



Stepping stones of life: natal dispersal in the group-living but noncooperative speckled warbler

JANET L. GARDNER*, ROBERT D. MAGRATH* & HANNA KOKKO†

*School of Botany and Zoology, Australian National University

†Department of Biological and Environmental Science, University of Jyväskylä

(Received 4 June 2002; initial acceptance 18 July 2002;
final acceptance 31 December 2002; MS. number: 7360)

In most cooperatively breeding birds the offspring of one sex, usually male, delays dispersal to remain on the natal territory and helps its parents to rear subsequent young. Thus delayed dispersal could be the first step in the evolution of cooperative breeding. We studied natal dispersal in a population of the group-living speckled warbler, *Chthonicola sagittata*, based on observations of a colour-banded population over 3 years. Unlike other group-living members of the Acanthizinae, all juvenile males in this population dispersed to settle on foreign territories as subordinates, which do not help rear the young. Speckled warblers showed all the life history traits that are thought to result in a saturated habitat and lead to delayed dispersal: they were sedentary, had high adult survival and had a male-biased sex ratio. However, they differed from other acanthizids in occurring at low density (0.18 birds/ha) on large breeding territories (6–12 ha), with a maximum of two males per territory. This may allow subordinates to live on foreign territories yet avoid aggression from dominants. A benefit of dispersal is that it provides an additional route to gaining a breeding vacancy. Dispersers can acquire vacancies on their new territory or on a neighbour's, but incest avoidance would be likely to constrain nondispersing males to neighbours' territories. A model of relative lifetime success showed that the survival benefits of natal philopatry are unlikely to outweigh this benefit of dispersal.

© 2003 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour.

A territorial bird has four options to obtain a breeding vacancy: (1) disperse directly to a vacancy; (2) disperse to float in search of a vacancy; (3) disperse to queue on a foreign territory; or (4) delay dispersal and queue on the natal territory. The offspring of most pair-breeding bird species leave the natal territory soon after reaching independence to disperse directly to a breeding vacancy or float until one becomes available (Koenig et al. 1992). Floating defines a strategy whereby individuals do not belong to any particular territory but move between territories in search of vacancies (Kempnaers et al. 2001). In contrast to pair-breeders, in the vast majority of cooperatively breeding bird species the offspring of one sex, usually male, delays dispersal to remain on the natal territory and helps the dominant pair to rear subsequent young (Brown 1987). The causes of delayed dispersal have been the focus of considerable interest, as it is widely accepted as the first step in the evolution of cooperative breeding (Brown 1987).

Correspondence: J. Gardner, School of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia (email: Janet.Gardner@anu.edu.au). H. Kokko is at the Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, 40351 Jyväskylä, Finland.

Two hypotheses have been proposed to account for the causes of delayed dispersal. The ecological constraints hypothesis (Emlen 1982) proposes that philopatric males have no opportunity to breed independently because of a lack of mates (Pruett-Jones & Lewis 1990; Walters et al. 1992) or territories (Selander 1964; Woolfenden & Fitzpatrick 1984), because conditions for breeding are harsh (Stacey & Ligon 1987; Komdeur 1992), or because they require time to develop skills appropriate for breeding (Heinsohn 1991). As well as constraints to dispersal, there may be benefits of philopatry (Zack 1990; Stacey & Ligon 1991; Koenig et al. 1992). These include increased survival, increased opportunity to obtain a high-quality territory and kin-selected benefits by helping to rear nondescendant young or increasing the survival of related breeders (Komdeur 1992, 1994; Ekman et al. 1999, 2000). In practice, the two hypotheses are complementary, differing only in the emphasis they place on the benefits of staying versus the costs of leaving, and they have now been incorporated within a broader ecological constraints model (Koenig et al. 1992; Mumme 1992; Emlen 1994; Hatchwell & Komdeur 2000).

The underlying premise of this model is that external factors such as seasonality, predation pressure and habitat

quality act to limit breeding opportunities (habitat saturation), leading to delayed dispersal (Koenig et al. 1992; Mumme 1992; Emlen 1994). Although useful in understanding dispersal strategies of particular species, the hypothesis is not a complete explanation for the evolution of cooperative breeding because the majority of bird species experience constraints on breeding, yet only about 3% of species worldwide are known to breed cooperatively (Brown 1987; Heinsohn et al. 1990; Arnold & Owens 1998). Furthermore, comparative studies have failed to show any ecological factors that consistently differ between cooperative and noncooperative species (Arnold & Owens 1999).

Given the limitations of ecological factors as an explanation for the evolution of delayed dispersal and cooperation, there has been renewed interest in the life history hypothesis which proposes that specific traits, such as longevity, clutch size and dispersal rate, may lead to slow turnover and therefore limited breeding opportunities (Arnold & Owens 1998). Life history traits are highly conserved in evolution (Owens & Bennett 1995) and may therefore explain why cooperation is largely restricted to species within particular taxonomic lineages (Russell 1989; Edwards & Naem 1993; Cockburn 1996; Arnold & Owens 1998). In attempting to identify the roles of life history and ecology, Arnold & Owens (1998) concluded that life history traits (low adult mortality) predispose species within particular lineages to delayed dispersal, and cooperation results, given the right ecological conditions. Hatchwell & Komdeur (2000), however, argued that the distinction is artificial and that life history and ecology are likely to act in concert to influence the rate of turnover of breeding positions. Opportunities for dispersal and breeding are a balance between the number of vacancies available and the number of competitors available to fill them, traits that are influenced by both ecology and life history (Hatchwell & Komdeur 2000; Kokko & Lundberg 2001).

