

Subordinate superb fairy-wrens (*Malurus cyaneus*) parasitize the reproductive success of attractive dominant males

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Explanations of cooperative breeding have largely focused on the indirect benefits philopatric offspring gain from investing in kin. However, recent molecular studies have revealed that in many species subordinates provision unrelated offspring. This has led to the re-evaluation of the direct and indirect benefits of helping behaviour. In this study, we used microsatellite genotyping to assess the extra-group reproductive success of subordinate superb fairy-wrens (*Malurus cyaneus*), a species with extremely high rates of extra-group paternity. Extra-group subordinate males sired 10.2% (193 out of 1895) of all offspring sampled between 1993 and 2000 and 21.4% (193 out of 901) of all illegitimate offspring sired by known males. The extra-group success of subordinates was greatly influenced by the attractiveness of their dominant male. Subordinates of attractive dominants sired more extra-group young than did average dominants. Evidence suggests that mate choice in superb fairy-wrens is error-prone and subordinates can gain direct reproductive benefits through parasitizing the reproductive success of attractive dominants.

Keywords: sexual selection; extra-pair copulation; avian mating systems; *Malurus cyaneus*; mate choice; hidden leks

1. INTRODUCTION

Traditionally, cooperative-breeding theory has emphasized the indirect benefits that philopatric offspring gain from investing in kin (Emlen *et al.* 1995; Emlen 1997). This perspective is now challenged by the increased recognition that helping can be influenced by deferred benefits such as group augmentation (Clutton-Brock 2002) and immediate benefits from access to reproduction (Magrath & Whittingham 1997; Cockburn 1998; Richardson *et al.* 2003).

Cockburn (2003) found that in 15 out of the 29 cooperatively breeding birds studied using molecular analyses, paternity was commonly shared within the group (more than 20% of broods) if the group contained more than one male to which the female was unrelated. In some cooperative breeders there is also considerable extra-group paternity (Seychelles warbler, *Acrocephalus sechellensis* (Richardson *et al.* 2001); western bluebird, *Sialia mexicana* (Dickinson & Akre 1998); red-billed buffalo weaver, *Bubalornis niger* (Winterbottom *et al.* 2001); white-browed scrubwren, *Sericornis frontalis* (Whittingham *et al.* 1997); splendid fairy-wren, *Malurus splendens* (Brooker *et al.* 1990); and the superb fairy-wren, *Malurus cyaneus* (Mulder & Cockburn 1993; Dunn & Cockburn 1999)) but it is unclear whether subordinates share these benefits.

Superb fairy-wrens show extreme rates of extra-group paternity (more than 60% of offspring; Mulder *et al.* 1994; Dunn & Cockburn 1999). High-quality males are most likely to sire extra-group young (Dunn & Cockburn 1999; Green *et al.* 2000), but subordinates are reproductively competent (Mulder & Cockburn 1993) and can achieve

both within-group (Cockburn *et al.* 2003) and extra-group success (Mulder *et al.* 1994; Dunn & Cockburn 1999). The high rates of extra-group paternity result in low levels of relatedness between subordinates and offspring but helpers always provision young (Dunn *et al.* 1995). However, evidence suggests that helping does not enhance group productivity (Green *et al.* 1995; Dunn & Cockburn 1996).

In order to reassess helping behaviour in this species, we used a microsatellite-based genotyping system to determine the reproductive success of subordinate males in a dataset of 1944 offspring sampled over eight breeding seasons. We examine the distribution of extra-group reproductive success among subordinate males and question why subordinate males sire any extra-group offspring.

2. METHODS

(a) Study species and study site

Since 1988 we have studied a colour-banded population of superb fairy-wrens breeding in and around the Australian National Botanic Gardens in Canberra. The study area covers ca. 70 ha (85 wren territories) and is surrounded by Canberra Nature Park and the Australian National University campus, which support contiguous wren territories.

Fairy-wrens are resident throughout the year, and during the breeding season a socially monogamous pair occupies each territory. While pairs have exclusive ownership of about half the territories, one to four subordinate males can also assist the pair. Male fairy-wrens show strong natal philopatry whereas juvenile females are forced to leave their natal territory to find a breeding vacancy (Mulder 1995). Females may later divorce their mates but will rarely move more than one or two territories (Cockburn *et al.* 2003). Owing to the high turnover of females and the extreme level of infidelity, males often help raise unrelated offspring (Dunn *et al.* 1995). The oldest and earliest-moulting male

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on a territory is always dominant. Subordinates defer to the dominant male during aggressive encounters and dominants will monopolize access to the female during her fertile period (Cockburn *et al.* 2003).

