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ORIGINAL ARTICLE

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A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxii*

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Abstract Bright colours of male birds have often been shown to be the target of sexual selection through female choice, yet few studies have looked at the role of colour expressed after pairing on female motivation and behaviour. Here we analyse the role of an integumentary colour in the spectral range of 400–700 nm, the foot colour in male blue-footed boobies, *Sula nebouxii*, which is prominently displayed during pair courtship. Measurements early in the breeding season showed that foot colour of courting males is pale (high values of brightness) and has an aqua-blue chroma, and females in better body condition were mated to males with brighter feet. We carried out an experimental manipulation which modified the foot colour of males in courtship, making it closer to the foot colour of males in low nutritional state. We found that females paired to experimental males courted less and were less likely to copulate than females in the control group. Male behaviour was apparently unaffected by the manipulation; thus the change in female behaviour can be attributed exclusively to foot colour manipulation. These results strongly support the hypothesis of female preference for an integumentary colour and suggest that this dynamic trait is used as a male ornament after pairing.

Keywords Dynamic traits · Female courtship · Integumentary colour · *Sula nebouxii.*

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Introduction

Since Darwin (1859, 1871), female choice has been considered the major evolutionary force responsible for the elaborate ornaments typically exhibited by males, those with elaborate traits gaining a mating advantage. In this context, bright sexually dimorphic colours in birds have been proposed as recurrent examples of female choice leading to the exaggeration of ordinary traits (e.g. Hill 1990; Andersson 1994; Møller and Birkhead 1994; Smiseth et al. 2001). In recent decades, the benefits gained by females paired with males with conspicuous colours have been the focus of intensive research. Females paired with colourful males may gain either direct benefits such as territorial resources, parental care and the avoidance of infectious diseases (Kirkpatrick and Ryan 1991), or indirect benefits derived from attractive offspring (Fisher 1930), and even enhance the viability of their offspring when selected colours indicate male genetic quality (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Grafen 1990).

In many monogamous birds, however, colourful traits are exhibited after pair formation and their function is not fully understood (Wachtmeister 2001). It has been suggested that colourful signals displayed after pair formation may have evolved to stimulate and motivate the females (Crews 1992), and thereby influence their reproductive decisions. Female motivation could be governed by sensory systems in which the amount of neural stimulation is related to the strength of male traits (Ryan 1994). In socially monogamous species, females may evaluate continuously the quality of their partners (de Lope and Møller 1993; Moreno et al. 1994) using sexual signals such as colour traits, and hence decide whether to stay or divorce, the proportion of offspring that the social mate will sire, or the amount of female reproductive investment (Black 1996; Cunningham and Russell 2000; Michl et al. 2002). The few studies that have manipulated sexual traits after pair formation in monogamous birds suggest that female indeed modify their breeding decisions according with male traits. For example, in zebra finches, *Taeniopygia guttata,* and barn swallows, *Hirundo rustica,* females invested more when the sexual trait of the mate was experimentally increased (Burley 1986; Gil et al. 1999; Saino et al. 2002). In bluethroats, *Lusciania svecica,* males with brighter throat patches had a greater pairing success (Johnsen and Lifjeld 1995). Bluethroat males that were blackened after pairing showed more intense mate-guarding than control males, suggesting that mate-guarding may be adjusted according to the male's sexual attractiveness, which may be assessed through female behaviour such as willingness to copulate (Johnsen and Lifjeld 1995).

