

Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens

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Despite great interest in the use of extra-pair mating as a tool for examining female choice and intersexual selection, the underlying assumption of female control has proved difficult to verify empirically. We combined microsatellite genotyping and radiotelemetry of fertile females in order to investigate mate choice in superb fairy-wrens *Malurus cyaneus*, the bird with the highest known rate of extra-pair fertilization. All five females radio tracked during the peak of fertility, two to four days before the first egg is laid, undertook pre-dawn forays. All extra-pair young produced by the female were sired by a male visited during their forays, indicating that females control extra-pair fertilizations. In a larger sample of paternity data, some broods were sired by two extra-group males. In virtually all the cases the territory of the two sires were on an identical linear trajectory from the female's territory. This again suggests that extra-group paternity in superb fairy-wrens is directly linked to female extra-territorial forays. In other species mixed paternity has been taken to indicate that females attempt to insure against infertile pairings or try to maximize the genetic diversity of their brood. However, in fairy-wrens the likelihood of multiple extra-group paternity increased greatly as females traversed more territories in order to mate, perhaps suggesting that females which foray further are more likely to have difficulties locating the preferred male.

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

1. INTRODUCTION

Socially monogamous birds often engage in extra-pair copulations (Westneat & Sherman 1997; Petrie & Kempenaers 1998). Although extra-pair fertilizations were once thought primarily to reflect male self-interest, there is growing acceptance that females control extra-pair mating in most birds (Gowaty 1996). Such control is of considerable theoretical interest as the benefits of mating with extra-territorial males should be dissociated from any choice of males for the purpose of obtaining paternal care or paternal resources. Extra-pair fertilizations therefore offer an insight into the indirect benefits females may obtain from mate choice. The benefits might include enhancement of the quality of their offspring by obtaining 'good genes' (Kempenaers *et al.* 1992; Hasselquist *et al.* 1996; Sheldon *et al.* 1997), avoidance of genetic incompatibility (Wetton & Parkin 1991; Zeh 1997; Kempenaers *et al.* 1999) and enhancement of the diversity of the brood (Birkhead & Møller 1992; Schulze-Hagen *et al.* 1993).

However, there are substantial caveats to the assumption that females control paternity. First, if females only initiate extra-pair matings on their own territory their choice will be limited to males that intrude into their territory and, hence, be a reflection of male-male competition rather than free female choice. Females might also accept mating to reduce subsequent harassment (Clutton-Brock & Parker 1995). More compelling evidence for female control has been provided by studies of blue tits (Kempenaers *et al.* 1992), hooded warblers (Neudorf *et al.* 1997; Stutchbury *et al.* 1997), red-winged blackbirds (Gray 1996, 1997a) and black-capped chickadees (Otter *et al.* 1998; Smith 1988). In these species females make extra-territorial forays during their fertile period, presumably to copulate with neighbouring males. However, females

may trade copulations with neighbouring males in return for extra foraging opportunities or simply be assessing potential extra-pair sires or future partners (Gray 1997b; Neudorf *et al.* 1997). Therefore, in these species extra-territorial forays could also have direct benefits and these forays have not been shown to influence paternity directly.

In this study we investigated extra-pair mating and paternity in the superb fairy wren (*Malurus cyaneus*). This species has the highest known rate of extra-pair paternity (76% of young and 95% of broods; Mulder *et al.* 1994) and available evidence suggests that extra-pair mating is under female control. First, during the female's fertile period dominant males do not guard females closely and often leave their territory to display to neighbouring females (Green *et al.* 1995; Mulder 1997). Second, the frequency of courtship displays by extra-pair males to fertile females cannot be used to predict the paternity of subsequent broods (Mulder *et al.* 1994; Dunn & Cockburn 1999). Finally, all observed copulations have been solicited by females (Mulder 1997). However, even within-pair copulations are rarely observed and only three possible extra-pair copulations have been recorded in more than 1000 h of observation (Mulder 1997). It has therefore been unclear whether females copulate covertly with intruding males or actively seek sperm from extra-group males through extra-territorial forays.

In this study, we used microsatellite genotyping and radiotelemetry to demonstrate that female superb fairy-wrens initiate pre-dawn extra-territorial forays which are highly stereotyped, confined to a narrow window during the fertile period and appear to be solely for the acquisition of sperm.

