

# Safe betting: males help dull females only when they raise high-quality offspring

Judith Morales · Roxana Torres · Alberto Velando

Received: 16 March 2011 / Revised: 7 September 2011 / Accepted: 10 September 2011  
© Springer-Verlag 2011

**Abstract** In evolutionary biology, whether parents should enhance or reduce parental care according to mate ornamentation is a subject of great debate. However, the evolution of female ornaments can shed light on this question. In theory, female ornamentation should be traded off against fecundity and thus cannot be wholly informative to males without a direct indication of fecundity. Hence, direct cues of offspring quality should affect the relationship between male investment and female ornamentation. Under this hypothesis, we manipulated two direct cues of offspring quality (egg size and color) after first egg laying in the blue-footed booby and registered male incubation patterns. In this species, foot color is a dynamic signal of current condition and in females is traded off with egg size. We found that males spent more time incubating when paired with dull females but only in nests with large eggs. Males also spent less time incubating small dull eggs.

Results indicate that egg size, a direct cue of reproductive value, affected the relationship between male effort and female ornamentation. Males may be willing to help females that have invested in offspring at the expense of ornamentation, which suggests compensation when females are in low condition. Another possibility is that males relax their effort when paired with highly ornamented and fecund females because they have high parenting abilities. Our findings suggest that the information conveyed by female ornaments may depend on direct cues of fecundity. Results also highlight that parental decisions are complex, modulated by a combination of information sources.

**Keywords** Differential allocation · Eggshell color · Information exchange · Life history tradeoffs · Parental care · Reproductive compensation · Reproductive value · *Sula nebouxii*

Communicated by S. Pruett-Jones

J. Morales (✉) · A. Velando  
Departamento de Ecología e Biología Animal,  
Facultade de Ciencias, Universidade de Vigo,  
36310 Vigo, Spain  
e-mail: jmorales@mncn.csic.es

R. Torres  
Departamento de Ecología Evolutiva,  
Laboratorio de Conducta Animal, Instituto de Ecología,  
Universidad Nacional Autónoma de México,  
AP 70-275,  
México DF 04510, Mexico

*Present Address:*

J. Morales  
Departamento de Ecología Evolutiva,  
Museo Nacional de Ciencias Naturales (CSIC),  
José Gutiérrez Abascal 2,  
28006 Madrid, Spain

## Introduction

One of the most fundamental decisions that sexually reproducing organisms face is how much of the resources available to them should be spent on a particular breeding attempt. In iteroparous species, any investment to increase the fitness of current offspring evokes costs in terms of future reproductive prospects (Williams 1966; Stearns 1992). Hence, long-lived species are more reluctant to increase current reproductive effort than are short-lived ones (Stearns 1992). Due to the trade-off between present and future reproduction, there is potential conflict between the male and the female parents over how much parental investment each should give (Trivers 1972). Particularly, in monogamous species, intersexual conflict may continue well after the partner has been chosen and arise over

parental duties such as incubation and feeding the young (Winkler 1987; Lessells 1999). Yet, when the costs in terms of future reproduction can be compensated for higher survival or reproductive success of current offspring, parents are expected to increase their current investment (Trivers 1972). Thus, the outcome of sexual conflict should be intimately associated with direct cues of current reproductive value (e.g., offspring size; Winkler and Wallin 1987; Davis et al. 1999).

One factor that may affect the fitness value of current reproduction (and thus parental conflict resolution) is the phenotypic or genetic quality of the mate relative to that of expected future mates. Therefore, it is thought that individuals should invest in parental care according to their mates' physical or behavioral attributes (e.g., ornamentation) if they obtain immediate benefits, such as access to food or mates' parental care (e.g., Hoelzer 1989), or indirect genetic benefits that increase offspring fitness (reviewed by Andersson 1994). The differential allocation theory (Burley 1986; Sheldon 2000) is built on this assumption and, in its original form, predicted that parents should invest more when paired with relatively attractive mates (Burley 1986); this positive covariation pattern would better be termed as "positive differential allocation" (Ratikainen and Kokko 2010). Support for this prediction has come from several experimental tests in a diversity of taxa (reviewed by Sheldon 2000; Harris and Uller 2009), although mostly in birds (e.g., Burley 1988; Roulin 1999; Cunningham and Russell 2000). However, other studies have found the opposite (Saino et al. 2002; Byers and Waits 2006; Bolund et al. 2009; Braga-Goncalves et al. 2010; Wiebe 2010), suggesting that individuals mated with non-preferred mates may increase their care to make up for likely offspring viability deficits ("compensation hypothesis"; Gowaty et al. 2007; Gowaty 2008). Alternatively, negative covariations between parental care and mate ornamentation may simply arise from a reduction in care by individuals paired with high-quality mates as revealed by ornaments ("negative differential allocation"; Ratikainen and Kokko 2010). So far, it is not resolved whether differential allocation or compensation governs parental decisions. In any case, the apparent flexibility in reproductive decisions that are based on signals of quality reveals a role for information exchange in the conflict over care (Hinde and Kilner 2007; Morales et al. 2009a).

