Do male paternity guards ensure female fidelity in a duetting fairy-wren?

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Most socially monogamous bird species engage in extra-pair mating, and consequently males may adopt various behavioral strategies to guard paternity. However, the relationship between mate guarding and extra-pair paternity is unclear: low levels of extra-pair paternity can be associated either with no mate guarding or with intense mate guarding. We investigate paternity guards in the purple-crowned fairy-wren (\textit{Malurus coronatus}), a duetting species where extra-pair paternity is rare. This species is unusual in a genus known for extremely high levels of extra-pair mating. We examine the behavioral interactions between the sexes underlying these low rates of extra-pair paternity and show that male purple-crowned fairy-wrens do not use frequent copulation or courtship feeding to assure paternity or guard females acoustically by duetting. Males maintain close proximity to females both when they are fertile and when they are not breeding and do not invest in courtship displays to extra-pair females. Consistent with predictions of theoretical models, low extra-pair paternity in this species may be related to female fidelity rather than male paternity assurance strategies, but short-term removal of males would be necessary to test this experimentally. 

\textit{Key words:} copulation duration, courtship feeding, duetting, extra-pair paternity, mate guarding, sexual conflict.

More than 75\% of socially monogamous passerine birds engage in extra-pair copulations (reviewed in Griffith et al. 2002). Males that invest in parental care should attempt to ensure paternity of the offspring they care for, and many studies have documented widespread use of a variety of paternity guards (reviewed in Birkhead and Møller 1992). Males may attempt to reduce the success of extra-pair copulations by frequent within-pair copulations (Møller and Birkhead 1991; Hunter et al. 1992). Alternatively, males may attempt to induce female fidelity by courtship feeding as a “bribe” or indicator of male quality (Green and Krebs 1995; Velando 2004; Kempenaers et al. 2007). Males may use song to repel rival males (Møller 1991; Sheldon 1994), and, in species where both sexes sing, if female song attracts males, then males may join their partners’ songs to form duets to repel extra-pair males (Levin 1996). Finally, males may attempt to prevent extra-pair copulations by maintaining close proximity to receptive females, this mate-guarding strategy is widespread, and male birds commonly accompany their partner closely during her fertile period (reviewed in Birkhead and Møller 1992; Møller and Ninni 1998). Though the use of paternity guards is widespread, the relationship between paternity guards and extra-pair paternity is unclear.

This is partly because extra-pair paternity is a population-level meta-trait that arises out of interactions between females, pair males, and extra-pair males, and progress in large-scale comparative analyses of factors underlying extra-pair paternity (EPP) has been hampered by poor knowledge of the fine-scale behavioral interactions between these players (Westneat and Stewart 2003). Thus far, no relationship between levels of extra-pair paternity and paternity-guarding behaviors has been detected across species (Møller and Ninni 1998), and within species the relationship is complex. Selection should favor paternity guards only if extra-pair paternity occurs because females or extra-pair males pursue extra-pair copulations, and some species with little or no extra-pair paternity do not show mate-guarding behavior (Robertson et al. 2001; Gill et al. 2005). However, low extra-pair paternity could also be a consequence of highly effective paternity assurance strategies. Consistent with this, mate guarding has been shown experimentally to be effective in reducing extra-pair paternity in some species (Westneat 1994; Chuang-Dobbins et al. 2001). However, female fidelity may also play a role, particularly when copulations are under female control (Lifjeld and Robertson 1992; Double and Cockburn 2000), and recent theoretical modeling predicts low levels of mate guarding when females are very faithful, but also when they are very unfaithful (Kokko and Morrell 2005).

