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## Male coloration and chick condition in blue-footed booby: a cross-fostering experiment

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**Abstract** Sexual selection models suggest that female choice is based on male traits that indicate their genetic or environmental condition, consequently enhancing her reproductive success by direct or indirect benefits. We investigated the relationship between male foot colour and offspring condition in the blue-footed booby, a socially monogamous seabird, with conspicuous and variably condition-dependent coloured feet that are selected by females. In a cross-fostering experiment, we found that chick condition was related to the foot colour of the foster father and, to some extent, to the foot colour of the genetic father; thus overall, the father's sexual ornamentation (genetic and foster) explained 32% of variance of chick condition. These data suggest that foot colour, a dynamic sexually selected trait, is mostly a signal of parental contribution. In species in which males provide parental care, females may choose mates with higher parental ability. Overall, our data suggest that colourful integuments are honest signals of parental ability.

**Keywords** Dynamic trait · Condition-dependence · Skin colour · Sexual selection · *Sula nebouxii*

### Introduction

Female choice has been considered one of the major evolutionary forces responsible for the elaborate ornaments typically exhibited by males (see review in Andersson 1994). Males with elaborate traits can gain a mating advantage. In this context, bright colours in birds have been proposed as the standard example of female choice leading to the exaggeration of ordinary traits (e.g. Andersson 1994; Møller and Birkhead 1994; Smiseth et al. 2001). In recent decades, the benefits gained by females paired with males with conspicuous colours have been the subject of an intense controversy and the focus of research. Overall, female preference should favour sexual displays that are closely linked to individual condition (Kodric-Brown and Brown 1984). Condition-dependent models suggest that females paired with colourful males may enhance the viability of their offspring when selected colours indicate male genetic quality (Grafen 1990; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Zahavi 1975), or direct benefits (Kirkpatrick and Ryan 1991; Price et al. 1993), when the male colour indicates the capacity to acquire nuptial gifts, a good territory or resources for offspring. One of the key predictions of sexual condition dependence is that females paired with attractive males enhance offspring fitness due to the genetic or environmental quality of attractive mates.

In many bird species, males provide substantial amounts of care, and direct fitness benefits derived from male contribution might be more important than indirect benefits (Griffith et al. 1999; Kirkpatrick and Barton 1997; Palokangas et al. 1994; but see Møller and Jennions 2001). The good parent hypothesis suggests that female choice is based in male traits that indicate their ability to acquire nutrients and perform better parental duties, consequently enhancing her reproductive success (Heywood 1989; Hoelzer 1989; Kirkpatrick 1985; Price et al. 1993). The good parent hypothesis is expected in socially monogamous species in which mating opportunities are few, and males in good condition may gain a greater increase in fitness by allocating resources into parental care than by attracting more potential mates (Kokko 1998; Massaro

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et al. 2003). The main source of support of the good parent hypothesis arises from studies that found an association between male ornamentation and male feeding rates (Grant and Grant 1987; Hill 1991; Linville et al. 1998; Norris 1990; Palokangas et al. 1994; Saetre et al. 1995; Wiehn 1997) or the proportion of feedings contributed by males (Voltura et al. 2002), but failed to quantify the quality of the food items (Saetre et al. 1995; Sundberg and Larsson 1994), and to differentiate environmental and genetic factors (Senar et al. 2002). The main prediction of the good parent hypothesis is that the offspring fitness is more dependent on the environmental (which includes direct parental effects) than on the genetic father's condition displayed by sexual ornaments (Møller and Thornhill 1998).

The blue-footed booby (*Sula nebouxii*), a socially monogamous seabird, is a good model to investigate the role of male ornaments as indicators of male parental ability. Males have conspicuous and variably coloured feet that are exhibited prominently during pair courtship (Nelson 1978). During courtship, males (especially) land in the territory with spread feet held flung up and in front of the underparts, producing a conspicuous contrast between the colour of the foot-web and the white underparts (salute-landing; Nelson 1978). The sexual advertising display is frequently preceded or followed by a parade, consisting of an exaggerated foot-raising, flaunting the webs upwards and outwards. A recent experimental study showed that the foot colour of males is a condition-dependent sexual selected trait that influences female motivation to court and the probability of pair copulations (Torres and Velando 2003). Particularly in long-lived birds, such as the blue footed-booby, females should optimise their reproductive decisions in relation to the partner quality and his level of investment (Chase 1980; Houston and Davies 1985; Winkler 1987). In this species, males provide a great amount of parental care (Anderson and Ricklefs 1992; Guerra and Drummond 1995) and their contribution influences offspring condition and the investment by females (Velando and Alonso-Alvarez 2003).

