Ecol Res (2010) 25: 77–82
DOI 10.1007/s11284-009-0632-3

ORIGINAL ARTICLE

Matteo Griggio · Valeria Zanollo · Herbert Hoi

UV plumage color is an honest signal of quality in male budgerigars

Received: 10 January 2009 / Accepted: 15 June 2009 / Published online: 16 July 2009

Abstract Elaborate and colorful feathers are important traits in female mate choice in birds. Plumage coloration can result from pigments deposited in feathers such as carotenoids and melanins, or can be caused by nano-scale reflective tissues (structurally based coloration), usually producing ultraviolet (UV) coloration. Structural colorations remain the least studied of the three most important feather colorations. Previous studies have found a female preference for UV color in the budgerigar, *Melopsittacus undulatus*, but it is not clear what information this ornament conveys, nor what is the possible cost associated with its production. We investigated possible correlations between immune response and plumage color of wild-type (green) male budgerigars. In particular we measured the wing web swelling resulting from injection of phytohaemagglutinin (PHA). We did not detect any correlation between the sedimentation rate and morphological and color variables. We found that UV chroma is the best predictor for the cutaneous immune activity. Indeed, male budgerigars with high UV reflectance in the breast feathers showed stronger immune responses. These results are consistent with the idea that UV colors are special signals conveying information about a bird's condition.

Keywords Feather coloration · Ornaments · Phytohaemagglutinin · Sexual selection · Structurally based coloration

Introduction

Female mate choice is an important driving force in sexual selection (Darwin 1871). Females use various signals to assess the quality of males, including sexual vocalizations, behavioral displays, pheromones, and morphological traits (Andersson 1994). For signals to contain reliable information, they must be costly to produce and/or to maintain (Zahavi 1975; Grafen 1990). Females may benefit from mating with high-quality mates, because such individuals may provide "direct" (e.g., territorial space and the resources therein) or "indirect" (e.g., good genes) benefits (see Andersson 1994). Whatever the benefit gained, the most obvious cues used in mate-choice decision are plumage ornaments, such as long feathers and brightly colored patches. Indeed, since Darwin (1871), plumage of birds has been an important focus for many evolutionary biologists interested in sexual selection. Many studies of birds have provided evidence that females can benefit by choosing a male according to the expression of colorful plumage ornaments (e.g., Andersson 1994). There is also increasing evidence that male mating preferences are based on female plumage ornaments, supporting the importance of plumage traits in sexual selection (e.g., Jones and Hunter 1993; Griggio et al. 2005). Plumage coloration can result from pigments deposited in feathers, such as carotenoids (giving feathers yellow to red coloration), melanins (brown and black coloration), or other pigments (such as are found in some parrot feathers, Masello et al. 2004; McGraw and Nogare 2005). Other than pigments, the coloration of feathers can be caused by nano-scale reflective tissues (structurally based coloration), usually producing ultraviolet (UV) and iridescent coloration (Gill 1995).

One of the most controversial issues in evolutionary biology is the identification of costs of particular ornaments used in mate choice. Many hypotheses try to answer the question: "Why should individuals have a sexual preference for exaggerated or particular colored traits?" Melanin-based ornamental colorations are under social control: in a number of species, melanin-based traits function as badges of social status (the "status signalling hypothesis" Rohwer 1975; Senar 1999; Hoi and Griggio 2008). Moreover, recent studies suggest that melanins may not be as inexpensive to produce as initially

M. Griggio (✉) · V. Zanollo · H. Hoi
Konrad Lorenz Institute for Ethology,
Austrian Academy of Sciences, Savoyenstrasse 1a,
1160 Vienna, Austria
E-mail: m.griggio@klivv.oeaw.ac.at
Tel.: +43-1-515812753
Fax: +43-1-515812800

thought, and so melanin-based traits can be honest signals (McGraw 2007). Indeed, these studies show that plumage melanization is related to resistance to ectoparasites (Roulin et al. 2001), to mating success (Parker et al. 2003) and to environmental growth condition (Fargallo et al. 2007). Several studies indicate that melanin ornaments are influenced by circulating testosterone and suggest that melanin ornament size can act as a reliable indicator of condition (reviewed in Jawor and Breitwisch 2003).

