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RESEARCH ARTICLE

Melanin plumage ornaments in both sexes of Northern Flicker are associated with body condition and predict reproductive output independent of age

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ABSTRACT

Melanin is a common pigment in the plumage of birds, but the extent to which its deposition in feathers is condition dependent and can be used as a reliable signal of quality and reproductive performance is still much debated. In addition, the existence and function of melanin ornaments in female birds or in birds of different age classes has rarely been addressed. We studied the size and color of 4 melanin ornaments in the Northern Flicker (*Colaptes auratus*), a woodpecker, and found that the plumage patches became larger or darker with age class in both sexes. Consistent with the partly reversed sex roles of Northern Flickers and sexual selection in both sexes, several melanin ornaments were the same size in males and females and were correlated with body size or body condition. There was assortative pairing according to melanin ornaments when controlling for age, and 1 or more ornaments predicted laying date or clutch size of the pair independent of age. The results suggest that melanin ornaments in Northern Flickers may contain multiple messages and be used as cues of quality.

Keywords: body condition, *Colaptes auratus*, melanin, Northern Flicker, ornament, plumage, reproduction, woodpecker

Los ornamentos de melanina en el plumaje de ambos sexos de *Colaptes auratus* se asocian con la condición corporal y predicen el rendimiento reproductivo independientemente de la edad

RESUMEN

La melanina es un pigmento común en el plumaje de las aves, pero aún existe bastante debate en cuanto al grado al que su presencia en las plumas es dependiente de la condición corporal y a si puede ser usada como una señal confiable de calidad y desempeño reproductivo. Además, la existencia y función de los ornamentos de melanina en hembras o en aves de diferentes clases de edad rara vez han sido evaluados. Estudiamos el tamaño y color de cuatro ornamentos de melanina en el carpintero *Colaptes auratus* y encontramos que los parches de plumaje se hacían más grandes o más oscuros con la edad en ambos sexos. De acuerdo con la inversión parcial de los roles sexuales y la selección sexual en *C. auratus*, varios ornamentos de melanina fueron del mismo tamaño en machos y hembras, y se correlacionaron con el tamaño o la condición corporal. Encontramos apareamiento asociativo de acuerdo a los ornamentos de melanina cuando controlamos por edad, y uno o más ornamentos predijeron la fecha de puesta de los huevos o el tamaño de la nidada de la pareja independientemente de su edad. Los resultados sugieren que los ornamentos de melanina en *C. auratus* podrían contener múltiples mensajes y podrían ser usados como indicadores de calidad.

Palabras clave: carpintero, *Colaptes auratus*, condición corporal, melanina, ornamento, plumaje, reproducción

INTRODUCTION

A foundational idea in sexual selection is that signals of individual quality are costly to express (Zahavi 1975, Andersson 1994), and a plethora of studies in birds have focused on the correlation between plumage color and an individual's age, dominance, condition, or reproductive performance. Plumage ornaments in birds can function intersexually in the context of mate choice or intrasexually

in assessment of dominance or quality (Hill 1991, Santos et al. 2011). Carotenoid-based colors have been studied intensively as reliable signals of health and quality because their expression depends on ingestion and extraction of chemical precursors in the diet (Badyaev and Hill 2000) and potential modification along biochemical pathways (Stradi 1998), which may be energetically costly (Senar et al. 2003). However, the cost and function of melanin-based colors, the commonest pigment in birds, has been more debated.

Melanin pigments that form the black, brown, or gray colors in birds are synthesized from the amino acid tyrosine in the body (Murphy 1994). Classic early work highlighted the importance of melanin ornaments as “badges of status” in sparrow flocks (Rohwer 1975), yet the cost of such ornaments was historically assumed to be mainly social rather than physiological (Jawor and Breitwisch 2003). The results of subsequent studies on the effect of nutritional limitation on the production of melanins have not been conclusive. For example, some studies have reported smaller black bibs in nestling House Sparrows (*Passer domesticus*) under nutritional stress (Veiga and Puerta 1996) or smaller black breast stripes in heavily parasitized Great Tits (*Parus major*; Fitze and Richner 2002), but others have not found a relationship between melanin pigmentation and environmental stressors (e.g., Badyaev and Hill 2000, Roulin and Dijkstra 2003, Senar et al. 2003). In some birds, melanin production may be under strong genetic control and be less sensitive to environmental effects than carotenoid colors (reviewed in Roulin 2004), but recent meta-analyses suggest that both carotenoid and melanin colors in birds may be sensitive to environmental factors (Griffith et al. 2006, Guindre-Parker and Love 2014).

Nevertheless, evidence is still scarce for condition-dependent melanin traits in birds and for links between melanin and correlates of fitness such as reproduction or survival (Saino et al. 2013). Among the few examples is the production of gray-colored (eumelanin) rump feathers by nestling male Eurasian Kestrels (*Falco tinnunculus*), which is associated with high prey supply and female body condition (Fargallo et al. 2007). In the same falcon species, Piau et al. (2012) experimentally manipulated the condition of nestlings and found that the young in better condition grew wider, black subterminal bands on their tail feathers. Male, but not female, Barn Swallows (*Hirundo rustica*) that had more eumelanin content in breast feathers survived longer (Saino et al. 2013); and in Barn Owls (*Tyto alba*), laying date and brood size varied with melanin traits but in a complex way that differed between sex and age classes (Dreiss and Roulin 2010).

