Factors influencing mate guarding and territory defence in the stitchbird (hihi) *Notiomystis cincta*

Matthew Low

Ecology Group, Massey University, Private Bag 11 222, Palmerston North, New Zealand
(E-mail: stitchbird@ihug.co.nz)

Abstract: Socially monogamous male birds are predicted to maximise their reproductive success by pursuing extra-pair copulations (EPCs) while engaging in anti-cuckoldry behaviour such as mate guarding. In the stitchbird, *Notiomystis cincta*, high levels of forced EPCs and a high proportion of nestlings resulting from extra-pair fertilisations lead to the prediction that males of this species should exhibit intense paternity guarding behaviours. While studying an isolated stitchbird population on Tiritiri Matangi Island – New Zealand (36°36´S, 174°53´E), I collected daily behavioural data throughout the breeding season from 15 males in 2000/01 and 27 males in 2001/02. In this study, male stitchbirds demonstrated clear paternity guarding by exhibiting: (1) an increased likelihood of being close to their mate during her fertile period, (2) an increased initiation of mate contact during her fertile period, (3) switching from site-specific territorial defence during the pre-fertile period to defending an area centring on the their female partner's location during her fertile period, and (4) an increased following of the female to communal feeding sites outside the territory during her fertile period. For polygynous males, mate guarding and territorial defence were conditional on which of their females was fertile. Additional evidence supporting the hypothesis that mate guarding in this species is a form of paternity assurance, rather than protection from harassment, is that males protected their partner from harassment by other stitchbird males but did not intervene when females were harassed by male bellbirds, *Anthornis melanura*. While mate-guarding intensity in many species is conditional on the stage of female fertility, male stitchbirds also modified their behaviour depending on the location of the female and the rate of intrusions by extra-pair males. Resident males adopted a best-of-a-bad-job tactic when they were unable to locate their female by defending an area around her last known location. Furthermore, when the rate of intrusions by extra-pair males increased they traded-off the area they could defend within their territory against their ability to guard the female. Territory takeovers were uncommon, but when they did occur older males displaced younger males and healthy birds displaced sick ones. Contrary to the prevailing view that mate guarding is a male response to female infidelity, male stitchbirds appear to use mate guarding primarily to prevent paternity losses from forced EPCs. Future assessments of mate guarding function should consider the possibility that mate guarding involves a combination of conflict and co-operation between the sexes.

Keywords: Mate guarding; paternity assurance; forced copulation; sexual coercion; extra-pair copulation; male intrusion; territory size; harassment; polygyny; sexual conflict.

Introduction

In order to maximise lifetime reproductive success, males of many bird species adopt a strategy where they combine monogamous pairing with attempting to sire additional young through extra-pair copulations (Trivers, 1972; Birkhead and Møller, 1992). Extra-pair fertilisations occur in over two-thirds of bird species studied to date, and can account for up to 80% of nestlings in a study population (Mulder and Cockburn, 1993; Griffith *et al.*, 2002). To maximise reproductive output, males should attempt to achieve extra-pair copulations while minimising the chance of being cuckolded. In birds, mate guarding is one of the most commonly observed forms of paternity assurance behaviours (Møller and Birkhead, 1991; Komdeur *et al.*, 1999). Mate guarding is usually described as a male closely following his female partner during her fertile period, but may also involve active repulsion of extra-pair males approaching his mate or intruding onto his territory (Lifjeld and Marstein, 1994; Komdeur *et al.*, 1999). While mate guarding has been most commonly studied in birds, it is also a common feature of mating systems in other species where paternity risks exist: e.g. insects (del Castillo, 2003), fish (Alonzo and Warner, 2000), reptiles (Shine, 2003) and mammals (Matsubara, 2003).

As mate guarding occupies a significant proportion

of the male's time, it is expected to incur considerable costs and should only be favoured in situations where the benefits of paternity assurance outweigh these costs (van Rhijn, 1991). It is predicted, therefore, that mate guarding will be traded-off against factors affecting the survival of the male (e.g. foraging; Komdeur, 2001) or other reproductive opportunities (e.g. attracting additional mates; Pilastro et al., 2002). Mate guarding is also influenced by environmental and social factors such as population density (Björklund and Westman, 1986), breeding synchrony (Thusius et al., 2001), degree of polygyny (Pilastro et al., 2002) and habitat structure (Mays and Ritchison, 2004).