Regardless of the degree to which ecology and life history contribute to the evolution of cooperation, cooperative breeding is not an inevitable consequence of delayed dispersal. For example, in three group-living species offspring may delay dispersal for one or more breeding seasons but never help to rear subsequent young produced on the territory (a northern population of the green jay, *Cyanocorax yncas*: Gayou 1986; a New Zealand population of Australian magpies, *Gymnorhina tibicen*: Veltman 1989; Siberian jays, *Perisoreus infaustus*: Ekman et al. 1994). In contrast, the offspring of some cooperative species do not delay dispersal, but disperse to foreign territories soon after reaching independence to form groups that cooperate to rear young (e.g. dunnoek, *Prunella modularis*: Davies 1992). Last, delayed dispersal is not restricted to group-living species; in some pair-breeding species males may remain on the natal territory over winter but disperse to a vacancy just before breeding begins again (e.g. brown thornbill, *Acanthiza pusilla*: Green & Cockburn 2001). Consequently, dispersal strategies and group living need to be considered separately from the question of why some individuals help to rear young that are not their own.

We investigated natal dispersal in the group-living speckled warbler, *Chthonicola sagittata*, and tested the hypothesis that habitat saturation resulting from life history traits (sedentariness, male-biased sex ratio, low adult mortality) leads to delayed dispersal. Although speckled warblers live in groups during breeding, subordinates never help to feed nestlings or fledglings (Gardner et al., in press). Thus, this species provides a rare opportunity to test the habitat saturation model in a group-living species in the absence of cooperative breeding. This is an important distinction, because most studies of delayed dispersal have focused on cooperative breeders, species that, in the vast majority of cases, associate in kin groups that by definition have offspring that delay dispersal (Ekman et al. 2001).

METHODS

Species and Study Site

The speckled warbler is a small (11–15 g) insectivorous passerine which is a sedentary resident of the temperate woodlands of eastern Australia (Blakers et al. 1984). It is either a member of the Acanthizinae within the Pardalotidae (Christidis & Boles 1994) or a member of the Acanthizidae, in which case the species has been renamed *Pyrrholaemus sagittatus* (Schodde & Mason 1999). We use Acanthizinae within the Pardalotidae here. The species is primarily ground dwelling, both nesting and foraging directly on the ground (Gardner 2002a). Males are slightly larger than females and can be distinguished by their black rather than rufous crown stripe (Blakers et al. 1984). Speckled warblers breed in the austral spring and summer, laying clutches in up to 8 months of each year (Gardner 2002a). Females are multibrooded and can fledge up to three broods per season, but, despite this, reproductive success is low with each female producing about 1.0 fledgling per season (Gardner 2002a). We studied a population of speckled warblers in open Eucalypt woodland, dominated by *Eucalyptus rossii*, *E. mannifera* and *E. macrorhyncha*, on the lower slopes of Mt Anslie in the Canberra Nature Park, ACT (149°9'E, 35°16'S) from 1997 to 2000. The study area was about 300 ha, within the larger 1500-ha reserve.

Field Techniques

The study population consisted of all individuals living within the 300-ha study area, and was monitored throughout the year. Adults were captured in mist nets and colour-banded to allow individual recognition; at least 90% of the resident adult population was banded in each year. We attempted to monitor all nesting attempts of resident adults and the majority of offspring hatched on the study site were banded as nestlings. We visited most territories at least three times a week during the breeding season and usually at least once every 2 weeks at other times. Repeatedly locating banded birds and

catching and banding unmarked individuals as they settled on the study site allowed us to document the nature and timing of social rearrangements, mortality and juvenile dispersal and recruitment.

We attempted to locate all birds that had dispersed outside the study area in the winters following two of the three breeding seasons, 1997 and 1998. We systematically searched most habitat within 2 km of the study site, checking all individuals located by sight or song. We found 61% (20/33) of banded birds that survived to independence and were thought to have dispersed (1997: 2/7; 1998: 18/26). After the 1999 season dispersers were located opportunistically, and we found only 34% (10/29) of birds. Dispersal distances were measured as straight-line distances from the centre of one territory to another on a map, or as the number of territories, calculated by dividing the straight-line distance by 300 m, since the mean size of breeding territories was 9 ha.

We assessed annual survival of banded individuals at the start of each breeding season, nominally 1 August. Breeding adults that disappeared were presumed to have died if they could not be found on the surrounding three territories (see Results), or if they disappeared during a breeding attempt, since neither member of the dominant pair was known to abandon an attempt after the first week of incubation (Gardner 2002a).

Bird trapping and banding were carried out under licence from the Australian Bird and Bat Banding Scheme, the ACT Parks and Conservation Service and the ANU Animal Experimentation and Ethics Committee.

Data Analyses

General

Data were analysed with JMP version 3 (SAS Institute 1994) or Genstat version 5.3.2 (Genstat 1993). Means were compared by *t* tests or ANOVA, providing that data were normally distributed with equal variances, or likelihood ratios from contingency tables if variables were categorical. Survival data were analysed with Generalized Linear Models (GLM) using the logit link function. Residual deviance was used as a scaling factor in calculating variances. Although individuals surviving from one year to the next constituted replication, the dispersion parameter from the GLM model was low (2) indicating that these individuals were not contributing disproportionately to the final result. Therefore the use of GLM rather than a Generalized Linear Mixed Model (GLMM) was warranted. Means are reported \pm SDs. Statistical tests are two tailed.

Dispersal model

Based on field data, we concluded that the benefits of dispersing from the natal territory would outweigh those of philopatry for speckled warblers (see Discussion). However, because philopatry was never observed, we could not test the assumption. We therefore used a model to

estimate how strong a philopatric benefit would have to be for philopatry to become a preferred option for males. The model calculates relative lifetime fitness of philopatric males (compared to dispersing males), based on rates of territory acquisition. We assumed that philopatric males could have higher survival because of familiarity or beneficial kin interactions, but that they also suffer a cost because they cannot breed while their mother is alive (Kokko & Ekman 2002). We used the model to answer the question: how much better should philopatric sons survive for philopatry to pay? Specific assumptions are as follows.

