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Color in a Long-Lived Tropical Seabird: Sexual Selection in a Life-History Context

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I. Introduction

Animals from a wide range of taxa display extravagant traits, such as the striking coloration displayed by some bird species. Darwin initially proposed that the advantages that the bearers of these extravagant traits gained in terms of mating success compensate for their survival cost (Darwin, 1871). Darwin's hypothesis was first validated by two elegant experimental studies conducted in fish. In the jewel fish (*Hemichromis bimaculatus*) red coloration of males was either increased or decreased, and females laid more eggs when closer to brighter colored males (Noble and Curtis, 1936). Similarly, three-spined stickleback females (*Gasterosteus aculeatus*) preferred males with brighter red coloration (Pelkwijk and Tinbergen, 1937). Despite these two demonstrations, the idea that mate choice was a driving force for the evolution of extravagant traits was largely ignored and almost a century had passed before researchers returned to the study of sexual selection (e.g., Burley et al., 1982, 1986; Endler, 1980, 1983; Hill, 1990, 1991; for experimental studies of colorful traits). After mate choice was recognized as one of the main forces for the evolution of secondary sexual traits, a vast body of theoretical and empirical studies has dealt with the information content in ornaments and the benefits of exerting such a choice (Andersson, 1994).

Commonly, males are ornamented, signaling to females, which are the receivers and choosy sex. Males with elaborate traits gain a mating advantage, but understanding why females are choosy is fundamental to understanding the evolution of male sexual traits. One influential model of sexual selection

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theory postulates that ornaments may be honest (i.e., reliable) signals of the phenotypic and/or genotypic quality of individuals (Andersson, 1994). It is believed that ornaments are costly, and these costs of signal production and/or maintenance enforce honesty of signaling (Zahavi, 1975). Therefore, female preference should favor sexual displays that are closely linked to individual condition (Kodric-Brown and Brown, 1984). Condition-dependent models suggest that females paired with colorful males may enhance the viability of their offspring when selected colors indicate male genetic quality (Grafen, 1990; Zahavi, 1975, 1977), or direct benefits (Kirkpatrick and Ryan, 1991; Price et al., 1993) when male color indicates the capacity to acquire nuptial gifts, a good territory or resources for offspring.

In organisms that reproduce several times over their lifespan, an increase in current reproduction should be penalized by a reduced residual reproductive value (Stearns, 1992). In this context, male attractiveness is often subject to life-history trade-offs and indicator mechanisms do not require that ornaments and survival be correlated, only that ornaments be correlated with male quality (Getty, 2006; Kokko et al., 2002). Indeed, in some species high-condition males may invest more in sexual signals, but die younger than low-condition males (e.g., Hunt et al., 2004). In a life-history context, males can adaptively adjust their current investment in sexual signals in response to environment, mate quality and availability, or future reproductive prospects (e.g., Candolin, 2000; Hunt et al., 2004).

Sexual selection includes any selection that arises as a result of variation in the number and/or quality of mates (Fuller et al., 2005). However, in long-lived organisms with prolonged parental care, such as seabirds, sexual selection does not necessarily end after mate choice, since mate quality can vary within a breeding event and may influence the optimal solution of resource allocation to current reproduction. Thus, one might expect that the use of sexual signals after pairing may be favored, as the information conveyed by ornamental traits affects the fitness value of current reproduction. In species with biparental care, sexual signals may strongly affect the negotiation between mates over offspring care (Johnstone and Hinde, 2006; McNamara et al., 1999; Morales et al., 2009a).

Here, we summarize the research on a sexual trait, foot color, in the blue-footed booby, a long-lived bird species with prolonged biparental care. In this species, males and females exhibit colorful foot-web after pairing. Males assist females with caring for nestlings and male condition and contribution to parental care is an important factor for female breeding success (Velando and Alonso-Alvarez, 2003). Therefore, females may adjust investment in response to current mate condition. Interestingly, since pigments present in these fleshy structures should be continuously allocated, sexual selection in a life-history context may shape the investment in coloration not only during a breeding season but also during the lifetime of individuals. In this species, females are also ornamented, but life history trade-offs governing signal expression in females may be significantly different compared with males.

II. Basis of Integumentary Color

A. General Basis of Integumentary Color Production

Among birds, the striking beauty of feathers has long attracted the attention of researchers. Consequently, the mechanisms of color production in feathers are well known. Although less studied, birds of a considerable number of species also display color in the skin, iris, bill, legs, and feet (Auber, 1957; Olson and Owen, 2005; Prum and Torres, 2003), and in some cases this coloration may play a role in social communication (e.g., Burley et al., 1982; Zuk et al., 1990). In bare parts of the body, the production of color may be either pigmentary or structural, or a combination of both (Bagnara et al., 2007; Prum, 2006; Prum and Torres, 2003). Pigmentary colors result from differential absorption and emission of wavelengths of visible light by pigment molecules (e.g., melanins, pteridines, or carotenoids); hence, the color produced by a pigment depends on the molecular structure of the pigment and its concentration (Hill and MacGraw, 2006). On the other hand, structural colors are those that result exclusively from the light interacting with nanometer-scale structures of the dermis (Prum, 2006; Prum and Torres, 2003). In some cases, the arrays of structural colors may include molecular pigments; however, as long as the color that arises depends on the arrays of pigment granules, not from their molecular properties, they produce what are considered structural colors (Prum, 2006). Additionally, skin color may result from the interaction among different components of the multilayered three-dimensional dermal system that often contains multiple pigment types and structural features (Bagnara and Hadley, 1973; Bagnara, et al., 1968; Grether et al., 2004). The interaction among these layers determines the overall reflectance spectrum of skin color, and changes in any one component can alter the resultant color (Grether et al., 2004). For instance, the combination of long-wavelength structural color and pigmentary mechanisms produces yellow and orange skin colors in some avian taxa; apparently, in these cases, the pigments are carotenoids within lipid vacuoles in the uppermost strata of the dermis (Prum and Torres, 2003). Hence, some yellow and orange skin colors in birds result from the interaction between pigments and structural components (Prum, 2006; Prum and Torres, 2003), as in some fishes, reptiles, and amphibians (Bagnara et al., 2007; Grether et al., 2004).

B. Can Avian Blue Integuments Depend on Pigments?

Integumentary blue colors in vertebrates are common and have been thought to be structurally based (Auber, 1957; Bagnara et al., 2007; Prum and Torres, 2003). Bagnara et al. (2007) reviewed the basis of blue color production in vertebrates and concluded that, regardless of Class, and with the exception of a blue pigment found in two species of callionymid fish (Goda and Fujii, 1995), blue is almost always a structural color based mainly on selective light scattering from elements of the animal surface that differ in refractive index. Prum and Torres (2003), in a very elegant work, analyzed the structure of the collagen layer of colored skin from 31 species of birds. Avian tissues were analyzed by transmission electron micrographs and two-dimensional Fourier analysis (Prum and Torres, 2003). This method allowed the theoretical evaluation of whether the biological arrays (the spatial frequency of collagen fibbers) were appropriately nanostructured to produce the observed colors by coherent scattering (Prum and Torres, 2003). Based on their results, the authors concluded that integumentary blue color in birds is structural (Prum and Torres, 2003). However, here we show evidences that, similar to the mechanisms for the production of some integumentary green, yellow, and orange colors (Bagnara et al., 2007; Grether et al., 2004; Prum and Torres, 2003), integumentary blue colors may be also produced by the combined effect of pigments and structural features.

