

Demography of male reproductive queues in cooperatively breeding superb fairy-wrens *Malurus cyaneus*

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Summary

1. Subordinate helpers in cooperative societies may gain both immediate and future benefits, including paternity and territorial inheritance. However, if such opportunities correlate with rank in the queue, it is unclear why such queues should be stable.

2. In cooperatively breeding superb fairy-wrens *Malurus cyaneus*, only males are generally philopatric, and form stable hierarchical queues for the dominant position.

3. Male opportunities for reproduction are influenced both by their dominance status within the group, and their relatedness to the breeding female. For young queuing subordinates, the breeding female is typically their mother. Because of incest avoidance, reproduction is possible only through extra-group mating, even if the dominant position is achieved while the mother is still on the territory. If the mother dies while the helper is still a subordinate, he can seek matings both outside the group, and with the unrelated replacement female within the group. Finally, males can achieve the dominant position and pair with an unrelated female by inheritance, dispersal to a neighbouring vacancy, or by forming a liaison with an immigrant subordinate female that causes fission of the natal territory.

4. On average males spent more time living with unrelated females than with their mother. Subordinate males gained no survival advantages when living with their mother rather than an unrelated female, contrary to the prediction that parents facilitate the survival of their offspring.

5. Dominants and subordinates also had similar survival. Mortality accelerated over time, probably because older males invest more in extra-group courtship display.

6. Fairy-wren queues are likely to be stable because older birds are superior, and because extra-pair mating provides direct benefits to subordinates.

Key-words: cooperative breeding, dominance, helper, *Malurus*, reproductive queue

Introduction

In many cooperatively breeding birds, philopatric young form queues on the natal territory, which they either inherit, or use as a staging post to gain vacancies in neighbouring territories. The outcomes of queuing can be quite diverse. In many species queues are stable as subordinates do not contest their position in the queue and individuals inherit their natal territory in a

predictable order (Wiley & Rabenold 1984). In other species, power struggles can erupt once the dominant bird dies (Heinsohn *et al.* 2000). However, in a few species territorial inheritance appears not to occur, so queuing only provides individuals with access to vacancies on neighbouring territories (Legge & Cockburn 2000; Ekman *et al.* 2001; Kokko & Ekman 2002). This variability suggests that the costs and benefits of queuing also vary; yet despite considerable early interest (Wiley & Rabenold 1984; Zack & Rabenold 1989; Zack 1990), there has been little recent empirical attention to this problem.

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The widespread observation that individuals do not contest their position in queues has led to growing theoretical interest in the question of why reproductive queues should be stable. There are four broad classes of explanations. First, queue members may collude to punish any individual that challenges for a higher rank, making such challenges impossibly costly (Maynard Smith 1983; Crespi & Ragsdale 2000). Second, the costs of fighting may be so great that the costs of fighting for dominance may exceed the benefits gained from promotion (Maynard Smith 1983). Third, the rank in the queue could be correlated with fighting ability, so there is no prospect of success for subordinates challenging for promotion (Maynard Smith 1983). Finally, subordinates may obtain fitness benefits while queuing.

The first two explanations are unlikely to be generally applicable. In the first case, the argument that many individuals can combine to punish challengers does not apply where the queue contains just one subordinate. In the second case, while arbitrary conventions may be feasible but difficult to assess empirically (Kokko, Lopez-Sepulcre & Morrell 2006), they may be difficult to apply when more than two individuals compete in the queue (Beacham 2003).

By contrast, differences in fighting ability with rank could easily arise because greater age could be correlated with greater ability or motivation (Krebs 1982) to defend ownership of the territory. However, this explanation has some limitation, as it deals less well with the case where same-aged individuals such as nest-mates are participants in the queue. There is also a growing literature associated with the benefits that subordinates may obtain while waiting to achieve the dominant position. Benefits can be direct if subordinates obtain some parentage, or indirect, if the subordinate obtains fitness by enhancing the production, quality or survival of relatives. Benefits can also be immediate, or deferred, in the form of territory inheritance or enhancement of the survival of relatives. Because it is a common benefit, considerable attention has been paid to whether eventual inheritance (Kokko & Johnstone 1999; Ragsdale 1999; Cant & Field 2001; Cant & English 2006; Cant, Llop & Field 2006), or privileged access to nearby vacancies (Kokko & Ekman 2002; Ridley, Yu & Sutherland 2005) can stabilize the benefits of adopting a subordinate position. In the latter case, membership of a queue allows repeated interactions with neighbours, and this gives neighbours, including subordinates, a benefit relative to floaters and intruders in contests over space. However, the stabilizing role of future inheritance is likely to depend on the relative mortality schedules of dominants and subordinates (Tsuji & Tsuji 2005; Mesterton-Gibbons, Hardy & Field 2006).