Traditionally, mate guarding was viewed from the perspective of the focal male and assumed, therefore, that the focal male was protecting himself from being cuckolded by extra-pair males (Trivers, 1972) or protecting his mate from the threat of EPCs (Gowaty et al., 1989). Recently, however, extra-pair paternity in birds has been viewed as a female fitness-enhancing strategy, where EPCs are a result of active female solicitation (Petrie and Kempenaers, 1998; Griffith et al., 2002) and the focal male instigates mate guarding in an attempt to make the best of a bad job (Wagner et al., 1996; Johnsen et al., 1998). The intensity of mate guarding is predicted, therefore, to be lower in mating systems where females do not engage in EPCs (Robertson et al., 2001; Wallander et al., 2001; Cuervo, 2003). However, this current focus on female pursuit of EPCs ignores mating systems where females do not encourage EPCs but, instead, are forced to copulate with extra-pair males. In such cases, the sexual conflict that is assumed to exist between the focal male and female may, instead, be replaced with sexual co-operation where both the male and female work together to minimise extra-pair male copulation attempts. Thus, in this study, I investigate mate-guarding intensity relative to the social mate's fertile period in a species, the stitchbird (or hihi, *Notiomystis cincta*), with high levels of forced copulation and female resistance to EPCs (see Low, 2005). This species provides an opportunity to test the prediction that the function of mate guarding is not simply limited to preventing female infidelity, but also to minimise paternity losses arising from sexual coercion of females by extra-pair males.

The stitchbird is a medium sized (28–43 g) endangered passerine, currently restricted to three islands off the coast of New Zealand. Stitchbirds are sexually dimorphic with respect to size and plumage colouration (Craig et al., 1982; Higgins et al., 2001). Social monogamy is the most common pairing arrangement, but the mating system also includes polygyny, and rarely, polyandry and polygynandry (Castro et al., 1996). Male stitchbirds defend their nest site, and also seek extra-pair copulations (Castro et al.,

1996; Ewen et al., 2004). The majority of these extra-pair copulations are forced and involve a unique face-to-face copulatory position (Anderson, 1993; Castro et al., 1996; Ewen et al., 1999, Low, 2005). Face-to-face forced EPCs are characterised by male force and extreme female resistance behaviours (fleeing, hiding, struggling, alarm calling and fighting), and can be readily distinguished from the usual avian mating position, where birds mate with the male standing on the female's back (Castro et al., 1996; Low, 2005). Extra-pair male intrusions and copulation attempts have been shown to increase during the female's fertile period, demonstrating that males can determine when females are likely to be fertile (Ewen et al., 2004; Low, 2004). Offspring resulting from extra-pair fertilisations are common (35–46% of young) and occur in the majority (80–82%) of nests (Ewen et al., 1999; Castro et al., 2004). Male stitchbirds do not feed their mates during courtship or incubation, but they do contribute to chick feeding, albeit at a lower rate than females (Castro et al., 1996; Ewen and Armstrong, 2000; Low et al., in press).

Threats to paternity, fertility cues, and male parental care suggest that stitchbird males should engage in intensive mate guarding as a form of paternity assurance (Komdeur, 2001). However, Castro et al. (1996) report that while a proportion of stitchbird males were observed mate guarding, many spent little time with any one female during the pre-laying and laying period; however, these observations were not quantified, and it is difficult to accurately assess the degree of mate guarding in that population. Furthermore, Ewen et al. (2004) concluded that paternity guarding by male stitchbirds is unusual in that it is restricted to defending the area around the nest site rather than defending the female *per se*. However, the timing of that study coincided with a strong male bias in the sex ratio and unusually cryptic female behaviour around the time of egg laying (Ewen, 1998), suggesting that males may have been unable to locate the female and implement an orthodox mate-guarding tactic. Observations of a third population suggest that male stitchbirds exhibit clear mate guarding (Isabel Castro, Massey University, Palmerston North, N.Z., pers. comm.).

To better document mate guarding in the stitchbird, my study aimed to quantify the form and extent of mate guarding and assess the effect of extra-pair male intrusions on the expression of the resident male's behaviour by addressing the following questions: (1) Do male stitchbirds exhibit typical mate guarding behaviours, such as maintaining proximity to their female during her fertile period? (2) Does mate guarding behaviour change relative to the reproductive cycle? (3) Is mate guarding restricted to nest-site defence or does it centre on the position of the female? (4) Does

the male adopt conditional behavioural tactics depending on the rate of extra-pair male intrusions and the location of the female within the territory?

Methods

Study population

Birds in this study were observed during the 2000/01 and 2001/02 breeding seasons on Tiritiri Matangi Island (36°36´S, 174°53´E), located off the northeast coast of New Zealand's North Island. The island is ca. 220 ha, with stitchbirds restricted to remnant and regenerating closed-canopy forest patches totalling around 30 ha. Depending on the age of the forest patch, the canopy height varied from 2–15 m with a regenerating understorey; this understorey, with the exception of the forest edges, was often sparse or patchy and generally allowed the birds to be easily followed within their territory once they were located. All birds on the island are uniquely colour banded with their ages and social parentage known. Stitchbirds on Tiritiri Matangi Island breed during the spring and summer (September to February) and may lay up to three clutches of between two and six eggs (4.05 ± 0.06, $n = 32$). Males and females generally return to the same nesting sites every year (M. Low, unpublished data). Stitchbirds were translocated to the island in 1995 as part of the ongoing management of the species by the New Zealand Department of Conservation where they now form a closed population. The population is small (27 females and 15 males in 2000/01; 32 females and 27 males in 2001/02) allowing all breeding attempts to be monitored. Supplementary food in the form of a 20% w/v sugar solution was provided year round at nine feeding stations and used by all birds on the island. These feeding stations were necessary due to a shortage of natural food and were situated at the forest edges and not contained within birds' territories. Stitchbirds usually require tree cavities for successful nesting; however these are not readily available on the island as the vegetation is predominantly young regenerating forest. Hence, small groups of two or three nest boxes were placed throughout potential nesting areas (78 in 2000 and 86 in 2001). Each nest box was attached to tree trunks approximately 1.5 m off the ground and had a hinged lid which allowed easy monitoring of nesting.

