

Post-fledging care, philopatry and recruitment in brown thornbills

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Summary

1. We describe patterns of post-fledging care, dispersal and recruitment in four cohorts of brown thornbills *Acanthiza pusilla*. We examine what factors influence post-fledging survival and determine how post-fledging care and the timing of dispersal influence the probability of recruitment in this small, pair breeding, Australian passerine.

2. Fledgling thornbills were dependent on their parents for approximately 6 weeks. Male fledglings were more likely than female fledglings to survive until independence. For both sexes, the probability of reaching independence increased as nestling weight increased and was higher for nestlings that fledged later in the season.

3. The timing of dispersal by juvenile thornbills was bimodal. Juveniles either dispersed by the end of the breeding season or remained on their natal territory into the autumn and winter. Juveniles that delayed dispersal were four times more likely to recruit into the local breeding population than juveniles that dispersed early.

4. Delayed dispersal was advantageous because individuals that remained on their natal territory suffered little mortality and tended to disperse only when a local vacancy was available. Consequently, the risk of mortality associated with obtaining a breeding vacancy using this dispersal strategy was low.

5. Males, the more philopatric sex, were far more likely than females to delay dispersal. Despite the apparent advantages of prolonged natal philopatry, however, only 54% of pairs that raised male fledglings to independence had sons that postponed dispersal, and most of these philopatric sons gained vacancies before their parents bred again. Consequently, few sons have the opportunity to help their parents. Constraints on delayed dispersal therefore appear to play a major role in the evolution of pair-breeding in the brown thornbill.

Key-words: delayed dispersal, natal philopatry, nestling weight.

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Introduction

For many species of birds and mammals, much of the variance in lifetime reproductive success among females can be attributed to differences in the survival of their offspring until recruitment (Clutton-Brock 1988). Factors that influence offspring survival until recruitment are therefore likely to play a major role in the evolution of life history traits. Consequently, studies examining what factors influence survival both during the period that offspring are dependent on their parents, and

from independence until recruitment, are important in understanding the adaptive significance of variation in life history traits among species.

Juvenile survival is frequently related positively to nestling weight or condition in birds (e.g. Magrath 1991) and birth weight in mammals (e.g. Clutton-Brock, Albon & Guinness 1988). This pattern may arise because body mass or condition has a direct affect on juvenile survival. For instance, heavy individuals may be better able to cope with short periods of food shortage than light individuals, or mass may affect dominance and hence the ability to access resources (Perrins 1965; Garnett 1981). Alternatively, size-dependent survival may arise indirectly, as differences in parental or territory quality affect both the size, and the subsequent survival, of juveniles.

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The timing of breeding also often influences juvenile survival (reviewed by Daan *et al.* 1988). In single-brooded species of birds, or mammals that reproduce only once a year, the probability that a juvenile survives to independence frequently declines as the breeding season progresses (e.g. Perrins 1970; Guinness, Clutton-Brock & Albon 1978). Juvenile survival may decline because of reduced food availability or because older, more experienced, females breed earlier in the year (Daan *et al.* 1988). However, in multibrooded birds and in mammals that produce multiple litters in a year seasonal variation in juvenile survival is often less pronounced (e.g. Ringsby, Sæther & Solberg 1998).

There is now a considerable amount of information on dispersal patterns in birds and mammals (Greenwood 1980; Clarke, Sæther & Røskaft 1997). Evolutionary interpretations focus on either the female-biased dispersal of birds and the male-biased dispersal of mammals (Pusey 1987), or delayed dispersal and group-living in the young of cooperative breeders (Emlen 1982; Stacey & Ligon 1987, 1991). Less attention has been paid to intrasexual variation in dispersal behaviour, and how different dispersal strategies influence the probability of recruitment. However, there is some evidence that hatch or birth dates (Nilsson 1989), dominance status (Ellsworth & Belthoff 1999), natal territory quality (Komdeur 1992) and population density (Hanski, Peltonen & Kaski 1991) may influence individual dispersal in both birds and mammals.

In this paper we examine juvenile survival and dispersal in the brown thornbill (*Acanthiza pusilla* (White), Acanthizidae), a small, pair-breeding, passerine endemic to Australia. The endemic Australian passerines (Corvida) have life histories typified by small clutch sizes, long breeding seasons with multiple nesting attempts, an extended period of post-fledging care, high juvenile survival and high adult survival (Rowley & Russell 1991). Parental care during the post-fledging period may be more important than nestling weight or the timing of breeding in explaining variation in juvenile survival and recruitment in species with these life history traits. Cooperative breeding is also far more prevalent among the Corvida than the Passerida, the well-studied Northern Hemisphere passerines (Russell 1989), and is thought to be the ancestral trait for some genera within this clade (e.g. *Aphelocoma*, Peterson & Burt 1992; *Acanthiza*, Nicholls *et al.* 2000). Cockburn (1996) has suggested that while prolonged philopatry may be advantageous to juveniles in both cooperative and non-cooperative species in the Corvida, the costs of juvenile retention to adults may sometimes result in the evolution of pair-breeding. In this study, we therefore aimed to: (1) examine what factors influence post-fledging survival to independence, (2) evaluate what prompts the dispersal of juveniles and (3) investigate how post-fledging care and the timing of dispersal influence the probability of recruitment in brown thornbills. We also discuss the implications of our results for life history evolution in the Corvida.

Methods

STUDY SPECIES AND POPULATION

The brown thornbill is a small (≈ 7 g) passerine that is common in the eucalypt forests and woodlands of south-east Australia (Blakers, Davies & Reilly 1984). Males are larger and heavier than females (Green & Cockburn 1999). We studied a colour-banded population of brown thornbills in and adjacent to the Australian National Botanic Garden in Canberra, Australia, between July 1995 and August 1999. The vegetation in the 40-ha Botanic Gardens consists of both plantations of Australian native plants, and natural woodland that is contiguous with a large area (≈ 9 km²) of dry sclerophyll forest in Canberra Nature Park. Brown thornbills bred both in the Garden and in the adjacent reserve. Approximately 30 pairs maintained permanent territories in the 80 ha study area. Pairs defended small (≈ 2 ha) territories year round. Females laid up to three clutches (98% of clutches contained three eggs) but rarely fledged more than one brood during a breeding season that extended from late July (mid-winter) to December (early summer). Females built nests and incubated without assistance, but males contributed to nest defence and the provisioning of nestlings and fledglings (Green & Cockburn 1999).