Fairy-wrens are cooperative breeders known for extremely high rates of extra-pair paternity, with up to 95\% of broods containing offspring sired by males outside the social group, and within-group subordinate males also occasionally gaining paternity (Brooker et al. 1990; Mulder et al. 1994; Karubian 2002; Webster et al. 2004). Extra-pair males frequently intrude onto the territories of nest-building females to perform courtship displays that may include presentation of a contrasting flower petal, but do not culminate in extra-pair copulations (Mulder 1997; Rowley and Russell 1997; Green et al. 2000; Karubian and Alvarado 2003). Males show physiological adaptations for intense sperm competition, with large testes and cloacal protuberances to produce and store large amounts of sperm (Mulder and Cockburn 1993; Rowe and Pruett-Jones 2006). Females control extra-pair copulations in superb fairy-wrens (\textit{Malurus cyaneus}), going on extra-territorial forays when they are fertile to mate with the extra-pair males that sire their offspring (Double and Cockburn 2000). Males in this species attempt to guard their own fertile females by maintaining close proximity to them (Mulder 1997), but these attempts at mate guarding appear largely ineffective as superb fairy-wrens have the highest known rate of extra-pair paternity in birds (Mulder et al. 1994).
In contrast, the purple-crowned fairy-wren (Malurus coronatus), a duetting sister species to the superb fairy-wren, has extremely low levels of extra-pair paternity; males are not physiologically adapted for intense sperm competition; and males do not invest in extra-pair courtship displays (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation). Purple-crowned fairy-wrens closely resemble their highly promiscuous congeners in their social system and aspects of their ecology, but nothing is known about behavioral interactions between the sexes when the female is fertile. We therefore test for a range of paternity assurance behaviors in this species, including acoustic paternity guarding by duetting. Specifically, we observed male and female behavior and interactions in nonbreeding and breeding pairs, quantifying copulation and courtship feeding rates, song rates, and proximity between partners in relation to time before egg laying to test the following hypotheses and predictions relating to paternity assurance:

1. Frequent copulation: If frequent copulation is used to assure paternity, then copulations should occur at a high frequency compared with other species when the female is receptive.
2. Courtship feeding: If males use courtship feeding to ensure access to their fertile partners, then copulation rates should peak after courtship feeding.
3. Acoustic mate guarding: If males use duetting to guard receptive females, then duets will be more common when females are receptive and males will "answer" a high proportion of female songs to form duets.
4. Physical mate guarding: If males guard receptive females physically, they will move toward their partner more often and spend more time close to them during the receptive period.

Additionally, because subordinate males in cooperatively breeding groups may also threaten paternity of the dominant male, we compare the behavior of males and females with subordinates to those without.

**MATERIALS AND METHODS**

**Study species**

Purple-crowned fairy-wrens are riparian specialists of the tropical north of Australia that are vulnerable to extinction due to destruction and fragmentation of their habitat by livestock (Rowley 1993). Like other Malurus spp., purple-crowned fairy-wrens are cooperative breeders, and breeding pairs often share their exclusive, year-round territory with male, and sometimes female, subordinate "helpers" (Rowley and Russell 1997). The sexes are seasonally dichromatic, both sexes sing, and breeding partners often overlap their songs to form duets (Rowley and Russell 1997). Purple-crowned fairy-wrens nest throughout the year, with seasonal peaks around April and August, depending on rainfall (Hall ML, personal observation of this population; Rowley and Russell 1993). Modal clutch size is 3 eggs. From July 2005, we studied a color-banded population resident on Annie Creek and the Adcock River in the Australian Wildlife Conservancy’s Mornington Wildlife Sanctuary (17°31’S, 126°6’E). We captured adults with mist nets and nestlings in the nest and marked each with a unique combination of colored leg bands for individual recognition (under permit from the Australian Bird and Bat Banding Scheme [Authority 2073] and the Western Australia Department of Conservation and Land Management [Licence BB002178]). Territories, group composition, and status within groups were documented by regular census (for details, see Hall and Peters 2008).

**Observations**

From May 2006 to December 2007, we conducted 135 focal watches on nonbreeding (N = 12 pairs, 13.3 h) and nest-building pairs (N = 29 pairs, 57 nests, 105.9 h; 6 of these pairs were also sampled as nonbreeding pairs). Nesting occurred in all months of the year, and nonbreeding observations were likewise conducted throughout the observation period (mean = 13 March 2007 for nonbreeding watches and 3 February 2007 for nest-building watches). Nonbreeding pairs showed no signs of nesting for at least 1 month after the focal watch (mean ± standard error [SE] = 123 ± 22.2 days to next nesting). Nonbreeding pairs were each observed on 1.3 ± 0.2 days for a total of 66.7 ± 11.0 min. Nest-building pairs were each observed on 4.1 ± 0.7 days at 2.0 ± 0.2 nests for a total of 219.1 ± 41.3 min. Nonbreeding pairs comprised 8 pairs with subordinate group members and 4 pairs without. Nest-building pairs included 19 pairs with subordinates, 7 pairs without, and 3 pairs that were sampled both with and without subordinate group members. Focal observations were conducted in the mornings, starting 74.5 ± 6.1 min after sunrise (range: 35 min before sunrise to 288 min after).

