

Juvenile sexual dimorphism, dichromatism and condition-dependent signaling in a bird species with early pair bonds

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Abstract Sexual selection in juvenile vertebrates is a rare and seldom studied phenomenon. Bearded Reedlings are passerines that form stable, life-long pair bonds within a few weeks after fledging. We investigated the degree to which juvenile Bearded Reedlings are sexually dimorphic and whether they possess condition-dependent ornaments. We found significant intersexual differences in the bill reflectance, reflectance and size of eumelanin-based plumage traits (lore and back patch) and morphological traits. Females that were in better body condition had longer tails and bills with greater red chroma, and lore size was negatively related to the occurrence of chewing lice. In males, body condition was positively related to melanic back patch length. Moreover, a positive relationship between bill color and feather mite load in males suggests a symbiotic, rather than parasitic, relationship. Our study provides the first evidence that sexually dimorphic traits in immature birds with pair bonds have the potential to signal condition and resistance to parasites.

Keywords *Panurus biarmicus* · Ornaments · Ecto-parasites · Mate choice · Carotenoids

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Zusammenfassung

Juveniler Geschlechtsdimorphismus, Dichromatismus und konditionsabhängige Signale bei einer Vogelart mit früher Paarbindung

Sexuelle Selektion bei juvenilen Wirbeltieren ist ein seltenes und wenig untersuchtes Phänomen. Bartmeisen sind Sperlingsvögel, die bereits wenige Wochen nach dem Ausfliegen stabile, lebenslange Paarbindungen eingehen. Wir haben untersucht, in welchem Ausmaß juvenile Bartmeisen sexuell dimorph sind und ob sie konditionsabhängige Ornamente aufweisen. Wir fanden signifikante Geschlechtsunterschiede in der Reflektivität des Schnabels, der Reflektivität und Größe von auf Eumelanin basierenden Gefiedermerkmalen (Zügel und Rückenfleck) und morphologischen Merkmalen. Weibchen in besserer Körperkondition hatten längere Schwänze und Schnäbel mit stärkerer roter Farbsättigung, und die Größe des Zügels stand in negativer Beziehung zum Auftreten von Kieferläusen. Bei Männchen stand die Körperkondition in positiver Beziehung zur Länge des melanistischen Rückenflecks. Darüber hinaus deutet eine positive Beziehung zwischen der Farbe des Schnabels und dem Federmilbenbefall darauf hin, dass diese Beziehung eher symbiotisch als parasitisch sein könnte. Unsere Studie liefert erste Belege dafür, dass sexuell dimorphe Merkmale bei noch nicht geschlechtsreifen Vögeln mit Paarbindungen möglicherweise Körperkondition und Parasitenresistenz signalisieren.

Introduction

In many bird species, males display brilliantly colored plumage or bare skin, elongated feathers, crests, wattles

and many other traits (reviewed in Andersson 1994; Hill and McGraw 2006), while females exhibit less elaborate traits. The evolution of male ornaments is usually explained by the process of sexual selection where individuals honestly advertise their quality to prospective partners (Andersson 1994; but see Amundsen 2000 for an alternative hypothesis). Because mate choice is inevitably linked with breeding, sexual dimorphism is usually restricted to adult, sexually mature individuals. Young birds typically exhibit no dimorphism (except body size) or dichromatism (reviewed in Kilner 2006). With few exceptions, immature birds lack bright colors, and color is limited to melanin-based shades of gray, brown and black, often appearing mottled (reviewed in Kilner 2006).

There are three classes of sexual dimorphism in immature birds. First, young birds may develop dimorphic traits that are retained until they moult into adult plumage. One example is the structurally colored rectrices of blue tits (*Cyanistes caeruleus*, Johnsen et al. 2003). Second, some form of juvenile dimorphism may persist only until the offspring fledge (or become independent), like the yellow breast coloration of blue tits (Johnsen et al. 2003) or the variable back coloration of European bee-eater (*Merops apiaster*, Kapun et al. 2011). In these examples, color is thought to signal gender to parents who may favor offspring of a particular sex (reviewed in Kilner 2006). Finally, immature, sexually dimorphic birds may form pairs and breed in the subsequent, or the same, season. In these species [e.g., Bearded Reedling (*Panurus biarmicus*, Bibby 1983) and Scottish and Common Crossbills (*Loxia scotica*, *L. curvirostra*; Edelaar et al. 2005)], juvenile dimorphism is slightly different from that observed in adults. These juvenile ornaments might be honest indicators of quality and be sexually selected; however, this hypothesis has never been tested.

The Bearded Reedling is a small, reed-dwelling Euro-Asiatic Passerine. Juvenile plumage differs with sex; males have bright orange bills and black lores, while females have brown bills and grey lores (Cramp 1998). Moreover, both sexes possess long, graduated tails (the tails are longer in males), black rectangular patches on their backs, and variable amounts of black color on tail feathers (Cramp 1998). Adult males also differ from females in their long, black, drooping moustaches and blue-gray heads (Cramp 1998). Adults of both sexes lack the black tails and rectangular black back patches that are well developed in juveniles (Cramp 1998). Pair formation takes place during the juvenile plumage stage (Feindt and Jung 1968; Wawrzyniak and Sohns 1986; Brocchieri et al. 1992), and these pair bonds last all year, usually for the life of the birds (van den Elzen 1977; Todte and Stępniewski 2002; Hořák et al. 2003). Several hypotheses have been proposed

to explain this phenomenon. Bibby (1983) suggested that the early duration and permanence of Bearded Reedling pairs enable small numbers of individuals to colonize and recolonize areas. Another explanation is that early pair formation increases fitness. Indeed, in a recent experimental study, Griggio and Hoi (2011) demonstrated that pair duration has a positive effect on the synchronization of nest building, the number of breeding attempts and breeding success.

