Paternal care declines with increased opportunity for extra-pair matings in fairy martins

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SUMMARY

Following the discovery that extra-pair fertilizations are common in many birds, it has been predicted that male participation in parental care may be influenced by their opportunity for extra-pair copulations. However, such a trade-off between male contribution to parental care and the availability of fertile females has not been confirmed. Here we use a novel remote monitoring technique to show that participation in incubation by male fairy martins, *Hirundo ariel*, declines with the increasing availability of fertile females in the breeding colonies. Furthermore, male contribution to incubation is most responsive to change in the availability of fertile females in the early morning, when most copulations occur, and also if their clutches are smaller than average. Both of these patterns support the presence of a trade-off between parental and extra-pair copulation effort. We suggest that this trade-off may be widespread among the 90% of bird species where males contribute to parental care.

1. INTRODUCTION

There is currently considerable interest in the consequences of extra-pair fertilizations for parental care behaviour in birds (Westneat *et al.* 1990; Birkhead & Møller 1992; Ketterson & Nolan 1994). Most research has focused on determining if males reduce their contribution to care in relation to a perceived loss of paternity of young in their nest. This idea has met with conditional theoretical support (Whittingham *et al.* 1992; Westneat & Sherman 1993), but the evidence from field studies has been equivocal (Westneat & Sargent 1996).

A second important prediction, which has received less attention, is that the participation of a male in care may vary in relation to his opportunity for extra-pair copulations (Werren *et al.* 1980; Westneat *et al.* 1990; Birkhead & Møller 1992; Ketterson & Nolan 1994; Whittingham & Lifjeld 1995). This prediction follows from the general evolutionary premise that male reproductive behaviour is expected to be a trade-off between parental effort and mating effort (Trivers 1972; Maynard Smith 1977; Beecher & Beecher 1979; Fitch & Shugart 1984). Despite this robust prediction, there has been no empirical support for an association between male contribution to parental care and the opportunity for extra-pair copulations. Male feeding rate of nestling and fledgling indigo buntings, *Passerina cyanea*, did not vary with the number of neighbouring females that were fertile (Westneat 1988), while there was no association between contribution to incubation

by male barn swallows, *Hirundo rustica*, and the proportion of fertile females in the colony (Smith & Montgomerie 1992). However, male contribution to these care activities was minimal in both species so they are not ideal for evaluating the effect of extra-pair copulation opportunity on paternal care behaviour.

Here we investigate the relationship between incubation by males and temporal variation in extra-pair copulation opportunity in naturally occurring colonies of socially monogamous fairy martins, *Hirundo ariel*. Fairy martins are excellent candidates for exploring this relationship for a number of reasons. First, males contribute substantially to all aspects of care, including construction of the mud nest, incubation of eggs and feeding of nestlings. Second, fairy martins nest in colonies and forage in groups, allowing frequent encounters between all individuals in the colony. Third, the retort-shaped nest, with a narrow tube entrance, ensures that incubation is incompatible with solicitation of extra-pair copulations. Fourth, the opportunity for extra-pair copulations varies widely and unpredictably through the course of the protracted breeding season (3–5 months) because laying is asynchronous, many pairs produce two or more clutches, and periods of adverse weather often result in widespread clutch or brood abandonment and subsequent re-laying. And finally, like other members of the Hirundinidae for which parentage data are available, fairy martins engage in extra-pair fertilizations. Microsatellite DNA fingerprinting of families in the study population revealed that 20% of 70 broods contained at least one extra-pair chick, while overall 14% of 203 chicks were sired by extra-pair males (M. J. L. Magrath, unpublished data).

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Our central prediction is that male incubation attendance will decline when a greater proportion of females in the colony is fertile. Several other ancillary predictions may also be advanced if males are trading off paternal care with the pursuit of extra-pair copulations. First, as both pair and extra-pair copulations in the Hirundinidae, and most other birds, occur more frequently in the morning (Birkhead & Møller 1992), the response of males to the availability of females should be greatest at this time of day. Second, males with smaller clutches may invest more time in the pursuit of extra-pair copulations because they have less to lose, and consequently relatively more to gain from successful extra-pair fertilizations (Westneat 1988). Therefore, the response of males to the availability of fertile females may vary in relation to their clutch size.

