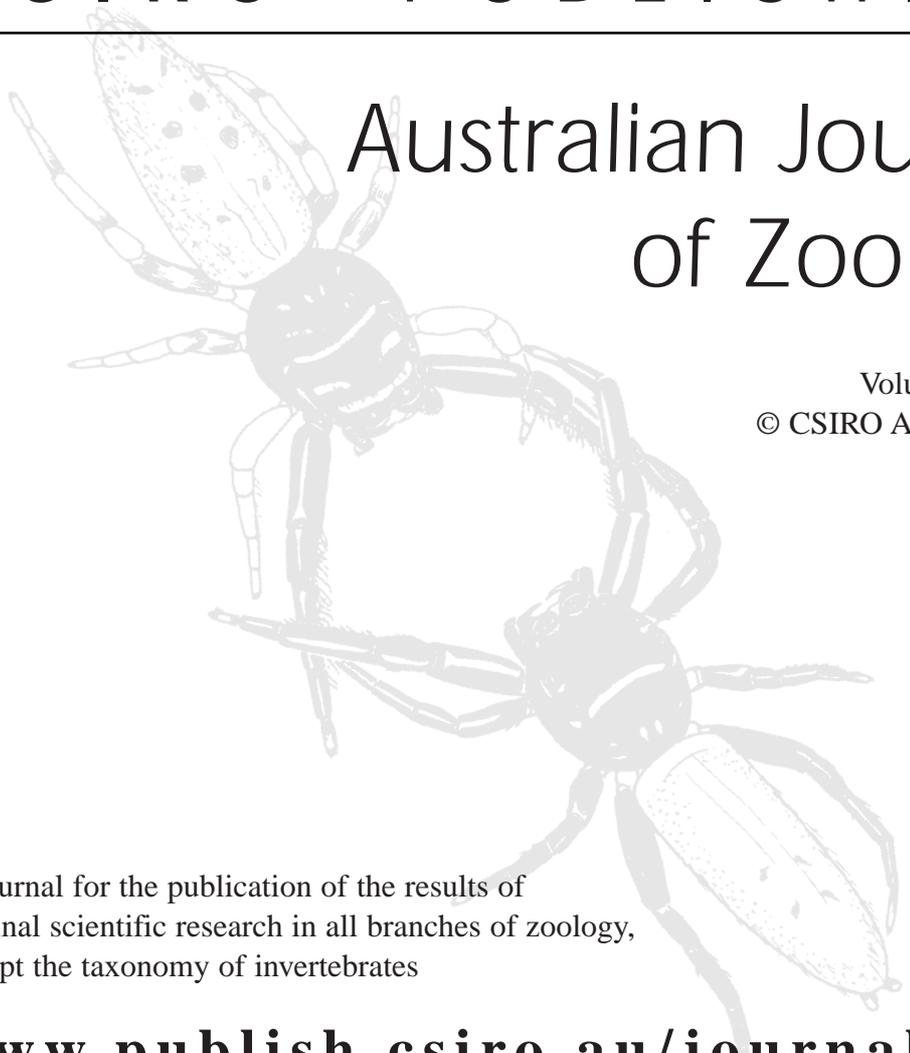

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Life history and demography of an uncooperative Australian passerine, the brown thornbill

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Abstract

The genus *Acanthiza* may be important in understanding the evolution of avian mating systems because while brown thornbills, *Acanthiza pusilla*, are thought to breed only in pairs, a recent phylogenetic analysis suggests that cooperative breeding is the ancestral trait within this genus. We provide a detailed account of the breeding biology of the brown thornbill, confirm that they breed exclusively in pairs, and compare their population demography with what is known for other members of the Pardalotidae. We found that brown thornbills produced small clutches (3 eggs) with a two-day laying interval, had a long incubation period (declining from 19 to 16 days through the season), and had a long breeding season (4.0 months) that allowed females to occasionally raise two successful broods. Brown thornbills, in our study, produced an average of 1.57 fledglings per pair and had relatively high annual survival rates (*c.* 63%). We found no evidence to suggest that the evolution of pair-breeding within the Pardalotidae is associated with a reduction in annual survival rates, a short breeding season with reduced productivity, or high levels of predation post-fledging. Since there also appear to be no ecological correlates with mating system in the Pardalotidae we suggest that examination of reproductive conflict between parents and young may shed light on the evolution of pair-breeding in this family.

Introduction

Studies of avian mating systems have recently begun to use a comparative approach to examine the life-history traits of pair-breeding and cooperatively breeding birds (Poiani and Jermin 1994; Poiani and Pagel 1997; Arnold and Owens 1998). Arnold and Owens (1998) conclude that extremely low adult mortality may predispose some avian families to breed cooperatively. This approach has been galvanised by the detailed phylogeny available for birds (Sibley and Ahlquist 1990), but is compromised by the lack of detailed data on the breeding biology of birds from the Southern Hemisphere (Martin 1996).

The Corvida, an ancient clade of passerines that evolved and radiated mostly within Australia, plays an important role in comparative analyses of life-history traits because cooperative breeding is much more prevalent in the Corvida than in the Passerida, the clade to which most well studied species belong (Russell 1989; Cockburn 1996). The Australian endemics are thought to possess a suite of life-history traits resulting in long, slow reproduction, but current analyses do not support the view that cooperative Corvida in Australia have different demography from non-cooperative taxa (Ford 1989; Rowley and Russell 1991; Poiani and Jermin 1994).

The Pardalotidae are a speciose family from the Corvida that contains both pair-breeding and cooperatively breeding members. They are known for their longevity, small clutch sizes, long incubation periods, and prolonged breeding seasons (Woinarski 1985; Yom-Tov 1987; Rowley and Russell 1991; Yom-Tov *et al.* 1992; Ricklefs 1993). Nevertheless only a few of the 49 species of Pardalotidae resident in Australia have been studied in detail, e.g. *Acanthiza pusilla* and *A. reguloides* (Bell and Ford 1986), *A. chrysorrhoa* (Ford 1963), *Sericornis frontalis* (Ambrose and Davies 1989; Magrath *et al.* in press). Even for these species, quantitative data often do not cover the whole breeding season and little is known about seasonal effects on reproduction.