In many monogamous birds, particularly among non-passerines, coloration is displayed in integuments such as wattles, caruncles, culmen or legs. The information expressed in integuments probably differs from plumage colours since pigments present in wattles, combs or skin can be mobilised facultatively (Lozano 1994). The colour of fleshy structures may reflect more recent physiological events and have the potential to indicate current physical condition (Zuk et al. 1990; Lozano 1994; Negro et al. 1998). This type of dynamic signals may be accurate indicators of quality because they respond rapidly to changes in condition (Folstad and Karter 1992) and, therefore, provide information useful for mate choice and for the evaluation of the partners quality after pairing. There are few experimental studies of female choice on integumentary colours, most of them in polygynous species and with mixed results. The yellow bill in the mallard, *Anas plattyrhnchos*, the red bill in least auklet, *Aethia pusila*, and the number of red-neck caruncles in wild turkeys, *Meleagris gallopavo,* affect female preference for mates (Jones and Montgomerie 1992; Buchholz 1995; Omland 1996); yet neither the red comb in red jungle fowl, *Gallus gallus*, nor the red wattle in ring-necked pheasants seem to influence female mate choice (Zuk et al. 1992; Mateos and Carranza 1995). Also, probably because of the lack of information on the role of integumentary colours as sexual signals they are often ignored in comparative studies on the evolution of sexual dimorphism in birds (e.g. Read and Harvey 1989; Møller and Birkhead 1994; Owens and Bennett 1994; Martin and Badyaev 1996; Badyaev and Hill 2000; Dunn et al. 2001; Bennett and Owens 2002; but see Johnson 1999). As far as we know, there are no studies of the role of integumentary colours of any bird after pair formation. In this study we investigated female behavioural response after pairing to experimental variation of male foot colour in the blue-footed booby, *Sula nebouxii*, a monogamous long-lived bird.

Blue-footed boobies are socially monogamous with a mixed-reproductive strategy, extra-pair copulations representing 13.3% of copulations by all females (Osorio-Berstain and Drummond 1998). Males have conspicuous and variably coloured feet that are exhibited prominently during pair courtship (Nelson 1978). Blue-footed boobies are dimorphic in the colour of the feet: male feet are brighter and aqua-blue while female feet are less bright and bluish (Stamps and Calderon, unpublished data; Espinosa and Torres, unpublished data). In a parallel study, we have recently found that male and female foot colour varies with reproductive status. After laying, brightness decreases and chroma saturation increases (Espinosa and Torres, unpublished data). We have also found that colour is a highly dynamic signal and its expression changes rapidly with nutritional state (Velando and Torres, unpublished data).

During courtship, males and females exhibit their feet to their partner. Males (especially) land in the territory with spread feet held flung up and in front of their underparts producing a conspicuous contrast between the colour of the foot-web and the white underparts (salute-landing; Nelson 1978). The sexual advertising display is frequently preceded or followed by a parading consisting of an exaggerated foot-raising, flaunting the webs upwards and outwards. It has been suggested that male pair courtship behaviour evolved to show the brightly coloured feet (Nelson 1978). Brilliant coloured feet are present in most of the species of Sulidae, from brilliant colour-lines along the digits to complete brilliant coloured feet. In spite of the fact that ornamental skin is among the most striking features of Sulids, there are no studies on their possible function as signals. In this study we evaluated the role after pairing of foot colour in the blue-footed booby on female motivation to court and copulate. We experimentally modified the foot colour of males in established pairs that were courting and recorded the females' courtship displays after the manipulation to evaluate the role of male colour on female behaviour after pairing.

Methods

Study area and animals

The study was carried out in the blue-footed booby colony at Isla Isabel, Nayarit, México, from January to March 2002. Both members of 30 pairs were captured by night-lighting and randomly assigned to the experimental or control treatments. Each bird was marked with a numbered metal leg-band and a number on the bill with an indelible black marker to facilitate identification during behavioural observations. Pairs were identified as birds that were standing 20 cm or less from each other during capture. Subsequent observations were also made. Pairs were captured during two consecutive nights at the same area to maximise the number of pairs that could be simultaneously observed and to increase the synchrony in reproductive timing among pairs; in the blue-footed booby colony at Isla Isabel there is a greater reproductive synchrony among closer pairs that among distant pairs (personal observation). We measured mass (±5 g) and ulna length (±1 mm) of all captured birds and, prior to the experimental manipulation, the colour of the left and the right feet of males using a colorimeter with CIELAB parameters (MINOLTA CR-200). We used the L^*, a^*, b^* colour space, where L^* indicates brightness, and a^* and b^* indicate the chromaticity co-ordinates. The saturation of the colour given by the co-ordinates a^* and b^* increases as a^* and b^* absolute values increase. All captured birds were monitored every 3 days until they completed a clutch. Twenty-five out of the 30 captured pairs and 13 out of 16 pairs included in the behavioural analyses eventually incubated a clutch.