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 and associated young, to determine when colour-banded juveniles gained a breeding vacancy or new birds entered the population, and to document adult mortality. During the breeding season we monitored pairs at least three times a week to ensure that we documented all nesting attempts even if they failed during incubation (73% of nests were found before laying was completed, $n = 173$). Hatching and fledging dates were determined by daily visits to the nest towards the end of the nestling period, respectively. The number of young fledging was estimated as the number banded, less the number known to have died before fledging. If the nest was damaged or found empty before the expected fledging date, only those seen alive were assumed to have fledged. Green & Cockburn (1999) provide additional details about the study area and study population.

NESTLING AGE AND STATUS

Nestlings were usually aged to within a day as nests were checked daily between 07:00 h and 10:00 h around the time of hatching. The few broods that were found when parents were provisioning nestlings, or that hatched prior to the routine daily visits were aged by comparing their plumage with the plumage of nestlings of known age.

Most clutches hatched synchronously (68%; Green & Cockburn 1999). Where the clutch did not all hatch on the same day, we identified the younger nestlings at

the time of banding using plumage development. We classified nestlings as being either early hatched young, if they hatched before or on the same day as their brood mates, or late hatched young.

NESTLING SEX, MASS AND CONDITION

We sexed all nestlings using a simple PCR-based molecular technique (see Griffiths *et al.* 1998 for details of the method) using DNA extracted from a small blood sample ($\approx 40 \mu\text{L}$) taken from the brachial vein. Nestlings were usually weighed, banded and bled when they were 6–9 days. In 1997 and 1998, nestlings were also weighed when they were 11–12 days. For these nestlings we also measured wing-length, from the carpal joint to the tip of the longest primary, to the nearest mm. To control for differences in the age at which nestlings were weighed we fitted separate logistic growth curves to both male and female nestlings (male nestling mass = $8.15/(1 + \exp[-0.48(\text{age} - 5.1)])$, $r^2 = 0.84$, $n = 204$; female nestling mass = $7.51/(1 + \exp[-0.39(\text{age} - 4.5)])$, $r^2 = 0.80$, $n = 185$) and used the residuals from these growth curves as an estimate of the relative mass of each nestling. We estimated the condition for those nestlings weighed and measured when 12 days old using the residuals from the weight–wing length regression (mass = $3.93 + [0.11 \times \text{wing}]$, $n = 78$, $r^2 = 0.13$, $P < 0.001$).

POST-FLEDGING CARE, JUVENILE SURVIVAL AND THE TIMING OF DISPERSAL

We conducted focal observations on 38 fledglings (24 broods) produced by 19 females in order to determine the duration of parental care, and to examine factors influencing provisioning rate during the fledgling period. Focal observations were conducted between mid-September and early January in 1996/97 and 1997/98. Observations, which were conducted at weekly intervals, began when fledglings were 2 weeks old and ended when fledglings were either no longer resident on their natal territory or had reached 8 weeks of age. All observations took place at 09.00–12.00 h and 14.00–17.00 h and lasted for 30 min. During focal observations we counted the number of times that a fledgling was fed and the identity of the parent providing each food item. To determine whether parental aggression prompted dispersal we also recorded the number of times the focal fledgling was displaced or chased by either parent during the 30-min focal observation.

Individual nestlings appeared to be fed predominantly by only one of their parents. We therefore conducted additional focal observations, in both 1996 and 1997, to determine which parent was provisioning a further eight fledglings (four broods). Each fledgling was observed on two occasions, separated by at least two days, when they were 3–4 weeks old. These focal observations lasted for between 20 and 30 min.

We monitored the survival of all colour-banded young that were known to have fledged ($n = 159$) until

they reached nutritional independence at 6 weeks (see Results) using weekly censuses that commenced when fledglings were 2 weeks old. No fledglings of 2–6 weeks that were missed in a census were ever subsequently found to have been alive. If a fledgling disappeared from their natal territory after 6 weeks we assumed they had dispersed rather than died. The timing of dispersal for those fledglings that survived to independence was determined either from the weekly censuses conducted during the breeding season or from the monthly censuses conducted from January until the start of the following breeding season in late July.

RECRUITMENT OUTSIDE THE STUDY AREA

We attempted to locate colour-banded brown thornbills that had dispersed from our study area by conducting systematic searches outside the study area. Searches were conducted during the autumn and winter (April–June) following each of the four breeding seasons. We searched all suitable habitat within 3 km of the study area in 1996, 1997 and 1998, and all habitat within 0.5 km of the study area in 1995. In each year, we split the area to be searched into blocks of approximately 25 ha and located thornbills by walking any available trail through each block, and walking along every ridge and gully within each block. Blocks were searched once per year. All thornbills located visually or by call (15–30/block) were examined for bands. Observers conducting systematic searches for other species in Canberra Nature Park also occasionally located banded birds. We relocated all the banded individuals found during any of these searches at the start of the next breeding season (August) to confirm that they had survived long enough to enter the breeding population. Additional nonsystematic searches were conducted throughout Canberra by volunteers from the Canberra Ornithologists Group without locating any additional banded birds. The number of territories that individuals traversed to obtain a vacancy was estimated by dividing the straight-line distance travelled from the centre of their natal territory by the mean diameter of a brown thornbill territory in natural bushland (≈ 160 m).

STATISTICAL ANALYSIS

Our data examining juvenile survival and dispersal were structured and not independent as individual fledglings often had siblings that had been raised in either the same brood or other broods produced by their parents. We therefore analysed our data using mixed models incorporating both random and fixed effects (Bennington & Thayne 1994), with ‘pair identity’ being specified as a random factor in all models. A new pair was considered to have formed when either member was replaced following a death or divorce. We also tested whether there was any evidence of dependency at the brood level by specifying ‘brood identity’ as an additional random factor in all mixed models. We found that there was

little variance associated with 'brood identity': the standard error of the estimate for the variance component was always large compared to the estimate, so 'brood identity' was not included as a random factor in our models.

