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Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*

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Female ornaments are expected to evolve through sexual selection when male parental investment is high. Blue-footed boobies are socially monogamous seabirds with a long period of biparental care. Males and females have colourful feet that are displayed ostentatiously during courtship, both before and after pairing, and extrapair copulations are frequent. We manipulated the foot colour of paired females to test whether this trait influences male courting behaviour, used here as an index of male preferences. There were no differences in time spent at the courting site, frequency of female courtship or frequency of copulations of 11 control and 15 experimental pairs. Experimental females, which had duller feet, received less intra- and extrapair courtship, suggesting that foot colour influences female attractiveness and opportunities for extrapair interactions. Our results support the idea that female foot colour in the blue-footed booby is favoured by sexual selection through male preference.

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In many animal species, males have elaborate ornaments as a result of sexual selection (reviewed in Andersson 1994). However, the reasons why females of some species express similar extravagant ornamental structures or colours are poorly documented (Amundsen 2000; Bounduriansky 2001). Female ornaments have been considered as selectively neutral or even detrimental, resulting from a genetic correlation between the sexes leading to the expression in females of traits selected for in males (Lande 1980; Muma & Weatherhead 1989; Hill 1993; Cuervo et al. 1996; Tella et al. 1997). Instead, female ornaments can themselves be promoted by selection, either through female–female competition or male mate choice (Darwin 1871; West-Eberhard 1983; Johnstone et al. 1996; Jones & Hunter 1999; Amundsen 2000). Female ornaments may indicate reproductive or genetic quality, and hence be preferred by choosy males (Jones & Montgomerie 1992; Johnsen et al. 1996; Potti & Merino 1996; Linville et al. 1998; Roulin et al. 2000, 2001; Domb & Pagel 2001; Velando et al. 2001; but see Hill 1993; Tella

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et al. 1997). Recent comparative and experimental studies on birds suggest that female ornaments are favoured by male choice (Jones & Hunter 1993, 1999; Irwin 1994; Amundsen et al. 1997; Hunt et al. 1999; Roulin 1999; Arnold et al. 2002), although other studies have failed to demonstrate male choice for female ornaments (Muma & Weatherhead 1989; Dale & Slagsvold 1994; Cuervo et al. 1996).

Female ornaments and male mate choice are expected to evolve when mating is costly to males (e.g. energy and time spent on the sexual behaviour, increased risk of disease and parasite transmission), when female quality (or fertility) is highly variable, and when males provide a substantial amount of parental care to the offspring (Trivers 1972; Johnstone et al. 1996; Cunningham & Birkhead 1998; Wachtmeister 2001). Accordingly, in socially monogamous species where males provide a large amount of parental care, female ornaments are common. An experimental study in the crested auklet, *Aethia cristalleta*, a socially monogamous seabird with monomorphic ornaments and biparental care, showed that in both sexes there is a preference for models with enlarged crests (Jones & Hunter 1993, 1999). Hence, similar preferences for ornaments in both sexes and similar competition within each sex can explain ornament monomorphism in some bird species (Jones & Hunter 1999).

In many socially monogamous birds, ornaments are displayed before and after pairing, but their function during this last stage is poorly understood. In monogamous species, partners may evaluate each other's quality continually (de Lope & Møller 1993; Moreno et al. 1994), and sexual signals could influence both male and female decisions such as whether to divorce or to stay with the same partner, or how much to invest in reproduction (Black 1996; Cunningham & Russell 2000; Saino et al. 2002). In the barn owl, *Tyto alba*, male contribution to parental care decreased when female plumage spottiness was experimentally reduced after mating (Roulin 1999), suggesting that males adjust their parental investment according to female attractiveness. More experiments are required to test whether male motivation and behaviour after pair formation are influenced by female traits.

After pairing, ornaments may also attract extrapair mates, and thereby function in a mixed reproductive strategy. In many monogamous species, females are able to adjust their initial mate choice with extrapair copulations (Kempenaers et al. 1997; Michl et al. 2002). By choosing between males, females can gain proximate benefits, such as fertility assurance or food resources, and genetic benefits (reviewed in Jennions & Petrie 2000). A female's choice of extrapair matings will be limited by the cost of searching and the number and quality of males courting her (Janetos 1980; Real 1990). In general, costs to males of extrapair matings are expected to be low; nevertheless, males may be selective when the costs of extrapair copulations increase, for instance when frequent copulations make the male temporarily infertile or when the risk of parasite transmission is high (Birkhead 1991; Birkhead & Møller 1992). As far as we know, there are no studies on the role of avian female ornaments in attracting extrapair mates.