2. METHODS

(a) *Study species and study site*

A colour-banded population of superb fairy-wrens has been studied in and around the Australian National Botanic Gardens

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in Canberra since 1988. This 40 ha reserve and the surrounding bushland contain *ca.* 85 territories which the fairy-wrens maintain year round. The study area is surrounded by Canberra Nature Park and the Australian National University campus which also support contiguous wren territories. Each territory is occupied by a socially monogamous pair, but in *ca.* 60% of territories in any year the pair are assisted by one to four helper males. The dominant male is usually unrelated to the female, but females are paired to their sons in *ca.* 5–10% of territories. Males are extremely philopatric and are usually recruited into the breeding population in the territory in which they are born. Most males achieve dominance by queuing. However, some males disperse to neighbouring territories when the female in that territory is widowed but lacks helpers which could inherit the vacancy (Mulder 1995). Males are capable of breeding at one year of age, regardless of social status (Mulder & Cockburn 1993; Dunn & Cockburn 1999). Both dominant and subordinate males achieve extra-pair fertilizations (Mulder *et al.* 1994; Dunn & Cockburn 1999). In contrast, while females overwinter in social groups, they are not tolerated by the dominant female once reproduction commences and females are forced to disperse to find a vacancy or die, leading to the death of many young females (Mulder 1995). Dispersing females typically accept the first vacancy that they encounter and also pair with the senior male in the queue if their social partner dies, regardless of their relatedness to the senior male in the queue. However, females prefer to divorce their sons if a vacancy becomes available in a neighbouring territory (A. Cockburn, unpublished data).

Female fairy-wrens build the nest and incubate the clutch of three or four eggs. Males help defend the nest and later help provision the nestlings and fledglings (Rowley 1965; Dunn & Cockburn 1996).

(b) *Microsatellite genotyping*

Using microsatellite genotyping we attempted to assign paternity to nestling fairy-wrens sampled between 1989 and 1996 (414 broods) and eight broods produced by females radio tracked during the 1998–1999 breeding season. Between five and eight 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 polymerase chain reaction products and allele sizes determined using GeneScan 2.1 (Perkin-Elmer, Norwalk, CT, USA).

The paternal alleles were identified by comparison with the maternal genotype for each offspring. A database of genotypes for every adult within the study population was searched for males which possessed all the paternal alleles found in the offspring. To reduce the probability of false exclusion through mutation, alleles sizes within two base pairs were considered identical. If more than one adult male matched the chick's genotype then paternity was assigned based on parsimony; males in which no mutation was required to assign paternity were preferred to males in which one or more single-step mutations had to be assumed and, more occasionally, older males in close proximity to the offspring's territory (four or less territories) were deemed more likely to sire chicks than young, distant males (Dunn & Cockburn 1999).

(c) *Radio tracking*

Previous observational studies have suggested that female fairy-wrens remain in their territory during daylight hours (Cooney & Cockburn 1995; Green *et al.* 1995; Mulder 1997).

Mulder (1997) recorded two instances where a female strayed into a neighbouring territory but in neither case was an interaction with extra-group males observed. However, it is possible that females make extra-territorial forays during periods when they were impossible to observe. In the 1998–1999 breeding season we fitted seven females with radiotransmitters (Holohil LB-2, Holohil Systems Ltd, Ontario, Canada). For six out of the seven females the radiotransmitters were attached as soon as possible after the loss of a clutch. Fairy-wrens usually lay a replacement clutch seven or eight days after nest predation. We recaptured the first of the six females after two days to inspect the bird and the transmitter's harness so only five of the females were tracked throughout their fertile period. One female was monitored during the laying period and at the start of incubation. The transmitters were usually removed once the transmitter's battery failed or the female laid the first egg of a replacement clutch.

The females were radio tracked each morning for 1 h either side of sunrise. If a female left her territory, the time, flight trajectory and final destination were noted. We also recorded the duration of the foray and the time the female returned to her own territory. Copulations or other conspicuous behaviours were also recorded. In total, the females were monitored for 41 mornings during the core of the breeding season from mid-October to late December 1998. We used microsatellite genotyping to assign paternity for all young produced in that season by the five females tracked during the peak of their fertile period (one to three broods per female).

In this paper we define 'dawn' as synonymous with sunrise and 'twilight' to be when the sky is not completely dark but when the light levels are still too low to follow the birds or read colour bands. The times of sunrise were taken from the Department of Industry, Science and Resources' Web site (<http://www.auslig.gov.au>).