Female superb fairy-wrens retain their brown plumage throughout the year, whereas males moult from a brown to a bright blue and black nuptial plumage up to eight months prior to the start of the breeding season. Almost all males attain full nuptial plumage and a few males (less than 2%) maintain nuptial plumage throughout the year. Males in nuptial plumage regularly display to neighbouring females (Rowley 1991; Mulder 1997; Green *et al.* 2000) and females appear to use the timing of the moult as an indicator of male quality. Males that retain or moult earliest into nuptial plumage almost always sire extra-group young (Dunn & Cockburn 1999; Green *et al.* 2000). Extra-group copulations are controlled by females and occur in a predictable context: 2–4 days prior to laying their first eggs, females conduct pre-dawn forays to nearby territories to copulate with extra-group males (Double & Cockburn 2000).

The study population was monitored throughout each year and the timing of the moult into nuptial plumage was recorded for every resident male. During each breeding season every territory was visited at least three times a week to assess breeding activity and group composition. In this paper, the term 'dominant' refers to the senior male on a territory but does not necessarily imply the presence of subordinate males.

(b) *Microsatellite genotyping*

Nestlings were banded between 5 and 7 days after hatching and a small blood sample was taken for DNA profiling (Double *et al.* 1997). We used microsatellite genotyping to assign paternity to all nestling fairy-wrens produced in the study area between 1993 and 2000. Between five and seven hypervariable microsatellite loci were amplified for each individual (Double *et al.* 1997) and run on an ABI377 sequencer (Perkin-Elmer). Internal size standards were run with all PCR products and allele sizes were determined using GENESCAN v. 2.1 (Perkin-Elmer).

Paternal alleles were identified by comparing the offspring and maternal genotypes. A search of genotypes for every male in the population identified those that possessed all the paternal alleles found in the offspring. To reduce the probability of false exclusion through mutation, we initially considered all allele sizes within two bases to be identical. If more than one adult male matched the chick's genotype, then males that mismatched the offspring's paternal alleles by more than a single base were excluded. In the rare cases where the pool of potential fathers still contained more than one male, paternity was assigned to any matching male that also unambiguously sired other chicks within the brood. If these criteria did not identify a single male then paternity was not assigned.

Genotypes were produced for 1944 offspring from 688 complete broods. Owing to multiple matches or genotyping errors, we could not assess the legitimacy of 49 offspring from 40 broods.

(c) *Statistical analyses*

A standardized male moult score was calculated for each adult male for each breeding season. This moult score was the number of standard deviations (s.d.) from the mean moult date for that year. For example, in 1993 the mean moult date in Julian days was 245.5 (s.d. = 56.6 days, $n = 186$). Therefore a male that was recorded as reaching full nuptial plumage on 26 April 1993 (113

Julian days) would have a moult score of -2.34 ($(113 - 245.5)/56.6$). Males that retained nuptial plumage throughout the year were assigned a moult date of 60 Julian days, one day prior to the earliest moult from eclipse to breeding plumage recorded between 1993 and 2000. Males that did not acquire full nuptial plumage were assigned a moult date of 340 Julian days, one day after the latest moult recorded between 1993 and 2000.

We used JMP v. 3.0.2 (SAS Institute Inc.) for most analyses and GENSTAT v. 5 (release 4.2, 2000) for logistic regression models of extra-group paternity. Modelling was used to examine the effect of male age, standardized moult score, breeding unit (pair or group), presence of subordinates and year on the probability of males successfully siring one or more extra-group offspring. We used presence or absence of success as we could not fully measure the success of males towards the edge of the study area and the data were dominated by unsuccessful males. If the social status of a male was ambiguous then that male was removed from the analysis. This can occur when a dominant male dies and the two remaining subordinates are the same age. We also examined the influence of female age and the number of territories between the female and the most distant extra-group sire on the probability that a female's brood contained a chick sired by a subordinate male.

Initially we fitted models containing all fixed and interaction terms. Terms were assessed by the change in deviance (which approximates a χ^2 distribution) and were progressively removed until the model contained only significant terms ($p < 0.05$). Results presented for non-significant terms were those predicted by the model that contained all significant terms.

3. RESULTS

The general paternity data from this study will be reported elsewhere (M. C. Double and A. Cockburn, unpublished data). In summary, microsatellite genotyping revealed that males from outside the female's social group sired 1151 of the 1895 offspring. The true sire could not be identified for 250 of these 1151 illegitimate offspring (21.7%) because the male was not resident within the study area. The remaining 901 offspring (78.3%) were successfully assigned to extra-group males within the study area. We did not find any cases of intraspecific brood parasitism.

