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## PERSPECTIVES IN ORNITHOLOGY

### MELANIN ORNAMENTS, HONESTY, AND SEXUAL SELECTION

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MANY STUDIES OF sexual selection have focused on the role of ornaments in mate choice (see Andersson 1994, Espmark et al. 2000). Birds have been a favorite taxon for those studies because of the prevalence of conspicuous ornaments, including brightly colored feathers, skin, and bills, and dramatically elongated feathers or feathers of elaborate structure. The colors of avian ornaments are the result of carotenoids, melanins, tissue structure, or some combination thereof. Carotenoid ornaments (e.g. bright reds, oranges, and yellows) have generated much interest. Those pigments can not be synthesized *de novo* by animals, but rather must be included in the diet (Brush 1990). That allows for the possibility that they are limited in nature or difficult to obtain (Hill 1994, 1996; Hudon 1994; Linville and Breitwisch 1997). Additionally, carotenoids have been implicated in a variety of critical physiological functions in animals. That recognition has stimulated much recent research on mate choice of carotenoid advertisement and the indicator value of carotenoid ornaments for several important aspects of individual condition.

Avian melanin ornaments have also received considerable research attention. In contrast to studies of carotenoid ornaments, however, the primary focus of studies of melanin ornaments has been on the advertisement of melanin

“badges” in intrasexual competition. Thus, the associations among expressions of melanin ornaments, mate choice, and individual condition have not been made to the same degree as for carotenoids. There are several possible reasons for that. First, melanins not only color ornaments but are also the basis of most inconspicuous appearances (i.e. camouflage), in contrast to the highly conspicuous carotenoids. Second, melanins are synthesized by animals and thus do not need to be included in the diet. Finally, it is perhaps incorrectly assumed that melanin ornaments are typically black or blackish-brown and thus show both less variation within species and less diversity across species than do carotenoid ornaments.

Here, we review a variety of aspects of the biology of avian melanin ornaments. We demonstrate that the color diversity of melanin ornaments is quite broad, including red (e.g. Red Junglefowl and Barn Swallow [*Hirundo rustica*]), orange (e.g. Red Junglefowl), yellow (e.g. Western Tanager [*Piranga ludoviciana*]), and green (e.g. Mallard), in addition to black and brown. Color differences in all melanin ornaments are, in part, a function of the ratio of the two types of melanins contained, and we outline the intriguingly different metabolic pathways to the formation of the two different categories of melanins. There are likely to be both significant physiological benefits and costs to melanin production, and those may well differ for the two types of melanins. Finally, we

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address new avenues of investigation concerning melanin ornaments in the context of sexual selection.

#### DIVERSITY OF MELANIN ORNAMENTS

All melanin-colored ornaments contain a mixture of the two types of melanin, eumelanin and pheomelanin. The reflectance spectrum of the ornament is, in part, a function of the ratio of the two types of melanin in feathers (Haase et al. 1992, 1995; Protá et al. 1995; Shiojiri et al. 1999). Additionally, the absolute amount of eumelanin is important, because its presence may overwhelm the contribution of pheomelanin to the reflectance spectrum. The two types of melanin have different spectral qualities (Sarna and Swartz 1998). Eumelanin is perceived by humans (and presumably by birds) as black to dark brown, whereas pheomelanin is perceived as light brown, buff, dull red, orange, and yellow (Protá et al. 1995). Some pheomelanin pigments have the potential to produce brighter reds, oranges, and yellows than may typically be thought to be due to melanins (e.g. the bright orange feathers of Red Junglefowl; J. Hudon pers. comm.). A field guide to the birds of any geographic region shows quite clearly that ornaments of such colors are widespread. Despite that diversity, investigators have focused predominantly on black to brown eumelanic ornaments (Table 1).

The question of the diversity of melanin ornaments is complicated by the findings that both melanins and carotenoids can occur in the same ornament (Hudon 1991, Saino et al. 1999; K. McGraw pers. comm.). Melanins occur in ornaments that were once considered to be pigmented solely by carotenoids, for example, the yellow feathers of Western Tanagers (Hudon 1991) (see also Stradi 1998). In addition, carotenoids have been found in what are commonly classified as melanin ornaments, for example, the rusty-orange feathers of Barn Swallows (Saino et al. 1999; see also Howell 1952, Nero 1954). Reflectance spectra (and color perception) of such mixed ornaments may well depend on both the carotenoid and melanin pigments contained. There are, however, possible technological problems in verifying that hypothesis, insofar as the carotenoid pigment contribution to the spectrum in some mixed ornaments may overwhelm that due to melanins (J. Hudon

pers. comm.), or melanins may overwhelm carotenoids (Theron et al. 2001). The alternative would thus be chemical extraction of pigments from an ornament (see below) and comparison of pigment amounts to reflectance spectra for a sample of individuals. To our knowledge, no one has yet done that. Moreover, no one has evaluated mate choice as a function of pigment composition in mixed ornaments assessed in the process of choice.

#### MELANIN PRODUCTION

The examinations of potential costs, controls, and material requirements of melanin production have focused on mammals, with less research on avian melanogenesis. We therefore present findings from studies on both mammals and birds in the following discussion. Melanogenesis involves the conversion of L-tyrosine into the two types of melanin. The biochemical pathway along which L-tyrosine is converted to melanin is complex and may have significant energy costs associated with it (V. Hearing pers. comm., Fig. 1). Both end products, eu- and pheomelanin, are large, negatively charged, insoluble, nitrogenous heteropolymers.

Melanogenesis takes place in melanocytes, which are derived from neural crest cells (Duval et al. 2002, Han et al. 2002). Melanocytes responsible for skin, hair, and feather pigmentation are found in the basal layer of the epidermis and in hair or feather follicles (Duval et al. 2002). Melanin production occurs in melanosomes, a melanocyte-specific organelle. The two types of melanosomes are rod-shaped eumelanosomes and spherical pheomelanosomes (Wolff 2003). Melanosomes move from the melanocytes into keratinocytes and become incorporated into growing hair or feathers, thus providing pigmentation (Duval et al. 2002). Pigments in skin, fur, or feathers represent a mixture of the two types of melanins that originate from multiple melanocytes.

There are at least three enzymes involved in melanogenesis that require metal cofactors. The copper-containing enzyme tyrosinase catalyzes the rate-limiting step in melanogenesis (Wolff 2003). The two enzymes Tyrp-1 and Tyrp-2 are required for eumelanogenesis. The latter enzyme requires zinc, and the former is thought to require iron (Furumura et al. 1998). There are ad-

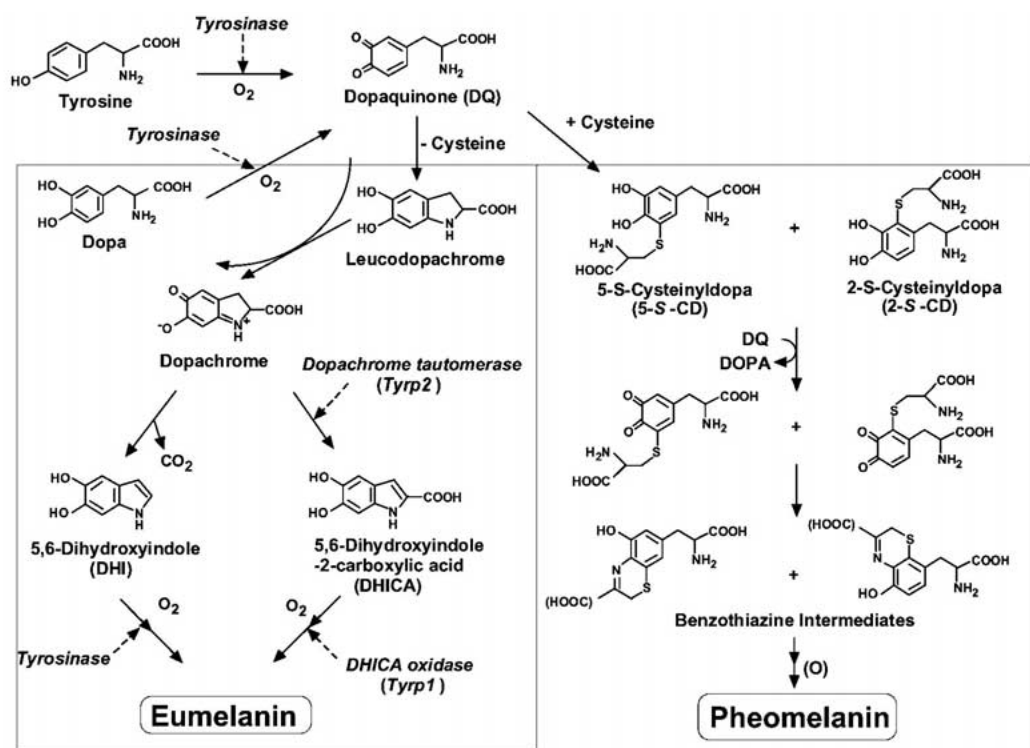


FIG. 1. Pathways for both eu- and pheomelanogenesis (reproduced from Wakamatsu and Ito [2002] with permission from Blackwell Publishing Ltd.).

verse health effects on birds when the diet has either too little or too much copper. Copper deficiency affects production of hemoglobin, with anemia as the result, whereas iron deficiency affects both production and maintenance of blood cells and the constituents of eggs (Arnall and Keymer 1975). The functions of zinc are not known with certainty. Whether deficiencies in those metal cofactors affect melanogenesis is also unknown.