Finally, for a genuine trade-off to exist between male contribution to parental care and extra-pair mating effort, there should be costs to the clutch associated with reduced paternal care. Females may compensate to some extent for reduced male participation, but complete compensation is unlikely because otherwise selection would favour males that provided less care (Houston & Davies 1985; Winkler 1987; Wright & Cuthill 1989). Consequently, we assessed whether male participation in incubation affected the incubation period or hatching success.

2. METHODS

(a) *Study population and estimation of breeding parameters*

The incubation and nestling feeding activities of 48 pairs of fairy martins, *Hirundo ariel*, were monitored at five naturally occurring colonies near Melbourne, Australia, between 1994 and 1996. Colonies varied in size from 11 to 29 pairs, and were spatially separated by at least 500 m. The contents of nests were examined every second day. The incubation period for a clutch was defined as the period from the laying of the last egg to hatching of the last chick. Nestlings were considered to have hatched on the day of inspection if they appeared to be newly hatched, otherwise they were deemed to be two days old.

Extra-pair copulation opportunity was quantified for each colony by estimating the number of fertile females that were present in the colony on each day, and expressed as a proportion of all females in the colony. Females were considered to be fertile from five days before they laid their first egg, through until the day they laid their penultimate egg (Møller 1994). A pre-laying period of five days was selected because this is the shortest known period of sperm storage in birds, and females are likely to be fertile for at least five days before laying commences (Birkhead & Møller 1992).

(b) *Microsatellite DNA parentage analysis*

DNA was isolated from blood samples using a high salt/ethanol extraction procedure following Bruford *et al.* (1992). Parentage testing was performed using three hyper variable microsatellite markers (HrU5, HrU6, HrU7), first identified in the congeneric barn swallow, *Hirundo rustica* (Ellegren 1992; Primmer *et al.* 1995). The DNA fingerprinting procedure followed Primmer *et al.* (1995). Chicks were assigned as extra-pair if at least two of their three markers were inconsistent with the putative parental genotypes. Two markers

provided an average exclusion probability of greater than 0.98 in this population of *H. ariel*. Males were assigned as extra-pair fathers if they possessed all three paternally inherited alleles of an extra-pair chick. We were able to assign parentage to extra-pair males because only one male in the population ever possessed all three of any particular extra-pair chick's paternally inherited alleles. All extra-pair fathers were from the same colony as the extra-pair young they sired.

(c) *Remote monitoring system*

Parental care data were collected using a novel, remote monitoring system that allows detection and identification of individuals as they arrive at and depart from their nest. Birds were identified by transponders (Trovan, 11 mm × 2 mm) that were attached to the leg bands of most individuals in the study colonies. Transponders are small passive devices that emit a unique identification code when in the close proximity of a powered antennae. Detection and identification occurred in the tube-shaped entrance to the nest. Existing nest entrances were replaced with a custom made artificial entrance of similar dimensions and external appearance to that of the natural nest entrance. These artificial entrance tubes included two infrared sensors, positioned 40 mm apart (less than a bird length), and several wire coils that functioned as an antenna. The antenna was activated for a period of one second when either of the two infrared beams were interrupted. Additionally, the time of interruption and re-establishment of each beam was recorded to a one hundredth of a second. The time sequence of beam interruptions allowed the direction of the bird's movement to be determined. An event (arrival or departure) was deemed to have occurred if interruption of the second beam occurred before re-establishment of the first beam, and re-establishment of the first beam occurred before re-establishment of the second. These criteria preclude the false assignment of an event in cases where the bird starts but does not complete an event (e.g. moves from inside the nest into the entrance then back into the nest). Multiple nests were monitored concurrently by multiplexing the reading unit to as many as eight artificial entrances, with beam identification allowing antenna activation only at the nest entrance where activity was detected.

The performance of the system was assessed by concurrent video-taping of ten monitored nests. Over 500 events occurred of which 95.5% were assigned correctly.

