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RESUMEN

La permanencia, actividad extra-pareja (cortejo y cópula con otro individuo además de la pareja) y la respuesta (acercamiento y agresión) de las parejas sociales se observó en una colonia de bobos de patas azules anidando en la Isla Isabel, Nayarit, México. Tratamos de contestar tres preguntas: 1) ¿Cómo es que los machos y las hembras resguardan a sus parejas?, 2) ¿qué tan efectivas son estas tácticas de resguardo?, y 3) ¿cómo pueden los individuos promiscuos evitar el resguardo de pareja?. De 18 parejas, 6 hembras y 11 machos tuvieron cópulas extra-pareja (EP). Todos los machos y 10 hembras cortejaron con otros individuos además de sus parejas sociales.

Los individuos con parejas promiscuas (que copularon EP) tuvieron la misma permanencia en el territorio que los individuos con parejas no promiscuas. Los inidividuos con parejas promiscuas salieron primero del territorio en igual proporción que sus rivales. Tanto los machos como las hembras hicieron cortejos intra-pareja en respuesta a los cortejos EP de sus parejas. Este comportamiento es consistente con la hipótesis de que el cortejo (y las cópulas) frecuentes pueden ser un tipo de resguardo de pareja. Las hembras amenzadas (apareadas con machos que hacían actividades EP) respondieron con más agresión y acercamiento cuando sus parejas estaban haciendo cortejos EP dentro del territorio.

Sin embargo, el cortejo intra-pareja y las respuestas inmediatas no fueron efectivas en disminuir la actividad EP de los machos y de las hembras. Para los machos y las hembras, la presencia parece ser la manera más efectiva en suprimir la actividad EP de sus parejas. En el bobo de patas azules, tanto los machos como las hembras han encontrado tácticas para evadir el resguardo de pareja. Las hembras promiscuas parecen evitar a sus parejas sociales modificando sus patrones de permanencia, mientras que los machos

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Tactics, effectiveness and avoidance of mate-guarding in the blue footed booby (*Sula nebouxii*)

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Abstract

Attendance, extra-pair activity (courtship and copulation with an individual other than the mate) and the response (approach and aggression) of social mates were observed in a colony of blue-footed boobies (Sula nebouxii) nesting on Isabel Island, Mexico. We sought to answer three questions: how do males and females guard their mates?, how effective is mate guarding?, and how can promiscuous individuals avoid mate guarding?. Of 18 pairs, 6 females and 11 males engaged in extra-pair (EP) copulations. All 18 males and only 10 females courted with individuals other than their social mate.

Cuckolded individuals did not increase their attendance in the territory and were as likely as rivals to leave the area first. Both male and female social mates performed intra-pair courtship as a response to EP courtships by their mates. This behaviour is consistent with the hypothesis that frequent courtship (and copulations) may serve as a form of mate guarding. Threatened females (mated to males that performed EP activities) were more likely to respond with approach and aggression towards the rival when their social mates were engaging in EP courtship inside the pair's territory rather than outside.

Intra-pair courtship and immediate responses (approach and aggression), however, were not effective in diminishing either male or female EP activity. For both male and female social mates, presence appears to be the most effective means of reducing EP activity of their partners. In the blue footed booby, both males and females have found ways to evade mate guarding. Promiscuous females, thus, seemed to avoid their social mates by modifying their attendance patterns, while promiscuous males avoided mate guarding by copulating away from the territory when the mate was present

Key words Mate guarding. Sula nebouxii. Extra-pair courtship. Extra-pair copulations

Introduction

In species with a large investment in parental care by both sexes, males are expected to follow a mixed reproductive strategy (Trivers 1972), copulating extra-pair while maintaining their pair bond and rearing offspring with their social mate. However, females may also benefit from this strategy. Males may achieve more fertilisations by copulating with as many females as possible, while females that copulate extra-pair may obtain genotypic or phenotypic benefits such as courtship feeding (reviewed in Westneat et al. 1990). However, these extra-pair copulations (EPCs) may also impose costs on cuckolded social mates (reviewed in Birkhead and Møller 1992). Thus, individuals are expected to evolve tactics, such as mate guarding, that prevent the social mate from engaging in extra-pair (EP) activity (courtship and copulation).

Most solitary territorial species guard their mates by close following prior to and during egg laying (Trivers 1972; Smith 1988). However, not all species can guard mates in this way. Colonial birds, for example, do not seem to follow their mates as they are limited in mate guarding by the need to perform other activities such as foraging (Birkhead and Møller 1992). Nonetheless, colonial birds can potentially protect paternity using tactics such as frequent pair copulations, aggression towards other individuals and maximisation of time spent with their mate (Birkhead and Møller 1992). The objective of this research was to answer three questions: how is mate guarding manifested by males and females in the blue-footed booby (Sula nebouxii)?, how effective is it in hindering EP activity?, and how do promiscuous birds side-step it?. We used the functional definition of mate guarding as any behaviour that reduces EP behaviour of the social mate. We did not assess the outcome of EP activity (i.e. paternity).

Mate guarding is not always completely effective in preventing EP activity. In

purple martins (Progne subis) and blue tits (Parus caeruleus), mate guarding seems to be relatively ineffective in protecting paternity (Morton et al. 1990; Kempenaers et al. 1992). Similarly, in tree swallows (Tachycineta bicolor) and European starlings (Sturnus vulgaris), frequent intra-pair (IP) copulations do not deter social mates from copulating with other females (Whittingham et al. 1994; Eens and Pinxten 1995). In contrast, in the northern cardinal (Cardinalis cardinalis) and in razorbills (Alca torda) it seems to account for EP fertilisations being infrequent (Wagner 1992a; Ritchison et al. 1994).

Individuals may have difficulty in escaping mate guarding (Slagsvold and Lifjeld 1997). Since mate guarding is a poor predictor of EP paternity in some species, this suggests that females have ways of preventing/avoiding mate guarding. For example, male budgerigars (Melopsittacus undulatus) restrict their EP courtship to times when the social mate is unable to observe them, although Baltz and Clark (1997) did not suggest that the function of this timing was to avoid mate guarding. Yet, in western bluebirds (Sialia mexicana), females are no more likely to participate in EPCs when the resident male is visually occluded than when he is present (Dickinson 1997). Other forms of avoiding mate guarding are: performing EPCs outside the territory (Hatch 1987; Smith 1988, Wagner 1991; Kempenaers et al. 1992; Heg et al 1993; Neurdorf et al. 1997; Sheldon 1994; Stutchbury 1998), moving away from the social mate as egg laying approaches, or having a prolonged receptive period (Davies 1985; Sheldon 1994; Lumpkin 1981; Hatch 1987). Males may also attempt to prevent female mate guarding by interference in female-female aggression (Summers 1990).

