Female tawny-bellied seedeaters do not prefer more colorful males in choice experiments

Carolina Facchinetti & Juan Carlos Reboreda

Journal of Ethology

ISSN 0289-0771

J Ethol
DOI 10.1007/s10164-013-0371-3

Springer

Your article is protected by copyright and all rights are held exclusively by Japan Ethological Society and Springer Japan. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Springer

Author's personal copy

J Ethol
DOI 10.1007/s10164-013-0371-3

ARTICLE

Female tawny-bellied seedeaters do not prefer more colorful males in choice experiments

Carolina Facchinetti · Juan Carlos Reboreda

Received: 12 October 2012 / Accepted: 19 March 2013
© Japan Ethological Society and Springer Japan 2013

Abstract Plumage coloration has long been studied as a sexually selected character. The tawny-bellied seedeater, *Sporophila hypoxantha*, is a sexually dichromatic species, with adult males the more colorful sex and juvenile males indistinguishable from females. We did choice experiments to evaluate female preferences for males that differ in age or plumage coloration. Females were evaluated in three experiments: (1) choice between males with similar breast brightness that differed in age, (2) choice between males of 2 years of age that differed in breast brightness, and (3) choice between males of 3 or more years of age that differed in breast brightness. We also repeated the latter experiment with estradiol-treated females. We did not find a clear female preference for brighter or older males, as females spent the same proportion of time with males of similar breast brightness that differed in age or with males of similar age that differed in breast brightness. Our results do not support the hypothesis that breast brightness is a cue used by female tawny-bellied seedeaters at the time of choosing males. We propose that, in this species, male plumage coloration might play a role in intrasexual competition.

Keywords Mate choice · Plumage coloration · Sexual selection · *Sporophila hypoxantha*

C. Facchinetti (✉) · J. C. Reboreda
Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires-IEGEBA-CONICET, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina
e-mail: cfacchinetti@ege.fcen.uba.ar

Introduction

Since Darwin (1871), it is widely accepted that elaborate ornaments exhibited by males have evolved or are maintained as a result of sexual selection. Accordingly, sexual differences in plumage coloration in birds are thought to have evolved in response of females preferring more colorful males (i.e. intersexual selection; Andersson 1994; Bradbury and Vehrencamp 1998; Hill 2006; Kigma et al. 2008), or they have evolved to signal the fighting ability of individuals in male–male competition (i.e. intrasexual selection; Morimoto et al. 2005; Senar 2006). Female preferences for mating males with the most elaborate expression of color or larger color patches has been experimentally tested in several passerine birds (summarized in Hill 2006; Kigma et al. 2008), while the resolution of male–male contests using plumage color cues has also been demonstrated in several studies (summarized in Senar 2006; Morimoto et al. 2005; Quesada and Senar 2007). Males of most sexually dichromatic passerines acquire the definitive plumage before the first breeding attempt (Humphrey and Parkes 1959). However, in some species, males retain a plumage similar to that of females during the first year of life or more, a phenomenon referred as delayed plumage maturation (DMP; Lyon and Montgomerie 1986; Hawkins et al. 2012). Adaptive hypotheses of DMP are focused on the benefits of expressing the age and inexperience of juvenile males, during both the non-reproductive and reproductive seasons (reviewed in Hawkins et al. 2012). A female-like coloration may increase the probability that juvenile males can enter adult male territories and gain access to females (Rohwer et al. 1980). Also, juvenile appearance may signal social status, decreasing older male aggression (Lyon and Montgomerie 1986; Senar 2006).