In the blue-footed booby, both females and males have conspicuous and variably coloured feet that are exhibited prominently during pair courtship (Nelson 1978). In an experimental study, we showed that the foot colour of males influences the frequency of pair copulations (Torres & Velando 2003). Here, we investigated the function of female foot colour after pairing. By manipulating female foot colour, we tested whether this trait influences the sexual behaviour of the mate and the sexual behaviour and attraction of extrapair males. In this species, males provide a large amount of parental care (Anderson & Ricklefs 1992; Guerra & Drummond 1995), and their contribution influences the female's investment (Velando & Alonso-Alvarez 2003). Blue-footed boobies are socially monogamous, but extrapair copulations are frequent: 53% of paired females engage in them (Osorio-Beristain & Drummond 1998).

METHODS

We carried out the study in the blue-footed booby colony at Isla Isabel, Nayarit, México from January to February 2003. Both members of 43 pairs were captured by night-lighting (i.e. directing a light to the bird's eyes and catching hold of the bird) and randomly assigned to the experimental or control treatments. Each bird received a numbered metal leg band and a number on the bill, applied using an indelible black marker. Pairs were captured during 3 nights between 23 January and 2 February at three sites of similar densities in the colony. We considered two birds to be a pair when at capture they were standing 20 cm or less from each other and 2 days later they were courting for more than 2 h. Before the experimental manipulation, we measured the colour of the left foot of females using a colorimeter with CIELAB parameters (MINOLTA CR-200, Minolta Co. Ltd., Osaka, Japan). We used the L*a*b* colour space, where L* indicates how bright a colour is (hereafter brightness), and a* and b* indicate the chromaticity coordinates. The saturation of the colour given by the coordinates a* and b* increases as the absolute values of a* and b* increase.
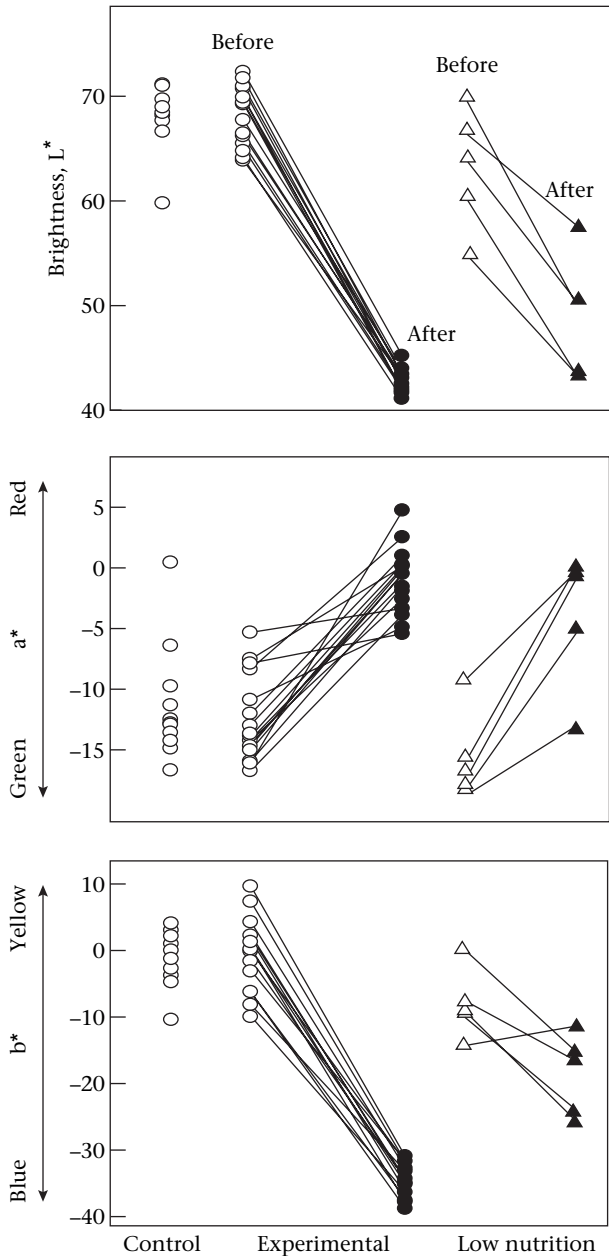
Experimental Manipulation