Molecular studies of the extent to which subordinates obtain immediate reproductive benefits in cooperatively breeding birds are burgeoning, but have revealed bewildering diversity (Cockburn 2004). These studies reveal one reasonably common pattern among species with natal philopatry; namely that helpers may experience two radically different circumstances before they become dominant. In the first of these, where they live on the territory with their opposite-sexed parent, mating may be constrained by avoidance of

nuclear family incest (Koenig & Haydock 2004). Immediate fitness benefits available during this phase are therefore restricted to augmenting the reproductive success of relatives, acquiring reproductive skills, and competing for any extra-group parentage. By contrast, if the opposite-sex parent dies, subordinates often obtain immediate fitness benefits via within-group reproduction (e.g. Rabenold *et al.* 1990; Haydock, Parker & Rabenold 1996; Lundy, Parker & Zahavi 1998; Cockburn 2004).

This dichotomy has not been explored theoretically, but has some profound implications. For example, Magrath (2001) has suggested that help provided by supernumerary white-browed scrubwren *Sericornis frontalis* principally benefits inexperienced yearling females. However, because all females disperse in this species, these subordinates are unlikely to be related to the yearling females they assist, and in general, subordinates in this species are more likely to provision unrelated offspring (Magrath & Whittingham 1997). By contrast (Ekman, Bylin & Tegelstrom 2000; Ekman *et al.* 2004; Ekman 2006) have argued that offspring living with a parent can potentially gain ongoing advantages from nepotistic favouritism allowing access to food and preferred feeding sites. If this is generally true, the probability of surviving to inherit the dominant position may depend on whether the subordinates are living with their mother or an unrelated female.

Here we document patterns of survival and transition probabilities between reproductive phases in the superb fairywren *Malurus cyaneus* (Ellis, 1782), a species in which males form queues for the dominant position on the territory. Dominant status is known to be the preferred state in this species, as experimental studies show that subordinate males will always disperse to join an unmated female on a neighbouring territory (Pruett-Jones & Lewis 1990). However, kinship is unlikely to be an important stabilizing force, as extra-group paternity is extremely common (Mulder *et al.* 1994a), and there is no evidence that the presence of helpers aids within-group productivity (Cockburn *et al.* 2008). However, the presence of helpers does enhance the life span of the breeding female (Cockburn *et al.* 2008), extending the period where incest avoidance governs within-group mating. Here we show that queues are extremely stable, and evaluate explanations for the stability of queuing by examining demography of subordinates in relation to dominant male survival and relatedness to the female.

Methods

STUDY AREA AND SPECIES

We have surveyed the social composition and breeding biology of a population of colour-ringed superb fairy-wrens at the Australian National Botanic Gardens since 1988 until data for this study were finalized in March 2007, though the study area was expanded from about 40 ha to 80 ha in 2001. Females are multibrooded. The first nests are usually initiated in September and the last nests fledge in February. The composition of groups is determined by weekly

census throughout the year. Details of the study area and census methods are provided in Cockburn *et al.* (2003), where a complementary analysis of relationships is reported from a female perspective.

To summarize key results from Cockburn *et al.* (2003), fairy-wrens live on year-round territories where a dominant male and a female form a pair-bond, which is easily recognized by close association, including counter-singing, joint territorial defence and mate-guarding. The pair-bonded male and female are hereafter called the dominant male and female, to distinguish them from the other individuals that also live on their territory. Further behavioural evidence of dominance comes from the ability of these individuals to win contests over food and by initiation of attacks on same-sexed individuals.

Females never breed on their natal territory, even if the dominant female dies and there are no neighbouring territories she can colonize. Intense aggression by the dominant female contributes to the elimination of female supernumeraries from the territory. By contrast, the dominant pair tolerates supernumerary subordinate males, so while the territory owners often breed unaided, they may be assisted by as many as four adult male subordinates (helpers), which provision and defend young.

