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MELANIN-BASED BLACK PLUMAGE COLORATION IS RELATED TO REPRODUCTIVE INVESTMENT IN CARDUELINE FINCHES

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Abstract. Avian color ornaments produced by different mechanisms (i.e., melanin, carotenoid, and structural colors) can communicate different sets of information due to differences in their condition or developmental constraints. Although this suggests that different color signals should be analyzed separately, few comparative studies have focused on specific types of coloration. In cardueline finches, interspecific variation in overall plumage brightness (which integrates all types of coloration) was previously shown to be affected by sexual selection and to covary with fecundity and parental care. Using a phylogenetic comparative approach, we extended this line of research and tested whether a specific component of plumage ornamentation, the melanin-based black frontal coloration of finches, showed a similar association with reproductive effort. We found that the extent of male melanization and melanin dichromatism increased in species with reduced clutch sizes, whereas female melanization was negatively correlated with incubation length. These results remained significant when we controlled for the effects of several ecological variables, and were also consistent between two alternative multivariate model-selection approaches. Our results are consistent with the hypothesis that interspecific variation in melanization may be related to fecundity and parental care through trade-offs between investment in sexual signals and parental efforts.

Key words: cardueline finches, color evolution, life history, melanin dichromatism, melanin ornaments, sexual selection.

La Coloración Negra del Plumaje Basada en Melanina se Relaciona a la Inversión Reproductiva en los Pinzones Carduelinos

Resumen. Los ornamentos de colores de las aves se producen por mecanismos diferentes (i.e., melanina, carotenoides y colores estructurales) y pueden comunicar distintos tipos de información debido a las diferencias en su condición o en las limitaciones impuestas por el desarrollo. Aunque esto sugiere que las diferentes señales de color deberían ser analizadas separadamente, pocos estudios comparativos se han enfocado en los tipos específicos de coloración. En estudios anteriores, se demostró que la variación interespecífica en el brillo general del plumaje (la cual integra todos los tipos de coloración) de los pinzones carduelinos ha sido afectada por la selección sexual y covarió con la fecundidad y el cuidado parental. Usando una perspectiva filogenética comparativa, extendemos esta línea de investigación y evaluamos si un componente específico de la ornamentación del plumaje, la coloración frontal negra basada en melanina de los pinzones, muestra una asociación similar con el esfuerzo reproductivo. Encontramos que el grado de melanización de los machos y el dicromatismo de melanina incrementaron en las especies con tamaños de nidada reducidos, mientras que la melanización de las hembras se correlacionó negativamente con la duración de la incubación. Estos resultados siguieron siendo significativos luego de que controlamos por los efectos de varias variables ecológicas, y fueron también consistentes entre dos enfoques alternativos de selección de modelos multivariados. Nuestros resultados son consistentes con la hipótesis de que la variación interespecífica en la melanización puede estar relacionada con la fecundidad y el cuidado de los padres a través de compromisos entre la inversión en señales sexuales y el esfuerzo de los padres.

INTRODUCTION

Recent studies of avian plumage coloration have suggested that the main types of color ornaments (carotenoid-based, melanin-based, and structural coloration) have distinct signal contents and may evolve in response to different selection pressures (Gray 1996, Owens and Hartley 1998, Badyaev and Hill 2000). For example, several experimental studies have demonstrated the differing functions of carotenoid and melanin ornaments. Carotenoid ornaments are often in-

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volved in female choice but not in signaling social status among competing conspecifics (Johnson et al. 1993, Hill 2002), whereas melanin ornamentation usually predicts dominance rank (reviewed by Senar 1999); however, evidence on females preferring more melanized males is equivocal (Møller 1988, Johnson et al. 1993, Senar et al. 2005, Tarof et al. 2005). In addition, careful experiments have shown that the expression of carotenoid but not melanin ornaments was influenced by nutritional condition (Hill 2002, McGraw et al. 2002) and endoparasite load (Hill and Brawner 1998, Brawner et al. 2000, McGraw and Hill 2000), whereas melanin but not carotenoid coloration was affected by ectoparasite infection (Fitze and Richner 2002).

Although these findings suggest that different color signals should be analyzed separately when studying selective forces influencing interspecific color variation, most comparative studies have made no such distinction between specific types of coloration (reviewed by Badyaev and Hill 2000). For example, in cardueline finches overall plumage brightness, which encompasses all types of coloration, covaried with ecological factors, as predicted by sexual selection theory, varying with the altitude of breeding (Badyaev 1997a) and nest height (Martin and Badyaev 1996). Furthermore, Badyaev (1997b) demonstrated that plumage brightness and dichromatism were linked to components of fecundity and duration of parental care. The latter result indicated that common mechanisms such as nest predation or adult mortality rates may affect variation in both sexual ornamentation and fecundity, and thus may mediate the relationships between investment in sexually-selected traits and reproductive efforts (Badyaev 1997b).