We modified the foot colour of experimental females with a nontoxic and water-resistant blue intensive make-up (Laukrom, Laurendor S. A., Barcelona, Spain) which was homogeneously applied over the dorsal interdactylar membranes of both feet. The feet of control females were sham coloured using a crayon in a plastic bag to imitate the manipulation and the handling time of experimental females. We applied a few blue marks to feathers on the lower belly of control females, to imitate the accidental staining of experimental females through contact of their feet on their bellies. The resulting foot colour of experimental females was measured immediately after the manipulation. For comparative purposes, the foot colour of five males in low nutritional state after they were food deprived for 48 h is reported here (Fig. 1). These males were used in a different experiment carried out during the courtship stage in the same colony during 2003. Foot colour of males and females naturally changes by similar amounts from courtship to the rearing period (I. Espinosa, unpublished data); hence, we have no reason to expect that female foot colour would respond differently to that of males in the same food deprivation treatment.

In the present study, the foot colour of control and experimental females before the manipulation did not differ (t tests: L*: $t_{24} = 0.35$, $P = 0.73$; a*: $t_{24} = 0.13$, $P = 0.90$; b*: $t_{24} = 0.32$, $P = 0.75$; Fig. 1). The experimental manipulation changed all the foot colour parameters of females (paired t tests: L*: $t_{14} = 38.57$, $P < 0.001$; a*: $t_{14} = 8.85$, $P < 0.001$; b*: $t_{14} = 28.28$, $P < 0.001$; Fig. 1). The modified foot colour of experimental females resembled in brightness and in the chroma parameter a* (green saturation) that of birds in low nutritional state (L*: $t_{18} = 2.31$, $P = 0.082$; a*: $t_{18} = 1.68$, $P = 0.1$; Fig. 1); the manipulation also increased the blue saturation (chroma parameter b*) in the same direction as that of undernourished birds, but with higher values (b*: $t_{18} = 8.91$, $P = 0.001$; Fig. 1).

Behavioural Observations

Two days after the manipulation we observed each pair continuously from 0645 to 1130 hours and from 1500 to

Figure 1. Foot colour of control ($N = 11$) and experimental ($N = 15$) females before and after the colour manipulation. The foot colours of five males in low nutritional state before and after food deprivation are also shown (see text). CIELAB colour parameters are reported: brightness (L*) and chromaticity parameters (a*, from green to red, and b*, from blue to yellow).

1800 hours, the periods of greatest courtship activity. Each of four observers, in hides, observed two to five focal pairs simultaneously, recording the frequency of courtship displays and copulations and noting whether they were performed within the pair or with another bird. From the 43 pairs that were manipulated, 26 pairs (15 experimental and 11 control) were observed; 17 pairs were not observed because they were out of sight from the hides. In the case of extrapair activity we recorded only displays performed or received by the focal female. Every 15 min, the presence of each of the focal birds in the observation

area was also recorded. The courtship displays recorded were sky-pointing (when the bird's neck was lengthening with the bill pointing skywards, accompanied by elevation of the tail and lateral spreading of the wings), parading (when the bird performed an exaggerated foot-raising, flaunting the webs upwards and outwards), and ritualized nest material presentation (when the bird picked up a fragment of any type of material and with an upward movement of the head in a smooth high arc deposited it near the feet of the courting bird; Nelson 1978). Copulations were recorded whenever the two birds' cloacae came into contact or when the male stood on a female's back and made tail movements typical of copulation (Osorio-Beristain & Drummond 1998).

Statistical Analysis

The foot colour, time spent at the courting site and courtship displays of control and experimental birds were compared using t tests, or Mann–Whitney U tests when the samples were not normally distributed. The confidence intervals of effect sizes are reported (Colegrave & Ruxton 2003). We analysed the rates of within-pair sky-pointings, parading and nest material presentation performed by males and females, and the total courtship a focal female received (all behavioural categories of within and extrapair pooled) over the total time (h) a pair was at the courtship site. The proportion of females that received extrapair courtship was analysed using a logistic regression with treatment as a factor and the total time females spent in the courting site as a covariate. Correlations between rates of courtship displays and copulations were evaluated with Spearman rank correlation tests. Means $\pm$ SE are reported throughout. All statistical analyses were two tailed.