Male helpers typically occur because they are philopatric on their natal territory, though occasionally helpers move with an older male when he disperses to take up a vacancy, disperse from their own territory to become a subordinate, return to their natal territory to help, or are relegated to a subordinate role when a senior male usurps ownership of the territory. This occurs most commonly when a bird that has previously been the dominant of the helper loses its own mate, causing the two adjacent territories to fuse.

Male dominant status is acquired via three paths. First, when the senior male dies, the senior helper can inherit the territory. Second, a subordinate can disperse to a neighbouring territory. Third, about 30% of territories attract foreign supernumerary female dispersers that join the group towards the end of the breeding season in which they fledge (Cockburn *et al.* 2003). At the start of the next breeding season such females sometimes pair with a subordinate and split the territory in two (fission).

It is important to realize that there is considerable complexity underlying the summary of interactions described here, as even the strongest of generalizations about fairy-wren society have rare exceptions. For example, incestuous pairing usually occurs because the death of the dominant leads to the promotion of a queuing son to dominant status (76 of 82, 93%). However, we recorded three cases where a male that had dispersed to a vacancy returned to pair with his mother, two where territorial fusion after the death of an opposite-sexed dominant led the widowed birds to form a mother/son pair, and one case of a territorial fission where the dominant male paired with a supernumerary leaving the female with her son. Hereafter, although we always report the true probabilities, we do not discuss rare (< 10%) exceptions unless they are particularly illustrative, as to do so would sharply increase the length of the paper without additional biological insight. We have excluded from analysis any brief periods (generally < 60 days) where the dominant male was left unpaired on his territory awaiting the arrival of a female disperser, as these males obtain mates at the start of the breeding season.

STATISTICAL ANALYSIS

Most analysis depends on simple loglinear models or binomial tests. We estimated the time in weeks spent in each of the reproductive roles using survival analysis (log-rank tests). In these analyses, death or change of status we assumed to be known to an accuracy of 1 week, as the ease of census and extreme philopatry of these birds

allows us to distinguish death from dispersal with unusual precision. In order to estimate duration in each reproductive role, we treated birds still alive at the end of the study as censored. However, to measure mortality risk during each of the phases, we also treated changing from one status to another as a censored observation. The censored data thus contribute to the estimate of sample size of individuals alive at any time, but not to the shape of the survival curve. We examined whether the distributions were consistent with constant mortality hazard (i.e. survival can be described with an exponential distribution) by fitting Weibull distributions, for which the exponent β is expected to equal 1 if the mortality hazard is constant.

Results

The data described here include two samples, males that were studied for their entire lives ($n = 596$), and a larger sample that also includes the males that were still alive at the end of the study ($n = 710$). Males that were of unknown age because they were banded as adults were not included. In total we describe data for 1647 years of male adult lives, i.e. from the start of the breeding season after they were fledged, when they potentially gain access to reproduction.

PHILOPATRY

Male fairy-wrens are extremely philopatric. Most males gain dominant status for the first time on their natal territory (Table 1; 282 of 471, 60%), and regardless of whether they attain dominant status, die on the natal territory (427 of 596, 72%). Males that do disperse generally move to an immediately neighbouring territory (179 of 189, 95%). When rare longer moves did occur, they were not always independent, as on separate occasions groups of three and two males moved together to establish a territory on unoccupied space. The longest movement in our data set was five territories (see below), though our sampling is biased against detection of rare very long movements.

WITHIN-GROUP CONTESTS OVER DOMINANT STATUS

Males formed strict and uncontested queues for dominant status. A Poisson distribution predicts the number of males in the queue (Fig. 1; $\chi^2 = 1.3$, d.f. = 4, $P = 0.85$, last two categories

Table 1. Location and mode for the initial acquisition of the dominant breeding position in male superb fairy-wrens ($n = 471$ males)

	Natal territory	Foreign territory	Total	%
Inheritance	179	22	201	43%
Fission	100	11	111	24%
Eviction of a dominant	1*	12	13	3%
Dispersal to a vacancy	2†	144	146	31%
Total	282	189	471	
%	60%	40%		

*In this case the dominant male became ill and skulked.