Here, we used a cross-fostering experiment to examine the relative roles of genetic *versus* environmental parental effects on the condition of blue-footed booby chicks. If parental quality is related to foot coloration, we predict that foot colour should be positively correlated to chick condition; the importance of environmental or genetic parental quality may be separated from the cross-fostering experiment. In the blue-footed booby, male investment is especially important in the first 2 weeks of the chick's life, and after that, the contribution of the male decreases progressively as chicks get older, in comparison to the female contribution (Guerra and Drummond 1995). Thus, we tested the above prediction using chick condition at 15 days of age.

## Methods

The study was carried out in the blue-footed booby colony at Isla Isabel, Nayarit, México from February to April 2002.

A total of 70 clutches of 2 eggs were marked and monitored daily near hatching. Egg length (L) and breadth (B) were measured (to the nearest 0.01 mm), and egg volume (V) was then calculated with the formula  $V=0.51LB^2$  (Hoyt 1979). We performed a cross-fostering experiment to isolate the effects on offspring condition of the genetic father from effects of the foster father operating during the rearing period. In our study, genetic effects are indistinguishable from pre-manipulation maternal effects. Nests where only one chick hatched were included in the experiment. Each experimental nest was paired with another according to hatching date (the maximum difference was 1 day). Chicks were individually marked on the bill with waterproof markers, and then swapped between paired nests within 1 day of hatching ( $n=44$ ). For the experiment, we preferably selected nests with one newborn and one unfertile egg or one egg that contained a dead embryo, determined by hand examination. In seven cases, the second egg was removed and placed in a newborn one-chick nest with similar chronology in the surroundings. As a result of this design, all nests remained with the original chronology and breeding effort of adults. At the age of 15 days, chicks' body mass (to the nearest gramme) and ulna length (to the nearest millimetre) were recorded. In addition, we measured T-cell-mediated immunocompetence (CMI) of chicks through the phytohaemagglutinin (PHA) skin-testing technique (Smits et al. 1999). We studied the response to an injection of 0.2 mg PHA in 0.1 ml phosphate buffered saline (PBS) in the left wing-web. The point of injection was marked with an indelible marker. Three replicate measurements of the patagium thickness were taken with a digital micrometer (to the nearest 0.001 mm) prior to the injection, and again 24 h later. Wing-web thickness measures were significantly repeatable, both for initial measures (intra-class correlation coefficient,  $r=0.93$ ,  $P<0.001$ ) and for final measures ( $r=0.98$ ,  $P<0.0001$ ). The CMI was measured as the change in thickness (mm) of the wing-web after 24-h post-injection.

We captured the male and female parents of cross-fostered nests when the chick was 15–17 days old. Chicks and adults were captured early in the morning to avoid heat stress and any variation related to circadian rhythms. We recorded body mass (to the nearest 5 g) and ulna length (to the nearest millimetre) of captured adult birds, and two measures of colour of the right foot of males using a colorimeter with CIELAB parameters (MINOLTA CR-200). We used the  $L^*a^*b^*$  colour space, where  $L^*$  indicates brightness, and  $a^*$  and  $b^*$  indicate the chromaticity co-ordinates. The saturation of the colour, given by the co-ordinates  $a^*$  and  $b^*$ , increases as  $a^*$  and  $b^*$  absolute values increase. Foot-colour chromaticity varies from dark blue (negative values of  $b^*$  and low absolute values of  $a^*$ ) to a light blue-green (positive values of  $b^*$  and negative values of  $a^*$ ). CIELAB parameters measure colour on the range of reflectance visible to the human eye, and many bird species have ultraviolet-sensitive retinal cones (e.g. Bennett et al. 1996; Johnsen et al. 1998; Siitari et al. 2002). However, it has been argued that quantifying coloration exclusively by human-perceived colour can be reasonable

for longer wavelengths (Andersson 1999; Zuk and De-cruyenaere 1994). As an index of adult body condition, we used the residuals from an ANCOVA analysis, with body mass as dependent variable, sex as factor and ulna length as covariate ( $R^2=0.987$ ,  $P<0.0001$ ). Sample size was reduced due to chick mortality during the nestling stage. We were not able to capture adults in 3 nests, and thus, adult and chick data were collected in 41 nests, and complete data (including data of foster and genetic parents) were obtained in 38 nests. The effect of chick size was standardised by introducing ulna length into the regressions relating foot colour to chick mass. We performed a backward multiple regression model with all confounding variables and the mean foot colour of genetic and foster parents; variables were removed from the full model when the variance explained did not significantly improve the model ( $\alpha=0.05$ ).