Most studies on mate guarding have focused solely on males, who risk losing paternity if the mate's EPCs result in fertilisations (Birkhead and Møller 1992). Even though the female does not need to ensure her maternity, it may also be in her best interest

to guard the social mate. Female mate guarding could produce a non-genetic benefit (Wagner 1992b), such as strengthening or defending the pair bond (Petrie 1992), especially if there is a risk of mate switching (Black 1996; Wagner 1991; Stamps 1998). This risk may be especially relevant if EPCs are a form of assessing future partners (Hatch 1987; Colwell and Oring 1989; Slagsvold and Lifjeld 1997). In principle, if females have promiscuous partners, they may be exposed to more sexually transmitted diseases or parasites (Hamilton 1990; Petrie 1992), receive insufficient sperm from the social mate for future clutches, or suffer a reduction in paternal investment (Petrie 1992; Hunter et al. 1993). Thus, females may attempt to monopolise males by remaining near their territories, and using frequent courtship and copulation (Yasukawa and Searcy 1982; Summers 1989; Wagner 1992b; Petrie 1992; Hunter et al. 1993; Eens and Pinxten 1995). Female blue-footed boobies' guarding strategies are of particular interest in this context.

The blue-footed booby is a long-lived colonial marine bird (Nelson 1978) in which both sexes participate in the rearing of the young (Guerra and Drummond 1995) Courtship and copulations are highly ritualised and visible (Nelson 1978), and individuals spend much of their time at or around their territories, leaving only for short foraging trips. Females are 32% heavier than males (Castillo and Chavez-Peón 1983) and their co-operation is apparently necessary for copulation (Osorio and Drummond 1998). Females are probably fertile for 1-5 days before laying each egg, plus an unspecified previous period (Birkhead and Møller 1992; Osorio and Drummond 1998). EPCs sharply decrease after the female has laid her first egg (Osorio in preparation; personal observation).

Previously, it has been determined that in the blue-footed booby 1) roughly half of paired males and females perform EPCs; 2) males copulate EP mainly outside of the social mate's presumed fertile period while females increase their EPCs during their fertile period;

3) male and female promiscuity declines in the presence of the social mate; 4) males and females appear to guard by being present with the mate and courting and copulating at the nest site (Osorio and Drummond 1998). The evidence for the above was a six-fold decline in females EPCs and approximately a 50% decline in male EPCs, when the social mate was present versus absent. Also, males and females increased attendance at the nest site as laying approached. Hence, attendance combined with pair courtship and copulation appear to serve a mate-guarding function.

The following hypotheses were tested:

Hypothesis 1: Individuals respond to EP activity of the social mate by remaining within or near the territory, engaging in intra-pair (IP) activity, approach and aggression. Hypothesis 2: Attendance, courtship, copulation, approach and aggression suppress EP activity of the social mate. Hypothesis 3: Promiscuous individuals evade guarding by modifying their attendance and performing EP activity away from the territory.

We use the following terminology. An unfaithful individual courts with other individuals in addition to the social mate A threatened individual is one whose social mate engages in EP courtship. A promiscuous individual copulates with another individual (rival) in addition to the social mate, while a cuckolded individual has a promiscuous partner.

Results

Of the 18 focal pairs observed, 11 males and 6 females were promiscuous. Males performed an average of 6.1 ± 4.6 EPCs, and these occurred in a median of –5 days previous to their mates first egg laid (range 0 to –22). Promiscuous females had an average of 12.3 ± 12.9 EPCs, and these occurred in a median of -4 days before egg laying, (range 0 to –9). Two of these females copulated EP with paired males (one of them copulating with an unpaired male too), three of them copulated with unpaired males and one with a male of unkown status. Six of the males copulated EP with paired females, four with unpaired males and one with a female of unkown status, none of these males copulated EP with more than one female. All 18 males courted with other females in addition to their social mate, while only 10 females actively courted with another individual. Because not all individuals received or performed the same types of courtship, sample sizes for individuals engaged in EP courtship vary.

Hypothesis 1 Tactics for Mate Guarding

Individuals respond to the EP activity of the social mate by remaining within or near the territory, engaging in IP activity, approach and aggression.

Prediction a: Cuckolded individuals should spend more their time at or near the territory than non-cuckolded individuals as laying approaches.

Comparing the median time spent daily by individuals at or near their territory over the 5-d period before egg laying, cuckolded males did not differ in their attendance compared to non-cuckolded males (cuckolded: 8.8 (6.1, 10.2) h, $n = 6$; non-cuckolded: 8 5 (7.7; 9.2) h, $n = 12$; Mann-Whitney test, $U = 30.0$, $P = 0.6$). There were no differences between the time that cuckolded or non-cuckolded females stayed at or near their territories

(cuckolded: 8.4 (6.4; 9.3) h, n = 11; non-cuckolded females: 7.9 (2.9; 9.0) h, n = 7; U= 36.0, P = 0.9).

Prediction b: When a pair of social mates and a rival are present, the cuckolded mate should be less likely than the rival to leave the area first.

Using all periods in which the rival and both social mates were present within or near the territory, we asked whether the rival or the cuckolded mate departed first. The whole period of observation for each focal pair was used. Sample sizes for these tests were small: of the promiscuous individuals, only 6 males and 3 females had a constant rival whose presence in the area could be monitored. Other rivals entered the observation area only sporadically or when the social mate was absent, and thus their attendance could not be compared to that of the social mate.

Female social mates were not more likely to leave the area first than were female rivals (5.5 (0.0; 6.0) vs. 8.5 (4.0; 15.0) first departures, respectively; Wilcoxon test, T = 18.0, n = 6, P =0.2), and male social mates departed first at a frequency similar to that of their rivals (9.0 (4.0; 24.0) vs. 13.0 (8.0; 26.0) first departures, respectively; Wilcoxon test, T = 0, n = 3, P = 0.2)

Prediction c: Threatened mates should increase IP activity after EP activity has occurred.

We compared the frequency of intervals with IP courtship by the threatened individual before vs. after a partner's EP courtship. Whenever an EP courtship occurred, we scored whether an IP courtship occurred during the remainder of that 5-min interval and also during the subsequent 5-min interval. The sum of these two one-zero scores was the

"after" score, and the sum of the two scores before EP courtship was the "before" score. When there was a block of consecutive 5-min intervals with EP courtship, IP courtship occurring during these intervals was not taken into account, so as not to confuse the sequence of events. The whole period of observation for each focal pair was used. The total one-zero scores across all these days were summed for each individual. Only reciprocal and non-reciprocal IP courtship performed by the threatened individual were taken into account.

When a male simply **received** EP courtship, there was no significant difference between the frequency of intervals with IP courtships by the threatened female occurring before vs. after EP courtship (Table 1). However, when a male actively performed a **non-reciprocal** or **reciprocal** EP courtship, there was a four-fold increase, for the lattter, in the frequency of intervals with IP courtship by the threatened female after EP courtship (Table 1).

After **reciprocal** EP courtship by a female, the frequency of intervals with IP courtships performed by the threatened male significantly increased four-fold (Table 2). However, when the female simply **received** or actively performed a **non-reciprocal** EP courtship, there was no significant increase in IP courtships by the threatened male after EP courtship (Table 2). Sample sizes varied because not all individuals received or performed all types of EP courtships. The sample size of IP copulations occurring before vs after EP copulations was insufficient to perform a test.

Prediction d: Threatened mates should respond with approach and aggression towards the rival after an EP courtship has occurred, and this response should be just as likely when the unfaithful individual is within or outside the social

pair's territory.

If approach and aggression occur as a response to a territorial threat then they should occur only when the unfaithful individual and the rival are within the social pair's territory, however if these behaviours occur within and outside the territory then they support the mate guarding hypothesis.