Melanogenesis begins with the oxidation of L-tyrosine and DOPA to dopaquinone by tyrosinase, the rate-limiting step in melanogenesis (Wolff 2003; Fig. 1). In addition to production of dopaquinone, tyrosinase also oxidizes two other eumelanin intermediates. Eumelanogenesis is stimulated by the binding of  $\alpha$ -melanocyte stimulating hormone ( $\alpha$ -MSH) to the G protein-coupled receptor MC1R (also called CMC1 in birds) in the melanocyte membrane (Takeuchi et al. 1996a, b; Bowers et al. 1997; Theron et al. 2001; Voisey and Van Daal 2002; Wolff 2003). When  $\alpha$ -MSH binds to MC1R, levels of tryo-

sinase, Typr1, and Typr2 increase, and levels of intracellular cysteine decrease. That favors production of eumelanin. Pheomelanogenesis occurs without  $\alpha$ -MSH stimulation. During pheomelanogenesis, following the production of dopaquinone, cysteine combines with dopaquinone to form cysteinyl-dopas that are oxidized via benzothiazines to pheomelanin (Wolff 2003). During pheomelanogenesis, the enzymes important to eumelanogenesis do not increase in concentration, and intracellular cysteine levels remain high. That favors the formation of pheomelanin. Additionally, pheomelanogenesis is increased when agouti signaling protein (ASP) interacts with MC1R (Hunt and Thody 1995, Wolff 2003).

Pheomelanogenesis has been suggested as the default pathway during pigment production (Wolff 2003). Presence of a default pathway is important. If there are significant differences in production costs of the two melanins, at least one production cost is nontrivial, and a changing ratio of melanin types affects the reflectance

TABLE 1. Species in which melanin ornament expressions have been measured and correlated with components of fitness.

| Species   | Melanin <sup>a</sup>                                | Status <sup>b</sup>                                 | Measure <sup>c</sup>   | Outcome   | Citation   |
|---|---|---|--|---|--|
| Mallard<br>( <i>Anas platyrhynchos</i> )              | P, E<br>P, E  | Ca<br>Ca  | Cn<br>Cn   | Testosterone affects amounts of two melanins in feathers<br>Testosterone dose affects amounts of two melanins in feathers   | Haase et al. 1995<br>Haase and Schmedemann 1992  |
| Eurasian Dotterel<br>( <i>Charadrius morinellus</i> ) | P, E  | F   | Co   | Brighter females more dominant and aggressive   | Owens et al. 1994  |
| Red Junglefowl<br>( <i>Gallus gallus</i> )            | P*<br>P*<br>P*<br>P*                                | Ca<br>Ca<br>Ca<br>Ca                                | Co<br>Co<br>Co<br>HSB  | Male plumage color not used in mate choice<br>Male plumage color not used in mate choice<br>Male plumage color used when combs altered<br>Male plumage color used secondarily   | Zuk et al. 1990a<br>Zuk et al. 1990b<br>Zuk et al. 1992<br>Johnsen and Zuk 1996  |
| Rock Dove<br>( <i>Columba livia</i> )                 | E, P  | F   | Cn   | Melanin content varies with color of feather  | Haase et al. 1992  |
| Barn Owl<br>( <i>Tyto alba</i> )                      | E<br>E<br>E<br>E, P<br>P<br>E                       | F<br>F<br>F<br>F<br>F<br>F                          | Spots<br>Spots<br>Spots<br>Spots and Co<br>Co<br>Spots             | Males prefer spottier females<br>Number of spots indicate genetic quality in females<br>Number of spots correlates with parasite resistance in females<br>Spot number and plumage color indicate genetic quality<br>Male color correlates with reproductive success and feeding rate<br>Female number of spots correlates with offspring quality  | Roulin 1999<br>Roulin et al. 2000<br>Roulin et al. 2001a<br>Roulin et al. 1998<br>Roulin et al. 2001b<br>Roulin et al. 2002  |
| Pied Flycatcher<br>( <i>Ficedula hypoleuca</i> )      | E<br>E<br>E<br>E<br>E<br>E<br>E<br>E<br>E<br>E<br>E | F<br>F<br>F<br>F<br>F<br>F, Ca<br>F<br>F<br>F<br>Ca | GCC<br>GCC<br>GCC<br>GCC<br>GCC<br>GCC<br>GCC<br>GCC<br>GCC<br>GCC | Song repertoire correlates with black color<br>Black males higher quality for several qualities<br>Black color signal for aggression<br>No difference in energy expenditure with color<br>Females prefer black males<br>Females prefer black males<br>Color associated with age and number of nest boxes, not intrasexual<br>Black males more efficient feeders<br>Females prefer black males | Lampe and Espmark 1994<br>Järvi et al. 1987<br>Huhta and Alatalo 1993<br>Sætre et al. 1997<br>Dale and Slagsvold 1996<br>Sætre et al. 1994<br>Slagsvold and Lifjeld 1988<br>Sætre et al. 1995<br>Slagsvold and Drevon 1999 |
| Great Tit<br>( <i>Parus major</i> )                   | E<br>E<br>E<br>E<br>E                               | F, Ca<br>F<br>F<br>F<br>F                           | A<br>A<br>A<br>A   | Stripe size used to signal status<br>Males with larger stripes mate with high quality female<br>Males with stripes more attentive at nest<br>Sexually dimorphic, stripe not used in status signal   | Järvi and Bakken 1984<br>Norris 1990a<br>Norris 1990b<br>Wilson 1992   |

TABLE 1. Continued.

| Species   | Melanin <sup>a</sup> | Status <sup>b</sup> | Measure <sup>c</sup> | Outcome  | Citation                  |
|---|----------------------|---------------------|----------------------|--|---------------------------|
| Great Tit   |                      |                     |                      |  |                           |
|   | E                    | F                   | A                    | Stripe size genetically based, correlates with viability             | Norris 1993               |
|   | E                    | F                   | A                    | Stripe most effective in interaction with strangers                  | Lemel and Wallin 1993     |
|   | E                    | F                   | A, HSB               | Stripe area affected by ectoparasites                                | Fitze and Richner 2002    |
| Black-capped Chickadee<br>( <i>Poecile atricapillus</i> )   | E                    | F                   | A, Edg               | Bib area dimorphic, and raggedness correlates with age               | Otter and Ratcliffe 1999  |
| Bluthroat<br>( <i>Luscinia svecia</i> )                     | P                    | Ca                  | GCC                  | Males prefer more colorful females                                   | Amundsen et al. 1997      |
|   | P                    | F                   | GCC                  | Female color does not correlate with parental quality                | Rohde et al. 1999         |
|   | P                    | F                   | HSB                  | Male color does not correlate with parental quality                  | Smiseth et al. 2001       |
| Yellow Warbler<br>( <i>Dendroica petecia</i> )              | P                    | F                   | A                    | More colored males more aggressive                                   | Studd and Robertson 1985a |
|   | P                    | F                   | A                    | Male color correlates with territory quality, not with paternal      | Studd and Robertson 1985b |
|   | P                    | F                   | A                    | Male color correlates with territorial effort                        | Studd and Robertson 1988  |
| American Redstart<br>( <i>Setophaga ruticilla</i> )         | E                    | F                   | A                    | Males with smaller bibs have high reproductive success               | Lemon et al. 1992         |
|   | E                    | F                   | GCC                  | Black males preferred by females                                     | Omeland and Sherry 1994   |
| Chestnut-sided Warbler<br>( <i>Dendroica pensylvanica</i> ) | P*                   | F                   | A                    | Males with larger badges nest earlier                                | King et al. 2001          |
| Harris's Sparrow<br>( <i>Zonotrichia querula</i> )          | E                    | F                   | A                    | Badge area used intrasexually  | Rohwer 1975               |
|   | E                    | F                   | A                    | Manipulated birds persecuted, intrasexual use                        | Rohwer 1977               |
|   | E                    | F                   | A                    | Color and hormone manipulated birds can "cheat"                      | Rohwer 1985               |
|   | E                    | F                   | A                    | Badge area weak use intrasexually                                    | Watt 1986                 |
|   | E                    | F                   | A                    | Badges do not signal status within age and sex class                 | Jackson et al. 1988       |
| Dark-eyed Junco<br>( <i>Junco hyemalis</i> )                | E                    | Ca                  | GCC                  | Hood darkness correlates with dominance rank                         | Ralph et al. 1979         |
|   | E                    | Ca                  | GCC                  | Hood darkness correlates with dominance rank                         | Holberton et al. 1989     |
|   | E                    | Ca                  | GCC                  | Hood darkness correlates with age and dominance                      | Holberton et al. 1990     |
| Eurasian Siskin<br>( <i>Carduelis spinus</i> )              | E                    | F                   | A                    | Badge used intrasexually   | Senar et al. 1993         |
|   | E                    | F                   | A                    | Badge correlates with molt and dominance rank                        | Senar et al. 1998         |
|   | E                    | Ca                  | A                    | Badge used intrasexually   | Senar and Camerino 1998   |
|   | E                    | Ca                  | A                    | Badge correlates with dominance, negative correlation with metabolic | Senar et al. 2000         |