Models were fitted using Genstat 5.4.1 for Windows (Genstat 5 Committee 1997). Continuous dependent variables were analysed using the restricted maximum likelihood (REML) procedure, while dichotomous dependent variables were analysed using the generalized linear mixed modelling (GLMM) procedure. When fitting models using either the REML or GLMM procedure we initially fitted a full model with all explanatory variables and their interaction terms. A final model was selected by progressively eliminating non-significant interaction terms, and then non-significant main effects until only significant terms remained. In the case of non-significant main effects the statistics presented refer to the results of dropping the term of interest from the final model plus the non-significant term. When examining continuous dependent variables the significance of a term was determined using the change in deviance when the term was dropped from the model. In contrast, when analysing dichotomous variables the significance of a term was determined using the Wald statistic for that term when it was the last to be entered in a model (see Genstat 5, Genstat 5 Committee 1997 for rationale). In all analyses residual plots and normal probability plots were used to examine for unequal variance and deviations from normality among residuals. Natural log transformations were applied to feeding rate and dispersal distance data so that they conformed to the assumptions of the mixed models. Model predictions in the text are presented with either standard errors or the average standard error of differences (SED).

Results

POST-FLEDGING CARE

Individual fledglings were usually fed almost entirely by one of their parents (44 of 46 fledglings; 25/26 broods), either because females re-nested and males consequently cared for all fledglings (nine fledglings; eight broods), a single parent cared for all fledglings (eight fledglings; five broods) or broods were divided with each parent providing more than 90% of all food delivered to individual fledglings (27 fledglings; 12 broods). Where broods were divided, males and females were as likely to take care of sons as they were daughters (males: 11 sons/6 daughters, females: 8 sons/10 daughters; $\chi^2_1 = 1.5$, $P = 0.22$).

Fledglings were dependent on their parents for food until they were 6 weeks old (Fig. 1). The amount of food received by a fledgling began to decline when they were 5 weeks old, although they continued to be fed at a low rate for a further 3 weeks (age effect: $\chi^2_6 = 266$, $P < 0.0001$). Post-fledging feeding rates also declined

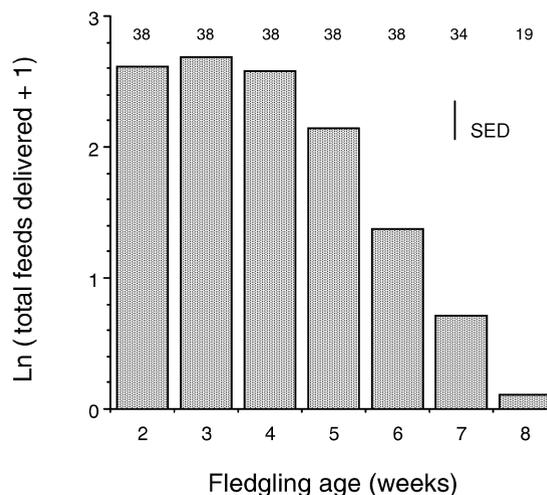


Fig. 1. Relationship between fledgling age and the amount of food delivered by their parents per 30-min focal observation. Bars show the predicted means from the REML model controlling for fledging date and the number of fledglings provisioned by the parent providing care. The line shows the average standard error of differences (SED).

across the breeding season (date effect: $\chi^2_1 = 8.1$, $P = 0.004$) and were affected by the number of fledglings in a parent's care (REML model predictions: one fledgling, $\ln [\text{total feeds} + 1] = 1.86$, two or more fledglings, $\ln [\text{total feeds} + 1] = 1.63$, $\text{SED} = 0.08$; workload effect: $\chi^2_1 = 7.3$, $P = 0.007$). Male thornbills tended to feed their fledglings at a higher rate than females (REML model predictions: males, $\ln [\text{total feeds} + 1] = 1.79$, females, $\ln [\text{total feeds} + 1] = 1.64$, $\text{SED} = 0.09$; parent effect: $\chi^2_1 = 2.9$, $P = 0.09$). Post-fledging feeding rates were not affected by the sex of the fledgling, the location of the territory, the time of day the focal observation was conducted or the year of the study (all $P > 0.10$).

Juvenile thornbills began to disperse when between 6 and 7 weeks old. None of the 38 fledglings that were the subject of focal observations disappeared from their natal territory between the ages of 2 and 6 weeks, but 50% had disappeared by 8 weeks (see sample sizes in Fig. 1). There was little evidence to suggest that dispersal was prompted by an increase in parental aggression. Males were occasionally observed to chase fledglings when fledglings were 6–8 weeks ($n = 5$ cases). However, these chases were short and directed only at fledglings that either repeatedly harassed them for food or approached a subsequent nesting attempt. Females were never observed to behave aggressively towards fledglings.

SURVIVAL TO INDEPENDENCE

Sixty-four per cent (102/159) of the colour-banded fledglings survived to nutritional independence at 6 weeks. Mortality was concentrated in the first few days after fledging; 51 of 57 fledglings that died before reaching independence disappeared within 2 weeks of fledging. Male fledglings were more likely to survive to independence than female fledglings (Fig. 2; sex

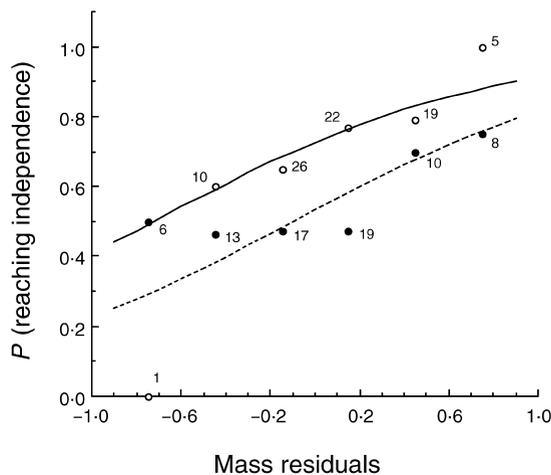


Fig. 2. Relationship between the standardized nestling mass of male and female fledglings and post-fledging survival until independence at 6 weeks. Nestling mass was standardized using the residuals from sex-specific logistic-growth curves. Lines show predictions from GLMM models controlling for fledging date (males, plain line; females, dashed line). Points show mean probabilities of reaching independence at 0.3-g intervals with associated sample sizes (males, open circles; females, closed circles).

effect: $\chi^2_1 = 4.8$, $P = 0.03$). For both sexes, the probability of surviving to independence increased as nestling weight increased (Fig. 2; mass effect: $\chi^2_1 = 6.2$, $P = 0.03$), and was higher for nestlings that fledged later in the season (date effect: $\chi^2_1 = 4.6$, $P = 0.03$).