## Results

The body condition of foster and genetic parents was not correlated (fathers:  $r=0.04$ ,  $P>0.5$ ; mothers  $r=0.06$ ,  $P>0.5$ ). Foot brightness, but not foot chromaticity, of foster and genetic fathers were correlated (Brightness:  $r=0.42$ ,  $P<0.05$ ; a\*:  $r=0.24$ ,  $P>0.1$ ; b\*:  $r=-0.04$ ,  $P>0.5$ ). Male foot-colour variables were not correlated with egg volume or hatching date ( $P>0.10$  in all cases).

The chick mass at 15 days of age (controlled by ulna length) was correlated with the foot colour of foster fathers (Table 1); foster fathers with more green (a\*) and yellow (b\*) feet had chicks with better condition. In addition, chick mass was also positively correlated with b\* chroma parameter of genetic fathers (Table 1). Furthermore, from a multiple regression analysis, the b\* parameter of the foster father was the colour variable with stronger correlation with chick condition (Table 2; see also Fig. 1a). After controlling for b\* parameter of foster father and female condition, the b\* parameter of genetic fathers had a slight, but significant, effect on chick condition at 15 days of age (Fig. 1b).

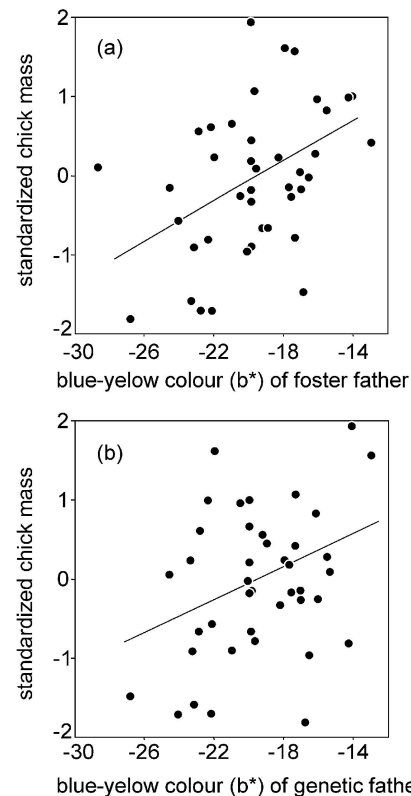
No correlation was detected between CMI and foot colour of genetic or foster fathers ( $P>0.10$  in all cases), not even after controlling by hatching date, egg size, chick mass, chick ulna or body condition of genetic or foster parents, all variables that did not correlate with chick CMI.

**Table 1** Regressions between chick mass at 15 days of age and foot colour parameter of foster and genetic fathers. Chick ulna was included in the models ( $n=41$  in all cases)

	$\beta$	$t$	$P$	Partial $r$
Foster father brightness	0.14	1.91	0.061	0.29
Foster father b*	0.20	2.81	0.008	0.41
Foster father a*	-0.19	2.67	0.011	-0.39
Genetic father brightness	0.13	1.73	0.091	0.27
Genetic father b*	0.16	2.10	0.042	0.32
Genetic father a*	-0.11	1.47	0.15	-0.23

**Table 2** Backward multiple regression model of potential sources of variation on chick mass at 15 days of age ( $n=38$ ); minimal adequate model, and variables included in the initial model

	$\beta$	$t$	$P$	Partial $r$
Variables in the model				
Foster father b*	0.24	3.58	0.001	0.52
Genetic father b*	0.15	2.19	0.035	0.35
Foster mother condition	0.13	1.88	0.069	0.30
Chick ulna length	0.87	12.88	<0.001	0.91
Variables not in the model				
Foster father brightness	-0.07	-0.79	0.44	-0.14
Foster father a*	-0.01	0.06	0.95	-0.01
Foster father condition	0.08	1.19	0.24	0.20
Genetic father brightness	-0.02	0.21	0.83	0.04
Genetic father a*	0.05	0.58	0.57	0.10
Genetic father condition	-0.11	1.7	0.10	-0.28
Genetic mother condition	0.06	0.96	0.34	0.16
Egg volume	0.10	1.44	0.16	0.24
Hatching date	0.01	0.87	0.93	-0.01



