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ORIGINAL PAPER

Parental conflict and blue egg coloration in a seabird

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Abstract When both parents provide offspring care, equal sharing of costly parental duties may enhance reproductive success. This is crucial for longlived species, where increased parental effort in current reproduction profoundly affects future reproduction. Indication of reproductive value or willingness to invest in reproduction may promote matching responses by mates, thus reducing the conflict over care. In birds with biparental care, blue-green eggshell color may function as a signal of reproductive value that affects parental effort, as predicted by the signaling hypothesis of blue-green eggshell coloration. However, this hypothesis has not been explored during incubation, when the potential stimulus of egg color is present, and has been little studied in longlived birds. We experimentally studied if egg color affected incubation patterns in the blue-footed booby, a longlived species with biparental care and blue eggs. We exchanged fresh eggs between nests of the same laying date and recorded parental incubation effort on the following 4 days. Although egg color did not affect male effort, original eggshell color was correlated with pair matching in incubation. Exchanged eggshell color did not affect incubation patterns. This suggests that biliverdin-based egg coloration reflects female quality features that are associated with pair incubation effort or that blue-footed boobies mate assortatively high-quality pairs incubating more colorful clutches. An intriguing possibility is that egg coloration facilitates an equal sharing of incubation, the signal being functional only during a short period close to laying. Results also suggest that indication of reproductive value reduces the conflict over care.

Keywords Blue-green eggshell coloration · Incubation · Life-histories · Pair matching · Parental care · Sexual conflict

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Introduction

In many animals, intersexual conflict (i.e., when one sex increases its reproductive success at the cost of the other) may affect the evolution of male and female reproductive behavior (Trivers 1972; West-Eberhard et al. 1987; Rice 1996). Particularly, in monogamous species, this conflict may continue well after the partner has been chosen and may arise over investment in parental duties such as nest building, incubation, feeding of young, and territorial defense (Winkler 1987; Lessells 1999; Royle et al. 2002). Because increased parental effort in current reproduction negatively affects future reproduction, organisms commonly restrict their parental effort in order to maximize lifetime reproductive success (Curio 1983; Stearns 1992). Consequently, either parent may profit if the other provides more care (Lessells 1999). These antagonistic "negotiations" between breeding parents over care may be costly and translate into reduced care (Royle et al. 2002; Arnqvist and Rowe 2005), with negative consequences on reproductive success (Royle et al. 2002). Thus, in many species where both parents provide extensive care for the offspring, an equal sharing of parental duties between mates is crucial for achieving successful reproduction (Black 1996). Excellent examples of such parental coordination are found in socially monogamous birds (Black 1996), where neither parent can successfully bring up the offspring alone. Therefore, conflict between parents over care may affect reproductive success (e.g., Davies 1982; Coulson and Wooller 1984; Burger 1987; Morris 1987; Bukacińska et al. 1996; Booth et al. 2000). How parental conflict is resolved in such systems is a question that remains controversial although it has been subject of much attention, both theoretical and empirical (e.g., Houston and Davies 1985; Jones et al. 2002; Johnstone and Hinde 2006; Harrison et al. 2009; Morales et al. 2009b).

Selection might favor variation of parental care according to offspring quality (Trivers 1972; Dawkins and Carlisle 1976; see Harrison et al. 2009 and references therein). For instance, when conditions are poor or unpredictable, we may expect that parents allocate resources preferentially to self-maintenance at the expense of parental care (e.g., Velando and Alonso-Álvarez 2003). On the contrary, under favorable conditions, parents may invest in reproduction without compromising their future survival (e.g., Weimerskirch et al. 2000, 2001) or may be willing to risk some of their future survival in order to produce young of high reproductive value (Erikstad et al. 1998). Moreover, it has been proposed that indication of reproductive quality may promote matching responses by mates (Johnstone and Hinde 2006), thus reducing the conflict over care. Studies performed in passerines agree with this idea (Lifjeld and Slagsvold 1991; Halkin 1997; Hinde 2006). Nevertheless, because of parental sex differences in the way that care is provided, parents may differ in the information they derive regarding offspring value (Halkin 1997). For instance, female birds profoundly influence offspring quality through maternal effects transferred to the eggs (Mousseau and Fox 1998; Mousseau et al. 2009) and may even attempt to manipulate paternal effort through the deposition of yolk hormones that affect offspring competitiveness and developmental rate (Müller et al. 2007). Exploring how mates exchange information regarding reproductive value and how this information affects the intersexual conflict over care may help us to understand the observed patterns of parental care (Jones et al. 2002; Harrison et al. 2009).