(1) A male that joins another group as a subordinate achieves a fraction p of paternity of that of the dominant male while he is a subordinate.

(2) Philopatric males do not achieve paternity while their mother is alive; incest avoidance thus forms a cost of philopatry.

(3) Philopatric males would have survival s_n which might differ from yearly survival s_i for subordinates that have dispersed. If $s_n > s_i$ individuals are able to use the natal territory as a 'safe haven' from which to vie for breeding opportunities, and this could in principle overcome the costs of restricted breeding opportunities at home (Kokko & Ekman 2002).

(4) Subordinates gain dominant status once the dominant male has died.

(5) Philopatric and dispersing males do not differ in how well they gain breeding vacancies on neighbouring territories in any given year, but the probability of being able to do so is linearly related to a subordinate's life span.

We estimated model parameters as follows. First, from our data we calculated that in 67% (6/9) of cases, acquisition of a breeding position would not have depended on the status of the male (philopatric versus disperser), because these males moved to neighbouring territories. Thus, the relative fitness (denoted R) of a philopatric male is

$$R = 0.67 \frac{1 - s_i}{1 - s_n} + 0.33 \frac{W_n}{W_i}$$

where $1/(1 - s_n)$ is the expected life span of a philopatric subordinate, and W_n/W_i is the relative success of natal versus immigrant individuals in the territory where they reside.

We then estimated W_n/W_i . A male who joins a pair, either as a natal offspring or as an immigrant, will enter a situation where both members of the pair are still alive ('B' for 'both'). For a natal offspring, the original pair are the parents. In the future, this might transform to a situation 'F', where only the female of the original pair is alive, 'M', where only the male is alive, and 'N', where neither are alive. Alternatively, the subordinate may die (state 'D'). Discrete transitions between states of a system can be modelled as a Markov chain (Puterman 1994). This is done by forming a transition matrix, \mathbf{P} , that describes the probability of moving from one state (e.g. both members of the original pair still alive) to another (e.g. only the original female is alive). Denoting female

survival by f , male survival by m , and subordinate survival by s , we obtain the matrix

$$P = \begin{bmatrix} fms & f(1-m)s & (1-f)ms & (1-f)(1-m)s & 1-s \\ 0 & fm & 0 & (1-f)m & 1-m \\ 0 & 0 & ms & (1-m)s & 1-s \\ 0 & 0 & 0 & m & 1-m \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

where the rows and columns 1–5 correspond to states B, F, M, N and D. Thus, for example, the probability of a B to F transition equals $f(1-m)s$, the value indicated in the first row (for B), second column (for F). This is the probability that the female survived (f), the male did not (m) and the subordinate did (s). As another example, the probability M to F (third row, second column) equals zero, because it is not possible that, first, only the male of the original pair is alive, and then only the female.

We next calculated the expected time that a system spends in 'transient states'; these are all possible states in which an individual lives before dying (Puterman 1994). We thus formed the 4×4 matrix Q of all transient states by omitting the last row and column of P . Denote by $\mathbf{t}(s) = [t_B(s), t_F(s), t_M(s), t_N(s)]$ the expected number of years that speckled warblers spend in each of the groups (B, F, M, N) before dying, when their survival as a subordinate equals s . The vector \mathbf{t} is calculated as the first row of the matrix $(\mathbf{I} - \mathbf{Q})^{-1}$, where \mathbf{I} is the 4×4 identity matrix (Puterman 1994).

The relative fitness gain in the residential territory is then calculated as $W_m = p t_M(s) + t_N(s)$ and $W_f = p t_B(s) + t_F(s) + p t_M(s) + t_N(s)$, where p refers to paternity. These expressions reflect our assumptions: males may obtain some paternity as subordinates, but while the female of the breeding pair is still alive (states B and F) there is no paternity gain for philopatric sons.

We ran the model using two estimates of subordinate survival, s_i , and two of subordinate paternity. The first survival value (0.83) was estimated by including all beta males in the analysis; the second (0.92) excludes the case where a subordinate moved to an empty territory before dying, thereby changing his status from a subordinate to a single male (i.e. one with no partner). Because the sample size of beta males was small ($N=12$) annual survival estimates are likely to be less reliable; 92% survival is very high compared with the more reliable estimate of 85% for alpha males. To overcome this problem, and to be conservative in our approach, we estimated relative fitness using both values and examined whether such differences in survival change the prospects for philopatry. We used estimates of 0 and 50% paternity for subordinate males, to span the potential range.

RESULTS

Population Size, Sex Ratio and Social Structure

There were 48–61 adults living on the 250–350-ha study site at the start of the breeding season in each year,

Table 1. Demographic characteristics of the study population at the start of each breeding season, nominally 1 August

Year	Study site area (ha)	Number of adults	Density (birds/10 ha)	Sex ratio (% male)
1997	250	48	1.9	58
1998	300	53	1.8	62
1999	350	61	1.7	56

resulting in a low population density at a mean of 1.8 birds/10 ha (Table 1). The percentage of adult males in the population averaged 59% (Table 1) and the sex ratio of juveniles just prior to dispersal was approximately even, at 47% male (29/62; range 41–57% in the 3 years).

Up to a third of breeding units in each year were trios, consisting of a female with two males; the remainder were pairs (Table 2). Alpha males were socially dominant to betas and maintained dominance through aggression in the form of chases and displacements. Alpha and beta males usually competed for copulations, with betas occasionally gaining paternity; shared paternity was recorded in 8.3% (1/12) of broods (Gardner et al., in press). In each year there were several empty territories or territorial males without partners, but there were no male 'floaters' (nonterritorial birds) in the population, since males that died or disappeared during breeding were not replaced by unknown individuals (Table 2).