spectrum, then the expression of a melanin ornament can serve as an honest indicator of condition. It is thus important that investigators begin to examine production costs more closely, measure pheomelanin and eumelanin content in melanin ornaments, and test whether different ratios of melanins are perceptually distinct to avian vision and affect the behavior of the perceiver.

The pathway of melanogenesis is complex, requiring several different enzymes and ions, appropriate amino acid precursors, a favorable pH environment, and the influence of keratinocytes and hormones. The products of >80 gene loci are involved in melanogenesis (Haase and Schmedemann 1992; Aroca et al. 1993; Haase et al. 1995; Hearing 1999, 2000; Ito et al. 2000; Takeuchi et al. 2000; Duval et al. 2002; Hoogduijn et al. 2003). In addition to complicated controls and requirements, melanogenesis is known to produce cytotoxic byproducts that are lethal to melanocytes (Tomita et al. 1984, Thody et al. 1991, Bowers et al. 1994; R. Bowers pers. comm.). Avian melanocyte cultures can be rescued by addition of antioxidants, suggesting that the cytotoxic byproducts are predominantly oxygen free radicals (Bowers et al. 1994; R. Bowers pers. comm.). It is not known, however, whether cytotoxic chemical production in melanogenesis affects either ornament expression or the body at large. In any case, complicated pigment production may provide information concern the health, genetic quality, or condition of an individual, as has been argued for other complicated types of pigments (Arnold et al. 2002).

#### MEASURING MELANIN ORNAMENT EXPRESSION AND VARIATION

The majority (58%) of studies on melanin ornaments cited in Table 1 measured only the size (or area) of discrete patches of melanic feathers (44 of 76 studies). Thirty-three of the 76 studies (43%) in some way measured color of melanin ornaments (including four studies that measured both size and color). Sixteen of the 33 studies measuring color recorded only gross color changes (e.g. brown vs. black), six used color chips (either Munsell or Methuen), and seven used color reflectance spectrophotometry (see below). Three studies measured melanin content of feathers.

In some species, there is obvious variation in color of melanin ornaments (e.g. a gradation from dark brown to black). In such species, only gross color differences have been measured (e.g. Slagsvold and Lifjeld 1988, 1992; Sætre et al. 1995, 1997 for Pied Flycatchers). Prior to the recent introduction of portable reflectance spectrophotometers, there were few other options for measuring color differences. The newly employed spectrophotometer technology can reveal variation unapparent to human vision (Johnsen and Zuk 1996, Hill 1998, Hill and Brawnner 1998, McGraw and Hill 2000, Smiseth et al. 2001, Jawor 2002). Whether that variation is perceived visually by birds must be empirically established, but obviously it is unwise to simply assume that it is not. That line of argument is even more relevant for melanin ornaments other than black, where even human vision can perceive variation. Reflectance spectrophotometry also yields measures of hue, saturation, and brightness of the color being measured (Hill 1998). Unfortunately, the correspondence between reflectance spectra (or measures of hue, saturation, and brightness) and melanin concentration or melanin ratios is unknown.

In a study of Northern Cardinals, we found variation in hue, saturation, and brightness of the black face mask of males (Jawor 2002). We also measured hue, saturation, and brightness of melanin ornaments of several other species (four eumelanic ornaments and one pheomelanic ornament) and found both intra- and inter-specific variability (Table 2). Those data demonstrate that, in some species, there is substantial variation in melanin color variables, whereas in others, there is essentially none (Table 2, Figs. 2 and 3).

A final measure of ornament expression involves extraction, identification, and quantification of the pigment contained in the ornament. That has been done for carotenoid pigments in feathers (Hudon 1991, Stradi 1998, McGraw et al. 2001). Both eu- and pheomelanin are difficult pigments to isolate and measure. The most common method is the analysis of the byproducts of eumelanin oxidation and pheomelanin acid hydrolysis (Haase et al. 1995, Ito and Wakamatsu 1998, Ito et al. 2000). That technique gives an estimate of the two types of melanin within feathers. Still to be determined are the relationships among melanin content and concentration



TABLE 2. Average hue, saturation, and brightness of melanin ornament coloration of bird species.

| Species  | Ornament   | Melanin <sup>a</sup> | Average hue <sup>b</sup> | Average saturation | Average brightness | n               |
|--|------------|----------------------|--------------------------|--------------------|--------------------|-----------------|
| Black-capped Chickadee                                       | Bib        | E                    | 1 (0–60)                 | 5 (0–30)           | 9 (5–14)           | 41              |
| Tufted Titmouse<br>( <i>Baeolophus bicolor</i> )             | Side patch | P                    | 30 (26–33)               | 54 (40–64)         | 46 (37–55)         | 24 <sup>a</sup> |
| White-breasted Nuthatch<br>( <i>Sitta carolinensis</i> )     | Forehead   | E                    | 187 (0–205)              | 13 (0–54)          | 12 (10–30)         | 5               |
| Dark-eyed Junco  | Hood       | E                    | 34 (0–60)                | 10 (4–20)          | 22 (15–32)         | 22              |
| Northern Cardinal<br>( <i>Cardinalis cardinalis</i> ) (male) | Mask       | E                    | 12 (0–60)                | 16 (5–32)          | 14 (9–28)          | 53              |
| Northern Cardinal<br>(female)                                | Mask       | E                    | 31 (17–43)               | 14 (6–19)          | 25 (17–33)         | 28              |

<sup>a</sup> E = eumelanin, P = pheomelanin.  
<sup>b</sup> For hue, saturation, and brightness, mean followed by range.

in ornamental plumage, reflectance spectra, and color perception by birds.

MELANIN ORNAMENTS AS HONEST INDICATORS

Environmental variables and physiological condition can influence melanogenesis and thus may also affect melanin ornament expression. Relevant influences on biosynthesis and deposition of melanin into ornaments include food availability and changing hormonal condition. Food availability is known to affect both gross color changes in and area of melanin plumage ornaments in some species (Slagvold and Lifjeld 1992, Veiga and Puerta 1996, Griffith et al. 1999a), but not in others (Hill 2000, McGraw et al. 2002). An unanswered question is whether a trade-off occurs at low food levels between melanin ornament expression and production of other proteins dependent on tyrosine. A similar trade-off has been suggested between expression of carotenoid ornaments and the need for those pigments in other cellular processes (Lozano 1994, von Schantz et al 1999).

Both types of melanins are initially produced from L-tyrosine, and cysteine is necessary for the production of pheomelanin (Ito et al. 2000). In birds, tyrosine is considered an essential amino acid (Murphy 1996, Hebert et al. 2002), whereas cysteine is synthesized from methionine, another essential amino acid (Griminger and Scanes 1986). Historically, amino acids have not been considered limiting, but that assumption needs to be reassessed. Indeed, some seed diets fed to cage birds are known to be protein deficient and specifically deficient in tyrosine, cysteine, or methionine (Arnall and

Keymer 1975). Changes in melanin coloration in molting captive birds have been observed when diets are insufficient in protein (e.g. Dark-eyed Juncos; E. Ketterson pers. comm.). It is not known whether levels of amino acids—and tyrosine in particular—become limiting during molt and ornament production. Given that amino acid availability may differ among individuals, that potential constraint on melanin ornament production needs to be addressed more fully.

