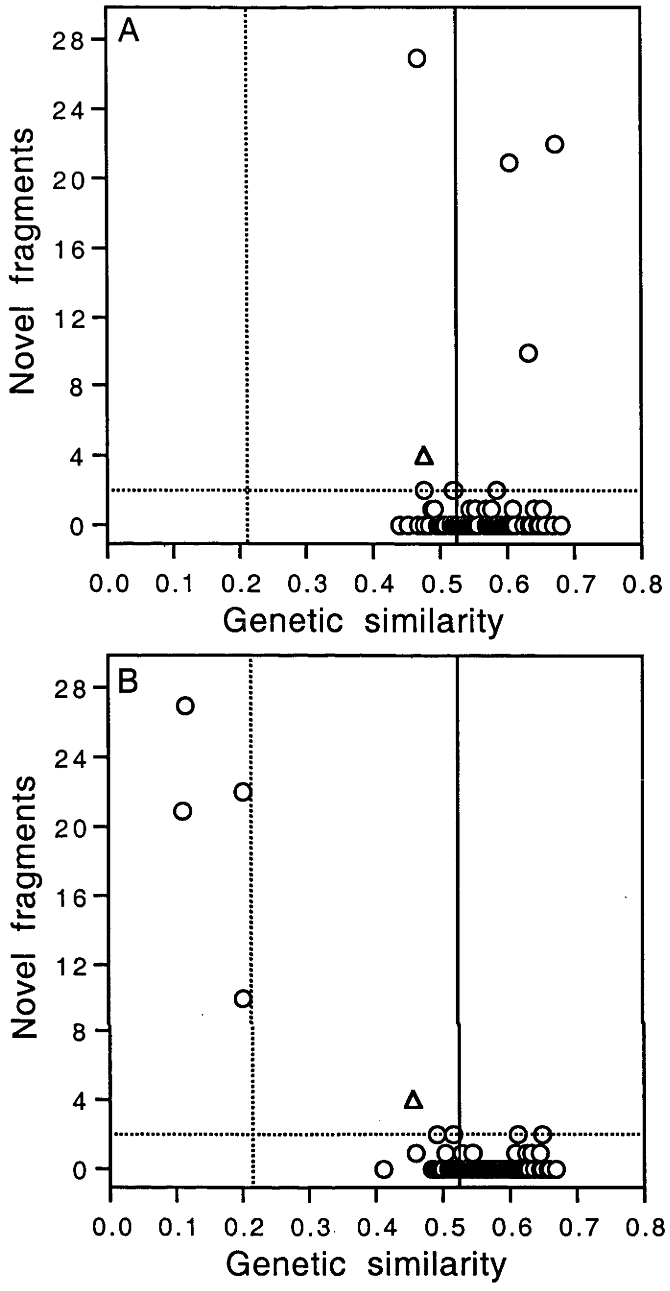

Figure 4.4. The number of novel fragments and the genetic similarity of yellow-rumped thornbill nestlings to their putative mothers (A) and fathers (B). Vertical lines depict lower (broken) and upper (solid) 99% confidence intervals for the distribution of genetic similarity of second order relatives (lower, 0.21; upper, 0.52). The lower 99% confidence limit for first order relatives was 0.41 (not shown). The horizontal line shows the threshold of 2 novel fragments, above which one or both of the putative parents were not the genetic parents of an individual. Triangle depicts a nestling of ambiguous parentage.

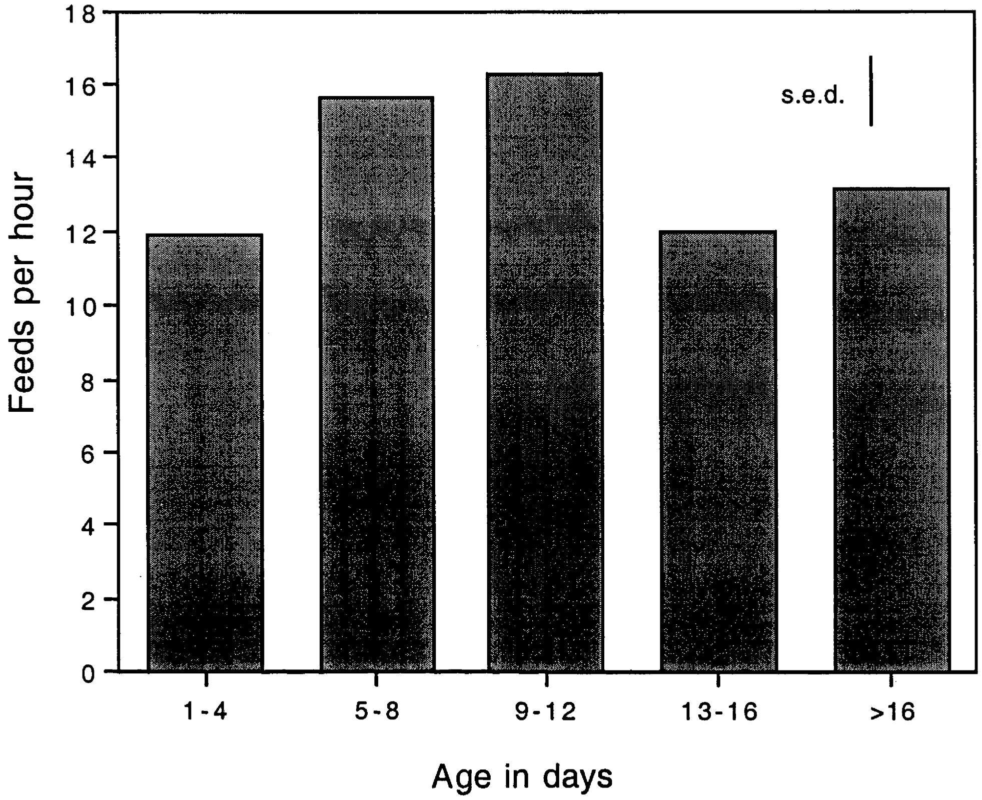

Figure 4.5. REML predictions of the effect of brood age on total feeding rate to broods in yellow-rumped thornbills, controlling for the effects of year, brood size and breeding unit (pair or group). The line shows the average standard error of differences (s.e.d. = 1.86).

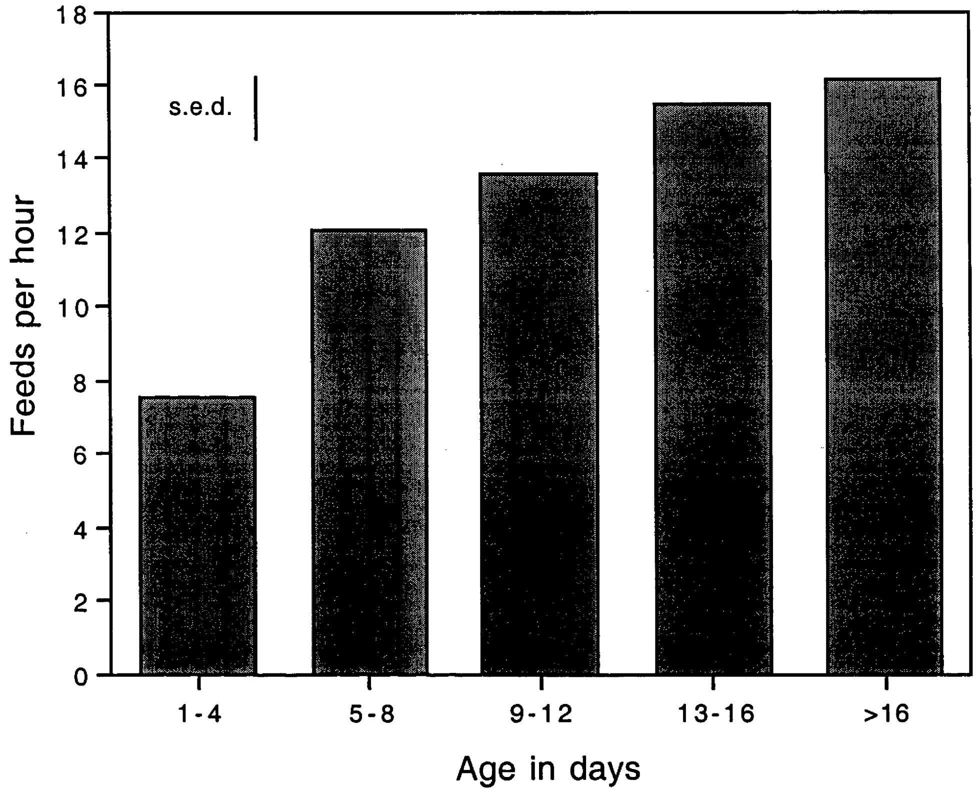

Figure 4.6. REML predictions of the effect of brood age on total feeding rate to broods in buff-rumped thornbills, controlling for the effects of year, brood size and breeding unit (pair or group). The line shows the average standard error of differences (s.e.d. = 1.74).

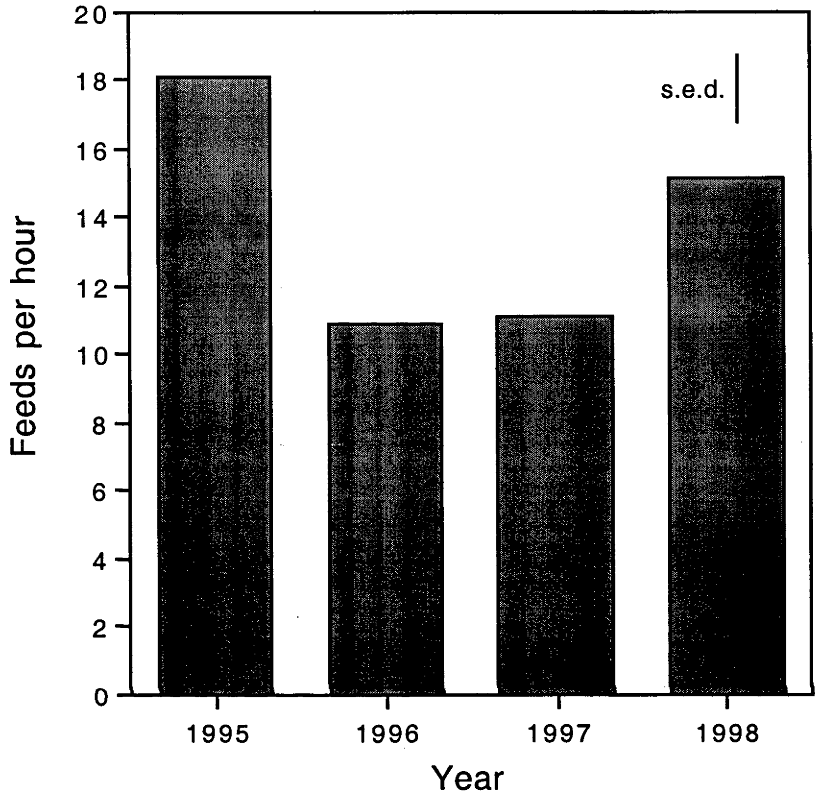

Figure 4.7. REML predictions of the effect of year on total feeding rate to broods in yellow-rumped thornbills, controlling for the effects of brood age, brood size and breeding unit (pair or group). The line shows the average standard error of differences (s.e.d. = 2.33).

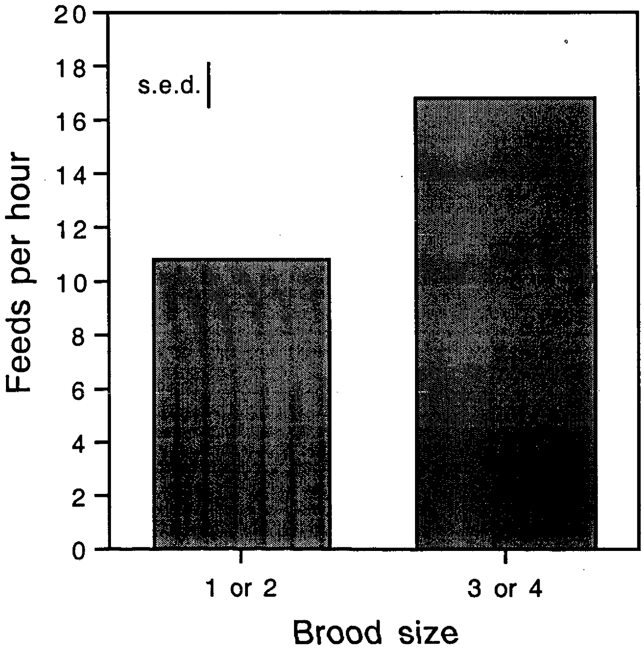

Figure 4.8. REML predictions of the effect of brood size on total feeding rate to broods in yellow-rumped thornbills, controlling for the effects of year and breeding unit (pair or group). The line shows the standard error of differences (s.e.d. = 1.66).

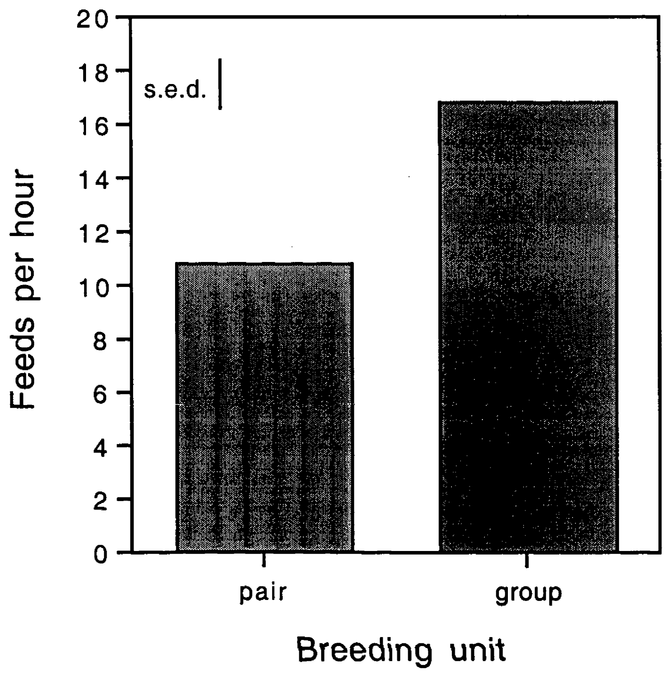

Figure 4.9. REML predictions of the effect of breeding unit (pair or group) on total feeding rate to broods in yellow-rumped thornbills, controlling for the effects of year and brood size. The line shows the standard error of differences (s.e.d. = 1.89).