Overall (inside or outside the territory), threatened males and females seemed more likely to respond with approach and/or aggression towards the rival when the social mate performed reciprocal EP courtship (Tables 3 and 4). When unfaithful males and females performed reciprocal EP courtship, the proportion of courtship events eliciting a response (approach) doubled compared to when unfaithful males and females performed non-reciprocal EP courtship (Tables 3 for threatened females and 4 for threatened males). Both threatened males and females appeared to be less likely to respond to EP courtship received by their social mates (Tables 3 and 4), in fact, of 18 threatened females, only one responded with approach when her mate received an EP courtship. Most of these approaches and aggressions resulted in the rival leaving the territory while the unfaithful mate usually stopped courting EP.

We compared the proportion of 5-min intervals with responses (aggression and approach pooled) by the threatened mate to EP courtship when the unfaithful individual was inside the territory vs. the proportion of intervals with responses by the threatened mate when the unfaithful individual was outside the territory. The whole period of observation was used for each focal pair.

There were not enough males that simply **received** EP courtship inside and outside the territory for us to analyze. When males actively performed **non-reciprocal** EP courtship, there was no difference between the proportion of courtship events eliciting a

response inside versus outside the territory (0.4 (0.0; 1.0) vs. 0.3 (0.0; 1.0), respectively; T = 27.5, n = 13, P = 1.00, Wilcoxon test). However, when males actively performed **reciprocal** EP courtship, the social mate was more likely to respond if the male was outside of the territory than inside (0.0 (0.0; 0.7) vs. 1.0 (0.2; 1.0), respectively, Wilcoxon test, T = 5.0, n= 10, P = **0.02**). That is, females defended and guarded their social mates, responding with approach and aggression more frequently when those males were courting outside the territory.

When females simply **received** EP courtship, there was a similar proportion of courtship events eliciting a response by the threatened mate inside versus outside the territory (0.5 (0.0; 1.0) vs. 0.4 (0.0; 1.0), n = 9, respectively; Wilcoxon test, T = 11.0, n = 6, P = 1.0). Too few females actively performed **non-reciprocal** EP courtship both inside and outside the territory to analyze (n = 3) When females actively performed **reciprocal** EP courtship, the social mate responded equally if the female was inside versus outside the territory (0 7 (0.0; 1.0) vs. 0.0 (0.0; 1.0), respectively, Wilcoxon test T = 15.5, n = 7, P = 0.31).

Hypothesis 2 Effects of Mate Guarding

Attendance, courtship, copulation, approach and aggression suppress EP activity of the social mate.

Prediction a: Extra-pair activity should be less frequent when the threatened mate is present than when absent.

We compared the rate of EP activity that occurred when the threatened mate was present vs. absent in the territory. This rate was calculated as the frequency of intervals of

EP activity in presence of the social mate over the total 5-min intervals in which both social mates were present vs. the frequency of intervals of EP activity in absence of the social mate over the total 5-min intervals in which only the unfaithful mate was present. The whole period of observation was analysed with the exception of day 0 (when females laid their first egg). Because not all unfaithful individuals received or performed the same types of EP courtships, sample sizes vary.

Males simply **received** EP courtship at the same rate when the social mate was present or absent (Table 5). However, active performance of EP courtship (**non-reciprocal** and **reciprocal**) by males occurred significantly more often when their mates were absent (Table 5). Male EP copulations did not increase significantly when the mate was absent (Table 5). Two promiscuous males were not included in this analysis because they performed EP copulations only during previous records when their attendance was not registered in 5-min intervals.

Females **received** more EP courtship in the absence of the social mate. Females also actively performed more **non-reciprocal** EP courtships in absence of the social mate as in its presence (Table 6), although female **reciprocal** EP courtship occurred equally in presence or absence of the social mate (Table 6). Female EP copulations did not seem to vary in presence or absence of the social mate (Table 6). Data on one promiscuous female were missing as she was registered during previous records as explained above.

Promiscuous males and females did not increase the number of EP copulation attempts (where there was mounting but no contact of the cloacas, see Methods), in the absence than in the presence of their social mate (males 0.0 (0.0; 0.0) vs 0.0 (0.0; 0.0), respectively; Wilcoxon test, $\underline{T} = 1.0$, $\underline{n} = 8$, $\underline{P} = 0.94$; females 0.0 (0.0; 0.0) vs. 0.0 (0.0; 0.0), $\underline{n} = 3$). Pooling EP copulations and copulation attempts did not yield a significant

result, either.

Prediction b: EP activity should be less frequent when the threatened mate is present and engaging in IP activity than when just present.

To test this prediction we compared:

A/B vs. C/D

where:

B = total number of intervals when the social mate was present and there was no IP activity

A = frequency of B intervals with EP activity

D = total intervals when social mate was present and there was IP activity

C = frequency of D intervals with EP activity

Only EP activity performed in the presence of the social mate, and active EP and IP courtships were taken into account. The whole period of observation was used for each individual.

The proportion of intervals in which males performed EP courtships was not different when there was IP courtship by the social mate than when the social mate was just present (0.1 (0.0; 0.2) vs. 0.0 (0.0; 0.1) respectively; Wilcoxon test, $\underline{T} = 34.0$, $\underline{n} = 13$, $\underline{P} = 0.45$). For unfaithful females, the proportion of intervals with EP courtships was also not different between intervals when the social mate had performed IP courtship and those when it was just present, (0.0 (0.0; 0.0) vs. 0.0 (0.0; 0.0) respectively; Wilcoxon test, $\underline{T} = 10.0$, $\underline{n} = 5$, $\underline{P} = 0.62$). IP copulations also did not appear to reduce the proportion of subsequent EP copulations (males and females pooled 0.0 (0.0; 0.0) EP copulation without IP copulation vs 0.0 (0.0; 0.0) EP copulation after IP copulation, Wilcoxon test, $\underline{T} = 15.0$, $\underline{n} = 6$, $\underline{P} = 0.44$).

Prediction c: The probability that an individual engages in EP courtship should increase as time passes after IP courtship.

Only active courtships were used for the whole period of observation. There was no clear tendency for a greater frequency of intervals with EP courtships as time advanced after the threatened mate had performed IP courtship (Fig. 1). Nevertheless, variation among successive 5-min intervals was significant (Friedman repeated measures test, males: $\underline{Fr} = 20.95$, $\underline{n} = 12$, $\underline{P} < \mathbf{0.01}$; females: $\underline{Fr} = 14.13$, $\underline{n} = 5$, $\underline{P} = \mathbf{0.03}$). Surprisingly, EP courtship increased during the interval immediately following IP courtship and then declined progressively over the next five intervals (Fig. 1).

Prediction d: Extra-pair courtship should be less frequent after the threatened mate has made some immediate response (courtship, approach or aggression) to the unfaithful mate's EP courtship, rather than when the threatened mate is only present.

We compared the proportion of 5-min intervals with EP courtship that occurred in the subsequent interval after: a) the threatened mate had made a response to the unfaithful mate's EP courtship, and b) the threatened mate had made no response and was only present.

These proportions were calculated as follows. The frequency of 5-min intervals with EP courtship immediately after an interval with a response was divided by the total number of intervals where a putative response had occurred. This was compared to the frequency of 5-min intervals with EP courtship immediately after an interval with no response (to the unfaithful mate's EP courtship) by the threatened mate, divided by the total

number of intervals where both social partners were present, and no response (to the unfaithful mate's EP courtship) occurred. The whole period of observation was used. Only active EP courtship performed when the social mate was present and the responses to this active EP courtship were taken into account. Responses could be courtship, approach and/or aggression (see Methods).