In general, darker, more eumelanin individuals are hypothesized to be more resistant to stress than lighter conspecifics (Ducrest et al. 2008) or may have higher levels of testosterone (Gonzalez et al. 2001), which may be associated with dominance and territoriality (Crary and Rodewald 2012). For example, in some species of North American warblers, males with large or dark melanin patches spent more time defending territories and were more successful in attracting extrapair matings than paler males (Yezerinac and Weatherhead 1997, Parker et al. 2003, Dunn et al. 2010), but this is not the case for all warbler species (Chiver et al. 2008). An intriguing “paternal care hypothesis” is that melanin badges signal

alternative reproductive strategies in male birds. Namely, males with larger melanin badges invest heavily in dominance and territory defense but less in provisioning and parental care than males with less melanin in the plumage (Studd and Robertson 1985, Jawor and Breitwisch 2003, Crary and Rodewald 2012).

We wanted to test whether the features of melanin ornaments were consistent with sexual selection and could signal quality in both males and females when both sexes are heavily involved in parental care. The Northern Flicker (*Colaptes auratus*) is well suited for investigation because the species has partly reversed sex roles. Males invest more in direct offspring care than do females (Wiebe 2008, Gow and Wiebe 2014), and females are facultatively polyandrous (Wiebe 2005), so the competition among females for access to high-quality males may be more intense than in many other birds. If both sexes display their quality through ornaments and compete for mates, we expected positive assortative pairing and that plumage traits would be correlated with some measure of reproductive output.

We focused on the relationship between the attributes of 4 melanin-based (Test 1940) plumage ornaments and individual traits including body size, body condition, sex, and age. The 4 black plumage ornaments (Figure 1) would be visible to opponents during conspicuous “wica” displays (Wiebe and Moore 2008) given to individuals of the same or the opposite sex in spring during territory establishment and mate selection. Because plumage color differs between age classes in many species (Dreiss and Roulin 2010, Saino et al. 2013) and because the allocation strategy of some feather pigments to competing functions has been shown to be age dependent (Cote et al. 2010), we analyzed age classes separately to determine whether individuals made decisions on plumage independent of the large-scale differences attributable to age. Furthermore, we controlled for age in models of reproductive success by including it as a factor.

METHODS

Study Area and Field Methods

K.L.W. studied Northern Flickers from 1998 to 2013 at Riske Creek in central British Columbia, Canada (51°52'N, 122°21'W), on a study area that covered ~100 km². The area contains grassland interspersed with clumps of aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and wetlands. Each year, the reproduction of 85–160 breeding pairs of Northern Flickers was monitored from arrival on territories after migration in late April until young fledged in late July. There is no perceptible difference in arrival time between the sexes or between yearling and adult birds, so the age classes can interact during mate choice. Clutch sizes range from 3 to 13 on the study area, incubation takes ~12 days,

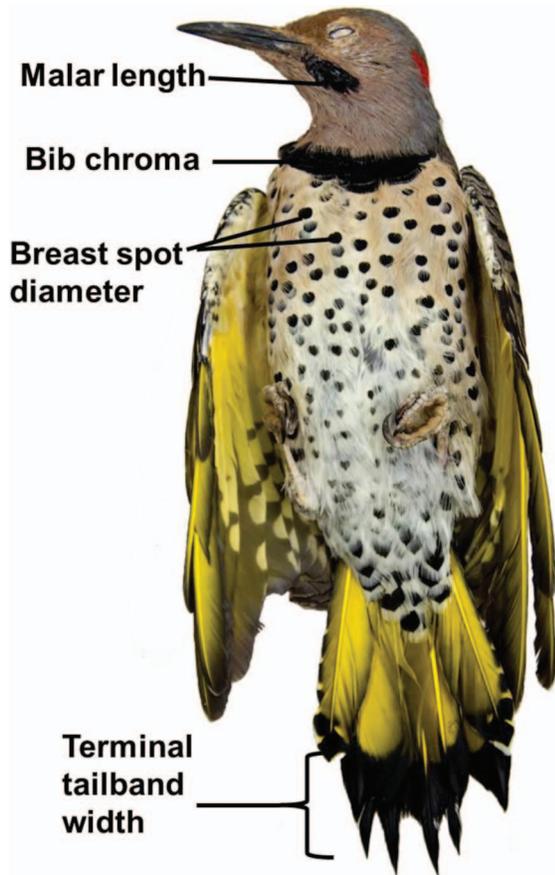


FIGURE 1. A male Northern Flicker, showing the 4 melanin-based ornaments that were analyzed. The plumage of females looks the same, except that it lacks the malar stripe.

and nestlings fledge at 25–27 days (Gow and Wiebe 2014). Only 1 brood is fledged per year. Flickers are normally socially and genetically monogamous, but ~5% of females per year may have 2 simultaneous nests with different males (Wiebe and Kempnaers 2009). Typically, both parents contribute to incubation, brooding, and provisioning of nestlings at both monogamous and polyandrous nests. Adults molt once a year, starting when the offspring fledge and extending into fall (September–October).

In spring, tree cavities on Northern Flicker territories were checked until eggs were found, and a small, replaceable “door” was cut into the tree trunk to give access to eggs and nestlings and to allow banding of adults. Birds were weighed with a Pesola scale, measured, and aged up to 4 yr according to molt patterns described in Pyle (1997), and each received a unique color-band combination. For a multivariate measure of body size (Rising and Somers 1989), we used the score on the first axis (PC1) of a principal component analysis (PCA) based on 6 measures: lengths of the wing, bill, tail, tarsus, and 9th primary, and bill depth. All measures loaded positively on the first axis, and separate PCAs were done for each sex

because of slight sexual size dimorphism (Wiebe and Moore 2008). For an index of energy reserves (“body condition”), we used the residuals of a regression of PC1 and body mass. K.L.W. trapped and measured all Northern Flickers to eliminate observer bias. The apparent annual mortality rate of adults is relatively high compared with that of other woodpeckers (~60%; Fisher and Wiebe 2006), so there is a rapid turnover of individuals in the population and most birds breed in their first year (summer after hatching; hereafter “yearlings”).