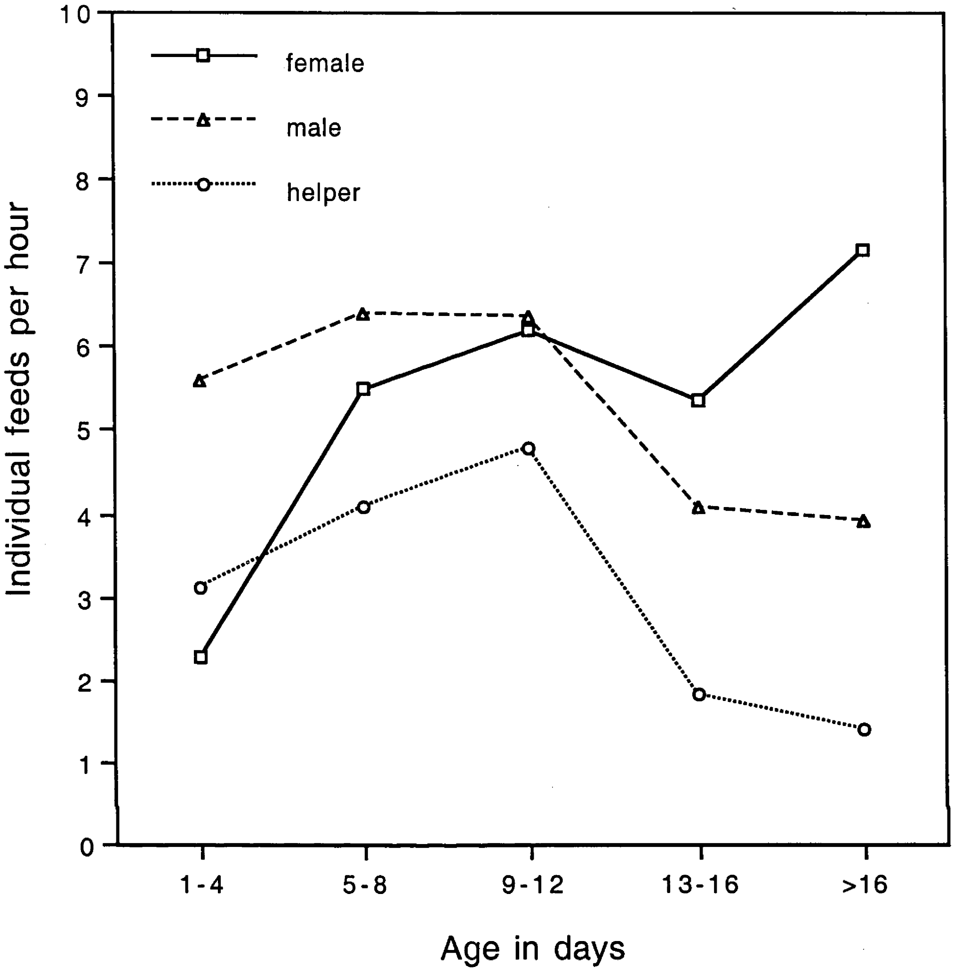

Figure 4.10. Model predictions of the effect of brood age on individual feeding rates of females, males and helpers in the yellow-rumped thornbill, controlling for effects of year and brood size (see text). The average standard errors of differences (s.e.d.) for the age*status (female, male or helper) interaction were 1.20 for the same age level, 1.20 for the same breeding unit level and 1.22 overall.

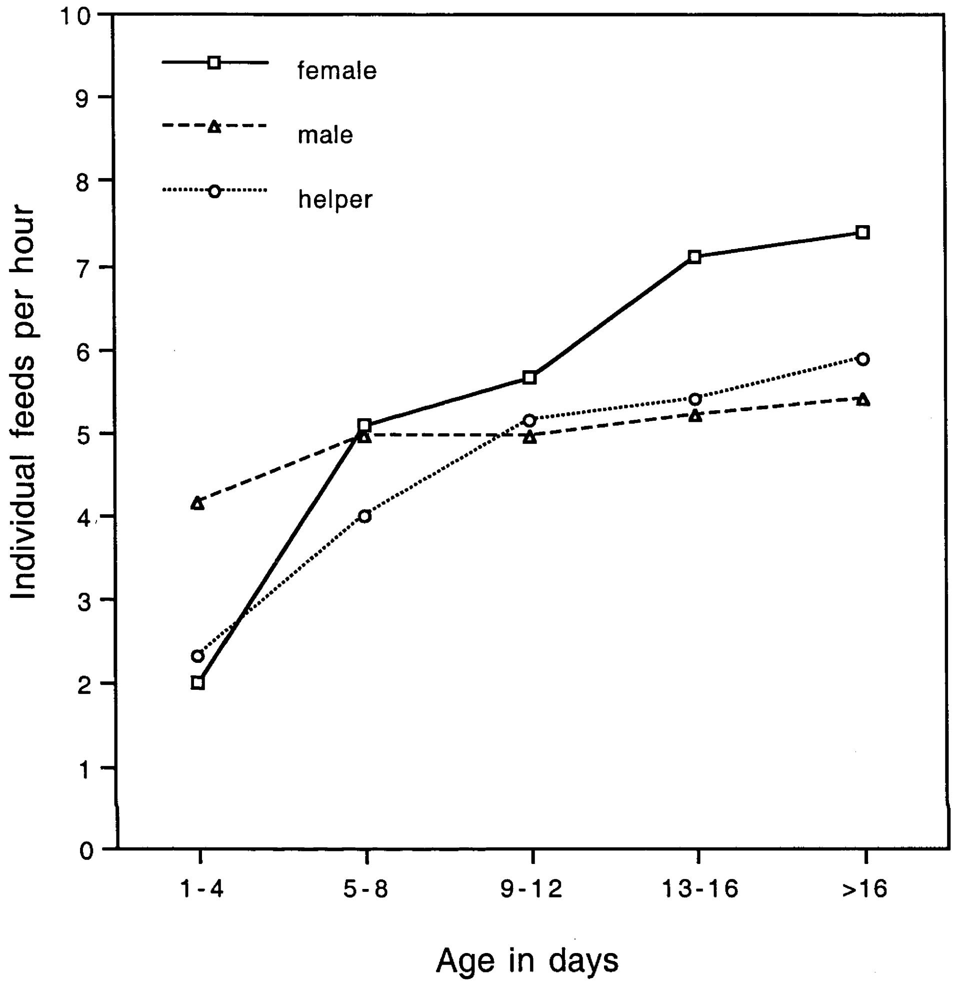

Figure 4.11. Model predictions of the effect of brood age on individual feeding rates of females, males and helpers in the buff-rumped thornbill, controlling for effects of year and brood size (see text). The average standard errors of differences (s.e.d.) for the age*status (female, male or helper) interaction were 1.16 for the same age level, 1.20 for the same breeding unit level and 1.20 overall.

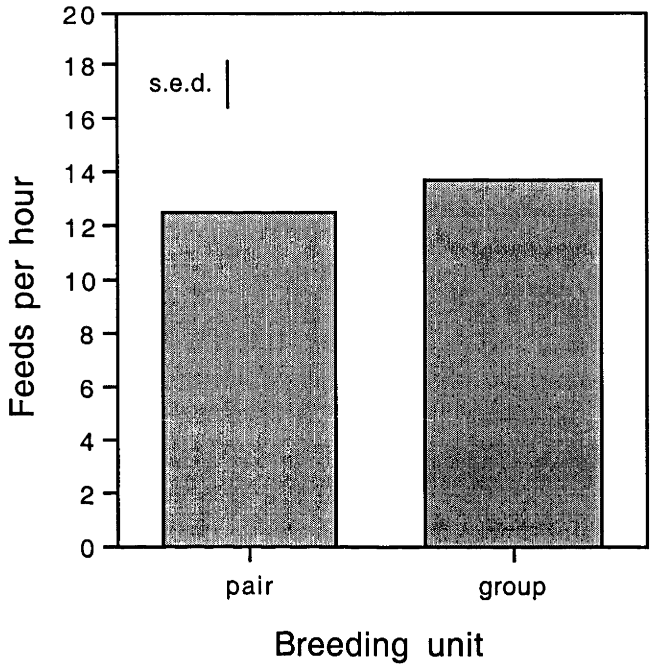

Figure 4.12. REML predictions of the effect of breeding unit (pair or group) on total feeding rate to broods in buff-rumped thornbills, controlling for the effects of year and brood size. The line shows the standard error of differences (s.e.d. = 1.72).

CHAPTER 5

The non-breeding social organization of the yellow-rumped thornbill

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INTRODUCTION

There have been numerous studies of the social organization of birds during the breeding season, including descriptions of parental care systems, mating systems, dispersal behaviour, and so on. This focus has intensified with the advent of molecular techniques for assessing parentage and relatedness, which allow a much finer resolution of the reproductive pay-offs to individuals that adopt different social, parental, mating or dispersal strategies. In contrast, the social organization of birds during the non-breeding season has received far less attention. This is despite the fact that many species are social to some extent over the non-breeding period, and that this period, commonly spanning winter, is often a critical period in terms of survival and is also often the period during which juvenile birds disperse and seek a mate or breeding territory. As such, social behaviour during the non-breeding period may influence important components of life-history, such as survival (Ekman 1990; Smith 1994; Koivula *et al.* 1996; Lahti 1998), dispersal (Smith 1984; Ekman 1989; Ekman *et al.* 2001) and future reproductive success (Ekman 1989; Ekman 1990; Koivula *et al.* 1996; Otter *et al.* 1999). Social organization in the non-breeding period is also closely linked to social aspects of breeding and may have implications for mate choice and pair-bonding (Ekman 1990; Matthysen 1990), and the occurrence of cooperative breeding (Nicholls *et al.* 2000; Hatchwell *et al.* 2001b; Kraaijeveld and Dickinson 2001; Russell and Hatchwell 2001).

The information that is available on non-breeding sociality comes from two main sources: long term studies of cooperative breeders (see Stacey and Koenig 1990 for examples), and the large body of work on northern hemisphere tits and chickadees (Parus spp, reviewed by Ekman 1989; Matthysen 1990). These two sources reflect a basic dichotomy in the form of non-breeding sociality exhibited by sedentary birds, particularly in regard to the relationship between non-breeding and breeding social organizations and underlying patterns of dispersal and kinship. Most cooperatively breeding species live in more or less permanent groups that are usually generated by natal philopatry (Emlen 1995). This commonly results in roughly equivalent social organizations in the breeding and non-breeding seasons, with relatively constant groups that are socially and genetically based on nuclear family units. In contrast, most *Parus* species are strictly pair-breeding, not natally philopatric, and only form groups outside the breeding season (Ekman 1989; Matthysen 1990). Not surprisingly, studies of cooperative breeders and *Parus* species have accentuated different factors in understanding the occurrence and evolution of avian social behaviour. Cooperative breeding studies have emphasised the causes and consequences of kinship in social groups (Emlen 1995; Emlen 1997; Cockburn 1998), with the focus overwhelmingly on the breeding season and reproductive costs and benefits of kin-based sociality. On the other hand, studies of *Parus* social systems have focused on the social and ecological factors at play within groups of non-relatives in a non-reproductive context.

As a consequence of the focus cooperative breeding our understanding of the role of kinship in avian social organization is biased toward its effects on reproduction while our knowledge of social systems characterized by sociality outside the breeding season is biased toward those, exemplified by *Parus* species, where kinship does not play a role. These biases do not reflect the diversity of avian social systems, particularly in regard to the relationship between breeding and non-breeding social organizations and the potential importance of kinship in the non-breeding season. Species such as the Siberian jay (*Perisoreus infaustus*) display aspects of kin-based sociality in the non-breeding season without breeding cooperatively (Ekman *et al.* 1994), demonstrating that kin-based social organization is not necessarily linked to, or explained by, the reproductive consequences of cooperative breeding. On the other hand the long-tailed tit (*Aegithalos caudatus*) displays kin-based cooperative breeding, but forms larger, and not strictly kin-based, social groups in the non-breeding season (Hatchwell *et al.* 2001b; Russell and Hatchwell 2001), suggesting that the kinship that underlies breeding social organization may not have the same importance in non-breeding social organisation. These examples highlight the diversity and complexity of non-breeding social organization and the fact that the role of kinship may be difficult to predict on the basis of breeding season social organisation. In this light, the dearth of studies that specifically address non-breeding social organization in birds with kin-based breeding systems represents a weak point in our understanding of avian social behaviour and evolution.

In this chapter I describe the non-breeding social organization of the yellow-rumped thornbill (*Acanthiza chrysorrhoa*) a member of the old endemic Australian passerine family Pardalotidae. The Pardalotidae is a relatively well known family in that there is some information on non-breeding social organization in a number of species. Two species, the strictly pair breeding brown thornbill (*Acanthiza pusilla*) and the group living, cooperatively breeding white-browed scrub-wren (*Sericornis frontalis*), are known to maintain essentially the same social structure throughout the year (Bell and Ford 1986; Green and Cockburn 1999; Magrath *et al.* 2000), although brown thornbill pairs often tolerate a single male offspring on their territories over the winter (Green and Cockburn 2001). Three other species, however, are known to display dramatically different breeding and non-breeding social organizations. The buff-rumped thornbill (*Acanthiza reguloides*) and the less well known striated thornbill (*Acanthiza lineata*) both breed cooperatively, and form stable and discrete pairs or small breeding groups of up to five individuals which occupy exclusive territories over the breeding season (Bell and Ford 1986, Chapter 4). When breeding concludes, pairs and cooperative groups coalesce and overwinter in stable, coherent flocks of up to 20 individuals (Bell and Ford 1986). In the better known buff-rumped thornbill, where natal philopatry was observed by Bell and Ford (1986) and genetic analysis has confirmed that cooperatively breeding groups are nuclear family units (Chapter 4), non-breeding flocks are likely to be kin-based. The speckled warbler (*Chthonicola sagittata*) also forms non-breeding flocks via the coalescence of previously territorial and discrete breeding pairs (Gardner 2004); however, this species is not natally philopatric and flocks are not comprised of kin (Gardner *et al.* 2003; Gardner 2004). An interesting feature of the Pardalotidae is the diversity of breeding systems displayed by its members despite relative uniformity in life-history traits (Green and Cockburn 1999; Green and Cockburn 2001). On the basis of available information, the family will continue to be of interest in the context of avian social evolution due to the equally diverse nature of non-breeding social organizations possessed by its members.