3. RESULTS

(a) *Extra-pair mating*

We successfully assigned paternity to all chicks within the brood for 253 out of the 414 broods sampled between 1989 and 1996. In 165 of these 253 broods, paternity was assigned to at least one extra-group male and the location of each sire's territory was known. In 29 out of the 165 broods two extra-group males gained paternity. Interestingly, broods were more likely to have more than one extra-group sire as the distance between the female's territory and the territory of the most distant extra-group sire increased (figure 1). Further, a close examination of the geographical distribution of these extra-group sires showed that, for each brood, the cuckolding males were usually on an identical linear trajectory from the female's own territory (figure 2). These data suggest that females conduct forays in a single direction and that the female is more likely to copulate with more than one extra-group male if she crosses several territory boundaries.

Radio tracking confirmed that females do leave their territories during their fertile period. All five females tracked three days before egg laying made an extra-territorial foray (figure 3). Some females also made forays on days -2 and -4 (figure 3). Each foray was the first movement made by the female after leaving the roost site and involved a rapid flight to the centre of the territory of another group or pair. After arriving in the extra-group territory, females remained stationary before making an

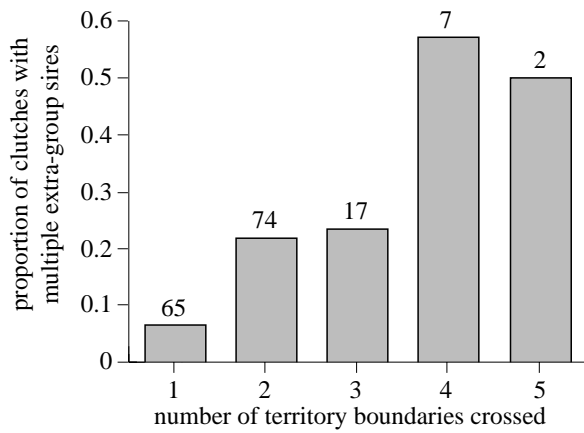


Figure 1. The frequency of broods with multiple extra-group sires increases with the number of territory boundaries between the female's territory and the most distant extra-group sire (logistic regression $\chi^2 = 11.22$ and $p < 0.001$). The number above each column is the sample size. These 165 broods were produced by 84 females. We repeated the analysis using a single clutch randomly chosen for each female. Again the relationship was highly significant (logistic regression $\chi^2 = 8.03$ and $p < 0.005$).

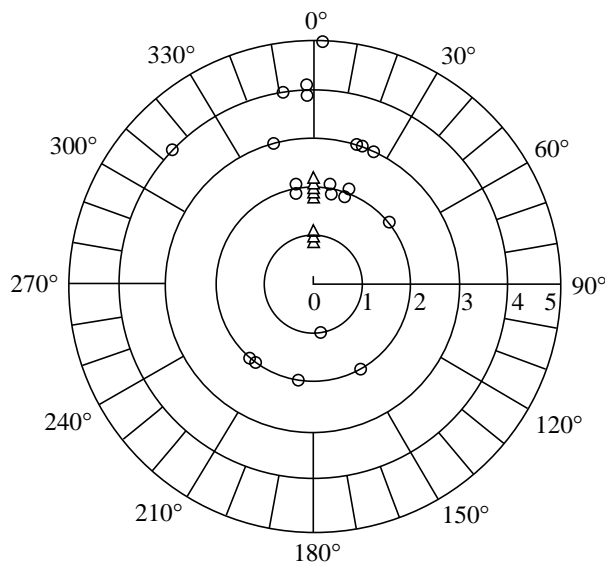


Figure 2. A polar plot representing the distribution of extra-group sires relative to the territory in which they gained paternity. Concentric circles represent the territory boundaries. Paternity was assigned for 165 clutches, 29 of which had two extra-group sires. For these 29 clutches (laid by 23 females), we found the number of territory boundaries between the female's territory and that of the most distant or oldest extra-group sire and set this male at 0° from the female. The divergence from zero indicates the trajectory to the territory centre of the second male to obtain paternity. Eight cases have zero divergence (denoted by triangles) because the two extra-pair sires were resident in the same territory. Points with identical coordinates are offset slightly so they can all be seen.

equally rapid return. Forays were initiated (mean time before sunrise = 20.5 min and range = 16–25 min) and usually completed before sunrise (mean = 7.0 min and range = 14 min before sunrise to 3 min after sunrise). The

