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Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*)

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Abstract Evolutionary biologists have shown much recent interest in the costliness and signal content of colorful plumage displays in birds. Although many studies suggest that both carotenoid- and structurally-based plumage colors are condition-dependent indicators of health and nutritional state at the time ornamental feathers are grown, there is little experimental evidence supporting the idea that melanin pigmentation is a reliable signal of condition during molt. Instead, melanin-based ornamental coloration often reveals the competitive ability and dominance of individuals throughout the year. However, this work does not indicate which proximate environmental factors shape the expression of melanin pigmentation at the time of feather growth. Because of the link between melanin coloration and the social environment, it is possible that the development of brightly colored plumage may be associated with aggressive social interactions during feather molt. Here, we show that melanin-based ornamental coloration in male house sparrows (*Passer domesticus*) is correlated with the degree to which individuals interact aggressively with conspecifics during molt. Males that were dominant (beta, but not alpha) within captive social groups during molt grew larger badges than subordinates. Groups of males that had higher rates of aggression during molt grew larger badges than less aggressive triads. To our knowledge, this is the first demonstration that melanin pigmentation and

plumage-based status badges are related to the competitive history of individuals during feather development. By coupling badge size directly with aggressive experiences during molt, birds can use their status signal to honestly indicate their likelihood of winning agonistic encounters throughout the year.

Keywords Aggressive behavior · Badge size · Competition · Melanin pigmentation · Plumage coloration

Introduction

Indicator models of sexual selection argue that secondary sex characteristics in animals function as honest signals of individual quality (Zahavi 1975; Clutton-Brock and Albon 1979; Andersson 1982, 1986, 1994; Johnstone 1995). Under this idea, exaggerated traits, which are more often found in males, are costly to produce or maintain (Kodric-Brown and Brown 1984). Only those individuals of the highest quality can pay the full complement of costs associated with elaborate displays (Grafen 1990).

Colorful plumage ornaments in birds have been the focus of many tests of honest signaling theory (Olson and Owens 1998; Hill 1999). Birds display three main types of color in their feathers (carotenoid-based pigmentation, melanin-based pigmentation, and structural coloration) and each is produced by a different mechanism (Fox and Vevers 1960). Many studies have focused on the nutritional and energetic constraints of producing these forms of bright coloration (Veiga and Puerta 1996; Keyser and Hill 1999; Hill 2000). Birds develop colorful feathers at one time of year (during the molt period), and experimental and correlational studies of nutritional state at the time of molt indicate that both carotenoid- (Hill and Montgomerie 1994; Hill 2000; <CitationRef and Hill 2000a) and structurally based (Keyser and Hill 1999, 2000; McGraw et al. 2002) ornamental colors are energetically and nutritionally demanding to produce in a number of avian species. Thus, they can reveal infor-

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mation to conspecifics about the health or condition of signalers at the time colorful plumage is grown.

Investigations into the energetic limitations of producing melanin-based plumage coloration in birds are less conclusive. One of the first studies offered a correlational link between nutritional condition and the degree of expression of melanin pigmentation (Veiga and Puerta 1996). In contrast, subsequent experiments have failed to support this notion that large patches of melanin-based feathers are nutritionally costly to produce (Gonzalez et al. 1999; McGraw and Hill 2000a; McGraw et al. 2002). Instead, researchers have emphasized the relationship between melanin ornamentation and aggressive competition among conspecifics (Rohwer 1975, 1977), such that males use exaggerated melanin displays to signal fighting ability and dominance throughout the year (Senar and Camerino 1998; reviewed in Senar 1999). Only those males that can withstand repeated aggressive attacks throughout the year display the largest status badges (Rohwer and Ewald 1981; Rohwer 1982).

