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Mate-guarding intensity increases with breeding synchrony in the colonial fairy martin, *Petrochelidon ariel*

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Extrapair paternity (EPP) is common in many socially monogamous species, influencing patterns of sexual selection and shaping many aspects of reproductive behaviour. However, factors explaining variation in the occurrence of EPP, both within and between populations, remain poorly understood. One ecological factor that has received considerable attention is breeding synchrony, but the proposed mechanisms remain contentious and the findings from the large number of correlational studies have been inconsistent. Mate guarding, a behavioural tactic to limit paternity loss, may be fundamental to any relationship between EPP and breeding synchrony. However, few studies have investigated how guarding behaviour varies with breeding synchrony, and the theoretical predictions are unclear. We examined how mate-guarding intensity in the colonial fairy martin varied with changes in breeding synchrony. To eliminate likely confounding effects of individual quality, we measured guarding intensity on multiple days during the fertile period of individual females and related this to daily variation in colony-level breeding synchrony. Similarly, we examined whether extrapair interest in fertile females varied with change in breeding synchrony. Both mate-guarding intensity and extrapair pursuit rate increased sharply several days prior to egg laying, before declining once laying commenced. When we controlled for this effect of female fertility status, guarding intensity increased with breeding synchrony. These novel findings suggest that the risk of paternity loss increases with breeding synchrony, at least among colonial species. Moreover, adjustment of guarding intensity to the risk of paternity loss may explain why most correlational studies do not reveal a relationship between EPP and breeding synchrony.

In many socially monogamous species, females regularly copulate with males other than their social partner (Westneat et al. 1990; Birkhead & Møller 1992a; Griffith et al. 2002). The benefits to females of engaging in these extrapair copulations (EPC) remain poorly understood, but include such possibilities as insurance against the infertility of their social partner or improvement of the genetic quality of their offspring by mating with males that are genetically superior or more compatible than their social mate (Jennions & Petrie 2000; Griffith et al. 2002). More obvious, however, are the potential costs of EPC to the female's social partner, because if they result in extrapair fertilization (EPF) he will sire fewer within-pair young and expend parental effort on unrelated offspring. Consequently, the males of many socially monogamous species show behaviours that appear to limit the likelihood of their partner engaging in EPC, reducing their risk of paternity loss (Birkhead & Møller 1998).

A commonly observed male tactic to reduce the likelihood of being cuckolded in birds is mate guarding, where males stay in close proximity to their partner during her fertile period (Beecher & Beecher 1979; Birkhead & Møller 1992a). Experimental studies show that mate guarding can be an effective way of minimizing paternity loss by both reducing the opportunities for females to seek EPC and limiting access to the female by other males (e.g. Chuang-Dobbs et al. 2001; Brylawski & Whittingham 2004; Komdeur et al. 2007). Moreover, by remaining in close proximity to their

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mate, males may maximize their own opportunity for within-pair copulations while she is fertile (Gowaty & Plissner 1987). However, guarding males are expected to incur some cost, and several studies show that mate guarding can be energetically costly (e.g. Møller 1987; Komdeur 2001; Low 2006) and may compromise their opportunity to gain additional social partners or EPC (e.g. Hasselquist & Bensch 1991; Marthinsen et al. 2005). Consequently, males are predicted to adjust their intensity of mate guarding in relation to their risk of losing within-pair paternity.

Perhaps the most significant factor determining a male's risk of within-pair paternity loss is the fertility status of his social mate. In birds, copulations that occur before the onset of laying can result in fertilizations because of sperm storage (which occurs for at least a week in passerines, Birkhead & Møller 1992b), although the chances of fertilization in the wild should generally increase closer to the start of laying because of passive sperm loss and last-male sperm precedence (Birkhead 1998). Females also remain fertile until the penultimate egg is laid (Birkhead & Møller 1992a; Birkhead et al. 1996), although strong declines in copulation rate are often observed after laying commences (Birkhead & Møller 1993). Consequently, males are predicted to guard their partner most intensely during this period of peak fertility and, consistent with this expectation, numerous studies have shown that mate guarding is most intense in the few days prior to the onset of egg laying (e.g. Birkhead 1982; Møller 1985; Riley et al. 1995; Krokene et al. 1996; Komdeur et al. 1999; Nicholls 2000; Low 2005).