In one of the first studies that focused on specific types of pigmentation, Gray (1996) showed that overall dichromatism in North American passerines was related to carotenoid-based coloration of males and was unrelated to their melanin-based and structural coloration. Similarly, Badyaev and Hill (2000) demonstrated in cardueline finches that much of the interspecific variation in overall dichromatism was explained by variation in carotenoid dichromatism, and they found no relationship between overall dichromatism and melanin dichromatism. Thus, Badyaev and Hill (2000) concluded that the relationships between overall plumage coloration and life-history traits in finches may be due to carotenoid rather than melanin ornaments. For other bird species, however, the evolution of melanin-based coloration has been related to parental care (Owens and Hartley 1998) and sexual selection (Bókony et al. 2003).

Our aim here was to expand previous comparative work in cardueline finches by investigating a specific component of plumage ornamentation, melanin-based black coloration. Determining factors that may affect interspecific variation in melanization is particularly important because recent advances in understanding the proximate basis of melanin-based coloration suggest that melanin ornaments may be costly to produce and can reflect individual condition (Jawor and Breitwisch 2003, McGraw 2003). Furthermore, an increasing number of case studies demonstrate that certain melanin ornaments may signal mate quality and predict mating success (Roulin 1999, Roulin et al. 2000, 2001, Parker et al. 2003, Tarof et al. 2005; for nonblack melanization see Siefferman and Hill 2003). This raises the possibility that the evolution of melanin ornaments may be related to variation in life-history traits, as shown for other sexually-selected traits (e.g., plumage brightness). For example, due to a trade-off between sexual and parental investment, in species where males increase their investment in sexual competition they may provide reduced parental care (Verner and Willson 1969, Trivers 1972, Badyaev 1997b). Thus, we hypothesized that if melanin ornaments are used in either form of sexual competition, such trade-offs may lead to a negative association between plumage melanization and reproductive investment (fecundity or parental care). Under this scenario, we predicted that (i) in species with more melanized males, females may lay smaller or fewer clutches or the incubation and nestling period may be prolonged because of decreased male parental care, (ii) in species with more melanized females, both fecundity and duration of care may be reduced because of females' increased investment in sexual competition, and (iii) the more competitive sex will dictate the relationship between melanin dichromatism and reproductive effort; in finches this would probably be the males.

In this study, we first assessed the extent of interspecific variation in melanin-based black coloration and its dichromatism in cardueline finches. We then tested whether melanization is

associated with variation in fecundity (i.e., clutch size and number of broods per year) and parental care (i.e., length of incubation and nestling periods) in the same manner as overall plumage brightness in finches (Badyaev 1997b). Although simultaneous investigation of several types of coloration (e.g., both melanin and carotenoid ornaments) would be the most powerful way to clarify their differences with respect to certain evolutionary processes, here we considered only melanin-based coloration because our method for quantifying melanization (Bókony et al. 2003) does not take into account hue and saturation (Hill 1998, McGraw et al. 2004). Lastly, we controlled for the possible confounding effects of ecological variables (nest height, breeding altitude, and body size) that are related to coloration and reproductive investment in cardueline finches (Martin and Badyaev 1996, Badyaev 1997a, 1997b, 1997c).

METHODS

MEASURING MELANIZATION

We measured the extent of melanization in the breeding plumage of male and female finches (n = 125 species) using color plates of Clement et al. (1993). We digitized illustrations that showed the birds in lateral view; in a few cases when no such image was available in Clement et al. (1993), color plates from Perrins (1998) were used. Using Scion Image software (Scion Corporation 2000), we then measured the area of black plumage patches on the head and breast, as bordered by the lower edge of the nape and the edge of the wing and a vertical line drawn from the base of the leg (frontal body region; Bókony et al. 2003). We restricted our measurements to the head and breast of finches because these areas are highly variable in melanization across species and are likely to be involved in sexual signaling (McNaught and Owens 2002, Bókony et al. 2003). If a species possessed several black patches within the frontal body region, we calculated the sum of the area of all patches. Melanization was expressed as the proportion of black area relative to the total area of the frontal body (Appendix); both areas were measured in pixels. Note that melanization values are proportions and thus have no unit of measurement. For sexually monomorphic species (i.e., those in which plumage was not illustrated separately for males and females), both sexes were given the same proportion of melanization. Although melanin pigments produce a range of colors (Jawor and Breitwisch 2003), we specifically measured black, which is produced by eumelanins (McGraw and Wakamatsu 2004) and usually does not reflect ultraviolet light (Bennett et al. 1994). See Bókony et al. (2003) for repeatabilities and justification of the method of measuring black plumage ornaments from lateral view on digitized illustrations.

DATA ON LIFE HISTORY AND ECOLOGY

We collected data on clutch size (average number of eggs per clutch), number of broods per season, and lengths of incubation and nestling periods (in days) using published sources (Badyaev 1997b, 1997c, Perrins 1998, Geffen and Yom-Tov 2000; Appendix). We also gathered published data on typical nest height relative to ground level (i.e., ground, shrub, or canopy) and altitude of breeding (i.e., average of lowest and highest elevation of breeding range), since these factors were shown to influence interspecific variation in plumage coloration among finches (Martin and Badyaev 1996, Badyaev 1997a). Because body size correlates with many life-history traits and thus may confound their relationships with coloration (Harvey and Pagel 1991), we collected data from Badyaev (1997a) on tarsus length as a skeletal measure of body size.