Although the status-signaling hypothesis provides an elegant explanation for the maintenance of signal honesty in these systems, it does not address the proximate factors that shape the expression of melanin-based plumage coloration at the time the ornament is produced. One interesting possibility is that, because of the link between melanin pigmentation and the social environment, the development of ornamental melanin pigmentation in birds is coupled with levels of aggressive social competition during feather growth (McGraw and Hill 2000a). Zuk and Johnsen (2000) and Setchell and Dixon (2001) recently found that the fleshy red coloration of male red junglefowl (*Gallus gallus*) and mandrills (*Mandrillus sphinx*), respectively, respond dynamically to changes in aggressive behavior and dominance among conspecifics. Whether melanin pigmentation or any plumage-based badge of status in birds is a reliable indicator of aggressive competition at the time of feather development has yet to be tested.

In this study, we investigated the relationship between social conditions during molt and the expression of melanin-based plumage coloration in male house sparrows (*Passer domesticus*). Male house sparrows display a sexually dimorphic patch of black throat feathers that is pigmented with melanin. Each autumn, males complete a single annual molt and replace their old badge with a new set of melanin-based feathers (Lowther and Cink 1992). Male sparrows that display larger badges throughout the year are socially dominant to males having smaller color patches (Møller 1987a, 1987b). We housed triads of male sparrows in captivity for the duration of their pre-basic molt and observed patterns of variability in melanin pigmentation and aggressive behavior within and among groups so that we could assess the relationship between social interactions during molt and the development of status badges at this time of year. Based on results from previous studies, we also tested whether alternate sources of environmental or genetic variation, such as prior residence (number of days spent in captivi-

ty; Holberton et al. 1990; Sandell and Smith 1991), body condition (Veiga and Puerta 1996), or previous badge size (Møller 1989) predicted aggression rates among cages, dominance within groups, and the size of melanin-based plumage patches.

Methods

Capture and housing conditions

We trapped 42 wild male house sparrows with mistnets and Potter traps in Tompkins County, N.Y., USA between 28 February and 1 May 2000. At capture, birds were marked with a unique combination of colored leg bands for individual identification. We arranged birds by capture date into groups of three and housed them in 14 stainless steel cages (0.6 m long x 0.45 m wide x 0.8 m tall) in an animal-approved indoor room (4.6 m x 4 m x 2.4 m) at Cornell University. Each cage contained wooden dowels as elevated perches and had an open top, front, and side that were covered in hardware cloth. Fluorescent light timers maintained natural day/light cycles. Daily temperatures ranged from 20–25°C and humidity ranged from 40–70%.

For the duration of time spent in captivity, male sparrows were fed an ad lib 50:50 diet of unmedicated game starter (26% protein, Agway, Batavia, N.Y.) and white millet. Water was treated with 6.6 drops l⁻¹ of Premium Multi-Drops high-potency multivitamins (Eight in One Pet Products, Hauppauge, N.Y.) and 0.26 g l⁻¹ of sulfadimethoxine (Sigma Chemical, St. Louis, Miss.), a drug that effectively controls coccidial infections in passerines (Hill 2000; McGraw and Hill 2000a). Food and water dishes were provided for each bird and spaced across the floor of the cages to ensure that all birds had equal access. At no point in the study were any males infected with obvious ectoparasites (e.g. ticks, avian pox, mites, lice).

Morphological measurements

At capture, we measured tarsus length to the nearest 0.1 mm with calipers and body mass to the nearest 0.1 g with an electronic balance. The size of melanin-based badges was also scored at this time by digitally photographing the ventral sections of each male against a grayboard and importing these images into Adobe Photoshop (Adobe Systems, San Jose, Calif) for analysis (*sensu* Dale 2000). We measured badge area (in cm²) by outlining the melanin-based pigmented area using the 'lasso' marquee and determining the number of pixels occupied using the 'histogram' function. Because photos varied slightly in distance from the subject, badge area was calculated relative to an area standard that was photographed next to each bird. Repeatability of badge area, calculated from separate photos of the same bird that were taken 5 s apart and after resetting each individual in front of the camera, was high using these scoring methods ($r=0.91$, $F_{22,23}=20.67$, $P<0.0001$). Birds began their pre-basic molt in the late summer (August), and at this time we again determined body mass so that we could calculate pre-molt body condition using the residuals of body mass regressed onto tarsus length (*sensu* Griffith et al. 1999). All birds completed molt by 1 November, and on this day we again measured body mass, tarsus length, and badge size. Freshly molted badges are partially obscured by buff feather tips in house sparrows, but our scoring technique, in which we placed the head of each bird flat against the grayboard surface, fully exposed the black-pigmented feather portions and allowed us to determine badge size in a repeatable fashion that was consistent before and after molt.