We describe the breeding biology of the brown thornbill, *Acanthiza pusilla*, a small (*c.* 7 g) insectivore common in forested areas of south-eastern Australia. Brown thornbills are one of 12 *Acanthiza* species endemic to Australia. This genus may be important in understanding the evolution of avian mating systems because while brown thornbills are thought to breed only in pairs (Bell and Ford 1986), a recent phylogenetic analysis suggests that cooperative breeding is the ancestral trait within the *Acanthiza* (Nicholls *et al.* in press).

Specifically, we aim (1) to provide a detailed account of the breeding biology of a small, sedentary, Australian endemic, and (2) to compare the population demography of this pair-dwelling member of the Pardalotidae with what is known for other species within the family that breed cooperatively.

Methods

Study population

We studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, from 1995 to 1999. The vegetation in the Botanic Gardens consists of both plantations of Australian native trees and shrubs, and natural woodland that is contiguous with a large area of dry sclerophyll forest (*Eucalyptus rossii*, *E. mannifera*, *E. macrorhyncha*) in Black Mountain Nature Reserve. We followed the fate of 15–32 pairs per year, monitoring the entire population resident in the 80-ha study area between 1996 and 1999.

General methods

We monitored the study population throughout the year. During the non-breeding season (January–June) we visited the study area at least once a month to census pairs, document survival, and identify when new birds entered the population. During the breeding season (July–December) each pair was monitored at least three times a week to document reproductive attempts. The location of birds during territorial disputes was used to determine territory boundaries.

Most birds monitored during the breeding season (>95% each year) were uniquely colour-banded. Adult birds were banded using a numbered Australian Bird and Bat Banding Scheme aluminium band and three plastic colour bands ($n = 136$). The four bands weighed a total of 0.09 g, approximately 1% of adult body mass, and did not appear to alter the behaviour of the birds in any way. We weighed birds to the nearest 0.1 g using Pesola spring balances whenever they were caught. We also measured wing and tail length to the nearest 1 mm using a stainless steel ruler, and tarsus length and head–bill distance to the nearest 0.05 mm using dial calipers.

Survival of banded individuals was measured from the start of one breeding season (1 August) until the beginning of the next. We assumed that birds had died if, after being a member of a breeding pair, they disappeared and were not seen again despite the study area and all suitable habitat within 0.5 km of the territory being searched.

We found nests by watching females building nests ($n = 126$), following females back to their nests during incubation ($n = 43$), or by watching adults feed nestlings ($n = 4$). The majority of nests (78%) were built within 1 m of the ground (mean height = 80 cm; range = 10 cm – 7 m). The progress of a nesting attempt was monitored by checking nests at 2–3-day intervals. In 1995 and 1996 we determined laying intervals by checking nests daily from the laying of the first egg until a clutch was completed. In 1997 and 1998 we checked nests only enough to determine the date that the first egg was laid. If we did not find the nest until after laying we estimated the clutch-initiation date from the hatching date and regression of incubation period on clutch-initiation date. For the few nests that were too high to be accessible ($n = 7$) we estimated the clutch-initiation date by backdating from the time that females were first seen incubating or when adults were first seen feeding nestlings.

We defined the incubation period as the interval between the laying of the last egg and the hatching of the last chick. We determined the date of hatching from daily visits to the nest after the female had been incubating for approximately 14 days combined with the appearance and size of nestlings. We banded the nestlings when 7–10 days old. All nestlings were weighed when banding took place and, in 1997 and 1998, were also weighed when 12 days old.

We calculated the nestling period as the interval between the hatching of the last chick and fledging of the last chick. We assessed the success of a nesting attempt by monitoring nests every 2–3 days for the first two weeks of incubation, and subsequently used daily visits to determine the date that broods fledged. For

breeding attempts that failed, nests were assumed to have failed on the day after the nest was last known to be active.

The survival of fledglings was determined by weekly censuses conducted 2–8 weeks after fledging. The duration of parental care was evaluated from 15-min observations on individual fledglings conducted at the same time as the censuses.

Sexing individuals

Brown thornbills are sexually monomorphic but only females are thought to build nests and incubate eggs. We initially sexed birds behaviourally but subsequently used a simple PCR-based molecular technique to confirm their gender (see Griffiths *et al.* 1998 for details of the method).

Statistical analysis

We used a modelling approach in statistical analysis. Our data contained pairs that were represented several times, as pairs could have multiple nesting attempts in any one year and be present for more than one year of the study. We therefore analysed our breeding data using mixed models incorporating both random and fixed effects, where 'pair' was included as a random factor in all models (Bennington and Thayne 1994). A new pair was considered to have formed when either member was replaced following a death or divorce.

We fitted separate models using eight dependent variables. The date that a pair initiated their first and their last clutch was used to examine the timing of breeding. We also examined the likelihood that a pair would re-nest following a successful or failed attempt, and the time interval between breeding attempts. The success of each nesting attempt was examined at three stages: hatching (for all clutches that were initiated), fledging (for all clutches that hatched), and post-fledging (for all broods that fledged).

We used four explanatory variables in our mixed models: year, month, date, and territory type (watered plantation or native woodland). A final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. To avoid any confounding order effects, any term that was close to significant ($P < 0.2$) was re-evaluated by adding and dropping it from the final model. We report only main effects or interactions from a model where they are significant ($P < 0.05$), a trend ($P < 0.1$), or it is of biological importance to find a non-significant result. In the case of non-significant effects the statistics refer to the results of dropping the non-significant term from the final model plus that term.

Models were fitted using Genstat ver. 5.3.2 (Genstat 1993). Continuous dependent variables were analysed using the restricted maximum-likelihood (REML) procedure while binary dependent variables were analysed using the generalised linear mixed-model (GLMM) procedure.

Analyses were restricted to pairs for which we documented all nesting attempts during the breeding season even if they failed during incubation. Sample sizes vary between analyses because nests were found, and failed, at different times during the breeding cycle. We also excluded 14 pairs whose nests were protected during an experiment in 1998 from analyses of hatching and fledging success.

Survival data were analysed using Cox's proportional hazards model as implemented in JMP ver. 3 (SAS Institute 1994). For other analyses, where birds were represented only once, we used conventional least-squares statistics. In all analyses residual plots and normal probability plots were examined for unequal variance and deviations from normality among residuals. We applied appropriate transformations if necessary. Means are presented with standard errors unless otherwise stated.

Results

Adult size

Male thornbills were significantly larger and heavier than females but there was overlap in all morphological measures (Table 1). Female thornbills could, however, be sexed accurately on the basis of nest-building and incubation behaviour as the molecular sexing technique always confirmed the gender of birds sexed using behavioural cues ($n = 136$).