Measuring Melanin Ornaments

In the field, the width of the terminal tail band (Figure 1) was measured with a ruler to the nearest 0.5 mm on the third (right side) rectrix from the proximal edge where the black touched the rachis to the distal feather tip. When the black band contacted the rachis asymmetrically on either side, the ruler was placed midway between the contact points. The length of the flattened malar patch (occurring in males only) was also measured to the nearest 0.5 mm with a ruler laid flush against the bird’s head, and the diameter of breast spots perpendicular to the rachis was measured with digital calipers to the nearest 0.01 mm. An average spot size was calculated using 3 feathers (each breast feather has a single spot) from the left side ~2 cm below the bottom edge of the chest bib. For bib color, 3–5 bib feathers were collected and stored in the dark for analysis in the lab.

In the lab, M.N.V. overlaid the plucked bib feathers to create a solid black surface on a white card and analyzed them using an OceanOptics USB4000 spectrometer equipped with a fiber optic probe with a PX-2 pulsed xenon light source. The probe was placed at an angle of 90° to the feather surface. Reflectance data were generated in relation to 2 standards: a white standard (Ocean Optics WS-1) and a dark standard (all light excluded). The SpectraSuite software package (Ocean Optics, Dunedin, Florida, USA) was used to record spectra, which were calculated as the average of 20 spectra with an integration period of 200 ms. Each measurement was repeated 3 times, with the probe lifted between scans, a process that has previously been shown to yield high repeatabilities for all measures of color (Safran et al. 2010). Brightness was computed from the raw ultraviolet–visible spectral data (300–700 nm) as the total amount of light reflected by the feather surface and chroma as reflectance in the 600–700 nm range divided by the total spectral range (300–700 nm). Melanic ornaments typically contain a mix of black eumelanin pigments and brownish phaeomelanins. Higher values of brightness and chroma can indicate higher concentrations of phaeomelanins and/or a smaller ratio of eumelanins to phaeomelanins (McGraw et al. 2005); however, these patterns are not universal (see, e.g., Gasparini et al. 2009).

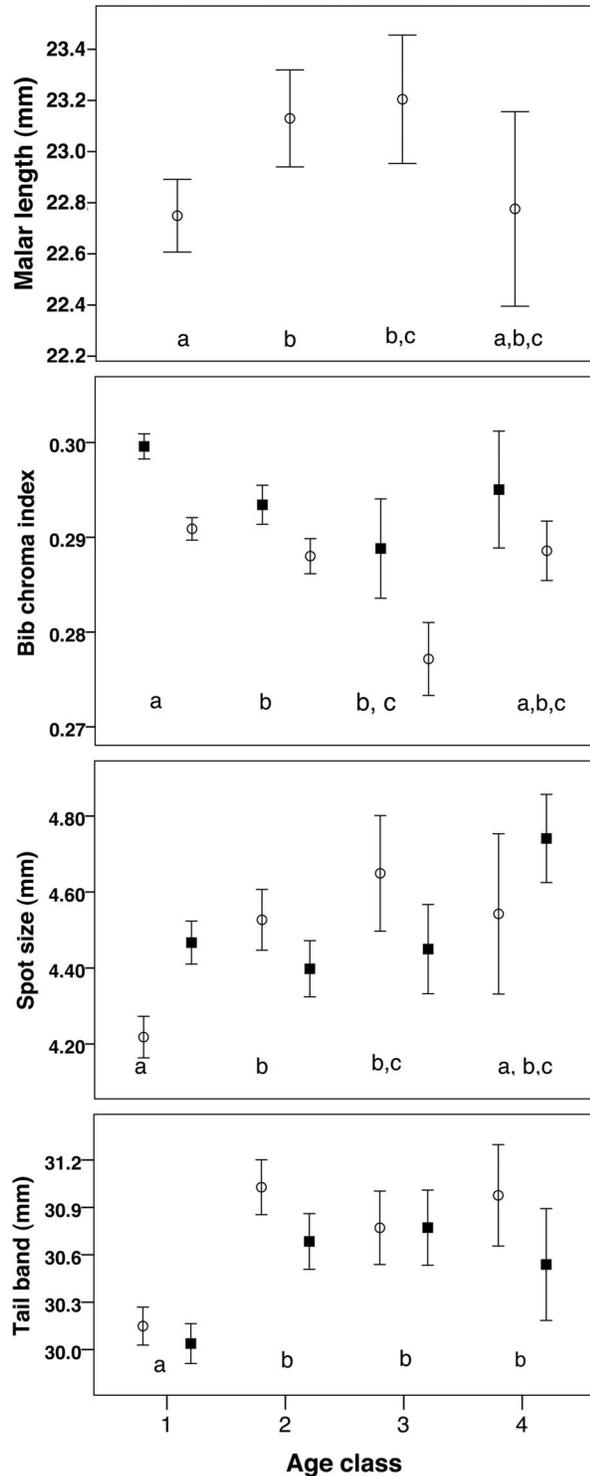


FIGURE 2. Attributes of 4 melanin plumage traits in Northern Flickers at Riske Creek in central British Columbia, Canada, according to sex and age class. Lower chroma indicates a darker color. Values are means \pm SE. Squares indicate females, and circles indicate males.