Behavioral observations

During the molt period, we videotaped each of the 14 cages to quantify the aggressive behavior of individuals within and among social groups. We conducted all observations during the first 3 h of morning daylight, and each cage was taped during two separate sessions that lasted 2 h each. Most (approximately 95%) of the aggressive interactions were chases or physical encounters that occurred on elevated perches. We tallied all of the aggressive encounters during the observation periods to determine overall interaction rate for each cage. We determined a winner and loser from each aggressive interaction when one individual withdrew from an encounter or failed to retaliate, and used these wins and losses to construct dominance hierarchies within groups. Although group hierarchies were linear within observation periods, they were not always consistent between sessions for individual cages, so we summed all wins and losses for each individual relative to others within a cage to assign overall dominance ranks (*sensu* McGraw and Hill 2000b). Individuals winning a greater percentage of interactions than their counterparts were given a higher rank in the hierarchy (1=alpha, 2=beta, 3=gamma).

Statistical analyses

First, to describe variation in badge size among our captive house sparrows, we compared the mean and variance in badge size measured at capture (grown in the wild) to that after males completed molt (grown in captivity) using an equality-of-variance *F*-test. We also calculated mean and variance for within- and among-cage badge size and cage aggression rate to determine variability in plumage expression and competitive behavior across social environments. To understand factors affecting aggression patterns across groups during molt, we used a forward stepwise multiple regression to compare the effects of body condition, pre-molt badge size, and capture date (an index of prior residence) on cage aggression rate. We included mean and variance measures of condition and melanin coloration as predictor variables in the regression because both the overall magnitude and the degree of difference between males in a cage may influence the intensity of competition in social groups. For this and all models to follow, we tested for collinearity among our predictors and found a significant positive correlation between pre-molt condition and post-molt condition ($r=0.8$, $n=42$, $P<0.0001$) and significant negative correlations between capture date and both condition measures (both $r<-0.35$, $n=42$, $P<0.03$). Thus, we excluded capture date from all models, and selected the one, most temporally relevant condition measure for other analyses (e.g. pre-molt condition as a statistical predictor of mid-molt aggression rate).

We used mixed-model ANOVAs to explore the effect of dominance rank during molt on two measures of the throat badge: (1) post-molt badge area, and (2) change in badge area. In these models, we entered rank as a fixed effect and the cage in which birds were housed as a random effect, to account for potential among-group differences in badge size. Post-hoc paired independent contrasts on least-squares means were conducted on significant model effects to determine specific group differences. Last, we used a forward stepwise multiple regression to investigate the full suite of predictors of badge size after captive molt. We included pre-molt badge size, pre-molt body condition, and aggressive interaction rate as independent variables in this model. Here, different regressions were performed using group/cage means (model A) and using values for individual birds (model B), and we again analyzed data using raw post-molt badge size measures and directional pre- to post-molt changes in badge size.

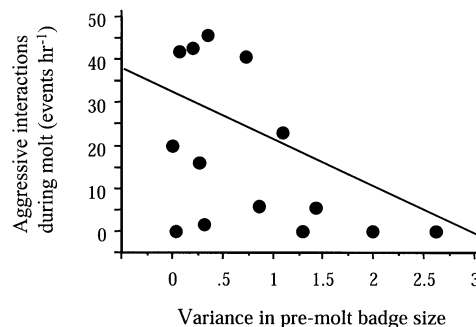


Fig. 1 Scatterplot of the significant relationship (from Table 1) between the variance in pre-molt badge size and the rate of aggressive interactions during molt within cages of captive male house sparrows

Table 1 Forward stepwise regression model comparing aggression rates of captive male house sparrows during molt to measures of body condition and badge size