Breeding groups defended large, usually contiguous territories whose boundaries changed little from year to year. The mean size of 20 breeding territories in 1997 was 9 ha (range 6–12 ha), and there was no difference in the size of territories held by pairs and trios (ANOVA: $F_{1,19}=0.91, P=0.4$).

Adult Mortality

Annual adult mortality was 22.7% (range 19.2–24.5%) and was significantly higher for females than males (GLM: $\chi^2_1=10.12, P=0.001$). Thirty-seven per cent (range 30–45%) of females died each year compared with 14% (range 7–20%) of males. There was no difference in mortality between years ($\chi^2_2=0.45, P=0.8$), but 26 of 32 (81%) individuals that died did so during the breeding season (seasonal effect: $\chi^2_2=15.66, P<0.001$).

Table 2. Social structure of the breeding population at the start of each breeding season, nominally 1 August

Year	Pairs	Trios (%)	Males with no partner	Empty territories*	Total territories
1997	14	6 (30)	0	1	21
1998	14	7 (33)	4	2	27
1999	20	5 (20)	2	3	30

*Empty territories were those without occupants but that supported a breeding pair or trio for the whole or part of a previous breeding season.

Juvenile Dispersal and Recruitment

All 64 young (from 36 broods) that survived to independence disappeared from the natal territory about 7 weeks after fledging ($\bar{X} \pm \text{SD} = 49 \pm 8.6$ days, range 38–68 days, $N=55$ fledglings from 31 broods for which accurate dates were known) and were assumed to have dispersed; no young of either sex remained on the natal territory over winter. Aggression by parents did not appear to trigger dispersal. Only one case of aggression by father to son was observed, and mothers were never seen to be aggressive towards their offspring.

Sixty-nine per cent (43/62; 19 females, 24 males) of juveniles were found at least once after they had left the natal territory (excludes two of 64 juveniles that were unbanded). Thirty-nine per cent (13/33) of females and 59% (17/29) of males settled on territories after dispersing, although we could not find six birds at the start of the following breeding season. All 10 known female dispersers became breeders as yearlings. In contrast, only one male gained breeding status in a pair; nine became subordinates within a group and four occupied territories without a female. Of these four, two dispersed and joined females that subsequently disappeared before breeding started again, leaving them alone on territories. The third joined a pair but switched to an empty territory before breeding began again, and the fourth was found on a territory as a subordinate to another male; whether there was a female on this territory when the juvenile arrived is unknown. Hence, juvenile males dispersed into subordinate positions rather than to empty territories.

Of eight juvenile females for which dates are accurately known, all filled vacancies within 6–68 days of leaving their natal territories. Two, however, switched to new territories in the following August, at the start of breeding, having repeatedly been located on the first territories during winter. Males also settled quickly; seven males settled on territories 1–45 days after dispersing.

Females dispersed greater distances than did males. Including only those individuals that gained vacancies on the study site, since males and females were equally likely to be found, females dispersed twice as far as males ($\bar{X} \pm \text{SE}$, range; females: 1235 ± 508 m, 400–2000 m, $N=10$; males: 608 ± 466 m, 0–1600 m, $N=12$; ANOVA: $F_{1,20}=9.1$, $P=0.007$; Fig. 1). If all individuals are included, those found off as well as on the study site, females did not disperse significantly further than did males (females: 1381 ± 225 m, 1300 m, 400–3100 m, $N=13$; males: 862 ± 197 m, 600 m, 0–3200 m, $N=17$; $F_{1,28}=3.0$, $P=0.09$). Distances equate to 2–10 territories for females and 1–11 for males.

Formation and Duration of Trio Groups

All trio groups formed through dispersal, since all 30 male fledglings that survived to independence in the three breeding seasons dispersed; no male was philopatric. Beta males, therefore, were not first-order relatives of the pair with which they lived. This was confirmed by DNA fingerprinting: the mean $\pm \text{SD}$ band-sharing coefficient between a beta male and the resident female

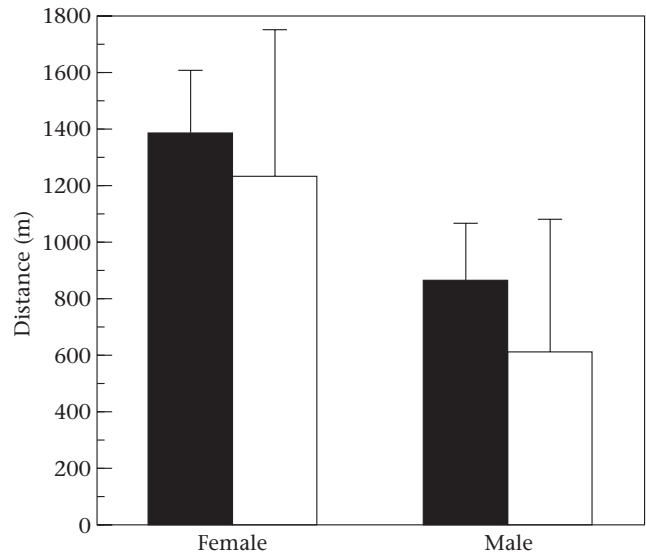


Figure 1. Dispersal distances $\pm \text{SE}$ of juvenile male and female speckled warblers. ■: All dispersal records, both on and off study site; □: only those on study site.

was 0.13 ± 0.16 , and between a beta and alpha male 0.20 ± 0.13 ($N=9$ beta males).