Statistical Analyses

Sample sizes were larger for the tail band and malar stripe, measured on all Northern Flickers since 1998, than for breast spots and bib color, which were measured for a subset of individuals in 5 yr (2009–2013) and 2 yr (2009–2010), respectively. Preliminary analyses showed that bib brightness and chroma were correlated ($r^2 = 0.24$, $P = 0.006$, $n = 256$), so only the chroma was used in subsequent statistical analyses. There were no significant bivariate correlations among the 4 melanin ornaments for females (Pearson correlations, all $P > 0.10$) or for males ($P > 0.15$), so they were treated as separate dependent variables. For analyses of assortative pairing, if a pair remained together for >1 yr, we used only data from the first year they appeared in the dataset. For analysis of reproductive success, only the first nest attempt of the season was used and we randomly chose 1 breeding record for an individual if there were data from multiple years. Year was included as a random factor in the analysis of covariance (ANCOVA) models to account for annual variation in reproduction. Age-related variation in melanin traits was first investigated with 4 age classes, with birds ≥ 4 yr old lumped into the oldest age class because the sample size of older birds was small. Because most of the variation in melanin traits occurred between the first and second years of life (see below) and because sample sizes were sometimes small for the oldest ages, models involving reproductive performance used ages classified as yearling versus older birds. Several dependent reproductive variables were modeled (laying date, clutch size, and fledging success) because each may reflect different proximate mechanisms that influence reproductive output at different stages of breeding. We confirmed that all continuous variables met the assumption of normality, conducted analyses with SPSS version 20 (IBM, Armonk, New York, USA), and used 2-tailed tests with $\alpha = 0.05$.

RESULTS

Relationship between Plumage Traits and Individual Traits

Width of the tail band did not differ between the sexes, but older individuals had wider tail bands than yearling breeders (2-way analysis of variance [ANOVA]: sex effect, $F_{1, 2,408} = 1.21$, $P = 0.21$; age effect, $F_{4, 2,408} = 7.51$, $P < 0.001$; Figure 2). The relationship between tail band width and age could not be explained only by differential mortality in the population, because tail bands also increased within individuals of both sexes measured in 2 consecutive years (repeated-measures ANOVA: time effect, $F_{1, 254} = 22.4$, $P < 0.0001$; sex*time interaction, $F_{1, 254} = 0.005$, $P = 0.96$). However, a significant interaction with age class showed that tail band width increased between years 1 and 2 of life but not

TABLE 1. Pearson correlations between 4 melanin-based plumage traits of Northern Flickers in relation to individual attributes of males and females at Riske Creek in central British Columbia, Canada, 1998–2013. Within each cell, correlations are shown for yearling breeders first and then for adult (≥ 2 yr old) breeders. Sample sizes of females and males, respectively, are 1,355 and 1,187 for tail band and malar variables, 249 and 253 for spots, and 131 and 124 for bib chroma. Significant values are in bold ($*P < 0.05$, $**P < 0.001$).

Trait	Female		Male	
	Body size	Condition	Body size	Condition
Tail band	0.30** , 0.32**	0.06, 0.08	0.22** , 0.27**	0.17** , 0.08
Bib chroma	−0.05, −0.21*	−0.32** , −0.03	0.01, 0.12	−0.21, −0.15
Spot size	0.04, −0.05	0.04, −0.03	−0.05, −0.01	0.13, 0.05
Malar length			0.17** , 0.25**	0.06, 0.03

significantly so in subsequent years (repeated-measures ANOVA: age class*time, $F_{1, 254} = 19.7$, $P < 0.001$).

For breast spot size, there was an interaction between sex and age class (2-way ANOVA: $F_{3, 504} = 5.26$, $P < 0.001$). This was explained by a significant increase in spot size with age among females ($F_{3, 248} = 4.69$, $P = 0.003$), mainly between yearlings and second-year birds, whereas the relationship with spot size and age in males was weaker ($F_{3, 254} = 2.11$, $P = 0.09$; Figure 2). Bib chroma differed between the sexes (2-way ANOVA, sex effect: $F_{1, 255} = 27.1$, $P < 0.001$) and according to age ($F_{3, 245} = 4.2$, $P < 0.001$; Figure 2). Males and older birds had lower chroma values, indicative of a purer black color. The length of the male's malar stripe also differed between age classes (ANOVA: $F_{3, 1,183} = 5.21$, $P = 0.001$), becoming longer from ages 1 to 3.

Yearlings had a smaller body size (PCA score) than adults (ANOVA: males, $F_{3, 1,376} = 10.3$, $P < 0.001$; females, $F_{3, 1,345} = 18.6$, $P < 0.001$), and the age classes also differed in body condition (ANOVA: males, $F_{3, 1,375} = 11.0$, $P < 0.001$; females, $F_{3, 1,344} = 7.76$, $P < 0.001$). The body condition of males increased between year 1 and year 2 of life, whereas the condition of females did not vary significantly in the first 3 yr of life but was higher in the oldest age class. Because of the covariance between age and the attributes of size and condition, we analyzed plumage traits and morphological measurements separately for each age class (yearling vs. older breeders) within each sex. The width of the tail band was positively correlated with structural size (PC1) within all 4 sex and age categories (Table 1). This correlation remained for yearling birds even when controlling for length of the tail feather (partial correlation: females, $r^2 = 0.10$, $P = 0.013$, $n = 639$; males, $r^2 = 0.09$, $P = 0.052$, $n = 572$) but not for older birds (all $P > 0.15$). In males, the length of the malar stripe was also positively correlated with body size in yearlings (Table 1).