†In these cases males that had dispersed to a subordinate role ultimately reclaimed the natal territory.

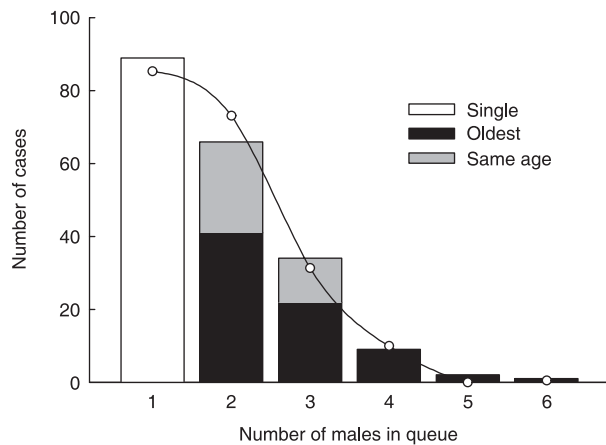


Fig. 1. The number of male *M. cyaneus* in reproductive queues at the time of death of the dominant. The classes distinguished are the case where just a single subordinate male was on the territory, where more than one male was present and either the sole oldest male inherited the vacancy, or nest-mates were the oldest birds when promotion took place. In the latter case, if there were three birds in the queue, all three were nest-mates in two of 12 cases, and just two were nest-mates in the remaining 10 of 12 cases. The curve describes the Poisson predictions for the number of males remaining after territorial inheritance (i.e. number of males in queue - 1).

pooled). We observed no cases of dominance reversal among subordinates. While in a substantial number of cases there was just one male in the queue on the death of the dominant (Fig. 1; 89 of 201, 44%), in 75 cases (37%) there was more than one bird in the queue and one was older than the others. This oldest subordinate was always promoted once the dominant died. In the remaining 37 cases (18%) two or more nest-mates were the oldest birds when the dominant died. In 27 of these latter cases we were able to compare the moult into nuptial plumage of the nest-mates in the season or seasons before the opportunity for promotion arose. Moult discrepancies that arise between nest-mates generally persist throughout life. In 24 cases (89%) the male that first achieved nuptial plumage as a subordinate subsequently became dominant (binomial test with continuity correction, $P < 0.001$). In two of these cases, the male that remained subordinate failed to achieve complete blue plumage, but in the remainder the difference was $16.7 \text{ days} \pm 10.6 \text{ SD}$ ($n = 24$, minimum = 7 days). In the three cases where dominance could not be predicted by moult, the males moulted at approximately the same time. In these cases, dominant status could be assigned to one of the males behaviourally. One of these three pairs of nest-mates moulted at similar times for 5 years, throughout which one bird dominated the other behaviourally.

We observed two cases where the dominant was replaced by his subordinate while still alive. In the first of these cases the dominant became ill and skulked on the territory for several months before death, allowing the subordinate to assert dominant status. The second case provided the only obvious case of successful violent overthrow of the hierarchy, but its extraordinary context emphasizes the usual strict observance

of queuing. In this case, a young male dispersed to take up a subordinate position. Uniquely, this male dispersed a long distance (five territories), and failed to acquire nuptial plumage for the first 2 years of its life, suggestive of an abnormal endocrine profile (Mulder & Cockburn 1993). In his third year he acquired nuptial plumage and shortly thereafter successfully fought and evicted the dominant.

Subordinates did sometimes take part of a territory from the dominant via fission. This process was typically resisted strongly by the dominant female, but the dominant male rarely intervened. The ability to achieve fission is contingent on whether the territory attracts a supernumerary dispersing female, and these females prefer to settle on territories with numerous supernumerary birds (Cockburn *et al.* 2003). In many cases fission was achieved where there was only one subordinate male ($n = 40$ of 138, 29%), or the oldest subordinates were a group of nest-mates (26, 19%). In the remaining cases where a contest occurred between males of different age (52%), the older male was more likely to gain the new dominant position on the new territory fragment, though not inevitably so (47 of 72, 65%; binomial test with continuity correction, $P = 0.003$).

BETWEEN-GROUP CONTESTS OVER DOMINANT STATUS

Ownership of the entire territory could also be gained directly by birds from outside the reproductive queue. Neighbouring birds gained ownership via three paths.