Trio groups were stable once formed, although relatively short lived compared with pairs. Beta males remained with the pair until a breeding vacancy became available; they did not move from one pair to another. Ninety per cent (9/10) of beta males whose fates were known gained a breeding vacancy (i.e. alpha status) during the study. Three replaced alphas on their own territories after alphas disappeared, and all subsequently bred with the females, two in the same season and the third in the following season, since the alpha disappeared in January towards the end of the breeding season. Six others gained breeding status in a pair, and one moved to an empty territory and subsequently died. Another four beta males disappeared. The distance moved by beta males from the first foreign territory to a vacancy was one ($N=6$) or two ($N=1$) territories. The mean duration of trio groups was 9.8 months (range 6–16 months; $N=6$ groups whose dates of formation and disintegration were known). Four additional trios had already formed before the study, but all split up during the following 5–14 months. Given the short duration of trios, beta males were typically first-year birds.

Changes in Group Composition

Groups changed composition when group members died or dispersed and were subsequently replaced. Fifty-nine per cent (37/63) of pairs or groups had a change in the dominant pair from the previous year (range 58–60% over 3 years). Most changes occurred as a result of death rather than divorce. Males and females behaved differently after the death of a partner (Fisher's exact two-tailed test: $P=0.01$). Females were equally likely to remain on the territory or leave it (four stayed, three left), whereas all males whose partners died remained on the territory

($N=19$ cases). Ten cases of divorce were recorded, where both adults were known to be alive after the split occurred. Both sexes appeared to initiate divorce; there were four cases of females leaving males and six of males leaving females. Causes of divorce were unknown but in the case of males leaving their partners, three of the six instances apparently resulted from another male forcing them off the territory. The three occasions involved two males; one was of a father displacing a son after the father lost his partner and the other was of two males displacing the same male with a different partner, after losing their own partners. Two of the four cases in which females divorced their partners did so immediately after a nesting attempt failed. Males moved a maximum of two territories after divorce ($N=6$ cases), and females moved a maximum of three territories after divorce or the death of a partner ($N=7$ cases).

Timing and Source of Replacements

Alpha males were replaced very quickly, often within 24 h. Replacement males came from within the territory or from adjacent territories, and competition for vacancies could be considerable, given the potential source of betas and territorial males without partners; additional males were always available to fill breeding vacancies. During the study 13 breeding positions were filled, mostly by beta males ($N=9$), or territorial males without partners ($N=2$), and one position was filled by a dispersing juvenile male and another by an immigrant. Excluding juvenile dispersal, the maximum distance moved by males to fill breeding vacancies was one ($N=10$) or two ($N=1$) territories.

Unlike males, females that died during the breeding season were not replaced until breeding had finished, unless a female nearby divorced her own partner to re-pair; there were no additional females to fill vacancies during the breeding season. Twenty-one breeding vacancies were filled during the study, half ($N=10$) by juvenile females hatched on the study site and the rest ($N=11$) by immigrant females. Some juveniles gained breeding territories in December or January each year when they were 2–3 months old, but in those cases the newly formed pair did not breed that season.

Model

We calculated that philopatric males would need to have annual survival rates of over 95% for philopatry to pay, using either 0.83 or 0.92 for subordinate survival (Fig. 2). Since males do not achieve 95% survival, even when dominant, it seems very unlikely that the 'safe haven' mechanism (Kokko & Ekman 2002) could make philopatry a better option. In addition, philopatry pays less if subordinates gain paternity within the group. This is because much of the paternity gain occurs when the original female is alive, which in the case of philopatric males is the mother with whom they cannot mate.

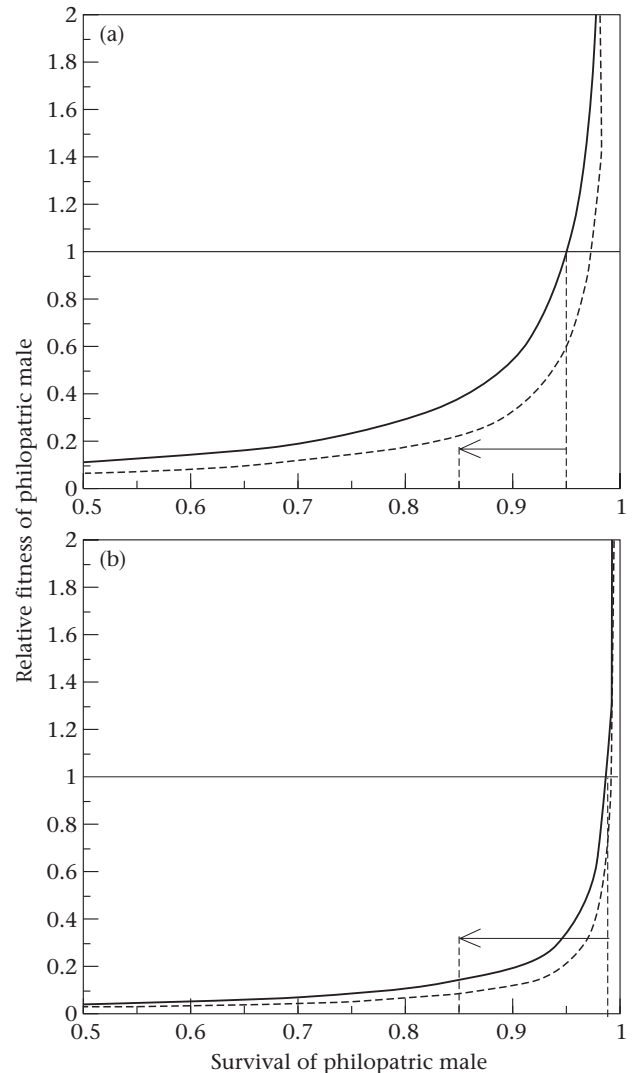


Figure 2. Relative fitness of philopatric males based on two values of annual subordinate survival, s_i (a) 0.83 and (b) 0.92. Both graphs assume annual survival of dominant males $m=0.85$, and females $f=0.63$. Solid lines: no paternity for subordinate males; dashed lines: 50% paternity. Vertical dashed lines joined by arrows indicate the difference between dominant male survival and that calculated for philopatric males. Philopatric males would need to achieve annual survival rates of over 95% for philopatry to pay (0.951 if $s_i=0.83$, 0.986 if $s_i=0.92$).