Spring body condition was positively correlated with darker black bib chroma in yearling females and by wider tail bands in yearling males, but not by any trait within the adult age class (Table 1 and Figure 3). Spring body

condition was assessed when birds were trapped during incubation or nestling rearing, although the melanin was deposited in the feather during the previous year's molt. Hence, we also tested whether tail band width was associated with body condition in the previous year. There was a positive correlation with the previous year's body condition among males ($r_{148}^2 = 0.19$, $P = 0.03$) but not among females ($r_{127}^2 = 0.07$, $P = 0.42$).

Assortative Pairing and Reproductive Success

There was strong assortative pairing according to age class. Among 401 yearling males, 72% had a yearling partner, whereas only 22% of 690 older males had a yearling partner ($\chi_1^2 = 261$, $P < 0.001$). Within yearling pairs, there was further positive assortative mating according to bib chroma ($r^2 = 0.11$, $P = 0.04$, $n = 30$; Figure 4) but not with spot size ($r^2 = 0.06$, $P = 0.24$, $n = 20$) or tail band width ($r^2 = 0.009$, $P = 0.87$, $n = 343$). Adult pairs mated assortatively according to bib chroma ($r^2 = 0.19$, $P = 0.02$, $n = 30$) and tail band width ($r^2 = 0.05$, $P = 0.01$, $n = 317$; Figure 4) but not spot size ($r^2 = 0.001$, $P = 0.94$, $n = 30$).

With age in the models to account for age-related reproductive success, the greatest variation in laying date was explained by age of both the male and female of the pair, but females with wide tail bands still had earlier laying dates (Table 2 and Figure 5). Female age and the covariate of laying date were the strongest predictors of clutch size, but with both these variables in the model, there was still a significant positive effect of the width of the male's, but not the female's, tail band (slope of the regression line = 0.06; Table 2). The length of the male's malar stripe was not associated with any fecundity parameter. Females with darker bib chroma also had earlier laying dates and larger clutches when age was controlled in the model (Figure 6).

Excluding depredated nests, the female's bib chroma was weakly associated with the proportion of the brood that fledged (Table 3), but the strongest predictor of fledging success was age of the male parent. The total number of fledglings produced was weakly positively associated with the width of the male's tail band when age and date were included in the model (ANCOVA: $F_{1, 441} = 2.12$, $P = 0.07$),

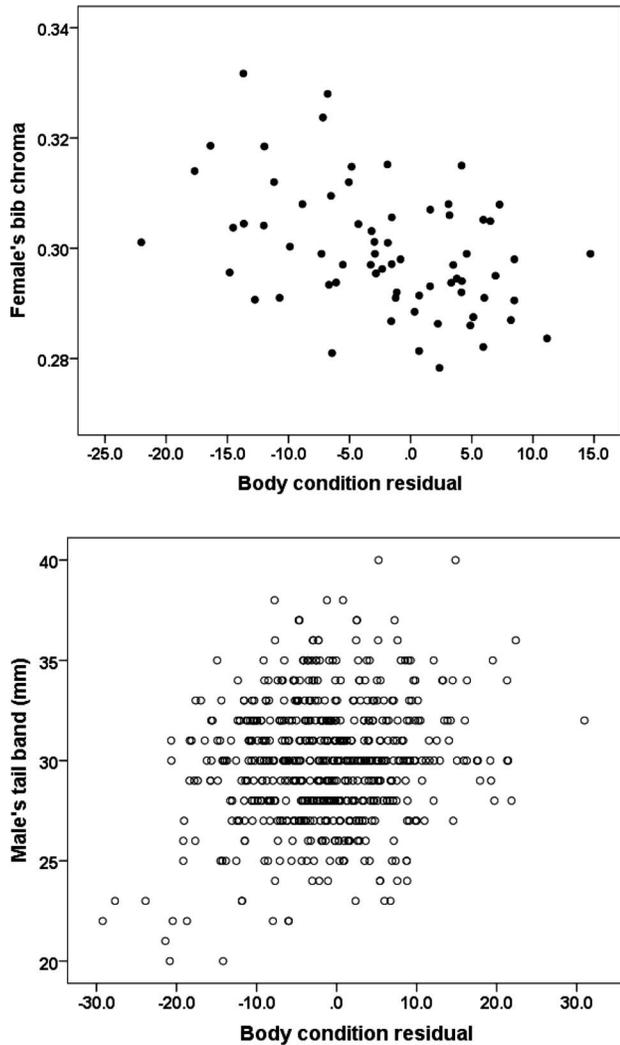


FIGURE 3. Significant negative relationship between body condition and bib chroma in yearling female Northern Flickers, and positive relationship between body condition and tail band width in yearling males, at Riske Creek in central British Columbia, Canada, 1998–2013.

as was the female's bib chroma ($F_{1, 95} = 3.92, P = 0.04$). The size of breast spots did not predict any aspect of reproductive performance in either sex.