Published online: 02 April 2013

Author's personal copy

Avian plumage coloration is produced by feather microstructure, pigments, or by a combination of both (Fox 1976; Prum et al. 1999), and both types of coloration may play an important role in female choice or in signaling fighting abilities (Andersson 1994; Hill 2006; Senar 2006). Melanin is the most frequent pigment among animals (McGraw 2006), and there are two forms: pheomelanin and eumelanin. These pigments absorb most of the wavelengths, resulting in dark colors, which are directly proportional to the pigment concentration (Proctor and Lynch 1993; McGraw et al. 2005). Studies on the function of melanin-based coloration have shown that it may act as signal of male competitive ability and social dominance (Senar 1999; Quesada and Senar 2007), and male parental quality (Roulin et al. 2001; Siefferman and Hill 2003; Siefferman and Hill 2005), and it is involved in mate choice (Kigma et al. 2008), by signaling aspects of individual quality. It is now accepted that environmental variables and physiologic condition, such as food availability (i.e. Griffith et al. 1999) and hormonal condition, can affect the production of melanin. In this scenario, it would be interesting to evaluate if male plumage coloration of tawny-bellied seedeaters, which is an age-dependent signal, could be used by females as an indicator of male condition in mate choice or by males to signaling fighting abilities. If plumage coloration is an indicator of male condition, males with more colorful plumage will be preferred by females.

The tawny-bellied seedeater *Sporophila hypoxantha* is a socially monogamous species with female-biased biparental care (Facchinetti et al. 2008) and delayed plumage maturation, with adult males more colorful than females and juvenile males (Facchinetti et al. 2011). Males are mostly brownish above, and have a tawny-rufous rump and underparts, this color extending to cover the cheeks and ear coverts, while females are brown above and buffy-brownish below (Ridgely and Tudor 1989). Male crown feathers are bright gray, while the color of the female crown is brownish (Ridgely and Tudor 1989). The pigment responsible for the brown breast coloration is melanin, while male crown coloration seems to be structurally based (Facchinetti 2012). Juvenile males look like females to the human eye, but spectrophotometric analyses reveal differences between them in the UV and visible regions of the spectrum (Facchinetti et al. 2011). Juvenile males differ from adult males in breast and crown color until their second prealternate molt (i.e. they look different from adults during their first breeding season).

The aim of this study was to test if females of tawny-bellied seedeaters prefer males with duller breast coloration. Because male plumage coloration is an age-dependent signal, we tested female preferences for more colorful males by controlling for male age. In addition, we also tested if females show preferences for older or younger males, by controlling for plumage coloration.

Materials and methods

We mistnetted tawny-bellied seedeaters at Reserva El Bagual, Formosa Province, Argentina (26°10′S, 58°56′E), and then moved the individuals to the Faculty of Exact and Natural Sciences at the University of Buenos Aires where we determined their sex genetically (see Facchinetti et al. 2011 for details). Birds were housed in wire cages of 120 × 40 × 40 cm in groups of 11–16 birds per cage. Adult males, adult females, and juvenile males were housed in different cages during their stay in captivity, so there were three groups: females, older males (males that arrived with adult plumage), and younger males (males that arrived with juvenile plumage). They were maintained in an indoor aviary on a natural light:dark cycle at room temperature, except during winter, when the minimum temperature was set to 15–18 °C (similar to the temperature they have in their winter range). Birds from different cages were visually but not acoustically isolated. They were provided with a diet of millet and canary seeds, vitamins, and water ad libitum.

Plumage measurements

We measured plumage reflectance using an Ocean Optics S2000 spectrometer and a PX-2 pulsed xenon light source and bifurcated fiberoptic probe (Ocean Optics). We calibrated reflectance measures against a white standard of barium sulphate, following Osorio and Ham (2002), and against a black standard. We took all measurements perpendicular to the body surface using a black plastic tube to minimize incident ambient light and keep the measurement distance constant (17.1 ± 0.1 mm). For the analysis, we used the average of three scans, taken on an arbitrary location on the breast (three measurements for each individual). We took each measurement in a 6-mm-diameter area and recorded reflectance from 350 to 700 nm in 0.35-nm steps (wavelengths between 300 and 350 nm showed considerable noise and the values of reflectance were very low, therefore we did not include them in the analysis). Data were obtained via spectral acquisition software package OOIBASE32 (Ocean Optics). We took dark and white reference measurements immediately before measuring each individual in order to minimize any error associated with drift of the light source and sensor. We summarized reflectance data by estimating breast brightness, calculated as the sum of the reflectance over the complete wavelength range (350–700 nm).