(a) *Moult score and extra-group paternity by subordinate males*

Extra-group subordinate males sired 10.2% (193 out of 1895) of all offspring sampled between 1993 and 2000 and 21.4% (193 out of 901) of all assigned illegitimate offspring. Subordinate males sired young in 25.5% of 386 complete broods where it was possible to identify the social status of every sire. On average 27.4% of subordinate males sired young in each season although this figure fluctuated greatly from 10% (7 out of 69) in 1994 to 43% (15 out of 35) in 1999.

A logistic regression model that included all subordinates was unduly influenced by the leverage of extremely high moult scores found only among late-moulting 1-year-old birds in some years. To avoid this, 1-year-old and older subordinates were initially modelled separately. All interaction terms in the model of first-year subordinates were not significant. Year effects were highly significant

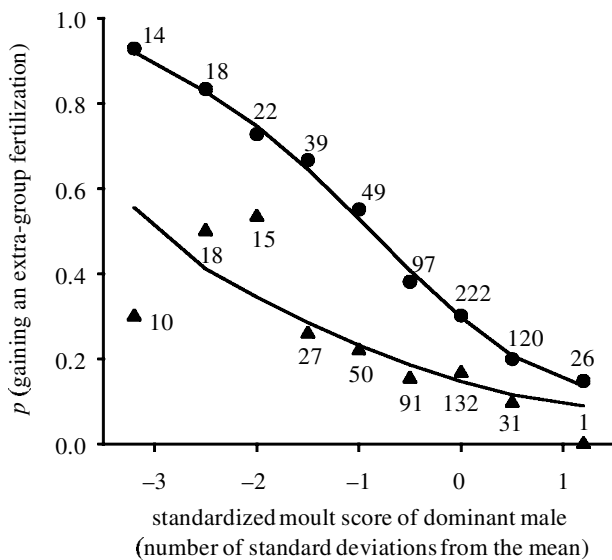


Figure 1. The effect of moult date on the probability of gaining at least one extra-group fertilization. Circles, dominant males; triangles, subordinate males. The curves are the logistic regression predictions of the probability of extra-group paternity on the standardized moult score of the dominant male in a model containing the interaction between status and moult score. Each data point represents the actual proportion of males that gained some extra-group paternity for each 0.5 s.d. category. The number of males in each category is given above the relevant data point. Categories at the extremities of this distribution have been pooled, and the points are located at the average value of the pooled data.

but were dominated by unstable estimates for years when many males failed to moult into full nuptial plumage ($\chi^2 = 23.0$, d.f. = 7, $p < 0.002$) and so were dropped from the model. The subordinate's own moult score did not influence extra-group success ($\chi^2 = 2.7$, d.f. = 1, $p = 0.1$) leaving the moult score of the subordinate's dominant as the only significant term in the model ($\chi^2 = 6.6$, d.f. = 1, $p = 0.01$). The modelling of older subordinates gave a similar outcome. Year was highly unstable but not a significant factor in the model ($\chi^2 = 11.2$, d.f. = 7, $p = 0.13$). Again, the reproductive success of older subordinates was not influenced by their own moult scores ($\chi^2 = 2.7$, d.f. = 1, $p = 0.1$) but increased if their dominant male moulted early in the season (figure 1; $\chi^2 = 8.3$, d.f. = 1, $p = 0.004$).

Both subordinate and dominant males were then included in a single model that examined the effect of status, the presence of subordinates and the moult score of the dominant male on the probability of siring chicks outside the social group. As in previous studies, extra-group reproductive success of dominant males was predicted almost perfectly by their own moult scores (figure 1; cf. Dunn & Cockburn 1999; Green *et al.* 2000). Status ($\chi^2 = 20.6$, d.f. = 1, $p < 0.001$), the dominant's moult score ($\chi^2 = 72.4$, d.f. = 1, $p < 0.001$) and the interaction between moult score and status ($\chi^2 = 5.2$, d.f. = 1, $p = 0.02$) all remained as significant effects in the model (figure 1). The difference in the probability of siring extra-group offspring between dominants and subordinates was higher when the dominants moulted earlier. However, subordinates of attractive dominants were more likely to