The female's fertile period is considered to begin six days prior to the laying of the first egg, when within-pair and extra-pair copulations begin, and to finish the day the penultimate egg is laid (8–10 day fertile period: Low, 2004; 2005). This period also coincides with the maximum extra-pair male intruder activity in the territory, which increases steadily from 6 days prior to the laying of the first egg, peaks on day of first egg laying at a mean of approximately 20 minutes territory^{-1} hour^{-1} (range 0–380), then rapidly declines to zero by the time egg laying finishes (Low, 2004). The estimated 8–10 day fertility period is consistent with observations from other stitchbird populations (Castro *et al.,* 1996) and that reported in other species (Birkhead and Møller, 1992; Komdeur *et al*., 1999).

Mate guarding indices

Stitchbird territories were located and the identity of pair members was established by following birds in all forested areas on the island during September, when male territorial calling and female nest site selection began. Each territory was observed for a continuous 30–60 min period each day when possible (mean ± SD, 39 ± 13 min, $n = 32$) from the onset of nest site selection until chick hatching. The timing of observation periods throughout the day was randomly distributed between territories to control for confounding temporal variables, as copulation rates (per hour) became less frequent in the afternoon than in the morning (0700–1300), when they were relatively static (Low, 2005). Stitchbirds generally ignore human observers within their territories and thus birds could be continuously followed (usually within 5–10 m) during each observation period without disturbing the birds. Most territories were roughly centred on the nest, and the observer returned to this point to re-establish contact if the birds were lost. Nest boxes were monitored daily to identify the date the first egg was laid and thereby estimate the start of the focal female's fertile period.

For each pair I recorded male and female displays, nest building and foraging, and the occurrence and nature of copulations (i.e. whether they were within-pair or extra-pair). Mate guarding behaviour was quantified in the territories of 23 males during first clutch attempts, between 21 days prior to the laying of the first egg (day –21) and 18 days after the first egg was laid (day +18) in 2001/02 (mean ± SD, 27 ± 6 observation periods per territory; range 10–38; average total observation time per territory 18 ± 4 hours) by measuring the six indices outlined below:

Time spent within the territory. The time the male or female left and re-entered the territory was recorded. From this, the total time that one or both resident birds were present was calculated.

Time spent by the resident male within 8 m of female. Every two minutes, the resident male was scored as present or absent within an 8-m radius of the female, when the location of both birds was known. Eight metres was chosen as this distance allowed the male to maintain visual contact with the female under most circumstances in the forest remnants this species inhabits on the island. If the male was chasing an extra-pair male within his territory at the time of recording,

which represents a form of mate guarding in itself, the distance measurement was delayed until the chase was complete and the male alighted.

Re-establishment of contact after separation. If the male and female were together (< 8 m) but contact was broken by one of them moving more than 10 m away, I recorded the identity of any individual which re-established contact within a two minute period. Re-establishment of contact was considered to be a measure of mate guarding because males that leave their female in order to chase away other males, but then return to her, are behaving differently from males that independently initiate movements away from the female. The two-minute time period was chosen as most male–male chases are of a shorter duration than this (M. Low, unpublished data).

Male response to a missing female during the fertile period. A comparison of the focal male's movement and calling behaviour within the territory during his female's fertile period was made when the female was present and visible versus when she was absent or at a location unknown to the male. I contrasted the 60-s period before and after the female's location became known to the focal male.

Resident male response to intrusions. To differentiate two hypotheses of mate guarding (paternity assurance versus protection from harassment) I measured behavioural responses of the focal male to: (1) territorial intrusions by extra-pair males and, (2) aggressive interactions between resident bellbirds and the focal female. In order to correlate mate guarding indices with extra-pair male intrusion rates, I recorded the sex and identity of any non-resident birds entering the territory, as well as their time of entry and exit (Low, 2004; 2005). If more than one extra-pair male intruder was present in a territory at the same time, then the period each spent in the territory was summed, giving total male intruder times of more than 60 min observation hour^{-1} in some territories.

Mate guarding at a communal site. When a female arrived at a supplementary feeding station outside of her territory, the male was recorded as accompanying the female if he was present within 30 s of her arrival and within 8 m of the feeder.