During focal observations, we recorded 1) nest-building rate—number of trips to the nest by the female per hour, 2) copulation rate—number of copulations per hour, 3) courtship feeding rate—number of times the female was fed by the dominant male or by subordinates per hour, 4) song rate—number of songs per hour, distinguishing solos and duets, and identifying the sex of the singer where possible, 5) time spent close—percentage of time that partners spent close to one another (see below for details), 6) flights toward partner—percentage of an individual's flights that were directed toward their partner, computed for each sex, and 7) intrusions—whether or not an intruder was seen on the territory. In addition to data collected during these focal observations, we also report copulations seen opportunistically. We used the method of Hall and Peters (2008) to score time spent close (5); we estimated the minimum distance between partners in each 1-min interval of the observation period, using the following distance intervals: 0–0.5, 0.5–2, 2–5, 5–10, and >10 m. Dense riparian vegetation imposed constraints on visibility, with no distance estimate possible for 63.6% of intervals per focal watch (N = 38 pair means), either because both birds were out of sight or because one bird was in sight but the vegetation around it was too dense to be sure that its partner was not within the critical distance. To control for this limitation, we computed proximity as the percentage of known intervals that the male and female were within a critical distance (0.5, 2, or 5 m) of one another (i.e., excluding intervals where distance between partners was unknown). We also checked for a relationship between visibility and proximity that might bias the results if, for example, partners that spent more time close together were more visible. However, the percentage of time that partners were within 2 m of one another did not depend on the percentage of intervals that distance between partners was known (effect size β ± SE = −0.02 ± 0.13, F1,98 = 0.02, P = 0.90, mixed model including pair identity as a random effect to take into account the non-independence of repeated observations on each pair).

The date on which the breeding female laid the first egg of the clutch was subsequently determined for 43 of 57 nests (82 focal observations), and behavior was summarized daily with respect to first-egg date (= Day 0). For analyses where sample sizes were small, we pooled all data for pairs observed during the female’s receptive period, defined as Day −5 to Day −3, based on peak copulation rates for this species (see Results). We use this "receptive period" conservatively in preference to the more commonly used "fertile period" because it is species specific and more directly relevant to mate-guarding behavior. Assumptions about female fertility in passerine birds are generally based on studies on zebra finches (Taeniopygia guttata) and Bengalese finches (Lonchura striata) (modal clutch size is 6 eggs) that showed females...
could store sperm for 8–10 days and eggs usually being fertilized 24 h before being laid (Birkhead et al. 1989; Birkhead 1992). However, most monogamous birds either stop or markedly reduce copulation rates after the first ovulation (Birkhead and Møller 1993); so for assessing male attempts at preventing extra-pair copulations, we focused on the time within the fertile period that copulations were occurring in purple-crowned fairy-wrens, using the term receptive period to avoid confusion.

**Statistical analysis**

To account for multiple observations from the same pairs, we fitted mixed models with pair identity as a random effect. For comparisons of means, or when residuals from mixed models did not satisfy the assumption of normality, we computed a mean for each pair observed more than once in any category so that each pair contributed equally to the analysis. Correlations between variables were examined using Spearman tests. The statistical software JMP 5.1 was used for computation. Means are presented with SEs throughout.

**RESULTS**

Nests were built exclusively by dominant females, who spent a week or more building, with the frequency of trips to the nest peaking on Day 2 at 18.9 ± 4.1 trips per hour (Figure 1a).