The bright blue feet of the blue-footed booby has been presented repeatedly as an example of an integumentary structural color (Bagnara et al., 2007; Prum and Torres, 2003). However, observational and experimental data from a wild population of blue-footed boobies contradicts this view. Integumentary structural colors once developed are apparently permanent and only in a few cases vary seasonally (Prum and Torres, 2003). In contrast, foot color in blue-footed boobies changes rapidly and varies seasonally, and rapid changes in foot color are influenced by food and carotenoid availability (Velando et al., 2006a). Male foot color varies from a bright blue-green turquoise (reflectance peak at 540 nm) to dull blue (reflectance peak at 440 nm; Fig. 1), and females prefer males with bright turquoise feet (Torres and Velando, 2003). Feet color varies rapidly with nutritional condition and dietary carotenoids (Morales et al., 2009b; Velando et al., 2006a). Experimental manipulation of the amount of food and dietary carotenoids showed that in 48 h foot color of courting males became duller when they were food-deprived and brighter when they were fed with fresh fish (Velando et al., 2006a). Variation of dietary carotenoids induced comparable (but amplified) changes in male foot color (Velando et al., 2006a). Furthermore, carotenoid supplementation of females following the laying of their first egg led to an increase 4 days later in foot green chroma (proportion of

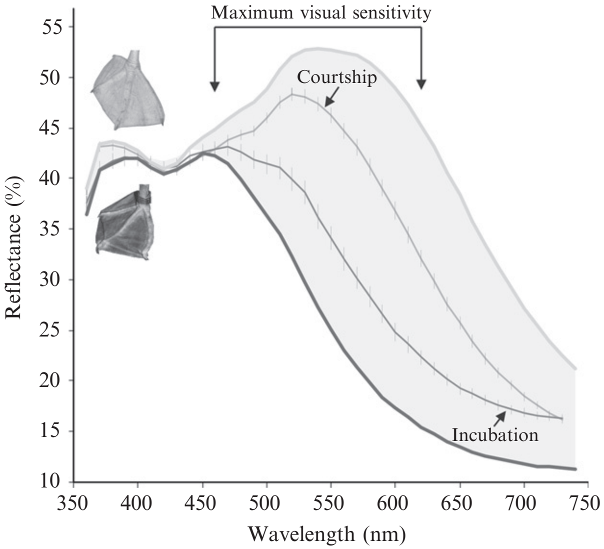

FIG. 1. Reflectance curves of blue-footed booby foot color of brightest (turquoise-green) and dullest (blue) males captured at Isla Isabel (Mexico). Foot color of male blue-footed boobies have high variability (shadowed area), especially in the wavelengths of maximum visual sensitivity (460–620 nm). Mean (±SE) of reflectance curves of males captured in courtship and incubation are given.

reflectance from 460 to 620 nm/total reflectance) in experimental females compared to control females (Morales et al., 2009b). Overall, results from both experiments indicate that carotenoid availability in the diet has a rapid impact on the expression of foot color and that foot color is a dynamic honest signal of current condition.

Foot color of male and female blue-footed boobies varies seasonally with the reproductive condition of the bird (Figs. 1 and 2). Foot color of males is on average green-turquoise (reflectance peak 520 nm), but becomes duller blue during incubation (reflectance peak 470 nm) and chick rearing (reflectance peak 430 nm). Female foot color is on average duller than males' during courtship. But similar to the male pattern of color variation through the breeding season, foot color of females is brighter during courtship and becomes duller during incubation and chick rearing (Fig. 2).

Previous examination of skin tissue from a male of unknown reproductive condition showed that collagen arrays predicted dark blue reflectance spectra (reflectance peak at 410 nm), and led to the conclusion that foot color in this species was the result only of tissue microstructure (Prum and Torres, 2003). More recently, the analysis of a skin sample from a courting

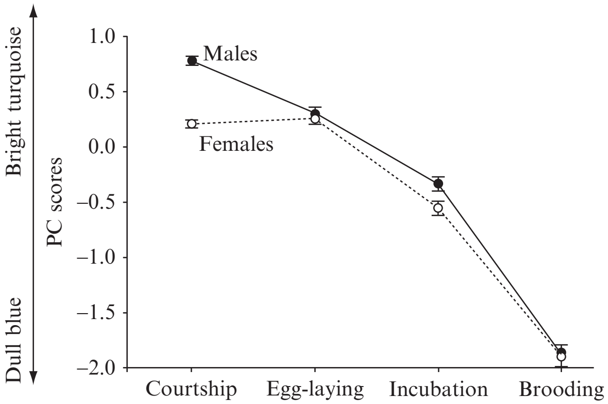

FIG. 2. Seasonal variability of foot color measurements on 680 males and 555 females of blue-footed boobies captured during seven years (2002–2008) at Isla Isabel (México) according to breeding stage. Color is expressed as the first principal component calculated from a factorial analysis with the correlation matrix of CIELAB parameters. PC1-negative values indicate dark blue and PC1-positive values indicate bright turquoise-green.

male (reflectance peak at 540 nm) revealed a thick dermal collagen layer below the epidermis (Fig. 2B in Velando et al., 2006a), and the presence of yellow lipid-soluble pigments (Velando et al., 2006a). These pigments in the foot-web were identified as zeaxanthin by HPLC analisys (Fig. 3). Hence, structural collagen arrays are probably responsible for the blue coloration of the foot-web, which, together with yellow pigments, becomes greener (Fig. 1). Overall, the fact that foot color can change rapidly and is influenced by dietary carotenoids, and the presence of yellow pigments in the foot-web, suggest that in the blue-footed booby integumentary foot color is produced by the combined effects of structural mechanisms (collagen arrays) and the yellow carotenoid pigments, a mechanism similar to the one described for the expression of green coloration in amphibians and reptiles (Bagnara et al., 2007).

C. RARE OR COMMON?

Is the mechanism of skin color production of blue-footed boobies a rare case among vertebrates? The evidence suggests that the color production (including green and bluish colors) by the interaction between pigmentary and structural components in a multilayer dermal system is quite common, at least in fishes, amphibians, and reptiles (see Bagnara and Hadley, 1973;

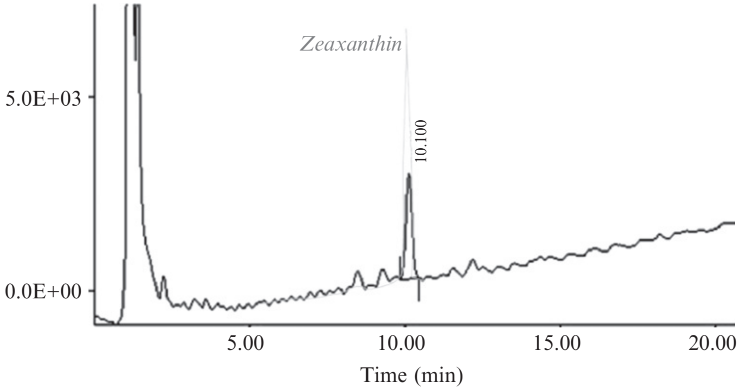

FIG. 3. HPLC chromatogram of pigments extracted from a foot web of a male blue-footed booby. Pigments were extracted from tissue with absolute ethanol and sonication. Samples were injected into a HPLC system (JASCO Comparison Proven) fitted with a SecurityGuard column and a C18 reverse phase analytical column. The mobile phase was methanol-milliQ water (90:10, v/v) in gradient elution and the flow rate 1.5 mL/min. Zeaxanthin was determined at 445 nm with a UV detector by use of external standard (in grey, provided by LGC Promochem SL, Barcelona, Spain) with a retention time of 10.1 min

Bagnara et al., 1968; Grether et al., 2004). As far as we know, there has been no pigment search performed in the blue-green skin of other bird or mammal species, besides the blue-footed booby. Nevertheless, there are many other birds and mammals with blue-green colors that display seasonal and rapid variation (see Prum and Torres, 2003, 2004). For example, in the Visayan tarictic hornbill (*Penelopides panini*), the bare facial skin changes from white to blue within minutes (Curio, 2004); in ruddy ducks (*Oxyura jamaicensis*), blue coloration is displayed only during the breeding season (Hays and Habermann, 1969); in spotted shags (*Phalacrocorax featherstoni* and *P. punctatus*) the skin at the bases of the upper and lower mandibles is opalescent blue and changes into blue sky during the courtship period (Johnsgard, 1993). Although collagenocyte activity or hydration in the dermis could produce structural color changes (Price et al., 1976; Prum and Torres, 2004), short-term color changes are probably best explained by changes in the basal melanin layer (Findlay, 1970; Hays and Habermann, 1969), or in the outermost pigmentary layer, if present (Grether *et al*., 2004). We predict that the combination of pigmentary and structural mechanisms will turn out to be common in species with short-term blue color variation as more studies of color production mechanisms are conducted.