For males, there was a significant increase in EP courtship after the threatened mate had shown a response compared to when there was no response (males 0.4 (0.0; 0.7) vs. 0.0 (0.0; 0.2), respectively; Wilcoxon test, $\underline{T}$ = 21.0, $\underline{n}$ = 15, $\underline{P}$= **0.02**). For females there was no difference in the amount of EP courtships occurring after a response or after no response from the social mate (females 0.0 (0.0; 0.5) EP courtships after a response vs. 0.0 (0.0; 0.0) EP courtships after no response, Wilcoxon test, $\underline{T}$ = 21.0, $\underline{n}$ = 7, $\underline{P}$= 0.29). Responses to EP copulations were too few to be analysed.

Hypothesis 3 Avoiding Mate Guarding

Promiscuous individuals evade guarding by modifying their attendance and performing EP activity away form the territory.

Prediction a: The temporal pattern of attendance within or near the territory should be different for promiscuous than for non-promiscuous individuals.

Only the 5 days previous to egg laying were analysed. The proportion of each hour that males spent within or near their territory was not different for both promiscuous and non-promiscuous individuals (Fig. 2). Promiscuous females, however, appeared to stay in the territory less time during the mid-morning hours and more during the afternoon than

non-promiscuous females (Fig. 3), and there was a significant interaction between female promiscuity and time of day (Two way ANOVA [with replication], $F = 2.60$, $df = 11$, $P < 0.01$). Promiscuous female attendance patterns may be a successful strategy for avoiding social mates, as cuckolded males seemed to decrease attendance progressively after 1400h (Fig. 4), while their promiscuous mates sustained a high level of attendance (Fig. 3). These promiscuous females could take advantage of this time in the late afternoon to perform EP courtships (Fig. 5), although they also spent a high proportion of the hours between 0800 and 1000h performing EP courtships, when their attendance was low relative to non-promiscuous females (Figs. 5 and 3) and when their social mates also decreased their attendance (Fig. 4).

Prediction b: Promiscuous individuals will overlap with the social mate within or near their territories during a lower proportion of their total attendance time than non-promiscuous individuals.

Only the 5 days of the prelaying period were used. The total frequency of 5-min intervals in which an individual overlapped with its social mate within or near the territory was divided by the total frequency of 5-min intervals in which the individual was present. These proportions were compared between promiscuous and non-promiscuous individuals. We expected promiscuous individuals to have a lower proportion of attendance overlap than non-promiscuous individuals. However, neither for males nor for females were there significant differences between the attendance overlap of promiscuous and non-promiscuous individuals (males 0.8 (0.5, 0.9) vs. 0.7 (0.2; 0 9), promiscuous $n=11$, non-promiscuous $n=7$, respectively, Mann Whitney test, $U= 29.00$, $P= 0.42$; females 0.8 (0.6; 0.9) vs. 0.8 (0.4; 1.0), promiscuous $n=6$, non-promiscuous $n=12$, respectively; $U = 33.0$ $P=$

0.82).

Prediction c: Individuals should perform EP activity farther from the territory when the threatened mate is present versus absent.

For males, the average distance at which active EP courtship took place was greater when the threatened mate was present than when absent (Males: 1.0 (0.0; 5.0) m, $\underline{n}$ =16, vs. 0.0 (0.0; 2.9) m, $\underline{n}$ = 18, respectively; Wilcoxon test, $\underline{T}$ = 74.0, $\underline{n}$ = 13, $\underline{P} < \mathbf{0.05}$). This difference was not significant for females (Females: 2.1 (0.0; 3.5) m, vs. 0.1 (0.0; 1.4) m, $\underline{n}$ = 10, respectively; $\underline{T}$= 38.0, $\underline{P}$ = 0.07).

The average distance from the territory at which male EP copulation took place was the same when the threatened mate was present versus absent (2.4 (0.7; 6.4) m, $\underline{n}$= 4 vs. 0.0 (0.0; 6.0) m, $\underline{n}$ = 11, respectively; Mann Whitney test, $\underline{U}$ = 8.5, $\underline{P}$ = 0.08). Females also seemed to engage in EP copulations at the same distance when the mate was present or absent (3.0 (0.0; 20.0) m, $\underline{n}$= 4 vs. 0.0 (0.0; 1.7) m, $\underline{n}$= 6, respectively; $\underline{U}$= 4.5, $\underline{P}$ = 0.11).

Prediction d: Individuals should perform a lower proportion of their EP activity within the territory (versus outside the territory) when the threatened mate is present rather than absent.

We compared the frequency of intervals with EP activity that occurred inside the focal pair's territory in the presence of the social mate divided by the total frequency of intervals with EP activity anywhere in presence of the mate, to the frequency of intervals with EP activity that occurred inside the focal pair's territory but in absence of the social mate divided by the total frequency of intervals with EP activity anywhere in absence of the mate. The whole period of observation was used.

Males performed a lower proportion of their active EP courtships inside the territory when the threatened mate was present than when absent, and this was not significant for females. Males ($\underline{n}$ = 18) performed 0.6 (0.0; 1.0) EP courtships in the presence of the mate vs. 1.0 (0.0; 1.0) EP courtships in her absence, Wilcoxon test, $\underline{T}$ = 15.0, $\underline{n}$ = 15, $\underline{P}$< **0.05**; females (n = 10) performed 0.1 (0.0, 0.6) EP courtships in presence of the mate vs. 0.2 (0.0, 0.6) EP courtships in his absence (Wilcoxon test, $\underline{T}$ = 8.0, $\underline{n}$ = 7, $\underline{P}$= 0.37).

Males also performed on average a significantly lower proportion of their EP copulations within the territory in the presence than in the absence of the threatened mate (0.0 (0.0; 0.7) vs. 1.0 (0.3; 1.0), respectively; Wilcoxon test, $\underline{T}$ = 0.00, $\underline{n}$ = 8, $\underline{P}$< **0.05**). Similarly, females in the sample seemed to perform on average a lower proportion of their EP copulations inside the territory when the threatened mate was present than when absent, but this difference was not significant (0.0 (0.0; 1.0) vs. 1.0 (0.6; 1.0), $\underline{n}$ = 6, respectively; Wilcoxon test, $\underline{T}$= 0.00, $\underline{n}$ = 5, $\underline{P}$ = 0.06).

Discussion

Female Infidelity

Promiscuous females copulated with EP males co-operatively, actively seeking EPCs with males within a 15 m diameter of their territories. In a previous study, 7 of 13 females copulated EP (Osorio and Drummond 1998), while in our sample, 6 of 18 females copulated EP. Although not all females were promiscuous, all 13 in the previous study and 10 (in our sample) actively courted EP. This behaviour suggests that although not all females may seek EP fertilisations, a majority of them may be trying to assess other males, perhaps as future partners (Wagner 1992a).

Male Mate Guarding

Males may need to guard their mates to protect their paternity. In species where males cannot follow their mates closely, attendance could serve as a tactic to avoid being cuckolded.