Annual survival

Adult survival of brown thornbills varied between a high of 85% in 1995 and a low of 37% in 1998 (year effect: $\chi^2 = 34.3$, d.f. = 3, $P < 0.001$). Overall, the survival of male and female thornbills was equal, although males showed more extreme year-to-year variation (gender effect:

Table 1. Comparison of mass and linear measurements for male and female brown thornbills

	Male		Female		<i>t</i> -test	<i>P</i>
	Mean ± s.d.	Range	Mean ± s.d.	Range		
Mass (g)	7.3 ± 0.4	6.6–8.0	6.4 ± 0.4	5.7–7.1	14.3	<0.0001
Head–bill length (mm)	26.9 ± 0.6	26.1–27.7	25.9 ± 0.4	25.0–27.1	10.6	<0.0001
Tarsus length (mm)	20.5 ± 0.6	19.4–21.3	19.7 ± 0.5	18.6–20.4	7.7	<0.0001
Wing length (mm)	52.0 ± 1.5	49–56	49.5 ± 1.5	45–52	10.0	<0.0001
Tail length (mm)	49.1 ± 2.5	45–56	47.2 ± 2.1	44–51	4.9	<0.0001
<i>n</i>		71		65		

$\chi^2 = 0.01$, d.f. = 1, $P > 0.9$, Table 2). Individuals in artificially watered territories were no more likely to survive than those in natural woodlands (watered plantation 62%, natural woodland 64%; $\chi^2 = 0.73$, d.f. = 1, $P > 0.25$). Mortality was observed at all times of the year; however, mortality was high during the autumn of 1997, and extreme during September and October in 1998 (Fig. 1).

Social organisation

Brown thornbills maintained territories, ranging in size from 0.4 to 3.1 ha, throughout the year. Pairs living in artificially watered plantations had significantly smaller territories than pairs living in natural woodland (1997 territories: plantations 1.3 ± 0.1 ha, $n = 15$; woodland 2.1 ± 0.1 ha, $n = 14$; *t*-test, $t = 3.87$, $P < 0.001$). Territory boundaries did not change significantly from year to year.

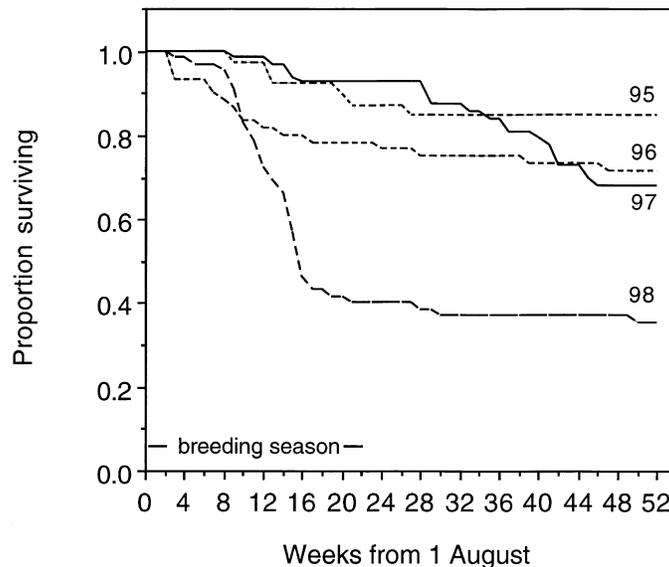


Fig. 1. Year-specific survival for colour-banded adult brown thornbills resident in the study area. Sample sizes for 1995 through 1998 are 39, 60, 63, and 65 respectively.

Table 2. Annual patterns of survival, timing of breeding, number of nesting attempts, and reproductive success in the brown thornbill

The data for each year refer to the year in which the breeding season commenced and cover the period from 1 August in that year until 31 July in the next. Survival data are for all colour-banded adults resident in the study area. Breeding data are for all pairs observed sufficiently that all nesting attempts have been documented. Fourteen pairs were excluded when calculating reproductive success in 1998 as their nests were protected

	1995	1996	1997	1998	Combined
Male survival (<i>n</i>)	0.95 (21)	0.74 (31)	0.66 (35)	0.30 (33)	0.63 (120)
Female survival (<i>n</i>)	0.72 (18)	0.69 (29)	0.71 (28)	0.41 (32)	0.62 (107)
<i>n</i> for timing	15	27	29	31	102
First clutch initiated ± s.d.	27 Aug ± 12 days	10 Aug ± 10 days	29 Aug ± 11 days	19 Aug ± 15 days	21 Aug ± 14 days
Last clutch initiated ± s.d.	7 Sep ± 22 days	22 Sep ± 29 days	26 Sep ± 28 days	16 Sep ± 31 days	19 Sep ± 29 days
<i>n</i> for reproductive success	15	29	29	18	91
Clutches laid – 0	0	2	0	1	3
1	11	7	15	7	40
2	4	18	8	8	38
3	0	2	6	2	10
Broods fledged – 0	6	12	14	8	40
1	9	15	15	9	48
2	0	2	0	1	3
Proportion of pairs that fledge young	0.6	0.59	0.55	0.55	0.57
Fledglings per pair ± s.d.	1.73 ± 1.49	1.72 ± 1.6	1.28 ± 1.31	1.67 ± 1.78	1.57 ± 1.52
Proportion of pairs that produce independent young	0.6	0.55	0.48	0.5	0.53
Independent young per pair ± s.d.	1.4 ± 1.3	1.03 ± 1.21	0.93 ± 1.1	0.89 ± 1.02	1.03 ± 1.15

Brown thornbills bred only in pairs ($n = 105$ pair-years). A single independent young sometimes remained with its parents in the natal territory through the autumn and early winter ($n = 20$ pair-years) but always dispersed or established a territory adjacent to its parents by the start of the breeding season. The late-dispersing young were almost always male (19 of 20 cases; Green, unpublished data). We never observed young from previous years or early broods assist their parents raise nestlings or fledglings produced at subsequent nesting attempts.