**Frequent copulation**

Copulation rates peaked at 0.74 ± 0.42 copulations per hour on Day 2 (Figure 1b). We observed 12 within-pair copulations in 7 pairs, occurring 3–6 days (N = 10) and 12 days (N = 1) before the female laid her first egg (first-egg date unknown for N = 1). In at least 8 cases, copulations were solicited by the female lowering and fluttering her wings. Mean duration of copulations was 8 ± 1.2 s (N = 9 with duration recorded). The 4 longest copulations (9, 10, 10, and 15 s, respectively) all occurred within 10 min of sunrise, and the latest copulation was observed 2.3 h after sunrise. During opportunistic observations, we saw a further 12 copulations or attempted copulations (male jumped onto the back of the female briefly). Five of these were between partners with active nests and between 2 and 7 days before the female laid her first egg. Three were between new partners, within 3 weeks of pair formation. The context of the remaining 4 observations was unclear (pairs were neither new nor known to have an active nest). We observed no extra-pair copulations or intrusions by extra-pair males during focal watches or opportunistically.

**Courtship feeding**

Courtship feeding by dominant males peaked at 2.9 ± 1.1 feeds per hour (N = 5 pairs) on the day before the first egg was laid (Figure 1c). There was a trend for males to feed females more...
on the day before they laid the first egg than they had during the receptive period (receptive: 0.62 ± 0.14 feeds per hour, N = 14; Wilcoxon Z = 1.88, P = 0.06). The rate at which males fed receptive females was not significantly higher than in non-breeding pairs (non-breeding: 0.35 ± 0.19 feeds per hour, N = 12; Wilcoxon Z = -1.4, P = 0.16). During the receptive period, courtship feeding rates by the dominant male did not differ significantly between pairs and groups (feeds per hour by males in pairs: 0.58 ± 0.27 feeds per hour, N = 6; in groups: 0.63 ± 0.19, N = 9; Wilcoxon Z = -0.12, P = 0.90).

The rate at which females received food from subordinates also peaked the day before the first egg was laid at 1.2 ± 0.9 feeds per hour (N = 3 pairs with subordinates) (Figure 1c). Mean courtship feeding rates by subordinates were higher on Day −1 than during the receptive period, but the difference was not statistically significant (receptive: 0.14 ± 0.09 feeds per hour, N = 9; Wilcoxon Z = 1.2, P = 0.25). Subordinates did not feed non-breeding females. Total courtship feeds received by receptive females in pairs and groups (i.e., male plus subordinate feeds in groups) did not differ significantly (pairs: 0.58 ± 0.27 feeds per hour, N = 6; in groups: 0.77 ± 0.23, N = 9; Wilcoxon Z = -0.49, P = 0.63). Subordinate group members (male N = 7; female N = 2) that fed the dominant female were all her offspring. We observed only one group with a subordinate male unrelated to the dominant female during the receptive period: this male did not feed the female but was chased by the dominant male and interrupted a copulation between the dominant pair (see Discussion).

Acoustic mate guarding

Daily changes in singing behavior did not show clear patterns as egg laying approached (Figure 1d). However, comparing duetting in non-breeding and receptive stages showed that a significantly lower percentage of songs were sung as duets when females were receptive (mixed model—receptiveness: \( F_{1,18} = 6.53, P = 0.02 \)), an effect that did not differ between pairs and groups (mixed model—group: \( F_{1,18} = 1.40, P = 0.25 \); receptiveness × group: \( F_{1,18} = 1.26, P = 0.28 \)).

The effect of nesting on male and female singing patterns differed (Figure 2). Females initiated no songs when they were receptive, a trend to reduce their song initiation rate from non-breeding (non-breeding: 0.50 ± 0.18 songs initiated per hour, N = 12; receptive: 0.01 ± 0.08 songs initiated per hour, N = 14; Wilcoxon Z = 1.90, P = 0.06). Because females were not seen initiating any songs in the 5 days leading up to egg laying (Figure 2a), males could not overlap their songs to form duets. Males did not initiate significantly more songs during the receptive than non-breeding stage (non-breeding: 0.78 ± 0.30 songs initiated per hour, N = 12; receptive: 1.54 ± 0.67 songs initiated per hour, N = 14; Wilcoxon Z = -1.71, P = 0.47). Females were 3 times less likely to duet with males when they were receptive, but this difference was not statistically significant (non-breeding: 48.0 ± 22.5% of male songs answered, N = 5 pairs where males sang; receptive: 13.0 ± 12.4% of male songs answered, N = 8 pairs where males sang; Wilcoxon Z = 1.26, P = 0.21).