Strikingly, most experimental tests have focused on maternal effort according to male attractiveness, but very few have investigated how male effort is affected by female attractiveness (see Burley 1988; Roulin 1999; Pilastro et al. 2003; Krebs et al. 2004; Matessi et al. 2009, all of which report positive associations between male care and female ornamentation). Female ornaments are probably subject to different selection pressures than male ornaments because

females usually provide the bulk of resources for the developing offspring. When the availability of such resources constrains both fecundity and ornamentation, the evolution of sexual signals in females becomes self-limiting (Fitzpatrick et al. 1995). The logic is that if males seek direct fecundity benefits, they should avoid favoring females that invest too heavily in signals at the expense of fecundity. As a consequence, female signals for direct benefits cannot be wholly informative to males without a cue of maternal allocation in the current offspring (Chenoweth et al. 2006). However, this uncertainty can be easily remedied once the offspring are produced, since males can directly assess maternal allocation. Given the theoretical trade-off in females, would not we expect males to rely on both cues (female attractiveness and fecundity) in order to adjust parental care? Although largely neglected, the evolution of female ornamentation may shed light on the debate between differential allocation and compensation (Ratikainen and Kokko 2010).

We hypothesized that the association between male parental effort and female ornamentation is affected by direct indications of offspring quality. To test this hypothesis, we chose as model species the blue-footed booby (*Sula nebouxi*), a long-lived seabird with intense biparental care. Both sexes share long periods of incubation (ca. 46 days) and chick brooding (Nelson 1978), as well as parental provisioning (140 days; Torres and Drummond 1999). In this species, egg mass accurately predicts hatchability (D'Alba and Torres 2007). Egg color reflects nutritional resources (e.g., carotenoids) of females at laying and is suggested to favor an equal sharing of parental care between the sexes (Morales et al. 2010a, b). We thus considered egg mass and color as direct cues of offspring quality. Foot color is subject to mutual sexual selection during the courtship period, prior to laying (Torres and Velando 2003, 2005). It is a highly dynamic trait that reflects current nutritional condition (Velando et al. 2006) and parental ability in males (Velando et al. 2005). Dynamic condition-dependent ornaments play a crucial role in the conflict over care, as they can be used to continuously evaluate the quality of partners and their parental ability (Torres and Velando 2010). In effect, rapid change in foot color causes parallel variation in mate investment (Velando et al. 2006; Dentressangle et al. 2008; Torres and Velando 2010). Intriguingly, the theoretical trade-off between female ornamentation and fecundity (Fitzpatrick et al. 1995) is supported in the study species. Correlative evidence indicates that females with larger clutches are paler (Torres and Velando 2010). Moreover, there is a negative relationship between foot color and egg size when resources are scarce (Morales et al. 2009b). However, when females are provided with extra carotenoids at laying, there is a positive association between both traits

(Morales et al. 2009b), as may be expected when individuals enjoy high resource levels (e.g., Reznick et al. 2000; Roff and Fairbairn 2007).

After first egg laying, we manipulated egg size and color, and on the following 2 days, we observed male incubation patterns according to female ornamentation. We were interested in the incubation period because the direct cues of offspring quality, males can evaluate at this stage (e.g., egg size and color), mostly depend on maternal investment. Additionally, male incubation effort is crucial for hatching success (García-Peña 2005). We were also interested in female nest attendance (female incubating or standing by the nest) to infer whether males were obliged or not to take their incubation shifts due to female absences. Nest attendance during egg laying may prevent aggressive attacks from neighbors and may function as a mate-guarding strategy to prevent extra-pair copulations by the mate (Pérez-Staples and Drummond 2005). According to the differential allocation theory, we may predict that males increase their effort when paired with ornamented females that have produced high-quality offspring. On the other hand, according to the compensation hypothesis, males should increase their investment when paired with dull females that have not risked fecundity.

## Methods

This study was conducted in a breeding colony of the blue-footed booby located on Isabel Island, Nayarit, Mexico (21°52'N, 105°54'W), from January to March of 2008. The study complies with the current laws of Mexico. Permission to conduct the study was granted by Parque Nacional Isla Isabel and the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT). As soon as a first egg was detected, its nest was randomly assigned to one of four treatment combinations in a 2×2 factorial design: (a) large and colorful ( $n=9$  nests), (b) large and dull ( $n=12$ ), (c) small and colorful ( $n=11$ ), or (d) small and dull ( $n=11$ ).