Variable	<i>F</i> -ratio	Coefficient	<i>P</i>
Pre-molt mean body condition	0.04	−0.06	0.84
Pre-molt variance in body condition	0.53	−0.21	0.48
Pre-molt mean badge size	1.32	0.32	0.27
Pre-molt variance in badge size	5.32	−0.55	0.04

Results

Variation in badge size

Males grew variably sized badges in captivity ($\bar{x} = 6.67 \text{ cm}^2$, $\sigma^2=0.69$, $n=42$), such that they were equally as variable as those that were grown in the wild and displayed prior to captive molt ($\bar{x} = 6.54 \text{ cm}^2$, $\sigma^2=0.81$) (Equality-of-variance *F*-test, $F=0.85$, $P=0.61$). There was no significant difference in the size of pre- and post-molt badges (paired *t*-test, $t=0.78$, $P=0.44$). Birds housed within the same cage for the duration of molt ($n=3$ per group) also grew badges that varied in size (mean intracage $\sigma^2=0.57$, $SD=0.49$, range of σ^2 s=0.003–1.574), similar to the degree of within-group badge-size variation exhibited prior to molt (mean intracage $\sigma^2=0.69$, $SD=0.70$, range=0.059–2.152; paired *t*-test, $t=0.53$, $P=0.60$).

Predictors of aggression rates within groups

Group aggression rates during molt varied from 0–46 interactions h^{-1} in our observation periods ($\bar{x} = 14.3$, $n=14$, $\sigma^2=222$). The lone significant predictor of mid-molt aggression rate within cages was the variance in pre-molt badge size between males (final model: $F_{1,12}=5.32$, $r^2=0.31$, $P=0.04$; Table 1). Cages in which males differed less in badge size prior to molt had higher rates of aggression during molt than groups in which males differed more in pre-molt badge size (Fig. 1). There were no significant effects of mean pre-molt body condition, vari-

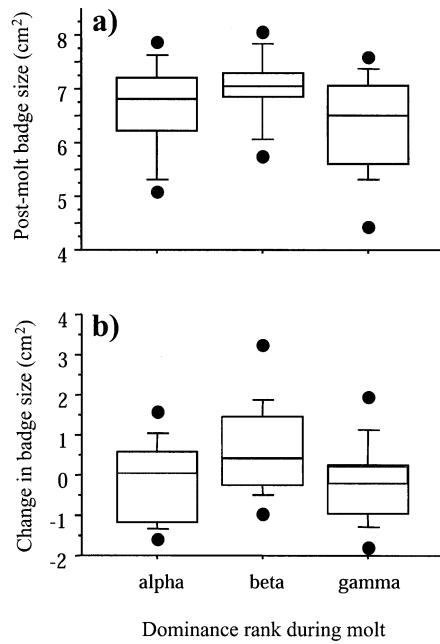


Fig. 2 Boxplot illustrating the relationships (from Table 2) between dominance rank during molt and **a** post-molt melanin pigmentation, and **b** change in badge size. Horizontal bars in the plot indicate the 10th, 25th, 50th, 75th, and 90th percentiles, and points give data for individuals outside of these ranges

Table 2 Mixed-model ANOVA tables for the effect of dominance rank during molt on two measures of plumage pigmentation in captive male house sparrows: (1) post-molt badge size, (2) change in badge size (post-pre molt). Here, dominance rank was entered as a fixed effect, and cage of origin as a random effect (to account for between-group differences in badge size that might confound relationships with dominance rank). Within each cage of males, dominance rank was categorically assigned on an integer scale from 1 (alpha) to 3 (gamma)

Model	Variable	r^2	F	P
Post-molt badge size	Full model	0.57	2.28	0.03
	Cage		2.05	0.06
	Rank		3.72	0.02
Change in badge size	Full model	0.46	1.46	0.19
	Cage		1.29	0.28
	Rank		2.57	0.04

ance in pre-molt body condition, or mean pre-molt badge size on group rates of aggression during molt (all $P>0.25$; Table 1).