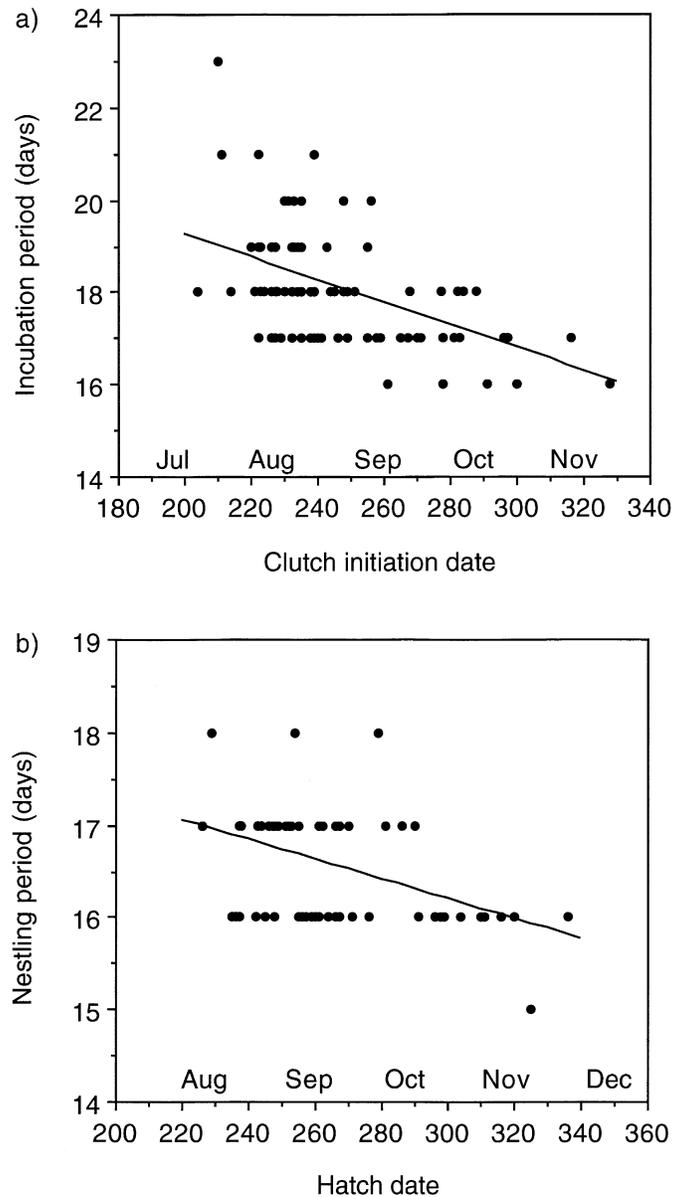


Fig. 2. Seasonal changes in (a) incubation period and (b) nestling period. Lines show predictions from the mixed models. The date used in models is the Julian date where 1 January = 1. Data are from all four years of the study. (a) $n = 92$ cases from 58 pairs with 47 females represented, (b) $n = 62$ cases from 43 pairs with 37 females represented.

Breeding biology

Brown thornbills typically laid three-egg clutches (97.6%, $n = 126$ clutches found before egg-laying), but occasionally produced two-egg (1.6%) or four-egg clutches (0.8%). Eggs were always laid at two-day intervals ($n = 23$ cases where the interval was known accurately).

Eggs were incubated for 18.0 ± 0.1 days (range: 16–23 days, $n = 92$ clutches). The incubation period decreased over the course of the breeding season ($\chi^2 = 29.3$, d.f. = 1, $P < 0.001$; Fig. 2a).

Female thornbills initiated incubation after the last egg was laid and clutches hatched relatively synchronously. In nests with no hatching failure the entire clutch hatched between daily nest visits 68% of the time ($n = 92$ cases). Of the remaining 29 cases, 28 clutches had finished hatching by the following day, and one clutch completed hatching two days later. Hatching was more likely to be totally synchronous early in the season (date effect: Wald $\chi^2 = 4.2$, d.f. = 1, $P < 0.05$).

Nestlings remained in the nest for 16.4 ± 0.8 days (range: 14–18 days, $n = 65$ broods). The nestling period declined over the breeding season ($\chi^2 = 14.7$, d.f. = 1, $P < 0.001$; Fig. 2b).

Thornbills started to initiate clutches between July and October, with 73% of first clutches being initiated in August and September. Pairs initiated second or, less frequently, third clutches between late August and November (Fig. 3, Table 2). MacArthur's (1964) index calculates the length of the breeding season as 4.0 months. The earliest that a clutch was initiated in this study was 23 July (1996), and the latest was 17 November (1997).

The length of the breeding season was determined more by when breeding started than when breeding stopped. Females initiated their first clutch early in 1996 and late in 1995 and 1997 ($\chi^2 = 61.0$, d.f. = 3, $P < 0.001$; Table 2). In contrast, the date that females initiated their last clutch did not vary significantly over the four years of this study ($\chi^2 = 4.2$, d.f. = 3, $P > 0.2$; Table 2).

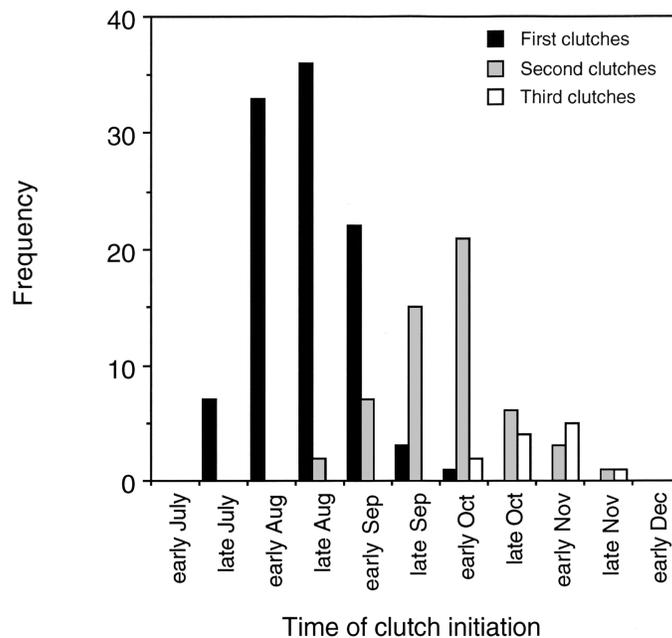


Fig. 3. Frequency distribution showing the number of first, second, and third clutches initiated through the breeding season. Data are for the four years combined. Sample sizes are 102, 55, and 12 respectively.