D. Foot Color Evolution in Sulids

Similar to blue-footed booby, the legs and feet in other sulid species are amazingly colored: red, yellow, orange, red, and turquoise. Since a reliable sulid phylogeny is available (Friesen and Anderson, 1997), it is possible to map the foot colors into the molecular tree to examine the evolution of blue-green color in this family. As far as we know, a part from the blue-footed booby, the mechanism of color production in the skin of other sulid species remains unknown. Nevertheless, the mechanism of color production in the feet of other Sulidae species is probably similar to that of the blue-footed booby, as shown by similar seasonal and geographic variation (Nelson, 1978). Gannet species (*Morus* spp.) display colorful lines above the foot digits that vary from green to yellow; the tomato red feet of red-footed boobies (*Sula sula*) is more intense during courtship; the foot color of male brown boobies (*Sula leucogaster*) varies from green to vivid yellow during courtship; and the feet of masked boobies (*Sula dactylatra*) exhibit substantial color variation from olive to orange (Nelson, 1978). The foot color of blue-footed boobies is quite similar to the color displayed by gannets. Unfortunately, no studies of reflectance spectra of gannets are available. More studies of the mechanisms of color production are required to disentangle color evolution in this family. Thus, depending on the assumptions relative to the mechanisms of color production, different evolutionary steps are required to reconstruct the evolution of foot color in this family. If we assume that mechanisms of color production are different for each foot color, five evolutionary steps are needed (Fig 4A and B). If we assume that mechanisms of color production of foot web and lines above the foot digits are the same, three evolutionary steps are required (Fig. 4C). In this case, colorful feet in tropical boobies (*Sula* spp.) were probably an ancestral state (Figs. 4B and C). Interestingly, blue-footed and Peruvian boobies (*Sula variegata*) are sister species that may have diverged recently (since the last interglacial period: Friesen and Anderson, 1997). Thus, Peruvian boobies have probably lost ancestral colorful feet (Fig. 4C). Assuming similar mechanisms of color production in gannets and boobies, the ancestor of sulids could have had some color in the feet, but the phylogenetic reconstruction is equivocal (Fig. 4D). Note that this ancestral state reconstruction depends on the phylogenetic position of Abbott's booby (*Papasula abbotti*) that needs to be confirmed (Friesen and Anderson, 1997).

III. The Blue-Footed Booby Mating System

The blue-footed booby is a long-lived colonial marine bird that nests on the tropical Pacific Ocean, between the Gulf of California and the northern extremity of the Peru Current (Nelson, 1978). Blue-footed boobies are

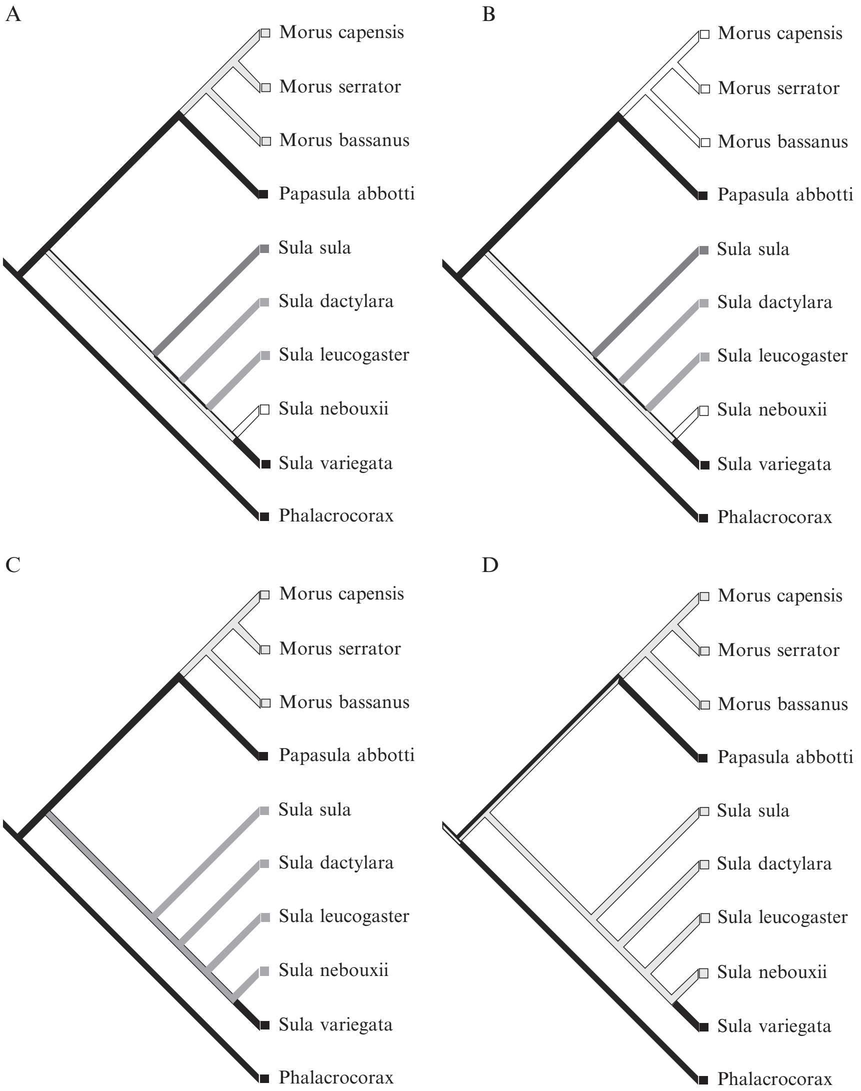

FIG. 4. Reconstruction of color mechanisms in the family Sulidae by parsimony ancestral state (Maddison and Maddison, 2006) under four different scenarios assuming that: (A) different mechanisms produce different colors in this family, (B) different mechanisms produce different colors in this family but are similar between blue-footed boobies and gannets, (C) only two mechanisms evolved: in foot webs and in digits, (D) similar mechanisms produce colorful feet and digits.

socially monogamous with an extended period of pair courtship (Nelson, 1978; Osorio-Beristain and Drummond, 1998). Males establish a territory and females fly over or walk around the colony prospecting for potential mates (Nelson, 1978). Pairs court for a period of about 40 days, progressively increasing attendance at the territory until they are together roughly half of the daylight period for the five days that precede egg-laying (Osorio-Beristain and Drummond, 1998). Though socially monogamous, during this long courtship period both sexes perform extrapair courtship and consensual extrapair copulations that peak in frequency during the female's presumed fertile period (Osorio-Beristain and Drummond, 1998; Pérez-Staples and Drummond, 2005). Extrapair copulations are typically performed with neighbors (paired and unpaired) and both promiscuous males and females perform extrapair courtship before copulating with the extra male/female, sometimes in the presence of the social mate (Osorio-Beristain and Drummond, 1998; Pérez-Staples and Drummond, 2005). However, although extrapair copulations are frequent, extrapair paternity seems to be low (Drummond, H., unpublished data).

The blue-footed booby has an extended period of parental care (Anderson and Ricklefs, 1992; Guerra and Drummond, 1995; Nelson, 1978). Modal clutch size is two eggs (range 1–3 eggs), which are laid with an average interval of four days and incubated for 42 days (D'Alba and Torres, 2007; Drummond et al., 1986). Both parents rear from one to three chicks and nestlings are fed sardines and anchovies that are regurgitated in their mouths (Drummond et al., 1986; Guerra and Drummond, 1995; Nelson, 1978). Parents feed their chicks roughly for four months (Torres and Drummond, 1999).