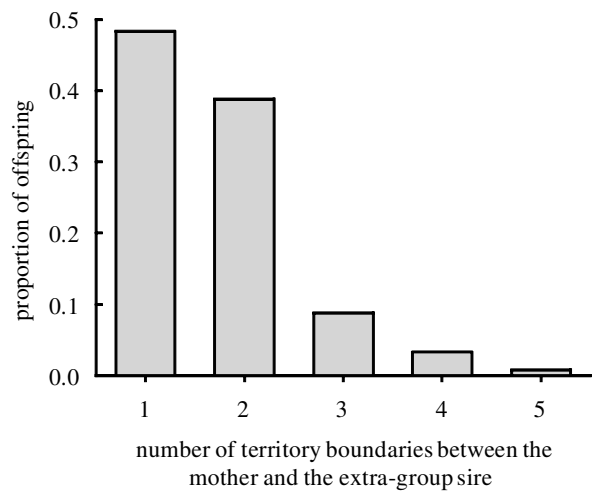


Figure 2. Males from territories adjacent to the mother's own territory most commonly sired extra-group offspring. This analysis included all offspring that were assigned to extra-group males within the study area ($n = 901$). If all the illegitimate offspring that could not be assigned to males in the study area ($n = 250$) were sired by distant males (3+ territories), over 68% (785 out of 1151) of illegitimate young would still be assigned to males within two territories of the mother.

sire extra-group young than were the dominants with average moult scores. The presence of subordinates did not affect the extra-group success of dominants ($\chi^2 = 0.3$, d.f. = 1, $p = 0.6$).

(b) *Extra-group forays and subordinate paternity*

The paternity data indicated that female fairy-wrens generally sought extra-group copulations over relatively short distances (figure 2). Males within one or two territories of the female accounted for the majority of extra-group paternities (87.1%; 785 out of 901), although in some cases paternity was assigned to males up to five territories (*ca.* 620 m) from the female's own territory. Subordinate males tended to be more likely to sire extra-group offspring if the female had travelled further to seek extra-group copulations (figure 3; $\chi^2 = 3.6$, d.f. = 1, $p = 0.06$) irrespective of the female's age ($\chi^2 = 2.9$, d.f. = 1, $p = 0.08$).

4. DISCUSSION

Subordinate males sired over one-fifth of all extra-group offspring of known parentage, and over one-quarter of all broods contained young sired by subordinate extra-group males. Such high rates of direct reproduction by subordinates have previously been reported only in cooperatively breeding birds where paternity is shared among unrelated members within a group (e.g. white-browed scrubwrens, *S. frontalis* (Whittingham *et al.* 1997); dunnocks, *Prunella modularis* (Burke *et al.* 1989); Galapagos hawks, *Buteo galapagoensis* (Faaborg *et al.* 1994); and brown skua, *Catharacta lombergi* (Millar *et al.* 1994)). By contrast, this is, to our knowledge, the first study to show that subordinate males can achieve high levels of reproductive success through extra-group copulations. Few minisatellite-based studies of cooperatively breeding birds have attempted to

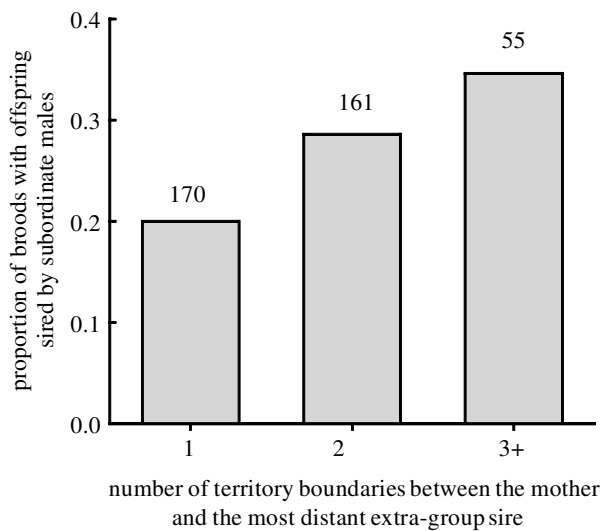


Figure 3. The proportion of broods with offspring sired by subordinate males increased with the number of territory boundaries between the female's own territory and that of the most distant extra-group sire. Only broods with complete paternity assignment and at least one illegitimate offspring were included in this analysis. The number above each column indicates the total number of broods in each class.

assign extra-group sires (Mulder & Cockburn 1993; Dunn & Cockburn 1999) and to date only one, to our knowledge, has used microsatellites to assign extra-group offspring. In Richardson *et al.*'s (2001) study of Seychelles warblers, 38% (21 out of 55) of offspring were found to be illegitimate. Although all successful extra-group sires were dominants, male help is rare in this species.