Blue-green eggshell coloration in species with biparental care may function as a post-mating female signal of quality to their mates (Moreno and Osorno 2003). The hypothesis is based on the idea that the pigment responsible for blue-green eggshell coloration, biliverdin, is a potent antioxidant in vitro (e.g., McDonagh 2001; Falchuk et al. 2002). Therefore, blue-green egg pigmentation could be costly in terms of the female's antioxidant defenses (Moreno and Osorno 2003), which has received experimental (Morales et al. 2008) and correlative support (Hanley et al. 2008). Also, the amount of biliverdin in the eggshell has been shown to relate with female body condition in the spotless starling *Sturnus unicolor* (López-Rull et al. 2008). Previous evidence in passerines indicates that blue-green egg coloration may reflect female quality traits (Moreno et al. 2005; Siefferman et al. 2006; Krist and Grim 2007; Soler et al. 2008), the nutritional conditions experienced at egg laying (Moreno et al. 2006a), and the quality of maternal effects transferred to the eggs, otherwise cryptic to the male (Morales et al. 2006; Hargitai et al. 2008; but see Cassey et al. 2008). Therefore, females may use blue-green egg coloration as a way to communicate the reproductive value to males. Interestingly, the bluer the eggs, the more care males allocate to offspring, both in comparative (Soler et al. 2005) and intra-specific studies (Moreno et al. 2006b; Hanley et al. 2008; Soler et al. 2008; but see Krist and Grim 2007). An experimental increase of clutch coloration in the pied flycatcher resulted in enhanced nestling condition (Moreno et al. 2008). Furthermore, blue-green egg coloration predicts the degree of polygyny in passerines (Soler et al. 2005).

However, blue-green egg pigmentation is also common in longlived socially monogamous species, such as seabirds and raptors, where the signaling hypothesis has only been tested in ring-billed gulls, *Larus delawarensis* (Hanley and Doucet 2009). In the latter experimental study, blue-green egg color was not associated with male individual effort after hatching or with female condition (Hanley and Doucet 2009). The allocation of resources to parental care is of particular interest in longlived species, where current reproductive investment and pair coordination may have large negative effects on lifetime reproductive success (Drent and Daan 1980; Linden and Møller 1989; Clutton-Brock 1991; Black 1996). In a recent review that questions egg coloration as a sexually selected signal, Reynolds et al. (2009) highlight that we still need to understand much more about the interactions between males and females at the nest and about the opportunities for males to see the eggs. Many longlived bird species exhibit prolonged biparental care already during incubation, when the stimulus of the egg is clearly visible for males. Yet, blue-green egg coloration has not been studied in relation to incubation patterns.