In blue-footed boobies, cuckolded males did not overlap with their mates within or near the territory for a greater amount of time than non-cuckolded males, and cuckolded males were just as likely as the rival to leave the territory first. Osorio and Drummond (1998) observed that both promiscuous and non-promiscuous females were left alone at the nest site during a similar proportion of daytime. However, male blue-footed boobies did increase nest site attendance as laying approached and were away from the nest site for significantly shorter periods of time during the 20 d before laying than females (Osorio and Drummond 1998). Thus, the male pattern of attendance is consistent with a male-guarding function, but we found no evidence that males facultatively adjust their attendance in response to infidelity of their social mates.

In addittion to the mate-guarding hypothesis, increased male attendance may also be related to territorial defence, pair bond maintenance, or copulation access (Lumpkin et al. 1982; Gowaty and Plissner 1987; Osorio and Drummond 1998). Males remained near their mates and continued courting with them after the pair had copulated, such behavior does not comply with the predictions of the copulation access hypothesis (Gowaty and Plissner 1987; Osorio and Drummond 1998).

The pattern of IP copulations by males is consistent with assuring paternity and there is no evidence that males facultatively adjust the pattern in response to the promiscuity of the social mate (Osorio and Drummond 1998); IP copulations did not increase after females had engaged in EPCs. However, IP copulations did increase progressively, peaking during the last 5 d before egg laying (Osorio and Drummond 1998).

We found evidence that males responded to the social mate's EP behaviour by courting and with approach and aggression. Threatened males responded with IP courtship to the reciprocal EP courtships of the social mate, but not to her non-reciprocal or received EP courtship. Male mates were just as likely to respond with approach and aggression when the unfaithful female was performing active EP courtship either within or outside the pair's territory. Thus, approach and aggression behaviours towards intruding rivals could serve a mate guarding function rather than territorial defence.

Effects of mate guarding

Although several male behaviours seem to reduce EP activity of the mate, they are not all effective. In fact, attendance seems to be the only effective mate guarding tactic that is capable of deterring female EP activity. In the present study, unfaithful females received

and performed non-reciprocal EP courtships less frequently in the presence of the social mate. Promiscuous females also copulated EP six times less frequently in the presence of the social mate and male attendance within or near the territory increased gradually as laying approached (Osorio and Drummond 1998).

The presence of a male within the territory possibly allows it to gather information on female promiscuity. Female boobies may tend to perform fewer EPCs in the presence of the mate to avoid the destruction of their eggs by the cuckolded male (Osorio in preparation, personal observation), and possibly to avert "retaliatory" desertion or reduction of parental investment by males (Gladstone 1979; Gowaty 1995).

By performing IP activity or approach and aggression, threatened males were probably not able to reduce EP activity of females. Thus, IP activity, approach and aggression are not effective mate guarding tactics. There was no evidence that IP courtship and copulation suppressed subsequent EP courtship or copulation, and there was no tendency for EP courtship to diminish after IP courtship or to increase gradually as time passed after IP courtship. This seems to suggest that IP activity or responses are not a mate guarding mechanism. Rather, they could be means of reinforcing or protecting the pair bond.

Males may risk loosing their partners to other rivals in the colony. Of our 18 focal pairs, one female switched to the EP male during the same reproductive season. The female deserted her social mate after courting, copulating and defending a common territory with him for 25 days. The pair spent on average 1.40 ± 1.08 hours together per day. During this time she engaged in frequent EPCs and laid 3 eggs, all of which were destroyed by the cuckolded male. Subsequently, she deserted the cuckolded male and paired with the EP male. Divorce between breeding attempts is also known to occur

(Torres, in preparation). Due to this risk, males could use IP courtship to prevent the female social mate from deserting the male or subsequently divorcing him rather than stopping her from engaging in EP activity or obtaining EP ejaculates.

Avoidance of mate guarding

Since effective male mate guarding is manifested by remaining within or near the territory, promiscuous females are expected to counteract this tactic by facultatively modifying their behaviour. Indeed data indicate that promiscuous females do differ from non-promiscuous females in their attendance, and tend to increase their EP courtship during the late afternoon when their social mate is absent. An extended period of IP activity and a prolonged receptive period may also attenuate the male's guarding (Osorio and Drummond 1998). In contrast, promiscuous females do not seem to avoid mate guarding by engaging in EP activity at a greater distance from the territory when the mate is present.

Male Infidelity

Males pursue a mixed strategy: Osorio and Drummond (1998) showed that males copulate with EP females, mostly outside their own mate's presumed fertile period; and copulate increasingly with their social mate as laying approaches. In the previous study, 7 out of 13 males performed EPCs, peaking about 5-15 d before their own mate's laying, then declining in frequency during the five d preceding laying (Osorio and Drummond 1998). EP courtship also appeared to decline steeply after the 10^{th} d before egg laying, approaching zero during the last 5 d (Osorio and Drummond 1998). In our study, 11 out of 18 males copulated EP, and all males actively courted with other females in addition to their own social mates.

Female Mate Guarding

Even though females do not risk losing paternity if their partners are promiscuous, they may also have other reasons to guard their mates. They may need to guard their mates to sustain the pair bond (Petrie 1992). The pair-bond hypothesis suggests that socially monogamous individuals may secure their mates through frequent courtship or copulations, thus developing a stronger affiliation (Petrie 1992; Stamps 1998). This pair bond may be put at risk by mate desertion or subsequent divorce.

At least one mate switching with the EP female has been observed. A male deserted his social mate after engaging in IP activity and defending a common territory with her for 12 days. They spent on average 7.06 ± 2.14 hours together per day. During this time he engaged in frequent EPCs with an unpaired neighbouring female. After the EP female laid her first egg the promiscuous male deserted his social mate to incubate the clutch with the EP female. Here we propose that to discourage mate switching and divorce (Torres, in preparation), females need to guard the mate and may do this through attendance. Females may guard their mates with more intensity than males if loosing a mate implies more costs for her (for example, if she is already carrying a fertilised egg).

Osorio and Drummond (1998) found female attendance to be a mechanism that females may employ to guard their mates, although in this study cuckolded and non-cuckolded females overlapped with their social mates within or near the territory for similar amounts of time. Nevertheless, female social mates were less likely than the female rival to leave the area first, although probably due to the small sample size, this difference was not significant. Yet this does suggest that given the presence of a rival, female mates tend to remain in the area possibly as a mate guarding tactic.

Although courtship is generally restricted to an animal finding a mate, determining that it is the correct species or synchronising sexual arousal, it also reinforces the pair bond (Barrows 1995). In the blue footed booby, IP courtship is very frequent whenever both social mates are together (Osorio and Drummond 1998), and this, together with approach and aggression, could be a response to threats to the pair bond. In this study, threatened females responded with significantly more IP courtship after active EP courtship had been performed by their social mate. Females were more likely to engage in approach and aggression when the unfaithful mate was performing active EP courtship outside the territory. Females may be especially vulnerable to abandonment when their social mate is courting EP outside the territory and thus may need to reinforce the pair bond. For example, in the poison dart frog (Dendrobates auratus), females use courtship and aggression as a means of preventing the social mate from mating with other females (Summers 1989), and indeed, females may use courtship (sexual responsiveness) and copulation soliciting as a means of manipulating male behaviour in general (Lumpkin 1981, 1983).