Physical mate guarding

Close proximity between non-breeding partners was reduced by nest-building activity, peaked on Day −3, and then decreased sharply on the day the first egg was laid (Figure 1e). The decrease in time spent in close proximity when laying commenced was statistically significant (Day −3 = 73.8 ± 5.7%; Day 0 = 39.4 ± 9.4%; t = 3.1, degrees of freedom [df] = 8.2, P = 0.01) and was not because females were on the nest (dis-

![Figure 2](https://academic.oup.com/beheco/article-abstract/20/1/222/215508/225)

Figure 2: Song initiation rates (solo songs + initiated duets per hour) by (a) females and (b) males in non-breeding and nest-building pairs. Data in each category are represented by box plots; boxes encompass the interquartile range (25th to 75th percentiles), the line through the box shows the median, and outliers are shown as points beyond the whiskers. Note that these data represent only that subset of all the songs sung where the sex of the singers could be identified: overall, the percentage of songs per focal observation where sex of the singer was identified = 23.0 ± 5.6% (N = 38 pair means).
3.30, \( P = 0.02 \)), but the significant effect of receptiveness on female flight patterns did not differ between pairs and groups (receptiveness: \( F_{1,20} = 19.20, P < 0.001 \); receptiveness for groups: \( F_{1,20} = 1.01, P = 0.33 \)). Male flight patterns did not differ between pairs and groups in the nonbreeding (Wilcoxon \( Z = -0.51, P = 0.61, N = 12 \) pair means) or receptive stages (Wilcoxon \( Z = 1.02, P = 0.31, N = 15 \) pair means; nonparametric tests presented because residuals of the mixed model did not meet the assumption of normality).

**Relationship between variables**

During the receptive period, there were no significant correlations between male courtship feeding, proximity, and duetting (proximity and courtship feeding; Spearman rho = 0.22, \( P = 0.45, N = 14 \); proximity and duetting; Spearman rho = 0.08, \( P = 0.80, N = 13 \), one pair did not sing; duetting and courtship feeding; Spearman rho = −0.48, \( P = 0.10, N = 13 \)). Likewise, in nonbreeding pairs, courtship feeding, proximity, and duetting were not correlated (proximity and courtship feeding; Spearman rho = 0.33, \( P = 0.29, N = 13 \); proximity and duetting; Spearman rho = 0.40, \( P = 0.22, N = 12 \); duetting and courtship feeding; Spearman rho = 0.25, \( P = 0.45, N = 12 \)).

**DISCUSSION**

We saw no intrusions by males in breeding plumage in more than 100 h of observations targeting nest-building females, confirming earlier reports that male purple-crowned fairy-wrens do not invest in the extra-pair courtship and petal displays (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation; Rowley and Russell 1997) that comprise a significant male investment in other members of the genus (Green et al. 1995; Mulder 1997; Karubian and Alvarado 2003).

**Frequent copulation**

Male purple-crowned fairy-wrens do not use frequent copulation to assure paternity. Peak copulation rate was less than 1 per hour, and most copulations were observed around sunrise and over a 4-day period (Day −6 to Day −3), suggesting that there would be fewer than 20 copulations per clutch and usually fewer than 2 per day, a low copulation rate according to the definition of Birkhead et al. (1987), and by comparison with other monogamous species where copulation rates can range up to 600 copulations per clutch in goshawks (Accipiter gentilis) and 40 copulations per day in house sparrows (Passer domesticus) (Birkhead et al. 1987). Most copulations in purple-crowned fairy-wrens were solicited by females after emerging from the nest, similar to within-pair copulation behavior reported for superb fairy-wrens, where females solicited copulations after leaving the nest around sunrise on Day −4 to Day −2 (\( N = 11 \), rate not given, Double and Cockburn 2000). Within-pair copulation rate in purple-crowned fairy-wrens peaked on Day −3, which was the day that superb fairy-wren females were most likely to make extra-territorial forays for extra-pair copulations (Double and Cockburn 2000) and also the day that copulation rate peaks in most monogamous bird species (Birkhead and Möller 1993). We saw no copulations during the laying period, and males also ceased maintaining close proximity to females once laying commenced, suggesting that females were no longer receptive to copulations then. Again, this reduction in copulation rate after the commencement of laying is a pattern common to many socially monogamous birds (Birkhead and Möller 1993).