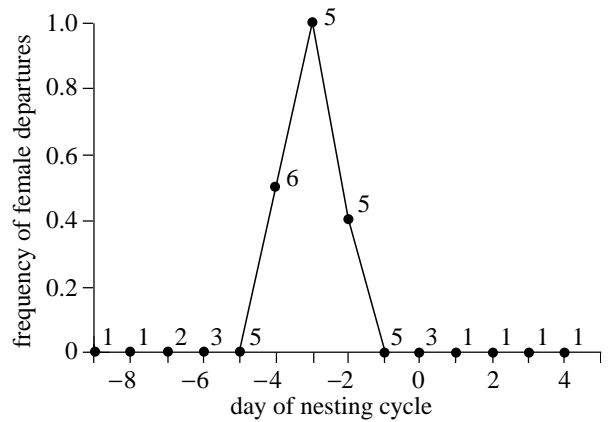


Figure 3. The frequency of female extra-territorial forays relative to the day of the nesting cycle. The first egg is laid on day 0. The numbers above each point indicate the number of females tracked during that day of the nesting cycle.

longest foray took 27 min (mean = 13.5 min and range = 8–27 min). Three out of the five females made forays on more than one morning, but on each occasion the route and final destination remained identical. Radio tracking was essential in detecting these forays. Even though one foray was completed after sunrise it was still too dark to track the bird by sight or read colour bands. During the hour after dawn, radio tracking did not detect any forays. We therefore have no reason to believe that previous observational studies failed to detect daylight extra-territorial excursions.

At least one brood from the 1998–1999 season was genotyped for each of the five females radio tracked throughout their fertile period (eight broods in total). All young within these broods were sired either by a male in the female's own territory ($n = 11$) or by a male on the territory visited by the female during the pre-dawn foray ($n = 12$). Only three of these broods were associated with the fertile period when the female was radio tracked. Even so, extra-group paternity within all broods with extra-group paternity ($n = 6$) could be predicted based on the trajectory and final destination of the females' forays. Two out of the five females produced more than one brood during the 1998–1999 season. One female produced two broods but only one clutch contained any extra-group paternity. The other female produced three broods and the same extra-pair sire gained paternity in each clutch.

During the 1993–1994 and 1994–1995 breeding seasons all broods produced within the study were genotyped. These data provide further evidence that females seem to repeat the same foray route for each fertile period. In total, there were 26 cases (from 24 different females) where a female produced two or more broods within a season, both of which contained at least one nestling sired by an extra-group male. In 13 of these 26 cases the same extra-group male sired at least one nestling in each clutch. In a further ten cases the extra-pair sires were either resident in the same territory ($n = 1$) or were neighbours ($n = 9$). In only three of the 26 cases did the paternity data suggest that the female appeared to have changed the direction of her extra-territorial foray.

(b) Within-pair interactions

Unusual, high-pitched calls, somewhat similar to an alarm call, were heard on several mornings ($n=3$) between days -4 and -2 . These calls were only heard just before the female moved away from the roost site and were suggestive of an antagonistic interaction between the resident fairy-wrens.

We also observed a total of 11 within-pair matings for three of the five females tracked during the fertile period. Prior to this study within-pair copulations had rarely been recorded (Mulder 1997). These copulations took place in a highly predictable context. Females would sit within their half-built nests for up to 12 min and on leaving would solicit a copulation from a resident male. Males appeared to anticipate these copulations and would perch near the nest entrance waiting for the female to leave the nest. All three females copulated with their social mate on day -3 , but one also copulated on day -4 and one on day -2 . The copulation on day -4 was not associated with a pre-dawn foray.

4. DISCUSSION

The geographical distribution of the extra-group sires suggested that females leave their territory to copulate with particular extra-pair males. This was confirmed by radio tracking females during their fertile period. Females left their territories just before dawn and often made repeated visits to the same territory over two or three mornings. Paternity analysis confirmed that only males visited during the extra-territorial forays sired chicks within the female's brood. These data show that in superb fairy-wrens both extra-pair mating and extra-pair paternity are controlled by the female and male reproductive success is largely dictated by female behaviour.