On the other hand, carotenoid-based ornaments correlate with the different aspects of individual quality such us parasite resistance, immunocompetence, and diet (for a review see Olson and Owens 1998). In particular, these pigments cannot be synthesized de novo but must be obtained from the diet (Hudon 1994; Møller et al. 2000). Carotenoids function as antioxidants and immunostimulants (Chew 1996), so a trade-off in carotenoid allocation between maintenance and ornamentation has therefore been hypothesized (Lozano 1994). In turn, males in better condition should require fewer carotenoids for maintenance (i.e., immune function) and therefore be able to allocate a larger portion of their limited carotenoid stores to ornamentation (see Hartley and Kennedy 2004 for a review). Indeed, several examples of honest signaling in animals are based on carotenoid-based ornaments (e.g., Hill 1991; Burley et al. 1992; Uller et al. 2006; Griggio et al. 2007; Serra et al. 2007).

In birds, structural colorations remain the least studied aspect of the three most important feather colorations, and they are largely unknown. Some studies suggest that the expression of structural coloration reflects the nutritional condition of an individual at the time of moult (Keyser and Hill 1999; Doucet 2002; but see Prum 2006), or the moult duration (Griggio et al. 2009). For example, male nestlings of the blue tit, *Parus caeruleus*, raised in reduced broods had higher UV reflectance in the UV/blue tail feathers, more carotenoid chroma and higher UV reflectance in the yellow breast plumage than nestlings in enlarged broods (Siefferman and Hill 2005). Others have suggested that UV colors may signal developmental stability and so genetic quality of the individual (Fitzpatrick 1998; Andersson 1999), but to our knowledge this idea remains untested.

UV colors have a relevant role in mate choice in budgerigars, *Melopsittacus undulatus*, but the message conveyed by this trait is not clear (Pearn et al. 2001, 2003; Zampiga et al. 2004). In particular, Zampiga et al. (2004) found that preened males were more attractive to females and that lack of preening decreased the UV reflectance of breast feathers. Moreover, reflectance from these feathers and female preference were eliminated when the UV light was manipulated (Pearn et al. 2001). So it seems that UV reflectance from the breast feathers could be involved in mate preference.

In this study we examined the possible relationship between immunocompetence and plumage color of wild-type (green) male budgerigars. We used sedimentation rate as a measure of general health (Biard et al. 2006) and response to a subcutaneous injection of phytohaemagglutinin (PHA) as a measure of immunocompetence (Martin 2005).

Methods

Body and color measurements

Three weeks before the experiment commenced, 40 male, wild-type adult (1 year old) budgerigars were selected randomly from four indoor aviaries and were placed in indoor cages (50 × 50 × 50 cm). Water and food were provided ad libitum before and during the experiment (for more details see Griggio and Hoi 2006). No individuals were moulting during this study. Due to the strong social behavior of this species, birds were caged in pairs, and cages were arranged in such a way that birds were not visually or acoustically isolated from the others. Body mass (to the nearest 0.1 g), tarsus, and wing length (to the nearest 0.1 mm) were measured (Svensson 1992). The body condition was calculated by dividing body mass by (tarsus length)^3; due to small values, the body condition indices were multiplied by 10^4 (e.g., Bókony et al. 2008). Commencement of breeding right after the experiment suggests that housing conditions were appropriate and that the birds were in a healthy condition.

The reflectance in the 300–700 nm range was measured with an Ocean Optics, Inc. USB 2000 spectrometer and a deuterium–halogen source (DH–2000). The probe was held at 45° to the feather surface (Griggio and Hoi 2006). A software package (Spectrawin 4.2) computed reflectance spectra relative to a white reference tile (SW–2). For each individual male, five measurements were taken, removing the probe between each measurement. We then averaged the five measurements for each male.