PHYLOGENETIC ANALYSES

To control for phylogenetic relationships among species, we used a composite phylogeny of finches that summarizes all recent systematic information available for extant carduelines. This consensus tree is well supported by molecular studies of both basal nodes and within-clade relationships (Badyaev et al. 2002). Since most branch lengths were not known, we set branch lengths to unity. This phylogenetic hypothesis has been used extensively in previous comparative work on cardueline finches (Badyaev 1997a, 1997b, 1997c, Badyaev and Ghalambor 1998, Tobias and Hill 1998, Badyaev and Hill 2000).

We calculated phylogenetically independent contrasts (Felsenstein 1985) as implemented by the CAIC 2.6 program (Purvis and Rambaut 1995). Male and female melanization were arcsine transformed and all other variables were log-transformed before the calculation of independent contrasts. Melanin dichromatism (i.e.,

the difference in the extent of melanization between sexes) was computed as contrasts in male melanization–contrasts in female melanization (Bókony et al. 2003). We tested the relationships between contrasts in melanization (or dichromatism; dependent variables) and contrasts in clutch size, number of broods per season, and length of incubation and nestling period (predictor variables) by least squares linear regressions forced through the origin (Harvey and Pagel 1991, Garland et al. 1992). Although the assumptions of the independent contrast method (Purvis and Rambaut 1995) were not met in some of our analyses, the method is robust to violations of these assumptions (Diaz-Uriarte and Garland 1996, 1998, Martins et al. 2002). Simulation tests showed that the independent contrasts method performs very well when there are no, or weak, constraints on the trait's evolution, and yields biased results only when evolutionary constraints are strong (Martins et al. 2002). In the latter case, however, analyses using raw data without phylogenetic control give reasonable results (Martins et al. 2002). Our results remained qualitatively unchanged when we treated each species as an independent datum (results not shown), so this consistency between the analyses suggests that our results are robust.

We used the information-theoretic approach as described by Burnham and Anderson (2002), based on the second-order Akaike's information criterion corrected for small sample size (AIC_c) to investigate the relative importance of life-history variables and to control for the potential confounding effects of nest height, breeding altitude, and body size. Since the very components of reproductive investment related to melanization were unclear *a priori*, an exploratory approach was taken and all possible subsets of the seven predictor variables were modeled and considered in the analysis (Gibson et al. 2004), excepting models that only contained confounding variables (i.e., nest height, breeding altitude, and tarsus length). As no single model was clearly superior compared with the others in the model set, we performed model averaging (Burnham and Anderson 2002), where model coefficients were weighted using Akaike weights and inference was based on the entire set of candidate models. We then compared the final sets of predictor variables selected by stepwise regression and AIC_c-based model averaging.

We used the R statistical computing environment (Ihaka and Gentleman 1996, R Development Core Team 2003) and SPSS for Windows 11.0 for statistical analyses. Sample sizes are different across statistical analyses, since life history and ecological data were not available for some species. Values of melanization and dichromatism are reported as means ± SE. All statistical tests are two-tailed with a 95% confidence level.

RESULTS

Melanization of the frontal body (proportion of the black area compared to the whole region) ranged from 0 to 0.97 in males and from 0 to 0.99 in females. Males were more extensively melanized (0.13 ± 0.02) than females (0.04 ± 0.01; paired *t*-test, $t_{124} = 5.9$, $P < 0.001$), although evolutionary changes in melanization of the sexes was positively correlated (linear regression of independent contrasts through origin; $r = 0.28$, $F_{1,72} = 6.2$, $P = 0.02$). The mean difference between male and female melanization (raw data) was 0.09 ± 0.02, ranging from −0.03 (more extensive female melanization) to 0.82 (more extensive male melanization).

Univariate regression analyses of independent contrasts showed that evolutionary increases in male melanization corresponded to reductions in clutch size (Fig. 1a), whereas they were unrelated to the number of broods, incubation length, or nestling period (Table 1). In females, evolutionary increases in melanization correlated with decreases in incubation length (Fig. 1b), but were not related to other life-history traits (Table 1). Increases in melanin dichromatism were strongly correlated with decreases in clutch size (Fig. 1c) and increases in nestling stage length (Table 1).