Copulations in purple-crowned fairy-wrens were of unusually long duration, with cloacal contact maintained for up to 15 s. In many birds, copulation duration is at most a few seconds, and durations greater than 1 s have been categorized as long (Birkhead et al. 1993). The function of such long-duration copulations is currently unknown. Because females can interrupt copulations by moving away from the male, maintaining cloacal contact for such long periods probably requires cooperation from the female and serve as a signal to the male, perhaps to secure subsequent paternal investment. Long-duration copulation could facilitate transfer of large quantities of sperm: long-duration copulations have also been observed in superb fairy-wrens (Cockburn A, personal communication) and, in general, fairy-wrens have unusually large testes, cloacal protuberances, and ejaculate sizes (Rowe and Pruett-Jones 2006), though the size of testes and cloacal protuberances are reduced in purple-crowned fairy-wrens (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation). Nevertheless, in one unusual opportunistic observation, we observed a nest-building female on Day −5 soliciting copulations from her partner 5 times, commencing 1 min after sunrise with a copulation 6 s in duration, followed by copulations of duration 5 s (15 min later), 3 s (7 min later), 3 s (25 min later), and 1 s (3 min later). Because ejaculate size diminishes with repeated copulations over a short period of time (Westneat et al. 1998), the decline in the duration of cloacal contact with successive copulations may have been associated with a reduction in ejaculate size.

**Courtship feeding**

Males do not use courtship feeding to assure paternity, as courtship feeding rates peaked on the day before the first egg was laid, when copulations were no longer occurring. Furthermore, courtship feeding rates by dominant males were not significantly higher during the receptive period than during nonbreeding, and female subordinates also fed dominant females. Whereas courtship feeding in some species reflects sexual conflict over mating, with females trading paternity assurance for food (Velando 2004), in others courtship feeding may be used to improve female condition prior to egg laying or to signal parental ability to females (Green and Krebs 1995). The latter seems more likely in purple-crowned fairy-wrens, as the peak in courtship feeding rates the day before the first egg is laid could represent direct investment by males and subordinate group members in egg production, though the peak might be expected to last for the 3 days of egg formation if this were the case.

**Acoustic mate guarding**

Fertile females do not use song to attract extra-pair males, and duetting does not function as an acoustic paternity guard. Partners were significantly less likely to coordinate their songs to form duets when females were receptive, and females did not initiate any songs during this period. Because females did not use song to attract extra-pair mates, males did not have reason or opportunity to use duetting to guard them. Our results are consistent with studies on other species with similarly low rates of extra-pair paternity that have rejected the paternity guard hypothesis for duetting after showing that females did not increase their song rate when they were fertile and that males were not more likely to answer the songs of their fertile partners (Hall and Magrath 2000; Gill et al. 2005). High rates of extra-pair mating among fairy-wrens had suggested potential for duetting functioning as a paternity guard in purple-crowned fairy-wrens, but recent results revealed that duetting was associated with low extra-pair paternity rates in this species (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation), like many other duetting species (but see Benedict 2008). Thus, there is currently no empirical evidence supporting the hypothesis that duetting is a consequence of sexual conflict over paternity, with
female attempts to solicit extra-pair copulations thwarted by their partners answering them in duet. It is unlikely that the absence of song initiations by receptive female purple-crowned fairy-wrens was a strategic attempt to prevent males from locating them because they still sometimes responded to their partner's songs to form duets. Female superb fairy-wrens also appear to sing at lower rates when they are fertile, indicating that even in this nonduetting congener with extremely high rates of extra-pair paternity females do not use song to attract extra-pair males (Mulder et al. 1994; Cooney and Cockburn 1995). The preying in female song rates may rather be a consequence of constraints imposed by nest building and egg production.