Given the amount of time and the extensive amount of parental care that both members of a pair invest over the course of a breeding event, selection should favor the evolution of traits that are honest indicators of individual parental quality or condition. Indeed, male condition is an important factor for female breeding success (Velando and Alonso-Alvarez, 2003). Experimental reduction of paternal effort has a strong negative effect on the condition, and hence, probable future reproduction of females (Velando and Alonso-Alvarez, 2003). Thus, in the blue-footed booby, one might expect the evolution of sexual traits that indicate the condition and quality of the bearer of such traits and, additionally, the ability to adjust parental investment in relation to current mate condition.

IV. Dynamic Colors in a Long-Lived Bird Living in a Stochastic Environment

A. Foot Color is a Sexual Signal in Males and Females

During courtship, blue-footed boobies are dimorphic in the color of the feet: male feet are brighter and green-turquoise while female feet are less bright and bluish (see Fig. 2). Blue-footed boobies are colonial and nest on variable types of terrains, typically fairly flat and open. Males and females exhibit their colored feet to their partners in a series of courtship displays that include ritualized locomotion and flight (Nelson, 1978; Osorio-Beristain and Drummond, 1998; Torres and Velando, 2003, 2005). Males (especially) land in the territory with spread feet flexed in front of their bellies, resulting in a conspicuous contrast between the color of the foot-webs and the white underparts, which is probably an effective display during landing to both territorial neighbors and potential mates (“salute landing”; Nelson, 1978; Fig. 5A). This elaborate landing occurs only during courtship; later in the season, during incubation and chick rearing, males land in the ordinary and more aerodynamic way (Nelson, 1978; personal observation). On land, the most frequent (and iconic) sexual advertising display in the blue-footed booby is the “sky-pointing”, when the bird’s neck is lengthened with the bill pointing skyward, accompanied by the elevation of the tail and the lateral spreading of the wings (Nelson, 1978; Fig. 5B). This sexual advertising display is commonly preceded or followed by a “parading”, consisting of exaggerated foot-raising, during which foot-webs are pointed upwards and outwards. “Sky-pointings” are displayed in different contexts (e.g. males display “sky-pointings” to overflying females), but probably the most

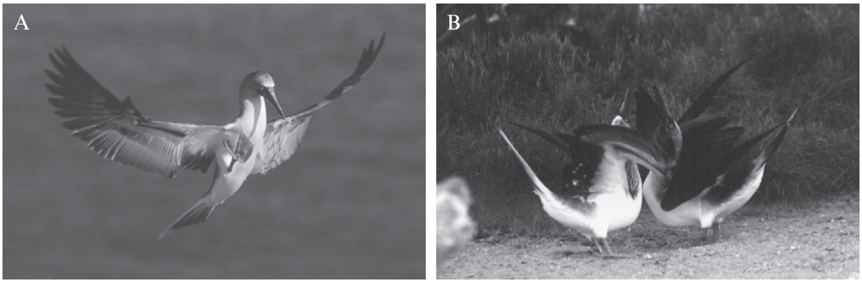

FIG. 5. Blue-footed boobies’ courtship displays. (A) Male showing off his foot color when landing to territorial neighbors and potential mates. (B) Mutual “sky-pointing” between partners. Photographs by (A) Claudio Contreras Koob and (B) Roxana Torres.

frequent situation is its use as a mutual display between partners that have already bonded (Fig. 5B). Nelson (1978), from his detailed observations on blue-footed booby courting behavior carried out during the breeding season of 1964 in Hood Island in the Galapagos, suggested that male courtship displays evolved to show the brightly colored feet.

Almost 40 years later, the idea that the brightly colored feet displayed by blue-footed booby males is a trait used during mate choice and pair evaluation was supported by a series of experiments. To evaluate the role of male foot color on female motivation to court and copulate, we colored the feet of courting males in established pairs and recorded the females' courtship displays after the manipulation (Torres and Velando, 2003). In the experimental group, male feet were colored using a nontoxic and water-resistant blue intensive make-up. The treatment changed the foot color of experimental males from green-turquoise to dull blue, similar in appearance to the foot color of males in poor nutritional condition (Torres and Velando, 2003; Velando et al., 2006a). Males in the control group were sham colored. Blue-footed booby females paired to experimental males courted less compared to control pairs, particularly decreasing their "sky-pointing" rate. Male behavior was apparently unaffected by the manipulation; thus, the change in female behavior can be attributed to the color manipulation. Furthermore, females were less likely to copulate when they were paired to males with duller feet. Although we did not test the potential role of foot color in mate selection, prior to the manipulation, male foot brightness was positively related to female body condition, suggesting that females in better condition may choose males with brighter feet. Overall, results from this first experiment support the hypothesis of female preference for male foot color and suggest that this trait is used as a male sexual ornament after pairing.

Female ornaments and male mate choice are expected to evolve when mating is costly to males (e.g., energy and time spent on sexual behavior, 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 offspring (Amundsen, 2000; Cunningham and Birkhead, 1998; Johnstone *et al*., 1996; Trivers, 1972), as in the blue-footed booby (see above). Although of a hue less bright than that of males, females display variably blue feet (see Fig. 2). To evaluate whether female foot color influences their mate's sexual behavior (an indication of male preference), female foot color during courtship was modified to a duller blue (Torres and Velando, 2005). Females with duller feet received less intra- and extrapair courtship than control females, suggesting that foot color influences female attractiveness and the opportunities for extrapair interactions (Torres and Velando, 2005). Taken together, the two experiments suggest that foot color in the blue-footed booby is favored by sexual selection through mutual mate preferences.

B. Dynamic Versus Static Traits

One of the intriguing features of the foot color display in blue-footed boobies is its dynamic change. The lability of the expression of sexual traits in animals varies greatly. Some traits, such as acoustic signaling and courtship displays, are highly dynamic and their expression varies rapidly in response to ecological, physiological, and motivational states, while others are relatively static with little or no change in expression after their development for a particular breeding season, examples of which are plumage coloration or tail length in birds. In theory, sexual traits have evolved because they allow individuals to assess variation in mate quality; consequently, selection should favor traits that are reliable indicators of quality (Hamilton and Zuk, 1982; Kodrick-Brown and Brown, 1984; Zahavi, 1975, 1977). Since they respond rapidly to changes in condition, dynamic sexual traits might be the most accurate indicators of a mate's current quality (e.g., Folstad and Karter, 1992; Hill et al., 1999; Lozano, 1994; Negro et al., 1998; Zuk et al., 1990). Conversely, static sexual traits might be more reliable indicators than dynamic traits because their expression is expected to be less sensitive to current environmental conditions. In addition, static traits are thought to be less likely to be deceptive because lower quality individuals will be unable to produce and sustain high-quality traits for long periods of time (Hill et al., 1999).

C. Why Dynamic Sexual Traits May Be Favored in Long-lived Tropical Birds

At first glance, it is odd that blue-footed booby males dance and display their colorful feet after pairing, and even during incubation. It is well established that many colors of male birds evolved due to female preference for more colorful males (Hill and MacGraw, 2006). Nevertheless, the reasons why males maintain costly ornaments after pairing need to be investigated. On the other hand, it is remarkable that females use a labile sexual trait, such as male foot color, that can vary in a few hours (Torres and Velando, 2003; Velando et al., 2006a). We performed some experiments to elucidate these questions, but first by examining the biology of blue-footed boobies, some answers can be found. Blue-footed boobies are long-lived birds with an extended period of parental care, and therefore breeding decisions should be adjusted within a life history context. Female breeding decisions may not be concluded when a mate is chosen, and after paring females can decide whether to stay with the present mate or to divorce, the proportion of offspring that the social mate will sire or the amount of reproductive investment to funnel into the current reproduction. In these contexts, dynamic traits may be useful to continuously evaluate the quality of partners.