The reflectance spectrum of the breast is double peaked: the first (usually smaller) peak being in the UV (300–400 nm), and the second in the green–yellow (500–600 nm). We quantified color using standard descriptors of reflectance spectra: brightness, hue, chroma, UV chroma, and green–yellow chroma. Mean brightness was calculated as the mean summed reflectance ($R_{300–700\ \mathrm{nm}}$). Hue ($\lambda_{(R\max)}$) was calculated as the wavelength at peak reflectance. Chroma was calculated as the difference between the highest and lower reflectance divided by the average reflectance (($R_{\max}$–$R_{\min}$)/R_{average}). Green–yellow chroma was estimated as the proportion of green–yellow reflectance on total reflectance ($R_{500–600\ \mathrm{nm}}/R_{300–700\ \mathrm{nm}}$). UV chroma was calculated as the proportion of the UV reflectance on total reflectance ($R_{300–400\ \mathrm{nm}}/R_{300–700\ \mathrm{nm}}$). These indices have been used in previous studies on birds (e.g., Hunt et al. 1999; Sheldon et al. 1999; Griffith et al. 2003).

Sedimentation rate measure

To state the general current condition of health of male budgerigars we measured the red blood cell sedimentation rate. Blood cell sedimentation rate is useful for detecting elevated levels of immunoglobulin and fibrinogen. A high sedimentation rate is indicative of infections and inflammatory diseases (Sturkie 1986; Biard et al. 2006). To measure sedimentation rate, we collected blood samples in heparinized capillary tubes, which were later placed upright in a refrigerator (4°C) for 4 h. Blood samples were then centrifuged for 5 min at 2,600 × *g*. Height of the red blood cell layer was measured and sedimentation rate was measured as the amount of red cells divided by the height of blood in the capillary occupied by blood (controlling for volume).

Assessment of T-cell-mediated immunity

Cutaneous immune activity was tested by a standard-protocol immunization with phytohaemagglutinin (PHA, Sigma L-8754). The subcutaneous injection of this plant lectin into the wing web induces a cell-mediated immune response that causes a local swelling. This test has been widely used in many captivity and field studies on birds (Davison et al. 1996; see also references in Martin et al. 2006 for a review of studies using this technique) since it reflects the combined responses of T cells, cytokines, and inflammatory cells. Each male was injected with 0.2 mg of PHA in 0.1 ml of physiological saline solution (PBS). Wing web thickness at the site of injection was measured with a spessimeter to 0.01 mm before injection and after 24 h. The immune response index was calculated as the difference between thickness after and before the injection. We injected the birds 3 weeks after they were placed in separate cages because stress hormone release (e.g., birds exposed to vigorous activity during capture phase) is a mediator of the suppression of PHA responses (Ewenson et al. 2003).

Statistical analyses

We used forward stepwise regression to identify which of the morphological (wing, body mass, tarsus measurements, and body condition index) and color variables (brightness, chroma, hue, UV chroma and green–yellow chroma) explained the significant amounts of the variation in wing web swelling and sedimentation rate. Statistical analyses were performed using SPSS v. 13.0 (Norušis 1993). Data were checked for normality, and appropriate transformations were used when necessary. All results are presented as mean ± standard error.

Results

Responses to PHA injection varied between males (1.53 ± 0.08 range: 0.36–2.88; Fig. 1). UV chroma was the only variable to enter the forward stepwise regression when wing web swelling was used as the dependent variable (Table 1; Fig. 1). We did not detect any correlation between sedimentation rate and morphological and color variables (all $P > 0.2$). A negative correlation was found between sedimentation rate (0.70 ± 0.01, range: 0.56–0.79) and PHA response (Pearson correlation: $r = -0.346$, $P = 0.029$, $N = 40$).

Discussion

Male budgerigars with high UV reflectance in the breast feathers showed stronger immune responses. Matching of captivity conditions (e.g., similar access to food) and age of all males used in this study ensure that differences in the quality of the individuals should not affect the activation of the immune system.