1. Subordinates can be regarded as competitors for neighbouring vacancies. Defining the appropriate pool of competitors is difficult for this pathway, as males that move to territories on the boundary of the study area are potentially competitors with unsampled males of unknown age. This problem is particularly pervasive before the expansion of the study area in 1991/1992. We therefore considered just the dispersal events that took place after 1992. There was no evidence that age conveyed an advantage in gaining neighbouring territories. We excluded from our sample 52 birds that dispersed to a boundary territory and four that dispersed more than one territory. In the remaining cases ($n = 42$) we defined the pool of potential dispersers as any male in a subordinate position on a territory adjacent to the vacancy. There was one instance where the vacancy was gained by the only subordinate on neighbouring territories. On six occasions (14%) the vacancy was gained by the oldest subordinate in the pool, and on 15 occasions (35%) by one of a pool of males from the same cohort. However, there were 20 cases (48%) where a younger bird gained the vacancy, and in five of these they did so despite the presence of an older subordinate on their own territory.
2. Usually prompted by the death of his own mate, an older bird sometimes subsumed a neighbouring territory, relegating any other residents to subordinate status ($n = 32$). In this latter case males often regained space that they had owned prior to territorial fission, so at least the senior subordinate had previously been their helper. With one exception, relegated males were always younger than the male that assumed the

Table 2. Frequency with which individual male superb fairy-wrens fill just one or combinations of social roles during their lives ($n = 596$ males)

	Type of female assisted				Total	%
	Mother only	Unrelated only	Both	Neither		
Helper and/or became dominant						
Help only	83	77	37	0	197	33%
Both	100	117	92	0	309	52%
Dominant only	0	0	0	90	90	15%
Total	183	194	129	90	596	
%	31%	33%	22%	15%		

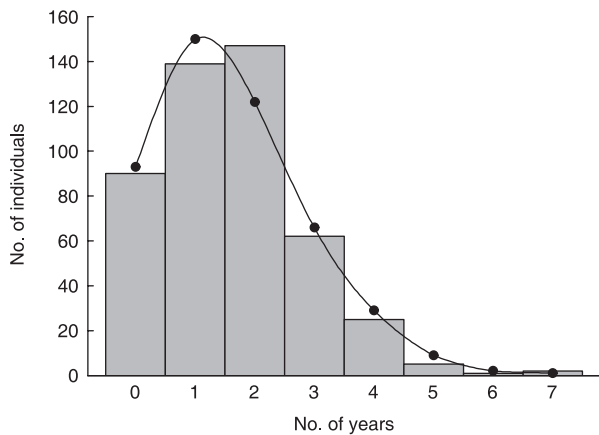


Fig. 2. The number of breeding seasons in which male *M. cyaneus* helped before gaining dominant status for the first time. A bird that obtains dominant status during a breeding season is counted as a helper for that season. The curve describes the Poisson predictions for the observed mean of 1.62 breeding seasons.

dominant position, and often pre-reproductive juveniles. In the exceptional case, a male relegated a same-aged nest-mate. **3.** Last, and least common, the usurper evicted any resident males ($n = 12$), usually forcing them to return to their natal territory and help. In these cases the males were generally of similar age (new dominant 1 year older, $n = 3$, same age, $n = 5$ and younger, $n = 3$). There was one exception, where the new dominant was 5 years younger than his predecessor, which was visibly ill with avian poxvirus.

INHERITANCE AND ITS CONSEQUENCES

Many males reached adulthood (1 year of age) but never attained dominant status (33%), but others did so before their first breeding season, so they had no prior opportunity to help (15%, Table 2). Males helped in as many as seven seasons before they obtained dominant status (Fig. 2, mean = 1.62 ± 1.23 SD, $n = 471$, median = 2 seasons). A Poisson distribution predicts the number of years males spend in helping roles (Fig. 2; $\chi^2 = 7.3$, d.f. = 5, $P = 0.20$, > 4 years pooled).