Virtually nothing is known of the non-breeding social organization of the yellow-rumped thornbill. The only quantitative information available is that of Bell and Ford (1986) who found that yellow-rumped thornbills occurred in groups, with an average size of 3.7 birds, during breeding and flocks, with an average size of 9 birds, when not breeding.

The yellow-rumped thornbill is natally philopatric and has a nuclear family based cooperative breeding system similar to that of the buff-rumped thornbill (Chapter 4) suggesting that non-breeding flocks might also be kin-based in this species. I used a combination of field observation and DNA fingerprinting to assess the social and genetic structure of yellow-rumped thornbill non-breeding flocks and investigate the potential significance of kinship in its non-breeding social organization.

METHODS

Study area and population

Campbell Park is a nature reserve on the eastern outskirts of metropolitan Canberra. Historic disturbance of the area has resulted in an open eucalypt woodland with a sparse understorey interspersed with cleared grassland patches. The area surveyed in this study was approximately 200 hectares in 1996 and 1997 and was expanded in 1998 to include an additional 40 hectares.

Yellow-rumped thornbills were banded with one numbered aluminium band, supplied by the Australian Bird and Bat Banding Scheme, and a unique combination of three coloured plastic bands. Many birds were banded during the breeding seasons from 1995 to 1997 and were therefore identifiable from the beginning of each non-breeding period. These birds included adult breeders and juveniles banded as nestlings. However a number of birds were banded during the non-breeding periods and were therefore not identifiable for the duration of each censusing period.

The individuals involved in non-breeding flocks fell into four categories, banded adults that bred in the preceding breeding season, banded juveniles fledged in the preceding breeding season, birds of unknown history that were banded during the non-breeding period and birds which remained unbanded.

Field methods

Censusing

The population of yellow-rumped thornbills in Campbell Park was censused during three non-breeding periods. In 1996 and 1997 censusing was from early May to late July and in 1998 from late March to early July. Each census consisted of searching a section of the study area until a flock of yellow-rumped thornbills was encountered whereupon individuals were counted, banded birds were identified and the location of the flock was recorded using a grid system and map. By alternating areas searched the entire study population was censused at a rate of approximately once every five days during the censusing periods. Birds were encountered in flocks ranging in size from two to more than twenty-five and due to the constant movement of individuals, and the flocks as a whole, censusing was imperfect in that it was often impossible to be sure that every bird in a flock was counted, or that every banded bird was identified. Error in estimating flock size and composition was minimized by counting both the whole flock and the number of banded birds repeatedly during a single observation. The maximum count was then recorded as the flock size and the observation was continued until at least the majority of banded birds present were identified. A typical record thus consisted of identifications for all, or almost all, banded birds and a count of the number of unbanded birds present. If during a single observation a flock moved more than 100 metres the new location was also recorded.

The area censused was not the same over the three non-breeding periods of the study. The expansion of the study area in 1998 resulted in the inclusion of a large number of yellow-rumped thornbills that were only partially censused in the preceding two years. The partial census data for the birds in this area for 1996 and 1997 are included in the results presented here although the small number of observations mean they are not included in some summary statistics.

Flock Home Ranges

Home range areas were estimated for each flock in each non-breeding period. Areas were calculated as minimum convex polygons including all locations recorded for the flock. One exception to this was flock D in 1998, (see Figure 5.1). An area which would be included in a convex polygon based on the locational fixes for this flock was excluded from the estimate of its home range as it was a paved carpark for a nearby office building and in none of the 34 observations of the flock were the birds seen to visit it.

Defining flocks

In the field - Foraging yellow-rumped thornbills move continuously, gleaning small invertebrates from the groundcover and regularly making small flights of several to tens of metres and returning to the ground to continue foraging. Flocks of birds are therefore highly dynamic in their dispersion and any instantaneous measure of proximity would be both impractical to estimate and of dubious validity as a measure of association. In light of this no formal criterion of proximity was used in the field to define flocks, however on the time scale of a single observation, ranging from 10 to 90 minutes, the association of individual birds in flocks was unambiguous. Individuals were rarely more than 15 metres, and were commonly only several centimetres, from their nearest neighbour while foraging. Birds observed at the more distant end of this range were usually only so "isolated" briefly before they were joined by others or flew to join others themselves. In this way a flock of foraging yellow-rumped thornbills moves continuously, but cohesively, in small steps with individuals making short flights of five to twenty metres to be quickly followed and joined by the rest of the flock. Also illustrative of the association of yellow-rumped thornbills in flocks was the cohesiveness displayed by flocks moving greater distances. During longer observations it was typical for flocks of birds to make one or two flights of 100 metres or more. These events almost always involved the synchronous flight of the entire flock and when this was not the case the remaining individuals typically followed within minutes. The only occurrence of groups of yellow-rumped thornbills splitting up during a single observation involved groups that were very large when first encountered and which presumably comprised more than one flock. Consistent with this assumption was the frequent observation of the opposite event, where a flock was observed to temporarily merge with another. Encounters of one flock with another could last 30 minutes or more and although the original flocks were not discernable within the larger group there was often an increase in what may have been aggressive singing and such encounters invariably ended with the departure of one of the original flocks, usually synchronously, in another long distance movement of 100 metres or more.

Over a single non-breeding period - Consistent groupings of birds were identified from census records for each non-breeding period. In most cases flocks consisted of a majority of banded birds however there were cases where flocks of mostly unbanded individuals were recorded (e.g. flock L, 1997, Figure 5.2). For each flock of mostly banded birds a core membership consisting of individuals repeatedly recorded together over a census period was unambiguous, however there were individuals associated with most flocks that were recorded less frequently and for whom membership of the flock was questionable. A large contributor to the variation in the number of records for individuals was technical. Forty-one percent of the banded birds recorded in flocks over the three years of the study were first captured and banded during the censusing periods. These individuals were not identifiable for the duration of the non-breeding period in which they were first recorded and irrespective of other factors were necessarily recorded in fewer censuses than many birds banded before the start of censusing. The combination of imperfect censusing and variation in capture date prompted the use of a rule of thumb to categorise individuals as flock members, if a bird was recorded three times or more with the same flock over a period spanning at least three weeks it was categorised as a member of that flock. This rule is arbitrary however under its application there were few individuals for whom flock membership was borderline and no individual was assigned membership of more than one flock in a single year. Individuals that were not assigned membership of a flock are discussed further below.

The three sightings over at least three weeks rule was not applied to records where the majorities of two flocks were included in a census record. Such records reflected the occurrence of interactions between flocks, a fact that was generally obvious in the field due to the observation of one of the flocks involved immediately before or after the interaction. Observations of two flocks at the same locations, although in some cases frequent enough to qualify pairs of flocks for reciprocal membership under the three sightings over at least three weeks rule, were also obvious in census records as they were considerably outnumbered by records of the individual flocks involved over the course of a census period.

Between years - The continuity and consistency of non-breeding flocks between years was assessed by comparison of flock membership determined for each non-breeding period from 1996 to 1998. There was no case of flocks in consecutive years having identical memberships however there was clear evidence for continuity of some flocks between years. Firstly, the birds surviving from one year to the next formed the same affiliations in that they were classified as flock-mates in both years. And secondly, in some flocks the birds surviving from one year to the next comprised a majority of the flock membership in the first year and they, and their offspring from the intervening breeding season, also comprised a majority of the flock membership in the second year. In these cases flocks in consecutive years were assumed to represent essentially the same social unit, despite some change of membership, and as such were regarded as the same flock. For some flocks however continuity between years was less clear-cut. The disappearance of banded birds between years combined with the presence of unbanded and recently banded birds resulted in some flocks where the majority of members were of unknown history in terms of their flock memberships, if any, in the preceding year. In these cases any continuity of membership and the absence of changes in membership, that is no surviving member of the flock from the first year changed affiliation between years and no member in the second year was a member of a different flock in the first year, was taken to indicate continuity and the flocks in consecutive years were regarded as the same.

Wherever changes in flock membership were apparent the possibility that a new flock had formed was considered. In cases where members of a flock had been classified as members of different flocks in the preceding year the proportion of the flock which was of known history, and the proportion of these individuals that were members of the same flock in the preceding year were both taken into account. Where most of the members of a flock were of known history and only one individual was a member of a different flock in the preceding year it was assumed that the outstanding bird had joined an old flock. Where there was no clear majority among the birds of known history in terms of their previous flock memberships the flock was assumed to be new.

Sexing

Yellow-rumped thornbills are sexually monomorphic and can only be sexed in the field by observing nesting behaviour as only females incubate. All sampled individuals were sexed using a simple molecular technique (see Griffiths *et al.* 1998 for method).

Fingerprinting Methods

Individuals were arranged on gels in sets based on flock membership in order to maximise the number of within flock pairwise comparisons that could be made. In total 118 individuals were fingerprinted on six gels with 21 to 23 lanes per gel. Although the arrangement of samples on gels prioritised within flock comparisons all gels contained individuals from different flocks to allow between flock comparisons. Two gels contained two flocks and four contained a single flock and a random selection of individuals from other flocks.

DNA was isolated from blood following standard procedures (Bruford *et al.* 1992). Ten to 20ug of DNA was digested overnight with HeaIII and 5ug of digested DNA was then electrophoresed at 3.5V/cm through a 40cm 0.8% agarose gel with 7.5ng of in-lane size standard (λ/EcoR1+HindIII Marker, 3 (MBI Fermentas)). Gels were run in 1 X TBE buffer for 72 hours at 4^0C. The running buffer was replaced after 36 hours. Gels were depurinated in 0.25M HCL for 10 minutes then denatured in 0.4M NaOH, 1.5M NaCl for 30 minutes and neutralised in 0.5M Tris, 1.5M NaCl for 30 minutes. DNA was then transferred to Hybond-Nfp membranes (Amersham) by capillary transfer and fixed by UV crosslinking at the energy level recommended by the membrane manufacturer. Membranes were separately hybridised to 33.15 and 33.6 (Jeffreys *et al.* 1985) and per (Shin *et al.* 1985) minisatellite probes followed by the in-lane size standard labeled with α-[^{32}P]-dCTP at 65^0C for a minimum of 6.5 hours. Unbound probe was removed from membranes by washing at least four times with 6XSSC at 65^0C or by washing three times with 2XSSC, 0.1% SDS at 65^0C followed by two washes with room temperature 1XSSC. Sealed membranes were exposed to X-ray film for 1 to 14 days with or without an intensifying screen at $^-70^0$C.

Scoring fingerprint profiles and pairwise comparisons

The presence or absence of hybridising bands was scored across all lanes of each autoradiograph. Autoradiographs were scored by eye by marking the position of bands from approximately 2 to 21kb on acetate overlays. Bands that differed in position by less than 1mm and in intensity by less than two-fold were scored as shared. Bands that may have been obscured by more strongly hybridizing fragments of similar mobility were excluded as were weakly hybridizing bands that may not have been discernible in fainter lanes of an autoradiograph. The scores for the three probes for each gel were pooled and the average of the total number of bands scored per lane was 32.1 (st. dev. = 7.6). Coefficients of similarity were calculated for every pair of individuals run on each gel following Wetton *et al.* (1987). Such comparisons were limited to pairs of individuals run on the same gel as bands were not scored across multiple autoradiographs; however, by running two different sets of flock-mates together or by including randomly selected individuals from other flocks each gel yielded numerous within-flock and between-flock pairs.

Genetic similarity

In total there were 951 unique pairwise comparisons (dyads) involving birds that were members of flocks in the same year. Dyads were classified firstly according to whether the two birds were from the same or different flocks and secondly by the sex of each bird such that six datasets were created (Table 5.1). Four within-flock versus between-flock comparisons were made, one overall comparison where the sex of the birds was not taken into account and one for each sex specific classification, male-male dyads, male-female dyads and female-female dyads. All datasets contained inter-dependent data in that individuals occurred in multiple dyads. The problems this presents for parametric statistics are well known (Lynch 1988; Lynch 1990; Danforth and Freeman-Gallant 1996) and the sub-sampling procedure of Danforth and Freeman-Gallant (1996) was used to estimate the standard error of the mean coefficient of similarity for each dataset using only independent pairwise comparisons. A computer program, written specifically for this purpose was used to take 2000 samples of *n* similarity coefficients from each dataset. Each sample was randomly selected except for one constraint: that no individual occurred more than once in a single sample. The mean similarity coefficient was calculated for each sample and the standard deviation of these means was used as an estimate of the raw mean's standard error. The number of random samples was arbitrarily set at 2000 for all datasets. The sample size, *n*, was also arbitrary and although it was the same for each within-flock versus between-flock comparison it was adjusted according to the total number of dyads in each dataset and the extent of interdependence among them. Where the variance of the sampled means was equal a standard Student's t-test with 2(n-1) degrees of freedom was used to assess any difference in the within-flock and between-flock mean coefficients of similarity. Where variances were unequal a modified t-test with n-1 degrees of freedom was used (Sokal and Rohlf 1995).

Relatedness

The power of minisatellite similarity coefficients to resolve levels of relatedness is limited by characteristics of the markers themselves, the potential for scoring error and bias and the interdependent nature of the pairwise datasets usually produced (Lynch 1988). The usual approach to classification of relatedness is to use distributions of similarity coefficients for dyads of known, or assumed, relatedness to set thresholds for the classification of dyads of unknown relatedness. The use of empirically derived reference distributions ameliorates the potential effects of scoring error or bias and incorporates the effect of background bandsharing, (the degree of minisatellite similarity not due to relatedness), in the determination of classification thresholds (Lynch 1990; Danforth and Freeman-Gallant 1996). However, the fundamental difficulty described by Lynch (1990); the overlap of distributions of similarity coefficients for adjacent and even non-adjacent levels of relatedness, remains. A two-step approach acknowledging these limitations was adopted here. First, a reference distribution created from dyads assumed to be unrelated, or at least not closely related, was used to set a "related" versus "unrelated" classification threshold. Second, the resolution of this threshold, in terms of the levels of relatedness likely to be defined by it, was assessed directly by comparison with a reference distribution for known first order relatives and indirectly by extrapolating theoretical distributions for lower order levels of relatedness. A sub-sampling procedure similar to that of Negro and Torres (Negro and Torres 1999) was used to estimate means and standard deviations for both empirically derived reference distributions in order to limit the potential for bias caused by the repetition of individuals within the datasets. In this procedure unique sub-samples of independent dyads, where no individual occurred more than once in a single sample and no sample was comprised of the same selection of dyads, were extracted and the averages of the sample means and standard deviations were used to describe normal distributions. The number of samples and sample size were determined by the number of dyads in each dataset and the extent of interdependence among them. All sub-sampling and calculation was done using a computer program written specifically for this purpose.