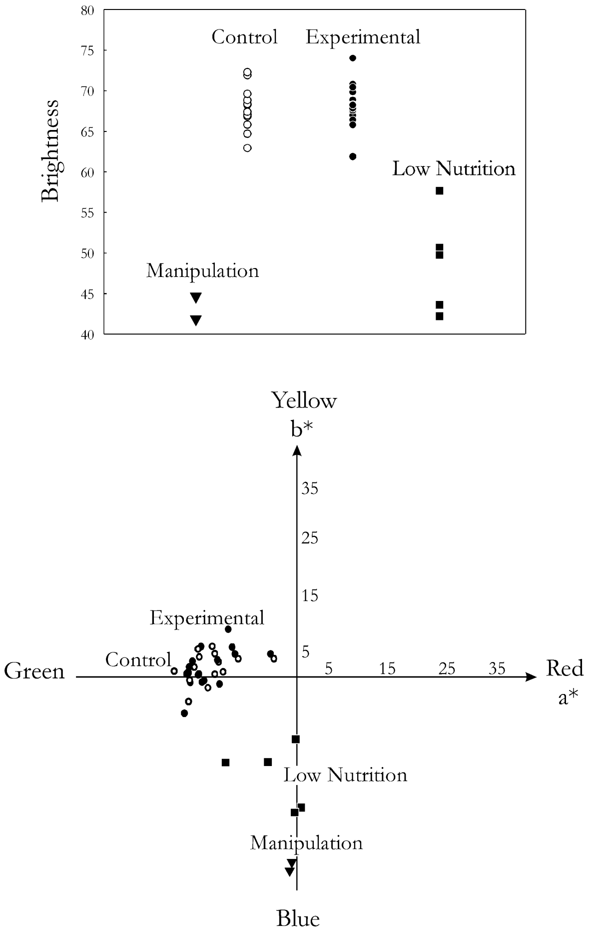

Fig. 1 CIELAB colour parameters of control (n=15) and experimental (n=15) blue-footed booby, *Sula nebouxii,* male feet prior to manipulation. The colour parameters of five males in low nutritional state (see text) and two experimental males after the manipulation are shown. Brightness (parameter L^*) in *upper figure* and chromaticity diagram (parameters a^* and b^*) in *lower figure*. Parameter a^* ranges from green to red and parameter b^* from blue to yellow

Experimental manipulation

Both feet of experimental males were coloured using a non-toxic and water resistant blue intensive make-up (Laukrom). The artificial colour was homogeneously applied over the dorsal interdactilar membranes of both feet. The feet of control males were sham coloured using a crayon in a plastic bag to imitate the manipulation and the handling time of experimental males. A few colouring marks were applied to feathers on the lower belly of control males, to imitate the accidental staining of experimental males through contact of their feet on their bellies. The foot colour of two experimental males after the manipulation was measured to quantify the magnitude of the colour modification. Handling time per bird was less than 5 min and the artificial colour on experimental males lasted for 5–6 days and apparently caused no irritation or other harm.

In addition, the foot colour of five males in low nutritional state captured during courtship is reported here (Fig. 1); these males were used in a different experiment carried out in the same colony during 2003, which involved food deprivation for 48 h (Velando and Torres, unpublished data).

Behavioural observations

Two days after the manipulation we observed each pair from 0700 to 1130 hours and from 1430 to 1800 hours, the periods of greatest courtship activity. Three observers recorded two to five pairs simultaneously. A total of seven experimental and nine control pairs was observed. We recorded the frequency of courtship displays, aggressions and copulations, and the time when a focal bird departed or arrived at the area. For all behaviours we noted whether they were performed within the pair or with an extra bird. Additionally, every 15 min the presence or absence of the focal birds in the observation area was noted. The courtship displays recorded were sky-pointing, when the bird's neck was lengthening with the bill skyward pointing, accompanied by the elevation of the tail and the laterally spreading of the wings; and symbolic nest-building, 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). In the category sky-pointing only high intensity behaviours were considered, but low and medium intensity sky-pointings (when the spreading of the wings was incomplete) were included in the total courtship category (Nelson 1978). Copulations were recorded whenever the two birds' cloacas came into contact or when the male stood on a female's back and made the typical tail movements that occur during copulation (Osorio-Beristain and Drummond 1998).