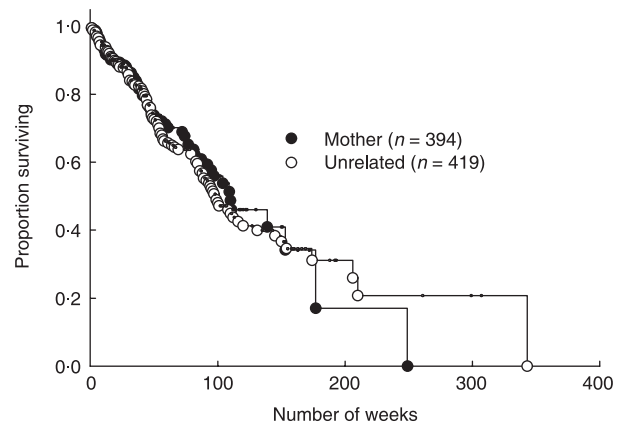


Fig. 3. Kaplan–Meier plots of the survival of subordinate males while living with their mother or an unrelated female. Circles denote death as a subordinate. Cases of transition to another social condition or persistence until March 2007 were treated as censored.

Similar numbers of subordinate males lived with their mother (312 of 596; 52%; Table 2) as did with an unrelated female (323 of 596; 54%). Some of these subordinates lived with both their mother and an unrelated female (129 of 596; 22%). Subordinate birds spent less time with their mother (mean = 42 weeks), than with unrelated females (mean = 53 weeks; log rank test, $\chi^2 = 10.1$, d.f. = 1, $P = 0.001$). A comparable result was obtained considering the restricted sample of males that were sampled with both their mother and an unrelated female (log rank test, $\chi^2 = 7.6$, d.f. = 1, $P = 0.006$). A small part of the difference between males living with their mother vs. an unrelated female could arise because mothers with helpers in the senior position on the territory will sometimes leave the territory (Cockburn *et al.* 2003). However, most of the effect occurred because while both classes of male have the opportunity for promotion on the death of the dominant male, males living with their mother will also change status if the female dies or initiates divorce, thus precipitating replacement by a female to which the male is unrelated (males with mother: 124 of 272 transitions, 46%; males with an unrelated female: 12 of 279 transitions, 4%; $\chi^2 = 137.0$, d.f. = 1, $P < 0.001$). Treating cases where there is a transition in status as censored allows survival prospects to be compared directly. Living with a mother vs. an unrelated female had no effect on male survivorship prior to a change in status (Fig. 3, log-rank test: $\chi^2 = 0.3$, d.f. = 1, $P = 0.61$).

Because of strict inheritance, a high proportion of males spent part of their lives paired to their mother (82 of 596, 14%). However, as we have reported previously, these relationships are often very short-lived, as females usually divorce their son and move to a vacancy as soon as one becomes available in the neighbourhood (Fig. 4).

Excluding the incestuous relationships, the survival of helpers and dominants was remarkably similar (Fig. 5a, log-rank test: $\chi^2 = 0.66$, d.f. = 1, $P = 0.44$). Weibull β was higher than 1 for both dominants (1.19, 95% confidence intervals 1.10–1.29) and helpers (1.12; 1.01–1.24), because mortality accelerates with length of occupancy, increasingly markedly after 4 years (Fig. 5b).

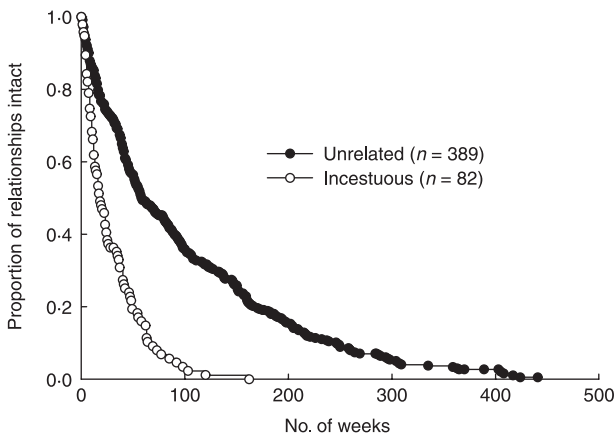


Fig. 4. Kaplan-Meier plots of the persistence of the relationships of males that have become dominant for the first time and either mated with an unrelated female or paired incestuously with their mother. Circles denote the end of the relationship. Relationships still persisting in March 2007 were treated as censored.