The effect of nestling mass on post-fledging survival did not arise simply because of hatch order effects on the mass of nestlings within broods (REML model predictions: mass residuals of early hatched nestlings = 0.02 g, late-hatched nestlings = 0.08 g, SED = 0.08; $\chi^2_1 = 1.9$, $P = 0.17$). Furthermore, hatch order had no effect on post-fledging survival to independence after controlling for sex, mass and fledging date (GLMM model predictions: early hatched nestlings = 0.63 ± 0.05 , late-hatched nestlings = 0.71 ± 0.11 ; hatch order effect: $\chi^2_1 = 1.0$, $P = 0.32$). The number of young fledged, the location of the territory and the year of the study also had no effect on survival to independence (all $P > 0.10$).

TIMING OF DISPERSAL

Natal dispersal was bimodal: juvenile thornbills either dispersed early and left their natal territory by the end of February, or delayed dispersal and remained in their natal territory into the autumn and winter (Fig. 3a). Males were far more likely to delay dispersal than females (males 25/63 juveniles, females 1/39 juveniles; $\chi^2_1 = 17.6$, $P < 0.0001$). Many of the males that finally 'dispersed' in June and July did not attempt to move to a vacancy in an established territory, but stopped associating with their parents and acquired a small territory by 'budding' (12 of 18 'dispersers'). Territories formed by 'budding' were initially established at the periphery of the male's natal territory but expanded into territory

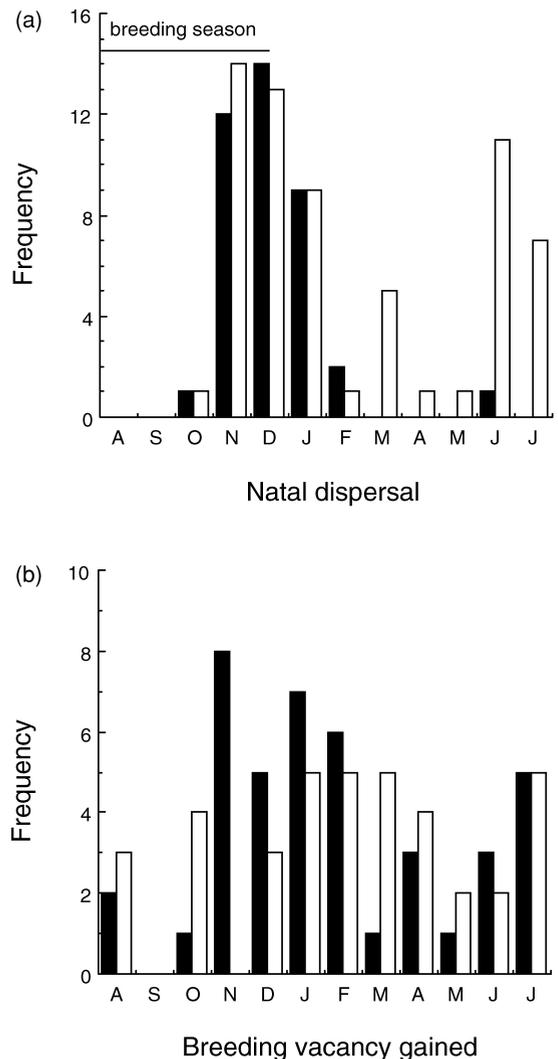


Fig. 3. Frequency distributions showing (a) the timing of natal dispersal of fledglings raised in the study population and (b) the time that breeding vacancies are taken up in the study area. Filled bars are females, open bars are males.

previously occupied by neighbours if an immigrant female joined the male.

Delayed dispersal was observed in only 54% of territories where one or more son was raised to independence ($n = 46$). Furthermore, a maximum of one male juvenile ever delayed dispersal even if pairs raised two or more sons to independence ($n = 17$ cases). We were unable to predict which males would remain in their natal territory and not disperse at the end of the breeding season. The probability that a male juvenile delayed dispersal was not influenced by their mass as a nestling ($\chi^2_1 = 0.0$, $P = 1.0$), their hatch order within the brood (GLMM model predictions: early hatched = 0.39 ± 0.08 , late hatched = 0.44 ± 0.20 ; $\chi^2_1 = 0.1$, $P = 0.75$) or the number of male siblings present at independence (GLMM model predictions: 0 sibs = 0.48 ± 0.11 , one or more sib = 0.32 ± 0.09 ; $\chi^2_1 = 1.8$, $P = 0.18$), suggesting that intrabrood dominance does not play a major role in dispersal decisions. In territories with two or more juvenile males there was also no suggestion that the

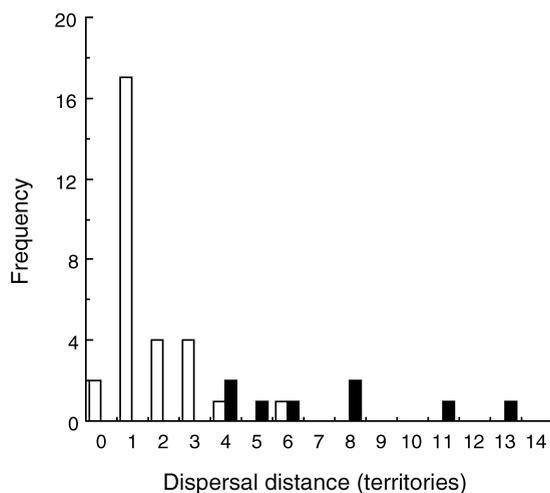


Fig. 4. Frequency distribution showing male (□) and female (■) natal dispersal distances (territories traversed) in brown thornbills.

male that stayed was heavier than his siblings prior to fledging (the heavier sib stayed in six of 11 cases, signed-rank test = 3.5, $P = 0.78$). The location of the territory had no effect on whether a male delayed dispersal (GLMM model predictions: watered plantation = 0.40 ± 0.12 ; natural woodland = 0.39 ± 0.09 ; $\chi^2_1 = 0.1$, $P = 0.75$). The date or year a juvenile fledged, the sex or workload of the parent that had provided care and the density of adult males in the study area at the end of the breeding season also had no effect on whether a male delayed dispersal (all $P > 0.1$).