The blue-footed booby (*Sula nebouxii*) is an interesting candidate model species for examining the role of blue-green eggshell coloration in the sharing of parental care. Both sexes share long incubation (around 40 days) and chick brooding periods (Nelson 1978; Guerra and Drummond 1995), as well as parental provisioning over this relatively long visiting period (140 days; Torres and Drummond 1999). Greater male incubation, which increases pair matching in incubation bouts, is known to enhance hatching success (García-Peña 2005) and offspring survival (Nelson 2005). Fresh eggs show a distinctly blue shell color. Thus, as in other species, blue-green eggshell color could provide information about reproductive value (Morales et al. 2006; Hargitai et al. 2008). In the blue-footed booby, as in other sulids, the shell is covered with a chalky layer of calcium carbonate, which becomes discolored and scratched soon after laying (Nelson 2005). Interestingly, both parents exhibit their highest rates of nest attendance as laying approaches, coinciding with the peak of intra- and extra-pair copulations (Osorio-Beristain and Drummond 1998). Furthermore, females allow males to see freshly laid eggs in a conspicuous manner, sometimes including parading and nest building movements (J. Morales and A. Velando, pers. observation; see Nelson 1978 in the north Atlantic gannet, *Sula bassana*). In addition, nest desertion often occurs soon after laying (Nelson 1978), males being more prompt to reduce parental care or even destroy the clutch when paternity is in doubt (Osorio-Beristain and Drummond 2001). All this poses an intriguing scenario at laying, because males are present at the nest when colorful eggs are laid and their color is still fresh, prior to any fading or discoloration.

In this study, we experimentally explored if blue-green egg color affected male and female incubation effort in the blue-footed booby. If blue-green egg color is positively associated with female quality traits (e.g., Moreno et al. 2005; Soler et al. 2008), males may respond to female quality and not to blue-green egg coloration itself. Therefore, we performed a cross-fostering experiment in order to separate egg color effects from other aspects of female quality. We searched for freshly laid first eggs and exchanged them between nests of the same laying date. As soon as eggs were exchanged, we recorded incubation behavior performed by both adults on the laying day and throughout the following 4 days. We predicted that egg color would affect the incubation pattern and reduce nest desertion. Also, we analyzed if eggshells in the study species contained biliverdin pigment.

Materials and methods

Field methods

We carried out the cross-fostering experiment in the breeding colony of the blue-footed booby *S. nebouxii* at Isla Isabel, Nayarit, Mexico, in February 2007. On the laying day and during the following 4 days, we searched for freshly laid first eggs every 1 or 2 h from 10:30 to 17:30 hours. Fresh eggs are easily detected, as their eggshell appears clean, blue, and wet. The blue-green eggshell color starts fading quickly, which in most cases is perceived visually throughout the laying day. Figure 1 shows the average sequential discoloration of two blue-footed booby eggs from different nests, represented by three reflectance spectra obtained on the laying day, on the first and on the second day after laying. Before obtaining the reflectance spectra of each egg, we gently rubbed the outer layer of the shell with a moist cotton cloth with water. Thus, the pattern of color loss that we represent is conservative, as the coloration perceived by the parents would be subject to the fading we report as well as discoloration from postlaying activities at the nest.

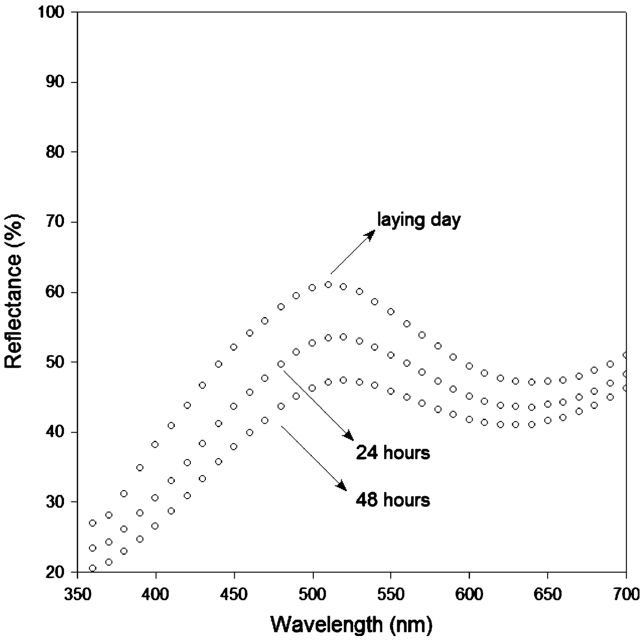

Fig. 1 Sequential discoloration of two blue-footed booby eggs from different nests, represented by three reflectance spectra obtained, respectively, on the laying day and 24 and 48 h later. Spectra represent the average reflectance of both eggs at each wavelength