Area defended by the resident male

The boundaries of each pair's territory were determined by watching both movement and feeding patterns of both individuals, as well as their interactions with neighbouring birds during the pre-fertile period. The territorial boundary was defined as the line that the pair fed within, and beyond which, an extra-pair male could call or be visible to the resident male without the resident male making an attempt to chase him away. Because this area remained generally stable for all pairs from September to February (M. Low,

unpublished data), it was used to denote each pair's territory and to gauge whether an extra-pair male was intruding. During the fertile period, the area used by the pair for feeding in did not change. However, in many cases males were found to trade-off repelling extra-pair males from their territory with maintaining proximity to the female. This was not simply a case of neighbouring males expanding their territory as the focal male's area contracted; many of the intruders came from other parts of the island (Low, 2005). Because of this observation, the effect of extra-pair male intruders on the size and location of the area actively defended by the resident male was also assessed. This was determined by comparing the pre-fertile territory area (i.e. the pair's exclusive feeding area that all extra-pair birds were excluded from during the majority of the breeding season) to the location and size of the area defended by the resident male at the time of peak intruder numbers during the female's fertile period. All territorial boundaries were entered onto digitised maps and their areas were calculated using GPS mapping software (Ozi-Explorer, 2000).

Data analyses

No pair was observed more than once per day and only first clutches were monitored for this study. Nesting was relatively asynchronous (mean ± SD of first egg dates in 2001/02: 20 October ± 13 days, range 56 days, $n = 32$). Consequently, I standardised data by using day relative to the date the first egg was laid for each pair (day 0). The periods before day -6 and after the penultimate egg was laid were classed as the pre-fertile and post-fertile periods respectively.

Mate guarding indices were compared between the three categories of fertility (pre-fertile, fertile and post-fertile) using a mean value that was generated from a standard interval of six days from each of the three time periods (day -12 to -7, -3 to +2, +6 to +12). All values were converted to per observation-hour to allow comparisons between territories. Mean values for each bird generated for these time periods were compared using matched-pair statistical tests or a Kruskal-Wallis ANOVA. For evaluating the changes in communal site mate guarding, the number of times each female arrived at the feeder accompanied by their male partner during each of the three fertility periods was converted to a percentage of all arrivals for each female, and these values were compared using a Sign test. When assessing the correlation between extra-pair male intrusion rates and percentage territorial area defended, data were arc-sin transformed prior to parametric analysis.

Not all territories could be surveyed or birds recorded in all sampling periods resulting in uneven numbers in some statistical tests. Parametric statistics were only used where data were normally distributed
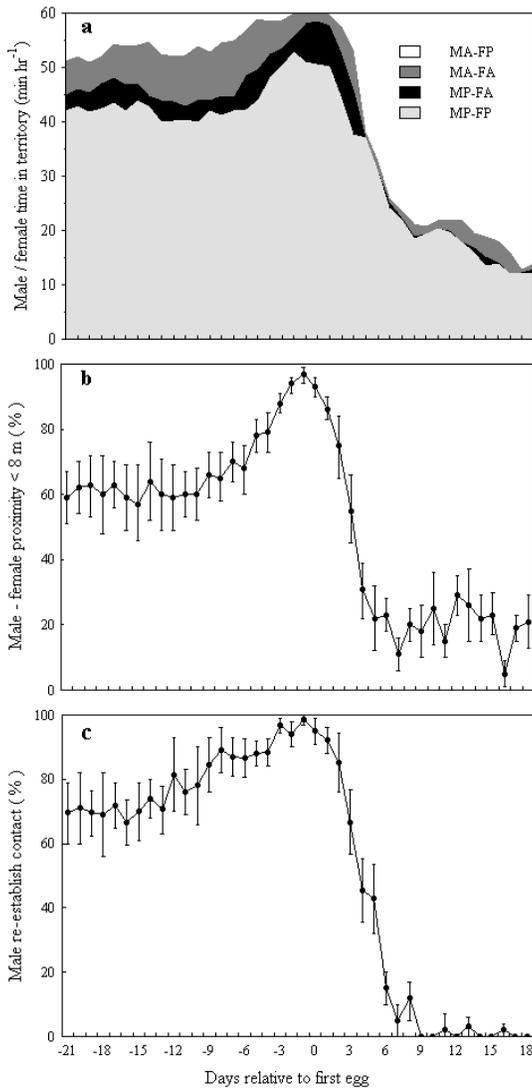
Figure 1. Mate guarding indices relative to first egg dates (day 0) in 23 territories during first clutches in 2001/02. **(a)** Average time (min hr^{-1}) spent within territory by males and females. The data are partitioned into four categories; male present – female present (MP–FP), male present – female absent (MP–FA), male absent – female absent (MA–FA) and male absent – female present (MA–FP). **(b)** Male proximity to female in relation to fertility stage (mean ± 1 SE; %). **(c)** Male re-establishes contact after a separation event of greater than 10 m (mean ± 1 SE; male %). Because not all territories were visited every day, the number of territories observed to generate each mean value ranged from 16–22. In the post-fertile period in (b) and (c), *n* is lower than the territories sampled as no number could be generated if the male was not present.

(Shapiro-Wilks test: $P > 0.05$) and variances were not significantly different (Levene's homogeneity of variance test: $P > 0.05$). When more than one test was performed on the same dataset, assessment of P-value significance took into account a sequential Bonferroni correction (Rice, 1989). Means are presented with standard errors, probability values are two-tailed and statistical significance recognised at $P < 0.05$ unless otherwise stated. The Statistica software package (StatSoft, 1997) was used for all analyses.