**Fig. 1** Relationship between chick mass at 15 days of age (standardised by ulna length) and b\* parameter of foot colour of foster father (a) and genetic father (b)

## Discussion

In our study, offspring condition correlated with both the foster and the genetic father's sexual ornamentation, which explained 32% of variance on chick condition. In agreement with key predictions of condition-dependent models of sexual selection (Andersson 1994), blue-footed booby females paired with colourful males improved their offspring condition. The multiple regression model indicated that the correlation between male colour and chick condition was mostly due to parental effects (23% of variance), although a small proportion was due to genetic effects (8%, of variance, including maternal effects). In the blue-footed booby, chick condition is highly dependent on male investment, especially in the first 2 weeks of chick life (Guerra and Drummond 1995; Velando and Alonso-Alvarez 2003). The blue hue of foster-father feet was the variable that better indicated chick body condition at 15 days of age. This was true even after controlling for the foster-mother condition, an indicator of post-hatching maternal effects. The conditions experienced during growth will probably affect offspring survival and their reproductive performance (Lindström 1999; Metcalfe and Monaghan 2001). Our results emphasise the importance of environmental sources of variation, such as direct paternal effects on offspring fitness, as other studies in blue-footed boobies have shown (Drummond and Garcia Chavelas 1989; Drummond et al. 2003; Torres and Drummond 1997, 1999; Velando 2002; Velando and Alonso-Alvarez 2003). Additionally, a previous experimental study showed that foot colour of male boobies is a trait that affects female choice (Torres and Velando 2003). Taken together, these results suggest that females paired with attractive males may enhance offspring condition, and hence their reproductive success, probably as a result of post-hatching male contribution to parental care (Heywood 1989; Hoelzer 1989). In addition, females could also increase their post-hatching contribution when paired with attractive males (see below).

The small, but significant, relationship between the foot blue hue of genetic fathers and chick condition suggests some influence of genetic factors expressed by foot coloration on chick condition. In cross-fostering experiments, maternal or environmental effects acting prior to the manipulation are indistinguishable from genetic effects (Merilä 1996; Mousseau and Fox 1998). Females could increase their egg investment when offspring have better chances of survival, as when they are paired with attractive males (Burley 1986; Cunningham and Russell 2000; Sheldon 2000; but see Mazuc et al. 2003). Maternal effects on eggs may be important; for instance, larger eggs provide greater lipid and water resources (Kennamer et al. 1997; Williams 1994), and in some bird species, physiologically active compounds, such as carotenoids, antibodies or hormones, which enhance the chick condition or immune system, are incorporated into eggs (Gil et al. 1999; Saino et al. 2002; Schwabl 1997). In our study, no correlation was detected between male foot colour and egg volume, a good indicator of nutrient content (Williams 1994). Consequently, on present evidence, the correlation between genetic-father

foot colour and chick condition cannot be attributed to a greater overall provisioning of nutrients into eggs.

Unexpectedly, we found a correlation of foot brightness between genetic and foster fathers. Adult males were paired by date and they could indirectly be paired by condition if male condition varies with breeding time; nevertheless, foot colour and male condition did not correlate with hatching date. Alternatively, foot brightness could be affected by weather at a particular time. In any case, foot chromaticity of foster and genetic fathers was not correlated, and thus the relationship between the foot blue hue of genetic fathers and chick condition was not due to the pairing method. Although more studies are required to confirm this, male foot chromaticity seems to indicate some heritable condition.

Few studies have considered the role in sexual selection of colours in integuments such as wattles, caruncles, culmen or legs (e.g. Burley 1986; Mateos and Carranza 1995; Torres and Velando 2003; Zuk et al. 1990, 1992), which are particularly widespread in non-passerine birds (Prumm and Torres 2003). In the blue-footed booby, male parental care is dependent on their foraging ability and condition, and influences the female contribution and chick condition (Velando and Alonso-Alvarez 2003). The relationship between foot coloration of foster father and chick condition suggests that foot colour is a reliable indicator of nutritional condition of males. In many birds, plumage coloration depends on the nutritional condition of the bearer at the time feathers were grown (Hill 1991; Hill and Montgomerie 1994), and serves as an honest signal of provisioning and parental ability (Hill 1991, 1999; Linville et al. 1998; Senar et al. 2002). The information expressed by colourful integuments displayed by many seabirds probably differs from plumage colours, since pigments present in fleshy structures can be mobilised facultatively (Lozano 1994), may reflect more recent physiological events, and have the potential to indicate current physical condition (Faivre et al. 2003; Lozano 1994; Negro et al. 1998; Zuk et al. 1990).