### Experimental manipulation of egg volume

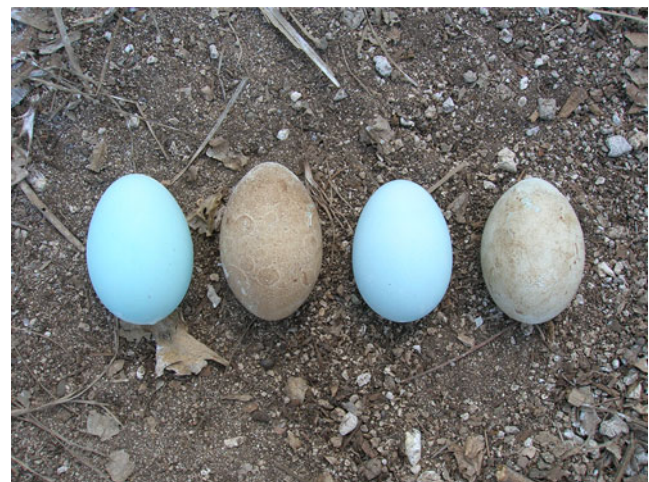
The manipulation of egg volume consisted of swapping the original first egg for a foster egg that was either large (volume, greater than 55.42 cm<sup>3</sup>) or small (volume, less than 54.28 cm<sup>3</sup>). This range was calculated with the mean volume ± SE (54.85±0.57 cm<sup>3</sup>) of the first eggs from 85 unmanipulated nests measured in the study population in 2007. We extracted the foster egg from a close non-experimental nest not farther than 20 m apart. The exact laying dates of foster eggs were not known with certainty in most cases; we tried to find nests where the birds had been seen courting very recently and were thus in an initial stage

of incubation. The original volume of first eggs did not differ between treatments ( $F_{1, 40}=0.42$ ,  $P=0.52$ ; egg volume could not be measured in one broken egg at manipulation). After manipulation, experimental groups differed roughly 25% from foster's egg volume (mean ± SE of large and small eggs, respectively, 60.85±1.10 and 47.90±1.07;  $F_{1, 41}=71.21$ ,  $P<0.001$ ). After the egg exchange, we proceeded to perform the color manipulation of the foster egg.

### Experimental manipulation of eggshell color

Fresh eggs show a distinctly blue-green color that is based on biliverdin pigmentation (Morales et al. 2010b). The shell is covered with an outermost layer, which is wet and blue in fresh eggs but soon solidifies and becomes scratched and whitish (Nelson 1978); color fading can be perceived gradually on the laying day (Morales et al. 2010b). If the whitish crust is removed with a cloth moistened with water, the blue-green color of the following lower layer comes to surface and the egg remains blue for various days (authors' personal observation). Thus, the egg color treatment consisted of either removing the shell crust of the foster egg or not, the way of obtaining nests with colorful and dull eggs (see Fig. 1).

The color of original and foster eggs after manipulation was measured with a portable spectrophotometer (MINOLTA CM-2600d, Minolta Co. Ltd, Osaka, Japan). We placed eggs directly on a target mask (diameter, 1 cm). 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. Blue-green chroma was estimated as the proportion of reflectance



**Fig. 1** Four blue-footed booby eggs photographed just after manipulation to illustrate the four treatment combinations: *from left to right* eggs are (a) large and colorful, (b) large and dull, (c) small and colorful, and (d) small and dull

between 400 and 570 nm divided by the sum of reflectance between 360 and 700 nm (Morales et al. 2010a, b). The color of the original first eggs did not differ between treatments ( $F_{1, 41}=0.21$ ,  $P=0.65$ ). After manipulation, the experimental groups differed on average of 23% from foster's egg color (mean  $\pm$  SE of colorful and dull eggs, respectively,  $0.565 \pm 0.007$  and  $0.450 \pm 0.007$ ;  $F_{1, 41}=130.66$ ;  $P<0.001$ ).

#### Foot ornamentation

At the night of laying or at the following night, we captured 37 females and 39 males (the other 6 females and 4 males were not found at capture or had deserted their nest; see the following section for details on nest desertion rate). There was no difference in male or female foot color according to Julian date, time of night when they were captured, or to whether they were captured on the night of laying or the following night (all  $P>0.11$ ). Thus, these variables were not included in the statistical models. The birds were captured at night to reduce perturbation in the colony. Handling time per bird was less than 2 min. To measure female and male foot color, reflectance spectra for each foot were automatically determined by the MINOLTA spectrophotometer as means of three sequential measures on the foot web by changing the position of the foot with respect to the apparatus. As the visual maximum sensitivity in this species occurs between 460 and 620 nm (Reed 1987), we analyzed the chroma of foot color in this range, estimated as the sum of the reflectance between 460 and 620 nm divided by the sum of reflectance between 360 and 700 nm (see Velando et al. 2006).

#### Behavioral observations

One hour after the egg exchange, we started to monitor each experimental pair with the aid of binoculars in order to record which sex was incubating and whether its mate was present at the nest or not. Blue-footed boobies are sexually dimorphic for many characteristics. Thus, differences between the sexes in physical appearance (eye color and body size) and vocal displays allow for unequivocal sex identification through observation (Nelson 1978). We performed one observation per hour for 24 h (i.e., 24 observations for each pair). All observations were performed during daylight hours (from 0630 to 1730 hours). In the blue-footed booby, foraging activities and the periods of greatest courtship are restricted to daylight hours (Torres and Velando 2005; Zavalaga et al. 2007). This suggests that incubation turns during this period of time may better reflect parental investment in relation to incubation costs. In this species, nest abandonment mostly occurs in the following hours after laying or in the following 2 days (Nelson 1978; authors' personal observation), suggesting