JUVENILE RECRUITMENT

Juvenile females were most likely to gain a breeding vacancy in the study area between November and February, when they filled vacancies left by adult females that had died during the breeding season, and between late June and early August, when they joined juvenile males that had established new territories by budding (Fig. 3b). The majority of females that settled within the study area originated from outside the study area (40/42 females). In contrast, very few of the male juveniles that settled within the study area came from outside the study area (6/38). There was also less variation in the timing of male recruitment as vacancies resulting from mortality early in the breeding season could be filled by young males from the previous year that had obtained a territory but had failed to attract a mate, while vacancies later in the year were filled by juveniles that had hatched earlier in the same breeding season (Fig. 3b).

Forty-six per cent (29/63) of the male fledglings and 21% (8/39) of the female fledglings that were known to have survived until independence were found to gain a breeding vacancy either inside or outside the study area. Male and female juveniles differed in the distance that they travelled to obtain a breeding vacancy (Fig. 4; sex effect: $\chi^2_1 = 21.2$, $P < 0.0001$). Males moved 0–900 m (median distance = 1 territory) while females moved

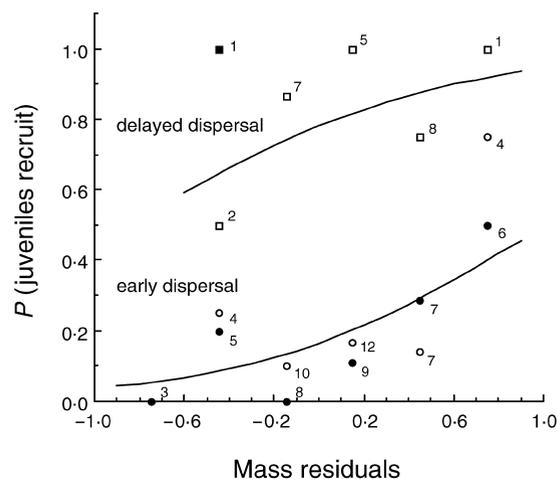


Fig. 5. Relationship between the standardized nestling mass of male and female thornbills and the probability that independent young recruit into the breeding population. Nestling mass was standardized using the residuals from sex-specific logistic-growth curves. Lines show predictions from GLMM models controlling for hatch order within the brood. Points show mean probabilities of recruitment at 0.3-g intervals for males (open symbols) and females (filled symbols) with associated sample sizes (early dispersal, circles; delayed dispersal, squares).

600–2000 m (median distance = seven territories). Systematic searches for juveniles were conducted in all habitat within 3 km of the study area so we are likely to have located all male recruits, but may have failed to locate a small proportion of the female recruits. Recruitment and dispersal distances of females may therefore be underestimated.

The distance both male and female juveniles moved to obtain a vacancy was dependent on the dispersal strategy used: juveniles that dispersed early travelled significantly further to gain a breeding vacancy (males: early = 2.4 ± 0.7 territories, $n = 8$, late = 1.3 ± 0.2 , $n = 21$; females: early = 7.9 ± 1.2 , $n = 7$, late = 4, $n = 1$; timing of dispersal effect: $\chi^2_1 = 9.1$, $P = 0.003$). The date or year a juvenile fledged, their mass as a nestling or hatch order within a brood, the number of siblings raised to independence, the sex or workload of the parent that cared for them and the location of the territory all had no effect on how far they travelled to gain a breeding vacancy (all $P > 0.10$).

The probability that a juvenile thornbill gained a breeding vacancy and lived to breed for the first time was influenced by three factors: the time that they dispersed from their natal territory, their weight as a nestling and the order they hatched within a brood. Juveniles that delayed dispersal were four times more likely to recruit than juveniles that dispersed early, and the probability of recruitment increased with nestling mass for both early and late dispersing juveniles (Fig. 5; timing of dispersal effect: $\chi^2_1 = 22.2$, $P < 0.0001$; mass effect: $\chi^2_1 = 4.9$, $P = 0.03$). In addition, juveniles that hatched early or at the same time as their nestmates were more likely to recruit than juveniles that hatched late (GLMM model predictions: early hatched = 0.38 ± 0.04 ,

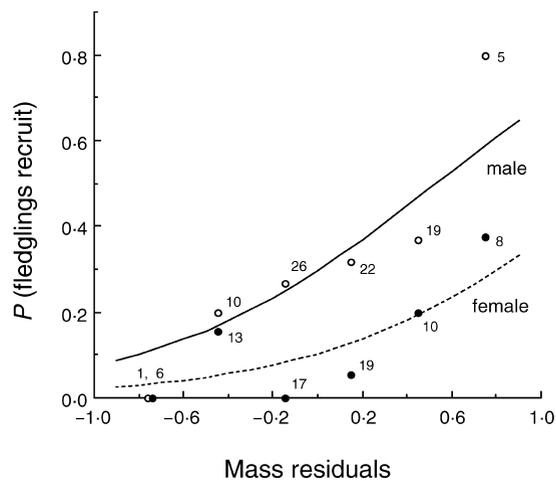


Fig. 6. Relationship between the standardized nestling mass of male and female fledglings and their probability of recruiting into the breeding population. Nestling mass was standardized using the residuals from sex-specific logistic-growth curves. Lines show predictions from GLMM models (males, plain line; females, dashed line). Points show mean probabilities of recruitment at 0.3-g intervals with associated sample sizes (males, open circles; females, closed circles).

late-hatched = 0.16 ± 0.07 ; $\chi^2_1 = 3.9$, $P = 0.05$). After controlling for dispersal, mass and hatch order effects, there was no difference in the recruitment of male and female juveniles (Fig. 5; sex effect: $\chi^2_1 = 0.0$, $P = 1.0$). The date or year a juvenile fledged, the number of fledglings raised to independence, the sex or workload of the parent that provided care, the location of the territory, and the density of adults in the study area at the end of the breeding season all had no effect on juvenile recruitment (all $P > 0.25$).