Statistical analysis

The mean value of the left and the right foot of each bird for the three colour parameters (L^*, a^*, b^*) were used for analyses. Male foot colour and time spent at the courting site by experimental and control birds were compared using t-tests. Female rates of sky-pointings, symbolic nest-building, and total courtship (high, medium and low intensity sky-pointings and symbolic nest-building categories pooled) were analysed using ANCOVAs with treatment as a factor. Because female behaviour can be influenced by the behaviour of the mate (Wingfield et al. 1994; Alonso-Alvarez 2001) and female body condition (Page 1994; Langmore et al. 1996), both of these variables were included as covariates in the analyses. For male courtship behaviour, body condition was not related to any of the variables analysed (sky-pointings by total observation time: $F_{1,14}=0.02$, $P=0.88$; symbolic nest-building by total observation time: $F_{1,14}=0.09$, $P=0.75$; total courtship displays by total observation time: $F_{1,14}=0.002$, $P=0.95$; sky-pointings by pair time: $F_{1,14}=0.94$, $P=0.34$; symbolic nest-building by pair time: $F_{1,14}=3.30$, $P=0.09$; total courtship displays by pair time: $F_{1,14}=2.94$, $P=0.10$), hence comparisons of courtship displays of control and experimental males were performed using t-tests. Both, the rate over the total observation time (min) and over the total time (min) a pair was at the courtship area were analysed.

As an index of body condition we used the residuals from a regression analysis of log body mass on log ulna length (linear regression: $F_{2,38}=140.66$, $P<0.0001$, $R^2_{59}=0.82$, $P<0.001$). Because we did not know the histories of the birds before they were captured only pairs that eventually incubated a clutch together (23 out of 30) were included in the analyses of female body condition and male foot colour.

The proportion of pairs that copulated was analysed using a Generalized Linear Model with binomial error distribution and a logit link function. The model included the total frequency of male courtship and female body condition as covariates.

Mean ± SE are reported throughout. All statistical analyses were two-tailed and the alpha level was set to 0.05.

Results

Before the manipulation, experimental and control males and females did not differ in body condition (t-test: males,

t=0.90, P=0.37, n=29; females, t =0.61, P=0.54, n=30). Also, there were no significant differences in the number of days from capture to laying between control (12.31±2.16 days) and experimental pairs (10.41±2.25 days; Mann-Whitney U-test: U=146.50, n_1=13, n_2=12, P=0.62).

Male foot colour during courtship had high brightness (67.90±0.47) and aqua-blue chroma (a^*, −15.77±0.45; b^* 1.17±0.54; Fig. 1). The manipulation modified the colour of male foot to lower brightness and a saturated blue, a colour similar to that of males with low nutritional state (Fig. 1). Control and experimental males did not differ in any of the colour parameters before the manipulation (L^*: t=0.56, P=0.58; a^*: t=0.10, P=0.92; b^*: t=0.01, P=0.99, n=15 control and 15 experimental males; Fig. 1).

Pair behaviour

Experimental and control pairs did not differ in the amount of time they spent at the courtship site (experimental 229.14±29.22 min, n=7; control 242.33±28.80 min, n=9; t=0.91, P=0.35). Also, the amount of time spent at the courtship site by females alone or males alone did not differ between treatments (female alone: t=0.87, P=0.40; male alone: t=0.58, P=0.57, n=16). Aggressions within the pair occurred in two experimentals and one control.

Male behaviour

Control and experimental males did not differ in the rates of courtship performed. The rates of courtship carried out by control and experimental males did not differ whether the rate of behaviours per total observation time (sky-pointings, t=0.89, P=0.38, Power of test 0.05; symbolic nest-building, t=2.00, P=0.06, Power of test 0.46; total courtship displays, t=1.03, P=0.31, Power of test 0.05) or total pair time were considered (sky-pointings, t=1.12, P=0.28, Power of test 0.07; symbolic nest-building, t=1.27, P=0.22, Power of test 0.11; total courtship displays, t=1.31, P=0.21, Power of test 0.12; for all comparisons n=16).