Females and males can base their mate choice on particular ornaments, such as exaggerated color traits. Many studies have demonstrated that colored plumages

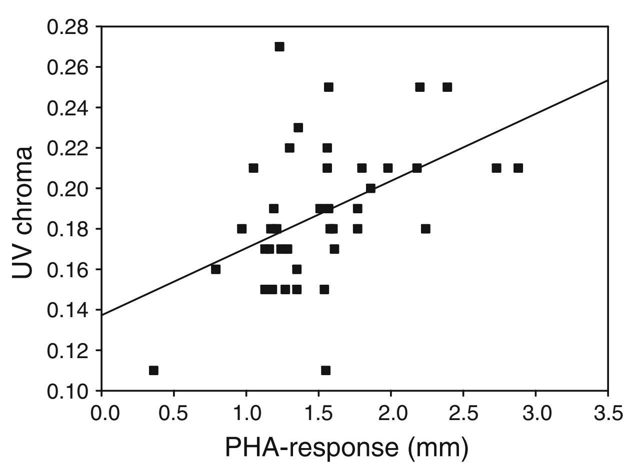

Fig. 1 Relationship between the immune response to phytohaemagglutinin (PHA response) and UV chroma

Table 1 Results of forward stepwise regression investigating the relationship between immune response (wing-web swelling in response to PHA) and morphology and color indices from 40 male budgerigars

	Wing	Body mass	Tarsus	Body condition	Brightness	Chroma	Hue	UV chroma	Gr–Yel chroma
Mean (±SE)	10.71 (0.09)	43.20 (1.12)	16.10 (0.70)	103.84 (2.94)	34.70 (1.09)	2.35 (0.10)	527.12 (7.82)	0.19 (0.01)	0.72 (0.01)
Partial correlation	−0.14	0.05	−0.25	0.13	0.08	0.09	−0.04	**0.45**	0.03
P value	0.39	0.78	0.13	0.41	0.65	0.59	0.81	**0.003**	0.87

Significant values are shown in bold

based on melanins and carotenoids are reliable signals correlating with aspects of individual quality such as parasite resistance, immunocompetence, diet, and social status (e.g., Lozano 1994; McGraw and Hill 2000; Blount et al. 2003; Griffith et al. 2003; Griggio et al. 2007). The situation for the UV reflecting structural colors is more controversial (see Prum 2006). We found that in budgerigars, UV plumage coloration that is known to have an important role in sexual selection (Pearn et al. 2001; Zampiga et al. 2004) signals male quality. In particular, the UV chroma is the best predictor for cutaneous immune activity. Our findings suggest that females choosing a partner with a higher UV reflectance should obtain a mate in good condition (Andersson 1994).

Our results add strength to previous studies proposing that UV colors are signals conveying information on birds' overall health (Doucet and Montgomerie 2003; Jourdie et al. 2004; Mougeot et al. 2005; Soler et al. 2007). In satin bowerbirds, *Ptilonorhynchus violaceus*, juveniles and females are greener than males, and the plumage reflectance is bimodal, with peaks in both the ultraviolet and green portions of the spectrum (as in the wild-type budgerigars). It was found that juvenile males exhibiting greater UV chroma had fewer blood parasites. It was proposed that a structural color ornament could signal the intensity of infection from blood parasites (Doucet and Montgomerie 2003). Another study suggesting UV chroma as an indicator of parasite resistance is the one by Mougeot et al. (2005) on the red grouse, *Lagopus lagopus*. They found that in both males and females fewer nematode parasites, *Trichostrongylus tenuis*, were predicted from brighter UV in combs. However, in both of these studies, the quality of individuals was investigated in terms of parasite numbers present in the blood. On the other hand, it has been suggested that individual immune system efficiency such as the genetic ability to respond against antigenic challenges can be a more appropriate measure of parasite resistance than a simple blood parasite count (Apanius 1998; Møller et al. 2000). Up to now, there have been a few studies investigating the individual immune response in relation to UV coloration, mostly on fleshy traits. It has been shown that in nestlings of both the common starling, *Sturnus vulgaris* (Jourdie et al. 2004) and spotless starling, *Sturnus unicolor* (Soler et al. 2007), there is a positive relationship between skin UV reflectance and T-cell-mediated immune response. Another study conducted on adult male king penguins, *Aptenodytes patagonicus,* failed to find any significant correlation between PHA immune response and the degree of UV reflectance from the beak (Nolan et al. 2006). On the contrary, in the mallard, *Anas platyrhynchos*, male bill UV reflectance was affected by the investment in antibody production consequent to immunization with sheep red blood cells (Peters et al. 2004). One other experiment testing the relationship between plumage coloration and immune response was conducted on fledgling blue tits, *Cyanistes caeruleus* (Peters et al. 2007). None of the color parameters measured was related to cell-mediated immune response (to PHA), humoral immune status and parasitism. Another study that failed to support the hypothesis that ornament expression signals quality in terms of cell-mediated immunity is the one by Pärn et al. on bluethroats, *Luscina s. svecica* (2005). They did not detect any correlation between the extent of the throat structural-based blue feathers and the swelling following a PHA-challenge in females, but this kind of immune response was strongly correlated with body condition. Our study is therefore one of the first to find a positive relationship between feather UV colors and individual immunocompetence. An experiment on immune response during the moult would be necessary to confirm our results. It must be noted that green breast coloration is a combined color containing both a yellow pigment component and a blue structural component. Future studies are necessary to understand the relative value of these two components. Moreover, budgerigars in captivity tend to be overweight, and this could be partially responsible for the fact that we did not detect a significant correlation between body condition and response to PHA injection. Future studies in the wild are necessary to confirm our results.

