

An update on the honesty of melanin-based color signals in birds

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Summary

The control mechanisms and information content of melanin-based color signals in birds have generated much recent interest and controversy among evolutionary biologists. Initial experimental studies on this topic manipulated coarse metrics of an individual's condition (i.e. food intake, disease state) and failed to detect significant condition-dependence of melanin ornament expression. However, three new lines of research appear profitable and target specific factors associated with the production of melanin pigments. These include the role of (i) metals, (ii) amino acids, and (iii) testosterone and social interactions in shaping the extent and intensity of melanin-colored plumage patches. Here, I review recent studies of and evidence for these honesty-reinforcing mechanisms.

Key words: amino acids/barn owl/barn swallow/house sparrow/metals/minerals/plumage/testosterone/zebra finch

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Melanin is the most common pigment in animal integuments and serves as the ground body color for many taxa (McGraw, 2006). Some animals, however, capitalize on melanin coloration as a sexual or social advertisement. Many birds, for example, develop bold patches of black or brown feathers that serve as honest signals of mate quality or aggressive ability (Hill, 2006; Senar, 2006).

In these instances of melanin-based quality signaling, there has been much interest in and controversy over the factors that keep the signals reliable (Jawor and Breitwisch, 2003). Traits must incur differential costs among individuals to evolve as honest advertisements,

such that only the highest-quality individuals can display the most exaggerated forms of a signal (Grafen, 1990; Zahavi, 1975). However, many early studies in birds showed little or no effect of an animal's condition on its ability to develop extensive or dark melanin-based plumage ornaments (i.e. McGraw and Hill, 2000; McGraw et al., 2002). A recent review and meta-analysis of data from the literature (Griffith et al., 2006) revealed that melanin-based color signals were equally condition-dependent as another signal type (carotenoid coloration) for which there was abundant evidence for condition-dependence. However, a re-analysis of these data, including citations overlooked by these authors and data from papers published since, showed in fact that melanin colors were not significantly condition-dependent (K.J. McGraw, A. Roulin, J.C. Senar and M.S. Rosenberg, unpublished data).

One important problem with much of the initial work on this topic was that the experimental challenges administered to birds were quite general. Factors such as total calorie intake (McGraw et al., 2002) or disease status (McGraw and Hill, 2000) were manipulated to determine their effects on ornamental melanin pigmentation, largely because these factors had strong effects on other condition-dependent (i.e. carotenoid) colors in birds. However, because of the very different processes associated with melanin and carotenoid color production, for example, one might presume that different factors, specific to melanin pigment production, are responsible for mediating the honesty of melanin compared with carotenoid colors. This view has led to at least three new lines of work that have attempted to pinpoint pigment-production-specific modulators of melanin color ornaments in birds. The goal of this mini-review is to highlight these new research avenues, to summarize the most updated evidence for each idea, and to offer suggestions for future study in these and other areas.

Metals as modulators of melanin coloration

It has long been known that, when in high supply, transition and alkaline earth metals (i.e. Cu, Zn, Fe, Ca, and Mg) can increase the production of melanin pigmentation in the hair of many domesticated mammal species (Prota, 1992). These minerals are often limited in the diets of wild animals (Klasing, 1998; McDowell, 2003)

and can serve roles as enzyme (i.e. tyrosinase) cofactors or in facilitating the molecular rearrangement of intermediate products (Solano and Garcia-Borrón, 2007). This metal-melanin hypothesis had never before been applied to melanin colors in bird plumage, however, until two studies were published 5 years ago on the topic (McGraw, 2003; Niecke et al., 2003). Supporting this hypothesis initially was the observation that several chemical elements are enriched in melanized as opposed to unmelanized feather regions in birds like eagles (reviewed in Niecke et al., 2003). Now, three new empirical papers seem to provide support for this idea.

First, Roulin et al. (2006) measured calcium concentrations in the bones of barn owl (*Tyto alba*; Figure 1A) specimens collected from the field and showed that bones from birds with heavier black spotting in their breast plumage (which is an honest signal of quality; reviewed in Roulin and Altwegg, 2007) had more calcium. This suggests that some dietary or physiological process underlies the accumulation of calcium for storage in bone and for increasing feather melanization.