The timing of pair bond formation and degree of sexual dichromatism in Bearded Reedlings suggest that females may use juvenile plumage to select the more ornamented males. Alternative explanations are that dichromatism may function only in sex recognition or that the traits function as intrasexual signals of social dominance. Here, for the first time, we investigate the possible function of juvenile ornaments in the Bearded Reedling. First, we examined intersexual differences in all potential traits to assess dimorphism and dichromatism. Next, we used feather reflectance coupled with avian visual models to quantify the degree of sexual dichromatism from the perspective of the avian eye. Finally, we investigated whether ornaments could act as indicators of partner quality by comparing ornaments with body condition and ecto-parasite load.

Methods

Field methods

We captured birds (44 males and 45 females) in mist nets from June to July 2007 at the Wonieć Reservoir (Western Poland). We measured the following morphology: tarsus length (caliper 0.01 mm), folded wing length (ruler 1 mm), mass (digital balance 0.01 g), tail length (ruler 1 mm) and back black patch length (ruler 1 mm). Back patch length was measured from the lower mantle to the central rump. Using standard positions, a size standard and digital camera, we photographed both sides of the head and spread tails. We collected the following feather samples: 3rd and 6th rectrice, 1st tertial and 10–15 breast feathers. Feathers were stored in the dark in tightly closed zip-lock bags until further analysis. We took several spectrometric measurements of bills and plumage (see below for details). Each bird was marked with an aluminum band.

Estimating ectoparasites load

All collected feathers (2 rectrices, tertial and breast feathers) were examined under a stereomicroscope at magnification of 1:40 to estimate feather mite (Acari: Astigmata) and chewing lice (Mallophaga) load.

Reflectance and size of ornaments

We measured the spectral reflectance of plumage and bills using an Ocean Optics spectrometer (USB 4000, range of 200–1,100 nm, Dunedin, FL, USA) and a PX-2 pulsed xenon lamp (Ocean Optics, Dunedin, FL, USA) that emits both UV and visible light (220–750 nm). We used a bifurcated fiber-optic measuring probe (R 200-7-UV/VIS, Ocean Optics, Dunedin, FL, USA) that provided illumination from the lamp and transferred reflected light from the feather to the spectrometer. To avoid ambient light and standardize measuring distance (1.5 mm), a black plastic tip was mounted on the ferrule of the probe. The probe was held at a 90° angle to the measured surface and illuminated an area of ca. 2 mm diameter. All reflectance data were generated relative to a white standard (WS-1-SL, Labsphere). Spectral measurements were expressed as percent reflectance of light per wavelength in relation to a white standard reflectance (100 %). We took two readings from the upper bill mandible, one on each side of the bill. Similarly, we took one measurement from the center of each of lore. Three measurements were taken from the middle of the black back patch, breast and crown. Black (3rd) and rusty (6th) rectrices were measured in the laboratory. In both cases, three readings were located approximately 10 mm from the feather tip. In case of multiple measurements, subsequent measurements were spaced by at least 2 mm.

We processed spectral data using RCLR v0.9.28 software (Montgomerie 2008). For all melanin-based colors (i.e., rusty and black), we calculated brightness as the mean reflectance for each wavelength (1 nm) between 300 and 700 nm (B2 in RCLR software). Brightness is a good predictor of the amount of melanin deposited in chestnut feathers (McGraw et al. 2003). Bill and rusty feathers showed the greatest reflection within the red wavelengths (Fig. 1); therefore, we calculated the red chroma (S1R in RCLR software) to describe those traits. Chroma is a measure of spectral purity and is expressed as the proportion of reflectance in the red region of spectra (600–700 nm) to the total reflectance (300–700 nm). Prior to further analysis, we averaged all values obtained from the same color patch and individual.

One researcher (MS) measured area of lore (mm²) from digital photographs using Lupa 2.0 software (Bajaczyk 2007). The areas of the left and right lores were averaged for each individual. Using digital images of the tails, one researcher (AS) quantified the proportion of the tail with black color using the following protocol. First, the ratio of black on the feather was assessed for each rectrice separately using an 11-point scale ranging from 0 (no black color in a feather) to 10 (entire feather is black). Then, the score for each feather was recalculated to reflect the ratio