Thornbills initiated up to three clutches during a breeding season but rarely fledged more than one successful brood (Table 2). The probability that a pair re-nested was much greater if the first attempt failed (79% of 52 failed attempts) than if it fledged (39% of 38 successful attempts; Wald $\chi^2 = 14.9$, d.f. = 1, $P < 0.001$). For nests that failed and for those that fledged young the

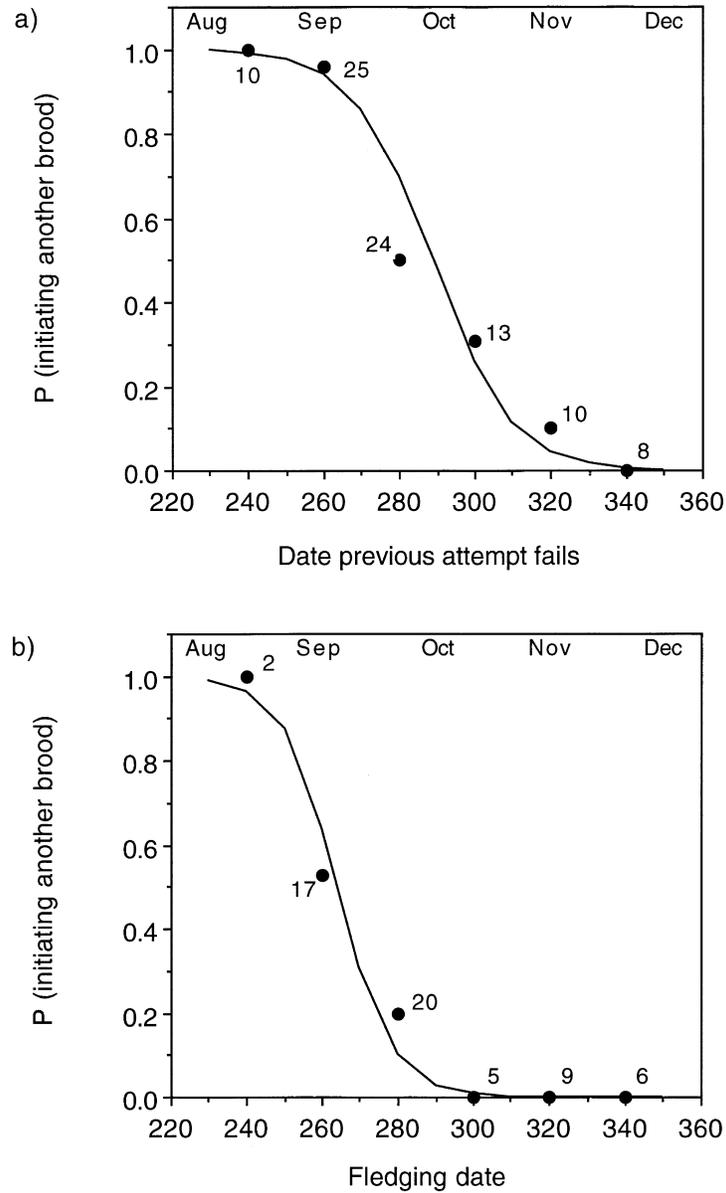


Fig. 4. Seasonal changes in the probability of initiating another clutch following (a) a failed nesting attempt, and (b) a successful nesting attempt. The date used in the model is the Julian date where 1 January = 1. The lines are predictions from the mixed models; points show 20-day means with sample sizes.

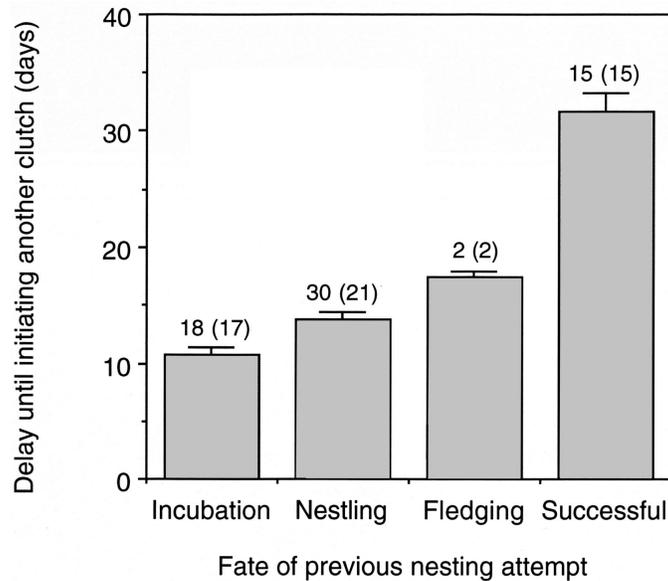


Fig. 5. Interval between nesting attempts according to the fate of the previous attempt. The delay to initiating another clutch is the number of days between the failure or fledging of a nesting attempt and the laying of the first egg in the next clutch. Timing of failure is divided into during incubation, during the nestling period, and immediately after fledging; a successful attempt produces at least one independent young. Bars show means + s.e. Numbers are sample sizes; the number of pairs represented is shown in parentheses.

date that the previous attempt ended affected the probability that a pair re-nested (failed attempts – Wald $\chi^2 = 24.0$, d.f. = 1, $P < 0.001$; successful attempts – Wald $\chi^2 = 9.3$, d.f. = 1, $P < 0.005$; Fig. 4). Since pairs that initiated their first clutch early had more time to re-nest if an early attempt failed the number of clutches initiated by a pair was dependent on when they started to breed ($\chi^2 = 10.4$, d.f. = 1, $P < 0.005$).

The interval between the date that a nest failed or fledged and the time that the next clutch was initiated increased with the amount of time invested in the previous nesting attempt ($\chi^2 = 61.2$, d.f. = 3, $P < 0.001$; Fig. 5).

Reproductive success

In all, 78% of clutches hatched successfully ($n = 157$ clutches). The major cause of failure was nest predation by birds ($n = 27$). We suspect this was principally due to pied currawongs, *Strepera graculina*, which are the most common avian predator in our study area. Additional causes of failure were predation by foxes or feral cats ($n = 3$), abandonment following the death of a female ($n = 3$) and nest loss due to high winds ($n = 1$). Hatching success tended to be lower in September and October than in other months (Wald $\chi^2 = 7.8$, $P < 0.1$; Fig. 6a).