**Physical mate guarding**

Partners stayed very close together in the receptive period, consistent with mate guarding, but maintained similarly close proximity when not breeding, suggesting other benefits of close proximity. The peak in close proximity in purple-crowned fairy-wrens coincided with the peak in copulation rate on Day –3 (Figure 1). At that time, partners spent 94% of the time within 5 m of one another (Figure 1e), and maintenance of close proximity was a consequence of male rather than female movements, suggesting strong mate-guarding behavior. Broadly similar patterns of proximity between partners peaking shortly before egg laying have been observed in other species with similarly low levels of extra-pair paternity (e.g., Hall and Magrath 2000; Green et al. 2002) and also in the highly promiscuous superb fairy-wren, though time spent in close proximity was lower in the more open habitat of this sister species: 4 days before the first egg was laid, when time spent in close proximity peaked, partners spent around 70% (55% if they had subordinates) of the time within 5 m of one another (from Figure 3 in Mulder 1997). Interestingly, in purple-crowned fairy-wrens, there was no significant difference in proximity in the nonbreeding and receptive period, suggesting a lack of mate guarding. However, because time spent in close proximity was high in nonbreeding pairs (this study and Hall and Peters 2008), the fact that both sexes were responsible for maintaining close proximity when not breeding and that close proximity was not maintained continuously but declined at the start of nest building (Figure 1e) suggests that close proximity could have different functions during the nonbreeding and receptive periods, with mate guarding playing a role in the latter.

Though subordinates could constitute a threat to paternity, males with subordinates did not guard receptive females more intensely, probably because most subordinates were related to the dominant female. Fairy-wren groups normally comprise a breeding pair with retained offspring (Rowley and Russell 1997), but when subordinate males are unrelated to the dominant female, they may compete with the dominant male for paternity (Mulder et al. 1994; Webster et al. 2004), and in our population, 2 dominant males lost paternity to an unrelated subordinate male, confirming that subordinate males can constitute a threat to paternity (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation). We showed that pair males did not use frequent copulation, courtship feeding, or acoustic mate guarding to assure paternity. Furthermore, although males guarded their partners by maintaining very close proximity to them when they were receptive to copulations, partners also maintained close proximity when they were not breeding (this study and Hall and Peters 2008). Females did not sing to attract extra-pair males, and unusually long-duration copulations suggested female cooperation in within-pair copulations. We suggest that female fidelity or lack of display by extra-pair males may be as or more important than mate guarding by pair males for explaining the dramatic reduction in extra-pair mating in purple-crowned fairy-wrens in comparison with their congeners (Kingma SA, Hall ML, Segelbacher G, Peters A, in preparation) because males did not use additional paternity assurance strategies to those used by male superb fairy-wrens (Mulder 1997), and extra-pair mating in this sister species is controlled by females (Double and Cockburn 2000). However, short-term removals of pair males (see, e.g., Brylawski and Whittingham 2004) would be necessary to experimentally test the relative importance of male mate guarding, female fidelity, and extra-pair male intrusions and determine whether a lapse in male mate guarding would lead to intrusions by extra-pair males, extra-territorial forays by fertile females, or solo singing by females that attracted male intruders (though interpretation of such experiments is not always straightforward, see Kempenaers et al. 1995).

**FUNDING**

“Sonderprogramm zur Förderung hervorragender Wissenschaftlerinnen” of the Max Planck Society.

We thank the Australian Wildlife Conservancy, in particular Sarah Legge, Steve Murphy, Joanne Heathcote, Dan Swan, and other staff at Mornington Wildlife Sanctuary for superb logistical support. Thanks also to A. Dalziell, S.A. Kingma, P. Villard, E. Kloczinski, S. Valderrama, L. Fairhurst, K. Delhey, R. Fell, J. Sardell, J. Rijpstra, R. Klooster, and A. Young who helped with finding and monitoring nests. Kaspar Delhey and Sjouke Kingma also provided helpful discussion and comments on the manuscript.

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