In conclusion, our study reveals that UV color is a reliable indicator of immunocompetence in male budgerigars. Our results seem to be in line with previous studies that found a positive relationship between structural plumage ornamentation and individual quality.

Acknowledgments We are grateful to C. Grabmayer and W. Pegler for support with animal husbandry.

References

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

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. doi:10.2307/3677129

Apanius V (1998) Stress and immune defence. In: Møller AP, Milinski M, Slater PBJ (eds) Advances in the study of behaviour, 27. Academic Press, San Diego, pp 133–153

Biard C, Surai PF, Møller AP (2006) Carotenoid availability in diet and phenotype of blue and great tit nestlings. J Exp Biol 209:1004–1044. doi:10.1242/jeb.02089

Blount JD, Metcalfe NB, Birkhead TR, Surai PF (2003) Carotenoid modulation of immune function and sexual attractiveness in zebra finches. Science 300:125–127. doi:10.1126/science.1082142

Bókony V, Liker A, Lendvai ÁZ, Kulcsár A (2008) Risk-taking and survival in the house sparrow *Passer domesticus*: are plumage ornaments costly? Ibis 150:139–151

Burley NT, Price DK, Zann RA (1992) Bill color, reproduction and condition effects in wild and domesticated zebra finches. Auk 109:12–23

Chew BP (1996) Importance of antioxidant vitamins in immunity and health in animals. Anim Feed Sci Technol 59:103–114. doi:10.1016/0377-8401(95)00891-8

Darwin C (1871) The descent of man and selection in relation to sex. Murray, London

Davison TF, Morris TR, Payne LN (1996) Poultry immunology. Carfax Publishing Company, Oxford

Doucet SM (2002) Structural plumage coloration, male body size, and condition in the blue–black grassquit. Condor 104:30–38. doi:10.1650/0010-5422(2002)104[0030:SPCMBS]2.0.CO;2

Doucet SM, Montgomerie R (2003) Structural plumage colour and parasites in satin bowerbirds *Ptilonorhynchus violaceus*: implications for sexual selection. J Avian Biol 34:237–242. doi:10.1034/j.1600-048X.2003.03113.x

Ewenson E, Zann R, Flannery G (2003) PHA immune response assay in captive zebra finches is modulated by activity prior to testing. Anim Behav 66:797–800. doi:10.1006/anbe.2003.2251

Fargallo JA, Laaksonen T, Korpimäki E, Wakamatsu K (2007) A melanin-based trait reflects environmental growth conditions of nestling male Eurasian kestrels. Evol Ecol 21:157–171. doi:10.1007/s10682-006-0020-1

Fitzpatrick S (1998) Colour scheme for birds: structural coloration and signals of quality in feathers. Ann Zool Fenn 35:67–77

Gill FB (1995) Ornithology. W. H. Freeman, New York

Grafen A (1990) Biological signals as handicap. J Theor Biol 144:517–546. doi:10.1016/S0022-5193(05)80088-8

Griffith SC, Örnborg J, Russell AF, Andersson S, Sheldon BC (2003) Correlations between ultraviolet coloration, overwinter survival and offspring sex ratio in the blue tit. J Evol Biol 16:1045–1054. doi:10.1046/j.1420-9101.2003.00550.x