Incestuous matings are extremely unlikely in the yellow-rumped thornbill (Chapter 4) and 35 dyads, including 39 individuals, that were comprised of birds that formed breeding pairs were used to create a reference distribution for dyads that were not closely related. Seventy-five unique samples of 17 independent breeding pair dyads gave an overall mean similarity coefficient of 0.107 and an overall standard deviation of 0.055. Assuming normality, the value that would exclude one percent of the upper tail of a distribution with this mean and standard deviation was 0.234 (0.107 + 2.33*0.055) and any dyad with a similarity coefficient larger than 0.234 was classified as "related".

A previous genetic study of parentage in the same study population (Chapter 4) allowed the classification of 30 dyads, including 29 individuals, as first order relatives, either parent-offspring or sibling relationships. These dyads were used to create a reference distribution for first order relatives by taking 32 samples of 12 independent dyads and calculating the average of the 32 means and standard deviations. The normal distribution characterised by a mean of 0.504 and a standard deviation of 0.054 was effectively non-overlapping with that estimated for unrelated dyads (the value excluding 1% from the lower tail was 0.377), suggesting that dyads related at a first order level were extremely unlikely to be classified as "unrelated" using the 0.234 threshold and indeed none of the 30 dyads known to be first order relatives were misclassified.

"Simulated" distributions of similarity coefficients were created for second and third order relatives using means predicted with the equation $\theta + r(1-\theta)$ (Lynch 1991) where θ, the mean similarity coefficient for non-relatives, was 0.107 and r, the coefficient of relatedness, was 0.25 and 0.125 for second and third order relatives respectively. On the assumption of equal variances the standard deviation of the empirically derived distribution for first order relatives was used to describe normal distributions around the predicted means. The 0.234 threshold for classifying a dyad as "related" was clearly not capable of resolving third-order relatives from non-relatives as the predicted mean similarity coefficient for third order relatives was 0.219 which was less than the threshold value. However, the predicted mean similarity coefficient for second order relatives was 0.33 and less than 4% of a normal distribution with this mean and a standard deviation of 0.054 would fall below the threshold value of 0.234. On this basis it was assumed that most second order relatives in this dataset would be classified as "related" using the 0.234 threshold.

In summary, although the use of threshold similarity coefficient to classify relatedness is arbitrary and assumes a degree of error almost all dyads related at a first order level (parent-offspring and siblings) and most related at a second order (grandparent, uncle/aunt and half-sib relationships) level were likely to be classified as "related" here. Similarly almost all dyads that were unrelated, in that they were at least as distantly related as breeding pairs, were likely to be classified as "unrelated". However dyads related at a third order level (e.g. cousins), or lower, were at least as likely to be classified as "unrelated" as "related" and in view of this dyads with a similarity coefficient less than 0.234 are referred to below as "unrelated" while those with higher similarty coefficients are referred to as "close relatives".

RESULTS

Flock size and home range area

Flock size ranged from 2 to 14 with an overall mean of 8 individuals per flock (Table 5.2). The number of banded birds recorded in censuses over the three non-breeding periods was 117. Nine of these were not assigned membership of a flock in any year while 59, 34 and 15 individuals were classified as flock members in one, two and three years respectively.

Flock home ranges varied substantially in area and in the extent of overlap between them (Figure 5.1). The smallest home range was 7.8ha for a flock of 10 birds in 1997 while the largest was 48.3ha for a flock of 11 birds in 1998. All but one of the well characterised home ranges, (excluding the southern most flock in 1996 and 1997), overlapped to some extent with one or two other home ranges. For those flocks with overlapping home ranges the minimum overlap with a single neighbouring flock was 2% of home range area and the maximum was 67%. Taking overlaps with more than one neighbouring flock into account the minimum shared area of a single flock's home range was 11% and the maximum was 77%.

Annual consistency

Within a single non-breeding period flocks were highly consistent in that the same individuals were repeatedly observed together and most individuals were recorded in the majority of census records for the flock to which they were assigned membership under the three sightings in at least three weeks rule (Figure 5.2).

Flock members

Nine individuals that were assigned membership of a flock were seen with other flocks. Eight of these were recorded only once or twice with another flock however one individual was seen several times with two different flocks, (without meeting the three sightings over three weeks requirement for membership), before being regularly and exclusively sighted with a third flock. This bird was a female of unknown history as she was first captured immediately before the censusing period in question. She subsequently bred with a male member of the third flock. The most likely explanation of her behaviour is that she was a juvenile in the process of dispersing when first recorded and that she briefly associated with the first two flocks before settling with the third.

Individuals not assigned flock membership

Eleven banded individuals that were observed during one or more non-breeding periods were not assigned membership of a flock under the three records in over three weeks rule of thumb. There are five possible explanations for birds not classified as members of a flock. First, they may have been members of the flock they were recorded with but were not so classified due to insufficient or imperfect censusing. Second, they might have been members of another flock that was not recorded at all. Third, they may have been solitary individuals that were recorded on the irregular occasion when they interacted with a recognised flock. Fourth, they may have been individuals with no strong flock affiliation that associated temporarily with more than one flock. And fifth, they may have died or dispersed out of the study population after being recorded in one or a few census records. Although imperfect censusing cannot be dismissed as a factor, death or dispersal is the most likely fate of nine of the eleven birds that were recorded in insufficient census records to be classified as flock members. Seven of these individuals were seen once or twice during a single non-breeding period and then never again in non-breeding or breeding observations. One was seen three times within one week with the same flock and then never again. And the last was a juvenile fledged in the preceding breeding season that was seen three times, spanning less than three weeks, in a non-natal flock and then never again.

In contrast to the nine individuals that most likely died or dispersed there were two birds not assigned membership of a flock that were known to be alive for the duration of the non-breeding period in which they were recorded. One of these was most likely not classified as a flock member in the 1996 non-breeding period due to insufficient censussing as it was recorded twice in 1996 with the flock it was classified as a member of in 1997 (see interannual continuity below). Notably the flock in question occupied the southern extremity of the 1996/1997 study area and was not censused as effectively as the rest of the population in those years. The second individual was classified as member of a flock in 1996 then was seen only twice in 1997 with a different flock before being classified as a member of that flock in 1998. It was unlikely that this individual was not classified as a flock member in 1997 simply because of insufficient censusing as the flock it was recorded with was censused 8 times over more than two months. It may have been a rare case of a bird that was unaffiliated over the course of a non-breeding period although it was never sighted alone or with another flock 1997. More likely this bird moved out of the study area in 1997 to associate with an uncensused flock and then returned to join a recognised flock in 1998.

Interannual consistency and continuity

Continuity of flocks between years was high and the affiliations of individuals generally did not change between years. There were nine cases where the majority of a flock in one year was banded and a majority of these birds survived to be present in non-breeding flocks in the following year. In eight of these cases the surviving individuals not only formed the same affiliations among themselves but also they and their offspring from the intervening breeding season comprised the majority of the memberships of their respective flocks in the second year. Thus it was typical for the members of a flock that survived between years to form a core of continuous flock membership in consecutive years. In this way the persistence of four flocks through the three years of the study (flocks A, B, C and D Figure 5.2) and one additional flock for two years (flock I Figure 5.2) was apparent despite some change of membership from year to year due to the loss of some individuals and the addition of others. Further evidence of consistency in the formation of flocks in consecutive years was the fact that most birds surviving between years were members of the same flock in both years. Over the three years of the study there were 49 occasions, involving 32 birds, where an individual was assigned membership of a flock in two consecutive non-breeding periods. On 39 occasions, 80%, the individual was a member of the same flock in both years. There were 17 individuals that were flock members in all three years of the study and 13 of these, 76%, were members of the same flock in all three years.

In contrast to the flocks with relatively stable memberships between years there were several cases where changes in membership were substantial enough to suggest that a new flock had emerged from the combination of birds from two flocks in the preceding year. The clearest example of this was flock I in 1997 (Figure 5.2) which was comprised of five banded birds and two unbanded birds. Four of the banded birds were known from the previous year and comprised two pairs of birds from two different 1996 flocks. Nine of the eleven members of the two original flocks were banded, four were presumed dead in 1997, while one was known to be alive but was not classified as a member of any 1997 flock. Given that most of the birds involved over the two years were banded, the affiliations of the four birds known to be flock members in both years were probably an accurate reflection of the merging of the remnants of two 1996 flocks into a new flock in 1997. Two slightly less clear-cut cases of changing flock memberships involved the flocks J in 1997 and M in 1998 (Figure 5.2). In both cases there were indications that the flocks represented new social units, that is that their memberships were substantially different from any flock in the previous year or included birds from more than one flock of the previous year, however the presence of birds of unknown history meant it was not possible to accurately describe the change of membership between years.

Flock composition

Breeding units and flock membership

Members of breeding pairs were always members of the same flock. Over the three years of the study there were16 cases where both members of a breeding pair were members of non-breeding flocks following a breeding season and in all 16 cases both were members of the same flock. There were 28 cases where both members of a breeding pair were members of flocks in a non-breeding period and again in all cases both were members of the same flock.

Flocks almost always included representatives of more than one breeding unit. The two smallest flocks were flock H, in 1996, which consisted of three birds and flock K, in 1997, which consisted of two birds (Figure 5.2). The two birds that comprised flock K were known to be a breeding pair in the preceding breeding season and it is possible that the three birds in flock H, one female and two males, also comprised a single breeding unit from the preceding season however it is very likely that flocks based on individual breeding pairs were rare. In 1996 three of the five flocks that contained birds known to have bred in the preceding breeding season contained members of more than one breeding pair. In 1997 and 1998, with improved knowledge of the breeding histories of the birds involved, twelve of the thirteen flocks that contained birds known to have bred in the preceding season contained members of more than one pair. The largest number of breeding pairs represented in a single flock was four. Flock G in 1996 contained four members that bred in four separate breeding pairs in the preceding season and flock C in 1997 contained six such individuals. Due to the presence of unbanded individuals in breeding pairs and the disappearance, most likely due to death, of breeders before the census periods there were few known occurrences of all members of multiple breeding pairs being members of a single flock. In two years, 1997 and 1998, flock A contained four individuals that comprised the same two breeding pairs in the preceding seasons and in 1997 flock C similarly contained four members that comprised two breeding pairs in the preceding season.

Juvenile birds

Only male juveniles became members of their natal flocks. Over the three years 20 male birds that were members of non-breeding flocks were of known parentage and geographical origin as they were banded as nestlings in the breeding seasons preceding census periods. Eighteen of these birds were members of their natal flocks, that is flocks that contained one or both of their parents. In addition to the two males that dispersed to join non-natal flocks, one female bird, fledged in the 1995 breeding season and then not recorded in 1996 or 1997, was subsequently discovered to be a member of a non-natal flock in 1998 when the study area was expanded. The fact that only one of 21 individuals fledged during this study and subsequently recorded in flock censuses was female is consistent with a strong sex bias in dispersal (Chapter 2).

A detailed example of flock composition

The membership of flock A (Figure 5.2) was especially well characterised over three years as almost all birds involved were banded and as such it was illustrative of the general characteristics of yellow-rumped thornbill flocks. flock A consisted of four birds in 1996, eight birds in 1997 and 11 birds in 1998 and apart from one individual in 1996 and another in 1997 all birds involved were banded. In 1996 the flock initially consisted of two banded males and one unbanded bird, which were joined by a fourth individual, a banded female which had been observed with two other flocks in the preceding weeks and appeared to be in the process of dispersing. These four birds formed two breeding units in the 1996/1997 breeding season and remained in the same flock in the 1997 non-breeding period. The four additional members of the flock in 1997 comprised two male offspring of one of the 1996/1997 breeding pairs and two other birds, one a banded female of unknown history and the other unbanded. Neither of these birds could have been juveniles natal to the flock as all offspring of the two breeding pairs from the 1996/1997 season were banded. The original two breeding pairs reformed in the 1997/1998 breeding season and one of the yearling males became a helper at the nest of his parents. The other natal yearling and both of the other new flock members were not involved in the 1997/1998 breeding season and must have died or dispersed (or continued to disperse) before breeding began. The 1998 flock of 11 birds were all banded and included the two breeding units, one pair and one trio, from the preceding season and four of their juvenile male offspring as well as two birds, one male and one female, of unknown history although known not to be natal juveniles. The male bird of unknown history was clearly in the process of dispersal in that he was known to be non-natal, was recorded with the flock only four times over approximately five weeks before disappearing and was recorded once with another flock during this period. The female bird of unknown history was also very likely a juvenile disperser although in her case she remained with the flock for the duration of the 1998 non-breeding period before taking up a breeding position within the flock. This female replaced one of the original breeding females from the flock after she disappeared immediately before the 1998/1999 breeding season. One of the juvenile males also disappeared during the 1998 non-breeding period while the other three remained and participated in the following breeding season. Two of them became helpers at the nest of the trio from the preceding season, making a breeding group of five, and the other formed a trio with his father and the new breeding female.

Flock A illustrated several characteristics that appear to apply generally to yellow-rumped thornbill flocks. First, the flock included two breeding units in all three years and although there were two cases where it was probably not the case, Flock K and Flock H (Figure 5.2), flocks comprised of multiple breeding units were typical. Second, flock membership was stable between years in that no surviving member left the flock. Again, there were exceptions but the overwhelming weight of evidence was for a stable core of flock membership continuing from year to year. Third, expansion of the membership of the flock occurred mostly through the natal philopatry of male juveniles. Excluding the breeding female captured immediately after the 1996 census period, six of the nine new flock members added in 1997 and 1998 were male offspring of the two breeding pairs in the flock. Fourth, there were two permanent dispersal events into flock A, both were female birds and both assumed a breeding position in the breeding season following their arrival.

DNA fingerprinting results

Genetic similarity

On average yellow-rumped thornbills were more genetically similar to individuals from the same flock than to individuals from different flocks (Table 5.1). Sex-specific comparisons revealed that this was largely due to relatively high genetic similarity between male birds from the same flock. On average male-male dyads comprised of birds from the same flock were significantly more genetically similar than dyads comprised of birds from different flocks (Figure 5.3, Table 5.1). Male-male dyads comprised of birds from the same flock were also more variable in their genetic similarity than those comprised of birds from different flocks (Figure 5.3, Table 5.1). The patterns of genetic similarity between male-female dyads were qualitatively similar to those for male-male dyads and the genetic similarity of birds from the same flock was both higher on average and more variable than for birds from different flocks, although the difference between the mean genetic similarity for within-flock and between-flock dyads was weaker and was not statistically significant at $\alpha = 0.05$ (Figure 5.3, Table 5.1). In contrast, female birds were on average no more genetically similar to other females from the same flock than they were to females from different flocks and nor were they more variable in their genetic similarity (Figure 5.3, Table 5.1).