Food availability may influence melanin ornaments by affecting the hormonal controls of melanogenesis as well as affecting essential amino acid availability. In mammals, the type of melanin produced by melanocytes is controlled by an interaction between  $\alpha$ -MSH and ASP (Lu et al. 1994, Hunt and Thody 1995, Hearing 1998, Graham et al. 1997). Eumelanogenesis is initiated by the stimulation of MC1R by  $\alpha$ -MSH, whereas pheomelanogenesis occurs without  $\alpha$ -MSH signaling, and is influenced by ASP (see above). Birds do not possess ASP but rather agouti related protein (AGRP), which has been suggested as functioning in a similar manner to ASP (Takeuchi et al. 2000). Agouti related protein is expressed in most tissues in birds and is known to interact with leptin (a hormone produced by adipocytes) and other melanocortin receptors (MC1R–MC5R or CMC1–CMC5) to regulate feeding behavior, metabolism, and neuroendocrine function both during periods of starvation and periods of satiation (Wilson et al. 1999, Takeuchi et al. 2000). Agouti related protein expression, by influencing pheomelanin production during molt, may affect the color of developing melanin ornaments, thus providing

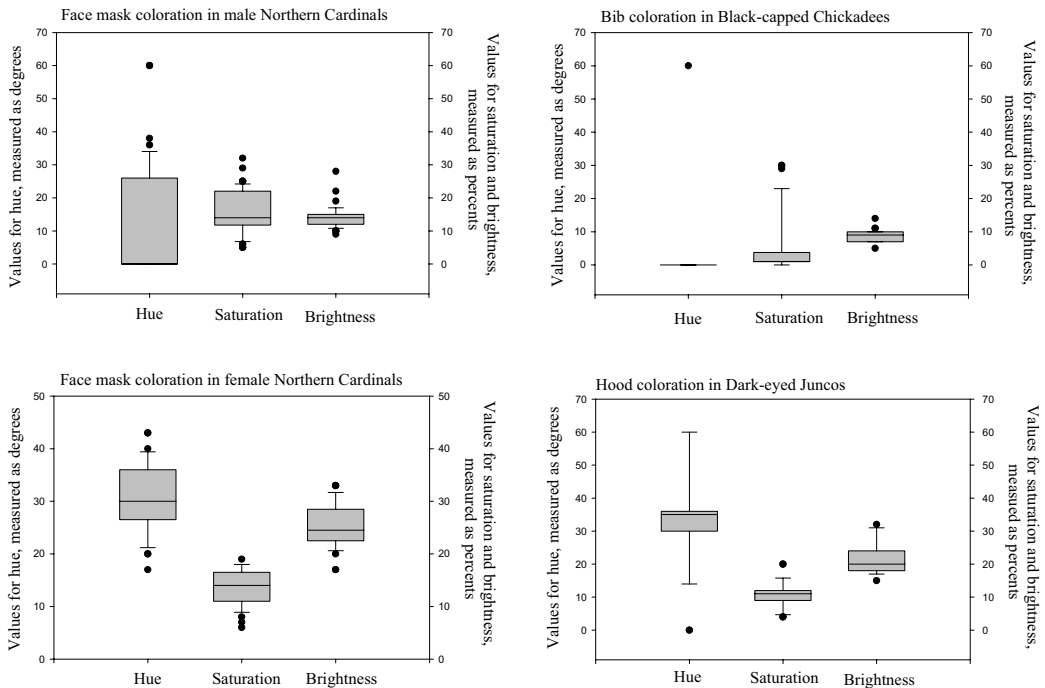


FIG. 2. Hue, saturation, and brightness measures of eumelanin ornament coloration from three different bird species. Left vertical axis represents the possible values of hue, which can occur anywhere along a 0–360° color space. The right axis represents the possible values of saturation and brightness, which are reported as a percentage and may range from 0 to 100% saturation or brightness.

information concerning an individual's food intake during molt. For example, the color of the black face mask in male Northern Cardinals is correlated with body condition early in the breeding season (J. M. Jawor and R. Breitwisch unpubl. data), which, in turn, may reflect nutri-

tional health during molt the previous autumn when the ornament is built. In contrast, in a controlled study of the effects of diet on melanin coloration in House Sparrows, McGraw et al. (2002) found that food deprivation did not influence brightness of melanin coloration. However, they did not measure ratios of the two melanin types in this study. The interaction between AGRP and  $\alpha$ -MSH, their effect on ornament pigmentation, and avian ability to perceive differences in the ratio of the two melanins in ornaments clearly warrants further investigation.

The production of cytotoxic compounds during melanogenesis also indicates that melanin ornaments can serve as indicators of condition and the ability to withstand physiological perturbation. Production of oxygen free radicals in melanogenesis should be particularly interesting in species that display both melanin and carotenoid ornaments, insofar as carotenoids can act as oxygen free radical scavengers (von Schantz et al. 1999). We hypothesize that in such species, the two types of ornaments have

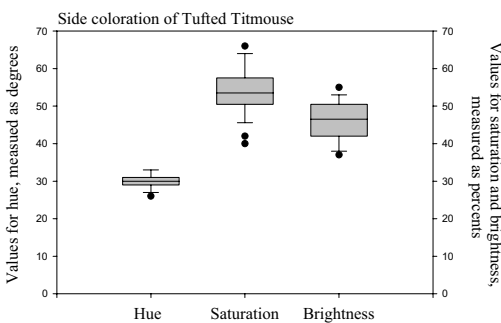


FIG. 3. Variation in Tufted Titmouse pheomelanin flank coloration. The left vertical axis represents the possible values of hue. The right vertical axis represents saturation and brightness of measured plumage.

a combined signaling function. Individuals can demonstrate their ability not only to withstand generation of cytotoxins but also their ability to ingest enough carotenoids to satisfy pigmentation, other physiological needs, and deactivation of the damaging byproducts from melanogenesis. That proposal may explain the apparent amplifier effect of melanin ornaments on carotenoid ornaments in, for example, guppies (*Poecilia reticulata*; Brooks 1996).

Melanin ornament expression may be influenced by titers of sex hormones during molt, during the breeding season, or both. Melanocytes are known to express cell surface receptors for both estrogen and progesterone, although the precise effects of those two hormones on melanogenesis are unknown (Hearing 1998). Although sex hormones are known to affect ornamental characteristics in birds, the type of effect varies with species (Haase and Schmedemann 1992, Haase et al. 1995). For example, in Mallards, higher levels of testosterone preceding molt influence the eclipse, nonbreeding plumage of males, with higher testosterone inducing a more complete eclipse plumage (Haase and Schmedemann 1992). Testosterone appears to affect melanogenesis so that feathers that are predominantly eumelanin in breeding plumage become mixed or predominantly pheomelanin in nonbreeding plumage (Haase et al. 1995). In House Sparrows, the area of the black bib is enlarged by testosterone during molt (Gonzalez et al. 1999, Evans et al. 2000, Gonzalez et al. 2001), but whether the ratio of the two types of melanins is affected is not known. Also in House Sparrows, testosterone enhances bill color, with higher levels of testosterone producing a blacker bill (Keck 1933, Haase 1975). There is an opposite effect of testosterone in European Starlings (*Sturnus vulgaris*), with higher levels of testosterone inhibiting melanin deposition in the bill and favoring carotenoid deposition (Witschi and Miller 1938). Those studies indicate that melanin ornaments are influenced by, and indicative of, levels of hormones that are important for breeding behavior.

It has been suggested that melanin coloration is generally unaffected by parasites. Hill and Brawnner (1998) and McGraw and Hill (2000) found no effect of an intestinal coccidian parasite, *Isospora* spp., on melanin coloration in House Finches and American Goldfinches, respectively. Additionally, Hill and Brawnner

(1998) found no effect of *Mycoplasma gallicepticum* (the cause of mycoplasmal conjunctivitis) on melanin coloration. In those same experiments, however, coccidian and mycoplasma infections negatively influenced carotenoid ornament expression. We present two caveats concerning those studies. First, the melanic feathers measured in Hill and Brawnner (1998) were tail retriix barring, which the authors acknowledge may not have been sexually selected as an ornament and thus unlikely to be so affected by condition. In McGraw and Hill (2000), on the other hand, the melanic feathers were the black forehead patch, and very likely an ornament subject to sexual selection. Second, melanins are derived from amino acids, and there is no reason to expect that coccidian parasites, which affect carotenoid absorption across the intestinal membrane, similarly affect the absorption of those melanin precursors. Active absorption of amino acids is mediated by transport proteins in healthy intestinal epithelium, whereas carotenoids are endocytosed by epithelial cells. When the epithelium is injured by coccidian activity, amino acids may still be able to enter or pass between epithelial cells, while carotenoids can no longer be absorbed (K. Crane pers. comm.). Although melanin ornaments may not be affected by endoparasites, they may be affected by ectoparasites. Fitze and Richner (2002) found that ectoparasites (hen fleas [*Ceratophyllus gallinae*]) affected the area of melanin ornamentation in Great Tits, but the color of both melanin and carotenoid pigmentation was not affected.