Griggio M, Hoi H (2006) Is preening behaviour sexually selected? An experimental approach. Ethology 112:1145–1151. doi:10.1111/j.1439-0310.2006.01270.x

Griggio M, Valera F, Casas A, Pilastro A (2005) Males prefer ornamented females: a field experiment of male choice in the rock sparrow. Anim Behav 69:1243–1250. doi:10.1016/j.anbehav.2004.10.004

Griggio M, Serra L, Licheri D, Monti A, Pilastro A (2007) Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. Behav Ecol Sociobiol 61:423–443. doi:10.1007/s00265-006-0270-5

Griggio M, Serra L, Licheri D, Campomori C, Pilastro A (2009) Moult speed affects structural feather ornaments in the blue tit. J Evol Biol 22:782–792. doi:10.1111/j.1420-9101.2009.01700.x

Hartley RC, Kennedy MW (2004) Are carotenoids a red herring in sexual display? Trends Ecol Evol 19:353–354. doi:10.1016/j.tree.2004.04.002

Hill GE (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339. doi:10.1038/350337a0

Hoi H, Griggio M (2008) Dual utility of a melanin-based ornament in bearded tits. Ethology 114:1094–1100. doi:10.1111/j.1439-0310.2008.01566.x

Hudon J (1994) Showiness, carotenoids, and captivity—a comment on Hill (1992). Auk 111:218–221

Hunt S, Cuthill IC, Bennett ATD, Griffiths R (1999) Preferences for ultraviolet partners in the blue tit. Anim Behav 58:809–815. doi:10.1006/anbe.1999.1214

Jawor JM, Breitwisch R (2003) Melanin ornaments, honesty, and sexual selection. Auk 120:249–265. doi:10.1642/0004-8038(2003)120[0249:MOHASS]2.0.CO;2

Jones IL, Hunter FM (1993) Mutual sexual selection in a monogamous seabird. Nature 362:238–239. doi:10.1038/362238a0

Jourdie V, Moureau B, Bennet ATD, Heeb P (2004) Ultraviolet reflectance by the skin of nestlings. Nature 431:262. doi:10.1038/431262a

Keyser AJ, Hill GE (1999) Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. Proc R Soc Lond B Biol Sci 266:771–777. doi:10.1098/rspb.1999.0704

Lozano GA (1994) Carotenoids, parasites, and sexual selection. Oikos 70:309–311. doi:10.2307/3545643

Martin LB (2005) Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*). Can J Zool 83:780–787. doi:10.1139/z05-114

Martin LB, Han P, Lewittes J, Kuhlman JR, Klasting KC, Wikelski M (2006) Phytohemagglutinin-induced skin swelling in birds: histological support for a classic immunoecological technique. Funct Ecol 20:290–299. doi:10.1111/j.1365-2435.2006.01094.x

Masello JF, Pagnossin ML, Lubjuhn T, Quillfeldt P (2004) Ornamental non-carotenoid red feathers of wild burrowing parrots. Ecol Res 19:421–432. doi:10.1111/j.1440-1703.2004.00653.x

McGraw KJ (2007) Dietary mineral content influences melanin-based ornamental coloration. Behav Ecol 18:137–142. doi:10.1093/beheco/arl059

McGraw KJ, Hill GE (2000) Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. Proc R Soc Lond B Biol Sci 267:1525–1531. doi:10.1098/rspb.2000.1174

McGraw KJ, Nogare MC (2005) Distribution of unique red feather pigments in parrots. Biol Lett 1:38–43. doi:10.1098/rsbl.2004.0269

Møller AP, Biard C, Blount JD, Houston DC, Ninni P, Saino N, Surai PF (2000) Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? Avian Poultry Biol Rev 11:137–159

Mougeot F, Redpath SM, Leckie F (2005) Ultra-violet reflectance of male and female red grouse, *Lagopus lagopus scoticus*: sexual ornaments reflect nematode parasite intensity. J Avian Biol 36:203–209. doi:10.1111/j.0908-8857.2005.03424.x