Young fledged from 48% of clutches that hatched young ($n = 123$ broods). The major cause of failure was nest predation by birds ($n = 39$), although some nests were lost to mammalian predators ($n = 4$) and a few broods were abandoned by males following the death of their mate ($n = 5$). Predation by snakes or birds was the likely cause of failure at a further 14 nests where nestlings were removed without any damage to the nest. There were also two known cases of cuckoo parasitism, one by a fan-tailed cuckoo, *Cuculus pyrrhophanus*, and one by a shining

bronze-cuckoo, *Chrysococcyx lucidus*. Fledging success did not change significantly over the breeding season, although the few broods that hatched in December appeared less likely to fledge ($\chi^2 = 3.6$, d.f. = 4, $P > 0.2$; Fig. 6b).

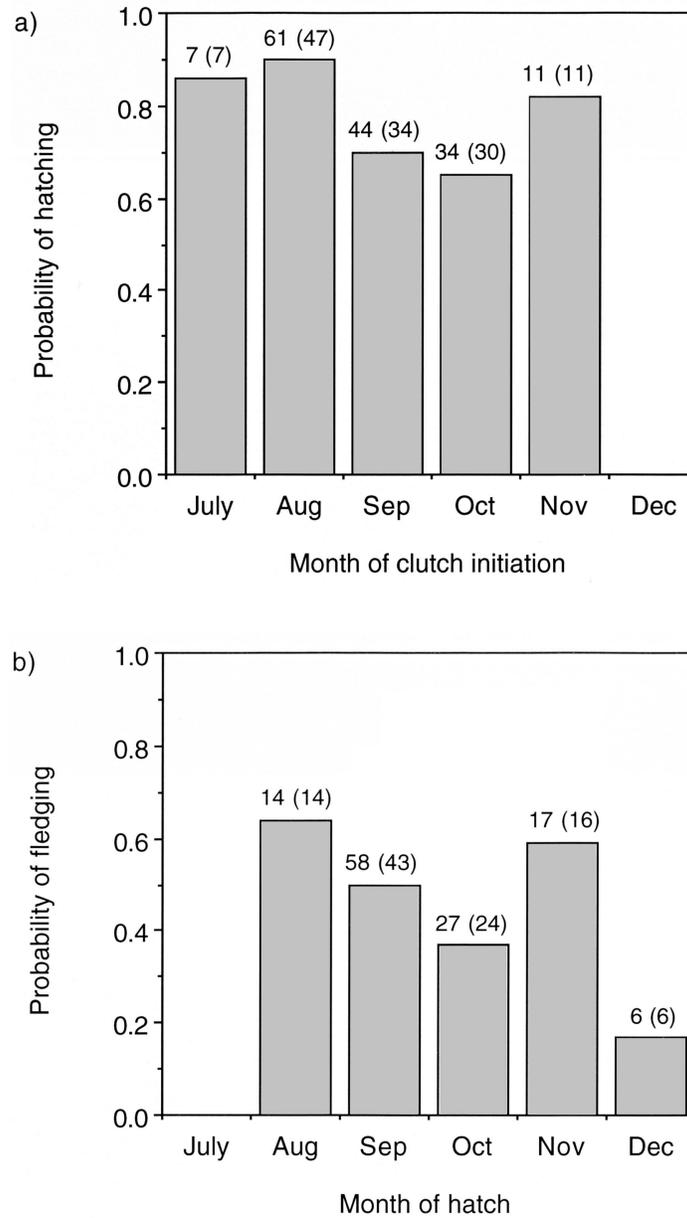


Fig. 6. Seasonal pattern to (a) hatching success (for all clutches completed) and (b) fledging success (for all clutches that hatch). Numbers above bars are numbers of clutches or broods; the number of pairs represented is in parentheses.

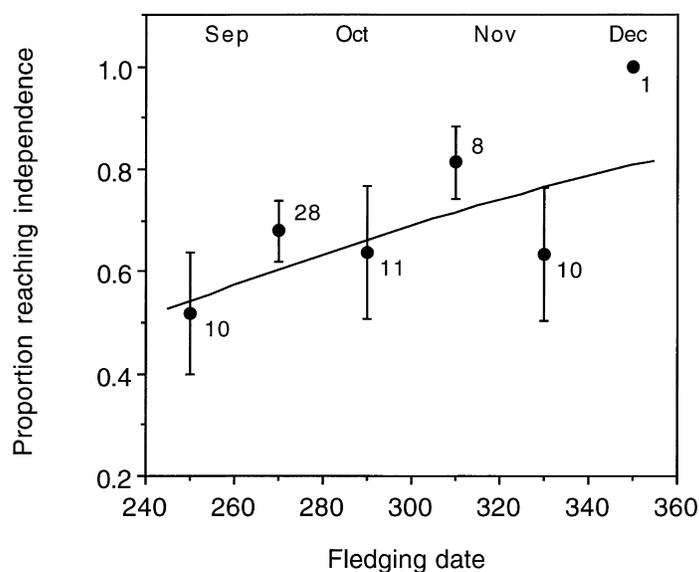


Fig. 7. Seasonal change in the proportion of a brood that survives to independence at six weeks. Fledging date used in the model is the Julian date where 1 January = 1. The line is the prediction from the mixed model; points show 20-day means with s.e. Numbers adjacent to points are number of broods; the number of pairs represented at each point are 10, 26, 11, 8, 10, and 1 respectively.

Fledglings were dependent on their parents for approximately six weeks. Overall, 64% of fledglings survived to independence ($n = 171$). The proportion of fledglings reaching independence tended to increase over the breeding season (Wald $\chi^2 = 3.4$, d.f. = 1, $P < 0.1$; Fig. 7).

Pairs in this study produced an average of one independent young per season, but only half the pairs in any year were successful (Table 2). Thornbills were significantly more productive in 1995 than in subsequent years principally because post-fledging survival was higher in that year (year effect: $\chi^2 = 9.8$, d.f. = 3, $P < 0.005$; Table 2). Territory type had no effect on the number of independent young that a pair produced ($\chi^2 = 0.13$, d.f. = 1, $P > 0.2$).

Discussion

Brown thornbills breed exclusively in pairs, although recent phylogenetic analyses suggest that cooperative breeding is the ancestral trait both within the genus *Acanthiza* and the family Pardalotidae (Cockburn 1998; Nicholls *et al.* in press). We found little to suggest that the evolution of pair-dwelling in this family is associated with changes to any life-history traits. In addition to being long-lived, brown thornbills possess all of the other life-history traits typical of the cooperatively breeding Pardalotidae (Russell and Rowley 1991; Magrath *et al.* in press). They lay small clutches, have long incubation periods, and are able to produce multiple broods over a long breeding season.