Female response to colour manipulation

Females in the experimental group performed less courtship behaviour than females in the control group. The mean rate of sky-pointings by observation time of experimental females (0.01±0.007) was 66% lower than that of control females (0.03±0.01; treatment, $F_{1,13}$=5.84, P=0.03, female body condition, $F_{1,13}$=4.09, P=0.06, male behaviour, $F_{1,13}$=0.55, P=0.46; Fig. 2a). Likewise, although non significant, the mean rate of symbolic nest-building was 74% lower in experimental (0.003±0.002) than in control females (0.01±0.005; treatment, $F_{1,13}$=2.54, P=0.13, female body condition, $F_{1,13}$=0.35, P=0.56, male behaviour, $F_{1,13}$=0.15, P=0.69; Fig. 2c).

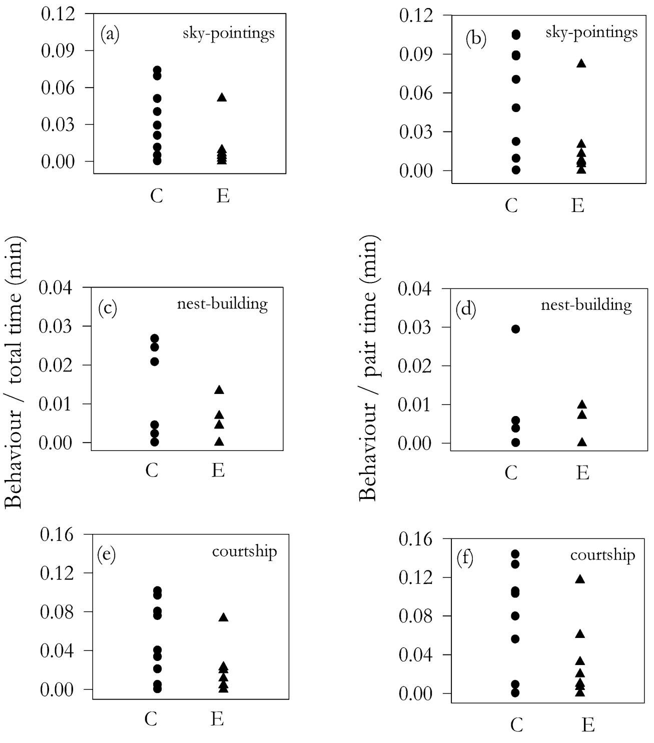

Fig. 2a–f Behavioural response of nine control (C) and seven experimental (E) females to male foot colour manipulation. The rates of sky-pointings, symbolic nest-building and total courtship displays by total observation time (**a–c**) and by the total time a pair was at the courting site (**d–f**) are shown

Overall, experimental females (0.02±0.01) courted at a rate 61% lower than control females (0.05±0.01; treatment, $F_{1,13}$=4.78, P=0.047, female body condition, $F_{1,13}$=3.24, P=0.09, male behaviour, $F_{1,13}$=0.53, P=0.47; Fig. 2e). Female body condition and the behaviour of the male were not significant in any of the comparisons performed. Similar results were found when the rate of displays over the time both members of the pair were present at the courtship site was analysed (sky-pointings: treatment, $F_{1,13}$=5.14, P=0.041, female body condition, $F_{1,13}$=1.08, P=0.31, male behaviour, $F_{1,13}$=0.33, P=0.57, Fig. 2b; symbolic nest-building: treatment, $F_{1,13}$=1.26, P=0.28, female body condition, $F_{1,13}$=0.16, P=0.68, male behaviour, $F_{1,13}$=0.48, P=0.49, Fig. 2d; and total courtship displays: treatment, $F_{1,13}$=4.90, P=0.045, female body condition, $F_{1,13}$=1.16, P=0.29, male behaviour, $F_{1,13}$=0.07, P=0.78, Fig. 2f).

Overall, the probability of copulation was related to the total frequency of male courtship (χ^2=5.78, df=1, P=0.02), but it was not related to female body condition (χ^2=3.34, df=1, P=0.07). Females in the experimental group were less likely to copulate than females in the control group (χ^2=7.07, df=1, P=0.008; Fig. 3). The proportion of experimental females that copulated was 55% lower than the proportion of control females (Fig. 3).