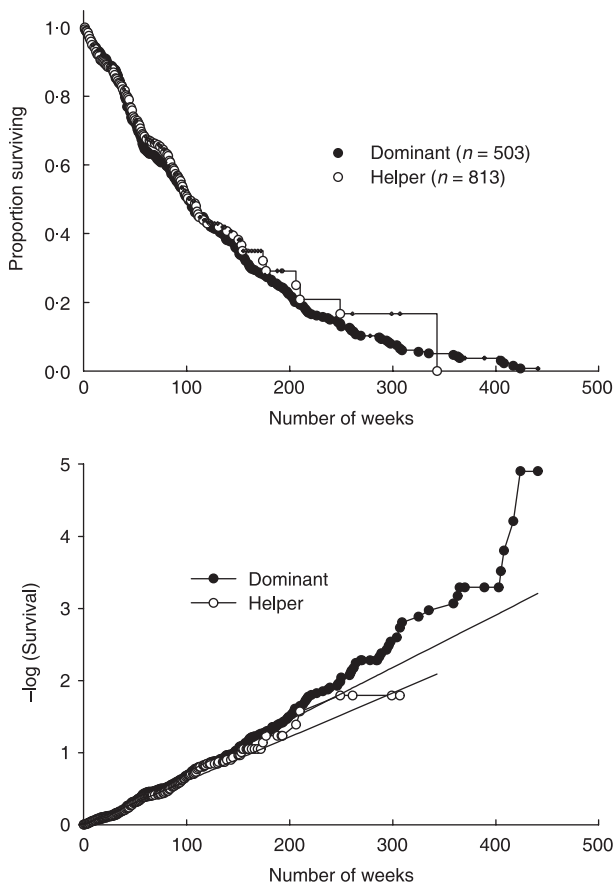


Fig. 5. Survival of dominant birds unrelated to the female and helpers. (a) Kaplan-Meier plots of the persistence of the relationships of dominants and helpers. Circles denote deaths. Changes from helper to dominant status and cases that persisted until March 2007 were treated as censored. Sample sizes include both cases that were censored and those terminated by death. (b) Plots of inverse log-transformed survivorship. Lines denote predictions for an exponential function, which would indicate constant survival.

Discussion

Male *Malurus cyaneus* form stable queues for dominant status, and the majority of birds achieve dominant status and die on their natal territory. Inheritance of the natal territory is the main path to dominant status, though dispersal to neighbouring vacancies and territorial fission are also common. While increases in ability and motivation among older birds may contribute, direct reproductive benefits while in the queue may also explain the stability of queues. We found no evidence that nepotism facilitates survival of offspring, or that the survival of dominants and subordinates was affected by fundamentally different processes.

Male *Malurus cyaneus* are extremely philopatric, with 60% of males gaining their first breeding vacancy on their natal territory. So far as we aware, this is the highest proportion reported for cooperatively breeding birds where just a single female usually nests on the territory, though more than 50% of males also achieve dominant status on their natal territory in two other species of *Malurus* (Russell & Rowley 1993, 2000) and *Campylorhynchus nuchalis* (Yáber & Rabenold, 2002).

The queues formed by male *M. cyaneus* are highly stable, with overturn of the hierarchy only occurring in two exceptional cases (of 596 males). This stability is unlikely to result solely from the prohibitive costs of fighting, as dominants could be overthrown by their neighbours. It is also unlikely that collusion among members of the queues to punish defectors is primarily responsible for enhancing stability, as there is often just a single subordinate, so any conflict is simplified to an interaction between the dominant and that subordinate. By contrast, asymmetries in fighting ability could contribute to the stability of queuing. First, violent contests leading to the eviction of neighbours were generally between males that were similar in age, and older males were also able to re-assert dominant status over younger birds when territories fused. Second, it is known that the males increase the time they spend in nuptial plumage, and hence in extra-group courtship display, for the first 5 years of life (Mulder & Magrath 1994b; Dunn & Cockburn 1999). Such improvement is suggestive of increased condition. However, this is unlikely to be a complete explanation, as neighbouring birds of similar or even lesser age do usurp vacancies. In addition, the competitors for inheritance are often same-aged nest-mates, yet appear to have adopted clear subordinate/dominant roles prior to the availability of the vacancy, usually allowing us to predict which nest-mate would gain the territory.