Relatedness

The comparison of sex-specific patterns of relatedness highlights three features of kinship in yellow-rumped thornbill flocks (Figure 5.4, Table 5.3). First, females from the same flock were rarely close genetic relatives. The few female-female dyads that did exceed the threshold value of genetic similarity used to distinguish relatives from non-relatives did so only marginally and if these pairs of birds were indeed relatives their degree of their relatedness was clearly low. This is in contrast to male-male and male-female dyads comprised of birds from the same flock among which close genetic relationships were comparatively common. Second, females tended to be either unrelated to males from their own flock or related to them at a first order level. This contrasts markedly with the distribution for male birds from the same flock among which intermediate level genetic relationships were almost as common as first order relationships. Third, unrelated dyads were common. Even among dyads of male birds from the same flock the majority of dyads were unrelated. Finally, a number of close genetic relationships were detected among birds from different flocks particularly among male-male dyads where there were a small number of first order genetic relationships between individuals from different flocks.

Due to nearly complete sampling the 1998 flocks provide the best information available on the fine scale details of relatedness among flock members and illustrate two general features of the genetic structure of flocks. First, it is very likely that flocks commonly contained individuals that were unrelated to any other member (Figure 5.5). In only one flock, which contained two unsampled birds, did every sampled individual have at least one relative among the other sampled birds from its flock. The lack of relatives among flock-mates probably applied to males and females although was probably more prevalent for female birds (Figure 5.5). Second, most individuals had at least one close relative among the other sampled birds from their flock and many individuals were closely related to several of their flock-mates (Figure 5.5). The occurrence of close relatives among the sampled individuals from a flock was sex biased and 78.6% (n=42) of males had at least one close relative as a flock-mate compared with 46.2% (n=26) of females.

Three 1998 flocks, involving 31 birds, were completely sampled (flocks A, D and M Figure 5.2) and further exemplified the general patterns described above. Ten birds from a flock of eleven, eight birds from a flock of thirteen and five from a flock of seven birds had at least one relative as a flock mate. Of the nine individuals that were not related to any of the other birds in their flocks five were female and four were male. The average number of related flock-mates per individual was 1.8 and ranged from zero to four.

DISCUSSION

The combination of field observations and genetic data presented in this study provides the first comprehensive description of non-breeding social organisation in the yellow-rumped thornbill. Census and genetic data established that non-breeding flocks were characterised by three features. First, they were stable social groups with memberships that were highly consistent over the course of a single non-breeding period and to a large extent continuous from year to year. Second, flocks occupied large home ranges that were not exclusive and usually overlapped substantially with the ranges of other flocks. Third, flocks consisted of adults from adjacent breeding ranges (pairs or groups), some of their offspring from previous breeding seasons and some immigrant individuals.

The combination of these features defines a highly unusual non-breeding social organization in which the role of kinship is of particular interest.

Dispersal and kinship in winter flocks

Genetic data on the sex and relatedness of individuals indicated that kinship in flocks was male biased and was generated by male natal philopatry. Juvenile birds that became members of their natal flocks were always male. Natal philopatry by males was reflected in the very high genetic similarities, indicative of first order relatedness, between some male-male and male-female dyads from the same flock. Male-male dyads related at a first order level may have been father and son or brothers, while male-female dyads related at a first order level were almost certainly all mothers and sons. In contrast to males, females were never philopatric. No pair of female birds from the same flock had a genetic similarity approaching that expected of a parental or sororal relationship and no female banded as a nestling became a member of its natal flock. These results indicate that dispersal of juvenile females was universal and occurred before the censusing period, either during or soon after the breeding season in which they fledged.

Relationships between male flock-mates were not limited to parentage or fraternity, and included many lower order relationships. Half-sibship, arising from the recruitment into the same flock of the sons of a parent that changed breeding partners, may explain some of these relationships. Changes in breeding partnerships between seasons, usually due to the death of one member, were not unusual in this population however there was evidence to indicate that some lower order relationships between males may not represent half-sibship but may have arisen through extended family relationships within flocks. Most flocks contained representatives of more than one breeding unit and in six of the fifteen cases where a pair of male flock-mates was comprised of two birds that were known to be breeders in the preceding breeding season they were found to be close relatives. Close kinship between breeding male flock-mates potentially links nuclear families producing extended families of male kin with various degrees of relatedness within some flocks.

Although genetic analysis highlighted the role of male natal philopatry in generating kinship within flocks it also revealed that such kinship was not universal. In 1998, the year with the most complete sampling (85%), most females (53.8%, n = 26) and a substantial proportion of males (21.4%, n = 42) were not closely related to any of their sampled flock-mates. Female birds without related flock-mates were found in all eight flocks while male birds without related flock mates were found in six of eight flocks, including all three of the flocks where every individual was sampled. These results are consistent with dispersal of some males; indeed two males marked as nestlings were found to be members of non-natal flocks. A second line of evidence further highlights the lack of universal male kinship in flocks. Although some pairs of male flock-mates comprised of birds that were known to be breeders in the preceding breeding season were found to be close relatives most, 9 of 15, were not. This suggests that where flocks contained elements of more than one nuclear family, they were often not linked by close kinship between male breeders and therefore often did not represent extended families of male kin.

The social structure of yellow-rumped thornbill flocks appears similar to that described in the buff-rumped thornbills by Bell and Ford (1986). Buff-rumped thornbill flocks also consist of stable social groups that persist between years and are based on the affiliation of adults and juveniles from several adjacent breeding groups (Bell and Ford 1986). However, juvenile females in the buff-rumped thornbill delay dispersal until the end of winter (Bell and Ford 1986); so kinship in flocks includes parent-daughter relationships and potentially also sibling relationships between female birds. Dispersal of male buff-rumped thornbills into non-natal flocks was not observed by Bell and Ford (1986) and all marked male juveniles were recruited into their natal flocks. A consequence of these dispersal patterns is that kinship within flocks may be more extensive in the buff-rumped thornbill than in the yellow-rumped thornbill, where all female juveniles disperse before winter and some males disperse into non-natal flocks. The apparent lack of male dispersal in the buff-rumped thornbill implies that flocks may be strictly kin-based in terms of male membership which is not the case in the yellow-rumped thornbill where male kinship is mixed and far from absolute. Dispersal and relatedness are crucial parameters in understanding social organisation and behaviour but are inherently difficult to measure and it is possible that a low level of male dispersal in the buff-rumped thornbill was not detected in the purely observational study of Bell and Ford (1986). Despite this it is clear that yellow-rumped thornbills are socially very similar to buff-rumped thornbills, and probably also to striated thornbills (Bell and Ford 1986), and kinship within non-breeding flocks, although differing in extent, is significant in these species.

Kinship can be an important modifier of the costs and benefits of social interaction (Hamilton 1964) and the prevalence of kin in the non-breeding flocks of yellow-rumped thornbills, buff-rumped thornbills and probably also striated thornbills suggests that relatedness arising from natal philopatry is an important factor in the social behaviour of thornbills. However, as exemplified by the social organisations of two related species kinship is neither necessary or sufficient for the occurrence of winter flocking in members of the Pardalotidae. The speckled warbler (*Chthonicola sagittata*), like the social thornbills, forms stable non-breeding flocks comprised of adults from adjacent breeding ranges and juvenile birds, however kinship within flocks is precluded in this species by the dispersal before winter of all juvenile birds, both male and female (Gardner *et al.* 2003; Gardner 2004). The contrary case is demonstrated by the brown thornbill (*Acanthiza pusilla*) which never breeds cooperatively or forms non-breeding flocks (Bell and Ford 1986; Green and Cockburn 1999; Nicholls *et al.* 2000). The absence of cooperative breeding and non-breeding sociality in the brown thornbill occurs despite the opportunity for kin-based social affiliations provided by philopatric male offspring remaining on their parent's territories over winter and commonly breeding on territories adjacent to their parents (Green and Cockburn 2001). The dissociation of natal philopatry and winter flocking in the Pardalotidae suggests that kinship may not be a causal factor in the flocking behaviour of the social members of the family. In the case of the yellow-rumped thornbill, kinship within flocks is probably a consequence of natal philopatry occurring within a broader, and not necessarily kin-based, social organisation.

Spatial arrangement of winter flocks

The spatial organization of yellow-rumped thornbill flocks was distinguished from that of buff-rumped thornbills and speckled warblers by the fact that flock home ranges overlapped extensively. Unlike yellow-rumped thornbills, speckled warblers and buff-rumped thornbills occupy exclusive flock ranges that appear to be actively defended (Bell and Ford 1986; Gardner 2004). It is unclear why yellow-rumped thornbill flocks do not defend exclusive areas, although observations during breeding in this study suggest that they also do not defend exclusive breeding territories, again in contrast with buff-rumped thornbills (Bell and Ford 1986) and speckled warblers (Gardner 2002). It is possible that differences in habitat requirements or food resources may result in larger, undefendable, home ranges in the yellow-rumped thornbill. However, all three species have similar diets, particularly in winter when they forage predominantly on ground-dwelling invertebrates (Ford *et al.* 1986; Recher 1989; Bell and Ford 1990). Furthermore, this study was undertaken at the same study site and overlapped with that of Gardner's (Gardner 2002;

Gardner 2004) study of the speckled warbler, suggesting that broad habitat differences do not explain differences in territoriality and, more importantly, allowing a direct comparison of home range size. Speckled warbler and yellow-rumped thornbill flocks at Campbell Park occupied home ranges of similar size: 7-30ha in the speckled warbler and 8-48ha in the yellow-rumped thornbill. Yellow-rumped thornbill flocks are themselves larger than those of the speckled warbler, 4-14 birds and 2-7 birds in 1998 respectively, which does not match expectation if the number of individuals relates directly to the capability of flocks to defend exclusive areas. Presumably the costs and benefits of territory defence for yellow-rumped thornbills differ in a significant way from those experienced by buff-rumped thornbills and speckled warblers, although where these differences lie remains unclear at this stage.

Yellow-rumped thornbills and speckled warblers at Campbell Park had similarly sized flock home ranges despite large differences in the size of breeding "territories". Although flock territories of speckled warblers are large, they directly correspond, both in size and outer borders, to the amalgamated breeding territories of their two or three constituent breeding pairs (Gardner 2004). In contrast, although yellow-rumped thornbill flocks generally encompassed the breeding ranges of their resident members flock ranges could be much larger than the sum of the breeding ranges they included. Breeding ranges were not systematically measured in this study but were approximately two to four hectares in size. Flocks generally contained two to four breeding units yet flocks home ranges were commonly 20 hectares or more in area, and were as large as 48 hectares, indicating that flock ranges were not directly related to the breeding ranges of their constituent members and could be much larger than their combined breeding ranges.

The fact that the space occupied by yellow-rumped thornbills expands in winter such that flocks occupy ranges of similar area to speckled warbler flocks may reflect a seasonal change in foraging mode or diet in the yellow-rumped thornbill and the potential importance of food resources in the spatial arrangement of winter flocks. Speckled warblers are relatively invariant in their foraging behaviour and forage on the ground year-round (Ford *et al.* 1986; Tzaros 1996). Yellow-rumped thornbills are also predominantly ground foragers (Ford *et al.* 1986; Higgins and Peter 2002) but may be more generalist than speckled warblers and also forage throughout various strata of the vegetation (Ford *et al.* 1986). No data are available on seasonal changes in yellow-rumped thornbill foraging, however, seasonal changes are well documented in other thornbills (Recher 1989; Bell and

Ford 1990; Ford *et al.* 1990) and it is possible that yellow-rumped thornbills become more restricted to ground foraging over winter (pers. obs) as has been observed in the buff-rumped thornbill (Bell and Ford 1990; Ford *et al.* 1990). Similarity in the food resources exploited by speckled warblers and yellow-rumped thornbills over winter may explain the similarly large areas occupied by flocks of both species.

The benefits of flocking

Over the three years of this study there was one case where a breeding pair of yellow-rumped thornbills persisted throughout an entire non-breeding period as a "flock" of only two individuals. This anomalous observation indicates that, at least in some circumstances, membership of a larger social group is not necessary. Given that non-breeding flocks are optional, they presumably provide some benefit to the majority of birds. The potential benefits of non-breeding sociality in sedentary birds have been addressed in two largely separate contexts. The large body of work on northern hemisphere *Parus* species has focused on the direct benefits gained by individuals in non-kin-based winter flocking systems (Matthysen 1990; Ekman and Rossander 1992). The equally large body of work on avian social systems based on natal philopatry has recently expanded beyond the study of cooperative breeding to explicitly include aspects of non-breeding sociality and has stressed the potential for fitness benefits arising specifically from overwintering with kin (Ekman and Rossander 1992; Ekman *et al.* 1994; Ekman *et al.* 2001; Kraaijeveld and Dickinson 2001). The mixture of kin and non-kin characteristic of yellow-rumped thornbill flocks suggests that both individual and inclusive fitness benefits may apply.

Kin-based benefits

The study of avian cooperative breeding has elucidated a number of benefits that can accrue to parents and offspring from natal philopatry (Emlen 1982; Brown 1987; Stacey and Ligon 1987; Koenig *et al.* 1992; Emlen 1994; Emlen 1995). These benefits are generally related to long-term reproductive consequences of delayed dispersal, largely ignoring aspects of non-breeding sociality beyond the effects of group augmentation, and often relate explicitly to survival benefits of living on a permanent territory or the acquisition of a territory and the breeding opportunity it represents. The parental facilitation concept (Brown and Brown 1984; Brown 1987) for example, explains natal philopatry in terms of long-term reproductive benefits to both parents and offspring. In populations where territories are a limiting breeding resource, or vary in quality, offspring may benefit from natal philopatry via the inheritance of their parent's territory. Territorial inheritance may also represent a fitness benefit to parents in that it promotes the reproductive success of their offspring. Benefits of philopatry such as parental facilitation that explicitly relate to the acquisition of breeding territories are unlikely to apply to yellow-rumped thornbills due to their lack of classical territoriality.