Author's personal copy

Mate choice

Dyads of males

Males were arranged according to their values of breast brightness and we then selected pairs of males that differed in breast brightness, keeping the difference approximately constant between pairs. During the breeding season 2009–2010, we performed three choice experiments. In the first one, females could choose between a pair of males with similar breast brightness that differed in age (brightness of older males: 474.8 ± 46.2; brightness of younger males: 470.6 ± 55.4; $t = 0.13$, $P = 0.71$, $n = 9$ pairs). In the second experiment, females could choose between a pair of males of 2 years of age that differed in breast brightness (brighter males: 573.6 ± 47.3; duller males: 473.4 ± 34.8; $t = 5.39$, $P < 0.001$, $n = 10$ pairs). In the third experiment, females could choose between a pair of males of 3 or more years of age that differed in breast brightness (brighter males: 521.9 ± 34.8; duller males: 431.5 ± 43.2; $t = 3.98$, $P < 0.01$, $n = 6$ pairs). In the breeding season 2010–2011, we repeated the third experiment with estradiol-treated females (brighter males: 1679.5 ± 133.0; duller males: 1228.9 ± 77.8; $t = 8.77$, $P < 0.001$, $n = 8$ pairs). The difference in brightness values between the two breeding seasons (higher values of brightness in 2010–2011) is because we used two different spectrometers. However, because we did not compare measurements between breeding seasons, this did not affect the analysis of the data. Because of the limited number of males, we decided to increase the number of pairs in the previous experimental groups and not include an experimental group in which females could choose between a pair of males of similar age and brightness.

Mate choice experiments

We conducted female choice experiments in an indoor room under artificial light conditions. In the room, there was an experimental arena consisting of three cages, one of 120 × 40 × 40 cm (length × width × height) for the female, and two of 30 × 20 × 20 cm for the males (Fig. 1). The cage of the female had three zones: near male 1 (the female could see male 1 but not male 2), near male 2 (the female could see male 2 but not male 1), and neutral (the female could not see either male). Males were visually but not acoustically isolated from each other. In all cages, there were food and water.

In each experiment, the pair of males was randomly assigned to the different females. Females were tested once in each experiment. We did not test females with the same male in different experiments within or across years, to avoid females choosing males with which they had previous experience. Mate choice experiments were conducted during the morning, between 0700 and 1200 hours. Each trial lasted 90 min. During the first 30 min, we allowed the birds to familiarize to the experimental arena. During this period, the female could hear the males but it could not see them (we put an opaque board in front of the cage of each male). Then, we removed the boards and the female could see both males and choose to stay close to either male or in the neutral zone (Ballentine and Hill 2003; Siefferman and Hill 2006; Fig. 1).

In the experiment with estradiol-treated females, 8 birds received a daily oral dose of 1 μg × g^{-1} of body mass of β-estradiol (Sigma Chemical) dissolved in a solution of 99 % water and 1 % alcohol. Each female received this treatment during 1 week previous to the start of the choice experiment to reduce the possibility that females were not receptive to the stimulus animals. Estradiol enhances the reproductive and productive functions in several species of songbirds; for example, increasing responsiveness to playbacks (O'Loghlen and Rothstein 2003; von Engelhardt et al. 2004; Elnagar and Abd-Elhady 2009).

Data analysis

The experiments were video-recorded and later analyzed using Etholog 2.2 program (Ottoni 2000). We started to record the time spent at the different zones after the female had observed both males. Those trials in which the female did not see both males were excluded (6 of 33). We compared the percentage of time spent in each male's zone using Wilcoxon tests. We performed statistical analyses

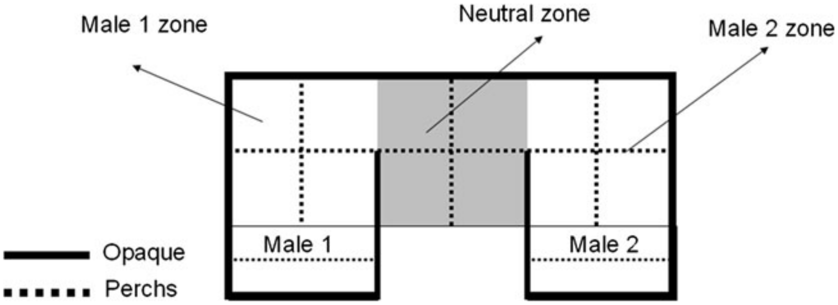

Fig. 1 The cages used in the choice experiments using tawny-bellied seedeaters *Sporophila hypoxantha*. The cage of the female had three zones: male 1, male 2, and neutral, delimitated by opaque partitions (indicated by *solid lines*). In the three zones, there were perches (*pointed lines*), food, and water