It has been hypothesized that different types of ornaments, and different aspects of a single ornament, may convey information on different components of condition. Through selection, ornaments have thus become associated only with those qualities for which they are most informative (Møller and Pomiankowski 1993, Hill and Brawnner 1998, McGraw and Hill 2000). Carotenoid ornaments may thus best convey information concerning endoparasitism and health of the immune system. In contrast, melanin ornaments may best display information concerning nutritional health, ectoparasitism, and hormonal titers related to aggression and intrasexual competitive abilities. We need a broader assessment of components of condition in relation to ornament expression to determine if that proposed division is generally the case.

We hypothesize that birds displaying both carotenoid and melanin ornaments provide more reliable indication of their overall quality than birds displaying only one or the other type of ornament.

#### SEXUAL SELECTION ON MELANIN ORNAMENTS

Gray (1996) and Badyaev and Hill (2000) have proposed that lack of sexual dimorphism in melanin ornaments in contrast to carotenoid ornament dimorphism is evidence against sexual selection of melanin ornaments. That proposition is based on two assumptions. The first is that sexual selection acts much more forcefully on males than on females (see Lande 1980), and the second is that the primary mechanism of sexual selection is unidirectional mate choice. However, there is reason to question both of those assumptions. First, Amundsen (2000) reviewed studies on ornaments in female birds and concluded that those frequently function both in mate choice and in intrasexual competition. Second, bidirectional mate choice has been demonstrated in some species, and that pattern should be common in monogamous, biparental birds (Burley 1981, Burley and Coopersmith 1987). If melanin ornaments function in bidirectional mate choice or female intrasexual competition, then the prediction of sexual dimorphism in those ornaments does not necessarily follow.

Ornaments function in both mechanisms of sexual selection (Berglund et al. 1996, Qvarnström and Frosgren 1998). Melanin ornaments, in particular, appear to function more commonly in intrasexual competition than in mate choice (Badyaev and Hill 2000). If intrasexual competition occurs in both sexes for resources, mates, or both, selection should favor ornaments that function in both sexes and thereby constrain evolution of sexual dimorphism. In that view, the apparent pattern of limited dimorphism in many melanin ornaments is not evidence against their evolution by sexual selection but of their current use by both sexes.

Findings from manipulative aviary studies of melanin ornaments have suggested that those types of ornaments are unreliable indicators of quality unless there is social control of "cheats" (Rohwer 1977, Møller 1987a). It seems likely that some proportion of social control is a result of experimental dissociation of behavior and

signal. Birds manipulated to signal dominance or subordination frequently do not act in accordance with their altered signal (Rohwer 1977). In contrast, signal integrity was maintained where either behavior was modified to match the new signal or birds were not allowed to interact physically with manipulated conspecifics (Rohwer and Rohwer 1978, Senar and Camerino 1998). In any case, social testing need not indicate signal dishonesty. Clearly, condition can vary seasonally and on much shorter time scales, even daily. We predict that social testing should become common if several conditions are met: ornaments are built during distinct periods, condition can change through time, potential benefits of social testing are high, and the cost of social testing is relatively low for the initiator.

Any social testing associated with melanin ornaments represents a cost of signaling by those ornaments. As signals of dominance rank, melanin ornaments stimulate aggressive interactions between individuals of similar dominance status (Rohwer 1977). As previously mentioned, individuals with experimentally altered melanin ornaments frequently experience aggression from unaltered conspecifics. House Sparrows that interact frequently with conspecifics during molt grow larger badges (McGraw et al. 2003), but whether badge color changes is not known. Whereas House Sparrows with large badges are dominant to those with smaller badges (Møller 1987b, 1988; Gonzalez et al. 2002), interactions between individuals with similarly sized badges can be prolonged and violent (J. M. Jawor pers. obs.). We suggest, then, that in addition to physiological costs of melanin production, melanin ornaments may be costly to individuals in terms of the time and energy spent (and risks of injuries incurred) defending dominance status from similarly ornamented and ranked individuals. Those ornaments thus would satisfy the requirement that honest signals be costly.

An intriguing finding in several species is that males with smaller melanin ornaments have higher reproductive success (Lemon et al. 1992, Qvarnström and Frosgren 1998, Griffith et al. 1999b). In some cases, less ornamented males are also preferred by females (Lemon et al. 1992, Qvarnström and Frosgren 1998, Griffith et al. 1999b). Those males are often better parents than more ornamented males, in terms of nest-

ling feeding rates (Studd and Robertson 1985a, b, 1988; Griffith et al. 1999b; but see Voltura et al. 2002). Melanin ornaments are positively affected by testosterone in some species (see above), as is aggressive behavior (Rohwer and Rohwer 1978). In contrast, paternal behavior can be negatively affected by high testosterone titers (Ketterson et al. 1992, Ketterson and Nolan 1994). The preference for less ornamented—and presumably less dominant or aggressive males—may represent a stronger preference for high-quality parents. Owens and Hartley (1998) found that male parental care is reduced in species with greater sexual dimorphism in the size of melanin ornaments. That suggests that melanin ornament size, which is affected by testosterone, can act as a reliable predictor of parental care behavior. Size of melanin ornaments in males, therefore, should be relevant to female mate choice in species to which the differential allocation hypothesis (Burley 1986) applies. Importance of paternal care, and the trade-offs in reproductive effort that females are willing to incur as a consequence of mate choice, need to be considered in studies addressing melanin ornaments that signal dominance status.

#### A HOLISTIC VIEW OF ORNAMENTS AND SEXUAL SELECTION

Our conclusion is that investigators should broaden their study of avian melanin ornaments. Techniques now available allow for increasingly rigorous measurement of melanin ornaments, and investigators should no longer simply assume that the apparently invariant color of eumelanin ornaments is so perceived by birds. Further, the known use of black eumelanic ornaments in intrasexual competition should encourage investigators to focus on the question of the types of information being communicated by each class of ornament. Any type of ornament may best display information on only limited aspects of condition, and we see no theoretical reason why melanin ornaments cannot be as informative as carotenoid ornaments regarding particular aspects of condition. Carotenoid ornaments may best indicate endoparasitism and general health, whereas melanin ornaments may best predict dominance, hormonal titer, foraging abilities, and ectoparasitism. Intrasexual competition undoubtedly precedes or constrains mate choice in many species

of birds, and the use of ornaments in those two mechanisms of sexual selection should receive equal investigative effort. Our hope is that investigators of avian ornamentation will develop a broader view of both the components of sexual selection and the diversity of ornaments displayed by birds.

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#### LITERATURE CITED

- AMUNDSEN, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution* 15: 149–155.
- AMUNDSEN, T., E. GORSGREN, AND L. T. T. HANSEN. 1997. On the function of female ornaments: Male Bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B* 264:1579–1586.
- ANDERSSON, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey.
- ARNALL, L., AND I. F. KEYMER. 1975. *Bird Diseases*. THF Publishers, Neptune, New Jersey.
- ARNOLD, K. E., I. P. F. OWENS, AND N. J. MARSHALL. 2002. Fluorescent signaling in parrots. *Science* 295:92.
- AROCA, P., K. URABE, T. KOBAYASHI, K. TSUKAMOTO, AND V. J. HEARING. 1993. Melanin biosynthesis patterns following hormonal stimulation. *Journal of Biological Chemistry* 268:25650–25655.
- BADYAEV, A. V., AND G. E. HILL. 2000. Evolution of sexual dichromatism: Contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society* 69: 153–172.
- BALPH, M. H., D. F. BALPH, AND H. C. ROMESBURG. 1979. Social status signaling in winter flocking birds: An examination of a current hypothesis. *Auk* 96:78–93.
- BERGLUND, A., A. BISAZZA, AND A. PILASTRO. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58:385–399.
- BOWERS, R. R., A. BIBOSO, AND O. CHAVEZ. 1997. The