In iteroparous organisms, life history predicts that investment in offspring is balanced against the negative effects on future reproduction (Stearns, 1992). Therefore, if increased parental effort in current reproduction has a negative effect on future reproduction, animals should continuously evaluate the value of their current reproduction and adjust investment accordingly. In monogamous species, the value of present reproduction may be affected by the current condition of the mate (Cunningham and Russell, 2000) and, particularly in long-lived animals, females should optimize their reproductive decisions in relation to partner quality and his level of investment (Winkler, 1987).

Interestingly, in tropical seabirds breeding conditions are influenced by a major environmental oscillation (the Niño/Niña events; Oro et al., 2010). Therefore, among seabirds (iteroparous species with long biparental care), mate quality probably varies annually and even within the same breeding event, from pair formation to chick feeding, influencing the value of current reproduction. In this context, evaluating current mate condition should be strongly selected and individuals may benefit by the use of dynamic sexual signals to continuously evaluate the quality of their partners.

D. Foot Color is an Honest Dynamic Signal of Current Condition

After finding that foot color in the blue-footed booby is a dynamic sexual trait in both sexes (Torres and Velando, 2003, 2005), the next step was to determine whether foot color honestly reflects the bearers' quality**.** As previously mentioned, by manipulating the amount of food, we found that carotenoid-based foot color is a rapid honest signal of current nutritional condition (Velando et al., 2006a). Additionally, we found that variation of dietary carotenoids induced comparable changes in cell-mediated immune function and foot color, suggesting that, in the blue-footed booby, carotenoid-pigmentation in the feet reveals the immunological state of individuals (Velando et al., 2006a). High immunocompetence probably reveals that individuals are well adapted to current infectious challenges, an important feature in long-lived animals. Velando et al. (2006a) only manipulated phenotypic condition, but it is likely that the ability to handle stressful conditions has some genetic basis (David et al., 2000; Hamilton and Zuk, 1982). This view was supported by a cross-fostering experiment (Fig. 6), where we found that blue-footed booby offspring condition was

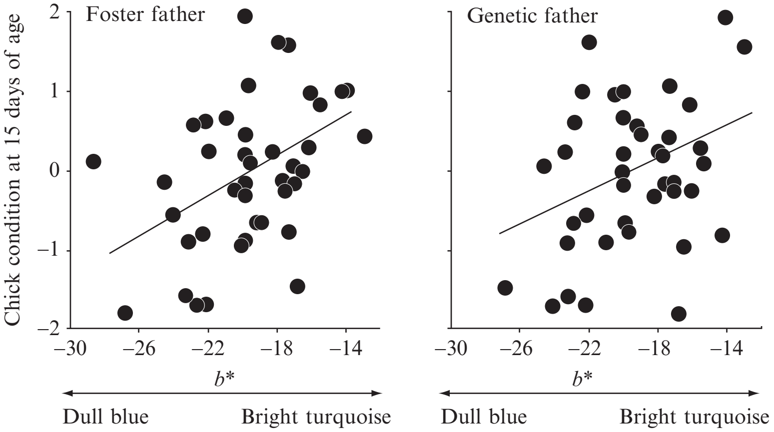

FIG. 6. Relationship between chick condition at 15 days of age (body mass standardized by ulna length) and foot color (*b** parameter of CIELAB color space) of foster father and genetic father from a cross-fostering experiment (Velando et al., 2005).

correlated with the foot color of the genetic father (Velando et al., 2005). Interestingly, chick growth was also correlated with the foot color of the foster father, indicating that colorful males are good parents (Velando et al., 2005). Therefore, looking at a mate's foot color, females may obtain reliable information of its current condition. A rapid decline in mate foot color probably indicates a decrease in health or condition, and consequently, a reduced ability to invest in the brood (Velando et al., 2005), and/or low genetic quality (David et al., 2000; Hamilton and Zuk, 1982).

E. Do Females Respond to Rapid Changes in their Mate's Foot Color?

Because sexual traits are part of a communication system, to understand signal evolution, we need to consider the selective forces acting at both ends: the signaler and the receiver. Communication occurs when the actions or cues given by an animal influence the behavior of another (Endler, 1993). Therefore, selection should favor dynamic traits when the receiver has the capacity to respond to the lability of the trait. Furthermore, the properties of the receiver can exert selective pressures on signal design, and signal design exerts reciprocal selective pressures on receiver behavior. Previous studies have found that females modify their breeding decisions after pairing in relation to male static sexual traits (de Lope and Møller, 1993; Limbourg et al., 2004) or artificial ornaments (Burley, 1986; Gil et al., 1999).

We investigated whether blue-footed booby females evaluate their mates after pairing and respond to rapid changes in their mate's foot color, a dynamic sexual trait, by adjusting their breeding decisions. If male foot color is a good indicator of male condition and paternal care, we expected that females should decrease their investment in reproduction when foot color deteriorates compared to females with males with colorful feet (Fig. 7).

We had previously found that females respond to sudden changes in the male's foot color during courtship by decreasing their rate of courtship and copulations. This suggested that female decisions do not end after pairing and that males with duller feet could possibly face a higher probability of being cuckolded (Torres and Velando, 2003). To investigate whether females adjust their investment in eggs according to the mate's condition we performed a series of experiments in which the foot color of experimental males was modified to a duller blue, as described above. In these new experiments, color manipulation was performed one day after the first egg was laid; this protocol allowed us to control for variation in reproductive stage among females (Dentressangle et al., 2008; Velando et al., 2006a). In the first experiment we found that females whose mate foot color suddenly changed to a duller blue decreased the size of their second egg compared to the second egg of control females (Fig. 8; Velando et al., 2006a). In the blue-footed booby egg size is positively related to hatching

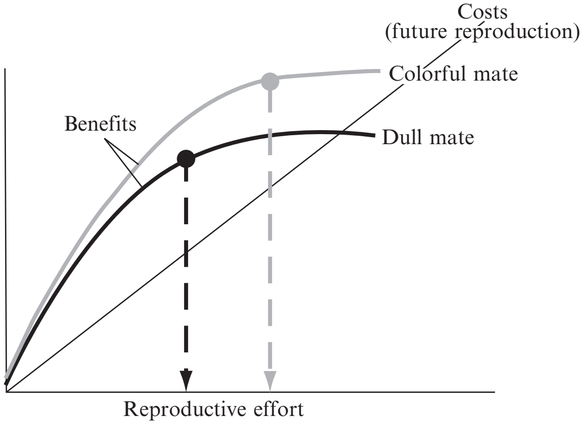

FIG. 7. Female decisions in relation to mate's foot color. Colorful feet are an honest signal of male individual quality, the ability to invest in the brood and high genetic quality. Females should be selected to fine-tune their reproductive investment according to mate quality. The balance between costs (future viable offspring) and benefits (current viable offspring) differs depending upon mate quality.

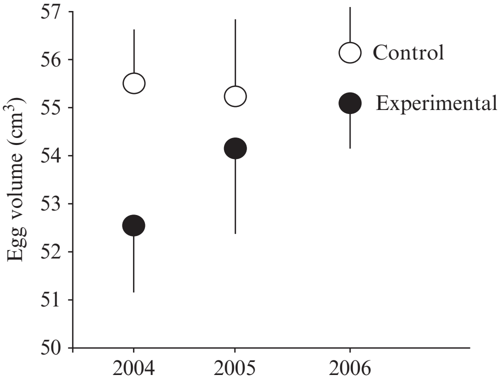

FIG. 8. Egg volume (mean ± SE) of second-laid eggs laid by females ($N = 107$) after manipulation of male foot web to duller blue color (experimental clutches; black circles) in three different years (see Dentressangle et al., 2008; Velando et al., 2006a). Females consistently reduced egg volume when mate foot color was experimentally reduced.

success and chick weight at hatching (D'Alba and Torres, 2007). Thus, experimental females probably facilitated brood reduction by decreasing egg size when the mates' foot color deteriorated. This first experiment indicated that females are able to rapidly respond to a highly dynamic sexual trait.