that this phase is important to release the appropriate incubation behavior of the pair. One observation per hour seems adequate to assess incubation effort by both mates. We have observed in this population that parents perform on average one or two changeovers per day on the following 6 days after laying (Morales and Velando, unpublished data). In addition, Nelson (1978) reports a minimum duration of incubation bouts of 4 h in males and 8 h in females. Nests were rarely left unattended and there was almost always 1 parent of either sex standing by the nest or incubating (the nest was found empty only in 8 among 900 records performed on the whole experiment). In all nests, we performed observations when the pair was incubating only the first foster egg; the blue-footed booby has a modal clutch size of two eggs, which are laid with an average interval of 5 days (D'Alba and Torres 2007). There was only one observer (JM) in order to avoid disturbance in the colony.

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 in their nest. Presence at the nest was calculated as the sum of records where each individual was found incubating plus those where the bird was not incubating but standing close to the mate, divided by the total number of observations. The number of observations differed among nests because ten pairs (23%) deserted their clutch during the experiment. It is not likely that nest desertion was due to egg manipulation, since parents seemed to accept the foster egg (note that they also accept eggs from common hens; García-Peña 2005). All eggs that were eventually deserted were incubated during various hours by both parents, except for one that was incubated only for 1 hour by the female. In this population, on average, 53% of the nests are abandoned during egg laying and incubation (range over 18 breeding seasons, 24–93%; Ancona et al. 2011). Thus, the proportion of abandoned clutches in our experiment was within the natural range. As soon as behavioral observations were completed, foster eggs were again exchanged for original eggs and put back in their nest (except in those cases where pairs had deserted their nest) to avoid that the natural incubation period of both nests was either shortened or lengthened.

#### Statistical analyses

As incubation efforts were estimated as proportions of the total number of observations performed, we fitted one generalized linear model with binomial distribution to test whether male incubation effort was affected by the experimental manipulations. The full model included the following independent variables: volume manipulation (large or small egg), color manipulation (colorful or dull

egg), the original egg volume and color, female foot color after laying, male foot color after laying, and the relevant double interactions (volume manipulation×color manipulation, volume manipulation×female foot color, color manipulation×female foot color). Female and male foot color after laying were not related with each other or with original egg volume and color (all  $P>0.24$ ). Original egg volume was positively associated with the original egg blue-green chroma ( $F_{1, 40}=15.27, P<0.001$ ). In this model, we excluded one nest that was deserted after two observations, during which the male was not found and probably did not see the exchanged egg. Then, the available sample size for female foot color was 36 nests. The results did not change when this nest was included (not presented but available upon request). We performed a similar model with binomial distribution to test whether nest desertion (deserted or not) was affected by the independent variables mentioned above. Interaction terms could not be included in the full model, probably because only two nests were deserted in the group with large eggs. The minimal models were obtained by a backward deletion procedure: first, the interaction terms and then the main effects were removed from the full model when the variance explained did not significantly improve the model ( $\alpha=0.05$ ). We show the  $P$  values for nonsignificant variables before excluding them from the full model. Data overdispersion was corrected using the Pearson scale parameter.

## Results

On average, males incubated more than females (mean  $\pm$  SD proportion of time spent incubating by males,  $0.51 \pm 0.16$ ; females,  $0.30 \pm 0.14$ ;  $t$  test,  $t_{36}=4.71, P<0.001$ ). Male incubation effort was not associated with female presence at the nest ( $F_{1, 34}=0.02, P=0.89$ ), suggesting that males were not forced to incubate because the female left the nest.

Male incubation effort was affected by the interaction between egg volume and color manipulations (Table 1). Small dull eggs received less incubation effort than small colorful eggs and large eggs (Fig. 2); regardless of their color, large eggs received a reasonably high incubation

effort by males (more than half the total number of observations performed; Fig. 2). The interaction between female foot color after laying and egg volume significantly affected male incubation effort (Table 1). In nests with small eggs, males devoted less incubation effort when female foot color was duller ( $\beta=0.36$ ; Fig. 3), while in nests with large eggs, males enhanced incubation effort when females showed dull feet ( $\beta=-0.62$ ; Fig. 3). Interestingly, the highest differences between these two relationships were found when female attractiveness was lowest (Fig. 3). The interaction remains significant when three outliers are removed ( $F_{1, 27}=4.79, P=0.038$ ;  $\beta=0.29$  and  $-0.98$  for small and large eggs, respectively; outliers detected with Cook's distance  $>4/(n-k-1)$ , where  $n$  is the number of cases and  $k$  the number of independent terms; Fox 1997), and the highest differences are still found when female attractiveness was lower (close to the value 0.52 of foot color in Fig. 3). All other covariates were not significant (female foot color×color manipulation,  $F_{1, 24}=0.26, P=0.62$ ; original egg color,  $F_{1, 25}=0.01, P=0.91$ ; male foot color,  $F_{1, 26}=0.14, P=0.71$ ; original egg volume,  $F_{1, 28}=3.18, P=0.09$ ).