(d) *Data analysis*

An average of 64 ± 34 (s.d.) daylight hours (06:00–20:00 h) of clutch attendance data were collected for the 48 nesting pairs during the incubation period. The extensive data set allowed the effect of factors that varied between days to be estimated 'within-bird', controlling for potential differences in incubation behaviour among birds that may be due to, or correlated with, the timing of nesting during the season. Importantly, this allowed assessment of the response of individuals to changes in the opportunity for extra-pair copulations, because the proportion of fertile females (PFF) in colonies usually varied during the average 14-day incubation period. ANCOVA models (with the bird as the factor, the PFF as a covariate, and the bird * PFF interaction term) were used to derive individual responses (slopes) to an increase in the PFF. Age of the clutch, mean daily ambient temperature, and day of the season were also included as covariates in ANCOVA models to control for their effects. Response slopes were derived for each individual for the effect of the PFF on incubation attendance (min h^{-1}), duration of incubation bouts (min), duration of recess periods (min), and the contribution

of the male relative to his mate. Data on bout and recess durations were log transformed to improve the normality of their distribution. These response slopes were used for all subsequent analyses. Deviation from zero of mean response slopes was assessed using one-sample *t*-tests, while ANOVA was used to test differences between groups of slopes. All tests were two-tailed.

The range in PFF experienced during incubation varied between pairs, so response estimates were only derived for individuals that experienced at least a 20% change in the PFF over those days on which they were monitored. This criterion was selected to maximize the range in PFF over which individuals were observed (linear slope estimates improve with greater range), while ensuring the sample still contained representatives from all colonies. Few individuals in the population experienced a 20% change in the PFF during their nestling feeding period, and for this reason we have not addressed the effect of extra-pair copulation opportunity on feeding behaviour in this paper. Statistical analyses were performed with SYSTAT 5.2 (Wilkinson 1992).

3. RESULTS

(a) Incubation attendance and the proportion of fertile females

During daylight hours of the incubation period (06:00–20:00 h), males attended the nest for an average of 27.7 min h^{-1} (s.d. = 4.7, $n=42$), which translated to a 44.8% (s.d. = 6.9) share of total incubation attendance. Males reduced incubation attendance by an average of 1.8 min h^{-1} per 0.10 increase in the PFF, while female attendance did not vary with an increase in the PFF (figure 1). Not surprisingly, the relative contribution by males also declined significantly with an increase in the PFF (one-sample *t*-test: $t=-4.5$, $n=18$, $p<0.001$). This reduction in male incubation attendance was apparent in each of the five colonies (with $p<0.05$ in four out of five).

The decline in male clutch attendance resulted primarily from an increase in the duration of recess periods (one-sample *t*-test: $t=3.97$, $n=18$, $p=0.001$), rather than a decrease in the duration of incubation bouts (one-sample *t*-test: $t=-0.91$, $n=18$, $p=0.38$).

Males were most responsive to the PFF in the early morning and least responsive in the afternoon. Between 06:00 and 09:00 h male attendance declined by an average of over 2.3 min h^{-1} per 0.10 increase in the PFF (figure 2). Females were not responsive to the PFF during any time period of the day (figure 2).

Males with smaller than average clutches (2–3 eggs) were significantly more responsive to the PFF than males with larger clutches (4–5 eggs) (mean slope $\pm$ s.d. for males with small clutches was $-2.4 \pm 1.5 \text{ min h}^{-1}$ per 0.1 increase in the PFF ($n=12$), compared with $-0.7 \pm 1.8 \text{ min h}^{-1}$ per 0.1 increase in the PFF for males with large clutches ($n=13$); ANOVA: $F_{1,23}=5.12$, $p=0.03$). This clutch-size related response suggests that the optimal solution to the trade-off between paternal care and extra-pair copulation effort varied with clutch size. Also consistent with this trade-off, there was no difference in incubation attendance between males with small or large clutches at times when there were no fertile females (i.e. when PFF = 0) (mean *y*-intercept $\pm$ s.d. for males with small

clutches was $31.2 \pm 5.4 \text{ min h}^{-1}$ compared with $29.8 \pm 4.7 \text{ min h}^{-1}$ for males with large clutches; ANOVA: $F_{1,23}=1.89$, $p=0.18$).