To explore the influence of mate and environmental conditions on female investment in eggs, we repeated the experimental protocol of male foot color manipulation during egg-laying, as described above, in two consecutive years: an El Niño year (poor breeding conditions) and a year with good breeding conditions. In both years, we investigated how females adjusted their reproductive investment after a sudden deterioration of the mates' foot color relative to mass, volume, and yolk androgen concentration (androstenedione and testosterone) of the second egg as well as laying intervals (Dentressangle et al., 2008). We found that females laid heavier second eggs during the poor year than during the good year. Similar to previous results (Velando et al., 2006a), females paired to males with duller feet reduced second-egg mass and volume (Fig. 8). Independently of the year, females paired to experimental dull males deferred the laying of the second egg by 0.77 days on average. Yolk testosterone of second eggs from experimental and control clutches did not differ in either of the two years. Absolute yolk androstenedione concentration in second eggs was higher during the poor year than during the good year. However, during the El Niño year, females paired with dull males decreased the relative concentration of yolk androstenedione in the second egg compared to control females. Altogether, results suggest that females are capable of fine-tuning various egg components, depending on prevailing mate and environmental breeding conditions. An increasing number of studies of birds indicate that even minor variations of maternally derived yolk androgens can have important fitness effects on offspring (e.g., Gasparini et al., 2007; Groothuis et al., 2005; Schwabl, 1996, 1997; Tobler et al., 2007). By decreasing egg size and the relative concentration of yolk androstenedione, females paired to males with duller feet may decrease hatchability of second eggs or facilitate brood reduction in case both chicks hatch. The blue-footed booby is a species with aggressive sibling competition (Drummond et al., 1986), thus postponing the laying of the second egg probably increases the competitive asymmetries between broodmates and therefore facilitates brood reduction.

Our results suggest that blue-footed booby females are able to perform rapid adjustments of maternal investment in eggs according to the expected conditions that may prevail during chick rearing. They do this by using a combination of signals, such as annual variations in food availability and mate foot color. The costs for females of rearing a brood with a mate in poor condition during a poor breeding year are probably high, either because females will have to compensate for a low paternal effort (Velando and Alonso-Alvarez, 2003; Velando et al., 2005) or because the reproductive value of the brood will decrease (Velando et al., 2005). Our studies suggest that, if foot color influences female sexual activity, the allocation of resources to eggs, and the risk of cuckoldry for males, blue-footed booby males are probably under strong selection to invest in foot coloration after pairing.

V. Life History Trade-offs of Sexual Ornamentation

A. Senescence on Reproductive Success and the Role of Sexual Ornaments

Senescence is an age-specific decline in residual reproductive value owing to deteriorating survival probability and/or reproductive performance of individuals, caused by somatic deterioration and a general progressive loss of physiological functions late in life (Hamilton, 1966; Kirkwood and Austad, 2000; Williams, 1957). Models on the evolution of senescence suggest that this apparently maladaptive process has evolved because in the wild, extrinsic mortality weakens the force of natural selection with age (Fisher, 1930; Hamilton, 1966; Medawar et al, 1952; Williams, 1957). Thus, for a long time it was believed that senescence was difficult to observe or even nonexistent in natural populations (Kirkwood and Austad, 2000; Williams, 1992). Consequently, much of the study of senescence is focused on mechanisms underlying this process in model animals in the laboratory (Kirkwood and Austad, 2000). However, an increasing number of studies in the wild across a wide range of taxa have recently provided compelling evidence of senescence in survival and some indicators of reproductive success (Jones et al., 2008; Nussey et al., 2008).

In the blue-footed booby, the analyses of longitudinal data of individually marked birds revealed that both males and females show reproductive senescence (Beamonte-Barrientos et al., 2010; Velando et al., 2006b). Males show a steady increase in reproductive performance (number of fledglings produced) until the tenth year, followed by progressive decline (Velando et al., 2006b). Similarly, females' reproductive performance increases until roughly the eighth or ninth year and then decreases (Beamonte-Barrientos et al., 2010).

After the onset of senescence, results suggest that the rate of decrease in reproductive performance of males and females differs among cohorts, although this effect was significant only in females (Beamonte-Barrientos et al., 2010; Velando et al., 2006b). As mentioned above, blue-footed boobies are exposed to strong annual variation in food availability, and cohorts differ in chick growth, recruitment probability, and age at first nesting (Drummond et al., 1986; Drummond et al., 2003; Oro et al., 2010). The differences in the rate of reproductive senescence among blue-footed booby individuals from different cohorts suggest that conditions experienced early during embryo and chick development and the years prior to recruitment may affect an individual's reproduction over the long term (Beckerman et al., 2003; Lindström, 1999; Metcalfe and Monaghan, 2001).

The decline in reproduction at older ages can result from a decrease in one or a combination of reproductive traits. For instance, reproductive success may decline in older males because aging males may be unable to acquire high-quality territories, suffer a decline in foraging abilities, and decrease their investment in parental care (e.g., Bogdanova et al., 2006; Catry et al., 2006). Furthermore, the capacity to invest in costly sexual traits may be constrained in ageing animals by general somatic deterioration (Torres and Velando, 2007). Thus, older males might be less attractive and consequently unable to obtain high-quality mates.

In the blue-footed booby, there is a progressive decline in the male's foot coloration with age (Fig. 9). Consequently, senescent males display duller foot color than younger and middle-aged males during courtship (Torres and Velando, 2007; Velando et al., 2010). The reduction of foot color in senescent males probably impairs male reproductive success (see above),

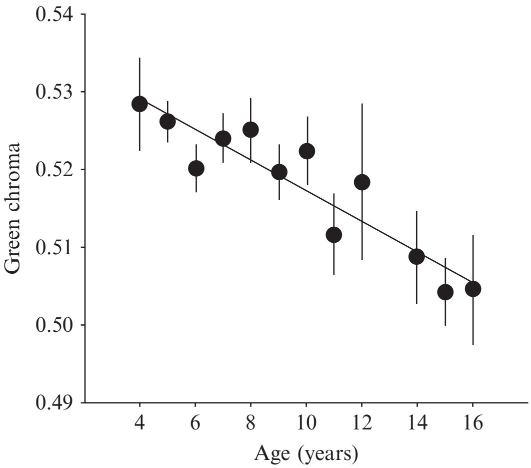

Fig. 9. Relationship between foot color (estimated marginal means ± SE, controlling by year) and age for 85 males captured during courtship (see Velando et al., 2010).

affecting mate choice, pair evaluation (Torres and Velando, 2003), and female investment in eggs (Dentressangle et al., 2008; Velando et al., 2006a). Hence, in the blue-footed booby, the decline in male reproductive success with age may be in part related to the decreased ability of senescent males to invest in costly sexual signals.

Despite the recent accumulation of evidence leading to the conclusion that senescence is a frequent process in natural populations, we know rather little about whether individuals differ in their rates of deterioration and, more importantly, which factors and mechanisms underlie these differences. Some studies suggest that accelerated senescence is associated with harsh environmental conditions, particularly during the first stages of development or soon after the independence from parental care (e.g., Beamonte-Barrientos et al., 2010; Nussey et al., 2007; Reed et al., 2008), or high reproductive effort early in life (Nussey et al., 2006). However, investment in sexual traits, a relatively neglected component of reproductive effort in terms of life history trade-offs (e.g., Griffith, 2000; Gustafsson et al., 1995; Siefferman and Hill, 2005), might influence the rate of senescence (Beck and Promislow, 2007; Beck et al., 2002; Promislow, 2003). Thus, it is possible that males that invest highly in sexual ornamentation early in life may suffer an earlier onset of senescence or an increase in the rate of decline, once senescence has started. This could be particularly plausible for carotenoid-based ornaments that need a continuous high influx of pigments, as in dynamic color signals. Interestingly, female preferences for young and middle-aged males (those that display the most attractive sexual ornaments in our study system) may accelerate senescence because selection should favor highest investment in ornaments in the age classes that are more likely to contribute to male reproductive success (Beck et al., 2002).