Model selection based on the information-theoretic approach confirmed the above results. For each dependent variable (male and female melanization, and melanin dichromatism) we built 120 regression models and ranked them according to their AIC_c values. Table 2 shows the maximized log-likelihood values (log[*L*]), number of estimated parameters (*k*), differences between the model with the lowest AIC_c value and each candidate model (ΔAIC_c), and relative Akaike weights (w_i) for models with $\Delta AIC_c < 4.0$ for each dependent variable. Models with ΔAIC_c values ≤2 have substantial support (Burnham and Anderson 2002), while ΔAIC_c values of

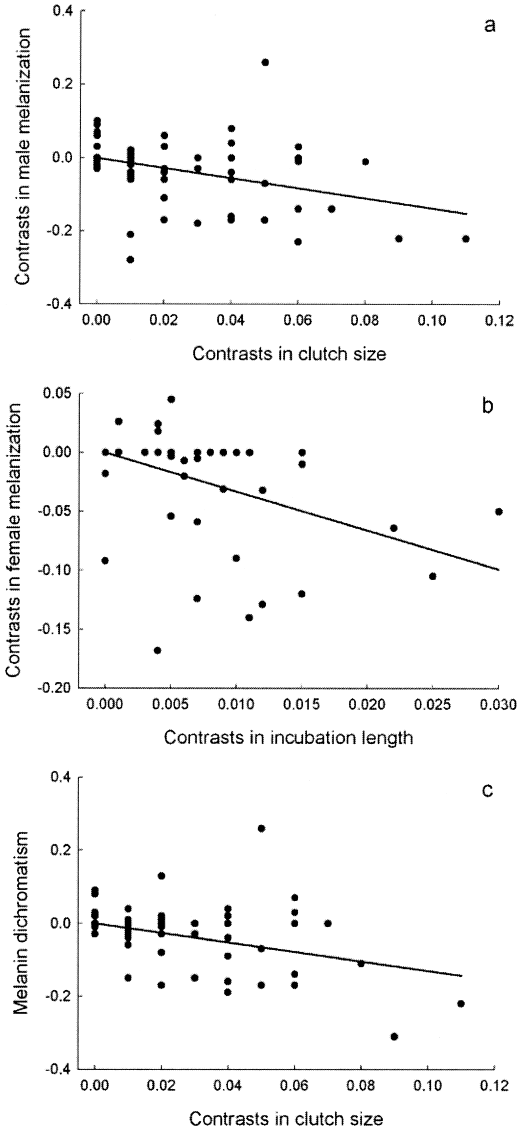

FIGURE 1. Relationship between phylogenetically independent contrasts in (a) clutch size and male melanization, (b) incubation length and female melanization, and (c) clutch size and melanin dichromatism in cardueline finches. Melanization was measured as the proportion of black area to the whole frontal body region; melanin dichromatism was computed as contrasts in male melanization–contrasts in female melanization. On each axis, positive values indicate increases in the given trait between sister taxa, while negative values correspond to decreases. Regression lines are forced through the origin (see Table 1 for statistics).

4–7 show considerably less support. For both male melanization and melanin dichromatism, the model with the lowest AIC_c included clutch size only, and of the top models 9 of 12 and 14 of 20 contained clutch size as a predictor, respectively. For female melanization, the best model included brood number and incubation length, but the second best included only incubation length, and all 16 top models contained incubation length as a predictor, while only 8 contained brood number.

Because w_i were similar across candidate models, suggesting substantial model selection uncertainty, we evaluated the relative importance of predictor variables using model averaging (Table 3). These results were consistent with the results of stepwise regressions: both male melanization and melanin dichromatism were most strongly related to clutch size, males being more melanized in species with smaller clutches. Female melanization related most strongly to incubation length, females being more melanized in species with shorter incubation periods. The remaining predictor variables explained much less interspecific variation in melanization.

DISCUSSION

We found that the extent of melanin-based black coloration and its dichromatism increased in cardueline species with aspects of decreased reproductive investment. Our results are robust since they remained significant after controlling for the possible confounding effects of the most relevant ecological factors known to influence coloration in carduelines. Furthermore, our results are consistent between two alternative multivariate model selection approaches: a conventional frequentist method and an information-theoretic model comparison. This latter finding is also noteworthy in light of the ongoing debate about whether employing information theory should exclusively replace frequentist procedures (Anderson and Burnham 2002) or whether the two approaches may be used in concert to get robust results (Stephens et al. 2005).

Our results suggest that melanization is related to some life-history traits in a similar way as overall plumage brightness (Badyaev 1997b). This finding is interesting given that melanin-based coloration is a minor constituent of sexual dichromatism in finches (Badyaev and Hill 2000), and melanin ornaments appeared not to

TABLE 1. Melanization of males and females, and melanin dichromatism in relation to life-history traits in cardueline finches. Least square linear regressions of independent contrasts were forced through the origin. Melanin dichromatism was computed as contrasts in male melanization–contrasts in female melanization.