The risk of cuckoldry may also vary with the synchrony of breeding across a population (Birkhead & Biggins 1987; Westneat et al. 1990). Typically, there will be some degree of asynchronous nesting in most avian populations, with early and later breeders generally more likely to experience lower synchrony than pairs breeding mid-season. The relationship between breeding synchrony and extrapair paternity (EPP) has received considerable attention, although empirical findings have been inconsistent. Some studies show an increase in EPP with synchrony (Stutchbury & Morton 1995; Stutchbury 1998), others show a decline (e.g. Conrad et al. 1998; Saino et al. 1999), but most reveal no systematic effect (Westneat & Sherman 1997; Bennett & Owens 2002; Griffith et al. 2002; Václav & Hoi 2002). In many species, mate-guarding behaviour and its effectiveness may be fundamental to the relationship between breeding synchrony and EPP (Birkhead & Biggins 1987; Westneat et al. 1990; Westneat & Gray 1998; Schwagmeyer & Ketterson 1999), and yet few studies have investigated whether guarding behaviour varies with changes in the level of synchrony within populations.

When synchrony is low, only a few females in the population will be concurrently fertile, and these individuals may attract more male-initiated EPC attempts than more synchronous females (Westneat et al. 1990), promoting the necessity for mate guarding (Wagner et al. 1996). Consequently, all else being equal, guarding may be expected to be most intense when the proportion of fertile females in the population is low (Wagner et al. 1996; van Dongen 2008). Alternatively, males may invest more effort into seeking EPC when a higher proportion of females in the population are fertile (greater synchrony) and/or synchrony may facilitate the ability of females to compare and choose among extrapair males, promoting their propensity to engage in EPC (Stutchbury & Morton 1995). In these two latter scenarios, the risk of cuckoldry may be predicted to increase with synchrony, resulting in more intense guarding to offset the greater risk.

These opposing predictions have been tested by comparing the intensity of mate guarding across pairs in relation to the current level of breeding synchrony, with two studies revealing a negative association between guarding intensity and local breeding synchrony, (black-throated blue warbler, *Dendroica caerulescens*: Chuang-Dobbs et al. 2001; golden whistler, *Pachycephala pectoralis*: van Dongen 2008), and three others finding no effect (barn swallow, *Hirundo rustica*: Møller 1987; purple martin, *Progne subis*: Wagner et al. 1996; house sparrow, *Passer domesticus*: Václav & Hoi 2002). While these studies are illuminating, further data are clearly required, particularly in view of the inconsistent findings for the relationship between EPP and breeding synchrony. Furthermore, correlations may be confounded by differences in quality between individuals that influence the time at which they breed relative to others, the guarding ability of the male, and the likelihood of the female participating in EPC (Wagner et al. 1996). For example, males that breed relatively late, when synchrony is low, are likely to be younger or of lower quality and perhaps less capable of guarding their mate than birds whose partners lay earlier. One solution to this problem would be to manipulate the natural chronology of nesting in an attempt to decouple timing of laying and level of synchrony (e.g. Václav & Hoi 2002). Alternatively, variation in mate-guarding intensity can be examined within individual pairs in relation to daily changes in the synchrony of fertile females in the population, which would fully account for individual differences.

In this study, we investigated how female reproductive status and breeding synchrony influence within-pair mate-guarding behaviour in the socially monogamous fairy martin. Fairy martins breed colonially and both sexes invest extensively in all aspects of parental care (Magrath 1999). Nevertheless, extrapair paternity is very common, with a previous study finding that 20% of broods contained at least one extrapair offspring (Magrath & Elgar 1997). Mate-guarding behaviour has also been observed previously in the fairy martin (M.J.L. Magrath, personal observation). Moreover, extrapair males are known to attempt copulations with females gathering nesting material, and chase fertile females in aerial pursuits (Magrath 1999, unpublished data). Indeed, both guarding behaviour and extrapair chases and copulations appear to be common among the Hirundinidae in general (e.g. Beecher & Beecher 1979; Møller 1985; Lifjeld & Marstein 1994; Riley et al. 1995; Nicholls 2000).

In line with predicted fluctuations in the risk of within-pair paternity loss, we expected the intensity of mate guarding and also the frequency of extrapair chases to peak a few days prior to the onset of egg laying and extend into the laying period. More importantly, we aimed to examine how the intensity of mate guarding varies with breeding synchrony, allowing us to discriminate between opposing predictions and improve our understanding of how breeding synchrony relates to the frequency of extrapair paternity, both between and within populations.

METHODS

Study Population and General Field Methods

We studied fairy martins at three naturally occurring colonies under concrete bridges along the Colleambally outflow channel near Booroorban, New South Wales, Australia (34°56′S, 144°52′E), between September and November 2006. These three colonies (here designated A, B and C) were separated by at least 10 km and contained a maximum of 13, 45 and 53 concurrently active nests, respectively. Nests were considered active from the time nest-lining material appeared in the nest until the brood fledged (about 21 days after hatching) or the nesting attempt failed. The mean lay dates ± SD (days) for colonies A, B and C were 13 November ± 6.29, 18 October ± 8.54 and 14 October ± 8.91, respectively.

Fairy martins construct bottle-shaped mud nests, often at high densities. Once under construction, each nest was numbered and then checked every second day. Nest contents were inspected by