Author's personal copy

with Statistica v.8.0 (Statsoft 2009) and G*Power v.3.1 (Faul et al. 2007). All P values were two-tailed with alpha (α) set at 0.05. The n values refer to pairs of males and the $1-\beta$ values to the statistical power.

Results

We first evaluated whether females had any side preference. In all cases, we did not find significant differences between the percentage of time spent at the left and right sides of the cage (experiment 1: $z = 1.18$, $P = 0.23$, $n = 7$; experiment 2: $z = 0.42$, $P = 0.67$, $n = 8$; experiment 3: $z = 0.94$, $P = 0.34$, $n = 5$; and experiment 4 with estradiol: $z = 0.84$, $P = 0.4$, $n = 8$).

In all the experiments, females spent more time in the males' zones than in the neutral zone (choice between same brightness males that differed in age: $z = 2.36$, $P < 0.01$, $n = 7$, Fig. 2a; choice between males of 2 years that differed in brightness: $z = 2.38$, $P < 0.01$, $n = 8$, Fig. 2c; choice between males of 3 or more years that differed in brightness: $z > 2.02$, $P < 0.04$, $n = 5$, Fig. 2e; and choice by estradiol treated females between males of 3 or more years that differed in brightness: $z = 2.52$, $P < 0.01$, $n = 7$, Fig. 2g).

Considering the time that females spent in the males' zones, we did not find significant differences in the percentage of time that females spent with males that differed in age but not in breast brightness ($z = 0.84$, $P = 0.39$, $1-\beta = 0.89$, $n = 7$; Fig. 2b), or with males that differed in breast brightness but not in age ($z = 0.84$, $P = 0.4$, $1-\beta = 0.97$, $n = 8$ for males of 2 years of age; Fig. 2d; and $z = 0.21$, $P = 0.68$, $1-\beta = 0.16$, $n = 5$ for males of 3 or more years of age; Fig. 2f). Similarly, when we repeated the experiment of choice between males of 3 or more years that differed in brightness, but using females hormonally treated with estradiol during 1 week, we did not observe differences in the percentage of time females spent with males that differed in breast brightness ($z = 0.21$, $P = 0.83$, $1-\beta = 0.9$, $n = 8$; Fig. 2h). We re-analyzed the data of the four experiments by measuring the first male with which the female spent a bout longer than 30 s, and the preferences of the female during the first 10 min of the trial, and in both cases we did not find evidence of female preferences for older (experiment 1) or brighter (experiments 2–4) males.