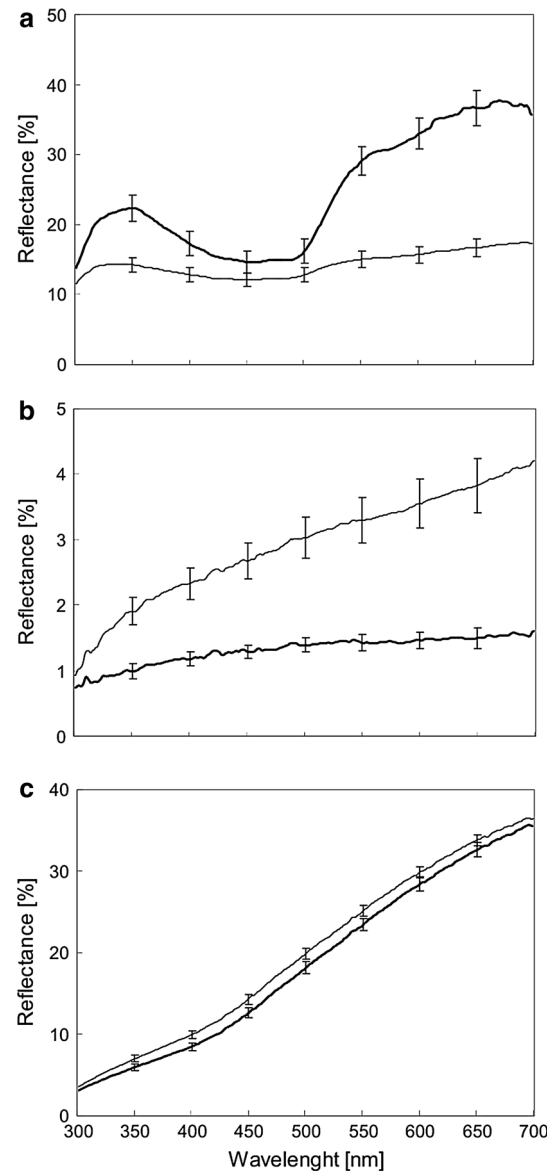


Fig. 1 Mean (\pm SE) reflectance spectra of male (*thick line*) and female (*thin line*) Bearded Reedlings: **a** bill, **b** lore, **c** flank

of the black area in relation to the entire tail area. The total score used in further analyses was the sum of percentages of the black area obtained from all 12 rectrices.

Carotenoid analysis

Carotenoid analyses were performed on a male specimen found dead in the study area in 2007. Two small (2×4 mm) shavings of upper bill mandible were collected and sent to the laboratory of Kevin McGraw at Arizona State University. The type and amount of carotenoids in the bill tissue were analyzed using high-performance liquid chromatography (HPLC) (see detailed methods in Juola et al. 2008).

Statistical analysis

Sample sizes vary between analysis and traits because we failed to take all measurements from all individuals. We tested for normality using Shapiro-Wilk tests. All data conformed to normality except for back patch brightness, lore brightness and flank red chroma in females and wing length in both sexes.

We used Pearson or Spearman correlations to investigate relationships between traits and *t* tests or Mann-Whitney tests to investigate differences between sexes. We corrected the alpha level using the sequential Bonferroni method whenever multiple testing occurred. To examine relationships between ornaments and body condition, we applied stepwise backward regression models. The following traits were used as independent variables: (1) tail length, (2) lore area, (3) back patch length and (4) bill red chroma. Body condition was expressed as body mass divided by tarsus length (Safriel and Lavee 1988; Zduniak and Yosef 2012). Back patch, tail length and lore area were not significantly correlated with tarsus in either sex ($p > 0.05$ in all cases), so we did not correct these measurements for body size. We used backwards logistic regression to determine whether variation in ornaments (see above)

explained the presence/absence of feather mites and lice.

Visual modeling

Reflectance spectrometer data yield very precise color measurements. Therefore, some intersexual differences in color parameters (Table 1) may be statistically significant, but not necessarily distinguishable to birds. To assess whether detected dichromatism was within the birds' perception abilities, we calculated chromatic contrast (ΔS) between reflectance of male and female feathers. Chromatic contrast (ΔS) is expressed in units called just noticeable differences (jnds). It is assumed that ΔS values >1.0 can be distinguished by birds (Vorobyev et al. 1998). Moreover, increasing values of ΔS suggests an increasing ability of birds to detect differences between two color patches. We calculated chromatic contrast (ΔS) in the following way. For average reflectance spectra from each region (i.e., lore, rusty tail and flank) and for each individual, we computed cone quantum catches (Q_i) for each cone type using the formula provided by Vorobyev et al. (1998):

$$Q_i = \int_{\lambda} R_i(\lambda)S(\lambda)I(\lambda)O(\lambda)d\lambda$$

Table 1 Sexual dimorphism (morphology and coloration) in juvenile Bearded Reedlings

Trait	Males		Females		<i>t</i> , <i>z</i>	<i>p</i>
	<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD		
Bill						
Red chroma	32	0.355 \pm 0.036	32	0.279 \pm 0.018	10.79*	<0.001
Tail						
Length	38	74.0 \pm 3.2	38	69.2 \pm 4.2	5.54*	<0.001
Black area	27	48.04 \pm 6.02	23	51.35 \pm 6.21	-1.91	0.062
Black brightness	29	0.053 \pm 0.010	29	0.056 \pm 0.007	-1.36	0.179
Rusty brightness	27	0.127 \pm 0.016	27	0.134 \pm 0.014	-1.72	0.091
Rusty red chroma	27	0.392 \pm 0.011	27	0.383 \pm 0.011	2.48*	0.002
Lore						
Area	31	15.04 \pm 1.90	32	10.85 \pm 2.67	7.15*	<0.001
Brightness	27	0.012 \pm 0.004	29	0.029 \pm 0.014	-5.35*	<0.001
Back patch						
Length	29	37.1 \pm 2.9	29	34.1 \pm 4.3	3.09	0.003
Brightness	29	0.023 \pm 0.006	27	0.022 \pm 0.005	0.41	0.682
Crown						
Brightness	32	0.122 \pm 0.023	32	0.122 \pm 0.017	-0.04	0.965
Red chroma	32	0.399 \pm 0.027	32	0.398 \pm 0.026	0.22	0.830
Flank						
Brightness	29	0.186 \pm 0.036	31	0.201 \pm 0.030	-1.81	0.075
Red chroma	29	0.420 \pm 0.025	31	0.404 \pm 0.026	2.12	0.034
Mass	44	14.020 \pm 0.710	43	13.562 \pm 0.610	3.21*	0.001
Tarsus	44	24.000 \pm 0.578	45	23.228 \pm 0.590	6.21*	<0.001
Wing	41	58.1 \pm 1.3	41	56.8 \pm 1.4	3.63*	<0.001