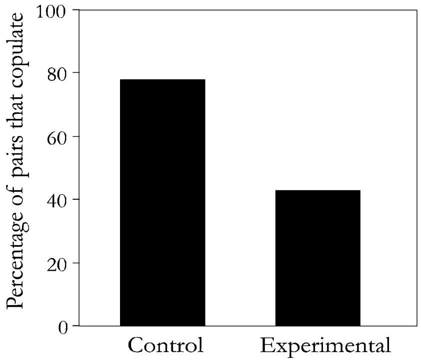

Fig. 3 Percentage of experimental and control pairs that copulated

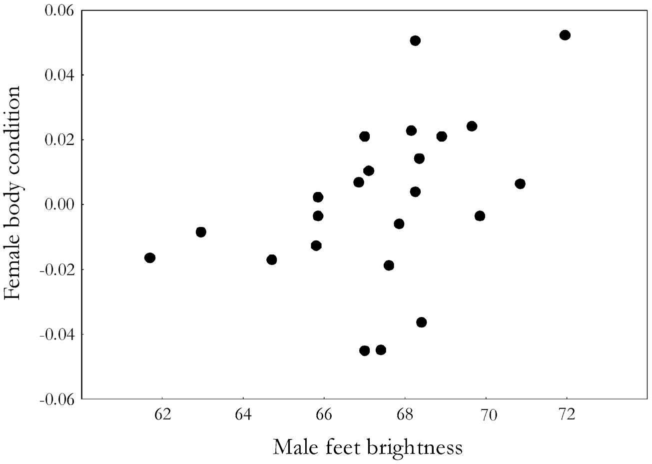

Fig. 4 Female body condition (residuals of log body mass on log ulna length) and male foot brightness measured by CIELAB prior to manipulation

Female body condition and male foot colour

Prior to manipulation female body condition was related to male foot brightness. Males whose feet had greater values of brightness were mated to females in better body condition (linear regression: $F_{1,21}$=4.87, P=0.038, r^2=0.19, n=23; Fig. 4). Chromatic parameters of male foot were not related to the condition of the female (linear regression: a^*, $F_{1,21}$=0.13, P=0.72, r^2=0.006; b^*, $F_{1,21}$=0.91, P=0.35, r^2=0.42, n=23).

Discussion

Our results indicate that male foot colour in the blue-footed booby is important for female motivation to court and to copulate within the pair. Females responded to experimental variation in male foot colour. After controlling for the female condition and the behaviour of the male, experimental females courted less compared to control pairs, particularly decreasing their sky-pointing rate. Individual variation in the rate of courtship behaviour by females in the control group was evident; however, most females in the experimental group (six out of seven) decreased their within pair courtship suggesting that variation in male foot colour had a strong effect on female behaviour (see Fig. 2). The only female in the experimental group that performed relatively high rates of sky-pointings and total courtship was in fact the female closest to laying in our whole sample. A possible confounding variable could be behavioural changes in experimental individuals associated directly to manipulation of their ornaments (Jones and Hunter 1993; Sanz 2001). In our study, males from experimental and control groups did not differ in the rate of their displays, although power of all tests was low (<50%). In addition, the amount of time at the courting site was similar for experimental and control pairs. Hence, on present evidence, the difference in behaviour of experimental and control females was apparently not related to variations in male behaviour or the amount of time the pair was at the courting site. Taken together, the results indicate that females respond negatively to mates with dull feet.

In the blue-footed booby, foot colour is a highly dynamic condition-dependent trait. Foot colour is related to the nutritional state of the individual and varies very rapidly (male foot colour after 48 h of food deprivation in Fig. 1 this study; Velando and Torres, unpublished data). Our colour manipulation simulated males of low nutritional state (Fig. 1), and females paired with males with duller feet reduced their courtship motivation. Hence, female motivation to court apparently depends on the condition of the male, expressed by foot colour.

Contrary to static traits, dynamic traits change very rapidly with ecological, physiological or motivational state having the potential to indicate current physical condition (Zuk et al. 1990; Lozano 1994; Negro et al. 1998; Hill et al. 1999). Because static and dynamic traits indicate different, and maybe complementary, information it is likely that both kinds of traits are been used in some species (e.g. Hill et al. 1999). In the blue-footed booby parental effort is high, both parents incubate and feed the chicks for a long period (up to 145 days; Torres and Drummond 1999; Guerra and Drummond 1995); hence females may benefit by having an extended courtship period to evaluate the current condition of the mate (other non-alternative explanations for extended courtship after pairing are possible; e.g. Wachtmeister 2001). In fact in this species courtship after pairing lasts a relatively long time (up to 40 days; Osorio-Beristain and Drummond 1998). A dynamic trait such as foot colour may play an important role in this extended evaluation allowing blue-footed booby females to adjust their present reproductive effort accordingly.