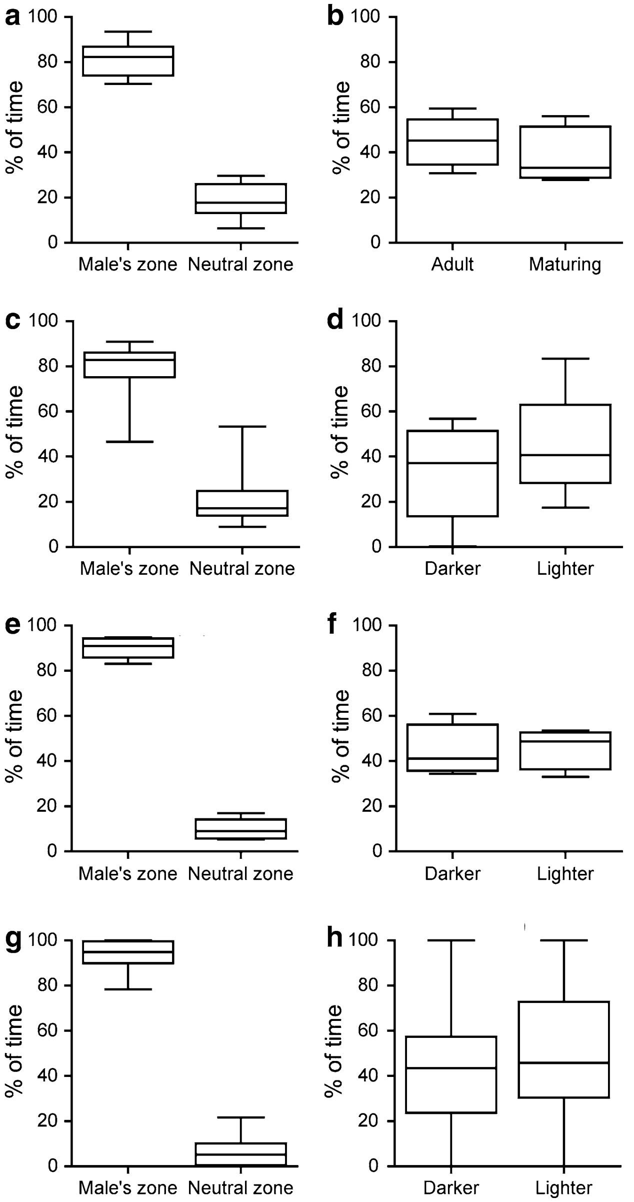

Fig. 2 *Box plots* indicate the percentage of time spent by females of tawny-bellied seedeaters *Sporophila hypoxantha* in the choice experiments (median, lower and upper quartiles, and smallest and largest values). *Numbers* on the *left* indicate the percentage of time spent by females in the males' zones (zone male 1 + zone male 2) and in the neutral zone, while *numbers* on the *right* indicate the percentage of time spent by females in the zones of each male. **a**, **b** The choice between males differing in age but not in breast coloration, **c**, **d** the choice between males of 2 years differing in breast brightness, **e**, **f** the choice between males of 3 or more years differing in breast brightness, and **h**, **g** the choice between males of 3 or more years differing in breast brightness by females hormonally treated with estradiol

Discussion

We did not find a pattern of preference for brighter or older males, as females spent the same proportion of time with males of similar breast brightness that differed in age or with males of similar age that differed in breast brightness. Negative results in a mate choice experiments can be interpreted as an evidence of lack of female preferences for the specific analyzed character only if the tested individuals

Author's personal copy

are receptive to the stimulus animals (Liu et al. 2007). To eliminate the later possibility, we hormonally treated females with estradiol and the results remained unchanged. In addition we also analyzed if there was a preference for the first male with which the female spent at least 30 s, and the preference of females during the first 10 min of the trial, and again, we did not find a pattern of preference for brighter males. Therefore, we did not find support for the hypothesis that male, breast brightness is a cue used by female tawny-bellied seedeaters at the time of choosing males. The statistical power for most tests was high ($1-\beta > 0.8$), except for one test ($1-\beta = 0.16$). These results should be reconfirmed by increasing the sample size or by conducting experiments in the field, where we can evaluate, for example, if there is a correlation between male coloration and the start of the breeding season or male reproductive success (i.e. Kigma et al. 2008).

An alternative explanation for the sexual dichromatism of tawny-bellied seedeaters would be that male plumage coloration plays a role in intrasexual competition. In many species, plumage coloration is an indicator of male social dominance and is involved in male–male competition (Senar 1999; Morimoto et al. 2005; Senar 2006). For example, melanin coloration in the great tit, *Parus major*, is associated with male aggression, including dominance and nest defense (Quesada and Senar 2007). The tawny-bellied seedeater shows delayed plumage maturation, with juvenile males looking different from adult males until their second breeding season (Facchinetti et al. 2011). The status signaling hypothesis (Lyon and Montgomerie 1986) is focused on the benefits that juveniles could obtain by showing their inexperience in male–male interaction (i.e. Morimoto et al. 2005; Mitrus 2007). Considering tawny-bellied seedeater biology, with males very territorial during the breeding season (A.G. Di Giacomo, personal communication; Benites 2012), the high frequency of extra-pair copulations (Facchinetti 2012), and the association with other conspecifics during the non-breeding season (Di Giacomo 2005), the occurrence of delayed plumage maturation in this species may act as a signal to avoid aggression from older males, during the reproductive as well as the non-reproductive seasons. Therefore, it would be important to evaluate if male coloration in tawny-bellied seedeaters is also involved in competition among adult males.