The "prolonged brood care" hypothesis (Ekman and Rossander 1992; Ekman *et al.* 1994; Ekman *et al.* 2001), although it too includes long-term reproductive benefits associated with territoriality, explicitly includes potential benefits arising from the association of parents and offspring in the non-breeding period. These benefits arise from nepotistic behaviour of parents that enhances the survival or fitness of their mature offspring in much the same way as classical parental care does for dependent offspring. Parents may facilitate access to food for their offspring (Ekman *et al.* 1994; Pravosudova *et al.* 1999) or actively protect them from predators (e.g. Griesser 2003). The extended association of parents and offspring in yellow-rumped thornbill flocks provides the potential for "prolonged brood care" which, if it occurs, would represent a benefit of flocking for juvenile males that remain in their natal flocks and their parents. Furthermore, the long-term nature of yellow-rumped thornbill flocks and the likelihood of non-parental relationships among males presents the possibility of nepotistic interactions beyond those of "prolonged brood care". Male birds banded as nestlings were known to remain in natal flocks for at least two years in this study which suggests that they may reach a level of independence and maturity whereby they might direct nepotistic behaviour toward their parents and, given the nature of male kinship in yellow-rumped thornbill flocks, inclusive fitness benefits of nepotism among brothers and other male kin are also possible.

Individual benefits

The direct benefits of flocking in *Parus* species include short term benefits associated with survival over winter, and longer term social benefits associated with maintaining or gaining a territory or mate for the ensuing breeding season (Ekman 1989; Matthysen 1990). The survival benefits of flocking can include a reduction in predation risk and an increase in foraging efficiency. An individual's risk of predation may be reduced in a flock through the increased vigilance of "many eyes" (Pulliam 1973; Elgar 1989) and the dilution of risk (Pulliam 1973; Bednekoff and Lima 1998). Where investment in vigilance trades off with investment in foraging, the reduction in individual vigilance can increase foraging time (Pulliam 1973; Elgar 1989), furthermore, social foraging itself, regardless of predation risk, can increase foraging efficiency (Krebs *et al.* 1972; Pulliam 1973; Baker *et al.* 1981; Beauchamp 1998) and reduce variation in foraging success (Clark and Mangel 1986; Ekman and Hake 1988).

The foraging habit of the yellow-rumped thornbill may entail a significant predation risk and thus promote the potential for group size benefits of flocking. Within the open habitats in which they occur the ground foraging yellow-rumped thornbill has a preference for sparsely vegetated grassland areas and often forage some distance from cover (pers. obs., see Higgins and Peter 2002). The confamiliar speckled warbler is also a ground foraging species with a preference for open habitats and Gardner (2004) found that benefits relating to group size were probably an important factor in the formation of winter flocks of speckled warblers.

The social organisation of speckled warblers differed between two years of observation by Gardner (2004). In one year flocks comprised only a single breeding pair and immigrant juveniles but in another year with unusually low rainfall speckled warblers formed larger, more thornbill like, flocks comprised of residents from adjacent breeding territories as well as immigrant juveniles (Gardner 2004). The formation of larger flocks when conditions are unusually harsh has also been observed in some *Parus* species (e.g. great tit, *Parus major* (Saitou 1978); willow tit, *Parus montanus* (Hogstad 1988)) and is thought to reflect the general importance of individual survival benefits arising from group size effects on individual vigilance and social foraging in winter flocking *Parus* species (Ekman 1989; Matthysen 1990). That flock size may be important to yellow-rumped thornbills was suggested by the amalgamation of the remnants of previously independent flocks after poor inter-year survival. Most yellow-rumped thornbill flocks persisted between years in that surviving birds usually formed a core of continuous membership from one year to the next and new flock members were probably mostly natal or immigrant juveniles. However, there were several instances where adult birds joined existing flocks or formed new flocks incorporating the surviving members of previously independent flocks. These mergers, occurring after a reduction in size of the original flocks, are consistent with yellow-rumped thornbills actively seeking to achieve larger group sizes in some circumstances.

Winter flocking may facilitate the acquisition of a breeding territory in some species but this is unlikely to be a major benefit of flocking in the yellow-rumped thornbill. *Parus* species typically form winter flocks via the association of juvenile birds with a territory holding adult pair (Ekman 1989; Matthysen 1990). Juveniles that join flocks early are often socially dominant over those that settle later and can benefit from priority over territory ownership, and hence access to a breeding vacancy, upon the death of a dominant bird. Access to a territory as a benefit of flocking in *Parus* systems has some power to explain the occurrence of flocking itself in that it applies differentially to juveniles that become flock members by settling with dominant territory holders and those that do not (Matthysen 1990). This benefit, as it applies in the context of universal juvenile dispersal and territoriality characteristic of *Parus* social systems, may not be relevant to the yellow-rumped thornbill. Unlike most *Parus* species breeding yellow-rumped thornbills do not occupy discrete and exclusive territories, which suggests that access to a "territory" or breeding range probably does not represent a critical breeding resource as it does in *Parus* systems. Furthermore, there was no direct relationship between the winter home range of yellow-rumped thornbill flocks and the breeding ranges of their constituent breeding pairs and groups. These characteristics suggest that membership of a winter flock is not significantly related to maintaining or achieving ownership of a breeding territory in the yellow-rumped thornbill.

Although flocking may not promote access to territorial vacancies, yellow-rumped thornbill flocks may facilitate breeding opportunities. In *Parus* species (Ekman 1989; Matthysen 1990), and in the speckled warbler (Gardner 2004), breeding pairs tend to consist of birds that were in the same flock in the preceding winter and this appears to also be true of the yellow-rumped thornbill. For male yellow-rumped thornbills breeding opportunities are probably constrained by a shortage of females. There were more males than females in flocks: in the 1998 flocks there were 42 males versus 26 females overall, and 20 males versus 11 females in the three completely sampled 1998 flocks. This sex bias suggests that male birds are probably in competition over access to mates. Social dominance hierarchies within flocks, such as those found in some *Parus* species (Ekman 1989; Matthysen 1990), might have important implications for male yellow-rumped thornbills to the extent that rank or status may influence their ability to attract or keep a mate. Furthermore, social dominance structures might be expected among males given that they vary in age, origin (natal or immigrant), and relatedness to other flock members.

Elucidating the potential social functions of flocking, such as the facilitation of pairing for the subsequent breeding season, requires detailed behavioural data not currently available for the yellow-rumped thornbill. However, although it may be the case that winter flocks provide the social context for important interactions among yellow-rumped thornbills with implications for subsequent breeding, it is not clear that this represents a benefit, rather than secondary consequence, of forming winter flocks.

CONCLUSION

Yellow-rumped thornbills display a non-breeding social organization that is unusual even among the social members of their family. The social affiliation of adults from multiple breeding units, sex biased dispersal, and the mixed dispersal strategies of male juveniles creates large non-breeding flocks with complex mixtures of related and unrelated individuals. Kinship may provide family based or inclusive fitness benefits to some birds in non-breeding flocks. However, although kinship arising from male natal philopatry is a feature of yellow-rumped thornbill flocks, the lack of correlation between natal philopatry and winter flocking in the Pardalotidae and the mixture of kin and non-kin in flocks suggests that kin-based benefits of sociality do not wholly explain the formation of winter flocks in the yellow-rumped thornbill. The individual benefits of winter flocking, as elucidated in the non-kin-based social systems of *Parus* species and the speckled warbler, probably also apply to the yellow-rumped thornbill and may be an important factor in the social affiliation of both kin and non-kin in flocks. Furthermore, changes in the use of space between breeding and non-breeding seasons suggests that seasonal changes in the food resources exploited by yellow-rumped thornbills may be an important ecological factor underlying the formation of winter flocks.

Table 5.1. Sample sizes and test statistics for differences between mean genetic similarity coefficients of within-flock and between-flock dyads. Standard errors for t-tests were calculated with a sub-sampling procedure following Danforth and Freeman-Gallant (1996) see text for explanation. Equality of variances assessed by F-tests, $\alpha = 0.05$.

	Coefficient of similarity mean ± SE				
Dyad type	Within	Between	**t**	**d.f.**	**p**
All	0.161 ± 0.0227	0.107 ± 0.0103	2.17	434 & 513^1	**0.031**
Male/Male	0.209 ± 0.0405	0.110 ± 0.0163	2.27	127 & 172^1	**0.025**
Male/Female	0.146 ± 0.0225	0.103 ± 0.0104	1.73	226 & 241^1	0.085
Female/Female	0.123 ±0.0150	0.108 ± 0.0146	0.75	177^2	0.45

[1] variances unequal

[2] variances equal.

Table 5.2. Flock size and home range size for the yellow-rumped thornbill over the winters of 1996, 1997 and 1998.

				Flock size			Home range size (ha)		
Year	**No. of flocks**	**Total flock members**	**% banded**	n[1]	range	mean±SD	n[2]	range	mean±SD
1996	8	57	78.9	8	4–12	7.1 ± 3.3	6	12.3 - 28.5	19.9 ± 5.8
1997	8	59	69.5	7	2–12	7.4 ± 2.9	5	7.8 - 20.4	15.6 ± 5.0
1998	9	83	84.3	9	4-14	9.3 ± 3.2	8	15.0 - 48.3	28.2 ± 10.3

[1] One flock was excluded on the basis of insufficient census data.

[2] Home ranges size was calculated for flocks with more than 10 location records.

Table 5.3. Numbers and proportions of related within-flock dyads. Dyads with similarity coefficients greater than the upper 99% confidence interval for the distribution of unrelated (breeding pair) dyads were classified as related. Of the dyads classified as related, those with similarity coefficients less than the lower 99% confidence interval for the distribution of known first-order relatives were classified as related at less than a first-order level.

	Total no. dyads	**No. related (as proportion)**[1]	**No. related at less than 1st order level (as proportion)**[2]
Male-Male	128	40 (0.31)	16 (0.40)
Male-Female	227	22 (0.10)	3 (0.14)
Female-Female	80	5 (0.06)	5 (1.00)

[1] Shown in parentheses as a proportion of the total number of dyads.

[2] Shown in parentheses as a proportion of the total number of related dyads.

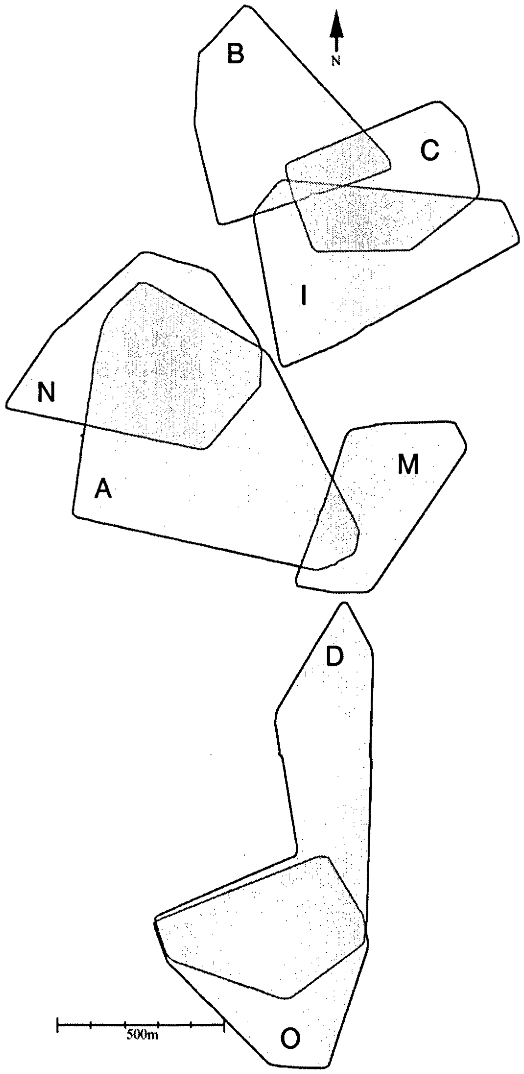


Figure 5.1. Home ranges of yellow-rumped thornbill flocks in 1998. Letter codes correspond to Figure 5.1.

Flock A → 1996	no. flock rec's = 15		Flock A → 1997	no. flock rec's = 9		Flock A 1998	no. flock rec's = 19	
flock size = 4	sex	individual rec's	flock size = 8	sex	individual rec's	flock size = 11	sex	individual rec's
yBWG	m	15	→		6	→		15
yGAY	f	5	→		8	→		15
yORW	m	15	→		8	→		18
			yRON	f	9	→		17
			yGbwM	m	8	→		17
			yArnY	m	8	X		
			yAOA	f	7	X		
						yRryB	m	17
						yMryO	m	15
						yNbw A	m	18
						yBbw R	m	11
						yABR	f	14
						yNWW	m	4

Flock B → 1996	no. flock rec's = 12		Flock B → 1997	no. flock rec's = 9		Flock B 1998	no. flock rec's = 15	
flock size = 10	sex	individual rec's	flock size = 12	sex	individual rec's	flock size = 10	sex	individual rec's
yRRG	f	12	→		8	→		14
yNBR	m	11	→		8	→		14
yBOW	f	12	→		7	→		12
yBAR	f	9	X					
yRMW	f	8	X					
yRAN	m	7	X					
yWNO	f	8	X					
			yABN	f	4	→		15
			yGGN	m	6	→		13
			yANA	m	3	X		
			yNOB	f	8	X		
			yBRN	f	6	X		
			yGGO	f	3	X		
			yMRW	m	3	X		
						yBrnO	m	15
						yOrnW	m	14
						yAWG	f	10
						yBGO	m	11

Flock C → 1996	no. flock rec's = 11		Flock C → 1997	no. flock rec's = 7		Flock C 1998	no. flock rec's = 11	
flock size = 10	sex	individual rec's	flock size = 10	sex	individual rec's	flock size = 8	sex	individual rec's
yNOO	m	5	→		6	→		9
yNMW	f	9	→		5	→		10
yBbw B	m	11	→		7	→		11
yWBN	f	10	→		4	X		
yNRA	f	8	→		5	X		
yOOW	f	8	X					
yANO	f	4	☆ see flock 97K					
			yRbw B	m	5	→		11
			yAGO	m	6	→		9
						yRRO	f	11