DISCUSSION

Life History

Speckled warblers in our study area showed all the life history traits that are thought to result in a saturated habitat and lead to delayed dispersal and yet young were never philopatric: they were sedentary, had a male-biased sex ratio and had high adult survival (Arnold & Owens 1998, 1999; Hatchwell & Komdeur 2000). Adult mortality was low at 23% and typical of the mean rate for passerines with a cooperative breeding system (30%) compared with those with a noncooperative system (44%: from the database of Arnold & Owens 1998, 1999; I. Owens, personal communication). Despite this, all speckled

warbler young dispersed from the natal territory 38–68 days after fledging. Juvenile males dispersed into subordinate positions with a breeding pair, rather than remaining on the natal territory or becoming floaters.

It was the lack of females that constrained independent breeding for young males, given that there were vacant breeding territories in each year. The skewed sex ratio probably resulted from a combination of higher mortality of females during breeding and dispersal. Only females incubate and brood the young and during this time they are particularly vulnerable to predation; most females that died during breeding did so during this period, and at least some were killed at the nest (Gardner 2002a). In addition to mortality during breeding, females dispersed further than males, which is likely to have increased mortality. Differential dispersal of the sexes is thought to be a strategy to avoid inbreeding, and higher mortality is associated with the sex that disperses further (Greenwood 1980). In this study, females dispersed about twice as far as males. Whether longer dispersal results in higher mortality in this species is unknown, but the sex ratio of independent young was roughly equal just prior to dispersal while that of all adults at the start of each breeding season was consistently male biased, suggesting that dispersal plays a role in mortality.

Is Dispersal an Active Choice?

Dispersal appeared to be an active choice on the part of speckled warbler males, since there was no evidence that parents evicted their offspring, as occurs in some species (e.g. green jays: Gayou 1986; grey jays, *Perisoreus canadensis*: Strickland 1991). Only one case of aggression by father to son was observed. Regardless of the lack of aggression, it seems unlikely that a father would force his own sons to leave but accept settlement by a neighbour's son if, for example, depletion of resources (food) on the territory were a reason for eviction (Koenig et al. 1992); two adult males had juvenile males settle on a territory after their own sons dispersed. It also seems unlikely that eviction would be possible by a single dominant male on such a large territory (6–12 ha), and in fact alpha males did not defend the territory once breeding began in earnest, but concentrated on defending the female (unpublished data).

Cost of Dispersal

Although the life history attributes of speckled warblers in our study were similar to those of other group-living acanthizids, they differed in two demographic characteristics that may promote opportunity for dispersal by minimizing the potential for aggression. They occupied very large, contiguous breeding territories and occurred at low density, with a maximum of two males per territory. All other acanthizids occur at high density, with up to five males occupying a single small territory (Table 3), and dominant males should be able to expel intruding males. Aggression may be an effective constraint on dispersal if all territorial males act to expel intruders,

territories are small enough for intruders to be easily detected and evicted, and territories are contiguous so that a disperser would be driven from one aggressive encounter to the next. In such cases the costs of dispersing may be prohibitive and may, at least in part, account for natal philopatry of male offspring in all the other group-living acanthizids (Table 3). The ability of juvenile speckled warbler males to avoid aggression may therefore substantially reduce dispersal mortality.

Benefit of Dispersal versus Philopatry

A benefit of dispersal for juvenile speckled warbler males is that it provides an additional route to gaining a breeding vacancy. Subordinates can replace the dominant male on the foreign territory on which they settle as well as on territories nearby; in this study three of nine subordinates replaced alphas when they disappeared and subsequently bred with the female. Assuming incest restriction, philopatric sons cannot replace their father until their mother has died, and this would take considerable time since females are not replaced until the following breeding season. Juvenile males that disperse, therefore, are likely to acquire breeding vacancies at a higher rate than would philopatric sons. A similar situation has been recorded for Siberian jays, whereby males that disperse gain vacancies at about twice the rate of philopatric sons because of inbreeding avoidance (Ekman et al. 2000; Kokko & Ekman 2002). However, survival of philopatric sons is about twice that of dispersers, which cancels the effect. The outcome is that first-ranking subordinates remain on the natal territory and others disperse.

Speckled warblers were not philopatric so we do not know whether survival would be improved on the natal territory or how quickly they would acquire a breeding vacancy. However, our model predictions showed that dispersal would almost certainly result in greater fitness, measured as lifetime reproductive success. Philopatric males would need to achieve annual survival rates of over 95% for philopatry to pay. Since males do not achieve 95% survival, even when dominant, it seems very unlikely that the 'safe haven' mechanism could make philopatry a better option. Our conclusion appears robust since the relative benefit of philopatry may be less than our model estimates. This is because we did not model the possibility that if a male were to die leaving a son and mother on the territory, the son would be evicted by an incoming male, as occurs in some other species (e.g. white-browed scrubwren, *Sericornis frontalis*; R. Magrath, unpublished data). Thus the relative benefit of philopatry may be even lower than our estimate.

Why Not Disperse to Float?