NESTLING MASS AND RECRUITMENT

During the course of this study 23% (37/159) of the young that were known to have fledged recruited into the local breeding population. We found that males were more likely to recruit than females, and that for both sexes, the probability of recruitment increased as nestling weight increased (Fig. 6; sex effect: $\chi^2_1 = 9.3$, $P = 0.002$; mass effect: $\chi^2_1 = 8.7$, $P = 0.003$). Although hatch order had an effect on juvenile survival between independence and recruitment, hatch order did not have a significant effect on the probability a fledgling was recruited (GLMM model predictions controlling for sex and mass effects: early hatched = 0.22 ± 0.04 , late-hatched = 0.13 ± 0.07 , $\chi^2_1 = 1.0$, $P = 0.32$). The date or year a nestling fledged, the number of fledglings in a brood, and the location of the territory all had no effect on the probability that a fledgling would gain a breeding vacancy (all $P > 0.25$).

Discussion

We found that brown thornbills vary in their dispersal strategy. Females tended to disperse early whereas males

either dispersed at the end of the breeding season or postponed dispersal and attempted to fill local vacancies when they became available. Juveniles that delayed dispersal suffered little mortality and were significantly more likely to gain a breeding vacancy in the local breeding population. This study demonstrates that delayed dispersal is not a strategy confined to species that breed cooperatively and suggests that prolonged philopatry may be associated with direct fitness benefits to offspring in both non-cooperative and cooperative species of Corvidae. Despite the apparent advantages of delayed dispersal, however, only half the pairs of brown thornbills which produced independent young retained offspring on their territory. Most of these philopatric sons gained vacancies before their parents bred again. As a result, few juvenile thornbills have the opportunity to help their parents. Constraints on delayed dispersal therefore appear to play a major role in the evolution of pair-breeding in the brown thornbill.

POST-FLEDGING SURVIVAL

Post-fledging survival to independence of brown thornbills was influenced by their mass as a nestling, the date on which they fledged and their sex. This is the first study to demonstrate that post-fledging survival of an Australian endemic passerine improves with nestling mass, although several studies on passerines from the Northern Hemisphere have found that the probability of surviving to independence is related to nestling body mass or body condition (e.g. dunnocks *Prunella modularis* (Linnaeus), Davies (1986); great tits *Parus major* Linnaeus, Perrins 1965, Tinbergen & Boerlijst (1990); song sparrows *Melospiza melodia* (Wilson), Hochachka & Smith 1991; and blackbirds *Turdus merula* Linnaeus, Magrath 1991).

Post-fledging survival may be influenced by nestling mass because heavier individuals are in better condition and are therefore better equipped to cope with short periods without food. We found that heavy thornbill nestlings are also in good condition ($r = 0.93$, $n = 78$, $P < 0.0001$) providing some support for this explanation. In addition, we found that male nestlings are, on average, in better condition than female nestlings (males = 0.29 ± 0.06 g, $n = 44$, females = -0.37 ± 0.07 g, $n = 34$, ANOVA, $F = 56.8$, d.f. = 1, $P < 0.0001$) which may help explain sex differences in post-fledging survival in the brown thornbill. Alternatively, mass and sex effects on post-fledging survival in brown thornbills may both arise because size influences dominance and hence access to resources provided by parents or vulnerability to predation. However, this explanation appears unlikely as we may then have expected other factors that could influence dominance, such as hatch order, to affect survival to independence. Furthermore, sex and nestling mass do not have any effect on the amount of food fledglings obtain from their parents during the nestling period (sex effect: $\chi^2_1 = 0.5$, $P = 0.48$; mass effect: $\chi^2_1 = 0.3$, $P = 0.58$; sex \times mass interaction: $\chi^2_1 = 0.4$, $P = 0.53$).

Post-fledging survival in birds is also often influenced by the timing of breeding (Daan *et al.* 1988). The survival rate of brown thornbill fledglings improved as the season progressed perhaps because environmental conditions improve dramatically between September and December when the average minimum daily temperature rises from 3.1 to 11.2 °C. Mortality of fledglings was concentrated in the first few days after fledging when they are likely to be most sensitive to environmental conditions, do not fly proficiently and are consequently vulnerable to predators. Other studies on multibrooded species have also found that the relationship between fledging date and survival may be positive (Brinkhof *et al.* 1993; Ringsby *et al.* 1998). In contrast, in most single-brooded species the survival rate of fledglings decreases as the breeding season progresses (Daan *et al.* 1988; Sæther 1990).

JUVENILE SURVIVAL TO RECRUITMENT

The most important factor influencing survival and recruitment of juvenile brown thornbills was the timing of dispersal. Delayed dispersal was advantageous because individuals that remained on their natal territory suffered little mortality and were able to inherit their natal territory (2/26), move into a nearby territory as soon as a vacancy became available (8/26) or acquire a small territory by budding (12/26). Individuals that gained a territory via the latter route could then either attract a mate and expand into territory previously occupied by their neighbours (8/12), or live on their small territory until a local vacancy became available (4/12). Consequently, juveniles that delayed dispersal had a high probability of obtaining a breeding vacancy. Prolonged juvenile philopatry and extended parental investment in retained offspring is linked to fitness benefits in other non-cooperative species of Corvida. For example, male Siberian jays *Perisoreus infaustus* (Linnaeus) that postpone dispersal for a year or more subsequently obtain territories of higher quality, and have higher lifetime reproductive success, than males that disperse in their first summer (Ekman, Bylin & Tegelstrom 1999). The results of our study and the long-term study on Siberian jays are important, as they demonstrate that delayed dispersal can have fitness benefits for offspring of non-cooperative as well as cooperative species. These results also suggest that delayed dispersal in cooperative species in the Corvida are more likely to be driven by direct fitness benefits to offspring rather than indirect benefits accrued by raising non-descendent kin.