Results of Student's *t* tests (normal type) and Mann-Whitney (*italics*) tests are given. Alpha level after sequential Bonferroni correction for multiple tests is 0.003

* $p < 0.003$

where λ is a wavelength, $R_i(\lambda)$ the sensitivity of cone type i , $S(\lambda)$ the reflectance spectrum, $I(\lambda)$ the irradiance spectrum and $O(\lambda)$ the transmittance of the ocular media.

We assumed that Bearded Reedlings, like the majority of passerines, use four cone types for color vision that are sensitive to very short (VS), short (S), medium (M) and long (L) wavelengths (Ödeen and Håstad 2003). Because no studies of cone sensitivities or the transmittance of the ocular media have been performed on Bearded Reedlings, we used data from Blue Tit, a species with UV-sensitive vision (Hart et al. 2000). We used Endler’s blue sky spectrum as irradiance spectrum (Endler 1993).

We calculated discriminability between two spectra using the following equation:

$$\Delta S^2 = (\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2) + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2 / \left((\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2 \right)$$

where:

$$\Delta f_i = \Delta q_i / q_i$$

where q_i is cone quantum catch (Q_i) normalized for the irradiance spectrum, and ω_i represents the receptor noise, which depends on scaling factor T , the relative abundance of cone types and the Weber fraction for the cone type. The scaling factor relates a proportion of the maximal cone catch to an absolute cone catch. We set T to 10,000, which roughly corresponds to bright illumination. We used a Weber fraction of 0.05 for all cone types and the following relative abundance of cones from blue tit: VS = 0.37, S = 0.70, M = 0.99, L = 1.00 (Hart et al. 2000).

The Vorobyev-Osorio model assumes that color discriminability does not depend on brightness (Vorobyev et al. 1998). We therefore calculated achromatic contrast (ΔL) using the formula provided by Siddiqi et al. (2004):

$$\Delta L = \Delta f_i / \omega$$

where:

$$\Delta f_i = \ln[q_i(\text{spec1})/q_i(\text{spec2})]$$

and q_i indicates double cone quantum catches for two reflectance spectra (spec1 and spec2). Double cones are assumed to be involved in achromatic vision (reviewed in Cuthill 2006). We used double cone sensitivity data provided by Hart et al. (2000). If ΔL values are >1.0, two reflectance spectra are considered to be distinguishable by birds (Siddiqi et al. 2004).

To assess whether birds perceive intersexual differences in color, we calculated chromatic and/or achromatic contrasts between averaged reflectance of each of female and

averaged reflectance of all males. The procedure was performed for each region separately. We confined analysis only to those traits where: (1) statistical differences were detected and (2) no intersexual differences occurred according to human vision. We used chromatic contrast (ΔS) to examine differences in chroma and achromatic contrast (ΔL) to examine differences in brightness. All calculations of cone quantum catches and chromatic discriminability were performed using SPEC.01 software (Hadfield 2004).

Results

Sexual dimorphism and dichromatism

Pairwise comparisons showed a number of differences between males and females. In general, males were larger and heavier than females (Table 1). Males had significantly longer tails, darker eumelanin lore traits, larger lores and marginally significantly longer back patches. We found no difference in the extent of black on tails between males and females (Table 1). Males displayed greater red chroma of the pheomelanin-pigmented tail and flank feathers (Table 1), but according to visual models, these differences were not distinguishable to the avian eye (see below). The bill color of males reflected significantly more red light and absorbed more blue light compared to females (Table 1; Fig. 1). The chemical analysis of male bill tissue revealed

Table 2 Correlation matrix among multiple traits in juvenile female and male Bearded Reedlings

	Tail length	Tail rusty red chroma	Lore area	Back patch length
Males				
Bill red chroma	0.53* (30)	-0.17 (27)	0.09 (32)	-0.16 (29)
Tail length		-0.14 (26)	0.13 (31)	-0.13 (27)
Tail rusty red chroma			-0.15 (27)	0.31 (26)
Lore area				0.24 (29)
Females				
Bill red chroma	0.03 (30)	0.31 (27)	-0.01 (32)	0.26 (29)
Tail length		0.29 (26)	0.42 (30)	0.35 (27)
Tail rusty red chroma			0.07 (27)	0.08 (25)
Lore area				0.31 (29)

Values are correlation coefficients with sample size in parentheses. Alpha level after sequential Bonferroni correction for multiple tests is 0.003

* $p < 0.003$

fair concentration of zeaxanthin (288 $\mu\text{g/g}$) and lutein (152 $\mu\text{g/g}$) with low concentrations of beta-cryptoxanthin (3 $\mu\text{g/g}$). Although female bill reflectance was overall flatter (Fig. 1), two weak peaks in UV and red range of light waves suggest a small contribution of carotenoids.