The alternative strategy to remaining on the natal territory or dispersing to a foreign territory is to disperse to become a floater (Koenig et al. 1992). We do not know why speckled warbler males do not become floaters but it may be related to survival in winter. Speckled warblers

Table 3. Some life history and demographic characteristics of group-living members of the Acanthizinae (all species are sedentary)

Species	Sex ratio (% male)	% breeding units that were groups*	No. of males per breeding territory	Population density (birds/ha)	Mean territory size (ha)	Annual adult mortality	Maximum longevity (years)	Source
Striated thornbill, <i>Acanthiza lineata</i> †	60	43 (6/14)	1–3	>1.4	<1	—	>17	Extrapolated from Bell & Ford 1986; Wilson 1995
Buff-rumped thornbill, <i>Acanthiza reguloides</i>	59	32 (6/19)	1–3	1.8	<2	46	>8	Extrapolated from Bell & Ford 1986; Anon. 1993
Yellow-rumped thornbill, <i>Acanthiza chrysorrhoa</i>								
Study 1	—	—	—	>2	<1	—	—	Extrapolated from Ford 1963
Study 2	—	—	1–3	—	<2	36	>7	Anon. 1997; D. Ebert, personal communication
White-browed scrubwren, <i>Sericornis frontalis</i>								
Study 1	—	54	1–5	8	(1.0–1.4)	—	≥17	Magrath et al. 2000; Higgins et al. 2002
Study 2	—	—	—	0.61	1–2.6 (1.8)	—	—	Brooker 1998
Study 3	—	—	—	0.6	(1.4–2.6)	—	—	Ambrose & Davies 1989
Speckled warbler, <i>Chthonicola sagittata</i>	59	28	1–2	0.18	6–12 (9)	23	>8	Anon. 1997; this study

*The groups of all species, except speckled warblers, form as a result of male philopatry.

†Striated thornbills were not sexed so these data assume one female per breeding group, consistent with all known species within the family.

form flocks in some winters which may increase foraging efficiency and thus survival when food is least abundant (Elgar 1989; Gardner 2002b). Flocks are composed of residents from two or three adjacent breeding territories as well as dispersing juveniles, and territorial residents are dominant to newly arrived dispersers. Membership of a territory and its associated rank may ensure access to resources and be important for survival in harsh winters (Desrochers et al. 1988).

Other Polyandrous Species

In two other polygamous species, territory size and population density have been shown to influence formation of the mating system. In the dunnoek, the extraordinary variability in mating systems (monogamy, polyandry, polygyny and polygynandry) has been attributed to different patterns of overlap between male and female territories (Davies 1992). Females establish territories relative to the dispersion of feeding sites and males establish territories relative to their ability to monopolize females. The ability of males to exclude rivals depends on the size of the female's territory. If a female's territory is large, a male cannot exclude other males, leading to polyandry. In a population of the closely related alpine accentor, *Prunella collaris*, in the French Pyrenees, terri-

ories are thought to be established in the same manner as dunnoeks, with females and males responding to different resources (Davies et al. 1995). However, a more dispersed and patchy distribution of food leads to large, undefended territories containing polygynandrous groups of males and females, since neither sex can defend exclusive areas.

In the dunnoek and alpine accentor, territory size and population density influence the mating system but in themselves do not promote opportunity for dispersal. In the speckled warbler, the polyandrous mating system appears to be a direct result of the opportunity for dispersal, made possible by large territories that cannot be defended by a single male, and low population density resulting in few males per area. Consequently, subordinates are apparently free to disperse and settle on a territory because they can avoid aggression by dominant males.

Conclusion

Delayed dispersal is not an inevitable consequence of a saturated habitat. Despite a saturated habitat, speckled warbler males dispersed to foreign territories, rather than remaining philopatric or dispersing to float. As such, the habitat saturation model fails to account for dispersal

behaviour in the speckled warbler. Similar cases have been documented for several pair-breeding species of tits (genus *Parus*), which also live in a saturated habitat and show life history characteristics that are typical of cooperative breeders, yet none delays dispersal (Ekman et al. 2001 and references within). These studies suggest that the focus on cooperatively breeding species for the study of delayed dispersal is unwarranted, and that patterns of dispersion should be examined in species with diverse life histories and social organization.

Acknowledgments

We thank Jan Ekman, Ian Owens and members of the Behavioural Ecology Group at the ANU for comments on the manuscript. Thanks also to Jeff Wood and Christine Donnelly from the ANU Statistical Consulting Unit for advice and Peter Marsack for assistance in the field. The study was supported by an ANU Postgraduate Scholarship, a Stuart Leslie Bird Research Award (Birds Australia) and a Cayley Memorial Scholarship (Gould League of New South Wales) to J.L.G.