B. Senescence and Physiological Trade-offs of Ornaments

Trade-offs between life-history traits are well documented and are thought to have physiological bases; however, the mechanistic underpinnings of these trade-offs are rarely addressed (Barnes and Partridge, 2003; Monaghan et al., 2009; Zera and Harshman, 2001). Physiological trade-offs have been typically considered in terms of energy allocation, where two or more functions compete for the same resources within the same individual (Stearns, 1992). However, these trade-offs can also result when one activity has negative effects on another activity (Alonso-Alvarez et al., 2004; Zera and Harshman, 2001). Oxidative stress is the imbalance between the production of damaging reactive oxygen species (ROS), which are by-products of normal metabolic activities, and antioxidant defenses, which scavenge ROS and limit their toxic effect (Finkel and Holbrook, 2000; Surai, 2002). The role played by oxidative stress in the ageing process has long been recognized (Beckman and Ames, 1998; Harman, 1957). More recently, it has been suggested that oxidative stress represents a cost of reproduction, and may be an important mediator in life history trade-offs (Alonso-Alvarez et al., 2004; Monaghan et al., 2009).

Furthermore, oxidative damage (or the capacity to avoid oxidative stress) might be one of the main proximal causes of the genuine information revealed to prospective females through carotenoid-based male sexual traits (Velando et al., 2008; von Schantz et al., 1999). Animals cannot synthesize carotenoids *de novo*, and have to ingest them with food. Consequently, it was first thought that carotenoid-based sexual signals were honest indicators of the individual ability to find high-quality food (Endler, 1980; Grether et al., 1999; Hill, 1990, 1991). However, beyond their role in the expression of colored signals, carotenoids have many other physiological functions as antioxidants, recycling other antioxidants and immunostimulants (Hill et al., 1999; Lozano, 1994; MacGraw, 2006; Pérez-Rodríguez, 2008; Surai, 2002; von Schantz et al., 1999). Hence, carotenoid-based ornaments may also function as indicators of the oxidative status of the bearer, with more intensely colored males signaling their enhanced ability to combat oxidative stress (Velando et al., 2008; von Schantz et al., 1999). Although the role of carotenoids as antioxidants is currently under debate, the function of carotenoid-based sexual traits as indicators of oxidative status has received some support from studies in fish and bird species (e.g., Helfestein et al., 2010; Pérez-Rodríguez et al., 2008; Pike et al., 2007, 2010).

The role of oxidative stress is thought to be one of the most important causes of senescence (Beckman and Ames, 1998). Older animals accumulate and are less able to prevent oxidative damage, probably due to a decline of antioxidant defenses and/or repair mechanisms (Beckman and Ames, 1998; Finkel and Holbrook, 2000). Thus, particularly in long-lived animals, females may benefit by preferring ornaments indicative of oxidative status, and probably the rate of senescence of potential mates. We assessed whether sexual attractiveness of blue-footed boobies is affected by immunologically induced oxidative damage (Torres and Velando, 2007). To induce oxidative damage in courting males, we injected a lipopolysaccharide, a bacterial cell wall component that mimics an infection without the negative effects of pathogens (Bonneaud et al., 2003), and is known to increase the formation of reactive oxygen species and lipid peroxidation products (a common type of oxidative damage; e.g., Wiesel et al., 2000; Escames et al., 2003). In this experiment, males of known age were immune-challenged and seven days later we analyzed the changes in the plasma levels of immunoglobulins and lipid peroxidation, along with changes in foot color. As expected, experimental males mounted an immune response, although, no differences were found between middle-aged (younger than ten years) and senescent males (older than ten years; Torres and Velando, 2007). The immune activation induced greater lipid peroxidation in senescent males than in middle-aged males (Torres and Velando, 2007). Interestingly, the immune challenge had no effect on the foot color of middle-aged males, but invoked changes in color expression of senescent males (Torres and Velando, 2007). Senescent males that were challenged immunologically suffered a decrease in foot color, changing to less attractive duller blue feet. Hence, senescent males, but not middle-aged ones, apparently suffered a cost when mounting an immune response in terms of oxidative damage and sexual attractiveness. Conversely, middle-aged males were able to defend against radicals produced by the immune response and did not lose sexual attractiveness. Thus, in the blue-footed booby, foot color of senescent males may mirror their oxidative status. These results also support the idea that oxidative stress is one of the proximal mechanisms of the trade-off between sexual signals and immune competence (von Schantz et al., 1999).

Interestingly, our results suggest that sexual ornamentation may be more honest in ageing animals, as theory predicts (Proulx et al., 2002). In iteroparous organisms, the trade-off between current and future reproduction varies through life. Thus, during the first breeding events high-quality individuals (those with high survival probabilities) may invest less in sexual signals than low-quality individuals due to residual reproductive costs, so that signal strength is not a reliable indicator of condition at this time (Lindström et al., 2009). Older animals should increase their current reproductive investment (including sexual signals) because their future breeding opportunities are relatively fewer (Velando et al., 2006b; Williams, 1966). Consequently, the honesty of sexual signals is expected to increase in old males, and our results support this idea. A recent experimental study of red-legged partridges also found that the reliability of sexual signals increases over the male's lifetime (Alonso-Alvarez et al., 2009).

C. Previous Reproductive Effort Versus Sexual Attractiveness

Life-history theory predicts that in iteroparous organisms investment in reproduction occurs at the expense of somatic maintenance and future reproductive output (Stearns, 1992). As a consequence, throughout their lives, animals accumulate somatic deterioration arising from the negative effects of reproductive effort, and among other things, this may constrain their ability to invest in sexual signals. As mentioned above, blue-footed boobies have an extended period of parental care, and reproductive effort has been shown to increase oxidative stress (Alonso-Alvarez et al., 2006). Therefore, we predicted that besides the age-dependent decline in foot color (see above), reproductive effort should have a negative effect on foot color. To separate the effects of age and previous reproductive effort, two variables inevitably related, we compared the foot color of males of known age and breeding histories that had skipped breeding the year before with males that bred during consecutive years (Velando et al., 2010). We found that foot color deteriorates as males age and accumulate reproductive effort (Velando et al., 2010). However, males that skipped the previous breeding event displayed more attractive foot color (more turquoise-green) compared to males that reproduced the year before, indicating that besides other intrinsic effects of somatic deterioration through life, reproductive effort by itself has a negative effect on foot coloration (Velando et al., 2010). These results suggest that in the blue-footed booby, reproductive effort in one year constrains the expression of foot color in the following breeding season. Alternatively, males might strategically invest in enhanced coloration following a skipping event. Further studies are needed to investigate the potential strategies of foot color investment by blue-footed booby males within a breeding season (with variable social contexts) and between breeding seasons.

By skipping a breeding event, individuals may avoid the costs of reproduction, and hence skipping has been considered an adaptive strategy to maximize lifetime reproductive success (Wooller et al., 1989). Our results show that males that skipped a breeding event were able to produce brighter foot color, a sexual trait that may influence male success (Velando et al., 2010). Thus, particularly for senescent males that on average have duller feet color compared to younger males, skipping a breeding event might be an adaptive strategy that allows recovery from previous breeding effort. To evaluate whether skipping is an adaptive strategy, we need to investigate the age-dependent costs and benefits of skipping in the blue-footed booby.