While the benefits associated with age are therefore ambiguous, some of the proposed general benefits from membership of queues apply in this species. Two-thirds of subordinates gained a dominant role before they died. Mesterton-Gibbons *et al.* (2006) have argued that for stabilization of the queue to occur exclusively as a consequence of future inheritance, subordinates must have lower early mortality and higher later mortality than dominants. That pattern was not supported in this case. Survival of dominants and helpers is extremely similar (Fig. 3a), and conforms closely to constant mortality hazard for the first 4 years of life (Fig. 3b), though the average time

helpers spend in queues (48 weeks) is less than a quarter of that time. There has been considerable recent controversy over whether higher survival is expected in dominants or subordinates. The once widespread view that subordinates suffer more stress than dominants has not been supported by a number of studies of social mammals, which found the converse to be true (Creel 2001, 2005), though high stress does appear to cause reproductive suppression in meerkats (Young *et al.* 2006). For fairy-wrens, we found no difference in the survival of dominants and helpers, although mortality of both accelerated after 4 years. Increased mortality in older individuals is compatible with hypotheses of both senescence and terminal reproductive effort. However, in this case, we suspect that the pattern arises because older birds invest in extra-group courtship over prolonged periods, and suffer consequential costs, which escalate most strongly at about 4 years of age (Peters 2000; Peters *et al.* 2000; Peters, Astheimer & Cockburn 2001).

Surprisingly, and contrary to Ridley *et al.*'s (2005) hypothesis that a primary benefit of queuing is the establishment of reciprocal relationships that facilitate gaining vacancies on neighbouring territories once vacancies arise, older males were not more likely to gain dominant status by dispersal. The failure of older subordinates to win neighbouring vacancies could arise if dispersal was perceived as an inferior option to inheritance, because territories where vacancies arise are of inferior quality, as has been suggested for *Campylorhynchus griseus* (Haydock *et al.* 1996). However, experimental evidence suggests this is unlikely to be true in *M. cyaneus*. Pruett-Jones & Lewis (1990) created territorial vacancies by removing unassisted pairs from territories. Subordinate neighbours ignored the vacant territories but immediately dispersed when the female was released back on to her territory, suggesting that the presence of a female rather than territory quality is the prompt for dispersal.

Fairy-wrens are not a good candidate for indirect benefits associated with aiding kin, as subordinates are very frequently unrelated to the dominant male (Dunn, Cockburn & Mulder 1995), and there is no evidence that helpers bolster productivity of the dominants (Cockburn *et al.* 2008). Indeed, we found that the number of males assisting their mother or unrelated females during their lives was comparable (Table 2), and that the assistance of unrelated females was more prolonged (Fig. 2a).

The greater duration of subordinate status for unrelated males was not caused by different survivorship, but rather because the status of males helping their mother changed both because of the death of the mother and death of the dominant male. Nepotism towards offspring after fledging has been implicated as a founding condition for natal philopatry, and hence ultimately cooperative breeding (Ekman *et al.* 2000, 2004; Ekman 2006). We found no survival benefits of living with a mother rather than an unrelated female, suggesting that such nepotism does not occur in fairy-wrens.

By contrast, there is considerable evidence that immediate fitness benefits could be important. The extra-group paternity that dominates parentage in fairy-wrens is gained during

pre-dawn forays by the female to the territory of an attractive sire (Double & Cockburn 2000). Subordinates of these attractive sires participate in the dawn chorus and are highly effective at reproductive parasitism, gaining 21% of all extra-group paternity (Double & Cockburn 2003). In addition, while there is a complete avoidance of nuclear family incest, subordinates living with unrelated females gain 22% of within-group paternity if they are not living with their mother (Cockburn *et al.* 2003). Hence, unrelated subordinates have both within- and extra-group opportunities for reproduction, while subordinates living with their mother are confined to extra-group opportunities. It is interesting that the presence of subordinates increases the survival of the breeding female (Cockburn *et al.* 2008), which should postpone the access to related subordinates to reproduction, and increase the probability of incestuous pairing if the subordinate is promoted.

We hope that these data illustrate some of the complexities posed by reproductive queuing in cooperatively breeding birds. We hope that our analysis will provoke similar approaches for other species, as the relevant data are obtained routinely in the long-term studies that have dominated the empirical approach to this question (Stacey & Koenig 1990), and may allow us to understand the diversity of mating systems and patterns of territorial inheritance among cooperative breeders.

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