References

- Ambrose, S. & Davies, S. 1989. The social organisation of the white-browed scrubwren *Sericornis frontalis* Gould (Acanthizidae) in arid, semi-arid and mesic environments of Western Australia. *Emu*, **89**, 40–46.
- Anon. 1993. Recovery round-up. *Corella*, **17**, 31–32.
- Anon. 1997. Recovery round-up. *Corella*, **21**, 131–132.
- Arnold, K. E. & Owens, I. P. F. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London, Series B*, **265**, 739–745.
- Arnold, K. E. & Owens, I. P. F. 1999. Cooperative breeding in birds: the role of ecology. *Behavioral Ecology*, **10**, 465–471.
- Bell, H. L. & Ford, H. A. 1986. A comparison of the social organization of three syntopic species of Australian thornbill, *Acanthiza*. *Behavioral Ecology and Sociobiology*, **19**, 381–392.
- Blakers, M., Davies, S. J. F. & Reilly, P. N. 1984. *The Atlas of Australian birds*. Melbourne: Melbourne University Press.
- Brooker, B. 1998. A comparison of the ecology of an assemblage of ground-dwelling birds in an arid environment. Ph.D. thesis, Murdoch University.
- Brown, J. 1987. *Helping and Communal Breeding in Birds*. Princeton, New Jersey: Princeton University Press.
- Christidis, L. & Boles, W. 1994. *The Taxonomy and Species of Birds of Australia and its Territories*. Melbourne: Royal Australasian Ornithologists' Union.
- Cockburn, A. 1996. Why do so many Australian birds cooperate: social evolution in the Corvida. In: *Frontiers of Population Ecology* (Ed. by R. B. Floyd, A. W. Sheppard & P. J. De Barro), pp. 451–472. Melbourne: CSIRO Publishing.
- Davies, N. B. 1992. *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Davies, N. B., Hartley, I. R., Hatchwell, B. J., Desrochers, A., Skeer, J. & Nebel, D. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. 1. Ecological causes and reproductive conflicts. *Animal Behaviour*, **49**, 769–788.
- Desrochers, A., Hannon, S. J. & Nordin, K. E. 1988. Winter survival and territory acquisition in a northern population of black-capped chickadees. *Auk*, **105**, 727–736.
- Edwards, S. V. & Naeem, S. 1993. The phylogenetic component of cooperative breeding in perching birds. *American Naturalist*, **141**, 754–789.
- Ekman, J., Sklepkovych, B. & Tegelström, H. 1994. Offspring retention in the Siberian jay (*Perisoreus infaustus*): the prolonged brood care hypothesis. *Behavioral Ecology*, **5**, 245–253.
- Ekman, J., Bylin, A. & Tegelström, H. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. *Proceedings of the Royal Society of London, Series B*, **266**, 911–915.
- Ekman, J., Bylin, A. & Tegelström, H. 2000. Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology*, **11**, 416–420.
- Ekman, J., Baglione, V., Eggers, S. & Griesse, M. 2001. Living under the reign of nepotistic parents. *Auk*, **118**, 1–10.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, **64**, 13–33.
- Emlen, S. T. 1982. The evolution of helping. 1. An ecological constraints model. *American Naturalist*, **119**, 29–39.
- Emlen, S. T. 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution*, **9**, 282–285.
- Ford, J. 1963. Breeding behaviour of the yellow-tailed thornbill in south-western Australia. *Emu*, **63**, 185–200.
- Gardner, J. L. 2002a. Breeding biology of the speckled warbler, *Chthonicola sagittata*. *Australian Journal of Zoology*, **50**, 169–181.
- Gardner, J. L. 2002b. *Social behaviour and breeding biology of the speckled warbler*. Ph.D. thesis, Australian National University.
- Gardner, J. L., Magrath, R. D. & Olsen, P. D. In press. Speckled warblers break cooperative rules: absence of helpers in a group-living member of the Pardalotidae. *Animal Behaviour*.
- Gayou, D. 1986. The social system of the Texas green jay. *Auk*, **103**, 540–547.
- Genstat 5 Committee 1993. *Genstat 5 Release 3 Reference Manual*. Oxford: Clarendon Press.
- Green, D. J. & Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology*, **70**, 505–514.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Hatchwell, B. J. & Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079–1086.
- Heinsohn, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged coughts. *American Naturalist*, **137**, 864–881.
- Heinsohn, R. G., Cockburn, A. & Mulder, R. A. 1990. Avian cooperative breeding: old hypotheses and new directions. *Trends in Ecology and Evolution*, **5**, 403–407.
- Higgins, P., Peter, J. & Steele, W. (Eds) 2002. *Handbook of Australian, New Zealand and Antarctic birds*. Vol. 6. *Pardalotes to Shrike-thrushes*. Melbourne: Oxford University Press.
- Kempnaers, B., Everding, S., Bishop, C., Boag, P. & Robertson, R. J. 2001. Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology*, **49**, 251–259.
- 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.
- Kokko, H. & Ekman, J. 2002. Delayed dispersal as a route to breeding; territorial inheritance, 'safe havens' and ecological constraints. *American Naturalist*, **160**, 468–484.
- Kokko, H. & Lundberg, P. 2001. Dispersal, migration, and offspring retention in saturated habitats. *American Naturalist*, **157**, 188–202.

- Komdeur, J.** 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature*, **358**, 493–495.
- Komdeur, J.** 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology*, **34**, 175–186.
- Magrath, R. D., Leedman, A. W., Gardner, J. L., Giannasca, A., Nathan, A. C., Yezerinac, S. M. & Nicholls, J. A.** 2000. Life in the slow lane: reproductive life history of the white-browed scrubwren, an Australian endemic. *Auk*, **117**, 479–489.
- Mumme, R. L.** 1992. Delayed dispersal and cooperative breeding in the Seychelles warbler. *Trends in Ecology and Evolution*, **7**, 330–331.
- Owens, I. P. F. & Bennett, P. M.** 1995. Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society of London, Series B*, **261**, 227–232.
- Pruett-Jones, S. G. & Lewis, M. J.** 1990. Sex-ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature*, **348**, 541–542.
- Puterman, M. L.** 1994. *Markov Decision Processes: Discrete Stochastic Dynamic Programming*. Chichester: J. Wiley.
- Russell, E. M.** 1989. Cooperative breeding: a Gondwanan perspective. *Emu*, **89**, 61–62.
- Schodde, R. & Mason, I.** 1999. *The Directory of Australian Birds*. Collingwood, Victoria: CSIRO Publishing.
- SAS Institute** 1994. *JMP Version 3 Users Guide*. Cary, North Carolina: SAS Institute Inc.
- Selander, R. K.** 1964. Speciation in wrens of the genus *Campylorhynchus*. *University of California Publications in Zoology*, **74**, 1–224.
- 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.
- Strickland, D.** 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. *Canadian Journal of Zoology*, **69**, 2935–2945.
- Veltman, C.** 1989. Flock, pair and group living lifestyles without cooperative breeding by Australian magpies. *Ibis*, **131**, 601–608.
- Walters, J. R., Copeyon, C. K. & Carter, J. H.** 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk*, **109**, 90–97.
- Wilson, S.** 1995. Survival of brown and striated thornbills in the Brindabella Range, ACT. *Corella*, **19**, 138–146.
- Woolfenden, G. & Fitzpatrick, J.** 1984. *The Florida Scrub Jay: Demography of a Cooperative Breeding Bird*. Princeton, New Jersey: Princeton University Press.
- Zack, S.** 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology*, **86**, 265–286.