Dependent	Predictor	r	F (df)	$b \pm$ SE	P
Male melanization	Clutch size	–0.46	14.9 (55)	–1.32 ± 0.34	< 0.001
	Number of broods	–0.24	1.9 (32)	–0.52 ± 0.37	0.17
	Incubation length	–0.15	0.9 (38)	–1.64 ± 1.73	0.35
	Nestling period length	0.25	3.3 (49)	1.09 ± 0.60	0.08
Female melanization	Clutch size	–0.03	0.1 (55)	–0.05 ± 0.20	0.82
	Number of broods	–0.06	0.1 (32)	–0.07 ± 0.20	0.72
	Incubation length	–0.57	18.5 (38)	–3.27 ± 0.76	< 0.001
	Nestling period length	–0.22	2.4 (49)	–0.46 ± 0.30	0.13
Melanin dichromatism	Clutch size	–0.49	16.9 (55)	–1.27 ± 0.31	< 0.001
	Number of broods	–0.23	1.8 (32)	–0.45 ± 0.34	0.20
	Incubation length	0.17	1.1 (38)	1.64 ± 1.54	0.30
	Nestling period length	0.39	8.8 (49)	1.55 ± 0.52	0.01

affect mate choice in cardueline species (Johnson et al. 1993, Senar et al. 2005). Our results further imply that sex differences in melanin-based pigmentation of the head and breast might have contributed to the previously reported association between sexual dichromatism and life-history traits in finches (Martin and Badyaev 1996, Badyaev 1997a, 1997b, Badyaev and Ghalambor 1998).

Although both melanization and overall brightness are related to life-history traits in finches, the mechanisms causing these associations need not be the same for melanization and overall brightness in all instances. On the one hand, Badyaev (1997b) found that male brightness was negatively linked to fecundity (both to the number of broods and to clutch size), and proposed that this relationship reflects the evolutionary responses of female fecundity to males' trade-off between parental effort and mating effort (i.e., females lay smaller clutches in species with reduced paternal care). Our finding that male melanization varies negatively with clutch size may be explained by a similar logic. Males may use extensive melanin ornaments in intense sexual competition, which is expected to reduce their parental effort (Verner and Willson 1969, Trivers 1972, Qvarnström 1997).

On the other hand, female brightness was positively related to clutch size and strongly negatively associated with incubation length. These relationships were interpreted as a result of multiple effects of nest predation; for example, high nest predation rate may select both for duller females and smaller clutches (Badyaev 1997b). Since male carduelines do not participate in incubation, the rate of nest predation constrains female but not male plumage brightness (Martin and Badyaev 1996). Although we also found a negative relationship between incubation length and female melanization, it is unlikely that nest predation constrains the evolution of frontal black patches of females as it does plumage brightness. Black plumage has very low brightness (i.e., reflects very little light), thus it is expected to be rather inconspicuous in most of the natural nesting habitats of finches (Endler 1990, McNaught and Owens 2002). Accordingly, experimental manipulation of the extent of black patches of incubating females did not alter nest predation rates in the Hooded Warbler (*Wilsonia citrina*, Stutchbury and Howlett 1995). The lack of an effect of melanization on nest predation may also explain why we did not find associations between either female melanization and clutch size (which is a characteristic prediction of the predation hypothesis; Badyaev 1997b) or between female melanization and nest height (nest height also reflects nest predation rate and is associated with female brightness; Martin and Badyaev 1996). In contrast, the negative association between incubation length and female melanization is consistent with the prediction of sexual selection theory that females may trade off extended parental care for intense sexual competition and sexual signaling.

Finally, Badyaev (1997b) found that overall dichromatism was strongly related to clutch size, and this was ascribed to either sex-specific differences in adult mortality or nest predation rates, both of which affect coloration and fecun-

TABLE 2. Results of AIC_c-based model selection: maximized log-likelihood function (log[L]), number of estimated parameters (k), AIC_c differences (ΔAIC_c), and Akaike weights (w_i) for models with $\Delta AIC_c < 4.0$ for male and female melanization and melanin dichromatism. Predictor variables are clutch size (C), number of broods per season (B), length of incubation (I), length of nestling period (N), nest height (H), breeding altitude (A), and tarsus length (T).

Dependent	Predictors	log[L]	k	ΔAIC_c[a]	w_i
Male melanization	C	87.22	2	0.00	0.20
	C, A	89.66	3	1.37	0.10
	C, I	88.48	3	1.96	0.07
	C, B	88.34	3	2.03	0.07
	C, H	87.92	3	2.24	0.06
	C, T	87.90	3	2.25	0.06
	C, N	87.38	3	2.51	0.06
	N	80.74	2	3.24	0.04
	B, N	85.72	3	3.34	0.04
	C, A, T	91.10	4	3.51	0.03
	C, I, A	90.98	4	3.57	0.03
	B	79.34	2	3.94	0.03
Female melanization	B, I	165.52	3	0.00	0.16
	I	159.22	2	0.55	0.12
	B, I, N	169.08	4	1.08	0.10
	C, I	161.14	3	2.19	0.06
	B, I, T	166.44	4	2.40	0.05
	I, N	160.70	3	2.41	0.05
	I, H	160.60	3	2.46	0.05
	C, B, I	166.16	4	2.54	0.05
	I, A	160.12	3	2.70	0.04
	B, I, H	165.78	4	2.73	0.04
	B, I, A	165.52	4	2.86	0.04
	B, I, N, H	171.80	5	2.88	0.04
	I, N ,H	165.24	4	3.00	0.04
	I, T	159.24	3	3.14	0.03
	C, I, H	164.46	4	3.39	0.03
	B, I, N, T	169.62	5	3.97	0.02
Melanin dichromatism	C	107.50	2	0.00	0.16
	C, N	110.82	3	0.94	0.10
	C, I	109.68	3	1.51	0.07
	C, A	109.62	3	1.54	0.07
	N	104.38	2	1.56	0.07
	C, B	108.60	3	2.05	0.06
	C, H	108.50	3	2.10	0.06
	C, N, A	113.94	4	2.23	0.05
	N, A	107.76	3	2.47	0.05
	C, T	107.56	3	2.57	0.04
	C, N, H	112.66	4	2.87	0.04
	C, B, A	112.28	4	3.06	0.03
	C, I, A	111.74	4	3.33	0.03
	C, I, N	111.22	4	3.59	0.03
	I	100.16	2	3.67	0.03
	N, H	105.28	3	3.71	0.02
	I, N	105.20	3	3.75	0.02
	C, B, N	110.86	4	3.77	0.02
	C, N, T	110.82	4	3.79	0.02
	B, N	104.84	3	3.93	0.02