- role of alpha-MSH, its agonists, and C-AMP in *in vitro* avian melanocytes. *Pigment Cell Research* 10:41–45.
- BOWERS, R. R., J. LUJAN, A. BIBOSO, S. KRIDEL, AND C. VARKEY. 1994. Premature avian melanocyte death due to low antioxidant levels of protection: Fowl model for vitiligo. *Pigment Cell Research* 7:409–418.
- BROOKS, R. 1996. Melanin as a visual signal amplifier in male guppies. *Naturwissenschaften* 83: 39–41.
- BRUSH, A. H. 1990. Metabolism of carotenoid pigments in birds. *Federation of American Scientists for Experimental Biology Journal* 4: 2969–2977.
- BURLEY, N. 1981. Mate choice by multiple criteria in a monogamous species. *American Naturalist* 117:515–528.
- BURLEY, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist* 127:415–445.
- BURLEY, N., AND COOPERSMITH, C. B. 1987. Bill color preferences of Zebra Finches. *Ethology* 76: 133–151.
- DALE, S., AND T. SLAGSVOLD. 1996. Mate choice on multiple cues, decision rules and sampling strategies in female Pied Flycatchers. *Behaviour* 133:903–944.
- DUVAL, C., N. P. M. SMIT, A. M. KOLB, M. RÉGNIER, S. PAVEL, AND R. SCHMIDT. 2002. Keratinocytes control the pheo/eumelanin ratio in cultured normal human melanocytes. *Pigment Cell Research* 15:440–446.
- ESPMARK, Y., T. AMUNDSEN, AND G. ROSENQVIST, EDS. 2000. *Animal Signals: Signalling and Signal Design in Animal Communication*. Tapir Academic Press, Trondheim, Norway.
- EVANS, M. R., A. R. GOLDSMITH, AND S. R. A. NORRIS. 2000. The effects of testosterone on antibody production and plumage coloration in male House Sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 47:156–163.
- FITZE, P. S., AND H. RICHNER. 2002. Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behavioral Ecology* 13:401–407.
- FURUMURA, M., S. FRANCISCO, M. MATSUNAGA, C. SAKAI, R. A. SPRITZ, AND V. J. HEARING. 1998. Metal ligand-binding specificities of the tyrosinase-related proteins. *Biochemical and Biophysical Research Communications* 242: 579–585.
- GONZALEZ, G., G. SORCI, AND F. DE LOPE. 1999. Seasonal variation in the relationship between cellular immune response and badge size in male House Sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 46: 117–122.
- GONZALEZ, G., G. SORCI, L. C. SMITH, AND F. DE LOPE. 2001. Testosterone and sexual signaling in male House Sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 50:557–562.
- GONZALES, G., G. SORCI, L. C. SMITH, AND F. DE LOPE. 2002. Social control and physiological cost of cheating in status signalling male House Sparrows (*Passer domesticus*). *Ethology* 108: 289–302.
- GRAHAM, A., K. WAKAMATSU, G. HUNT, S. ITO, AND A. J. THODY. 1997. Agouti protein inhibits the production of eumelanin and pheomelanin in the presence and absence of  $\alpha$ -Melanocyte stimulating hormone. *Pigment Cell Research* 10:298–303.
- GRAY, D. A. 1996. Carotenoids and sexual dichromatism in North American passerine birds. *American Naturalist* 148:453–480.
- GRIFFITH, S. C., I. P. F. OWENS, AND T. BURKE. 1999a. Environmental determination of a sexually selected trait. *Nature* 400:358–360.
- GRIFFITH, S. C., I. P. F. OWENS, AND T. BURKE. 1999b. Female choice and annual reproductive success favour less-ornamented male House Sparrows. *Proceedings of the Royal Society of London, Series B* 266:765–770.
- GRIMINGER, P., AND C. G. SCANES. 1986. Protein Metabolism. Pages 326–358 in *Avian Physiology*, 4th ed. (P. D. Sturkie, Ed.). Springer-Verlag, New York.
- HAN, R., H. P. BADEN, J. L. BRISSETTE, AND L. WEINER. 2002. Redefining the skin's pigmentary system with a novel tyrosinase assay. *Pigment Cell Research* 15:290–297.
- HAASE, E. 1975. The effects of testosterone propionate on secondary sexual characters and testes of House Sparrows, *Passer domesticus*. *General and Comparative Endocrinology* 26:248–252.
- HAASE, E., AND R. SCHMEDEMANN. 1992. Dose-dependent effect of testosterone on the induction of eclipse coloration in castrated wild Mallard drakes (*Anas platyrhynchos*). *Canadian Journal of Zoology* 70:428–431.
- HAASE, E., S. ITO, A. SELL, AND K. WAKAMATSU. 1992. Melanin concentrations in feathers from wild and domestic Pigeons. *Journal of Heredity* 83: 64–67.
- HAASE, E., S. ITO, AND K. WAKAMATSU. 1995. Influences of sex, castration, and androgens on the eumelanin and pheomelanin contents of different feathers in wild Mallards. *Pigment Cell Research* 8:164–170.
- HEARING, V. J. 1998. Regulation of melanin formation. Pages 423–438 in *The Pigmentary System: Physiology and Pathophysiology* (J. J. Nordlund, R. E. Boissy, V. J. Hearing, R. A. King, and J. P. Ortonne, Eds.) Oxford University Press, New York.

- HEARING, V. J. 1999. Biochemical control of melanogenesis and melanosomal organization. *Journal of Investigative Dermatology* 4:24–28.
- HEARING, V. J. 2000. The Melanosome: The perfect model for cellular responses to the environment. *Pigment Cell Research* 13:23–34.
- HEBERT, C. E., J. L. SHUTT, AND R. O. BALL. 2002. Plasma amino acid concentrations as an indicator of protein availability to breeding Herring Gulls (*Larus argentatus*). *Auk* 119:185–200.
- HILL, G. E. 1994. House Finches are what they eat: A reply to Hudon. *Auk* 111:221–225.
- HILL, G. E. 1996. Redness as a measure of the production costs of ornamental traits. *Ethology Ecology and Evolution* 8:157–175.
- HILL, G. E. 1998. An easy, inexpensive means to quantify plumage coloration. *Journal of Field Ornithology* 69:353–363.
- HILL, G. E. 2000. Energetic constraints on expression of carotenoid-based plumage coloration in male House Finches. *Journal of Avian Biology* 31:559–566.
- HILL, G. E., AND W. R. BRAWNER III. 1998. Melanin-based plumage coloration in the House Finch is unaffected by coccidial infection. *Proceedings of the Royal Society of London, Series B* 265: 1105–1109.
- HOLBERTON, R. L., K. P. ABLE, AND J. C. WINGFIELD. 1989. Status signalling in Dark-eyed Juncos, *Junco hyemalis*: Plumage manipulations and hormonal correlates of dominance. *Animal Behaviour* 37:681–689.
- HOLBERTON, R. L., R. HANANO, AND K. P. ABLE. 1990. Age-related dominance in male Dark-eyed Juncos: Effects of plumage and prior residence. *Animal Behaviour* 40:573–579.
- HOOGDUJN, M. J., N. P. SMIT, A. VAN DER LAARSE, A. F. VAN NIEUWPOORT, J. M. WOOD, AND A. J. THODY. 2003. Melanin has a role in  $Ca^{2+}$  homeostasis in human melanocytes. *Pigment Cell Research* 16:127–132.
- HOWELL, T. R. 1952. Natural history and differentiation in the Yellow-bellied Sapsucker. *Condor* 54:237–282.
- HUDON, J. 1991. Unusual carotenoid use by the Western Tanager (*Piranga ludoviciana*) and its evolutionary implications. *Canadian Journal of Zoology* 69:2311–2320.
- HUDON, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). *Auk* 111: 218–221.
- HUHTA, E., AND R. V. ALATALO. 1993. Plumage colour and male-male interactions in the Pied Flycatcher. *Animal Behaviour* 45:511–518.
- HUNT, G., AND A. J. THODY. 1995. Agouti protein can act independently of melanocyte-stimulating hormone to inhibit melanogenesis. *Journal of Endocrinology* 147:R1–R4.
- ITO, S., K. WAKAMATSU. 1998. Chemical degradation of melanin: Application to identification of dopamine-melanin. *Pigment Cell Research* 11:120–126.
- ITO, S., K. WAKAMATSU, AND H. OZEKI. 2000. Chemical analysis of melanins and its application to the study of regulation of melanogenesis. *Pigment Cell Research* 13:103–109.
- JACKSON, W. M., S. ROHWER, R. L. WINNEGRAD. 1988. Status signaling is absent within age-and-sex classes of Harris's Sparrows. *Auk* 105: 424–427.
- JÄRVI, T., AND M. BAKKEN. 1984. The function of the variation in the breast stripe of the Great Tit (*Parus major*). *Animal Behaviour* 32:590–596.
- JÄRVI, T., E. RÖSKAFT, M. BAKKEN, AND B. ZUMSTEG. 1987. Evolution of variation in male secondary sexual characteristics: A test of eight hypotheses applied to Pied Flycatchers. *Behavioral Ecology and Sociobiology* 20:161–169.
- JAWOR, J. M. 2002. Multiple ornaments and sexual selection in a socially monogamous passerine, the Northern Cardinal (*Cardinalis cardinalis*). Ph.D. dissertation, University of Dayton, Dayton, Ohio.
- JOHNSEN, T. S., AND M. ZUK. 1996. Repeatability of mate choice in female Red Junglefowl. *Behavioral Ecology* 7:243–246.
- KECK, W. N. 1933. Control of the bill color of the English Sparrow by injection of male hormone. *Proceedings of the Society for Experimental Biology and Medicine* 30:1140–1141.
- KETTERSON, E. D., AND V. NOLAN JR. 1994. Hormones and life histories: An integrative approach. Pages 327–353 in *Behavioral Mechanisms in Evolutionary Ecology* (L. A. Real, Ed.). University of Chicago Press, Chicago.
- KETTERSON, E. D., V. NOLAN, JR., L. WOLF, AND C. ZIEGENFUS. 1992. Testosterone and avian life histories: Effects of experimentally elevated testosterone on behavior and correlates of fitness in the Dark-eyed Junco (*Junco hyemalis*). *American Naturalist* 140:980–999.
- KING, D. I., R. M. DEGRAAF, AND C. R. GRIFFIN. 2001. Plumage coloration and reproductive success in male Chestnut-sided Warbler. *Wilson Bulletin* 113:239–242.
- LAMPE, H. M., AND Y. O. ESPMARK. 1994. Song structure reflects male quality in Pied Flycatchers, *Ficedula hypoleuca*. *Animal Behaviour* 47: 869–876.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305.
- LEMEL, J., AND K. WALLIN. 1993. Status signaling, motivational condition and dominance: An experimental study in the Great Tit, *Parus major*. *Animal Behaviour* 45:549–558.