Females in our experiment were less likely to copulate when mated with males with duller feet. Hence, males with experimentally dull feet may increase their probability to be cuckolded. Although we did not record any copulations with birds other than the social mate, a relatively high occurrence of extra-pair copulations has been reported in this species (Osorio-Beristain and Drummond 1998). Male boobies increase the frequency of copulation and courtship as laying approach, apparently as a male guarding tactic (Osorio-Beristain and Drummond 1998). In many socially monogamous birds, copulation is under female control (Birkhead and Møller 1992; Hunter et al. 1993; Lens et al. 1997; Delehanty et al. 1998), and females are able to adjust their initial mate choice after pairing, particularly those paired with unattractive male (e.g. Kempenaers et al. 1992; Liefjeld et al. 1993; Hasselquist et al. 1996; Michl et al. 2002). Our data show that in the blue-footed boobies female motivation to court and copulate is affected by the partners' foot colour, suggesting that females may be able to adjust their mate choice by reducing intra-pair copulations when mated with unattractive males.

In addition, other female decisions, that we did not test, may be influenced by the mate attractiveness. Particularly in long-lived birds, females should optimise their reproductive decisions after pairing in relation to partner quality and his level of investment (Chase 1980; Houston and Davies 1985; Winkler 1987). Thus, a female paired with a low-quality mate may delay breeding to the next season (Jouventin and Dobson 2002), switch mate (Black 1996), and/or reduce the investment (Gil et al. 1999). In seabirds, there is some evidence that parents are able to exchange information about their current body condition, and adjust their investment accordingly (Tveraa et al. 1997). The results of a brood size manipulation experiment in blue-footed booby suggest that males paired with a female that laid two eggs may allocate more resources to reproduction than males paired with a female that laid one egg (Velando and Alonso-Alvarez 2003). Whether females adjust clutch size to male quality using foot colour as a cue remains an open question. Moreover, foot colour may be also an important trait in mate selection in this species. We did not test this hypothesis. However, prior to the manipulation, male foot colour explained a small (19%) but significant proportion of the variability in female quality in terms of body condition. These data suggest that females in better body condition choose males with brighter feet. Nevertheless foot colour varies very rapidly; hence more data are needed to know whether this trait is important before pair formation.

Many bird species have ultraviolet-sensitive retinal cones and there is increasing evidence that ultraviolet (UV) colour displayed in plumage is important for male attractiveness and possibly for mating success (e.g. Bennett et al. 1996; Andersson and Amundsen 1997; Johnsen et al. 1998; Siitari et al. 2002). We do not know whether UV reflection plays a role as part of a signalling system for mate choice in the blue-footed booby. There is some evidence that Sulids are sensitive to near-UV radiation (Reed 1987). An analysis of behavioural psychophysical responses (visual nystagmus) to different monochromatically illuminations showed a high spectral sensitivity in the near-UV in the Peruvian booby, but a moderate sensitivity in the blue-footed booby, and no response in the red-footed booby, *Sula sula* (Reed 1987). Our experimental manipulation modified the colour in our visual spectral range and probably masked UV reflectance; hence we cannot differentiate the relative importance of these colour components on female courtship behaviour. The role of UV reflectance in intraspecific mate choice and mate assessment in the blue-footed booby needs to be evaluated.

In conclusion, our results show that female decisions after pairing are influenced by male foot colour, a highly condition-dependent dynamic signal. As far as we know this is the first study that evaluates the role of an integument signal after pair formation. More studies on the role that foot colour plays in mate choice or in decisions of parental investment, and which proximal mechanism is responsible for the colour production, are required to understand the evolution of foot colour in the blue-footed booby. The current evidence suggests that colour in integuments, a labile trait, can play an important role as a sexual signal and should be considered in future studies.

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