[a] Lowest AIC_c values were –39.06, –75.62, and –49.20 for male and female melanization, and melanin dichromatism, respectively.

TABLE 3. Model-averaged regression coefficients (*b*) and their unconditional standard errors (SE) for each life-history and ecological variable, for male and female melanization and melanin dichromatism. Coefficients of a given predictor were weighted using the Akaike weight of each candidate model containing that predictor.

Predictor	Male melanization $b \pm$ SE	Female melanization $b \pm$ SE	Melanin dichromatism $b \pm$ SE
Clutch size	–1.58 ± 0.38	–0.03 ± 0.15	–1.37 ± 0.34
Number of broods	–0.13 ± 0.17	–0.13 ± 0.16	0.04 ± 0.14
Incubation length	–0.41 ± 0.34	–1.07 ± 0.44	0.45 ± 0.31
Nestling period length	0.39 ± 0.27	0.12 ± 0.20	0.65 ± 0.27
Nest height	–0.05 ± 0.13	–0.01 ± 0.10	–0.04 ± 0.11
Breeding altitude	0.02 ± 0.06	< 0.001 ± 0.03	0.02 ± 0.05
Tarsus length	–0.17 ± 0.23	–0.07 ± 0.16	–0.04 ± 0.19

dity. As for overall dichromatism, we found that melanin dichromatism increased in species with smaller clutch sizes, but it is unclear whether the effects of adult or nest predation rates can explain this relationship (see above). This result may have arisen simply because only male melanization is linked to clutch size. Furthermore, melanin dichromatism is more strongly correlated with male melanization (linear regression of independent contrasts through origin: $r = 0.85$, $F_{1,72} = 191.9$, $P < 0.001$) than with female melanization ($r = -0.26$, $F_{1,72} = 5.2$, $P = 0.03$), which may also explain why melanin dichromatism is negatively related to clutch size but not to incubation length.

We suggest that the relationship between reproductive investment and melanization may be mediated by levels of sex hormones, particularly testosterone. High levels of plasma testosterone are involved in the regulation of melanization in several vertebrate species, including birds (Haase et al. 1995, Tadokoro et al. 1997, Evans et al. 2000, Buchanan et al. 2001, Gonzalez et al. 2001, Hill and McGraw 2003, Quinn and Hews 2003). Increased testosterone levels of males have also been shown to reduce paternal care in several species (Hegner and Wingfield 1987, Ketterson et al. 1992, Saino and Møller 1995), including House Finches (Stoehr and Hill 2000). These multiple effects of testosterone may result in females laying smaller clutches in species with more melanized males that provide less care. However, the effects of testosterone on the fecundity and behavior of female birds are not well understood. In one relevant study, experimentally increased testosterone levels of female Dark-eyed Juncos (*Junco hyemalis*) had no effect on female parental behavior or clutch size, but prolonged interclutch intervals (Clotfelter et al. 2004). Thus, if melanization is linked to testosterone in female finches, females can afford to develop extensive melanization in those species where the incubation period is relatively short. It is unknown, however, whether interspecific variation in melanin-based coloration of the sexes is related to variation in responsiveness to, or concentration of, sex hormones.

Since we could not measure carotenoid-based coloration in our study, we cannot exclude the possibility that the relationship between melanization and reproductive efforts is a by-product of carotenoid ornaments. However, this is unlikely because there is no known correlation between melanin dichromatism and carotenoid dichromatism in carduelines (Badyaev and Hill 2000). To our knowledge, this is the second study that specifically investigated the factors influencing the interspecific variation of melanin-based coloration in male and female birds. In a former comparative study we demonstrated the role of sexual selection in the evolution of male melanization for a group of shorebirds with no known carotenoid plumage traits (Bókony et al. 2003). Here, we provide additional support for the result that sexual selection may influence melanin ornamentation from finches, which exhibit both types of pigmentation.

In conclusion, we found that melanin-based ornaments in finches, in spite of being a minor constituent of sexual dichromatism, are related to components of reproductive investment in a similar way as overall plumage brightness (Badyaev 1997b), which may be determined mainly by carotenoid ornaments (Badyaev and Hill 2000). This result adds to other recent findings that melanin-based coloration may be a potent means of sexual signaling, its expression being linked to important life-history variables.