Effect of mate guarding

Female presence did have an effect on the social mate's EP courtship, which can be interpreted as having a mate guarding function. In this study, unfaithful males performed less non-reciprocal and reciprocal EP courtships in the presence of the mate. Also Osorio and Drummond (1998) found that promiscuous males copulated EP at half the rate when the social mate was present. However, this decline in promiscuity could be a trade-off between male EP activity and a male's need to guard his partner.

Even though females are responding with IP courtship to EP courtship, this does not

serve a mate guarding function because it is not effective in reducing the social mate's subsequent EP activity. Aggression and approach are also not effective in reducing EP courtship. This could indicate that these behaviours are attempts by the females to sustain the pair bond and retain the social mate. Even though these behaviours were not effective in reducing EP activity, perhaps they could prevent an increase in the social mate's EP activity.

Two results seemed to indicate that aggression/approach and courtship by females actually provoke increased EP courtship by their social mates. Unfaithful males performed more EP courtships after the female social mate had responded with IP courtship. It could be that once partners are performing IP courtship, there is a lower threshold for performing courtship with another individual, or perhaps IP courtship attracts and stimulates potential rivals who then court the social mate, however it seems more likely that when IP courtship occurs as a response to EP courtship (see female mate guarding), EP courtship is only briefly suppressed and then promptly resumed. EP courtship may also increase after approach and aggression by the threatened female for this same reason.

Avoidance of mate guarding

As males can potentially increase their reproductive success through copulation with multiple mates, they should be adept at avoiding mate guarding This study documented males courting EP at almost twice the distance away from their territories when the social mate was present than when absent. As blue footed boobies are highly territorial (Nelson 1978, Osorio and Drummond 1993), a male may avoid mate guarding by engaging in EP activity a few meters away even though he may be in full view of the social mate. Female social mates are not able to reenforce their mate guarding when the social mate is outside

their territory. An alternative hypothesis would be that males are more likely to engage in EP activity if the mate is already within the territory defending it. However these males also performed a lower proportion of EP activity within the territory when the social mate was present.

Conclusions

How is intersexual conflict over EP activity resolved? Even though both males and females guard their social mates through attendance, this tactic is not successful in eliminating it altogether, although it does decrease the opportunities for EP behaviour. IP courtship seems to be a means of strengthening the pair bond for both sexes as mate switching is a risk. For the blue-footed boobie, both males and females have found ways to side-step mate guarding, either by modifying attendance patterns to avoid the social mate or by engaging in EP activity away from the territory when the social mate is present (Table 7).

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Figure legends

Fig. 1. Probability of males (n =12) and females (n = 5) performing active EP courtship following active IP courtship by the social mate. IP = the 5-min interval with IP courtship by the social mate. Friedman repeated measures test, males $P < 0.01$, females $P = 0.03$.

Fig. 2. Proportion of each hour that promiscuous (n = 11) and non-promiscuous males (n= 7) spent within or near their territories during the five days before laying by their mates.

Fig. 3. Proportion of each hour that promiscuous (n = 6) and non-promiscuous males (n= 12) spent within or near their territories during the five days before laying.

Fig. 4. Proportion of each hour spent by cuckolded males (n = 6) within or near their territories during the five days before laying by their mates.

Fig. 5. Proportion of each hour spent by promiscuous females (n = 6) performing active EP courtship, during the five days before laying.

Table 1. Frequency of intervals with intra-pair courtships by threatened females responding to the EP courtships of the social mate. Median (minimum; maximum). P values are from Wilcoxon tests, two tailed.

	IP courtships				
EP courtship	**Before**	**After**	**n**	**T**	**P**
Simply received	1.0 (0.0; 3.0)	1.0 (0.0; 5.0)	5	4.0	0.87
Non-reciprocal	2.0 (0.0; 9.0)	1 0 (0.0; 20.0)	15	12.5	**0.03**
Reciprocal	1.0 (0.0; 10.0)	4.5 (0.0; 15.0)	10	1.5	**0.02**

Table 2. Frequency of intervals with IP courtships by threatened males responding to the EP courtships of the social mate. Median (minimum; maximum). P values are from Wilcoxon tests, two tailed.

	IP courtships				
EP courtship	**Before**	**After**	**n**	**T**	**P**
Simply received	2.5 (0.0; 21.0)	3.5 (0.0; 35.0)	10	1.0	0.06
Non-reciprocal	2.5 (0.0; 12.0)	3.0 (1.0; 21.0)	6	5.0	0.31
Reciprocal	1.0 (0.0; 4.0)	4.0 (0.0; 9.0)	7	2.5	**0.05**

Table 3. Proportion of responses by threatened females to EP courtship events of their social mates. Median (minimum; maximum). All 18 females had unfaithful mates.

EP activity of males	Approach	Aggression	n	T	P
Simply received	0.0 (0.0; 0.4)	0.0 (0.0; 0.0)	5	-	-
Non-reciprocal	0.1 (0.0; 0.3)	0.0 (0.0; 0.3)	15	36.0	0.13
Reciprocal	0.2 (0.0; 1.0)	0.1 (0.0; 0.6)	10	20.0	0.06

Table 4. Proportion of responses by threatened males to EP courtship events of their social mates. Median (minimum; maximum). Ten males had unfaithful social mates.

EP activity of female	Approach	Aggression	n	T	P
Simply received	0.2 (0.0; 1.0)	0.1 (0.0; 1.0)	10	18.0	0.16
Non-reciprocal	0.1 (0.0; 0.8)	0.0 (0.0; 0.4)	6	6.0	0.25
Reciprocal	0.2 (0.0; 1.0)	0.5 (0.0; 1.0)	7	6.0	0.81

Table 5. Proportion of 5-min intervals with male EP activity in presence or absence of the threatened female mate. EP courtship divided into three categories: simply received, non-reciprocal and reciprocal courtship. Median (minimum; maximum). P values are from Wilcoxon tests, two tailed.

	Attendance of threatened female				
EP activity	**Present**	**Absent**	**n**	**T**	**P**
Simply received	0.0 (0.0; 0.0)	0.0 (0.0; 0.0)	7	3.5	0.08
Non-reciprocal	0.0 (0.0; 0.1)	0.1 (0.0; 0.4)	18	5.0	**< 0.0001**
Reciprocal	0.0 (0.0; 0.1)	0.0 (0.0; 0.2)	14	9.0	**< 0.01**
Copulations	0.0 (0.0; 0.0)	0.0 (0.0; 0.0)	9	9.0	0.13

Table 6. Proportion of 5-min intervals with female EP activity in presence or absence of the threatened male mate. EP courtship divided into three categories: simply received, non-reciprocal and reciprocal courtship. Median (minimum; maximum). P values are from Wilcoxon tests, two tailed.

	Attendance of threatened male				
EP activity	**Present**	**Absent**	**n**	**T**	**P**
Simply received	0.0 (0.0; 0.1)	0.0 (0.0; 0.3)	13	11.0	**0.01**
Non-reciprocal	0.0 (0.0; 0.0)	0.0 (0.0; 0.2)	7	1.0	**0.03**
Reciprocal	0.0 (0.0; 0.0)	0.0 (0.0; 0.2)	7	3.0	0.08
Copulations	0.0 (0.0; 0.0)	0.0 (0.0; 0.1)	5	1.0	0.12

Table 7. Significant results (*, $p < 0.05$) supporting predictions of hypotheses 1, 2 and 3. O refers to a difference in the opposite direction than the expected. Actv. = activity, cuck = cuckolded, court. = courtship, ind. = individual, NR = not relevant). Active EP courtship = non-reciprocal plus reciprocal courtship.