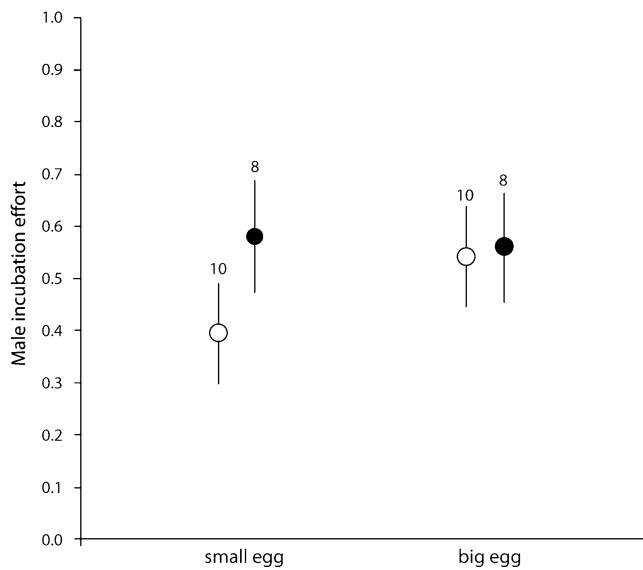
Egg volume manipulation affected nest desertion probability, larger eggs being less likely to be abandoned (Table 1). Only 2 nests were deserted among 21 with large eggs, while 8 nests were abandoned among 22 with small eggs. The rest of covariates were not significant (female foot color,  $X^2_{1, 27}=0.01, P=0.91$ ; original egg color,  $X^2_{1, 32}=0.08, P=0.77$ ; original egg volume,  $X^2_{1, 33}=0.45, P=0.50$ ; color manipulation,  $X^2_{1, 35}=1.64, P=0.20$ ). There was a nonsignificant association between male foot color after laying and nest desertion probability ( $X^2_{1, 36}=3.50, P=0.06$ ; nests were more likely to be deserted when male foot color was high).

## Discussion

Male incubation effort measured during our experiment seemed representative of the whole incubation period; previous observations performed after egg laying to the end of the incubation indicate that males incubate on

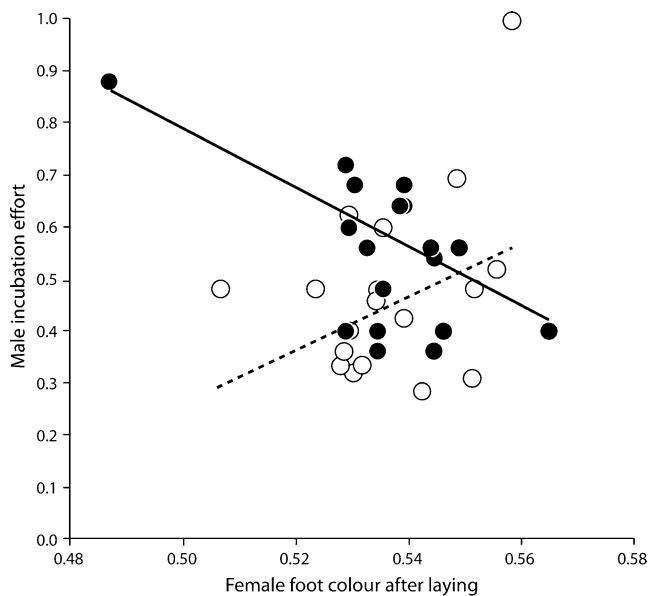
**Table 1** Final generalized linear models (GENMOD procedure in SAS) with binomial distribution showing the significant effects on male incubation effort (expressed as a proportion of the total number of observations performed) and on the rate of nest abandonment ( $X^2$  values are shown because the variable only admits two possibilities: deserted or not)

	Male incubation effort			Nest abandonment		
	$F$	$df$	$P$	$X^2$	$df$	$P$
Volume manipulation	13.98	1, 30	<0.001	4.59	1, 41	0.032
Color manipulation	5.34	1, 30	0.028			
Female foot color	0.20	1, 30	0.660			
Volume manipulation×color manipulation	5.31	1, 30	0.028			
Volume manipulation×female foot color	13.77	1, 30	<0.001			



**Fig. 2** Effect of the interaction between the manipulations of first egg volume and color on male incubation effort (no. of observations in which the male was found incubating divided by the total number of observations performed at the nest). *Full dots* are colorful eggs and *empty dots* are dull eggs. Values are means  $\pm$  SE. Sample sizes are reported *over the bars*

average during 52% of the time (García-Peña 2005) vs. 51% in our study. Importantly, male effort was not related



**Fig. 3** Effect of the interaction between egg volume manipulation and female foot color (chroma) after laying on male incubation effort (no. of observations in which the male was found incubating divided by the total number of observations performed at the nest). *Full dots and solid line* are big eggs and *empty dots and dotted line* are small eggs. *Lines* represent the values of male incubation effort predicted by the model. The interaction remains significant when three outliers are removed (see “Results” section)

to female nest attendance, which suggests that males were not “forced” to incubate because of females' absences.