Results

Mate guarding indices

Time spent within the territory by the resident male and female

Data on individual and simultaneous presence of each sex were collected from 23 territories (Fig. 1a). The analyses assume that both sexes were equally likely to be seen, and were not within their territory if they could not be seen. During the two weeks prior to the female's fertile period (day -21 to day -8) males spent an average of 44.9 ± 0.5 min hr^{-1} within their territory and females spent 48.5 ± 0.5 min hr^{-1}. For males, this increased during the fertile period to 53.7 ± 1.3 min hr^{-1} and peaked on day 0 at 58.5 ± 0.9 min hr^{-1}. The time spent within their territory by females during the fertile period (49.0 ± 1.1 min hr^{-1}) did not increase from the pre-fertile period. In the post-fertile period, when resident males were seeking extra-pair copulations, they spent less the time within their territory (19.7 ± 1.8 min hr^{-1}) and their intrusion rates into other territories increased (0.09 ± 0.02 territories per day during fertile period versus 0.45 ± 0.06 territories per day during incubation; Wilcoxon matched-pairs: $Z = 4.25$, $n = 26$, $P < 0.001$). In contrast, females spent more time in their territories during the post-fertile period (57.4 ± 0.4 min hr^{-1}), because they were incubating their eggs. Females were present in their territory while their mate was absent for 6.9 ± 0.4 min hr^{-1} during the pre-fertile period. This proportion decreased significantly during the fertile period to 0.7 ± 0.3 min hr^{-1} (paired-sample t-test: $t_{20} = 10.82$, $P < 0.001$), and from day –2 to day 0, females were never seen in their territory without their mate also being present.

In 2000/01 and 2001/02 a female-biased sex ratio existed and thus a number of males mated with more than one female. Because of nesting asynchrony the male would associate with his primary female until she laid her clutch, upon which time he would move to a new area (usually adjacent to his primary territory) and begin associating with a secondary female. In three cases the male then moved to a tertiary female's territory once the secondary female had laid her eggs.

Table 1. Mean time (min hr^{-1})[A] polygynous males spent in the territory of their primary (1), secondary (2) and tertiary (3) female during each of these females' peak fertile periods (between day –3 and +1). In all cases, the resident male predominantly associated with the female who was fertile (see mean values); for example m/rr spent 60 min hr^{-1} with his primary female when she was fertile and did not associate with either the secondary or tertiary females at this time. However, when his secondary female was fertile, he spent 48 min hr^{-1} in her territory and significantly reduced his association with his primary female to 6 min hr^{-1}. The tertiary female was ignored until she became fertile, whereupon m/rr increased his time in her territory to 48 min hr^{-1}.

Male ID	female 1 fertile			female 2 fertile			female 3 fertile		
	1	2	3	1	2	3	1	2	3
m/ow	49	0	-	0	60	-	-	-	-
m/rr	60	0	0	6	48	0	10	0	48
m/wg	60	0	-	3	55	-	-	-	-
om/r	46	4	0	8	42	9	3	7	50
wm/yw	53	0	-	0	52	-	-	-	-
bm/bb	47	13	-	10	50	-	-	-	-
rm/bo	59	0	-	6	48	-	-	-	-
rm/bw	60	0	0	0	60	0	5	0	35
rm/g	59	0	-	12	26	-	-	-	-
wb/bm	60	0	-	0	58	-	-	-	-
wy/bm	60	0	-	0	60	-	-	-	-
yo/bm	49	10	-	4	53	-	-	-	-
Mean	55	2	0	5	51	3	6	2	44

[A] Times for each male may add to less than 60 mins hr^{-1} in cases when the whereabouts of the male was unknown for some periods

For 12 males with territory occupancy data for their primary, secondary and tertiary females (where applicable), they spent most of their time in the territory of the female who was fertile at the time (Table 1). Overlap of the female fertile periods only occurred for three of these males (Male ID; om/r, bm/bb and yo/bm; Table 1), and in these cases males divided their attendance between these sites on those days; this is reflected in the lower mean values for those males. When a male moved into the territory of a secondary female, he would mate guard her and ignore intrusions into his primary territory. In Table 1 it is clear that males traded-off any territorial defence of their primary territory when they moved into the territory of secondary and tertiary females. Once secondary and tertiary females laid their clutches, the male generally associated with the primary female and territory, usually to engage in feeding offspring (Low *et al.,* in press).

Time spent by the resident male within 8 m of female

Males spent a significantly greater proportion of time within 8 m of the female during her fertile period than during her pre-fertile and post-fertile periods (Kruskal-Wallis ANOVA: $\chi^2 = 37.1$, df = 2, $P <0.001$), with this reaching a maximum mean value of 58 min hr^{-1} on day -1 (Fig. 1b).