DISCUSSION

Consistent with the hypothesis of sexual selection in both sexes of Northern Flicker, at least 1 of the 4 melanin plumage ornaments was correlated with body size or body condition in both males and females, even when controlling age class. Furthermore, there was positive assortative pairing within age classes according to melanin ornamentation, and at least 1 melanin ornament predicted a component of reproductive performance in both males and females. Hence, it appears that Northern Flickers can

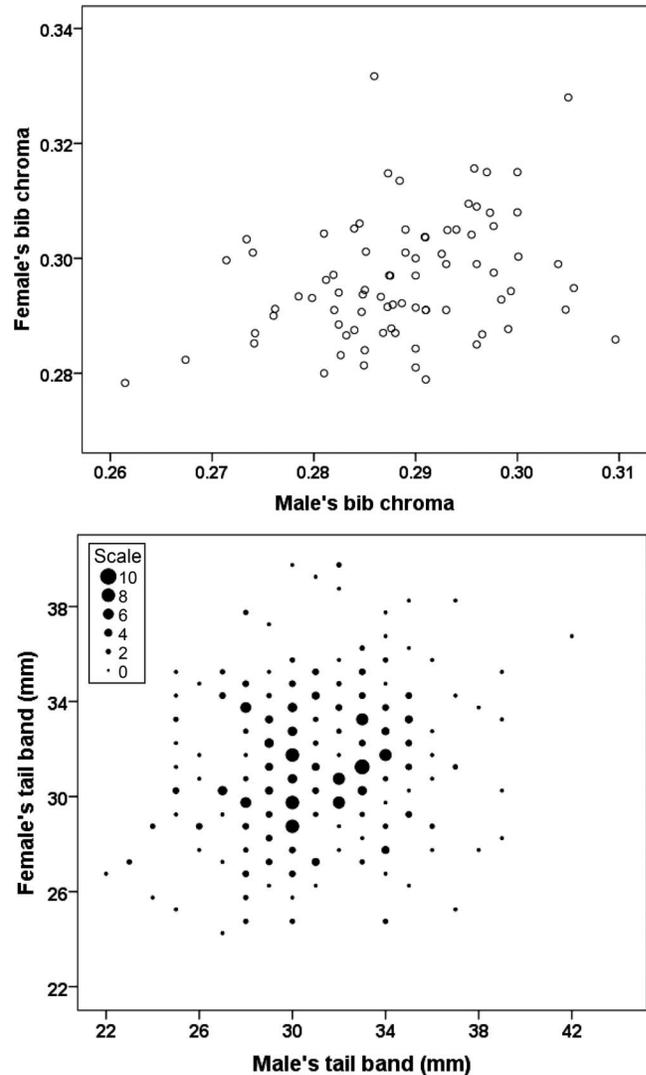


FIGURE 4. Positive assortative pairing within Northern Flickers at Riske Creek in central British Columbia, Canada, 1998–2013, according to bib color (age classes combined) and tail band width (adult pairs only). Size of the circles in the lower panel corresponds to the sample size of pairs.

use information based on the melanin deposited in the feathers during the previous fall to select mates adaptively during the following spring.

Melanin Ornamentation in Relation to Age and Sex

In contrast to many other species with exaggerated melanin ornaments only in males (e.g., Tarof et al. 2005), there is little sexual dimorphism in the plumage of Northern Flickers, with the exception of the malar stripe, which seems to function as an unambiguous signal of sex (Noble 1936). Unlike the case in Northern Flickers, tail bands and breast spots differ in size between the sexes in Barn Owls (Dreiss and Roulin 2010) and Eurasian Kestrels (Palokangas et al. 1994), respectively. Piau et al. (2012)

TABLE 2. Reproductive performance of Northern Flicker pairs at Riske Creek in central British Columbia, Canada, 1998–2013, according to female age class, male age, widths of parents' tail bands, and length of the male's malar stripe. Results are from ANCOVA models on first nesting attempts of the season only and include year as a random factor. Sample sizes of nests are 730, 703, and 550 for the models of laying, clutch size, and fledging success, respectively. Fledging success is defined as the proportion of hatched nestlings that fledged, excluding cases of total loss from depredation. Significant predictors are in bold.

Source	Laying date				Clutch size				Fledging success			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Year	15	316	6.75	0.001	15	4.96	3.46	0.001	15	0.10	1.57	0.07
Female age	1	438	9.33	0.002	1	21	15.1	0.001	1	0.10	1.06	0.20
Male age	1	402	8.58	0.004	1	0.10	0.07	0.78	1	0.45	7.06	0.008
Female tail band	1	249	5.32	0.021	1	0.79	0.55	0.45	1	0.15	2.36	0.12
Male tail band	1	123	2.63	0.10	1	6.05	4.29	0.036	1	0.06	0.89	0.34
Malar stripe	1	0.02	0.01	0.99	1	0.18	4.15	0.72	1	0.01	0.17	0.68
Laying date					1	246	171	0.001	1	0.08	1.20	0.27
Female age*Male age	1	784	16.7	0.001				NS				NS

suggested that the tail band in female Eurasian Kestrels may be only a side effect of selection on males, but in another study of the same species, tail band width of females was positively correlated with body mass (Kim et al. 2013), suggesting that it could signal condition. Clearly, more studies are needed on the function of melanin colors in female birds, especially those that may compete for high-quality male partners that invest heavily in paternal care, as is the case among woodpeckers with partly reversed sex roles (Wiebe 2005, 2008).