(b) Do males pursue extra-pair copulations during their incubation period?

The participation of males in extra-pair copulations during their incubation period was supported by the fact that four out of the five extra-pair fathers, identified by DNA genotyping, had already commenced incubating at their own nest by the time the extra-pair female with whom they had mated had initiated her clutch. Furthermore, males intruded into the nests of other pairs during their own incubation and nestling periods (M. J. L. Magrath, unpublished data), possibly to solicit extra-pair copulations, although the purpose of these intrusions was unknown.

(c) Costs of reduced paternal care

The incubation period was longer at nests where males were less attentive to the clutch (figure 3a). Furthermore, the duration of the incubation period was positively correlated with the mean proportion of fertile females during the incubation period (figure 3b). However, the probability of at least one egg in the clutch failing to hatch was not affected by male attendance ($F_{1,42}=0.99$, $p=0.33$, $n=44$), or the mean PFF during the incubation period ($F_{1,42}=0.28$, $p=0.60$, $n=44$).

4. DISCUSSION

Male fairy martins appear to pursue a mixed reproductive strategy whereby they generally contribute substantially to parental care, but solicit extra-pair copulations at times when the opportunities are greatest. Males reduced participation in incubation attendance, in all five colonies, on days when more fertile females were available, providing strong support for the existence of a reproductive trade-off between paternal and extra-pair mating effort.

The response of males to the availability of fertile females varied diurnally, as predicted. Males were most responsive to an increase in the proportion of fertile females in the early morning, reducing incubation attendance by over 14 min h^{-1} over the observed range in the PFF. Most birds, including the hirundinids, copulate more frequently in the early morning (Birkhead *et al.* 1987; Møller 1987), so it was expected that any trade-off between the pursuit of extra-pair copulations and incubation attendance would be most pronounced at this time.

Furthermore, males with smaller than average clutch sizes were more responsive to the availability of fertile females. This is consistent with a trade-off between paternal care and mating effort because the relative fitness benefits of obtaining an extra-pair fertilization will be greater for males with small clutches than for those with large clutches (Westneat 1988). Consequently, the greater the opportunity for extra-pair copulations, the greater the difference in effort that should be

Figure 1. Change in incubation attentiveness of individual (a) male and (b) female fairy martins in relation to an increase in the proportion of fertile females (PFF) in the colony. Males reduced attendance as the PFF increased (one-sample t -test using slopes for each individual; $t = -4.8$, $p < 0.001$, $n = 18$), while females were not responsive ($t = 0.12$, $p = 0.91$, $n = 18$). Furthermore, the mean response of males and females differed significantly (ANOVA: $F_{1,35} = 14.1$, $p = 0.001$). Bold lines indicate the mean response slope.

expended in pursuing extra-pair copulations between males with small and large clutches. Conversely, when there is little opportunity to obtain extra-pair copulations, neither males with small or large clutches will benefit from soliciting additional matings, so the difference in parental effort should be negligible. Consistent with this idea, the disparity in attentiveness between males with small versus large clutches was absent when there were no fertile females, but became increasingly apparent as the proportion of fertile females increased.

We have assumed that the clutch size of a male is unrelated to his ability to obtain extra-pair copulations. This may not be true if, for example, males paired to

Figure 2. Change in male and female incubation attentiveness ($\pm$ s.e.) in relation to the proportion of fertile females (PFF) for different time periods of the day. Males reduced attendance with an increase in the PFF in both early (06:00–09:00 h) and late morning (09:00–12:00 h) time periods (repeated measures ANOVA using slopes for each individual in each time period; early morning: $F_{1,17} = 20.7$, $p < 0.001$; late morning: $F_{1,17} = 5.79$, $p = 0.029$; other time periods $p > 0.05$). The response of males in the early morning period was greater than for all other time periods ($F_{1,76} = 6.27$, $p = 0.014$). Females were not significantly responsive to the PFF in any time period.

females that produce small clutches are generally less likely to be successful at obtaining extra-pair fertilizations. However, there was no difference in mean clutch size between males that obtained extra-pair fertilizations and those that did not ($F_{1,54} = 0.4$, $n = 56$, $p = 0.53$). Nevertheless, experiments involving the manipulation of clutch size would clearly be helpful.