Ethical Note

The birds were captured and manipulated at night to reduce perturbation. Handling time per bird was less than 5 min. The artificial colour on experimental females lasted for 5–6 days and the number painted on the bill disappeared in 3 days. Neither of these manipulations caused irritation or other detectable harm. The method of colour modification has been used before on this species with no negative effects on the birds (Torres & Velando 2003). In the food-controlled experiment reported here for methodological purposes, the birds were kept individually confined in cages (31×48 cm and 30 cm high) that were placed in the forest away from heat and noise stress. This method has been used before without any adverse effects on the birds (Osorio-Beristain & Drummond 2001). The duration of the food deprivation treatment (48 h) is within the natural range that blue-footed boobies can go without any food or water; during incubation, a male's shifts can last up to 75 h (Nelson 1978). Males on the food-deprived treatment lost on average $11 \pm 0.47\%$, (range 10–11%) of their original mass. After the 48 h of food deprivation the birds were fed, every 12 h for 36 h,

Table 1. Mean rates (behaviour/h $\pm$ SE) of intrapair courtship behaviour by females and males of 15 experimental and 11 control pairs

Behaviour	Experimental	Control	t or U^*	P	Confidence interval for effect size
Female					
Nest material presentation	0.41 ± 0.13	0.43 ± 0.13	0.10	0.91	-0.64–0.36
Sky-pointing	1.51 ± 0.38	2.31 ± 0.58	1.18	0.24	-2.18–0.59
Parading	0.31 ± 0.12	0.42 ± 0.23	0.18^*	0.85	-0.61–0.38
Male					
Nest material presentation	1.75 ± 0.44	3.56 ± 0.51	2.68	0.013	0.41–3.20
Sky-pointing	5.75 ± 0.90	8.09 ± 1.33	1.50	0.14	-5.84–0.87
Parading	1.46 ± 0.42	1.34 ± 0.23	0.22	0.82	-0.99–1.23

*Mann–Whitney test.

with fresh fish until they partially recovered their original mass. Before release, experimental males were on average $5.4 \pm 2.1\%$, (range 1–7%) below their initial mass. Although we did not search systematically, two of the five males used in this experiment were later seen in the colony. Permission to conduct the study was granted by the Parque Nacional Isla Isabel and the Secretaria de Medio Ambiente y Recursos Naturales.

RESULTS

The time spent at the courtship site by control and experimental pairs, females alone, and males alone did not differ (pairs: $t_{24} = 0.18$, $P = 0.85$; males alone: $t_{24} = 0.03$, $P = 0.97$; females alone: $t_{24} = 0.72$, $P = 0.48$). Overall, control and experimental females performed similar rates of intrapair courtship displays (Table 1). Females in our study were not very willing to initiate extrapair behaviour; only one sky-pointing and one nest material presentation, by two control females, were recorded.

Males in the experimental group performed less intrapair behaviour than males in the control group. The rate of nest material presentation by experimental males was 51% lower than that of control males (Table 1). The rate of nest material presentation by males was correlated with total intrapair courtship by females (Pearson correlation: $r_{25} = 0.57$, $P = 0.002$), but even after we controlled for female courtship the effect of the experimental manipulation on rate of nest material presentation remained significant (ANCOVA: $F_{1,24} = 4.91$, $P = 0.037$). The rate of sky-pointings by experimental males was lower (29%) than that by control males, but not significantly so (Table 1). No differences were found in the rate of parading between experimental and control males (Table 1).

Compared with experimental females, more control females received extrapair courtship (Fig. 2a). Overall, the probability of receiving extrapair courtship was related to the total time females spent in the courting site ($\chi_1^2 = 5.22$, $P = 0.022$); however, after we controlled for the time females spent in the courting site, control females were 5.4 times more likely than experimental females to receive extrapair courtship ($\chi_1^2 = 6.43$, $P = 0.011$; Fig. 2a). Furthermore, experimental females received 38% less courtship (total extra- and intrapair courtship pooled) than control females ($t_{24} = 2.28$, $P = 0.032$; Fig. 2b).