At least for tail bands, the longitudinal age analysis showed phenotypically plastic changes within individual Northern Flickers. In other species, the width of tail bands increased with age class in Eurasian Kestrels (Palokangas et al. 1994), and breast spot size increased in female but not male Barn Owls during the first 2 yr of life (Dreiss and Roulin 2010). In Northern Flickers, tail band width (both sexes) and spot size (mainly females) primarily distinguished the youngest breeding age class (yearlings) from older birds; the maximum expression of these ornaments could be achieved after the second prebasic molt in the second calendar year of life. By contrast, bib chroma became blacker and malar length increased until the third calendar year, after which time it declined again (Figure 2). Galván and Alonso-Alvarez (2008) suggested that oxidative stress related to aging could influence both breeding potential and melanin-based traits, and it would be interesting to study whether Northern Flickers begin to senesce after their third year of life.

Melanin and Measures of Quality

The generally weak or absent correlations between the melanin traits within individuals suggests that the plumage ornaments were not redundant but, rather, could convey multiple messages about the individual. Multiple messages may be important when signaling dominance to members of the same sex (Chaine et al. 2013) while at the same time signaling quality to a potential mate (Tarof et al. 2005).

Insofar as body size and condition were related to age, choosing larger or darker melanin ornaments would tend to secure a better-quality mate. However, even within age classes, tail band width (both sexes), malar stripe length (males), and bib chroma (females) were still positively associated with body size. Simple allometry cannot explain the relationship of chroma with body size, or the relationship of chroma with tail band size for yearlings. We did not control for head size, so allometric effects on malar length are possible. If size is important in intrasexual contests over resources, as it is in many species (Robinson-Wolrath and Owens 2003), the size of such melanin patches might reliably predict fighting ability or dominance. Achromatic plumage ornaments signaled territory size in Snow Buntings (*Plectrophenax nivalis*; Guindre-Parker et al. 2013), but Northern Flickers do not defend feeding territories (Elchuk and Wiebe 2003), so it is more likely that the ornaments signaled the individual's traits rather than the resources it held.

The condition-dependence of melanin traits in Northern Flickers was supported by the finding that males in better condition produced wider tail bands in the previous molt. Similarly, the width of the tail band ornament in nestling Eurasian Kestrels was shown experimentally to depend on food levels during growth (Piault et al. 2012). If melanin ornaments depend on food supply during molt, one would expect the relative body condition of individuals to be consistent between fall and spring if ornaments are to indicate body reserves at the time of breeding. Spring body condition was indeed indicated by melanin ornaments among yearling Northern Flickers, but not among adults. Yearlings may be generally under greater energetic stress than adults or show greater variation in nutritional condition, which is more likely to be expressed through variation in melanin ornamentation. Although wide tail bands were associated with body condition at the coarse scale measured between age classes, the trait did not appear to be as sensitive to the smaller differences in body condition

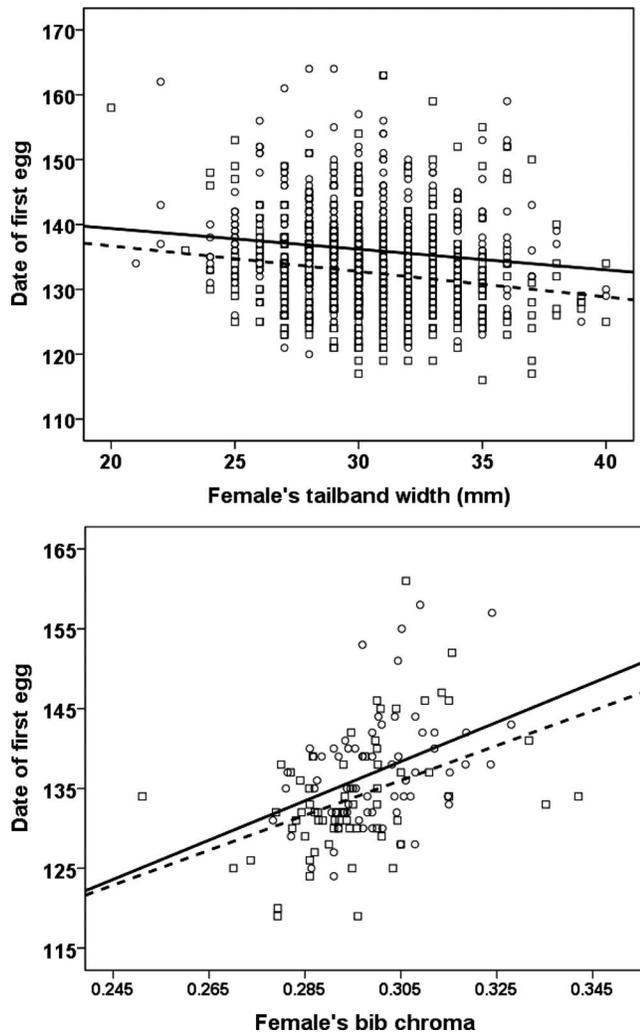


FIGURE 5. Relationship between the initiation of egg laying and 2 melanin plumage ornaments of female Northern Flickers at Riske Creek in central British Columbia, Canada, 1998–2013. Slope of the regression line is -0.35 for tail band (ages combined) and 172 for chroma. A smaller chroma indicates purer black color. Solid regression line and circles indicate yearling females, and dashed line and squares indicate females ≥ 2 yr old.

within age classes as bib chroma or malar length. Similar to the pattern in Northern Flickers, Great Tits in better body condition grew darker black cap feathers (Hegyí et al. 2007); this may be attributable to more melanin precursors in a nutritious diet (Poston et al. 2005), which leads to an increase in the amount of melanin deposited (Bonser 1995).