Then, in the only experimental study of its kind, McGraw (2007) manipulated calcium content in the diet of young and adult male zebra finches (*Taeniopygia guttata*; Figure 1B), which display a central patch of black, eumelaninic feathers on the breast, and found that calcium enrichment increased the number of black feathers grown and thus the size of the black plumage patch. In a granivorous species where calcium is typically limited in the diet, this result pinpoints specialized dietary regulation of a melanin ornament. Last, a recent paper capitalized on a unique environmental circumstance—heavy metal city pollution—to study the relationship between metals and avian melanin coloration. Dauwe and Eens (2008) measured differences in the black breast stripe width of great tits (*Parus major*) among sites with varying degrees of lead and cadmium contamination and found that tits grew wider stripes when captured from the most polluted areas. This result is counter to what one might predict about the effect of pollution on sexual traits (Hill, 1995), especially given that carotenoid coloration in tits showed the opposite relationship with pollution intensity, but is consistent



Figure 1. Color photos showing the melanin-based ornamental traits in four species that have been well-studied in the context of metals, amino acids, and hormones. (A) Black breast spotting and chestnut breast coloring in a barn owl, © Alex Roulin. (B) Black breast striping and patch in a male zebra finch, © Kevin McGraw. (C) Black throat badge of male house sparrow, © Janine Russell. (D) Brown forehead and throat plumage in a barn swallow, © Kevin McGraw.

with the special link between metals and melanins, even if it means a decoupling of melanin coloration from general condition/health.

Amid this recent burst of support for the metal-melanin hypothesis, much work still awaits to improve our understanding of their associations. Almost nothing is known of the natural intake and use of these minerals in wild birds, save from several calcium supplementation experiments in the context of acid rain contamination, eggshell formation, and/or nestling growth (Dawson and Bidwell, 2005; Mand et al., 2000; Ramsay and Houston, 1999; St Louis and Breebaart, 1991). Still needed is careful experimentation in wild-caught (not domesticated) species to confirm that melanin pigment production and coloration (ornamental or not) can naturally respond to dietary or physiological variation in minerals. There also has been a limited focus on a few minerals (calcium, in particular), so research on other transition and alkaline earth metals is encouraged. Trade-offs in use of these minerals (i.e. in bone, as co-factors) would also be an exciting area to pursue. Finally, McGraw (2003, 2006) speculated that feathers may be a means of voiding large amounts of potentially toxic minerals accumulated for enhancing melanin pigment production, but there still has been no study or evidence of the chemoprotective need for metal binding in sexually or socially selected melanic feathers.

Amino acid restrictions for melanin coloration

As with minerals, there has been an abundance of literature on the effects of amino acid concentrations on melanin pigment production in non-avian animals (Prota, 1992). This comes out of the basic observation that amino acids such as tyrosine, phenylalanine, and cysteine are the building blocks for endogenous melanin synthesis. Prominent studies within the last decade have been performed on domestic cats, showing that variation in dietary amino acids can change melanin composition and color of the coat (Anderson et al., 2002; Morris et al., 2002). A very recent study in a malnourished population of human children also showed that growing dark hair requires adequate nourishment (perhaps dietary tyrosine; McKenzie et al., 2007).

The amino acid composition of bird feathers has been considered in other contexts (Murphy and King, 1982; Murphy et al., 1990), and, as reported in an excellent review by Grau et al. (1989), early work in domesticated fowl (i.e. turkey, chickens, quail) showed that dietary restrictions of several amino acids (i.e. lysine, phenylalanine, tyrosine) can reduce melanin deposition in non-ornamental feathers. However, to date only one study has been published on the relationship between melanin feather ornamentation and amino acid intake. Poston et al. (2005) recently manipulated dietary concentrations of phenylalanine and tyrosine to understand their effects

on the development of the black melanin throat badge (a known signal of social status) and other plumage traits in male house sparrows (*Passer domesticus*; Figure 1C). Low amino acid intake reduced the darkness (presumably the eumelanin concentration) of the badge, but did not affect the size of the patch, which is the most variable aspect of the plumage that functions as a signal (but see Vaclav, 2006 for associations among melanic traits in a house sparrow population). In this same species, protein concentrations in the bloodstream positively correlate with the size of the black badge (Veiga and Puerta, 1996).

Clearly, this body of information is too limited at present to draw firm conclusions about the role of amino acids as honesty reinforcers of avian melanin signals. Amino acid restrictions can impact egg production in wild birds (Ramsay and Houston, 1998), so there is precedent for their life-history importance. However, we need to prioritize improving our understanding of how amino acid intake and use varies among individuals, among species with different diets, and in relation to protein status (Hebert et al., 2002), feather formation (Murphy and King, 1984a,b,c), and ultimately melanin formation. Moreover, in other melanin studies, substrate availability is not necessarily the rate-limiting step for melanin synthesis, but instead it is the activity of the melanin-synthesizing enzymes, such as tyrosinase, that govern melanin pigment production (Prota, 1992). Tyrosinase was studied in relation to sex-specific plumage colors in birds over 40 years ago (Hall, 1966; Hall and Okazaki, 1966; Okazaki and Hall, 1965), but since the advent of the handicap principle no research has considered the degree to which its activity is condition-dependent or primary in feather melanin accumulation within a sex.