In addition, tawny-bellied seedeaters are socially monogamous and males defend their territories from conspecific intruders (A.G. Di Giacomo, personal communication; Benites 2012). In this scenario, good-quality individuals are also likely to have good-quality territories, and discrimination between female choice over territories or males becomes difficult (Griffith and Pryke 2006). Therefore, it is possible that females do not chose males based on plumage coloration but on territory quality that is associated with male coloration (Alatalo et al. 1986). In this case, females may not exhibit a preference for male coloration in a mate choice experiment (Griffith and Pryke 2006). Alatalo et al. (1986) found that females simply selected the best territory, irrespective of the quality of the male defending that territory. It would be interesting to evaluate whether, in tawny-bellied seedeaters, male coloration is correlated with the quality of the territory and if females choose males indirectly by choosing territories.

Acknowledgments We thank Alejandro Di Giacomo who help us capture the birds at Reserve El Bagual and Alparamis SA, and Aves Argentinas/Asociación Ornitológica del Plata for logistical support at this Reserve. We also thank two anonymous reviewers and the corresponding editor for helpful comments on a previous version of this manuscript. C.F. was supported by a fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). J.C.R. is Research Fellow of CONICET.

References

Alatalo RV, Lundberg A, Glynn C (1986) Female pied flycatchers choose territory quality and not male characteristics. Nature 323:152–153

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

Ballentine B, Hill GE (2003) Female mate choice in relation to structural plumage coloration in blue grosbeaks. Condor 105:593–598

Benites P (2012) Análisis de las diferencias de coloración y vocalizaciones en especies de aves cercanamente emparentadas y simpátricas, y su importancia como mecanismos de aislamiento reproductivo. Dissertation, University of Buenos Aires, Argentina

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland

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

Di Giacomo AG (2005) Aves de la Reserva El Bagual. In: Di Giacomo AG, Krapovickas SF (eds) Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Aves Argentinas/Asociación Ornitológica del Plata, Buenos Aires, pp 203–465

Elnagar SA, Abd-Elhady AM (2009) Exogenous estradiol: productive and reproductive perfomance and physiological profile of Japanese Quail Hens. Int J Poult Sci 8:634–641

Facchinetti C (2012) Coloración del plumaje, sistema de apareamiento y elección de pareja en el Capuchino Canela (*Sporophila hypoxantha*). Dissertation, University of Buenos Aires, Argentina

Facchinetti C, Di Giacomo AG, Reboreda JC (2008) Parental care in tawny-bellied (*Sporophila hypoxantha*) and rusty-collared (*S. collaris*) seedeaters. Wilson J Ornithol 120:879–883

Facchinetti C, Mahler B, Di Giacomo AG, Reboreda JC (2011) Stages of plumage maturation of the tawny-bellied seedeater: evidence of delayed plumage maturation and cryptic differentiation between juveniles and females. Condor 113:907–914

Faul F, Erdfelder E, Lang AG, Buchner A (2007) G*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Meth 39:175–191

Author's personal copy

Fox DL (1976) Animal biochromes and structural colors. University of California Press, California

Griffith SC, Pryke SR (2006) Benefits to females of assessing color displays. In: Hill GE, McGraw KJ (eds) Bird coloration, vol II: function and evolution, Harvard University Press, Cambridge, pp 233–279

Griffith SC, Stewart IRK, Dawson DA, Owens IPF, Burke T (1999) Contrasting levels of extra-pair paternity in mainland and island populations of the house Sparrow (*Passer domesticus*): is there an 'island effect'? Biol J Linn Soc 68:303–316

Hawkins GL, Hill GE, Mercadante A (2012) Delayed plumage maturation and delayed reproductive investment in birds. Biol Rev 87:257–274

Hill GE (2006) Female mate choice for ornamental coloration. In: Hill GE, McGraw KJ (eds) Bird coloration, vol II: function and evolution, Harvard University Press, Cambridge, pp 137–200