Re-establishment of contact after separation

The percentage of times the male re-established contact with the female after a separation event was significantly higher during the peak fertile period ($90.8 \pm 2.2\%$) than during the pre-fertile ($72.7 \pm 3.2\%$) and post-fertile ($18.9 \pm 4\%$) periods (Kruskal-Wallis ANOVA: $\chi^2 = 35.3$, df = 2, $P < 0.001$; Fig. 1c). This reached a maximum of $98.6 \pm 1.4\%$ on day -1.

Male response to a missing female during the fertile period

Resident males generally sat beside their mates giving a variety of one, two and three-note calls and only leaving to chase territorial intruders (3-note calls as percentage of total: $29 \pm 5.5\%$, $n = 20$). However, if the male lost contact with his mate he would fly in an outward spiral around her last known position giving loud characteristic three-note calls (3-note calls: $100 \pm 0\%$, $n = 20$). The male would then move rapidly between four or five key locations, including the nest site and the last known position of the female, while vigorously calling and aggressively defending the area around and between these sites. This continued until the female was relocated, when the resident male's movement and calling behaviour abruptly changed once more. The male ceased moving around the territory

and remained within a few metres of the female, often in a stationary position. During the first minute after contact was re-established, in 43% of cases, the male was silent. In the remaining 57% of cases, the male generally changed his calling from three-note calls to two and one-note calls (last five calls prior to male-female contact: 3-note = 100%; first five calls after male-female contact: 3-note = 10%, 2-note = 77%, 1-note = 13%, $n = 20$).

Resident male response to intrusion

The resident male responded immediately to any extra-pair male intrusions with raised head and tail-feather threat displays, calls and aggressive chasing. Any intruding extra-pair males managing to engage the female in a chase when the resident male was present in the territory ($n = 291$) were aggressively chased in turn by the resident male. The resident male was alerted to the chase by the female's specific 'forced copulation' alarm call (Low, 2005). On these occasions, if the intruding male successfully brought the female to the ground, the resident male would physically attempt to remove the extra-pair male from on top of the female by pecking and striking at him with his claws, before chasing him away. No retaliation (copulation or aggression) against the female by the resident male was ever noted after these encounters (*contra* Clutton-Brock and Parker, 1995; Valera *et al.* 2003). In contrast, when the female was aggressively chased by a bellbird, *Anthornis melanura* (a honeyeater of similar size to the stitchbird), the male reacted and followed only 22% of these chases and never actively defended the female ($N = 119$).

Of the territories with detailed male occupancy data, the male territory holder changed between the beginning of nest building and the laying of the first egg during first clutches on six out of fifty-two occasions. In four of these instances, a first-year male had begun calling and associating with the female in a territory that, in previous years, had belonged to an older male (mean age of older male: 5.2 ± 0.9 years, range 4–8); however, the older male was still alive and frequently seen on other parts of the island. In all instances the older male displaced the younger male prior to the female's fertile period, reclaimed the territory and instigated mate guarding when the resident female was fertile. The four displaced first-year males then established territories nearby and paired with late nesting first-year females. In the fifth territory, a first-year male displaced another first-year male when the original territory holder became sick; his song was hoarse and he appeared unwell. However, in this case
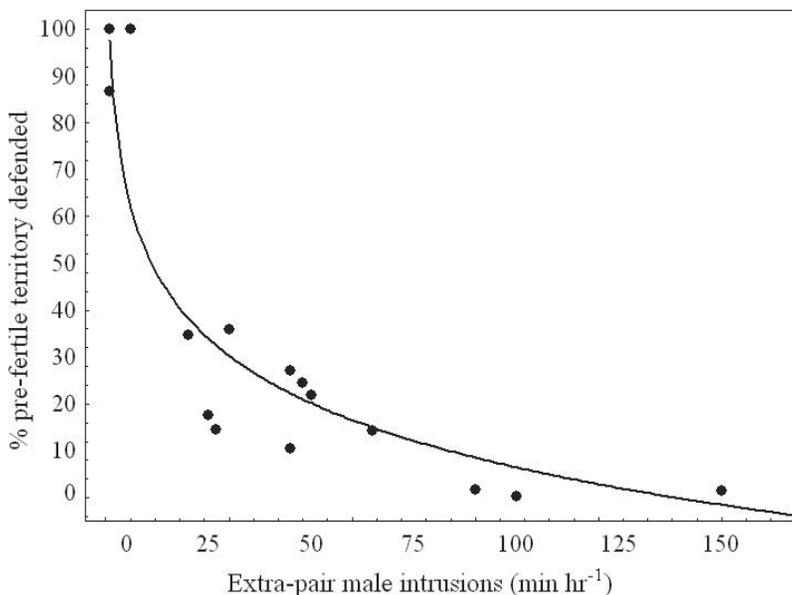

Figure 2. The percentage of the territory from the pre-fertile period that is defended by the resident male during his female's fertile period in relation to the amount of extra-pair male intrusion during that same period. The data in this figure are untransformed, with each point representing an individual nesting attempt. A logarithmic trend-line has been fitted to the data.

the original territory holder recovered from illness and reclaimed the territory two days before the first egg was laid and immediately began mate guarding. In the final instance, a first-year male displaced a six-year-old male; the old male was probably unwell at the time as he died of a respiratory infection 10 days later.