Flock D → 1996	no. flock rec's = 7		Flock D → 1997	no. flock rec's = 6		Flock D 1998	no. flock rec's = 17	
flock size = 11	sex	individual rec's	flock size = 7	sex	individual rec's	flock size = 13	sex	individual rec's
yRBO	m	5	→		4	→		15
yARG	f	6	→		3	→		16
yOWO	f	6	→		6	→		11
yNWR	f	3	→		3	→		12
yYGG	m	5	→		4	X		
yOWY	m	3	X					
yNAN	m	5	X					
yMRN	m	4	X					
yBBM	m	3	X					
yGWN	f	3	X					
			yWGW	f	3	X		
						yBbw G	m	16
						yRbw N	m	16
						yRmW	m	15
						yNRR	m	13
						yOGO	m	14
						yARN	f	10
						yNMA	m	14
						yMAR	f	14
						yGWNii	f	9

Legend

Bird IDs

eg. yAAA	Individual marked as an adult
eg. yAaaA	Individual marked as a nestling
eg. yAaaA	Individual known to be in non-natal flock

Individual Fates

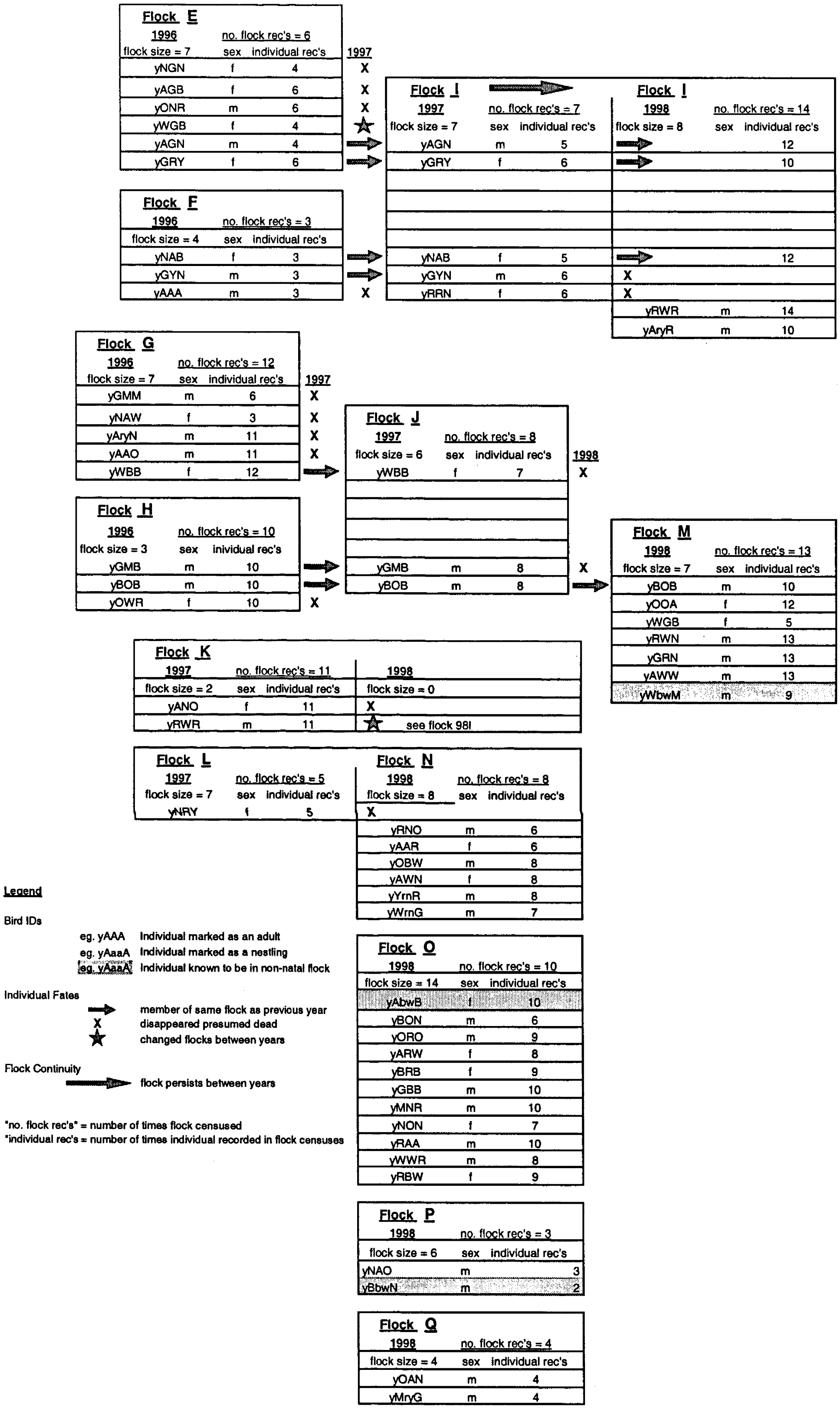
→	member of same flock as previous year
X	disappeared presumed dead
☆	changed flocks between years

Flock Continuity

→	flock persists between years

"no. flock rec's" = number of times flock censused
"individual rec's = number of times individual recorded in flock censuses

Figure 5.2. Flocking patterns over the winters of 1996, 1997 and 1998.



Flock E

1996 no. flock rec's = 6

flock size = 7	sex	individual rec's	1997
yNGN	f	4	X
yAGB	f	6	X
yONR	m	6	X
yWGB	f	4	★
yAGN	m	4	→
yGRY	f	6	→

Flock F

1996 no. flock rec's = 3

flock size = 4	sex	individual rec's	
yNAB	f	3	→
yGYN	m	3	→
yAAA	m	3	X

Flock I → **Flock I**

1997 flock size = 7 no. flock rec's = 7	sex	individual rec's	1998 flock size = 8 no. flock rec's = 14	sex	individual rec's
yAGN	m	5	→		12
yGRY	f	6	→		10
yNAB	f	5	→		12
yGYN	m	6	X		
yRRN	f	6	X		
			yRWR	m	14
			yAryR	m	10

Flock G

1996 no. flock rec's = 12

flock size = 7	sex	individual rec's	1997
yGMM	m	6	X
yNAW	f	3	X
yAryN	m	11	X
yAAO	m	11	X
yWBB	f	12	→

Flock H

1996 no. flock rec's = 10

flock size = 3	sex	inividual rec's	
yGMB	m	10	→
yBOB	m	10	→
yOWR	f	10	X

Flock J

1997 no. flock rec's = 8

flock size = 6	sex	individual rec's	1998
yWBB	f	7	X
yGMB	m	8	X
yBOB	m	8	→

Flock M

1998 no. flock rec's = 13

flock size = 7	sex	individual rec's
yBOB	m	10
yOOA	f	12
yWGB	f	5
yRWN	m	13
yGRN	m	13
yAWW	m	13
▨ yWbwM	m	9

Flock K

1997 flock size = 2 no. flock rec's = 11	sex	individual rec's	1998 flock size = 0
yANO	f	11	X
yRWR	m	11	★ see flock 98I

Flock L

1997 no. flock rec's = 5

flock size = 7	sex	individual rec's	1998
yNRY	f	5	X

Flock N

1998 no. flock rec's = 8

flock size = 8	sex	individual rec's
yRNO	m	6
yAAR	f	6
yOBW	m	8
yAWN	f	8
yYrnR	m	8
yWrnG	m	7

Flock O

1998 no. flock rec's = 10

flock size = 14	sex	individual rec's
▨ yAbwB	f	10
yBON	m	6
yORO	m	9
yARW	f	8
yBRB	f	9
yGBB	m	10
yMNR	m	10
yNON	f	7
yRAA	m	10
yWWR	m	8
yRBW	f	9

Flock P

1998 no. flock rec's = 3

flock size = 6	sex	individual rec's
yNAO	m	3
▨ yBbwN	m	2

Flock Q

1998 no. flock rec's = 4

flock size = 4	sex	individual rec's
yOAN	m	4
yMryG	m	4

Legend

Bird IDs

eg. yAAA	Individual marked as an adult
eg. yAaaA	Individual marked as a nestling
▨ eg. yAaaA	Individual known to be in non-natal flock

Individual Fates

→	member of same flock as previous year
X	disappeared presumed dead
★	changed flocks between years

Flock Continuity

→	flock persists between years

"no. flock rec's" = number of times flock censused

"individual rec's = number of times individual recorded in flock censuses

Figure 5.2 continued.

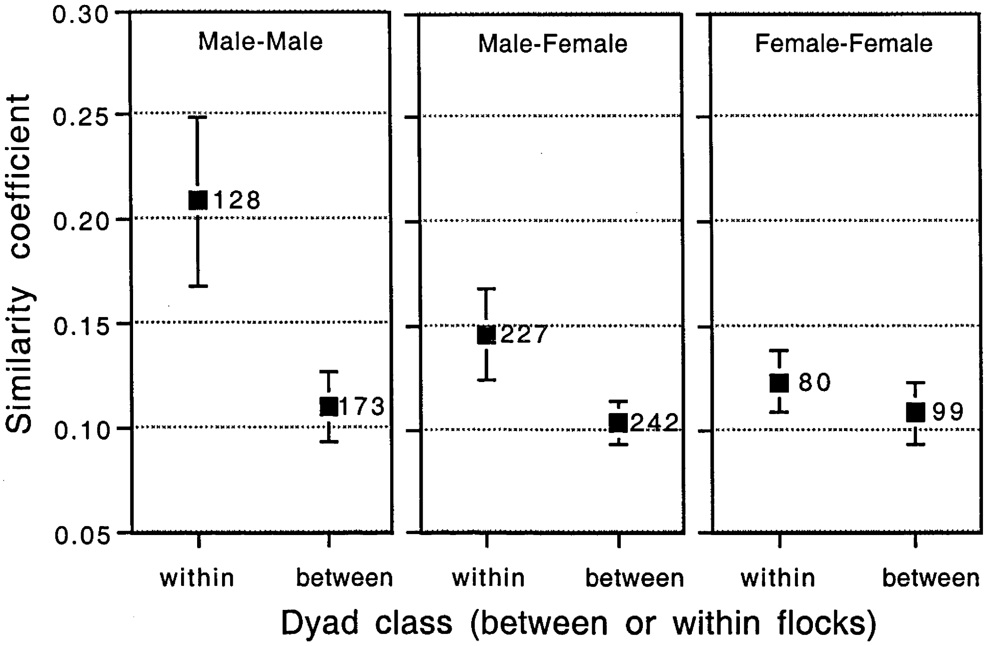


Figure 5.3. Mean genetic similarity coefficients and standard errors for within-flock and between flock comparisons of male/male, male/female and female/female dyads. Numbers of dyads in each class are shown beside each mean.

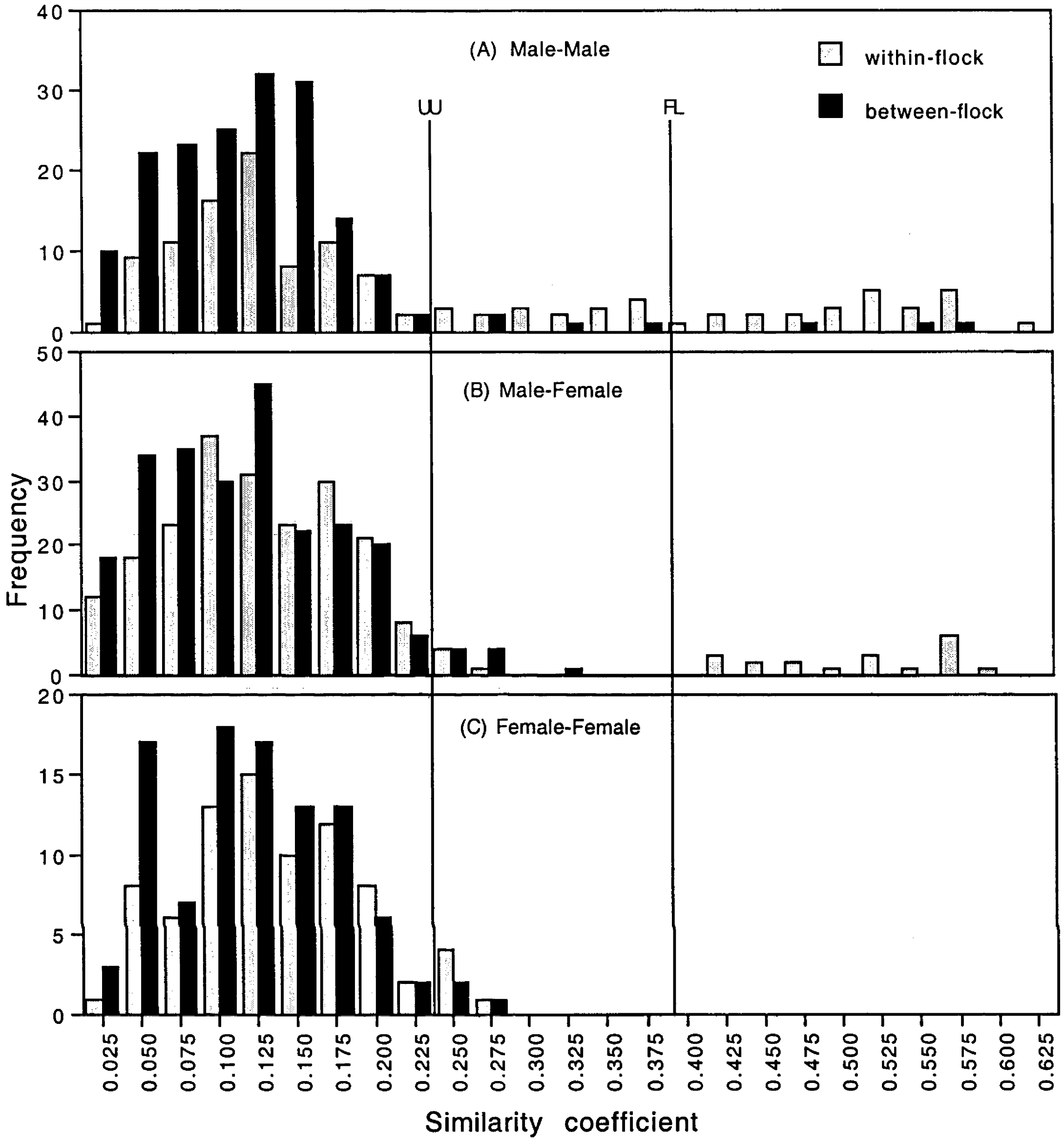


Figure 5.4. Frequency distributions of within-flock and between-flock genetic similarity coefficients for male-male, male-female and female-female dyads. Vertical lines indicate confidence limits used to classify dyads with respect to relatedness. UU = The upper one-tailed 99% confidence interval for a reference distribution of unrelated dyads (breeding pairs). FL = The lower one-tailed 99% confidence interval for a reference distribution of known first order relatives. Dyads falling to the right of UU were classified as related and of these those that fell to the left of FL were considered unlikely to be first order relatives.