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APPENDIX. Data on male and female melanization (proportion of the black area to the whole frontal body region), clutch size (number of eggs per clutch), number of broods per season, incubation, and nestling period length (in days) of cardueline finches. See text for further explanation of melanization values and data sources.

Species	Proportion of melanization		Clutch size	Number of broods per season	Incubation period (days)	Nestling period (days)
	Male	Female				
Callacanthis burtoni	0.41	0.00	2.0	–	–	–
Carduelis ambigua	0.23	0.00	4.0	–	12.5	18.5
Carduelis atrata	0.97	0.99	–	–	–	–
Carduelis atriceps	0.21	0.17	–	–	–	–
Carduelis barbata	0.18	0.00	–	–	–	–
Carduelis cannabina	0.00	0.00	4.7	2.0	12.6	13.4
Carduelis carduelis	0.15	0.12	4.9	2.0	12.0	14.7
Carduelis chloris	0.01	0.01	4.8	2.0	12.9	15.1
Carduelis crassirostris	0.33	0.00	–	–	–	–
Carduelis cucullata	0.44	0.00	4.0	1.0	12.0	15.0
Carduelis dominicensis	0.36	0.00	–	–	–	–
Carduelis flammea	0.03	0.03	4.8	2.0	10.7	11.5
Carduelis flavirostris	0.00	0.00	5.7	2.0	12.5	11.5
Carduelis hornemanni	0.02	0.02	4.8	2.0	11.5	11.0
Carduelis johannis	0.01	0.01	–	–	–	–
Carduelis lawrencei	0.16	0.00	4.5	–	12.5	12.0
Carduelis magellanica	0.47	0.00	–	–	–	–
Carduelis monguilloti	0.39	0.25	–	–	–	–
Carduelis notata	0.54	0.38	–	–	–	–
Carduelis olivacea	0.45	0.00	–	–	–	–
Carduelis pinus	0.00	0.00	3.5	2.0	13.0	14.5
Carduelis psaltria	0.47	0.00	4.5	2.0	12.0	15.0
Carduelis siemiradzkii	0.40	0.00	–	–	–	–
Carduelis sinica	0.00	0.00	5.0	2.0	12.5	14.5
Carduelis spinescens	0.10	0.00	–	–	–	–
Carduelis spinoides	0.19	0.00	4.0	1.0	13.0	–
Carduelis spinus	0.13	0.00	4.3	2.0	12.5	14.0
Carduelis tristis	0.10	0.00	5.2	2.0	13.0	14.0
Carduelis uropygialis	0.71	0.63	–	–	–	–
Carduelis xanthogastra	0.68	0.00	2.5	–	–	–
Carduelis yarrellii	0.17	0.00	–	–	–	–
Carduelis yemenensis	0.00	0.00	–	–	–	–
Carpodacus cassinii	0.00	0.00	4.5	2.0	13.0	14.0
Carpodacus edwardsii	0.00	0.00	–	–	–	–
Carpodacus eos	0.00	0.00	–	–	–	–
Carpodacus erythrinus	0.00	0.00	4.9	1.0	12.1	11.6
Carpodacus mexicanus	0.00	0.00	4.2	–	13.5	15.0
Carpodacus nipalensis	0.00	0.00	–	–	–	–
Carpodacus pulcherrimus	0.00	0.00	3.0	–	–	–
Carpodacus puniceus	0.00	0.00	4.0	–	–	–
Carpodacus purpureus	0.00	0.00	4.5	2.0	13.0	14.0
Carpodacus rhodochlamys	0.00	0.00	4.0	1.0	15.0	16.5
Carpodacus rhodochrous	0.00	0.00	4.5	–	–	–
Carpodacus rhodopeplus	0.00	0.00	–	–	–	–
Carpodacus roborowskii	0.02	0.00	–	–	–	–
Carpodacus roseus	0.00	0.00	4.0	–	–	–
Carpodacus rubescens	0.00	0.00	–	–	–	–
Carpodacus rubicilla	0.00	0.00	4.8	1.0	16.0	17.0
Carpodacus rubicilloides	0.00	0.00	5.0	–	–	–
Carpodacus synoicus	0.00	0.00	4.5	2.0	13.5	15.0
Carpodacus thura	0.00	0.00	3.7	–	–	–
Carpodacus trifasciatus	0.11	0.00	–	–	–	–
Carpodacus vinaceus	0.00	0.00	–	–	–	–
Coccothraustes coccothraustes	0.09	0.08	4.4	1.0	12.0	12.5
Eophona migratoria	0.26	0.00	4.5	–	–	–
Eophona personata	0.21	0.21	–	–	–	–
Haematospiza sipahi	0.00	0.00	–	–	–	–
Hesperiphona abeillei	0.46	0.21	–	–	–	–
Hesperiphona vespertinus	0.09	0.01	3.0	1.0	13.4	14.1
Leucosticte arctoa	0.00	0.00	4.0	1.0	–	15.0
Leucosticte brandti	0.07	0.07	3.5	–	–	–
Leucosticte nemoricola	0.00	0.00	4.8	1.0	14.0	17.5

APPENDIX. Continued.