Relationships among traits

We found only one significant correlation among traits in both sexes (Table 2). In males, the red chroma of the bill was positively correlated with tail length. No significant correlations were found in females.

Visual models

Chromatic contrast (ΔS) between female and male pheomelanic tail feathers was >1.0 only for one female (3 %; mean \pm SE 0.29 ± 0.04). Achromatic contrast (ΔL) of eumelanic lore exceeded the perception threshold in all cases (mean \pm SE 15.70 ± 2.92). Chromatic contrast of pheomelanic flank feathers was >1.0 in only three cases (13 %; mean \pm SE 0.52 ± 0.08). The above results suggest that differences in coloration were well perceived only in the lores.

Condition dependence and ecto-parasites

Feather mites were found only on rectrices and tertials. Their prevalence was 30 % for males and 48 % for females. The total number of mites varied from 1 to 7 in males, and from 1 to 101 in females; however, the mean number of mites did not differ significantly with sex ($Z = -1.29$, $p = 0.20$). Chewing lice were found only on the breast feathers of 57 % of males and 55 % of females. In all cases, single louse specimens were found. There was no difference in the prevalence of lice between the sexes ($\chi^2 = 0.02$, $p = 0.89$).

In males, body condition was significantly related to the length of back patches ($F_{1,26} = 4.46$, $p = 0.04$, $R^2 = 0.12$; $B = 0.04 \pm 0.02$, $t = 2.11$, $p = 0.04$); however, no other ornaments were significantly related to body condition (tail length: $t = -0.30$, $p = 0.77$; bill red chroma: $t = -0.35$, $p = 0.73$; lore area: $t = 0.92$, $p = 0.37$). There were no significant relationships between male ornaments and the occurrence of feather lice ($\chi^2 = -1.76$, $p = 0.18$). On the other hand, males with greater red chroma of the bill were more likely to have feather mites ($\chi^2 = 7.956$, $p = 0.02$; $B = 51.50 \pm 23.01$, Wald = 5.01, $p = 0.03$).

In females, body condition was positively related to tail length ($F_{2,25} = 8.82$, $p < 0.01$, $R^2 = 0.39$; $B = 0.004 \pm 0.002$, $t = 2.58$, $p = 0.02$, Fig. 2) and red bill chroma ($B = 0.79 \pm 0.29$, $t = 2.73$, $p = 0.01$). The remaining ornaments were not significantly correlated with body

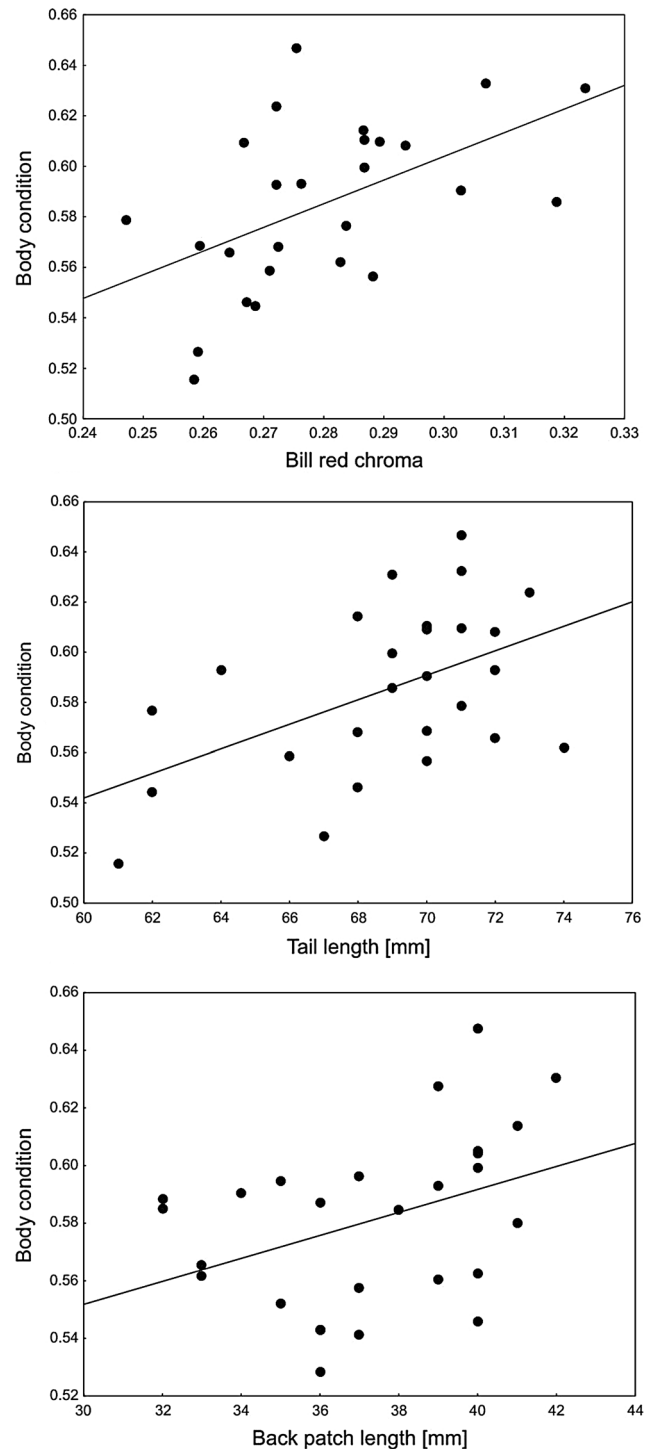


Fig. 2 Relationships between body condition and red chroma of the bill (female), tail length (female) and back patch length (male)