As soon as we detected fresh first eggs, we estimated their volume in mm^3 ($0.51 \times \text{length} \times \text{width}^2$) and swapped them between nests of the same laying date ($n=32$ nests). To explore whether blue-footed booby eggshells contained biliverdin pigment, we collected five fresh eggs from nests that were not included in the experiment. Egg exchanges were performed as quickly as possible between close nests (no farther than 20 m apart). Alternative approaches such as keeping males in captivity before egg laying to prevent them from observing their original eggs would not be appropriate. Males removed from the territory for 10–12 h on a single day during the females' supposed fertile period (1–5 days before the first egg was laid) expelled the first laid egg from the nest (Osorio-Beristain and Drummond 2001). Egg measurements and color estimation were completed in 2 min in all cases. To measure eggshell color, we placed eggs directly on a target mask (diameter 1 cm) of a CM-2600d portable spectrophotometer (Minolta Co. Ltd., Osaka, Japan). The reflectance spectra for each egg were automatically obtained as means of three sequential measurements of each egg by changing the position of the egg with respect to the apparatus. Eggs completely filled the measuring port. Blue-green chroma (hereafter called "egg color") was calculated as the proportion of reflectance in the blue-green part of the spectrum ($R_{400–570}/R_{360–700}$), following Siefferman et al. (2006) and Moreno et al. (2006a). Blue-footed boobies show maximum visual sensitivity between 460 and 620 nm (Reed 1987), coinciding to a large extent with the curve of egg color. The coefficient of variation of blue-green egg coloration in the study population was 0.023 (mean ± SE, 0.551±0.002). The mean change in eggshell color in each nest was calculated as swapped minus original color (0.005±0.004).

On the laying day and on the following 4 days, each experimental pair was monitored hourly with the aid of binoculars in order to record which sex was incubating. The number of observers was kept at minimum (two) in order to avoid disturbance in the colony. In this species, foraging activities and the periods of greatest courtship are restricted to daylight hours (Torres and Velando 2005; Zavalaga et al. 2007), suggesting that incubation turns during daylight hours may better reflect parental investment in relation to incubation costs. There is a marked difference between the sexes in physical appearance (eye color and body size) and behavior, which allows sex discrimination visually (Nelson 1978). On the laying day, observations were performed hourly from the moment in which eggs were swapped until 17:30 hours, while for the following 4 days, observations were done every hour from 7:30 until 17:30 hours. Male and female incubation effort were estimated as the sum of observations in which, respectively, the male or the female were found incubating, divided by the total number of observations performed. For each experimental pair, we calculated pair matching in incubation effort as the absolute value of female minus male number of observations divided by the total number of observations performed. Parents never left the nest unattended (unless they deserted) so either the male or the female were found incubating in the hourly records. Thus, among coordinated pairs, there were no cases in which both adults "agreed" to spend either less or more time incubating. In all cases, as pair matching increases, the number of records in which each adult was found incubating was closer to half the total number of observations. Finally, we counted the number of shifts in incubation turns (hereafter "nest reliefs") performed by each pair, divided by the total number of observations. We decided to test the relationships between egg color and incubation parameters only for the following 4 days after laying, as on the laying day, the number of records was very low and variable (mean ± SE number of observations: 6.8±0.4 compared with 44.0±0.0 on the following 4 days) and blue-footed boobies usually perform long incubation shifts (Nelson 1978). Also, incubation behavior on the laying date could have been altered due to our disturbance while swapping eggs. On average, pairs performed 7.0±0.3 nest reliefs on the following 4 days after laying. The number of net reliefs was not associated with pair matching in incubation ($\chi_{1,17}{}^2=0.58$, $p=0.45$).