The frequency of intrapair copulations was not affected by the treatment ($t_{24} = 1.08$, $P = 0.28$). Intrapair copulations were correlated with total female courtship (Spearman rank correlation: $r_S = 0.47$, $N = 26$, $P = 0.01$; Fig. 3), but even after we controlled for female courtship,
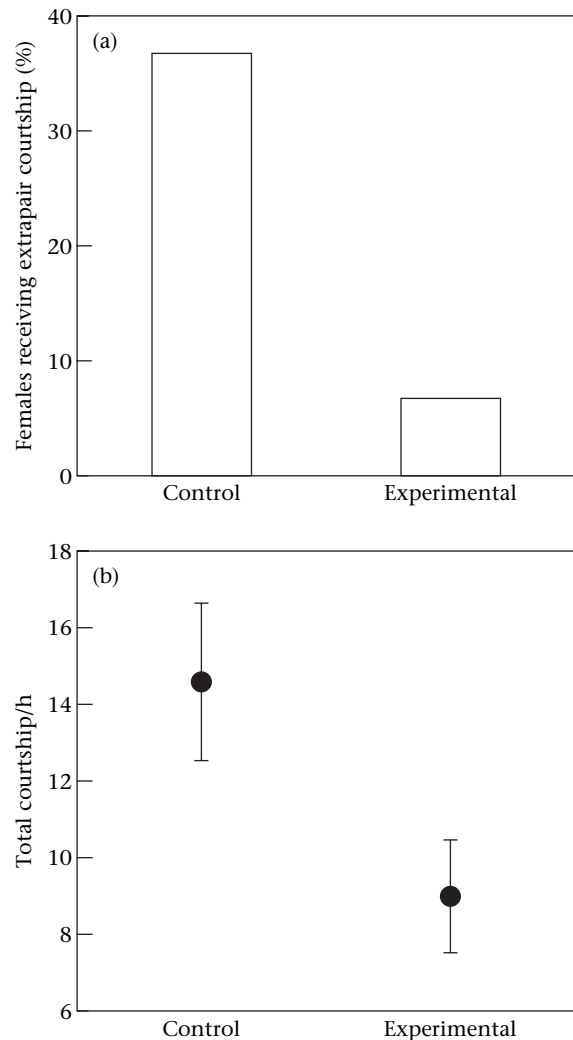
Figure 2. Courtship behaviour received by control and experimental females. (a) Percentage of females that received extrapair courtship. (b) Rates of total courtship (intrapair and extrapair pooled) received by females.
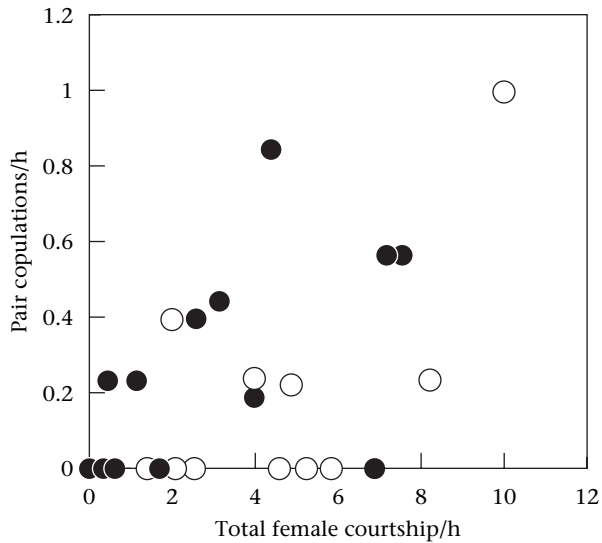
Figure 3. Rates of intrapair copulations of experimental (●) and control (○) pairs and total female courtship. $N = 26$ females. Two data points represent two females per point.

the effect of the experimental manipulation on the frequency of copulations was not significant (ANCOVA: $F_{1,25} = 2.02$, $P = 0.17$). The frequency of intrapair copulations was correlated with male behavioural rates, but significantly so only for the nest material presentation display (Spearman rank correlation: nest material presentation: $r_S = 0.46$, $P = 0.01$; parading: $r_S = 0.34$, $P = 0.08$; sky-pointing: $r_S = 0.27$; $P = 0.16$; $N = 26$ in all cases). No extrapair copulations were recorded.

DISCUSSION

The results suggest that female foot colour plays an important role after pairing in the blue-footed booby. The frequency of intrapair courtship by paired males was affected by the foot colour of females. We did not detect any difference in the amount of courtship or in the frequency of copulations of control and experimental females, nor did we find differences in the time that control and experimental pairs spent in the courting site. However, experimental males performed fewer nest material presentations than control males, although they not differ in the frequency of sky-pointings and paradings displayed. Sky-pointing and parading are frequently performed at the time of pair formation and according to context they may attract individuals of the opposite sex, increase short-term coordination of sexual activity, or entice the mate to a particular site in the territory (Nelson 1978). Nest material presentation, on the other hand, occurs more frequently after pair formation than before the pair is established (Nelson 1978), and in our study it was the only display significantly associated with the occurrence of intrapair copulation; but we have no information about the relation between male nest presentation rate and male parental investment. A negative response to mates with duller feet suggests that males continually assess the attractiveness of their mates, and

may change their initial mate choice. Male blue-footed boobies could also adjust their parental investment to the magnitude of female ornaments, as has been shown in other species (Roulin 1999).