condition (lore area: $t = 0.45$, $p = 0.66$; back patch length: $t = -0.82$, $p = 0.42$). Females with smaller lores were more likely to have feather lice ($\chi^2 = 7.02$, $p < 0.01$; $B = -0.49 \pm 0.23$, Wald = 4.95, $p = 0.03$, Fig. 3), but no ornament was related to feather mite occurrence ($\chi^2 = 3.42$, $p = 0.06$).

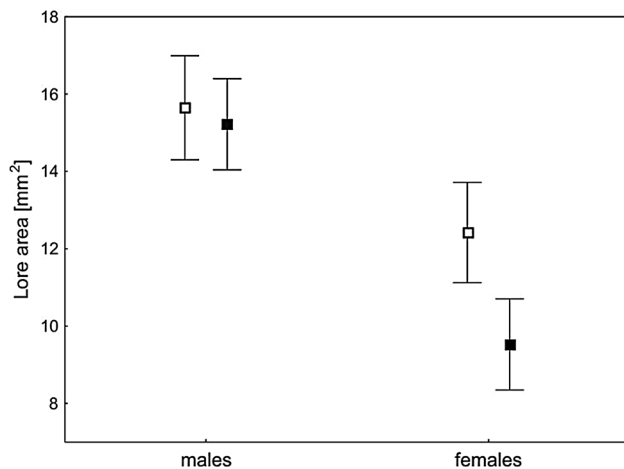


Fig. 3 Mean ($\pm 95\%$ CL) lore area of male and female Bearded Reedlings in relation to the presence of chewing lice. *Open squares* not infested; *filled squares* infested

Discussion

Our study provides the first complete description of sexual dimorphism in juvenile Bearded Reedlings including spectral reflectance measures of plumage coloration. We found that juvenile Bearded Reedlings are highly dimorphic. In addition to corroborating Cramp's (1998) work on tail length, bill and lore coloration (Cramp 1998), we reveal several other dimorphic characteristics. Males display larger lores and more extensive back patches compared to females. Males also display more elaborate rust-colored flanks and tails; however, these differences are not likely to be perceptible to the avian eye. The most dimorphic ornaments are bill and lore coloration, and lore area, while variation in other traits largely overlaps between males and females. According to predictions of sexual selection, males can be considered the more ornamented sex; male plumage characteristics suggest greater concentrations of carotenoids, eumelanins and pheomelanins deposited in their integuments.

Our study provides the first evidence that ornaments in juvenile birds that form early pair bonds signal a condition similar to honest signaling of adult birds. Heavier females displayed longer tails and bills with greater red chroma, and females with feather lice displayed smaller lores. A similar relationship has been previously reported among adult females; tail length was positively correlated with both condition (measured as body size index) and clutch size (Hoi and Hoi-Leitner 1997). Long graduated tails likely require a great deal of energy to produce and are often the result of sexual selection (see Andersson 1994). In adult Bearded Reedlings, birds exhibit mutual preferences for mates with longer tails (Romero-Pujante et al. 2002). Moreover, a recent study by Hoi and Griggio (2012)

found a negative relationship between the number of contacts that males initiate toward unpaired females and the relative tail length of his partner. Together, these findings suggest that male mate choice in Bearded Reedling is influenced by female tail length. As indicated by the reflectance curves, the yellowish bill of females may be, at least partially, colored by carotenoid pigments. Carotenoid-based bill colors have been shown to reflect many aspects of avian condition (e.g., Faivre et al. 2003; Hill et al. 2009; Rosenthal et al. 2012) and play a role in female mate choice (e.g., Simons and Verhulst 2011). There is a possibility that young male Bearded Reedlings use female carotenoid-based color to assess female quality (Griggio et al. 2009), but it is also possible that female bill color functions in intrasexual selection (Murphy et al. 2009). In addition to carotenoids, melanin pigments (particularly pheomelanin) may contribute to the red chroma of female bills. This type of coloration may also accurately reflect bird body condition (e.g., Siefferman et al. 2007). The trait that reflected female parasite load was lore size; individuals without lice had larger lores. It is important to note that, in females, there was a negative relationship between lore size and brightness; larger lores were darker, while the opposite was true for smaller lores ($r_s = -0.48$, $p = 0.007$, $n = 29$). Thus, lore size and brightness may honestly signal resistance to feather lice, as there is some evidence that lice avoid highly melanized feathers (Kose and Møller 1999; but see Bush et al. 2006).