- LEMON, R. E., D. M. WEARY, AND K. J. NORRIS. 1992. Male morphology and behavior correlate with reproductive success in the American Redstart (*Setophaga ruticilla*). *Behavioral Ecology and Sociobiology* 29:399–403.
- LINVILLE, S. U., AND R. BREITWISCH. 1997. Carotenoid availability and plumage coloration in a wild population of Northern Cardinals. *Auk* 114: 796–800.
- LOZANO, G. 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70:309–311.
- LU, D., D. WILLARD, I. R. PATEL, S. KADWELL, L. OVERTON, T. KOST, M. LUTHER, W. CHEN, R. P. WOYCHIK, W. O. WILKISON, AND R. D. CONE. 1994. Agouti protein is an antagonist of the melanocyte-stimulating hormone receptor. *Nature* 371:799–802.
- MCGRAW, K. J., J. DALE, AND E. A. MACKILLOP. 2003. Social environment during molt and the expression of melanin-based plumage pigmentation in male House Sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 53: 116–122.
- MCGRAW, K. J., AND HILL, G. E. 2000. Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proceedings of the Royal Society of London, Series B* 267:1525–153.
- MCGRAW, K. J., G. E. HILL, R. STRADI, AND R. S. PARKER. 2001. The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American Goldfinches (*Carduelis tristis*) and Northern Cardinals (*Cardinalis cardinalis*). *Physiological and Biochemical Zoology* 74: 843–852.
- MCGRAW, K. J., E. A. MACKILLOP, J. DALE, AND M. E. HAUBER. 2002. Different colors reveal different information: How nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology* 205:3747–3755.
- MØLLER, A. P. 1987a. Social control of deception among status signalling House Sparrows *Passer domesticus*. *Behavioral Ecology and Sociobiology* 20:307–311.
- MØLLER, A. P. 1987b. Variation in badge size in male House Sparrows *Passer domesticus*: Evidence for status signalling. *Animal Behaviour* 35: 1637–1644.
- MØLLER, A. P. 1988. Badge size in the House Sparrow *Passer domesticus*: Effects of intra- and intersexual selection. *Behavioral Ecology and Sociobiology* 22:373–378.
- MØLLER, A. P. 1989. Natural and sexual selection on a plumage signal of status on morphology in House Sparrows *Passer domesticus*. *Journal of Evolutionary Biology* 2:125–140.
- MØLLER, A. P., AND J. ERRITZØE. 1988. Badge, body and testes size in House Sparrow *Passer domesticus*. *Ornis Scandinavica* 19:72–73.
- MØLLER, A. P., R. T. KIMBALL, AND J. ERRITZØE. 1996. Sexual ornamentation, condition, and immune defence in the House Sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology* 39: 317–322.
- MØLLER, A. P., AND A. POMIANKOWSKI. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* 32: 167–176.
- MURPHY, M. E. 1996. Nutrition and metabolism. Pages 31–60 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.
- NERO, R. W. 1954. Plumage aberrations of the redwing (*Agelaius phoeniceus*). *Auk* 71:137–155.
- NORRIS, K. 1993. Heritable variation in a plumage indicator of viability in male Great Tits *Parus major*. *Nature* 362:537–539.
- NORRIS, K. J. 1990a. Female choice and the quality of parental care in the Great Tit *Parus major*. *Behavioral Ecology and Sociobiology* 27: 275–281.
- NORRIS, K. J. 1990b. Female choice and the evolution of the conspicuous plumage coloration of monogamous male Great Tits. *Behavioral Ecology and Sociobiology* 26:129–138.
- OMLAND, K. E., AND T. W. SHERRY. 1994. Parental care at nests of two age classes of male American Redstart: Implications for female mate choice. *Condor* 96:606–613.
- OTTER, K., AND L. RATCLIFFE. 1999. Relationship of bib size to age and sex in the Black-capped Chickadee. *Journal of Field Ornithology* 70: 567–577.
- OWENS, I. P. F., AND I. R. HARTLEY. 1998. Sexual dimorphism in birds: Why are there so many different forms of dimorphism? *Philosophical Transactions of the Royal Society of London, Series B*. 265:397–407.
- OWENS, I. P. F., T. BURKE, AND D. B. A. THOMPSON. 1994. Extraordinary sex roles in the Eurasian Dotterel: Female mating arenas, female-female competition, and female mate choice. *American Naturalist* 144:76–100.
- PRICE, D. K. AND N. T. BURLEY. 1994. Constraints on the evolution of attractive traits: Selection in male and female Zebra Finches. *American Naturalist* 144:908–934.
- PRICE, T. D. 1984. Sexual selection on body size, territory and plumage variables in a population of Darwin's Finches. *Evolution* 38:327–341.
- PROTA, G., M. L. LAMOREUX, J. MULLER, T. KOBAYASHI, A. NAPOLITANO, M. R. VINCENSI, C. SAKAI, AND V. J. HEARING. 1995. Comparative analysis of melanins and melanosomes produced by vari-