Longevity and annual survival rates

Australian passerines have been found to be longer-lived and have higher annual survival rates than equivalently sized passerines in temperate regions of the Northern Hemisphere (Fry

1980; Rowley and Russell 1991; Yom-Tov *et al.* 1992). Pardalotid species can be extremely long-lived and the maximum recorded longevity for a brown thornbill is 17 years (Woinarski 1985; Baker *et al.* 1999). The estimates for annual survival rates of members within the Pardalotidae based on long-term studies reflect the longevity of this family (Table 3). We estimated the annual survival rate of adult brown thornbills to be 63% which is substantially lower than the estimate of 87% for brown thornbills in New South Wales (Bell and Ford 1986). However, Bell and Ford's three-year study spanned a drought when breeding was partly suspended, which may have reduced mortality (H. Ford, personal communication). Our estimate is strongly influenced by the extreme mortality that occurred over two months in 1998. This short period was also a time of unusually high mortality for both superb fairy-wrens, *Malurus cyaneus* (Cockburn, unpublished data) and white-browed scrubwrens, *Sericornis frontalis* (R. Magrath, personal communication) in the Botanic Gardens. The high mortality does not appear to have been associated with unusually cold or wet conditions, but may have been the result of a local avian virus to which small passerines were particularly vulnerable. Excluding this year gives an annual survival rate for brown thornbills of 73%. This is likely to be a more accurate estimate as the oldest bird in our study was a minimum of 11 years old when last re-sighted, and three are currently at least 7 years old.

Social organisation

Most well studied *Acanthiza* species have been reported to breed cooperatively, although the proportion of birds that breed in groups rather than pairs varies considerably between species and also between populations within species. For example, although striated thornbills, *A. lineata*, in northern New South Wales frequently breed in groups (43% of breeding units, $n = 14$: Bell and Ford 1986), yellow-rumped thornbills *A. chrysorrhoa*, in the Australian Capital Territory rarely do so (7% of breeding units, $n = 46$: D. Ebert, personal communication). In contrast, we found that brown thornbills breed exclusively in pairs. No pairs were helped by additional birds at any stage of the breeding cycle over the four years of this study ($n = 105$ pair-years). Brown thornbills are also reported to breed strictly in pairs in New South Wales, South Australia, and Tasmania, so are likely to be pair-breeding throughout their range (Wheeler 1960; Thomas 1965; Bell and Ford 1986).

The pair defended a permanent territory that ranged in size from 0.4 to 3.1 ha throughout the year. Territory size may reflect food availability in different habitats as territories in artificially watered plantations were smaller than those in natural woodland. Additional support for this hypothesis is provided by Bell and Ford (1986), who found that although territory sizes varied they contained approximately the same amount of understorey, the preferred foraging niche of brown thornbills.

Breeding biology

Brown thornbills typically laid a clutch of three eggs. Small, relatively invariable, clutches are characteristic of the Pardalotidae and seem likely to be ancestral traits within the Corvida (Yom-Tov 1987; Woinarski 1989; Ricklefs 1993; Magrath *et al.* in press). Small clutch sizes may have evolved in response to an aseasonal environment where there is little or no peak in food availability to support reproduction (Ashmole 1963; Woinarski 1985). The relatively minor winter decline in arthropod abundance in the foliage of forests in south-eastern Australia supports this hypothesis (Woinarski and Cullen 1984; Woinarski 1985). The lack of seasonal variation in the clutch size of brown thornbills is also consistent with a lack of seasonality in conditions for breeding (Crick *et al.* 1993). However, at this point we have no direct evidence that food supply during the nestling period constrains clutch size.

The two-day laying interval that appears to be a feature of the Pardalotidae (Magrath *et al.* in press) has also been attributed to an inadequate food supply (Thomas 1974). However, the fixed two-day laying interval in brown thornbills and other members of the Pardalotidae suggests that food is unlikely to be a proximate factor in this family. The two-day laying interval may allow

females to lay relatively large eggs and thus improve the growth or survival of young without impairing their foraging ability or making them more vulnerable to predation (Williams 1994; Magrath *et al.* in press). Female thornbills do produce large eggs (a clutch weighs approximately 61% of their body weight), providing some support for this hypothesis.

Long incubation periods are characteristic of the Pardalotidae (Ricklefs 1993). Ricklefs (1992, 1993) has suggested that long incubation periods may assist in the maturation and subsequent efficiency of the immune system, and found that long incubation periods are associated with high annual adult survival and low prevalence of blood parasites. Brown thornbills have a mean incubation period of 18.0 days, which is much longer than the 12.4 days predicted for a passerine with a mass of 6.4 g, or the 12.7 days for a passerine laying an egg of 1.3 g (Rahn *et al.* 1995). Brown thornbills also have high annual adult survival rates and individuals may live for up to 17 years, which is consistent with Ricklefs' hypothesis (Bell and Ford 1986; Wilson 1995; Baker *et al.* 1999; this study).

We found that both the incubation and nestling periods declined over the breeding season. The marked seasonal decline in the incubation period probably reflects the change in temperature between August (mean daily maximum = 13°C) and November (mean daily maximum = 23°C) when clutches are being incubated. Females are presumably able to keep eggs at optimal temperatures for a greater proportion of the time when it is warmer. It is less clear why the nestling period also declined through the season. We found no evidence to suggest that nestlings grow faster when ambient temperatures are higher; age-specific nestling mass does not increase through the season (unpublished data). Perhaps the time at which nestlings fledged changed because of a shift in the relative predation rates in and out of the nest; nest predation rates increased slightly while fledgling loss decreased over the breeding season.

Species within the Australian endemic family, the Pardalotidae, are thought to have long breeding seasons compared with similar insectivorous birds in the Northern Hemisphere, which typically breed for 2–3 months (Woinarski 1985). We found that brown thornbills do have a comparatively long breeding season (4.0 months): clutches were initiated from mid-winter until late spring.

Brown thornbills were thought not to re-nest if their first clutch was successful (Bell and Ford 1986). However, we found that pairs not only initiated a second clutch if their first failed, but also frequently (*c.* 40%) re-nested if their first attempt was successful. Multi-brooding was more common in years when breeding started early as pairs that did not fledge their first brood early in the season were unlikely to re-nest. Brown thornbills may not have been reported to fledge two broods in northern New South Wales (Bell and Ford 1986) because high predation rates meant that females were unable to fledge their first brood sufficiently early in the season.