These results alone do not necessarily show that females actively discriminate between extra-group males. Females may simply conduct linear forays in any direction. However, available evidence suggests that this is not the case. First, the males which gain extra-pair fertilizations can be predicted from the date they moult into nuptial plumage (Dunn & Cockburn 1999), suggesting that females are deliberately choosing particular males during their forays. Second, females show repeated choice for the same male. For example, in this study one of the radio-tracked females allowed the same extra-group male to sire offspring in each of her three broods. More remarkable evidence comes from females that change position but still visit the same male. Throughout her life, broods laid by a female (BWM) were consistently sired by a long-lived extra-group male (GBN) (30 out of 33 offspring). On two occasions in seven years BWM divorced her son and moved territory. Even though each move radically changed the trajectory required to reach GBN's territory (89, 310 and 355° from North), GBN remained the sire of her offspring.

Multiple extra-group paternity occurred in 29 broods in our sample. In other species multiple mating has been suggested to reflect insurance against infertility (Wetton & Parkin 1991; Hunter *et al.* 1992) or the desirability of enhancing the variability of offspring (Birkhead & Møller 1992). These hypotheses seem inapplicable to fairy-wrens. First, despite multiple paternity, female

choice leads to consistent success by a limited range of male phenotypes (Dunn & Cockburn 1999). Second, multiple extra-group paternity is much more likely when the foray undertaken by the female traverses many territories (figure 1). Sampling to minimize infertility or maximize diversity should be possible in nearby territories. We suspect that multiple extra-group paternity is better explained by 'errors' on the part of the female. In nine of the 29 cases of mixed extra-group paternity the female crossed at least three territory boundaries to reach the most distant extra-group sire (figure 3). In all but one of these nine cases the two extra-pair sires were in neighbouring territories. This suggests that females do not copulate with males *en route* but copulate with males within or close to the territory of the intended extra-group sire. Alternatively, some females may target clusters of high-quality males and copulate with more than one male during an extra-territorial foray.

The possibility of errors draws attention to the difficulty in understanding how females locate particular males. Females can obtain information about the characteristics of extra-group males through frequent displays made by the extra-group males on the female's territory (Rowley 1991; Mulder 1997) and displays made months before the start of the breeding season seem most important in determining female choice (Dunn & Cockburn 1999). However, it is not obvious how females relate these displays to the geographical position of the male. Perhaps the group-specific type II song (Langmore & Mulder 1992) or the conspicuous extra-group displays encode geographical information which can be used by the female.

Each extra-territorial foray followed the same pattern. The female left the roost site, flew off the territory during twilight and returned before sunrise. Our previous observational studies suggested that the females then remain in the territory for the rest of the day. Interestingly, Smith (1988) found evidence which suggested that extra-pair copulations in black-capped chickadees were also concentrated close to dawn. So why do forays occur before dawn? It seems unlikely that, if the female leaves at this time, her foray goes unnoticed by within-group males. Indeed, the high-pitched calls prior to the female's departure may be indicative of males attempting to prevent the female's foray. However, the female may be able to avoid being followed if the foray occurs in the dark or in dim light. Similarly, Davies (1992) showed that female dunnocks in territories with dense vegetation can avoid alpha males more successfully than females in territories with little cover. Another explanation for the timing of the forays is that females are only assured of finding a dominant male in his territory before dawn, as after that time it is extremely likely that the chosen male will be displaying in other female's territories (Green *et al.* 1995).

A third possibility is that many females could visit a high-quality male in one morning and the earlier a female reaches that male the more sperm she is likely to acquire. Tuttle *et al.* (1996) found that up to eight billion sperm were stored in a male fairy wren's cloacal protuberance. The density of sperm in ejaculates and the lack of conspicuous copulations led Tuttle *et al.* (1996) to propose that these sperm reserves are used 'in massive ejaculates for a single or few copulations' (p.1363). Although our

data reveal copulations of which Tuttle *et al.* (1996) were unaware, our observations still strongly support this conclusion. The number of copulations a female fairy wren initiates during a fertile period is probably very low compared to other species with large cloacal protuberances and high sperm counts such as dunnocks, alpine accentors and Smith's longspurs (Nakamura 1990; Birkhead *et al.* 1991; Briskie 1992). A single massive ejaculate may reflect the low number of copulations and the close proximity of within- and extra-group copulations at dawn, but may create problems with sperm depletion.

The combination of observational data with paternity assignment provides the most convincing evidence for female control of extra-pair mating. The timing, duration and distance of the forays suggest that female fairy-wrens are driven by the indirect benefits associated with the acquisition of sperm. We have shown elsewhere that only a few males achieve extra-group fertilizations and that these males share a common phenotype (Dunn & Cockburn 1999). Our new data show that this asymmetrical mating success is the product of female choice.

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