Male incubation effort was influenced by the interaction between egg volume and color manipulations. Large eggs, independent of their color, received higher incubation effort by males (roughly half of the total number of observations) and were less likely to be abandoned than small eggs. On the contrary, small dull eggs received significantly less paternal care. Previous evidence in this species indicates that heavier eggs show higher hatching success and produce heavier hatchlings (D'Alba and Torres 2007; in the current study, egg mass was strongly associated with egg volume, adjusted  $r^2=0.98$ ). Small but colorful eggs received as much paternal effort as large ones, suggesting that egg color reduced the conflict over care in nests with a small egg. This is the first experimental evidence that eggshell color affects male incubation behavior in birds. In the blue-footed booby, blue egg color reflects nutritional resources (e.g., carotenoids) of females at laying (Morales et al. 2010a) and is related to parental coordination during incubation (i.e., equal sharing of incubation; Morales et al. 2010b). If egg color signals female quality to males (as hypothesized by Moreno and Osorno 2003), our results regarding egg color would partly support positive differential allocation by males. Additionally, egg color could directly affect fitness if the embryo benefited from shell biliverdin pigment, a molecule with strong immunostimulant and antioxidant properties (Stocker et al. 1987). However, egg color did not affect the probability of nest desertion (supporting previous results in the study population; Morales et al. 2010b), which indicates that egg size might be a more important cue in the decision to desert the nest.

As expected, male care was affected by the interaction between female foot color and egg volume manipulation. When females showed colorful feet, males cared similarly for small and large eggs. However, when female foot color was dull, an indication of low nutritional condition (Velando et al. 2006), males incubated more in nests with a large egg. This result suggests that female foot coloration conveys relevant information to mates when combined with direct information on fecundity. Given that female blue-footed boobies suffer a trade-off between resource allocation to egg size and foot color (Morales et al. 2009b), one possibility is that egg size is used by males as an indicator of how much the female has invested in offspring relative to signaling. Thus, by looking at female foot color and egg volume, males can favor dull females that have not risked fecundity for ornamentation, a pattern that points to the idea of compensation. On the other hand, females could manipulate males by reducing ornamentation and, thus, by pretending low condition (regulation of body reserves has been suggested as a strategy to force mates to provide care; Barta et al. 2002; Osorno and Székely 2004). But, if this was the case, they could only manipulate

males after a high investment in eggs. It is surprising, though, that males did not work harder for females that were superior in all regards (highly attractive and with high-quality offspring), as expected by positive differential allocation. One likely explanation is that males reduced care in nests of “super females” because highly ornamented females are in good body condition and can thus provide more care than pale ones (note that foot color signals parental ability in males; Velando et al. 2005). This possibility would not necessarily support the hypothesis of compensation, because rather than improving on an adverse situation males would be merely relaxing their investment level when their mate is in good condition (i.e., “negative differential allocation” according to Ratikainen and Kokko 2010). Measuring the change in foot color from the day before laying to the laying day would help to interpret our results, although it would require the researchers' ability to detect the pre-laying state of females. In any case, our results indicate that information on reproductive value affected the relationship between male incubation effort and female ornamentation, and even if males were able to directly assess offspring quality, the mate's foot color conveyed useful information to them.

One of the intriguing features of the color display in the feet of blue-footed boobies is its dynamic change in a few hours. Given that they respond according to rapid changes in condition, short-term dynamic signals might be the most accurate indicators of mate current quality (Folstad and Carter 1992; Hill et al. 1999). This flexibility in signaling is key during the sexual conflict over care, since parents may evaluate each other continuously and adjust their investment in offspring accordingly (Torres and Velando 2010). Blue-footed booby parents might express dynamic signals of condition to exchange information about their current ability to provide care (Velando et al. 2005). This is probably critical after laying, when females have just allocated the bulk of resources to eggs. Our results differ from those found in species where female ornaments are less dynamic (Burley 1988; Roulin 1999; Pilastro et al. 2003; Krebs et al. 2004; Matessi et al. 2009) or reflect genetic quality rather than immediate benefits (Roulin et al. 2010). The resolution of parental conflict might be different in these cases where it may pay males to help highly ornamented mates. Indeed, all these studies found positive associations between female ornamentation and male effort, but it would be very interesting to test whether current offspring value may affect these associations. We found that male foot color was not related with incubation effort, but nest desertion probability showed a nonsignificant tendency to increase with male ornamentation. Highly ornamented males could be young individuals with low reproductive experience or those seeking extra-pair copulations. We could not assess male age in this study neither could we test

whether male ornamentation in interaction with egg color or size manipulations played a role in nest desertion. Further studies should investigate the interplay between dynamic male and female ornamentation on the conflict over care.