In the blue-footed booby, foot colour is a dynamic condition-dependent trait, whose expression changes rapidly with nutritional state; in a food-controlled experiment, there was a strong correlation between body-mass loss and changes in foot brightness and hue (chroma parameters  $a^*$  and  $b^*$ ) (Torres and Velando 2003). Thus, attractive males (Torres and Velando 2003) are the ones with good nutritional condition. Future studies should evaluate the assumption that male nutritional condition during courtship (expressed by foot colour) and during chick growth covary. Another factor that will provide a better insight into the role of foot colour in the blue-footed booby is the understanding of the proximal mechanisms of colour production.

The lack of relationship between foot coloration of foster and genetic fathers with T-cell-mediated immune response of chicks at 15 days of age stresses the low influence of paternal effects (genetic and environmental) on early chick immunocompetence. In early life stages, chicks have a poor immunocompetence that is compensated for by maternal immune factors contained in the eggs (Apanius 1998; Lung et al. 1996). Other studies have shown that T-cell proliferative response of chicks has a

largely environmental component (Christe et al. 2000; Saino et al. 1997; Sorci et al. 1997; Tella et al. 2000). However, in blue-footed booby chicks at 15 days of age, the T-cell response was not affected by the chick-rearing conditions. Further studies are needed to clarify the factors governing early chick immunocompetence in this species.

In summary, we found that condition of blue-footed booby chicks was related to foot colour of the foster father and, to some extent, to foot colour of the genetic father. The data suggest that foot colour, a dynamic sexually selected trait, indicates paternal quality. Therefore, female blue-footed boobies may assess and choose colourful males due to their better parental abilities and probably better genetic quality in order to produce heavier chicks. Blue-footed boobies are socially monogamous, with low mating opportunities (Osorio-Beristain and Drummond 1998) and, in theory, males should enhance their reproductive success by allocating resources into parental care rather than mate attraction (Kokko 1998). Although complementary studies are required to assess the exact role of potential maternal effects, the results stress the importance of non-genetic effects indicated by condition-dependent sexual ornaments, and more likely, the interaction between genetic and environmental effects expressed by sexual traits in species with parental care.