Three pairs deserted just after manipulation and nine more on the following days after laying. We excluded all the abandoned nests, as we had less than four observations for them. On average, roughly 30% of blue-footed booby clutches are abandoned during incubation in normal years (Nelson 1978) and may reach 85% during an El Niño year (García-Peña 2005). In our study, which was conducted in a weak El Niño year, 12 pairs deserted (i.e., 37.5%). Thus, the proportion of abandoned clutches in our experiment is within the natural range.

Pigment analysis

The eggshells from collected eggs were broken in small pieces and kept in Eppendorf tubes in liquid nitrogen until laboratory analyses. Biliverdin was detected by high-performance liquid chromatography (HPLC) following Mateo et al. (2004) with the modifications described in Moreno et al. (2006a). Biliverdin was extracted from individual eggshells by adding, in this order, 0.6 ml of acetonitrile and 0.5 ml of HCl 3 N in glass vials. After 5 min of the addition of reagents, the vials were vortexed for 15 s and sonicated for 10 s. Samples were then centrifuged for 10 min at 12,000 rpm, and 0.35 ml of organic supernatant was transferred to glass vials for HPLC. The UV detection was performed at 377-nm wavelength (the peak of absorbance of biliverdin). The standard of biliverdin showed a retention time of 8.4 min (Frontier Scientific Europe, Carnforth, UK).

Statistical analyses

We used SAS software (SAS Institute 2001) for statistical analyses. As incubation efforts were estimated as proportions of the total number of observations performed, we fitted generalized linear models (GENMOD procedure in SAS) with binomial distribution to test whether the incubation patterns (male absolute incubation effort, pair matching in incubation effort, and the number of nest reliefs) were affected by the original and swapped egg color, which were included together as covariates (see Zuur et al. 2009). The original and swapped egg volume, laying date, and the interaction between the original and the swapped egg color were also included as covariates. We fitted a similar model (with binomial distribution and with the same covariates), including the probability of nest desertion as dependent variable. Final models were obtained by a backward deletion procedure; first, the interaction term and then the other covariates were removed from the full model when the variance explained did not significantly improve the model (α=0.05). The odds (odds ratio (OR)) of the effects (an estimation of effect size in logistic regression) of the original and swapped egg color were calculated for an increase in color of 0.005, which is the mean change between swapped and original eggs (OR was the exponential of the slope multiplied by 0.005; see Hosmer and Lemeshow 1989, for the calculation of OR in logistic regression with continuous dependent variables).

Results

The color of the original eggs was not related with the color of swapped eggs (r=0.16, p=0.42). There was neither an association between the volume of original and swapped eggs (r=0.01, p=0.94). The color and volume of original eggs were not associated (r=0.14, p=0.49). The same was true for the color and volume of swapped eggs (r=0.14, p=0.47). We found that all collected eggshell samples (n= 5) contained biliverdin pigment. Thus, a single peak with a retention time of 8.4 min was found, identified as biliverdin by the standard.

On the 4 days after laying, male absolute incubation effort was not related to any explanatory variable (all p>0.13). Interestingly, pair matching in incubation effort was associated with the original egg color, so that the more pigmented the original egg, the higher the pair matching ($\chi_{1,17}{}^2$=7.93, p=0.005; Fig. 2; all other p>0.19). Thus, for example, pairs matched their incubation effort (on average, 0.11±0.02; Fig. 2) above certain value of blue-green egg coloration (0.555) compared with pairs that had originally paler eggs (0.36±0.07; Fig. 2); this suggests a stronger conflict over parental care in the latter group. The 95% confidence intervals of the slopes for the original and swapped egg color were (−76.84, −11.25) and (−69.44, 15.17), respectively. Estimated odds were 0.80 and 0.87, respectively, for the original and swapped egg color. The number of nest reliefs was not related to any incubation parameter (all p>0.16; 95% confidence limits: original egg color (−9.09, 7.13) and swapped egg color (−15.68, 5.74)).