To conclude, we found that the association between male parental effort and female ornamentation was conditioned by egg volume, a direct cue of offspring value. Results support that parental decisions are complex, modulated by a combination of information sources, and highlight the role of signals in the outcome of sexual conflict (Hinde and Kilner 2007; Morales et al. 2009a). Foot color conveys accurate information about female's current condition and parental ability, a message that seems to release different male responses in different reproductive phases. Blue-footed booby males prefer colored females during the courtship period before laying (Torres and Velando 2005). Our results suggest that males either compensate for dull females with large eggs or perform negative differential allocation when paired with superior females during incubation. Thus, the information conveyed by female signals to males is probably plastic and depends on direct cues of fecundity. These findings highlight that both differential allocation and compensation are possible under different circumstances. Any covariation pattern between investment and mate's signaling is only a part of a more complex picture and depends on a tangle of relationships with other life history traits and information sources (see Harris and Uller 2009). Endeavors to fit a determined covariation pattern into the predictions of compensation or differential allocation may oversimplify our vision of parental strategies, since both processes may arise from the same life history principles and even pose non-opposing predictions (Ratikainen and Kokko 2010).

**Acknowledgments** We are grateful to four anonymous reviewers for valuable and constructive comments. We thank René Beamonte-Barrientos, Natalia Lifshitz, and Alejandro Mendez for help in the field. We thank the fisherman from San Blas and Camichín, the staff from Parque Nacional Isla Isabel, and the Armada de México for logistic support. SEMARNAT gave working permissions and approved the research. This work was supported by the Universidad Nacional Autónoma de México (PAPIIT IN211406, IN228309), Consejo Nacional de Ciencia y Tecnología (47599, 81823) of México, Ministerio de Ciencia e Innovación (CGL2006-10357-C02-01/CGL2009-10883-C02-01 and Juan de la Cierva fellowship to JM) of Spain, and a research grant (2007) from the Association for the Study of Animal Behaviour to JM.

## References

- Ancona S, Sánchez-Colón S, Rodríguez C, Drummond H (2011) El niño in the warm tropics: local sea temperature predicts breeding parameters and growth of blue-footed boobies. *J Anim Ecol* 80:799–808
- Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton

- Barta Z, Houston AI, McNamara JM, Székely T (2002) Sexual conflict about parental care: the role of reverses. *Am Nat* 159:687–705
- Bolund E, Schielzeth H, Forstmeier W (2009) Compensatory investment in zebra finches: females lay larger eggs when paired to sexually unattractive males. *Proc R Soc Lond B* 276:707–715
- Braga-Goncalves I, Mobley KB, Ahnesjö I, Sagebakken G, Jones AG, Kvarnemo C (2010) Reproductive compensation in broad-nose pipefish females. *Proc R Soc Lond B* 277:1581–1587
- Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. *Am Nat* 127:415–445
- Burley N (1988) The differential allocation hypothesis: an experimental test. *Am Nat* 132:611–628
- Byers JA, Waits L (2006) Good genes sexual selection in nature. *Proc Natl Acad Sci U S A* 103:16343–16345
- Chenoweth SF, Doughty P, Kokko H (2006) Can non-directional male mating preferences facilitate honest female ornamentation? *Ecol Lett* 9:179–184
- Cunningham EJA, Russell AF (2000) Egg investment is influenced by male attractiveness in the mallard. *Nature* 404:74–77
- D'Alba L, Torres R (2007) Seasonal egg-mass variation and laying sequence in a bird with facultative brood reduction. *Auk* 124:643–652
- Davis JN, Todd PM, Bullock S (1999) Environmental quality predicts parental provisioning decisions. *Proc R Soc Lond B* 266:1791–1797
- Dentressangle F, Boeck L, Torres R (2008) Maternal investment in eggs is affected by male feet colour and breeding conditions in the blue-footed booby, *Sula nebouxi*. *Behav Ecol Sociobiol* 62:1899–1908
- Fitzpatrick S, Berglund A, Rosenqvist G (1995) Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biol J Linn Soc* 55:251–260
- Folstad I, Carter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Fox J (1997) Applied regression analysis, linear models, and related methods. Sage, Thousand Oaks
- García-Peña GE (2005) Efectos y costos de la termorregulación durante la incubación del ave marina *Sula nebouxi*. Mater thesis, Universidad Autónoma Nacional de México, México
- Gowaty PA (2008) Reproductive compensation. *J Evol Biol* 21:1189–1200
- Gowaty PA, Anderson WW, Bluhm CK, Drickamer LC, Kim YK, Moore AJ (2007) The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. *Proc Natl Acad Sci U S A* 104:15023–15027
- Harris WE, Uller T (2009) Reproductive investment when mate quality varies: differential allocation versus reproductive compensation. *Phil Trans R Soc B* 364:1039–1048
- Hill JA, Enstrom DA, Ketterson ED, Nolan V Jr, Ziegenfus C (1999) Mate choice based on static versus dynamic secondary sexual traits in the dark-eyed junco. *Behav Ecol* 10:1–96
- Hinde CA, Kilner RM (2007) Negotiations within the family over the supply of parental care. *Proc R Soc Lond B* 274:53–60
- Hoelzer GA (1989) The good parent process of sexual selection. *Anim Behav* 38:1067–1078
- Krebs EA, Hunte W, Green D (2004) Plume variation, breeding performance and extra-pair copulations in the cattle egret. *Behaviour* 141:479–499
- Lessells CM (1999) Sexual conflict in animals. In: Keller L (ed) Levels of selection in evolution. Princeton University Press, Princeton, pp 75–99
- Matessi G, Carmagnani C, Griggio M, Pilastro A (2009) Male rock sparrows differentially allocate nest defence but not food provisioning to offspring. *Behaviour* 146:209–223
- Morales J, Alonso-Álvarez C, Pérez C, Torres R, Serafino E, Velando A (2009a) Families on the spot: sexual signals influence parent-offspring negotiations. *Proc R Soc Lond B* 276:2477–2483
- Morales J, Velando A, Torres R (2009b) Fecundity compromises attractiveness when pigments are scarce. *Behav Ecol* 20:117–123
- Morales J, Velando A, Torres R (2010a) Biliverdin-based egg coloration is enhanced by carotenoid supplementation. *Behav Ecol Sociobiol* 65:197–203
- Morales J, Torres R, Velando A (2010b) Parental conflict and blue egg coloration in a seabird. *Naturwissenschaften* 97:173–180
- Moreno J, Osorno JL (2003) Avian egg color and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecol Lett* 6:803–806
- Nelson JB (1978) The Sulidae: gannets and boobies. Oxford University Press, Oxford
- Osorno JL, Székely T (2004) Sexual conflict and parental care in magnificent frigatebirds: full compensation by deserted females. *Anim Behav* 68:337–342
- Pérez-Staples D, Drummond H (2005) Tactics, effectiveness and avoidance of mate guarding in the blue-footed booby. *Behav Ecol Sociobiol* 59:115–119
- Pilastro A, Griggio M, Matessi G (2003) Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment? *Anim Behav* 66:265–271
- Ratikainen II, Kokko H (2010) Differential allocation and compensation: who deserves the silver spoon? *Behav Ecol* 21:195–200
- Reed JR (1987) Scotopic and photopic spectral sensitivities of boobies. *Ethology* 76:33–55
- Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol Evol* 15:421–425
- Roff DA, Fairbairn DJ (2007) The evolution of trade-offs: where are we? *J Evol Biol* 20:433–447
- Roulin A (1999) Non-random pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behav Ecol* 10:688–695
- Roulin A, Altwegg R, Jensen H, Steinsland I, Schaub M (2010) Sex-dependent selection on an autosomal melanic female ornament promotes the evolution of sex ratio bias. *Ecol Lett* 13:616–626
- Saino N, Bertacche V, Ferrari RP, Martinelli R, Møller AP, Stradi R (2002) Carotenoid concentration in barn swallow eggs is influenced by laying order, maternal infection and paternal ornamentation. *Proc R Soc Lond B* 269:1729–1733
- Sheldon B (2000) Differential allocation: tests, mechanisms and implications. *Trends Ecol Evol* 15:398–402
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Stocker R, Yorihiro Y, McDonagh AF, Glazer AN, Ames BN (1987) Bilirubin is an antioxidant of possible physiological properties. *Science* 235:1043–1046
- Torres R, Drummond H (1999) Does large size make daughters of the blue-footed booby more expensive than sons? *J Anim Ecol* 68:1133–1141
- Torres R, Velando A (2003) A dynamic trait affects continuous pair assessment in the blue-footed booby (*Sula nebouxi*). *Behav Ecol Sociobiol* 55:65–72
- Torres R, Velando A (2005) Male preference for female foot color in the socially monogamous blue-footed booby *Sula nebouxi*. *Anim Behav* 69:59–65
- Torres R, Velando A (2010) Color in a long-lived tropical seabird: sexual selection in a life-history context. *Advances* 42:155–188
- Trivers RL (1972) Parental investment and sexual selection 1871–1971. In: Campbell BG (ed) Sexual selection and the descent of man. Aldine, Chicago, pp 136–179
- Velando A, Torres R, Espinosa I (2005) Male coloration and chick condition in blue-footed booby: a cross-fostering experiment. *Behav Ecol Sociobiol* 58:175–180
- Velando A, Beamonte-Barrientos R, Torres R (2006) Pigment-based skin colour in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. *Oecologia* 149:535–542



- Wiebe KL (2010) Negotiation of parental care when the stakes are high: experimental handicapping of one parent during incubation leads to short-term generosity. *J Anim Ecol* 79:63–70
- Williams GC (1966) Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am Nat* 100:687–690
- Winkler DW (1987) A general model of parental care. *Am Nat* 130:526–543
- Winkler DW, Wallin K (1987) Offspring size and number: a life history model linking effort per offspring and total effort. *Am Nat* 129:709–720
- Zavalaga CB, Benvenuti S, Dall'Antonia L, Emslie SD (2007) Diving behavior of blue-footed boobies *Sula nebouxii* in northern Peru in relation to sex body size and prey type. *Mar Ecol Prog Ser* 336:291–303