Male thornbills were far more likely than females to delay dispersal and obtain the advantages associated with natal philopatry. This pattern may result because the benefits of early dispersal may be greater for females than males. However, our data suggest that early dispersing females were no more likely to recruit than early dispersing males (GLMM model predictions: males = 0.17 ± 0.06 , females = 0.17 ± 0.06 ; sex effect:

$\chi^2_1 = 0.0$, $P = 1.0$). Furthermore, the date on which early dispersers left their natal territory did not affect the recruitment of either males or females (date effect: $\chi^2_1 = 0.1$, $P = 0.75$, sex \times date interaction: $\chi^2_1 = 0.8$, $P = 0.37$). Alternatively, females may be less likely to delay dispersal because they disperse a greater distance than males and are therefore less likely to benefit from spending the autumn and winter on their natal territory. Female-biased dispersal is extremely common in birds (Greenwood 1980; Clarke *et al.* 1997). Greenwood (1980) argued that sex biases in dispersal arose because male birds, which often defend resource-based territories, are more likely to benefit from remaining near their natal area, while females will benefit from dispersal as it allows them to assess and choose among males and/or to avoid inbreeding.

Nestling mass also has a significant effect on recruitment in thornbills. This result is surprising since most studies on northern hemisphere passerines, which do not have such an extended period of post-fledging care, find that nestling weight does not influence juvenile survival after young have reached independence (Magrath 1991; but see Sullivan 1989). It is possible that the effect of nestling mass on recruitment arises because parents that produce heavier nestlings also provide better care during the fledgling period. Alternatively, since nestling weight reflects differences in structural size as well as differences in condition in brown thornbills ($r = 0.36$, $n = 78$, $P = 0.001$), larger, heavier individuals may be dominant to smaller, lighter individuals and therefore at an advantage when attempting to disperse successfully. This may also explain why hatch order, which often influences dominance in birds (e.g. Hahn 1981; Stanback 1994), has a significant effect on recruitment in brown thornbills.

IMPLICATIONS FOR LIFE HISTORY EVOLUTION IN THE CORVIDA

Small clutch sizes in tropical and southern hemisphere birds are argued to have evolved in response to high nest predation rates, which select for reduced parental activity near the nest, and selection for high numbers of re-nesting attempts (Skutch 1949; Cody 1966). However, predation rates on nestlings can be relatively low in Corvida species (e.g. brown thornbill, 4% per day, Green & Cockburn 1999; white-browed scrubwren *Sericornis frontalis* (Vigors and Horsfield) 5.3% per day, R. Magrath, personal communication). Furthermore, many genera within the Corvida have long nesting periods (Ricklefs 1993), which is at odds with the evidence that higher nest predation rates are usually associated with faster nestling development and shorter nesting periods (Martin 1995). Small clutch sizes and an extended nesting period may both be explained by food limitation, since reduced food availability can lead to both small clutch sizes and a long slow developmental period (Lack 1948, 1968; Martin 1987). Our study suggests that there is likely to be a trade-off between the number and the quality of

nestlings that a brown thornbill can raise. This implies that small clutch sizes are more likely to have evolved in response to a limited food supply than high predation rates.

IMPLICATIONS FOR THE EVOLUTION OF PAIR-BREEDING IN THE ACANTHIZA

Cooperative breeding is likely to be the ancestral trait in the Acanthizidae (Nicholls *et al.* 2000). In order to understand mating system evolution within this family we therefore need to explain why species such as the brown thornbill have evolved pair-breeding, rather than attributing pair-breeding to some phylogenetic lag. There are no obvious differences in either the life history or ecology of pair-breeding and cooperatively breeding species in the Acanthizidae. Pair-breeding species do not have lower annual survival rates or lower productivity than cooperative species (Green & Cockburn 1999) and both pair-breeding and cooperative species are found in all habitat types across the entire geographical range of the family (Nicholls *et al.* 2000). Cockburn (1996) has suggested that while prolonged parental investment and juvenile philopatry may be advantageous for both cooperative and pair-breeding species in the Corvida, the costs of juvenile retention may sometimes be too great for parents to allow offspring to remain on their natal territory. The retention of juveniles may be costly to parents either because they subsequently compete with adults for opportunities to reproduce (Cockburn 1996), or they depress limiting resources on the natal territory (Koenig *et al.* 1992). Our study confirms that delayed dispersal is advantageous for juveniles even in a pair-breeding species, but did not find any evidence for conflict between parents and offspring over the timing of dispersal. Nevertheless, no juveniles were retained on 52% of the territories where one or more juvenile reached independence ($n = 54$). This suggests that even though delayed dispersal has fitness benefits for both parents and offspring the ability of juveniles to remain on their natal territory is constrained, perhaps because food availability on the small permanent territories is limited during the non-breeding season. Juveniles that are likely to have poor foraging skills compared to their parents may then be forced to leave their natal territory to obtain sufficient food.

The prevalence of cooperative breeding in the Acanthizidae suggests that for some species there are likely to be fitness benefits associated with both delayed dispersal and helping behaviour. However, while some brown thornbills have the opportunity to help, because they live adjacent to their parents and fail to attract a mate in their first year, they never assist their parents. These males may not help raise young because the fitness benefits associated with conducting forays in search of breeding vacancies in the local area are greater than the fitness benefits of helping. The benefits of helping may be low because young males are unable to increase the

reproductive success of their parents. Male brown thornbills breeding as a 1-year-old are less likely to fledge young than older males, perhaps because they are less proficient at delivering food to the nest without attracting the attention of predators (Green 2001). Furthermore, help by auxiliary males in a cooperative species from the Acanthizidae, the white-browed scrubwren, was only found to increase reproductive success when females were in their first year (Magrath 2001).

In conclusion, we suggest that three factors appear to have influenced the evolution of pair-breeding in brown thornbills. First, few juveniles have the opportunity to delay dispersal and remain on their natal territory despite the advantages associated with natal philopatry. Secondly, there is a high probability that the few juveniles that do delay dispersal obtain a breeding vacancy, reducing the number that are available to help their parents raise young in subsequent years. Finally, as the individuals that obtain a territory by budding but fail to attract a mate are young males, they may not help because they are more likely to reduce, rather than enhance, the reproductive success of their parents.