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## References

- Anderson D, Ricklefs RE (1992) Brood size and provisioning in masked and blue-footed boobies (*Sula* spp). *Ecology* 73:1363–1374
- Andersson M (1994) Sexual selection. Princeton University Press, New Jersey
- Andersson S (1999) Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *J Avian Biol* 30:193–204
- Apanius V (1998) The immune system. In: Starck JM, Ricklefs RE (eds) Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, Oxford, pp 130–145
- Bennett ATD, Cuthill I, Patridge J, Maier EJ (1996) Ultraviolet vision and mate choice in zebra finches. *Nature* 380:433–435
- Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. *Am Nat* 127:415–445
- Chase ID (1980) Cooperative and noncooperative behaviour in animals. *Am Nat* 115:827–857
- Christe P, Moller AP, Saino N, Lope F de (2000) Genetic and environmental components of phenotypic variation in immune response and body size of a colonial bird, *Delichon urbica* (the house martin). *Heredity* 85:75–83
- Cunningham EJA, Russell A (2000) Egg investment is influenced by male attractiveness in the mallard. *Nature* 404:74–77
- Drummond H, García Chavelas C (1989) Food shortage influences sibling aggression in the blue-footed booby. *Anim Behav* 37:806–819
- Drummond H, Torres R, Krishnan VV (2003) Buffered development: resilience after aggressive subordination in infancy. *Am Nat* 161:794–807
- Faivre B, Grégoire A, Prévault M, Cézilly F, Sorci G (2003) Immune activation rapidly mirrored in a secondary sexual trait. *Science* 300:103
- Gil D, Graves J, Hazon N, Wells A (1999) Male attractiveness and differential testosterone investment in zebra finch eggs. *Science* 286:126–128
- Grafen A (1990) Sexual selection unhandicapped by the Fisher process. *J Theor Biol* 144:473–516
- Grant BR, Grant PR (1987) Mate choice in Darwin's finches. *Biol J Linn Soc* 32:247–270
- Griffith SC, Owens IPF, Burke T (1999) Environmental determination of a sexually selected trait. *Nature* 400:358–359
- Guerra M, Drummond H (1995) Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. *Behaviour* 132:479–496
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Heywood JS (1989) Sexual selection by the handicap mechanism. *Evolution* 43:1387–1397
- Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339
- Hill GE (1999) Mate choice, male quality, and carotenoid based plumage coloration. In: Adams N, Slotow R (eds) Proceedings of 22nd International Ornithological Congress. BirdLife, Johannesburg, pp 1654–1668
- Hill GE, Montgomerie R (1994) Plumage colour signals nutritional condition in the house finch. *Proc R Soc Lond B* 258:47–52
- Hoelzer GA (1989) The good parent process of sexual selection. *Anim Behav* 38:1067–1078
- Houston AI, Davies NB (1985) The evolution of cooperation and life history in the dunnoek, *Prunella modularis*. In: Sibly R, Smith R (eds) Behavioural ecology: the ecological consequences of adaptive behaviour. Blackwell, Oxford, pp 471–487
- Hoyt DG (1979) Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73–77
- Johnsen A, Andersson S, Ornborg J, Lifjeld JT (1998) Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. *Proc R Soc London B* 265:1313–1318
- Kennamer RA, Alsum SK, Colwell SV (1997) Composition of wood duck eggs in relation to egg size, laying sequence, and skipped days of laying. *Auk* 114:479–487
- Kirkpatrick M (1985) Evolution of female choice and male parental investment in polygynous species: the demise of the ‘sexy son’. *Am Nat* 125:788–810
- Kirkpatrick M, Barton NH (1997) The strength of indirect selection on female mating preferences. *Proc Natl Acad Sci USA* 94:1282–1286
- Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38
- Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favoured by sexual selection. *Am Nat* 124:309–323
- Kokko H (1998) Should advertising parental care be honest? *Proc R Soc Lond B* 265:1871–1878
- Lindström J (1999) Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348
- Linville SU, Breitwisch R, Schilling AJ (1998) Plumage brightness as an indicator of parental care in northern cardinals. *Anim Behav* 55:119–127
- Lozano GA (1994) Carotenoids, parasites, and sexual selection. *Oikos* 70:309–311