D. Trade-offs in Female Ornamentation

Even though blue-footed booby females display duller feet than males during courtship, male behavior is affected by female foot color. Research on female ornamentation is particularly relevant in understanding sexual signals because the trade-offs governing signal expression may be significantly different for males compared with trade-offs for females (Bonduriansky, 2001; Heinsohn et al., 2005; LeBas, 2006). During egg formation and egg-laying, females should invest in the size and quality of the eggs. It has been suggested that this investment in offspring may be enough to constrain the evolution of elaborate female ornaments. Females that invest in ornaments at the expense of offspring lose direct fitness, and males should prefer to mate with females that invest in offspring rather than ornaments (Chenoweth et al., 2006; Fitzpatrick et al., 1995). Alternatively, ornamentation might have evolved because such a trade-off is resolved through the investment of different resources in ornaments and eggs (Fitzpatrick et al., 1995). Thus, we first investigated whether resources required for ornament expression (carotenoids) are also a limiting factor for female fecundity.

We performed a carotenoid supplementation experiment in female blue-footed boobies in the wild (Morales et al., 2009b). On the laying day of the first egg, females were captured by night-lighting and randomly assigned to the control or experimental groups. Females from the experimental group received single doses of a solution of dietary carotenoids in drinking water while control females received only drinking water. Increased pigment availability at laying allowed blue-footed booby females to boost foot color, confirming that, similar to males, the ornament is highly dynamic. Moreover, carotenoid supply enhanced the mass of second eggs and clutch volume. Interestingly, in the control group we found a negative relationship between egg quality and foot color changes, but a positive relationship between these variables for females supplied with carotenoids (Morales et al., 2009b). These results suggest a trade-off between ornamentation and fecundity mediated by carotenoid availability in blue-footed booby females. Pigment limitation may thus represent a key environmental factor for an evolutionary pathway to male choosiness and, potentially, to the evolution of sexual dimorphism during courtship in this species (Bonduriansky, 2001).

The trade-off between female ornamentation and fecundity is also evidenced by the negative relationship between clutch size and foot color of females during courtship (Fig. 10). Given this trade-off between investment in eggs and foot color, why do females in this species display colorful feet during courtship? And, why are males looking at female foot color? One untested possibility is that female ornamentation is maladaptive and males are caught in a sensory trap favoring colorful females in spite of their reduced fecundity (LeBas and Hockham, 2005). Conversely, stabilizing selection on female coloration may be predicted, such that males select females with intermediate coloration over females that invest so heavily in coloration that they incur a fecundity cost (Chenoweth et al., 2006). We do not have the data to explore these possibilities but female ornamentation in this species is also a dynamic trait that may be functional during courtship but not during egg-laying. Finally, preliminary data suggest that the dynamic female coloration expressed after pairing may convey relevant information to mates when it is combined with direct information on fecundity (clutch size, egg size, or egg color; Morales, J., unpublished data). Further studies of life-history trade-offs and female ornamentation will be particularly promising to understand sexual color dimorphism and sexual selection.

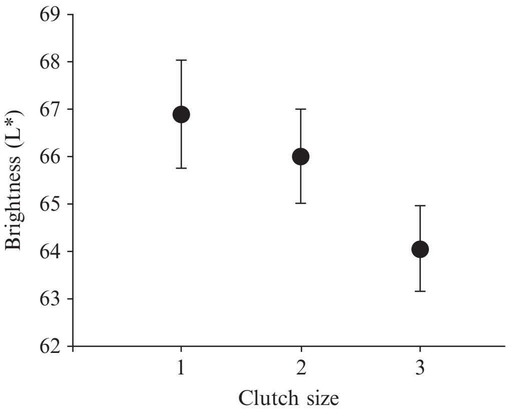

FIG. 10. Relationship between clutch size and foot color (estimated marginal means ± SE, controlling by year, laying date and time to laying) of 161 females captured during courtship.

VI. CONCLUSIONS

Mate choice has been considered as the main force favoring the evolution of sexual ornaments (Andersson, 1994). However, in many species, once a pair has been established, days or even weeks may be spent in courtship before a clutch is laid. This allows for plenty of opportunities to evaluate the mate, and sexual signals may play an important role during pair evaluation. Our studies of the blue-footed booby indicate that sexual traits are used after mate choice to continuously evaluate mate condition. After a sudden change in the mate's foot color, males and females decrease their courtship behavior and females decrease the frequency of copulations. Hence, in this socially monogamous seabird with an extended period of biparental care, both sexes are probably choosy and evaluate their mate after pairing. These findings suggest that foot coloration in the blue-footed booby has been favored by sexual selection through mutual mate choice.

Theory predicts that females should vary investment in offspring in a way that optimizes their inclusive fitness in specific contexts. Seabirds depend on unpredictable and highly variable resources. Hence, the quality of mates probably varies annually and within a breeding event, altering the value of current reproduction. In this context, individuals might use dynamic sexual signals to continuously update information regarding their mates' condition and adjust their breeding effort accordingly. In the blue-footed booby, foot color is a dynamic honest signal indicating an individual's current nutritional and immunological state, and is related to the condition of the chicks, suggesting that more colorful males are good parents. Based on their mate's foot color, females modify their breeding decisions. During three different years, females decreased the volume of the eggs and, during a year with poor food availability, also decreased the relative concentration of yolk androstenedione when the mate's foot color became duller. Thus, in this seabird, selection has apparently favored the evolution of dynamic sexual traits and the ability of females to rapidly respond and fine-tune their breeding decisions in response to changes in their mates' phenotype. This could be particularly adaptive in long-lived animals that depend on unpredictable resources.

Investment in offspring may constrain the evolution of elaborate ornaments in females when the same resources are used for ornaments and maternal investment. In the blue-footed booby, carotenoid availability influences both female foot color and investment in the clutch volume and there is a trade-off between ornamentation and fecundity mediated by carotenoids. These results suggest that in this species carotenoid limitation may represent an evolutionary pathway to male choosiness and, possibly, to the evolution of foot color dimorphism during courtship.

Life history theory has been a powerful tool in explaining both adaptation and constraint in phenotypic evolution. According to life history theory, investment in reproduction occurs at the expense of somatic maintenance and future reproductive output, and individuals should balance the costs and benefits between current and future reproduction to maximize life-time reproductive success (Stearns, 1992). Sexual traits have a strong influence on individual reproductive success and are frequently costly to produce and maintain (Andersson, 1994). Hence, allocation of resources to sexual displays should be considered as any other life history trait (Getty, 2006; Höglund and Sheldon, 1998; Proulx et al., 2002). Furthermore, as expected for other life-history traits, patterns of allocation of resources to sexual displays are expected to be individually optimized and trade-offs between investment in sexual display and other life history traits are expected (Höglund and Sheldon, 1998; Lindström et al., 2009), and have been found in some experimental studies (Griffith, 2000; Gustafsson et al., 1995; Siefferman and Hill, 2005).

In the blue-footed booby, foot color decreases as individuals age and accumulate breeding events. This loss of sexual attractiveness may partly explain the decline in reproductive output found in older males. Additionally, by diminishing the attractiveness of older males, senescence may influence male breeding strategy. Interestingly, after nonbreeding events males display more colorful and attractive feet compared with males that reproduced the year before, suggesting that males can mitigate the negative effects of senescence on sexual ornaments by modifying their breeding schedules. If skipping a breeding event helps recovering to be able to produce attractive ornaments, taking a breeding sabbatical could be an adaptive strategy, particularly for senescent males.

It has been suggested that oxidative damage is the genuine information revealed to prospective females through carotenoid-based sexual traits (Velando et al., 2008; von Schantz et al., 1999). Accordingly, in the blue-footed booby, experimental activation of the immune system induced greater oxidative damage and invoked negative changes in color expression, particularly in senescent males. This study suggests that oxidative stress affects senescence of a sexual trait. Also, as theory predicts, our results suggest that sexual ornamentation may be more honest in ageing animals (Proulx et al., 2002). Future directions of research should investigate whether blue-footed booby males and females optimize investment in sexual coloration and whether the pattern of investment in sexual ornamentation compromises other traits of their life history, such as senescence. Overall, our studies in the color of blue-footed booby emphasized the idea that sexual ornaments and preferences are parts of the reproductive investment of individuals and subject to complex life history tradeoffs.

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