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References

- Bennington, C.C. & Thayne, W.V. (1994) Use and misuse of mixed model analysis of variance in ecological studies. *Ecology*, **75**, 717–722.
- Blakers, M., Davies, S.J.J.F. & Reilly, P.N. (1984) *The Atlas of Australian Birds*. Melbourne University Press, Victoria.
- Brinkhof, W.G., Cave, A.J., Hage, F.J. & Verhulst, S. (1993) Timing of reproduction and fledging success in the coot: evidence for a causal relationship. *Journal of Animal Ecology*, **62**, 577–587.
- Clarke, A.L., Sæther, B.E. & Røskaft, E. (1997) Sex biases in avian dispersal – a reappraisal. *Oikos*, **79**, 429–438.
- Clutton-Brock, T.H., ed. (1988) Reproductive Success. *Studies of Individual Variation in Contrasting Breeding Seasons*. University of Chicago Press, Chicago.
- Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1988) Reproductive success in male and female red deer. *Reproductive Success: studies of individual variation in contrasting mating systems* (ed. T.H. Clutton-Brock), pp. 325–343. University of Chicago Press, Chicago.
- Cockburn, A. (1996) Why do so many Australian birds cooperate: social evolution in the Corvida? *Frontiers in Population*

- Ecology* (eds R.B. Floyd, A.W. Sheppard & P.J. De Barro), pp. 541–572. CSIRO Publishing, Melbourne.
- Cody, M.L. (1966) A general theory of clutch size. *Evolution*, **20**, 174–184.
- Daan, S., Dijkstra, C., Drent, R. & Meijer, T. (1988) Food supply and the annual timing of avian reproduction. *Proceedings of the International Ornithological Congress*, **19**, 392–407.
- Davies, N.B. (1986) Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledging success. *Journal of Animal Ecology*, **55**, 123–138.
- Ekman, J., Bylin, A. & Tegelstrom, H. (1999) Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proceedings of the Royal Society London B*, **266**, 911–915.
- Ellsworth, E.A. & Belthoff, J.R. (1999) Effects of social status on the dispersal behaviour of juvenile western screech-owls. *Animal Behaviour*, **57**, 883–892.
- Emlen, S.T. (1982) The evolution of helping. I. An ecological constraints model. *American Naturalist*, **119**, 29–39.
- Garnett, M.C. (1981) Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis*, **123**, 31–41.
- Genstat 5 Committee (1997) *Genstat 5, release 4.1. Command Language Manual*. Numerical Algorithms Group, Oxford.
- Green, D.J. (2001) The influence of age on reproductive performance in the brown thornbill. *Journal of Avian Biology*, **32**, 6–14.
- Green, D.J. & Cockburn, A. (1999) Life history and demography of an uncooperative Australian passerine, the brown thornbill. *Australian Journal of Zoology*, **47**, 633–649.
- Greenwood, P.J. (1980) Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Guinness, F.E., Clutton-Brock, T.H. & Albon, S.D. (1978) Factors affecting calf mortality in red deer. *Journal of Animal Ecology*, **47**, 817–832.
- Hahn, D.C. (1981) Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Animal Behaviour*, **29**, 421–427.
- Hanski, I., Peltonen, A. & Kaski, L. (1991) Natal dispersal and dominance in the common shrew *Sorex araneus*. *Oikos*, **62**, 48–58.
- Hochachka, W. & Smith, J.N.M. (1991) Determinants and consequences of nestling condition in song sparrows. *Journal of Animal Ecology*, **60**, 995–1008.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. & Stanback, M.T. (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, **358**, 493–495.
- Lack, D. (1948) The significance of clutch-size. Part III. Some interspecific comparisons. *Ibis*, **90**, 25–41.
- Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, Bristol.
- Magrath, R.D. (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology*, **60**, 335–351.
- Magrath, R.D. (2001) Group size dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? *Journal of Animal Ecology*, **70**, 370–385.
- Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.
- Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs*, **65**, 101–127.
- Nicholls, J.A., Double, M.C., Rowell, D.M. & Magrath, R.D. (2000) The evolution of cooperative and pair breeding in thornbills *Acanthiza* (Pardalotidae). *Journal of Avian Biology*, **31**, 165–176.
- Nilsson, J.-A. (1989) Causes and consequences of natal dispersal in the marsh tit, *Parus palustris*. *Journal of Animal Ecology*, **58**, 619–636.
- Perrins, C.M. (1965) Population fluctuations and clutch size in the great tit, *Parus major* L. *Journal of Animal Ecology*, **34**, 601–647.
- Perrins, C.M. (1970) The timing of birds' breeding seasons. *Ibis*, **112**, 242–255.
- Peterson, A.T. & Burt, D.B. (1992) Phylogenetic history of social evolution in the Aphelocoma jays. *Animal Behaviour*, **44**, 859–866.
- Pusey, A.E. (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution*, **2**, 298–299.
- Ricklefs, R.E. (1993) Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. *Current Ornithology* (ed. D.M. Power), pp. 199–276. Plenum Press, New York.
- Ringsby, T.H., Sæther, B.E. & Solberg, E.J. (1998) Factors affecting juvenile survival in house sparrow *Passer domesticus*. *Journal of Avian Biology*, **29**, 241–247.
- Rowley, I. & Russell, E. (1991) Demography of passerines in the temperate southern hemisphere. *Bird Population Studies: relevance to conservation and management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 22–44. Oxford University Press, Oxford.
- Russell, E.M. (1989) Co-operative breeding – a Gondwanan perspective. *Emu*, **89**, 61–62.
- Sæther, B.-E. (1990) Age-specific variation in reproductive performance of birds. *Current Ornithology* (ed. D.M. Power), pp. 251–283. Plenum Press, New York.
- Skutch, A.F. (1949) Do tropical birds rear as many young as they can nourish? *Ibis*, **91**, 430–455.
- Stacey, P.B. & Ligon, J.D. (1987) Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist*, **130**, 654–676.
- Stacey, P.B. & Ligon, J.D. (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *American Naturalist*, **137**, 831–846.
- Stanback, M.T. (1994) Dominance within broods of the cooperatively breeding acorn woodpecker. *Animal Behaviour*, **47**, 1121–1126.
- Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Animal Ecology*, **58**, 275–286.
- Tinbergen, J.M. & Boerlijst, M.C. (1990) Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology*, **59**, 1113–1128.

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