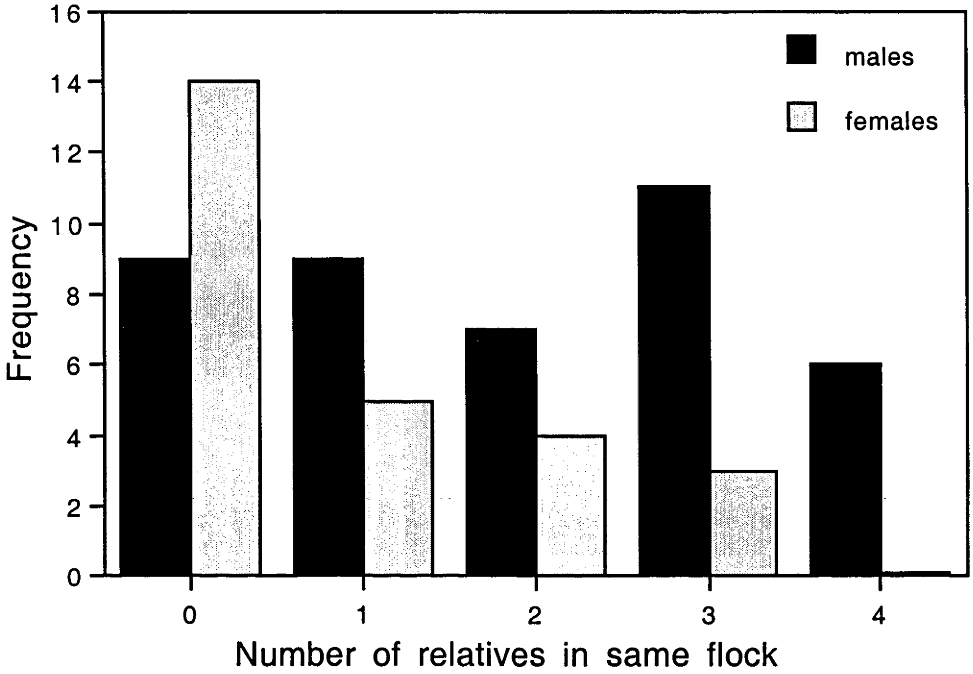


Figure 5.5. Frequency distributions of the number of flock-mates that were relatives for male and female yellow-rumped thornbills in 1998. Statistical tests were not carried out due to non-independence of the data.

CHAPTER 6

Conclusions and future directions

INTRODUCTION

This thesis investigated the breeding biology, mating system and social organization of the yellow-rumped thornbill and the mating and parental care systems of the buff-rumped thornbill. In part, the study was designed to add to the body of knowledge on the ecology of members of the Pardalotidae, a large and socially diverse group of old endemic Australian passerines. In addition, earlier anecdotal reports strongly suggested that the yellow-rumped thornbill would exhibit a complex two-tiered social organization, similar to that described for the buff-rumped thornbill, where adjacent breeding units of two or more individuals coalesce during winter to form stable flocks. A central aim of this study was therefore to describe the social organization and mating system of the yellow-rumped thornbill breeding units, and also the non-breeding social organization of winter flocks. As well as relying on standard observational techniques, I used molecular methods to examine the genetic relationships among individuals during the breeding and non-breeding seasons. These techniques have greatly accelerated and improved our abilities to investigate social structures.

In this final chapter, I briefly summarise the main findings of the thesis, and discuss the most promising avenues for future research.

Social organization – breeding season

Members of the Pardalotidae studied to date have shown little variation in aspects of their demography and breeding biology. They tend to be long-lived, lay small clutches, have long incubation and nestling periods, and lay multiple clutches over a long breeding season. At the species level yellow-rumped thornbills do not differ from this model and exhibit typical "long and slow" life history traits. However, the comparison of the population studied here and that described by Ford (1963) revealed marked differences in reproductive success. This appeared to be due to a much longer breeding season and much lower rates of nest predation in Ford's West Australian population than in the Canberra population described in this study.

In contrast to the homogeneity of life history characteristics, the Pardalotidae display a diverse range of social organisations and mating systems, which has proven valuable to researchers interested in the evolutionary basis for complex breeding sociality, particularly the evolution of pair-breeding in cooperative clades (Green and Cockburn 1999; Green and Cockburn 2001). Some species, like the brown thornbill, breed as simple pairs, the buff-rumped thornbill has been reported to breed in nuclear family groups, while the white-browed scrubwren breeds in pairs or cooperative groups comprised of both related and unrelated individuals. The application of genetic techniques has revealed the genetic mating systems of a small number of species. The brown thornbill has been shown to breed monogamously (Green *et al.* 2002), the speckled warbler has been found to have low rates of shared paternity within groups and low rates of extra-group paternity (Gardner *et al.* 2004), while the white-browed scrubwren has a moderately high incidence of both shared paternity within groups and extra-group paternity (Whittingham *et al.* 1997). In keeping with this diverse theme, the thornbills studied here had a breeding social organisation and mating system that are unique within the family, although yellow-rumped thornbills and buff-rumped thornbills shared many breeding system characteristics. Like buff-rumped thornbills, yellow-rumped thornbills often bred in pairs, but formed cooperatively breeding groups based on nuclear family units via the philopatry of male offspring. However, cooperative groups were less common in the yellow-rumped thornbill population studied here than they were for buff-rumped thornbills both in this study, and an earlier study by Bell and Ford (1986). DNA fingerprinting revealed that the mating system of both species was overwhelmingly monogamous with very low rates of extra-group paternity and no within-group shared paternity.

Both yellow-rumped thornbill and buff-rumped thornbill helpers made substantial contributions to the provisioning of nestlings. The only clear difference between the cooperative breeding systems of the two species was the provisioning behaviour of individuals in groups. Buff-rumped thornbills reduced their individual contributions when assisted by helpers, so that groups and unassisted pairs fed at the same overall rate. This was not true of the yellow-rumped thornbill, where the contribution of helpers was additive and groups fed at a higher overall rate than pairs. This difference is important because it suggests that the costs and benefits of helping behaviour differ between the two species in some critical way, and thus the underlying basis for cooperative breeding in the two species may differ.

Social organization – non-breeding season

The diversity of non-breeding social organizations within the Pardalotidae is comparable to the diversity of breeding systems within the family. For example, whereas the brown thornbill and white-browed srubwren continue to defend their breeding territories throughout the winter, speckled warblers, buff-rumped thornbills and striated thornbills form multi-member flocks with varying space-use patterns.

During this study, yellow-rumped thornbills formed flocks through the amalgamation of adjacent breeding units. Flock membership was stable throughout the non-breeding season, and was even stable, to a large extent, among years. In this respect, yellow-rumped thornbill flocking patterns are similar to that reported for buff-rumped thornbills. However, whereas buff-rumped thornbill flocks are reported to use and defend exclusive territories delineated by the shared borders of the breeding territories, yellow-rumped thornbill flocks ranged widely over winter and used areas that overlapped considerably with neighbouring flock ranges. This points to critical differences in diet and/or resource use between the two species, in the same way that the different provisioning patterns of yellow and buff-rumped thornbills suggested a key divergence in foraging constraints.

Nest predation

Most studies of the factors that influence nest predation have focused on traits of prey species that affect the vulnerability of nests to predation. Characteristics of nest concealment and parental and nestling behaviour are generally considered to influence rates of nest predation via their effects on the detectability of nests to predators. Patterns of predation on yellow-rumped thornbill nests strongly suggested that the behaviour of predators is also an important influence on the timing and intensity of nest predation. The coincidence of heightened predation specifically on yellow-rumped thornbill nestlings and the brood rearing period of the predatory pied currawong (*Strepera graculina*) indicated that pied currawongs actively targeted nests containing nestlings when they were feeding their own broods. These results point to a weakness in the study of nest predation from the exclusive perspective of the prey species. The yellow-rumped thornbill population studied here represents an example where information on the behaviour of a particular predator was required to explain patterns of predation at different stages of the nesting cycle and over the course of the breeding season.

Future directions

This study suggests three major avenues for future work on the thornbills:

1) What is the basis for the large variety of social systems in the Pardalotidae during the breeding season?

Before this question can be answered, more detailed information is required on the breeding and social systems of various species in the family. When cooperative breeding does occur, we need to know how helpers and breeders benefit from the system, and what the constraints and options for individual birds are. With regard to the thornbills, this study clearly showed that helpers did not gain any substantial access to mating opportunities, either within or outside their groups. Thus cooperative breeding is not driven by direct reproductive benefits to helpers. In addition, provisioning by helpers was unconditional, unlike the facultative helping displayed by white-browed scrubwrens (Magrath and Whittingham 1997), and therefore not linked to paternity in the brood. Helpers of both species were close relatives of the breeders and their young, so inclusive fitness benefits may be important. This study could not address this question adequately, partly because the incidence of cooperative breeding was low, and thus the sample of groups was small. Preliminary indications were that helpers did not increase the success of breeding attempts, but yellow-rumped helpers *may* have increased the quality of young produced, and buff-rumped thornbill helpers *may* have benefited the longer-term survival and/or fecundity of their parents by reducing their provisioning workload. These issues need to be examined in more detail, either by studying a larger population (and thus increasing the sample of cooperative groups) or by studying a population with a higher incidence of cooperative breeding. In addition, an experimental approach to some problems may be warranted, to avoid the problem of confounding effects that plague studies of cooperative breeding (Cockburn 1998). For example, it may be possible to design experiments to test whether a fundamental difference in foraging constraints is responsible for the different provisioning patterns in the buff and yellow-rumped thornbills.

Breeding buff-rumped thornbills could be given supplementary food to reduce their foraging costs, and the effect of this on load-lightening, fledgling weight and post-fledging survival measured. If foraging costs have a proximate role in load-lightening the amelioration of these costs may induce additive provisioning by parents and helpers. If additive provisioning was induced, the measurement of fledgling weight and post-fledging survival may provide valuable information on the potential costs of load-lightening in relation to the optimal provisioning of nestlings. Similarly, the foraging costs of yellow-rumped thornbills could be experimentally increased by adding small weights to their tails (e.g. Wright and Cuthill 1989), in order to test whether heightened foraging constraints induce load-lightening in this species. Again, the measurement of fledgling weight and survival may point to the costs of load-lightening in relation to the consequences of sub-optimal provisioning of nestlings.

2) What is the basis of the diverse non-breeding social organizations in the Pardalotidae?

The diversity of social systems in the Pardalotidae has only recently come to light after several long-term studies that were not restricted to aspects of breeding biology and behaviour (e.g. Bell and Ford 1986; Green and Cockburn 2001; Gardner 2004). The description of group size and composition, and space use, in the non-breeding period for other species is likely to increase the range of social systems known to occur within the family. Based on the comparison of the few species studied to date, an important factor in non-breeding social organization is likely to be diet, or resource dispersion, during winter. Although buff-rumped thornbills and yellow-rumped thornbills are similarly sized insectivores with broadly similar foraging modes, there may be a subtle difference in diet or patterns of resource dispersion that influence foraging requirements, and hence space use, in winter. Unlike buff-rumped thornbills, yellow-rumped thornbill flock home ranges overlapped considerably with those of neighbouring flocks. This may point to a difference in the area required to sustain flocks over winter and the defendability of these areas. Quantification of home range, or territory, size in winter in buff-rumped thornbills and other species may provide some clues as to the importance of the area flocks occupy and their tendency to be territorial. Issues of resource availability and dispersion could be addressed by providing supplementary food to flocks to reduce foraging costs and change the spatial requirements of foraging. The resulting effects on the size of flock ranges, territorial defense and possibly even the tendency to form flocks may provide an explanation for some of the variation in social organization within the Pardalotidae.

The non-breeding social organization of the yellow-rumped thornbill is unique within the Pardalotidae and may present an ideal opportunity to study the role of kinship in some aspects of avian sociality. As social units yellow-rumped thornbill flocks are unusual in that they are qualitatively different social groupings from those of the breeding season and they are mixtures of kin and non-kin. As such, the detailed observation of flocks, quantifying aspects such as dominance, aggression, foraging efficiency and vigilance with regard to relatedness among individuals, may provide valuable insight into the role of kinship in social groups in a context not directly related to reproduction. The application of new genetic techniques (e.g. microsatellite genotyping) that allow the rapid assessment of relatedness would be invaluable in such studies and would allow observational protocols to be designed with advance knowledge of relationships among individuals.

3) What is the basis of mixed male dispersal strategies in the yellow-rumped thornbill?

Juvenile male yellow-rumped thornbills displayed two discrete dispersal strategies, some males dispersed to become members of non-natal flocks, while others were natally philopatric and became members of their parent's flock. It is unclear what the costs and benefits of either strategy are, who decides whether a juvenile stays or leaves, and whether the individuals that adopt each strategy differ in some way, such as individual quality or social status. Studies in other species with mixed dispersal strategies have found that juvenile philopatry entails a survival benefit to those individuals that delay dispersal (e.g. gray jay, *Perisoreus canadensis*, Strickland (1991); Siberian jay, *Perisoreus infaustus*, Ekman *et al.* (2000); brown thornbill, Green and Cockburn (2001)). There is also evidence in some species of competition among siblings over who stays and who leaves with larger and/or socially dominant individuals more likely to delay dispersal (gray jay, Strickland (1991); Siberian jay, Ekman *et al.* (2002); red-cockaded woodpecker, *Picoides borealis*, Pasinelli and Walters (2002)). However, in the brown thornbill, although a maximum of one male ever delays dispersal even when broods include multiple males, there is no evidence of intra-brood competition over dispersal and larger brood mates are not more likely to delay dispersal (Green and Cockburn 2001).

The costs and benefits of alternative dispersal strategies in the yellow-rumped thornbill could be addressed in a long-term study comparing survival and recruitment rates of individuals that disperse and those that do not. It may also be possible to test some of the costs of dispersal by comparing the fates of birds that are forced to “disperse”, by translocation, with those of a control group. Detailed behavioural observations of flocks may elucidate the issue of how dispersal decisions are made. By quantifying aggression between parents and offspring, between siblings, and more generally between juvenile birds and their flock-mates, it may be possible to establish whether individuals are evicted from their natal flocks or choose to disperse. Related to this issue is the possibility that dispersing birds differ in quality or social status from those that are natally philopatric. Measurement of size and condition of juvenile birds, either as nestlings or, preferably, at the point of independence, may point to differences in quality that could be related to subsequent dispersal decisions.

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