From the dataset presented here Cockburn *et al.* (2003) reported that 65 within-group young were sired by subordinate males. Therefore, of offspring sired by males of known status, 26.7% (258 out of 966) of all *extra-pair* offspring and 15.7% (258 out of 1645) of all young sampled between 1993 and 2000 were sired by subordinates. Such direct reproductive success may provide an incentive for subordinates to remain on their natal territory and could explain the paradox that helpers often rear young to which they are unrelated (Dunn *et al.* 1995). However, experimental evidence indicates that subordinates will always disperse to a breeding vacancy if possible, despite having access to direct reproductive success (Pruett-Jones & Lewis 1990). This implies that within-pair matings are the major motivation for dispersal by subordinates of attractive males.

The extra-group reproductive success of subordinate superb fairy-wrens appears to be linked to the quality of their dominants rather than to their own prowess. Subordinate males on territories with early-moulting dominant males were more likely to sire extra-group offspring, irrespective of their own moult score. By contrast, the success of dominant males depended on the timing of their own moult into nuptial plumage, as reported elsewhere (Dunn & Cockburn 1999; Green *et al.* 2000).

These data indicate that subordinates can parasitize the attractiveness of high-quality dominants and may explain why the song posts used during the pre-dawn period are highly clustered (C. Blackmore, personal communication). Studies of lekking species, such as black

grouse (*Tetrao tetrix*) and marine iguanas (*Amblyrhynchus cristatus*), have shown that less attractive males can increase their chances of copulating with a visiting female if they display close to a highly attractive male (Alatalo *et al.* 1991; Rintamaki *et al.* 1995; Wikelski *et al.* 1996; Partridge *et al.* 2002). This is the basis of the 'hotshot model' of lek formation, which predicts that subordinate males will cluster around highly competitive or attractive males because females are more likely to seek copulations from these males (Beehler & Foster 1988; Hoglund & Robertson 1990). Wagner (1997) extends this model to socially monogamous territory-holding species and suggests that 'hidden leks' may exist where territories aggregate around high-quality males because females will preferentially settle with or close to a high-quality male. However, in fairy-wrens it is the males rather than the territories that are aggregated and so this system more closely resembles the hidden leks of socially monogamous non-territorial species such as razorbills (*Alca torda*; Wagner 1992).

Illegitimate offspring were more likely to have been sired by subordinates if the female had traversed more territories in search of extra-group copulations. Similarly, Double & Cockburn (2000) showed that females that travelled further to seek extra-pair copulations were more likely to produce a clutch sired by more than one extra-group male. These data indicate that females may not always be able to locate and identify the intended extra-group sire accurately. An anecdotal event supports this view. During the 1999 breeding season a dominant male (BnaR) that had remained blue throughout the winter was not seen on his territory for 10 days, and a 1-year-old subordinate from a neighbouring territory (MgwR) took up the vacancy. During BnaR's absence a female whose previous extra-group offspring had been sired by BnaR became fertile, and the two extra-group young in the subsequent clutch were sired by MgwR. BnaR then returned and usurped MgwR. In the following season BnaR sired all 10 of the female's illegitimate offspring. Although we cannot confirm the reason for the absence in this case, in other groups the temporary absence of a dominant has reflected disability caused by disease or injury.

The hotshot model of lek formation predicts that skew in male mating success is a reflection of skew in male dominance rather than a female preference for particular male phenotypes. This prediction may explain why females appear to be unable to identify particular males and why females sometimes copulate with subordinate males in neighbouring territories. Perhaps females decide to visit an area because it is occupied by an early-moulting male but then rely on male-male competition to decipher the identity of the high-quality dominant. If the high-quality male is absent or with another extra-group female then the subordinate will have the opportunity to copulate with the visiting female. Such error-prone mate choice will greatly reduce the intensity of sexual selection in this species, and was proposed as a resolution of the 'lek paradox' by Randerson *et al.* (2000).

The presence of subordinates did not increase the attractiveness of dominants so it is unclear why dominants tolerate subordinates that apparently reduce both their within-pair (Mulder *et al.* 1994) and extra-group success. Green *et al.* (1995) showed that helpers reduce the dominant's workload and this provides greater opportunity to

display to extra-group females. However, display rate *per se* does not influence extra-group success (Green *et al.* 2000). Perhaps, because females conduct pre-dawn forays during a very brief period, dominants cannot copulate with multiple females. Thus subordinates do not necessarily reduce the dominant's extra-group success and can even provide indirect benefits if the subordinate is a legitimate son.

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