Species	Proportion of melanization		Clutch size	Number of broods per season	Incubation period (days)	Nestling period (days)
	Male	Female				
Linurgus olivaceus	0.44	0.00	2.0	–	–	–
Loxia curvirostra	0.00	0.00	3.7	2.0	15.0	23.0
Loxia leucoptera	0.00	0.00	4.0	3.0	14.5	23.0
Loxia pytyopsittacus	0.00	0.00	3.8	2.0	15.0	22.0
Loxia scotica	0.00	0.00	3.7	2.0	13.2	21.0
Mycerobas affinis	0.41	0.00	–	–	–	–
Mycerobas carnipes	0.78	0.00	3.2	2.0	16.0	21.0
Mycerobas icterioides	0.40	0.00	2.5	–	–	–
Mycerobas melanozanthos	0.54	0.40	2.5	–	–	–
Neospiza concolor	0.00	0.00	–	–	–	–
Pinicola enucleator	0.00	0.00	3.8	1.0	13.5	14.0
Pinicola subhimachala	0.00	0.00	–	–	–	–
Pyrrhoplectes epauletta	0.82	0.00	–	–	–	–
Pyrrhula aurantiaca	0.09	0.09	3.5	–	–	–
Pyrrhula erythaca	0.05	0.05	3.0	–	–	–
Pyrrhula erythrocephala	0.07	0.05	3.5	–	–	–
Pyrrhula leucogenys	0.15	0.18	–	–	–	–
Pyrrhula nipalensis	0.02	0.02	–	–	–	–
Pyrrhula pyrrhula	0.18	0.12	4.7	2.0	13.0	16.0
Rhodopechys githaginea	0.00	0.00	5.0	2.0	13.5	13.5
Rhodopechys mongolica	0.00	0.00	5.0	2.0	–	18.0
Rhodopechys obsoleta	0.02	0.00	4.8	2.0	13.8	13.5
Rhodopechys sanquinea	0.05	0.00	4.5	1.5	14.0	14.0
Rhynchostrustus socotranus	0.34	0.13	–	–	–	–
Serinus alario	0.46	0.00	–	–	–	–
Serinus albogularis	0.00	0.00	3.5	–	–	15.0
Serinus ankoberensis	0.00	0.00	3.0	–	–	14.0
Serinus atrogularis	0.00	0.00	3.0	–	12.5	16.5
Serinus burtoni	0.00	0.00	–	–	–	–
Serinus canaria	0.00	0.00	3.8	2.0	13.5	16.0
Serinus canicollis	0.00	0.00	3.5	–	13.0	17.0
Serinus capistratus	0.10	0.00	3.0	–	–	–
Serinus citrinella	0.00	0.00	4.5	2.0	13.5	16.5
Serinus citrinelloides	0.08	0.00	2.5	–	–	–
Serinus citrinipectus	0.00	0.00	3.0	–	13.0	16.8
Serinus donaldsoni	0.00	0.00	–	–	–	15.0
Serinus dorsostriatus	0.00	0.00	3.0	–	–	19.5
Serinus estherae	0.10	0.04	–	–	–	–
Serinus flavigula	0.00	0.00	–	–	–	–
Serinus flaviventris	0.00	0.00	4.0	–	–	15.0
Serinus gularis	0.00	0.00	3.0	–	13.5	15.5
Serinus koliensis	0.00	0.00	–	–	–	–
Serinus leucopterus	0.00	0.00	–	–	–	–
Serinus leucopygius	0.00	0.00	3.5	–	–	19.5
Serinus menachensis	0.00	0.00	–	–	–	14.0
Serinus mennelli	0.07	0.03	3.0	–	13.0	17.0
Serinus mozambicus	0.03	0.00	3.0	–	13.5	20.5
Serinus nigriceps	0.55	0.00	2.5	–	–	16.5
Serinus pusillus	0.62	0.21	3.7	1.0	12.0	14.0
Serinus rothschildi	0.00	0.00	–	–	–	15.5
Serinus rufobrunneus	0.00	0.00	–	–	–	–
Serinus scotops	0.07	0.00	3.5	–	–	18.0
Serinus serinus	0.04	0.06	3.8	2.0	12.7	14.6
Serinus striolatus	0.00	0.00	3.5	–	–	15.0
Serinus sulphuratus	0.00	0.00	3.0	–	–	15.0
Serinus symonsi	0.00	0.00	3.5	–	–	–
Serinus syriacus	0.00	0.00	4.0	2.0	13.0	15.0
Serinus thibetanus	0.02	0.05	–	–	–	–
Serinus totta	0.00	0.00	–	–	–	–
Serinus tristriatus	0.00	0.00	3.5	–	–	14.0
Serinus xantholaema	0.01	0.01	–	–	–	–
Uragus sibiricus	0.00	0.00	4.5	1.0	–	–
Urocynchramus pyzlowi	0.00	0.00	–	–	–	–