Among males, we found a positive relationship between body condition and back patch size. In other species, melanin-based badge size is rarely correlated with body condition (e.g., Senar et al. 2003; Hegyi et al. 2007), and no such relationship has been found in adult Bearded Reedlings (Hoi and Hoi 2001). However, recent work suggests associations between melanin concentration and many physiological processes (McGraw 2006). Indeed, some studies have found that melanic traits signal body condition (Bortolotti et al. 2006) or ecto-parasite infestation (Fitze and Richner 2002). The positive correlations between feather mite occurrence and bill color that we found in the current study confirm a symbiotic, rather than parasitic, relationship between birds and feather mites (Galván et al. 2012). Preen oil may be an important component of the feather mite diet, and its production promotes mite abundance (Galván and Sanz 2006). Simultaneously, application of uropygial gland secretions may elaborate the reflectance of long-wavelength carotenoid-based colors (López-Rull et al. 2010). Thus, the positive relationship between coloration and mite occurrence that we observed in male juvenile Bearded Reedlings might occur because both are promoted by preen oil production.

It is possible that the ornaments of juvenile Bearded Reedlings may be associated with other aspects of

condition that we did not measure in our study. For example, carotenoid-based bill color changes with experimental alternation of the immune system (Faivre et al. 2003), nutrition and endo-parasites load (Hill et al. 2009). The fact that some potentially condition-dependent traits, such as bill color and tail length in males, are positively correlated suggests that they may function like multiple ornaments, conveying information on multiple overlapping aspects of condition (redundant signal hypothesis, Møller and Pomiankowski 1993). To fully understand the importance of condition-dependent ornaments in juvenile Bearded Reedlings, studies should be designed to investigate how well juvenile traits correlate with adult traits and whether the environment influences traits at both ages.

In Bearded Reedlings, extra-pair paternity is an important component of the mating strategy, and females often incite extra-pair copulations, which result in 14.4 % of offspring having extra-pair fathers (Hoi and Hoi-Leitner 1997). There is evidence that females choose extra-pair partners based on moustache length (Hoi and Hoi-Leitner 1997). Although the juveniles do not display moustaches, they have lores. It is possible that lore characteristics plays no role in juvenile mate choice but occurs as a precursor to the adult moustache. Alternatively, analogous to moustaches in adults, the lore characteristics may signal of social dominance among flocks of juvenile males (Hoi and Griggio 2008).

In summary, we found that juvenile birds with early pair bonds are capable of producing dimorphic traits, which could signal various aspects of their condition.

Future research is needed to determine the signaling function of juvenile ornaments, including mate choice experiments and more detailed condition measures. Moreover, following individuals to monitor how variation in juvenile traits influences variation in adult traits displayed after the completion of the pre-basic moult is warranted.

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References

- Amundsen T (2000) Why are female birds ornamented? *Trends Ecol Evol* 15:149–155
- Andersson M (1994) *Sexual selection*. Princeton University Press, Princeton
- Bajaczyk R (2007) *Lupa*, version 2.0. Adam Mickiewicz University, Poznań
- Bibby CJ (1983) Studies of west Palearctic birds: bearded tit. *Br Birds* 76:549–563
- Bortolotti GR, Blas J, Negro JJ, Tella JL (2006) A complex plumage pattern as an honest social signal. *Anim Behav* 72:423–430
- Brocchieri L, Matessi C, Marin G (1992) Inference of pair bonds from capture data based on low variation of the sex ratio among catches. *Am Nat* 140:492–508
- Bush SE, Kim D, Moyer BR, Lever J, Clayton DH (2006) Is melanin a defense against feather-feeding lice? *Auk* 123:153–161
- Cuthill IC (2006) Color perception. In: Hill GE, McGraw KJ (eds) *Bird coloration. Mechanisms and measurements*, vol 1. Harvard University Press, Cambridge, pp 41–89
- Cramp S (1998) *The complete birds of western Palearctic on CD-ROM*. Oxford University Press, Oxford
- Edelaar P, Phillips RE, Knops P (2005) Sexually dimorphic body plumage in juvenile crossbills. *Wilson Bull* 117:390–393
- Endler JA (1993) The color of light in forests and its implications. *Ecol Monogr* 63:1–27
- Faivre B, Grégoire A, Prévault M, Cézilly F, Sorci G (2003) Immune activation rapidly mirrored in secondary sexual trait. *Science* 300:103
- Feindt P, Jung K (1968) Barmeisen—Einblicke in ihr verborgenes Leben. *Zeitschrift des Museum Hildesheim, Neue Folge* 20:1–75
- Fitze PS, Richner H (2002) Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behav Ecol* 13:401–407
- Galván I, Sanz JJ (2006) Feather mite abundance increases with uropygial gland size and plumage yellowness in great tits *Parus major*. *Ibis* 148:687–697
- Galván I, Aguilera E, Atiénzar F, Barba E, Blanco G, Cantó JL, Cortés V, Frías Ó, Kovács I, Meléndez L, Møller AP, Monrós JS, Pap PL, Piculo R, Senar JC, Serrano D, Tella JL, Vágási CI, Vögeli M, Jovani R (2012) Feather mites (Acari: Astigmata) and body condition of their avian hosts: a large correlative study. *J Avian Biol* 43:273–279
- Griggio M, Devigilia A, Hoi H, Pilaastro A (2009) Female ornamentation and directional male mate preference in the rock sparrow. *Behav Ecol* 20:1072–1078
- Griggio M, Hoi H (2011) An experiment on the function of the long-term pair bond period in the socially monogamous bearded reedling. *Anim Behav* 82:1329–1335
- Hadfield J (2004) *SPEC. User manual*. Department of Biological Sciences, Imperial College at Silwood Park, Ascot
- Hart NS, Partridge JC, Cuthill IC, Bennett ATD (2000) Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J Comp Physiol A* 186:375–387
- Hegyí G, Szigeti B, Török J, Eens M (2007) Melanin, carotenoid and structural plumage ornaments: information content and role in great tits *Parus major*. *J Avian Biol* 38:698–708
- Hill GE, McGraw KJ (2006) *Bird coloration. Mechanisms and measurements*, vol 1. Harvard University Press, Cambridge
- Hill GE, Hood WR, Huggins K (2009) A multifactorial test of the effects of carotenoid access, food intake and parasite load on the production of ornamental feathers and bill coloration in American goldfinches. *J Exp Biol* 212:1225–1233
- Hoi H, Griggio M (2008) Dual utility of a melanin-based ornament in bearded tits. *Ethology* 114:1094–1100
- Hoi H, Griggio M (2012) Bearded Reedlings adjust their pair-bond behaviour in relation to the sex and attractiveness of unpaired conspecifics. *PLoS ONE* 7(2):e32806