Humphrey PS, Parkes KC (1959) An approach to the study of molts and plumages. Auk 76:1–31

Kigma SA, Szentirmai I, Székely T, Bókony V, Bleeker M, Liker A, Komdeur J (2008) Sexual selection and the function of a melanin-based plumage ornament in polygamous penduline tits *Remiz pendulinus*. Behav Ecol Sociobiol 62:1277–1288

Liu M, Siefferman L, Hill GE (2007) An experimental test of female choice relative to male structural coloration in eastern bluebirds. Behav Ecol Sociobiol 61:623–630

Lyon BE, Montgomerie RD (1986) Delayed plumage maturation in passerine birds: reliable signalling by subordinate males? Evolution 40:605–615

McGraw KJ (2006) Mechanics of melanin-based coloration. In: Hill GE, McGraw KJ (eds) Bird coloration, vol I: mechanisms and measurements, Harvard University Press, Cambridge, pp 243–294

McGraw KJ, Safran RJ, Wakamatsu K (2005) How feather colour reflects its melanin content. Funct Ecol 19:816–821

Mitrus C (2007) Male aggressive behaviour and the role of delayed plumage maturation in the red-breasted flycatcher *Ficedula parva* (Bechstein, 1792) during the breeding season. Biol Lett 44:51–59

Morimoto G, Yamaguchi N, Ueda K (2005) Plumage color as a status signal in male–male interaction in the red-flanked bushrobin, *Tarsiger cyanurus*. J Ethol 24:261–266

O'Loghlen AL, Rothstein SI (2003) Female preference for the songs of older males and the maintenance of dialects in Brown-headed Cowbirds (*Molothrus ater*). Behav Ecol Sociobiol 53:102–109

Osorio D, Ham AD (2002) Spectral reflectance and directional properties of structural coloration in bird plumage. J Exp Biol 205:2017–2027

Ottoni EB (2000) EthoLog 2.2—a tool for the transcription and timing of behavior observation sessions. Behav Res Methods Instrum 32:446–449

Proctor NS, Lynch PJ (1993) Manual of ornithology. Yale University Press, New Haven

Prum RO, Torres R, Williamson S, Dyck J (1999) Two-dimensional fourier analysis of the spongy medullary keratin of structurally coloured feather barbs. Proc R Soc Lond B 266:13–22

Quesada J, Senar JC (2007) The role of melanin- and carotenoid-based plumage coloration in nest defence in the Great Tit. Ethology 113:640–647

Ridgely RS, Tudor G (1989) The birds of South America, vol I. Oxford University Press, Oxford

Rohwer S, Fretwell SD, Niles DM (1980) Delayed plumage maturation in passerine plumages and the deceptive acquisition of resources. Am Nat 115:400–437

Roulin A, Riols C, Dijkstra C, Ducrest AL (2001) Female- and male-specific signals of quality in the barn owl. J Evol Biol 14:255–267

Senar JC (1999) Plumage colouration as a signal of social status. In Adams NJ, Slotow RH (eds) Proceedings of the 22 international ornithological congress, Durban. Bird Life South Africa, Johannesburg

Senar JC (2006) Color displays as intrasexual signals of aggression and dominance. In Hill GE, McGraw KJ (eds) Bird coloration, vol II: function and evolution, Harvard University Press, Cambridge, pp 87–136

Siefferman L, Hill GE (2003) Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. Behav Ecol 14:855–861

Siefferman L, Hill GE (2005) Blue structural coloration of male eastern bluebirds *Sialia sialis* predicts incubation provisioning to females. J Avian Biol 36:488–493

Siefferman L, Hill GE (2006) An experimental test of female choice relative to male structural coloration in eastern bluebirds. Behav Ecol Sociobiol 61:623–630

Statsoft Inc (2009) STATISTICA (data analysis software system), version 8.0. www.statsoft.com

von Engelhardt N, Dijkstra C, Daan S, Groothuis TGG (2004) Effects of 17-b estradiol treatment of female zebra finches on offspring sex ratio and survival. Horm Behav 45:306–313