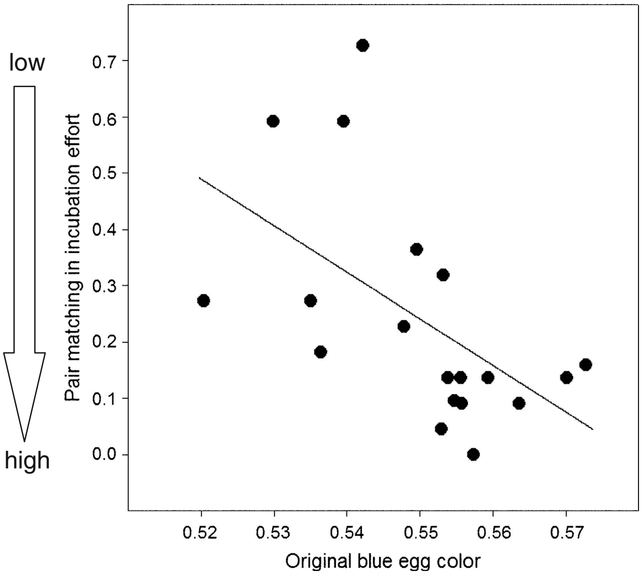

Fig. 2 Relationship between the color of the original egg (proportion of reflectance in the blue-green part of the spectrum) and pair matching in incubation effort (the absolute value of female minus male number of observations, divided by the total number of observations performed on the following 4 days after laying)

The probability of desertion (deserted or not deserted nest) was only associated with laying date ($\chi_{1,27}{}^2$=4.32; p=0.038), so that earlier pairs were more prompt to desert their nest (all other p>0.19; 95% confidence limits: original egg color (−102.84, 40.82) and swapped egg color (−62.85, 98.15)).

Discussion

Previous studies in passerines have found that blue-green egg color may induce a higher parental effort by males (Moreno et al. 2006b; Hanley et al. 2008; Soler et al. 2008). However, there has been less attention on the effect of blue-green egg coloration on the patterns of parental care in longlived species, where both sexes allocate similar care to offspring for long periods of time. In this study performed in the socially monogamous blue-footed booby, we found that, although absolute male parental effort was not affected by egg color, parental sharing in incubation was associated with the original eggshell color: the bluer the original egg, the higher the matching in incubation effort. As incubation patterns were not associated with the exchanged egg color, pair matching could be related to female (or pair) quality features correlated with the original egg color. Additionally, blue egg coloration may affect pair incubation effort and reduce the conflict over care between mates, as previously proposed for other signals of brood value (Johnstone and Hinde 2006). In any case, our results support that the reproductive value of a breeding event affects parental conflict between mates (Harrison et al. 2009).

The incubation time devoted by males to colorful clutches was not enhanced, but interestingly, was more coordinated with the mate. Egg color was associated with pair matching in incubation and not with absolute male incubation effort. Note that pair matching and absolute male (or female) incubation effort show a U-shaped (quadratic) association (r^2=0.95). Thus, for low values of egg color, males invested either less or more in incubation, while for higher values of egg color, pairs showed a coordinated effort. Since incubation effort may result in long-term fitness costs (Hanssen et al. 2004), pair matching in colorful clutches probably reflects a lower pair conflict during incubation shifts (i.e., similar costs shared by both parents). Enhanced matching during incubation prevents overcompensation for the low effort performed by the mate and facilitates that both adults spend similar time foraging and engaging in self-maintenance activities. Besides, low matching during incubation could reduce the feeding efficiency of one parent, therefore increasing the probability of reproductive failure (Bukacińska et al. 1996). Hence, coordination in incubation may enhance reproductive success and possibly reduce the conflict over care (Jones et al. 2002). Accordingly, pair matching in incubation has been found to reduce nest failure in the blue-footed booby (the probability of hatching success is higher in nests where males incubate between 50% and 64% of the time; García-Peña 2005), which agrees with previous evidence in other longlived seabirds (e.g., Burger 1987; Morris 1987; Bukacińska et al. 1996; Booth et al. 2000). In addition, a more equal sharing of incubation may allow females to recover from laying effort (Houston et al. 1983; Alonso-Alvarez et al. 2002; Öst et al. 2002). In our study, blue-green egg coloration may have affected parental conflict by inducing pair coordination rather than male incubation effort alone. Nevertheless, we cannot infer from incubation records whether coordination was initiated by the male, the female, or both, as incubation behavior of mates may interfere with each other (see for instance Alonso-Alvarez 2001). Further studies are needed to disentangle these possibilities.