The condition-dependence of melanin ornaments has been questioned, but meta-analyses show that it may be much more widespread in birds than previously thought (Griffith et al. 2006, Guindre-Parker and Love 2014). The underlying mechanism of the link between condition and melanin deposition is still unknown, but it may be related to corticosterone levels in some species (Roulin et al.

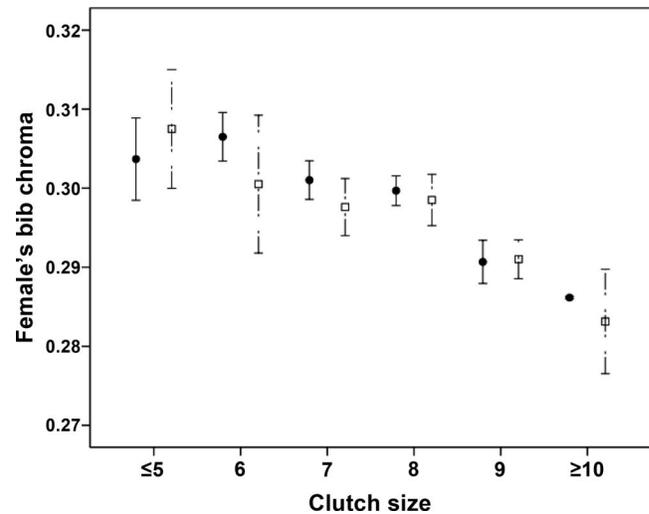


FIGURE 6. Relationship of clutch size to bib chroma in female Northern Flickers at Riske Creek in central British Columbia, Canada, 1998–2013. Circles indicate yearling females ($n = 61$), and squares indicate birds ≥ 2 yr old ($n = 55$). Values are means \pm SE.

2008). Recent work suggests that the production of eumelanin covaries with physiological pathways that regulate energy metabolism, immunity, and response to stressors (Roulin et al. 2008, Saino et al. 2013), and this could explain how melanin-based plumage traits have the potential to reflect nutritional status, hormone titers, or individual quality at the time the feathers are grown. However, the mechanisms underlying the condition-dependence of phaeomelanin pigments appear to differ from those identified for eumelanin pigments (Galván and Solano 2009, Jenkins et al. 2013), so future work in Northern Flickers could quantify concentrations of phaeomelanins versus eumelanins to help elucidate the physiological mechanisms involved.

Melanin, Mate Choice, and Reproductive Output

Even within age classes, bib chroma and tail band width appeared to be criteria for mate selection, and those traits were associated with body condition or body size. The high parental investment by male and female Northern Flickers means that both may be choosy of partners (Trivers 1972) and, especially because extrapair offspring in Northern Flickers and in woodpeckers are almost unknown (Wiktander et al. 2000, Wiebe and Kempnaers 2009), the choice of social mate also determines the genetic makeup of the offspring.

Age-related reproductive success is widespread in birds (Forslund and Pärt 1995), so it was not surprising that age was the strongest determinant of fecundity in Northern Flickers. Insofar as melanin ornaments were correlated with age class, they reliably indicated a more productive older

TABLE 3. Reproductive performance of male and female Northern Flickers at Riske Creek in central British Columbia, Canada, 1998–2013, according to their age class and the color of their bib feathers. Fledging success is the proportion of hatched nestlings that fledged, excluding complete failures from depredation. Results are from ANCOVA models on first nesting attempts of the season only. The top row of values is for males ($n = 106$), and the bottom is for females ($n = 112$). Significant predictors are in bold.

Source	Laying date				Clutch size				Fledging success			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Age	1	150	3.53	0.02	1	6.6	5.06	0.02	1	0.06	1.21	0.27
		100	3.76	0.05		2.2	2.15	0.14		0.04	1.01	0.31
Bib chroma	1	58	2.14	0.15	1	0.41	0.31	0.58	1	0.02	0.56	0.46
		402	15.1	0.001		12.7	12.6	0.001		0.11	3.21	0.07
Laying date						34	26.1	0.001	1	0.001	0.02	0.88
						18.7	18.5	0.001		0.03	0.80	0.37

partner. More intriguing was that, independent of age, wide tail bands and dark bib chroma in females predicted the ability to initiate egg laying early in spring, consistent with the idea that good body condition may facilitate mobilization of reserves for the formation of eggs. Females with darker bibs laid larger clutches, but they also laid more eggs when paired with a male that had a wide tail band. Because male Northern Flickers invest more in parental care than females (Gow and Wiebe 2014), it is possible that females adjust the number of offspring to the male's perceived condition. Fledging success, which mainly reflected the ability of parents to feed nestlings, was predicted mainly by the male's age and weakly by the female's bib chroma.

Experiments involving manipulation of plumage color are needed to confirm that Northern Flickers are indeed using the melanin traits as cues for mate selection, but our results point to the utility of such ornaments as indicators of individual quality and reproductive performance, even for females. Thus, the present study adds to a growing body of evidence that melanin coloration may be condition-dependent (Guindre-Parker and Love 2014) and can signal aspects of fitness linked to reproductive capacity. In contrast to the paternal investment hypothesis based on wood warblers (reviewed in Crary and Rodewald 2012), male Northern Flickers with large melanin ornaments did not trade off parental care with territorial behavior and the acquisition of extrapair mates. Rather, both sexes seemed to signal age, quality, and parental effort by larger melanin ornaments. Black terminal or subterminal tail bands are widespread across bird taxa, and their function has long been assumed to provide resistance to feather wear (e.g., Burt 1986), but future studies on this trait may also reveal a widespread signaling function.

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