Hypotheses & predictions	EP activity	Males	Females
1. Tactics for mate guarding	----------	-------	---------
a) overlapping time, cuck. > non-cuck.	NR		
b) 1st departures, social mate < rival	NR		
c) more IP courtship	simply received		
after EP courtship by the social mate	non-reciprocal		*
	reciprocal	*	*
d) equal responses (approach and	simply received		
aggression) to social mate's	non-reciprocal		
EP courtship on vs. off the territory	reciprocal		* more resp. off terr.
2. Effects of mate guarding	----------	-------	---------
a) less EP activity in social mate's	simply received		*
presence	non-reciprocal	*	*
	reciprocal	*	
	EP copulations		
b) less EP actv. when social mate is	active EP courtship		
performing IP actv.	EP copulations		
c) increase in EP court. as time passes after	active EP courtship	* **O**	* **O**
IP court. by social mate			
d) less EP court. after response by mate	active EP courtship	* **O**	
3. Avoiding mate guarding	----------	-------	---------
a) different attendance if promiscuous	NR		*
b) promiscuous ind. overlap less with mate	NR		
c) EP actv. farther when mate is present	EP copulation		
	active EP courtship	*	
d) less EP actv. inside the	EP copulations	*	
territory when mate is present	active EP courtship	*	

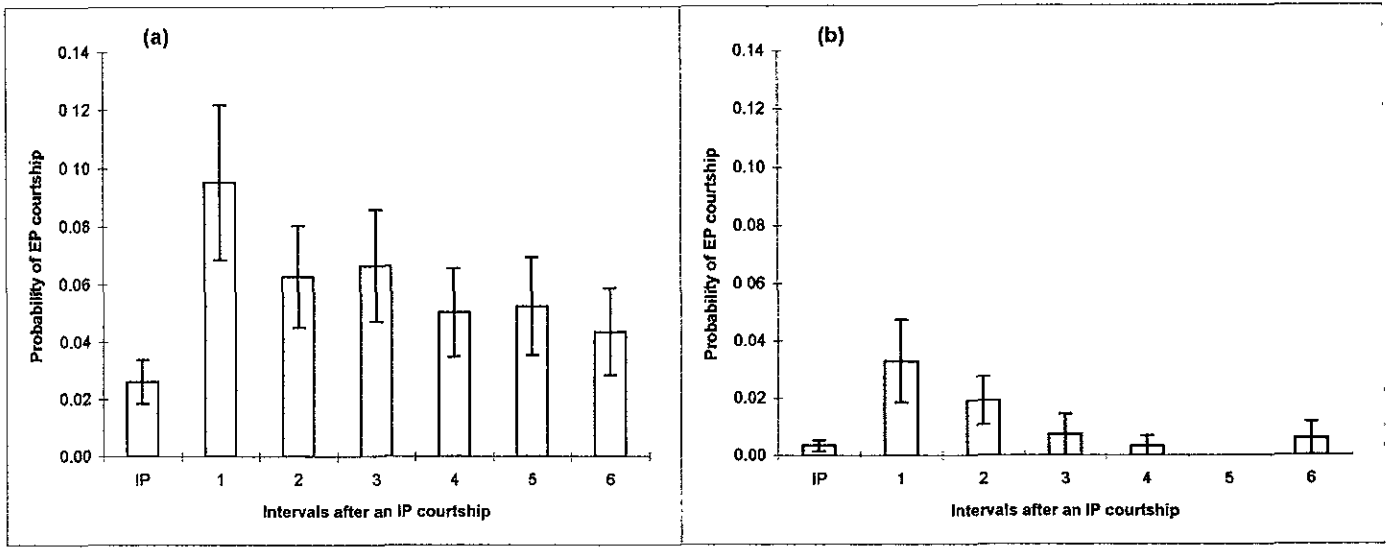

Fig. 1 Probability of (a) males (n = 12) and (b) females (n =5) performing active extra-pair courtship following active intra-pair courtship by the social mate IP = the 5-min interval with intra-pair courtship by the social mate

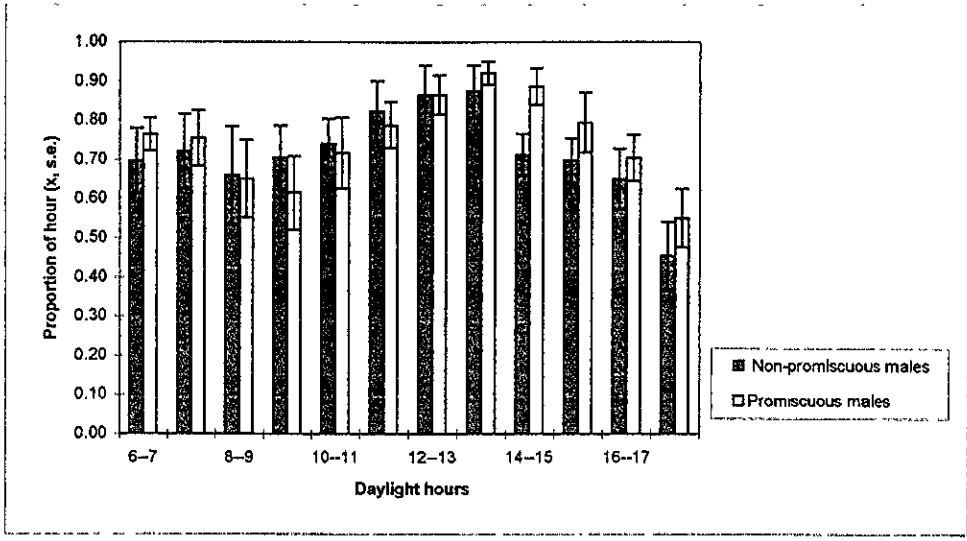

Fig. 2. Proportion of each hour that promiscuous (n =11) and non-promiscuous males (n = 7) spent at or near their territories during the five days before laying by their mates.

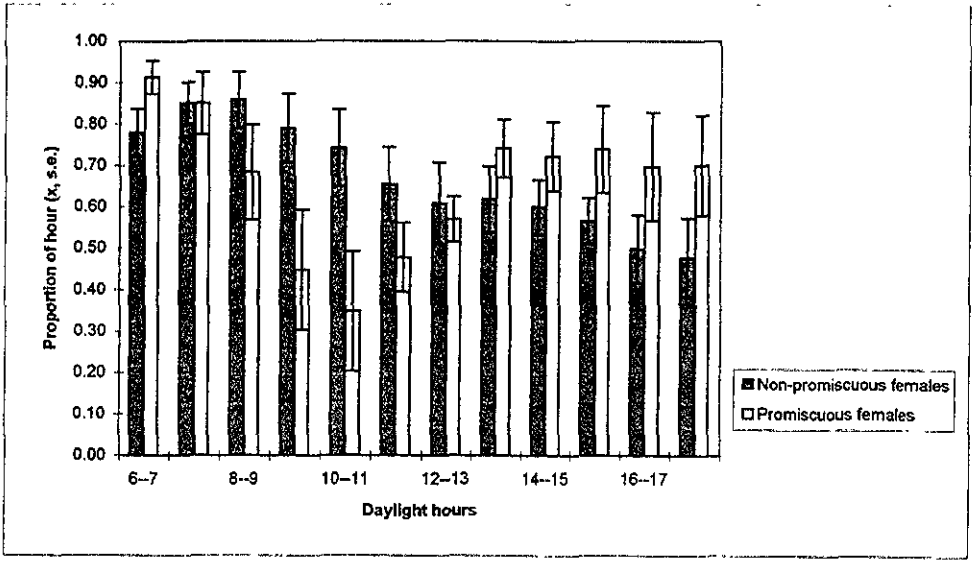

Fig. 3 Proportion of each hour that promiscuous (n = 6) and non-promiscuous females (n = 12) spent at or near their territories during the five days before laying.