- Lung NP, Thompson JP, Kollias GV, Olsen JH, Zdziarski JM, Klein PA (1996) Maternal immunoglobulin G antibody transfer and development of immunoglobulin G antibody responses in blue and gold macaw (*Ara ararauna*) chicks. *Am J Vet Res* 57:1162–1167
- Massaro M, Davis LS, Darby JT (2003) Carotenoid-derived ornaments reflect parental quality in male and female yellow-eyed penguin (*Megadyptes antipodes*). *Behav Ecol Sociobiol* 55:169–175
- Mateos C, Carranza J (1995) Female choice for morphological features of male ring-necked pheasant. *Anim Behav* 49:737–748
- Mazuc J, Chastel O, Sorci G (2003) No evidence for differential maternal allocation to offspring in the house sparrow (*Passer domesticus*). *Behav Ecol* 14:340–346
- Merilä J (1996) Genetic variation in offspring condition: an experiment. *Funct Ecol* 10:465–474
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Møller AP, Birkhead TM (1994) The evolution of plumage brightness in birds is related to extra-pair paternity. *Evolution* 48:1089–1100
- Møller AP, Jennions MD (2001) How important are direct fitness benefits of sexual selection? *Naturwissenschaften* 88:401–415
- Møller AP, Thornhill R (1998) Male parental care, differential parental investment by females and sexual selection. *Anim Behav* 55:1507–1515
- Mousseau TA, Fox CW (1998) Maternal effects as adaptations. Oxford University Press, New York
- Negro JJ, Bortolotti GR, Tella JL, Fernier KJ, Bird DM (1998) Regulation of intergumentary colour and plasma carotenoids in American kestrels consistent with sexual selection theory. *Funct Ecol* 12:307–312
- Nelson B (1978) The Sulidae: gannets and boobies. Oxford University Press, Oxford
- Norris KJ (1990) Female choice and quality of parental care in the great tit *Parus major*. *Behav Ecol Sociobiol* 27:275–281
- Osorio-Beristain M, Drummond H (1998) Non-aggressive mate guarding by the blue-footed booby: a balance of female and male control. *Behav Ecol Sociobiol* 43:307–315
- Palokangas P, Korpimäki E, Hakkarainen H, Huhta E, Tolonen P, Alatalo RV (1994) Female kestrels gain reproductive success by choosing brightly ornamented males. *Anim Behav* 47:443–448
- Price TD, Schluter D, Heckman NE (1993) Sexual selection when the female directly benefits. *Biol J Linn Soc* 48:187–211
- Prumm RO, Torres R (2003) Structural coloration of avian skin: convergent evolution or coherently scattering dermal collagen arrays. *J Exp Biol* 206:2409–2429
- Saetre GP, Fossnes T, Slagsvold T (1995) Food provisioning in the pied flycatcher: do females gain direct benefits from choosing bright-coloured males? *J Anim Ecol* 64:21–30
- Saino N, Bolzern AM, Møller AP (1997) Immunocompetence, ornamentation and viability of male barn swallows (*Hirundo rustica*). *Proc Natl Acad Sci USA* 97:579–585
- Saino N, Ferrari RP, Martinelli R, Romano M, Rubolini D, Møller AP (2002) Early maternal effects mediated by immunity depend on sexual ornamentation of the male partner. *Proc R Soc Lond B* 269:1005–1009
- Schwabl H (1997) A hormonal mechanism for parental favoritism. *Nature* 386:231
- Senar JC, Figuerola J, Pascual J (2002) Brighter yellow blue tits make better parents. *Proc R Soc Lond B* 269:257–261
- Sheldon B (2000) Differential allocation: tests, mechanisms and implications. *Trends Ecol Evol* 15:397–402
- Siitari H, Honkavaraa J, Huhta E, Viitala J (2002) Ultraviolet reflection and female mate choice in the pied flycatcher, *Ficedula hypoleuca*. *Anim Behav* 63:97–102
- Smiseth PT, Ornborg J, Andersson S, Amundsen T (2001) Is male plumage reflectance correlated with paternal care in bluethroats? *Behav Ecol* 12:164–170
- Smits JE, Bortolotti GR, Tella JL (1999) Simplifying the phytohemagglutinin skin testing technique in studies of avian immunocompetence. *Funct Ecol* 13:567–577
- Sorci G, Moller AP, Boulinier T (1997) Genetics of host-parasite interactions. *Trends Ecol Evol* 12:196–200
- Sundberg J, Larsson C (1994) Male coloration as an indicator of parental quality in the yellowhammer *Emberiza citrinella*. *Anim Behav* 48:885–892
- Tella JL, Bortolotti GR, Forero MG (2000) Environmental and genetic variation in T-cell-mediated immune response of fledgling American kestrels. *Oecologia* 123:453–459
- Torres R, Drummond H (1997) Sex-biased mortality in nestlings of a bird with reversed sexual size dimorphism. *J Anim Ecol* 66:859–865
- Torres R, Drummond H (1999) Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* 118:16–22
- 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
- Velando A (2002) Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. *Behav Ecol* 13:443–449
- Velando A, Alonso-Alvarez C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *J Anim Ecol* 72:846–856
- Voltura KM, Schwagmeyer PL, Mock DW (2002) Parental feeding rates in the house sparrow, *Passer domesticus*: are larger-badged males better fathers? *Ethology* 108:1011–1022
- Wiehn J (1997) Plumage characteristics as an indicator of male parental quality in the American kestrel. *J Avian Biol* 28:47–55
- Williams TD (1994) Intra-specific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol Rev* 68:35–59
- Winkler DW (1987) A general model for parental care. *Am Nat* 130:526–543
- Zahavi A (1975) Mate selection. A selection for a handicap. *J Theor Biol* 53:205–214
- Zuk M, Decruyenaere JG (1994) Measuring individual variation in colour—a comparison of two techniques. *Biol J Linn Soc* 53:165–173
- Zuk M, Thornhill R, Ligon JD, Johnson K, Austad S, Ligon SH, Thornhill NW, Costin C (1990) The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. *Am Nat* 136:459–473
- Zuk M, Ligon JD, Thornhill R (1992) Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. *Anim Behav* 44:999–1006