Mate guarding at communal sites

A total of 433 observations of females arriving at feeding stations and the presence or absence of their mate was collected during 39 observation periods in 2001/02. The likelihood of a male accompanying his mate to a feeding station increased significantly from $37 \pm 4.8\%$ in her pre-fertile period to $66.3 \pm 4.7\%$ during her fertile period (Sign test: $Z = 4.58$, $n = 25$, $P < 0.001$). Male accompaniment dropped significantly from the fertile period soon after incubation began ($6.4 \pm 1.8\%$: $Z = 4.69$, $n = 25$, $P < 0.001$). Males at the feeding stations would usually feed alongside their mate, but would sometimes wait nearby and follow her when she left.

Area defended by the resident male

The area defended by the resident male on the day of peak extra-pair male intruder activity during his female's fertile period ($1104 \pm 352\,m^2$) was significantly smaller than the area he defended during the pre-fertile period ($3274 \pm 175\,m^2$; paired sample t-test: $t_{15} = 7.68$, $P < 0.001$). The percentage of the pre-fertile territory that was actively defended during the time of peak intruder activity was negatively correlated with the amount of intruder male activity at that site (Pearson correlation: $r = -0.83$, $n = 16$, $P < 0.001$) (Fig. 2). For the lowest three intrusion rates recorded (< 1 minute per hour), males continued to defend almost all of their pre-fertile territory area (range 86–100%). For the highest three intrusion rates (range 120–300 min hr^{-1}), males defended only the immediate area around the female (range 0.09–1.5% of pre-fertile territory area). In these instances, the female continued feeding and the resident male moved with her, while displaying to and chasing away any extra-pair males that approached within one to two metres of the female. This can be contrasted with lower intrusion rates, where the resident male would chase away extra-pair males at much greater distances from the female (up to 30 m). In all cases of mate guarding during the fertile period, the defended area centred on the female as she moved around the territory.

Discussion

Stitchbird mate guarding behaviour and its temporal relationship to the females' fertile period was similar to that documented in most bird species (e.g. Komdeur

et al., 1999; Hall and Magrath, 2000; Chuang-Dobbs *et al.*, 2001). This was expected, since the forced copulations frequently made by extra-pair males pose a considerable paternity threat to the resident male (Ewen *et al.*, 1999). Previously, mate guarding in the stitchbird has been described as inconsistent (Castro *et al.*, 1996) or traded off with defending the nest site (Ewen, 1998; Ewen *et al.*, 2004). I found no such inconsistency or trade-off in this study as all males would defend an area centred on the position of the female, provided her location was known, regardless of whether she was within the territory or at a communal feeding site.

Costs or trade-offs associated with mate guarding suggest that mate guarding is subject to conflicting demands (Westneat and Stewart, 2003), with it being traded-off against: (1) courtship feeding and copulation (Mougeot *et al.*, 2002), (2) pursuit of extra-pair copulations (Chuang-Dobbs *et al.*, 2001; Pilastro *et al.*, 2002; but see Stutchbury, 1998), (3) attraction of secondary females (Pinxten and Eens, 1997), (4) male foraging and body weight (Askenmo *et al.*, 1992; Westneat, 1994; Komdeur, 2001), and (5) nest construction or defence (Cuervo, 2003; Ewen *et al.*, 2004). In this study there was evidence for a trade-off between mate guarding and polygyny, as well as a trade-off between territorial defence and mate guarding. For most polygynous males little trade-off was observed; males generally spent all of their time in the territory of the female who was fertile (see Table 1). However, when an overlap between the fertile periods of the male's female partners occurred (see the males om/r, bm/bb and yo/bm in Table 1), the male was forced to divide his attentions between females on those days (see also Pilastro *et al.*, 2002).

The negative correlation between the size of the defended area around the female and intrusion pressure by extra-pair males during her fertile period suggests that the focal male trades-off territory size for paternity assurance. While I am unaware of any previous study showing this effect in species where intrusion is primarily aimed at securing EPCs (but see Mougeot *et al.*, 2002 for a correlation between intrusion rates and mate guarding behaviour), it has been well documented in species where intrusion pressure is related to accessing food resources (Myers *et al.*, 1979; Norton *et al.*, 1982). In the sanderling, *Calidris alba*, territory holders could repel sporadic intrusions of single birds, being able to dispatch them with aggressive displays and chases (Myers *et al.*, 1979); a pattern also seen in this study. However, as the number of both intrusions and intruders increased, a threshold point was reached where males could not simultaneously chase away all territorial intruders, resulting in a smaller defended area centred on the contested resource: in the stitchbird this was the fertile female. From Fig. 2 this threshold

appears to be an intrusion rate of approximately 10 min hr^{-1}, above which resulted in a best-of-bad-job situation with the male trading-off the area defended with his ability to guard the female.