- Hoi C, Hoi H (2001) Intrasexual selection in bearded tits: beard length—a reliable predictor for dominance rank. In: Hoi H (ed) The ecology of reed birds. Austrian Academy of Sciences Press, Wien, pp 121–138
- Hoi H, Hoi-Leitner M (1997) An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. *Behav Ecol* 8:113–119
- Hořák D, Procházka P, Cepák J, Zárbynický J (2003) Tahové poměry sýkořic vousatých (*Panurus biarmicus*) na území České republiky a Slovenska. *Sylvia* 39:79–94
- Johnsen A, Delhey K, Andersson S, Kempenaers B (2003) Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proc R Soc Lond B Biol* 270:1263–1270
- Juola FA, McGraw K, Dearborn DC (2008) Carotenoids and throat pouch coloration in the great frigatebird (*Fregata minor*). *Comp Biochem Phys B* 149:370–377
- Kapun M, Darolová A, Křištofik J, Mahr K, Hoi H (2011) Distinct colour morphs in nestling European bee-eaters *Merops apiaster*: is there an adaptive value? *J Ornithol* 152:1001–1005
- Kilner RM (2006) Function and evolution of color in young birds. In: Hill GE, McGraw KJ (eds) Bird coloration. Function and evolution, vol 2. Harvard University Press, Cambridge, pp 201–232
- Kose M, Møller AP (1999) Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow. *Behav Ecol Sociobiol* 45:430–436
- López-Rull I, Pagán I, Garcia CM (2010) Cosmetic enhancement of signal coloration: experimental evidence in the house finch. *Behav Ecol* 21:781–787
- McGraw KJ (2006) Mechanics of melanin-based coloration. In: Hill GE, McGraw KJ (eds) Bird coloration. Mechanisms and measurements, vol 1. Harvard University Press, Cambridge, pp 243–294
- McGraw KJ, Dale J, MacKillop EA (2003) Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 53:116–122
- Montgomerie R (2008) RCLR, version 0.9.28. Queen's University, Kingston
- Møller AP, Pomiankowski A (1993) Why have birds got multiple sexual ornaments? *Behav Ecol Sociobiol* 32:167–176
- Murphy TG, Rosenthal MF, Montgomerie R, Tarvin KA (2009) Female American goldfinches use carotenoid-based bill coloration to signal status. *Behav Ecol* 20:1348–1355
- Ödeen A, Håstad O (2003) Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Mol Biol Evol* 20:855–861
- Romero-Pujante M, Hoi H, Blomqvist D, Valera F (2002) Tail length and mutual mate choice in bearded tits (*Panurus biarmicus*). *Ethology* 108:885–895
- Rosenthal MF, Murphy TG, Darling N, Tarvin KA (2012) Ornamental bill color rapidly signals changing condition. *J Avian Biol* 43:553–564
- Safriel UN, Lavee D (1988) Weight changes of cross-desert migrants at an oasis—do energetic considerations along determine the length of stopover? *Oecologia* 76:611–619
- Senar JC, Figuerola J, Domenech J (2003) Plumage colouration and nutritional condition in the great tit *Parus major*: the roles of carotenoids and melanins differ. *Naturwissenschaften* 90:234–237
- Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K (2004) Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol* 207:2471–2485
- Siefferman L, Wang Y-J, Wang YP, Yuan H-W (2007) Sexual dichromatism, dimorphism, and condition-dependent coloration in Blue-tailed bee-eaters (*Merops philippinus*). *Condor* 109:577–584
- Simons MJP, Verhulst S (2011) Zebra finch females prefer males with redder bills independent of song rate—a meta-analysis. *Behav Ecol* 22:755–762
- Todte I, Stepniewski J (2002) Paarzusammenhalt und Neuverpaarungen bei der Bartmeise (*Panurus biarmicus*). *Otis* 10:87–94
- Wawrzyniak H, Sohns G (1986) Die Bartmeise. Neue Brehm-Bücherei, A. Zeiensen, Wittenberg Lutherstadt
- van den Elzen R (1977) Paarzusammenhalt bei der Bartmeise (*Panurus biarmicus*): eine Auswertung von Ringfunddaten. *Vogelwarte* 29:122–125
- Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC (1998) Tetrachromacy, oil droplets and bird plumage colours. *J Comp Physiol A* 183:621–633
- Zduniak P, Yosef R (2012) Crossing the desert barrier: migration ecology of the Lesser Whitethroat (*Sylvia curruca*) at Eilat, Israel. *J Arid Environ* 77:32–38