By swapping the eggs we tried to disassociate female quality from egg coloration, to determine if pairs coordinated based on egg cues or female cues. We found that the color of the original egg was associated with the incubation pattern, while the color of the exchanged egg did not. Since we found enhanced pair matching in original colorful clutches (i.e., before egg swapping), we cannot separate the effect of egg color from other female quality features correlated with the original egg color. Previous studies in Passerines have found that biliverdin-based egg coloration reflects female quality (Moreno et al. 2005; Siefferman et al. 2006; Krist and Grim 2007; Soler et al. 2008). In a previous study in ring-billed gulls the association between blue eggshell color and paternal care after hatching was compared between control and experimental nests where eggs had been cross-fostered at the beginning of incubation (Hanley and Doucet 2009). Egg color was associated with proportional male feeding in control nests but not in cross-fostered ones (Hanley and Doucet 2009), which may support that male feeding effort was affected by other not measured female traits that in turn were associated with egg color. Our results may also suggest that blue-green egg coloration reflects female quality. Nevertheless, egg volume or laying date, known to be related with female quality in the study species (Beamonte-Barrientos et al. in press), were not associated with pair matching during incubation. In addition, egg color was not associated with egg volume neither in original nor in swapped eggs. At present evidence, pair matching seems not clearly affected by female cues correlated with egg color. Nonetheless, we cannot exclude that high-quality females laid bluer eggs and were more likely to mate with high-quality males, high-quality pairs being more coordinated.

Another explanation for our results is that the color of the original egg, which is conspicuous during a short period after laying, affected the patterns of parental care during incubation. Males are usually present at the nest during the laying event (Nelson 1978) and can observe freshly laid eggs with peak values of eggshell color. Also, it has been proposed that the first sight of the egg by males releases the appropriate incubation behavior in sulids (Nelson 1978). In species where males provide a large amount of parental care, signals indicative of reproductive value are expected to evolve (Trivers 1972; Black 1996; Cunningham and Birkhead 1998; Wachtmeister 2001). Biliverdin-based eggshell coloration in Passerines reflects egg quality traits, such as the amount of maternal antibodies and carotenoids transferred to the egg (Morales et al. 2006; Hargitai et al. 2008). Therefore, we may expect that biliverdin-based eggshell coloration in the study species conveys information about reproductive quality. In the blue-footed booby, females also display sexually selected colorful blue feet after laying (Torres and Velando 2003, 2005). However, this trait is traded-off against egg quality (Morales et al. 2009a) and probably does not inform directly about the reproductive value of eggs (Chenoweth et al. 2006). Additional information about the clutch value is expected to reduce the constraint imposed by fecundity costs on the elaboration of female sexually selected traits (Fitzpatrick et al. 1995; Chenoweth et al. 2006).

Our findings suggest that pair matching in incubation is associated with female (or pair) quality traits correlated with egg color. Additionally, egg color may enhance pair matching in incubation, the signal being functional only during a short period close to laying. In any case, our study highlights the role of reproductive value (clutch or female quality) on parental conflict between mates. More studies should test the role of egg coloration in signaling maternal quality. Biliverdin-based eggshell pigmentation could directly affect the embryo due to anti-bacterial properties, as proposed by Soler et al. (2008), or as a free-radical scavenger against oxidative stress.

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