

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

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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.

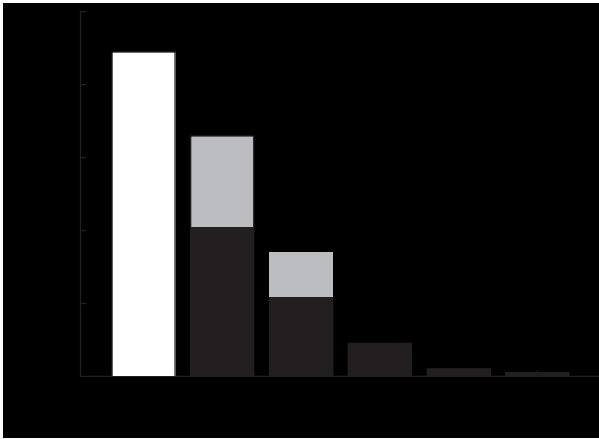
To summarize key results from Cockburn *et al.* (2003), fairy-wrens live on year-round territories where a dominant male and a female form a pair-bond, which is easily recognized by close association, including counter-singing, joint territorial defence and mate-guarding. The pair-bonded male and female 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. A subordinate male can usurp ownership of the territory if he wins a contest with the dominant male. This is observed in 21% of territories.

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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,  $P = 0.003$ ).

B  
A

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

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.

— A A



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

- Double, M. & Cockburn, A. (2000) Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society of London Series B Biological Sciences*, **267**, 465–470.
- Double, M.C. & Cockburn, A. (2003) Subordinate superb fairy-wrens (*Malurus cyaneus*)