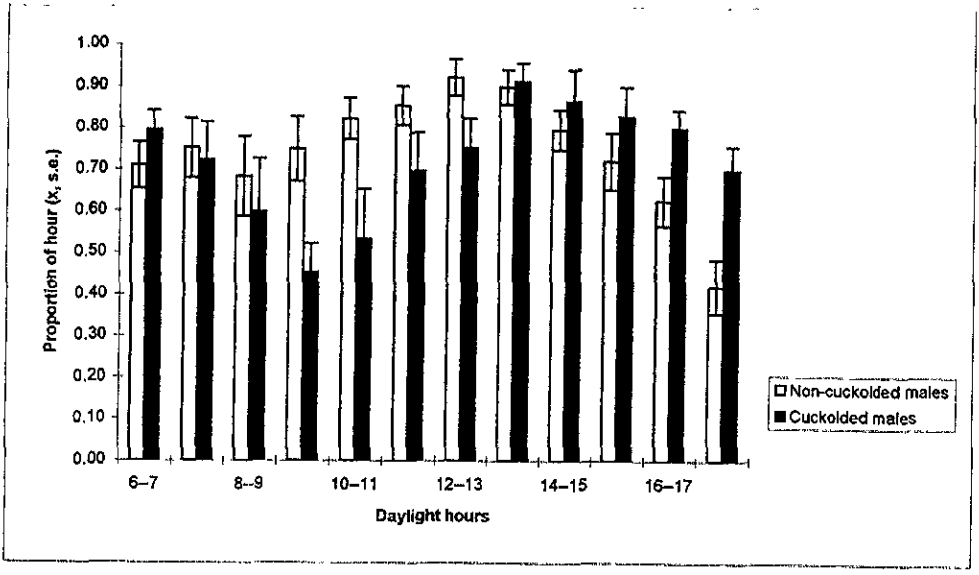

Fig. 4. Proportion of each hour spent by cuckolded (n = 6) and non-cuckolded males (n = 12) at or near their territories during the five days before laying by their mates.

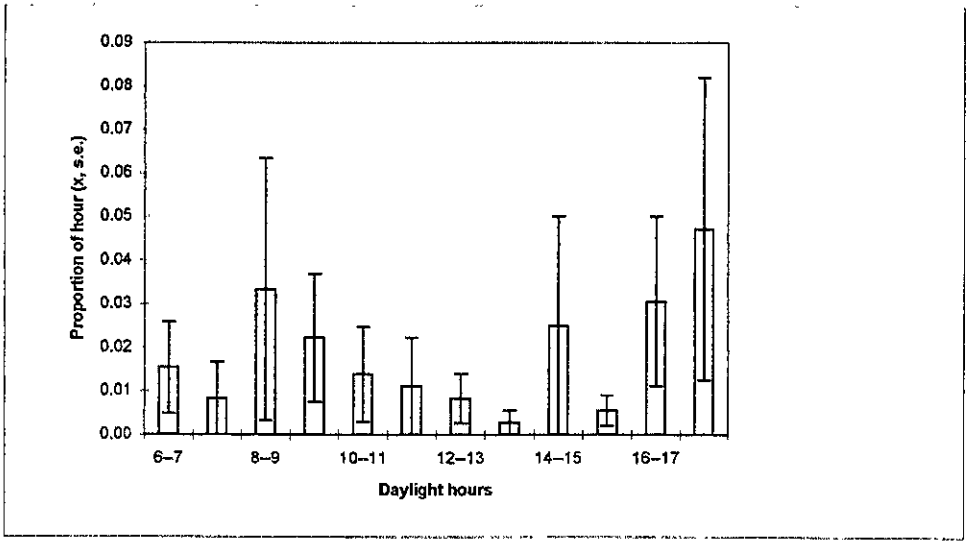

Fig. 5. Proportion of each hour spent by promiscuous females (n = 6) performing active extra-pair courtship (non-reciprocal and reciprocal) during the five days before laying.

Appendix A. Social pairs observed during the 1997 reproductive season (January-April) at Isabel Island, Nayarit Mexico. (*) Individuals were promiscuous before acquiring social mate, or after partnership dissolved. (*[2]) Ex –social partner was male C822.

Male Social mate	Female Social mate	Male's extra-pair mate(1)	Female's extra-pair mate (2)	Extra-pair mate (1) has partner and territory?	Extra-pair mate (2) has partner and territory?
B883	E297	NO BAND	C477	UNKOWN	YES
B886	E271	C168	NO	BRIEFLY	----------
C781	A271	C168	NO*	BRIEFLY	----------
B821	E238	NO	NO	----------	----------
C486	E549	NO*	NO	----------	----------
C536	B877	NO	NO	----------	----------
B923	C525	B835	NO	YES	----------
C822	E103	B468	NO	TERRITORY ONLY*[2]	----------
A270	A696	B497	NO	NO	----------
B231	B941	B497	NO	NO	----------
BRB	E371	NO	NO	----------	----------
C845	NO BAND (spots)	E237*	NO BAND (male 1)	YES	TERRITORY ONLY
NO BAND (male 3)	E237	NO	NO*	----------	----------
E381	F078	F147	NO BAND	TERRITORY ONLY	UNKOWN
G040	B856	E237	Male 1, E429	YES	TERRITORY ONLY
C877	B669	NO	NO	----------	----------
NO BAND (male 1)	NO BAND (eye)	NO*	E429, C845, A650, NO BAND	----------	E429= Territory; C845=Territory, had ex–social partner; A650=Territory and partner; No band=unkown
A650	B665	NO BAND (eye)	NO BAND (male 1)	YES	Male 1= Territory, had ex-social partner

Appendix B. Social partners not used for analyses (see observations).

Male Social mate	Female Social mate	Male's extra-pair mate(1)	Female's extra-pair mate (2)	Extra-pair mate (1) has partner and territory?	Extra-pair mate (2) has partner and territory?	Observations
E269	C230	NO	NO	---------	---------	Methods changed
B025	B749	NO	NO	---------	---------	Partnership dissolved
C974	B835	NO	B923	---------	YES	Partnership dissolved
E266	B875	NO	NO	---------	---------	Apparently they were 2 males
C572	C568	NO	NO	---------	---------	Observations interrupted
B093	A600	NO	NO	---------	---------	No copulations. Observations interrupted
B855	E262	NO	NO			Observed 4 days