Females are less likely to re-nest after a successful breeding attempt than after a failed attempt presumably because of the long period of post-fledging care provided and the costs associated with caring for fledglings. Females also take longer to re-nest after attempts that fail during the nestling period or immediately after fledging than after attempts that fail during incubation. Furthermore, females provisioning young weigh less than at other times of the year (Green, unpublished data). These data all suggest that females face energetic constraints that limit when and if they are able to initiate a new clutch.

Seasonal patterns to reproductive success

Predation rates on the domed nests built by female brown thornbills were low both prior to hatching (1.2% per day), and during the nestling period (4.0% per day). This is much lower than the rates reported for similar Northern Hemisphere species (mean predation rates on eggs and nestlings 9.3% and 8.4% respectively; Clark and Wilson 1981). Predation rates were relatively constant throughout the breeding season, although there was some suggestion that predation rates on both eggs and nestlings increased in September and October. This coincides with the period when pied currawongs are foraging on a diversity of avian prey; they switch to a diet composed largely of fairy-wren nestlings later in the breeding season (Prawiradilaga 1996).

Table 3. Comparison of the population demography of pair-dwelling and cooperatively breeding species in the Pardalotidae

The data presented are restricted to long-term studies conducted on colour-banded populations of birds. The length of the breeding season was calculated from the original data using the index of MacArthur (1964)

		Social system	Survival			Breeding season (months)	Productivity (fledglings per pair or group)	Post-fledging survival to independence (%)	Reference
			Male	Female	Adult				
Brown thornbill <i>Acanthiza pusilla</i>	(i)	Pair-dwelling	0.63	0.62	0.63	4.0	1.57	64	This study
	(ii)	Pair-dwelling	–	–	0.87	3.8	–	–	Bell and Ford (1986)
Grey gerygone <i>Gerygone igata</i>		Pair-dwelling	–	–	0.82	3.6	4.04	54	Gill (1982)
Buff-rumped thornbill <i>Acanthiza reguloides</i>	(i)	Cooperative	–	–	0.58	3.3	1.11	83	Bell and Ford (1986)
	(ii)	Cooperative	–	–	–	4.6	1.70	–	Ebert, pers. comm.
Yellow-rumped thornbill <i>Acanthiza chrysorrhoa</i>	(i)	Cooperative	–	–	–	5.5	3.60	–	Ford (1963)
	(ii)	Cooperative	0.68	0.59	0.64	3.8	1.45	–	Ebert, pers. comm.
White-browed scrubwren <i>Sericornis frontalis</i>		Cooperative	0.85	0.79	0.82	5.4	2.80	63	Magrath and Yezerinac (1997)
Speckled warbler <i>Chthonicola sagittata</i>		Cooperative	0.69	0.61	0.66	5.0	0.84	64	Gardner, pers. comm.

Post-fledging survival to independence at six weeks tended to increase over the breeding season. We are not certain why this should be the case. Most mortality occurred in the first few days after fledging, which suggests that predation may play a role. Perhaps pied currawongs expend less effort hunting fledgling thornbills later in the season when their principal prey, nestling fairy-wrens, are at their most abundant. Alternatively, harsher climatic conditions in September may simply make it harder for fledglings to survive the first few days out of the nest early in the season.

Demography of pair-dwelling and cooperatively breeding species in the Pardalotidae

Cooperative breeding in birds is rare and has generally been assumed to be a derived condition that has evolved from pair-breeding (Lack 1968). Recent phylogenetic analyses, however, suggest that evolution can progress in both directions (Peterson and Burt 1992; Cockburn 1998). Within the Pardalotidae it is now apparent that pair-breeding has evolved independently at least four times, twice within the genus *Acanthiza*, once within the genus *Gerygone* and once within the genus *Sericornis* (Nicholls *et al.* in press). Examination of the demography of species within the Pardalotidae provides little evidence to suggest that pair-breeding within the family is linked to an increase in adult mortality, a short breeding season with reduced productivity, or high levels of predation post-fledging (Table 3). This conclusion is consistent with those of a comparative analysis that found no difference between the life-history traits of cooperatively and non-cooperatively breeding Corvida within Australia (Poiani and Jermy 1994).

Arnold and Owens (1998, in press) have argued that while variation in life history is important in determining which avian lineages are predisposed to cooperative breeding, ecological factors will determine which species in these predisposed lineages actually breed cooperatively. However, there appear to be no broad ecological factors that correlate with the occurrence of pair- or cooperative breeding within the Pardalotidae. Ford *et al.* (1988) and Cockburn (1996) have suggested that species living in dense habitat are more likely to breed in pairs. Although brown thornbills do breed in habitat with dense understorey, the two species of *Acanthiza* that breed exclusively in rainforest appear to both breed cooperatively (Nicholls *et al.* in press). Similarly, although the one pair-breeding member of *Sericornis* (*S. citreogularis*) typically breeds in dense forest gullies the cooperatively breeding congeners also breed in dense habitat (Keast 1978; Nicholls *et al.* in press).

The absence of any life-history or broad ecological correlates with mating system in the Pardalotidae makes it unclear why pair-breeding has evolved several times in this family. Cockburn (1996) has suggested that although there may be general advantages to juveniles of prolonged philopatry and extended parental care in the Corvida, the costs of juvenile retention to adults may sometimes result in a conflict of interest between parents and young. The active eviction of young from their natal territory in the pair-breeding white-throated treecreeper, *Cormobates leucophaea*, which does not occur in two cooperatively breeding species (*Climacteris picumnus* and *C. erythrops*), provides evidence of such conflict (Noske 1991). Retention of juveniles may be costly to parents if food supply is limited outside the breeding season. This appears unlikely to result in the evolution of pair-breeding in brown thornbills as juveniles frequently remain in their natal territory until just before the start of the following breeding season. Furthermore, age-specific nestling mass does not decline towards the end of the breeding season, suggesting that dispersal is unlikely to be prompted by a reduction in food availability (Green, unpublished data). An alternative cost to parents of young remaining on their natal territory is conflict over reproduction. The species of *Acanthiza* have extremely large testes for their body mass, which suggests that sperm competition could be intense (Birkhead and Møller 1992). Further study focussed on reproductive conflict between parents and young may therefore shed light on the evolution of pair-breeding in *Acanthiza*.

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