An alternative explanation may be that males reduced their courtship rate to females with duller feet because they did not recognize them (Whitfield 1986). Many bird species have ultraviolet (UV) vision and increasing evidence suggests that UV colour is an important component of a signalling system for mate choice (e.g. Andersson & Amundsen 1997; Siitari et al. 2002). Our manipulation, besides modifying the colour in our visual spectral range (400–700 nm), may also have produced females with an unnatural appearance by changing the colour in the UV range, a part of the spectra we did not measure. No data are yet available to discuss this possibility. However, females with duller feet received less intra- and extrapair courtship, which is consistent with the hypothesis that foot colour plays a role in mate assessment and probably in mate choice.

In a previous study where the colour of male feet was manipulated, blue-footed booby females mated to males with duller feet decreased their courtship (sky-pointings and nest material presentation pooled), suggesting that male foot colour is important in the courting motivation of females (Torres & Velando 2003). Hence, foot colour in the blue-footed booby seems to be important for partner assessment in both sexes. Mutual sexual selection is expected in seabirds because the parental roles of males and females are similar (Johnstone et al. 1996; Jones & Hunter 1999), and many seabird species have sexually monomorphic ornaments which are used by both sexes in courtship displays (e.g. Velando et al. 2001). Few experimental studies have investigated the function of ornament expression in females of monomorphic bird species. In addition to the blue-footed booby, mutual sexual selection has been experimentally confirmed in two monomorphic species, the crested auklet (Jones & Hunter 1993, 1999) and the budgerigar, *Melopsittacus undulatus* (Arnold et al. 2002).

Males may benefit by mating with females with paler feet if foot colour is a signal of female quality (Velando et al. 2001; Roulin et al. 2003). Condition-dependent traits are important in mate choice (Pryke et al. 2002), and increasing evidence suggests that dynamic traits, those that change very rapidly, are reliable indicators of current condition (Zuk et al. 1990; Lozano 1994; Negro et al. 1998; Hill et al. 1999). Dynamic traits may be particularly important in species with a long period of parental investment, where continual evaluation may allow individuals to adjust their investment. In the blue-footed booby, the colour of the feet is a highly dynamic condition-dependent trait: in a feeding experiment the foot colour of five males kept for 48 h without food changed from an aqua blue, typical of birds during courtship, to a dark/opaque blue (Fig. 1), and then increased near to the original colour when the birds were fed until they recovered their original mass (unpublished data). Hence, our manipulation modified the foot colour of females to a duller/opaque coloration within the natural range which resembled the foot colour of low-condition birds, and accordingly both intra- and extrapair courtship directed to the female decreased. In addition, in

the blue-footed booby, females with paler feet lay larger clutches (I. Espinosa, unpublished data). Hence, male preference for paler feet may be driven by choosing more fecund females in better nutritional condition.

Experimental females were less likely than control females to receive extrapair courtship. Indirect evidence suggests that females copulate with extra males consensually; typically there is precopulatory courtship before an extrapair copulation, and no forced copulations have ever been documented in this species (Osorio-Beristain & Drummond 1998). By attracting extrapair males, females reduce their searching costs and increase their opportunity to exercise choice after pair formation (Janetos 1980; Real 1990). Similarly, females of several species use calls to attract potential mates (e.g. Montgomerie & Thornhill 1989; Langmore et al. 1996; Hoi 1997; Sæther 2002). In our study, experimental females received less total courtship (intra- and extrapair). Hence, females with duller feet are probably losing opportunities for extrapair copulations, and if extrapair mates are higher-quality males, females with duller feet are probably decreasing their reproductive performance. Alternatively, females can seek extrapair copulations to obtain other benefits such as beneficial sexually transmitted microbes, fertility assurance, reduction of harassment from other males, or mate assessment for future mate choice or divorce (Wagner 1991; Heg et al. 1993; Lifjeld 1994; Lovell-Mansbridge & Birkhead 1998; Lombardo et al. 1999). Ornament display after pairing may allow attractive females to adjust their initial choice through extrapair copulations or to gain other direct or indirect benefits. Male boobies may assure their paternity by mate guarding (Osorio-Beristain & Drummond 1998), but data on extrapair paternity in this species are not yet available. If attractive females are more likely to obtain extrapair copulations, males paired with attractive females should guard their mates more closely. Hence, the costs of being paired to an attractive female should be considered in future models of female ornament evolution, particularly in socially monogamous species.

Acknowledgments

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