If male parental behaviour is influenced by the availability of fertile females, as this study suggests, males must be able to gain information on the reproductive status of individual females. Sexually receptive females may be identified using cues such as the female carrying nesting material (Pinxten *et al.* 1987; Brown & Brown 1996), exhibiting more laboured flight during egg production (Beecher & Beecher 1979; Jones 1986), or being closely guarded by her social partner (Møller 1991). We observed males attempting copulations with females that were collecting mud for nest construction and feathers for nest lining. Carrying feathers is likely to be a particularly good indication that the female is fertile because the nest is lined with feathers only a few days before she starts laying.

The pursuit of extra-pair copulations by males while their mate is incubating has been reported in a range of species including indigo buntings, *Passerina cyanea* (Westneat 1988), barn swallows, *Hirundo rustica* (Møller 1985), rock ptarmigan, *Lagopus mutus* (Brodsky 1988), cliff swallows, *H. pyrrhonota* (Brown & Brown 1996), and superb fairy wrens, *Malurus cyaneus* (Green *et al.* 1995). In this study, the laying dates of clutches with

Figure 3. Duration of the incubation period in relation to (a) the mean attendance of the male over the incubation period, and (b) the mean proportion of fertile females in the colony during the incubation period. The duration of the incubation period was longer when males were less attentive ($n=42$, $r=-0.40$, $p=0.03$), and if the mean availability of fertile females was greater ($n=42$, $r=0.54$, $p=0.001$). Only birds monitored for at least five days during the incubation period were included in the first analysis.

extra-pair young suggest that male fairy martins not only pursue extra-pair copulations during their incubation period, but also that these copulations can be successful. Nevertheless, the activity of individuals could not be monitored once they left their nest, so it was not possible to show directly that individual males actually used the time saved by incubating less to pursue extra-pair copulations. However, there appear to be no other plausible explanations to account for the relationships between clutch attendance and the PFF described above.

The incubation period would seem an ideal time for males to solicit extra-pair copulations because the

constraints of mate guarding have been removed, but opportunities for extra-pair copulations often remain high. Mate guarding occurs in many socially monogamous species, including many hirundinids (Hoogland & Sherman 1976; Beecher & Beecher 1979; Møller 1985; Riley *et al.* 1995), and is both time consuming and largely incompatible with pursuing extra-pair copulations (Møller 1985; Brodsky 1988). Once egg laying concludes, the male is released from these constraints and will be able to devote more time to other activities, such as pursuing extra-pair copulations. For most males in this study, the opportunity for extra-pair copulations was substantially greater during their incubation period than the nestling periods, and this is likely to be true for most species.

Longer incubation periods with reduced contribution by males to clutch attendance suggests that both members of the pair incur costs associated with reduced male care. Reduced clutch attendance has been associated with prolonged incubation periods in snow buntings, *Plectrophenax nivalis* (Lyon & Montgomerie 1985), marsh tits, *Parus palustris* (Nilsson & Smith 1988), and European starlings, *Sturnus vulgaris* (Ricklefs & Smeraski 1983; Smith *et al.* 1995). Longer incubation periods are likely to be costly because the risk of nest failure increases, while the probability of producing a subsequent brood declines. In this study, 30% of clutches were lost during incubation, so prolonging the incubation period would increase the risk of complete failure by over 2% per additional day, assuming a consistent likelihood of clutch failure over the incubation period.

Trade-offs between paternal and extra-pair copulation effort may be widespread among birds because extra-pair fertilizations and nesting asynchrony are both common. Furthermore, this study reveals that the expression of this trade-off is likely to vary in relation to diurnal variation in copulation behaviour and also between individuals depending on the relative costs and benefits of parental care and solicitation of extra-pair copulations.

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