In both my study and Ewen *et al.*'s (2004) when the female was absent or could not be located by the male, the male adopted a conditional tactic whereby he defended the area that was most likely to contain the female or that the female was most likely to return to (i.e. around the nest site or where she was last seen). Thus, nest site defence under these circumstances should not be viewed as something traded-off against mate guarding (*contra* Ewen *et al.*, 2004), but rather a best-of-a-bad-job tactic contained within a wider strategy to maximise paternity assurance. Other indices of mate guarding support this conclusion: males were more likely to be close to the female and initiate contact during her fertile period, the defended area was mobile and based on the location of the female, and the resident male significantly increased his following of the female to communal sites outside the territory during this time.

On the six occasions when the resident male was replaced between the beginning of nest building and egg laying, this change in the resident male appeared to be correlated with male age or health. In all cases it appeared that the stronger male waited and usurped the female from a weaker competitor when: 1) the female approached her fertile period, or 2) the other male showed signs of ill health. Such takeovers are predicted from models of resource guarding (see Hardling *et al.* 2004 and references therein).

While not specifically measured in this study, it appears likely that the resident male is effective at limiting EPCs. On all occasions when EPCs occurred ($n = 47$; Low, 2005), the male was temporarily absent from the female. If the male was present, however, he was able to chase away any extra-pair males. An alternative interpretation of mate guarding is that the male is trying to protect the female from harassment (Gowaty and Buschhaus, 1998; Komdeur *et al.,* 1999). This does not appear to be the primary motivation in the stitchbird, as females are also harassed and chased by male bellbirds and yet the resident male does not interfere or chase these away. In contrast, when other male stitchbirds chased their mate, the resident male was extremely responsive to the chase and aggressively attempted to remove that male from the vicinity of the female.

What is the function of mate guarding in birds?

Mate guarding has increasingly been viewed as a best-of-a-bad-job tactic whereby males attempt to limit paternity losses in situations where females largely control paternity (Wagner *et al.*, 1996; Johnsen *et al.*, 1998; Double and Cockburn, 2000; Griffith *et al.*,

2002). However, detailed behavioural observations in a number of bird species suggest that EPCs are resisted by females to some degree (e.g. Brown, 1978; Birkhead *et al.*, 1985; Cunningham, 2003; Low, 2005), with often little evidence to distinguish between female pursuit of EPCs and situations where females concede to copulate as a form of convenience polyandry (Westneat and Stewart, 2003). If it can be shown that females do not exclusively control patterns of paternity in birds (e.g. Vaclav and Hoi, 2002) then our current understanding of mate guarding function must be similarly revised.

In the stitchbird it appears that males primarily guard their mates in order to maximise their paternity in the face of forced copulation attempts by intruding extra-pair males. However, while female extra-pair copulation forays were never observed and are considered unlikely (Low, 2005) they might have occurred at times observers were absent (Double and Cockburn, 2000). The idea that male stitchbirds mate guard because of the intrusive behaviour of extra-pair males is hardly surprising considering the high levels of forced extra-pair copulation and overt female resistance characteristics of this species (Castro *et al.*, 1996; Ewen *et al.*, 1999; Low, 2005). In mating systems where sexual coercion exists, one prediction is that the male and female should co-operate to prevent EPCs as neither party is expected to benefit from them. However, this does not necessarily lead to the conclusion that females should exhibit similar behaviours as expressed by the male (e.g. maintaining proximity and following) in order to gain protection from forced EPCs; thus, initiating movement away from her mate does not necessarily imply that the female is avoiding the male (*contra* Creighton, 2001). In the stitchbird, males are heavily engaged in repelling extra-territorial intruders during the females' fertile period; a time when she is almost constantly feeding in order to gain the weight necessary prior to egg laying (Low, 2004). Thus, the male and female have conflicting needs at this time; this is solved by the female optimising her feeding patterns and using a specific 'forced copulation' call to alert her mate to the presence of any extra-pair male intruder that approaches her: his response being to immediately fly in her direction and chase the intruding male away (Low, 2005).

Rather than seeing the stitchbird's mating system as an odd exception to the currently established view of mate guarding and extra-pair paternity, this study suggests that the male's role in determining mate guarding function should not automatically be assumed to be of secondary importance: a best-of-a-bad-job response to the female's infidelity. Indeed, discussions of mate guarding have implied that only one function should be attributed to mate guarding for each species; mate guarding has been interpreted as males protecting

their paternity from marauding extra-pair males (e.g. Gowaty *et al*., 1989), or protecting their paternity from their marauding female partner (e.g. Johnsen *et al*., 1998). Future assessments of mate guarding function need to consider that both possibilities may coexist. Males may use mate guarding to reduce the chance of their female being subjected to sexual coercion from non-preferred males, while at the same time preventing her from soliciting extra-pair copulations from preferred males. Because sexual coercion and female copulation solicitation may be subtle (Smuts and Smuts, 1993; Double and Cockburn, 2000) or show superficial similarities (Westneat and Stewart, 2003), differentiating the relative importance of these two mate guarding functions, both between and within species as ecological circumstances vary, presents a serious challenge for future researchers.

Acknowledgements

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