- ous coat color mutants. *Pigment Cell Research* 8:153–163.
- QVARNSTRÖM, A., AND E. FORSGREN. 1998. Should females prefer dominant males? *Trends in Ecology and Evolution* 13:498–501.
- REYER, H. -U., W. FISCHER, P. STECK, T. NABULON, AND P. KESSLER. 1998. Sex-specific nest defense in House Sparrows (*Passer domesticus*) varies with badge size of males. *Behavioral Ecology and Sociobiology* 42:93–99.
- ROHDE, P. A., A. JOHNSEN, AND J. T. LIFJELD. 1999. Female plumage coloration in the Bluethroat: No evidence for an indicator of maternal quality. *Condor* 101:96–104.
- ROHWER, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29: 593–610.
- ROHWER, S. 1977. Status signalling in Harris's Sparrows: Some experiments in deception. *Behaviour* 61:107–129.
- ROHWER, S. 1985. Dyed birds achieve higher social status than controls in Harris's Sparrows. *Animal Behaviour* 33:1325–1331.
- ROHWER, S., AND F. C. ROHWER. 1978. Status signalling in Harris's Sparrows: Experimental deceptions achieved. *Animal Behaviour* 26: 1012–1022.
- ROULIN, A. 1999. Nonrandom pairing by male Barn Owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology* 10:688–695.
- ROULIN, A., C. DIJKSTRA, C. RIOLS, AND A. -L. DUCREST. 2001b. Female- and male-specific signals of quality in the Barn Owl. *Journal of Evolutionary Biology* 14:255–266.
- ROULIN, A., A.-L. DUCREST, R. BALLOUX, C. DIJKSTRA, AND C. RIOLS. 2002. A female melanin ornament signals offspring fluctuating asymmetry in the Barn Owl. *Proceedings of the Royal Society of London, Series B* 270:167–171.
- ROULIN, A., T. W. JUNG, H. PFISTER, AND C. DIJKSTRA. 2000. Female Barn Owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London, Series B* 267:937–941.
- ROULIN, A., H. RICHNER, AND A.-L. DUCREST. 1998. Genetic, environmental, and condition-dependent effects on female and male ornamentation in the Barn Owl *Tyto alba*. *Evolution* 52: 1451–1460.
- ROULIN, A., C. RIOLS, C. DIJKSTRA, AND A.-L. DUCREST. 2001a. Female plumage spottiness signals parasite resistance in the Barn Owl (*Tyto alba*). *Behavioral Ecology* 12:103–110.
- SÆTRE, G.-P., T. FOSSNES, AND T. SLAGSVOLD. 1995. Food provisioning in the Pied Flycatcher: Do females gain direct benefits from choosing bright-coloured males? *Journal of Animal Ecology* 64:21–20.
- SÆTRE, G.-P., S. DALE, AND T. SLAGSVOLD. 1994. Female Pied Flycatchers prefer brightly coloured males. *Animal Behaviour* 48:1407–1416.
- SÆTRE, G.-P., T. SLAGSVOLD, A. KRUSZEWICZ, AND H. VIJUGREIN. 1997. Paternal care in Pied Flycatchers *Ficedula hypoleuca*: Energy expenditure in relation to plumage colour and mating status. *Ardea* 85:233–242.
- SAINO, N., R. STRADI, P. NINNI, E. PINI, AND A. P. MØLLER. 1999. Carotenoid plasma concentration, immune profile, and plumage ornamentation of male Barn Swallows (*Hirundo rustica*). *American Naturalist* 154:441–448.
- SARNA, T., AND H. M. SWARTZ. 1998. The physical properties of melanins. Pages 333–358 in *The Pigmentary System: Physiology and Pathophysiology* (J. J. Nordlund, R. E. Boissy, V. J. Hearing, R. A. King, and J. P. Ortonne, Eds.). Oxford University Press, New York.
- SENAR, J. C., AND M. CAMERINO. 1998. Status signalling and the ability to recognize dominants: An experiment with siskins (*Carduelis spinus*). *Proceedings of the Royal Society of London, Series B* 265:1515–1520.
- SENAR, J. C., M. CAMERINO, J. L. COPETE, AND N. B. METCALFE. 1993. Variation in black bib of the Eurasian Siskin (*Carduelis spinus*) and its role as a reliable badge of dominance. *Auk* 110: 924–927.
- SENAR, J. C., J. L. COPETE, AND A. J. MARTIN. 1998. Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the siskin *Carduelis spinus*. *Ibis* 140:661–669.
- SENAR, J. C., V. POLO, F. URIBE, M. CAMERINO. 2000. Status signaling, metabolic rate and body mass in the siskin: The cost of being a subordinate. *Animal Behaviour* 59:103–110.
- SHIOJIRI, N., T. NIWA, K. WAKAMATSU, S. ITO, AND A. NAKAMURA. 1999. Chemical analysis of melanin pigments in feather germs of Japanese Quail *Bh* (black at hatch) mutants. *Pigment Cell Research* 12:259–265.
- SLAGSVOLD, T., AND T. DREVON. 1999. Female Pied Flycatchers trade between male quality and mating status in mate choice. *Proceedings of the Royal Society of London, Series B* 255:917–921.
- SLAGSVOLD, T., AND J. T. LIFJELD. 1988. Plumage colour and sexual selection in the Pied Flycatcher *Ficedula hypoleuca*. *Animal Behaviour* 36: 395–407.
- SLAGSVOLD, T., AND J. T. LIFJELD. 1992. Plumage color is a condition-dependent sexual trait in male Pied Flycatchers. *Evolution* 46:825–828.
- SMISETH, P. T., J. ORNBORG, S. ANDERSSON, AND T. AMUNDSEN. 2001. Is male plumage reflectance correlated with paternal care in Bluethroats? *Behavioral Ecology* 12:164–170.
- STRADI, R. 1998. *The Colour of Flight*. Solei Gruppo Editoriale Informatico, Milan, Italy.

- STUDD, M. V., AND R. J. ROBERTSON. 1985a. Evidence for reliable badges of status in territorial Yellow Warblers (*Dendroica petechia*). *Animal Behaviour* 33:1102–1113.
- STUDD, M. V., AND R. J. ROBERTSON. 1985b. Sexual selection and variation in reproductive strategy in male Yellow Warblers (*Dendroica petechia*). *Behavioral Ecology and Sociobiology* 17: 101–109.
- STUDD, M. V., AND R. J. ROBERTSON. 1988. Differential allocation of reproductive effort to territorial establishment and maintenance by male Yellow Warblers, (*Dendroica petechia*). *Behavioral Ecology and Sociobiology* 23: 199–210.
- TAKEUCHI, S., H. SUZUKI, S. HIROSE, M. YABUUCHI, C. SATO, H. YAMAMOTO, AND S. TAKAHASHI. 1996b. Molecular cloning and sequence analysis of the chick melanocortin 1-receptor gene. *Biochimica et Biophysica Acta* 1306:122–126.
- TAKEUCHI, S., H. SUZUKI, M. YABUUCHI, AND S. TAKAHASHI. 1996a. A possible involvement of melanocortin 1-receptor in regulating feather color pigmentation in the chicken. *Biochimica et Biophysica Acta* 1308:164–168.
- TAKEUCHI, S., K. TESHIGAWARA, AND S. TAKAHASHI. 2000. Widespread expression of agouti-related protein (AGRP) in the chicken: A possible involvement of AGRP in regulating peripheral melanocortin systems in the chicken. *Biochimica et Biophysica Acta* 1496:261–269.
- THERON, E., K. HAWKINS, E. BIRMINGHAM, R. E. RICKLEFS, AND N. I. MUNDI. 2001. The molecular basis of an avian plumage polymorphism in the wild: A melanocortin-1-receptor point mutation is perfectly associated with the melanistic plumage morph of the Bananaquit, *Coereba flaveola*. *Current Biology* 11:550–557.
- THODY, A. J., E. HIGGINS, K. WAKAMATSU, S. ITO, S. BURCHILL, AND J. MARKS. 1991. Pheomelanin as well as eumelanin is present in human epidermis. *Journal of Investigative Dermatology* 97: 340–344.
- TOMITA, Y., A. HARIU, C. KATO, AND M. SEIJI. 1984. Radical production during tyrosinase reaction, dopa-melanin formation and photo-irradiation of dopa-melanin. *Journal of Investigative Dermatology* 82:573–576.
- VÁCLAV, R., AND H. HOI. 2002. Different reproductive tactics in House Sparrows signalled by badge size: Is there a benefit to being average? *Ethology* 108:569–582.
- VEIGA, J. P. 1993. Badge size, phenotypic quality, and reproductive success in the House Sparrow: A study on honest advertisement. *Evolution* 47:1161–1170.
- VEIGA, J. P. 1995. Honest signaling and the survival cost of badges in the House Sparrow. *Evolution* 49:570–572.
- VEIGA, J. P., AND M. PUERTA. 1996. Nutritional constraints determine the expression of a sexual trait in the House Sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London, Series B* 263:229–234.
- VOISEY, J., AND A. VAN DAAL. 2002. Agouti: From mouse to man, from skin to fat. *Pigment Cell Research* 15:10–18.
- VOLTURA, K. M., P. L. SCHWAGMEYER, AND D. W. MOCK. 2002. Parental feeding rates in the House Sparrow, *Passer domesticus*: Are larger-badged males better fathers? *Ethology* 108:1011–1022.
- VON SCHANTZ, T., S. BENSCHE, M. GRAHN, D. HASSELQUIST, AND H. WITZELL. 1999. Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London, Series B* 266:1–12.
- WAKAMATSU, K., AND S. ITO. 2002. Advanced chemical methods in melanin determination. *Pigment Cell Research* 15:174–183.
- WATT, D. J. 1986. Relationship of plumage variability, size and sex to social dominance in Harris's Sparrows. *Animal Behaviour* 34:16–27.
- WILSON, B. D., D. BAGNOL, C. B. KAELEN, M. M. OLLMANN, I. GANTZ, S. J. WATSON, AND G. S. BARSH. 1999. Physiological and anatomical circuitry between agouti-related protein and leptin signaling. *Endocrinology* 140: 2387–2397.
- WILSON, J. D. 1992. A re-assessment of the significance of status signaling in population of wild Great Tits, *Parus major*. *Animal Behaviour* 43: 999–1009.
- WITSCHI, E., AND R. A. MILLER. 1938. Ambisexuality in the female starling. *Journal of Experimental Zoology* 79:475–487.
- WOLFF, G. L. 2003. Regulation of yellow pigment formation in mice: A historical perspective. *Pigment Cell Research* 16:2–15.
- ZUK, M., K. JOHNSON, R. THORNHILL, AND J. D. LIGON. 1990a. Mechanisms of female choice in Red Junglefowl. *Evolution* 44:477–485.
- ZUK, M., J. D. LIGON, AND R. THORNHILL. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in Red Junglefowl. *Animal Behaviour* 44: 999–1006.
- ZUK, M., R. THORNHILL, J. D. LIGON, K. JOHNSON, S. AUSTAD, S. H. LIGON, N. W. THORNHILL, AND C. COSTIN. 1990b. The role of male ornaments and courtship behavior in female mate choice of Red Junglefowl. *American Naturalist* 136: 459–473.