Nolan PM, Dobson FS, Dresp B, Jouventin P (2006) Immunocompetence is signalled by ornamental colour in king penguins, *Aptenodytes patagonicus*. Evol Ecol Res 8:1325–1332

Norušis MJ (1993) SPSS for Windows base system user's guide release 6.0. SPSS, Chicago

Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? Trends Ecol Evol 13:510–514. doi:10.1016/S0169-5347(98)01484-0

Parker TH, Stansberry BM, Becker CD, Gipson PS (2003) Do melanin- or carotenoid-pigmented plumage ornaments signal condition and predict pairing success in the Kentucky warbler? Condor 105:663–671. doi:10.1650/7335

Pärn H, Lifjeld JT, Amundsen T (2005) Female throat ornamentation does not reflect cell-mediated immune response in bluethroats *Luscina s. svecica*. Oecologia 146:496–504. doi:10.1007/s00442-005-0209-y

Pearn SM, Bennet ATD, Cuthill IC (2001) Ultraviolet vision, fluorescence and mate choice in a parrot, the budgerigar *Melopsittacus undulatus*. Proc R Soc Lond B Biol Sci 268:2273–2279. doi:10.1098/rspb.2001.1813

Pearn SM, Bennet ATD, Cuthill IC (2003) The role of ultraviolet-A reflectance and ultraviolet-A-induced fluorescence in budgerigar mate choice. Ethology 109:961–970. doi:10.1046/j.0179-1613.2003.00936.x

Peters A, Delhey K, Denk AG, Kempeners B (2004) Trade-offs between immune investment and sexual signalling in male mallards. Am Nat 164:51–59. doi:10.1086/421302

Peters A, Delhey K, Johnsen A, Kempeners B (2007) The condition-dependent development of carotenoid-based and structural plumage in nestling blue tits: males and females differ. Am Nat 169:S122–S136. doi:10.1086/510139

Prum RO (2006) Anatomy, physics, and evolution of structural colors. In: Hill GE, McGraw KJ (eds) Bird coloration. Vol. I. Mechanisms and measurements. Harvard University Press, Cambridge, pp 295–353

Rohwer S (1975) The social significance of avian winter plumage variability. Evol Int J Org Evol 29:593–610. doi:10.2307/2407071

Roulin A, Riols C, Dijkstra C, Ducrest AL (2001) Female plumage spottiness signals parasite resistance in the barn owl (*Tyto alba*). Behav Ecol 12:103–110. doi:10.1093/beheco/12.4.506

Senar JC (1999) Plumage coloration as a signal of social status. In: Adams NJ, Slotow RH (eds) Proceedings of the International Ornithological Congress, vol 22. BirdLife South Africa, Johannesburg, pp 1669–1686

Serra L, Griggio M, Licheri D, Pilastro A (2007) Moult speed constraints the expression of a carotenoid-based sexual ornament. J Evol Biol 20:2028–2034. doi:10.1111/j.1420-9101.2007.01360.x

Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J (1999) Ultraviolet colour variation influences blue tit sex ratios. Nature 402:874–877. doi:10.1038/47239

Siefferman L, Hill GE (2005) Evidence for sexual selection on structural plumage coloration in female eastern bluebirds (*Sialia sialis*). Evol Int J Org Evol 59:1819–1828

Soler JJ, Aviles JM, Cuervo JJ, Perez-Contreras T (2007) Is the relation between colour and immune response mediated by nutritional condition in spotless starling nestlings? Anim Behav 74:1139–1145. doi:10.1016/j.anbehav.2006.09.026

Sturkie PD (1986) Avian physiology, 4th edn. Springer, Berlin Heidelberg New York

Svensson L (1992) Identification guide to European passerines. British Trust of Ornithology, Thetford

Uller T, Andersson S, Eklöf J (2006) Juvenile cell-mediated immune response is negatively correlated with subsequent adult ornament size in quail. Evol Ecol 20:1–9. doi:10.1007/s10682-005-2006-9

Zahavi A (1975) Mate selection—a selection for handicap. J Theor Biol 53:205–214. doi:10.1016/0022-5193(75)90111-3

Zampiga E, Hoi H, Pilastro A (2004) Preening, plumage reflectance and female choice in budgerigars. Ethol Ecol Evol 16:339–349