Testosterone, melanin, and social interactions

Among these melanin-specific lines of research that I review here, hormonal control of melanin coloration has perhaps had the longest history of study in domesticated (Cone et al., 1996; Slominski et al., 2004) and wild animals (Hadley and Oldman, 1969; Ralph, 1969), as well as for ornamental melanin colors (i.e. Quinn and Hews, 2003). Birds in particular have received increased attention on this subject in recent years (Buchanan et al., 2001; Evans et al., 2000; Gonzalez et al., 2001; Strasser and Schwabl, 2004). Although all of this work has been performed on a single hormone, testosterone (T), and a single species, the house sparrow, it has yielded consistent support for the notion that high T levels are required for developing an extensive black badge. More recently, this T-melanin hypothesis has been tested and supported in a comparative phylogenetic study of birds (Bokony et al., 2008). These researchers found in two clades (the shorebirds and

corvids) that T levels were higher in species with more extensive melanin ornaments (Bokony et al., 2008), but that this relationship did not hold in species where the male plumage is not androgen-dependent (i.e. in gamebirds and ducks). From this, it is clear that more empirical/experimental studies are needed in more species and with attention to other hormones that may interplay (see more below).

If T serves as an honesty reinforcer of melanin ornaments, the exciting question in the context of signal evolution then becomes: what makes T costly? Several have discussed the immunosuppressive effects of T in this context (Evans et al., 2000; Poiani et al., 2000), and there is some evidence in species like the house sparrow that T impairs immune system function (Buchanan et al., 2003). However, in these same studies, the role of a different hormone, corticosterone (CORT), has also received attention and in fact has been linked to aspects of immunocompetence (Buchanan et al., 2003; Evans et al., 2000). Until very recently, the idea that CORT mediates melanin expression remained untested. Roulin et al. (2008) manipulated CORT levels in nestling barn owls growing their melanin plumage ornaments and discovered that birds with high CORT had experimentally decreased phaeomelanin breast pigmentation. CORT and T have complex physiological interactions (Roberts et al., 2007), so in the coming years we should push more studies that aim to understand how these hormones separately or jointly impact melanin pathways or localization. Other hormones, such as those that mediate melanin darkening in other animals (i.e. melanocyte stimulating hormone, Balm and Groneveld, 1998; catecholamines, Korzan et al., 2002), and their effects (i.e. on metabolic rate; Buchanan et al., 2001) also should not be ignored.

One additional aspect of hormonal enforcement of melanin honesty has very recently been pursued, and that involves how an individual's behavior feeds into its hormonal state and thus its pigmentation. As much as animal behaviors are controlled by the hormonal milieu, hormone titers can also respond to one's actions (Oliveira, 2004). In effect, an animal's social experiences might then impact the extent to which T governs melanin signal expression; those who fight or win more might have higher T levels and thus bigger badges (McGraw et al., 2003). Social testing and enforcement of status signals has long been discussed (Senar, 2006), but only recently was a relationship between an animal's competitive behavior at the time of ornament development found to be linked to its melanin badge expression (i.e. in house sparrows; McGraw et al., 2003). Thus, rivals could directly learn about the social experiences and hormonal background of their opponents by assessing exaggeration of the plumage badge. Even more recently, Safran et al. (2008) experimentally tested an extension of this phenomenon in barn swallows (*Hirundo rustica*; Figure 1D), where they were

interested in the degree to which the melanin plumage signal itself influences an individual's hormonal state, presumably through how birds were perceived and treated by conspecifics. Birds whose plumage was experimentally darkened were found to have higher T levels (Safran et al., 2008). This result revolutionizes our perspectives on the physiological costs of animal signals, which now must be evolutionarily viewed and mathematically modeled as important both before and after trait production.

Conclusions

Rapid advances in the control and function of melanin signals have been made since the turn of the millennium. A wealth of new ideas have been introduced and have stood up to brief empirical testing. Others, such as the notion that melanins are antioxidants and thus may directly serve to improve health and coloration (much like carotenoid pigments do; Moreno and Møller, 2006), await rigorous tests in the context of ornamental melanin signals. There are hints that melanin signals are susceptible to antioxidant damage in the results from Chernobyl, where barn swallows captured nearer to the disaster site had fewer antioxidants (Møller et al., 2005) and were less colorful (Camplani et al., 1999; Møller and Mousseau, 2001). New approaches like these, and especially those that incorporate techniques from other subdisciplines where melanin biology and chemistry are key (i.e. cancer research), are very much welcomed as we push forward the field of melanin color research and improve our understanding of how unique melanin colors are compared with other colors and sexual traits in animals.

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