Dominance rank during molt and badge size

In our mixed-model ANOVAs, dominance rank had a significant effect on both post-molt badge size and change in badge size (Table 2). Post-hoc paired comparisons run for both models revealed a significant differ-

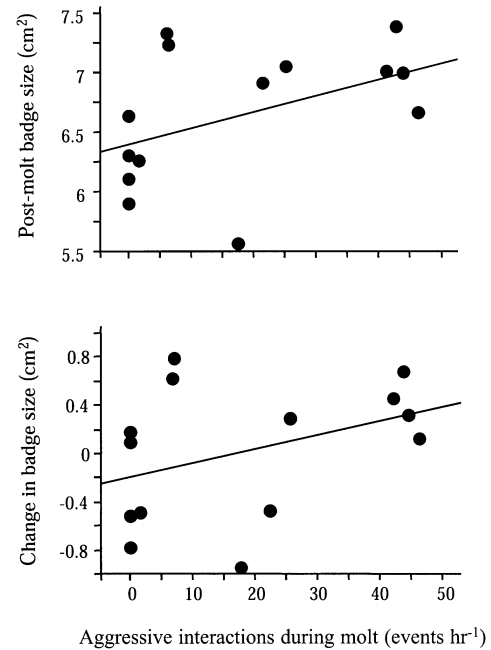


Fig. 3 Scatterplot of the significant relationships (from Table 3) between the group rate of aggressive interactions during molt and **a** mean post-molt badge size, and **b** mean change in badge size of caged male house sparrows

ence in badge size between beta and gamma individuals within a cage (Fig. 2), with beta males growing larger badges than gamma birds (paired independent contrasts on least squares means, both $t>2.0$, both $P<0.05$; $P>0.1$ for all other contrasts). There were no significant effects of cage of origin on dominance rank (Table 2).

Group aggression rate during molt and badge size

In model A (using cage means), we found that the overall rate of aggressive interactions during molt within a cage explained a significant portion of the variation in mean post-molt badge size per group (full model: $F_{1,12}=4.03$, $n=14$, $r^2=0.25$, $P=0.04$; Table 3). Birds from more aggressive groups during molt grew larger badges in captivity than males from less aggressive groups (Fig. 3a). There were no significant effects of mean post-molt body condition or pre-molt badge size on the size of badges grown during our study (all $P>0.15$; Table 3). Aggressive interaction rate during molt also was significantly predictive of individual variation in badge size in model B (using values for individual birds) (final model: $F_{1,40}=4.05$, $n=42$, $r^2=0.10$, $P=0.05$; Table 3). We again found no significant effects of condition or previous badge area on the expression of melanin coloration (all $P>0.1$; Table 3). We also analyzed these data using changes in badge size and found similar results to those reported for post-molt badge size (Table 3, Fig. 3b).

Table 3 Forward stepwise multiple-regression models comparing post-molt badge size of captive male house sparrows to previous badge size, rate of aggressive interactions, and post-molt body

condition. Two regressions (models A and B) were built to analyze each of our two measures of throat pigmentation in house sparrows: (1) post-molt badge size and (2) change in badge size

Response	Predictor variables	Group-means model (A)			Individual-values model (B)		
		<i>F</i> -ratio	Coefficient	<i>P</i>	<i>F</i> -ratio	Coefficient	<i>P</i>
Post-molt badge size	Pre-molt badge size	1.90	0.37	0.19	2.50	0.24	0.12
	Aggressive interaction rate	4.03	0.50	0.05	4.10	0.30	0.03
	Pre-molt body condition	0.00	0.00	0.98	0.12	0.05	0.73
Change in badge size	Pre-molt badge size	0.09	0.03	0.77	0.00	0.00	0.99
	Aggressive interaction rate	3.94	0.46	0.05	4.02	0.31	0.04
	Pre-molt body condition	0.35	0.12	0.56	0.13	0.09	0.72

Discussion

In this study, we tested whether social conditions during plumage molt were related to the development of sexually dichromatic, melanin-based feather patches in male house sparrows. The size of melanin-based plumage ornaments was variable both within and among groups of birds after completing molt in captivity. During feather growth, the degree to which groups of birds aggressively competed against one another was linked significantly to the magnitude of difference in badge size among individuals within a group, such that groups of males that had more similar badges prior to molt competed more intensely among one another. This finding supports the fundamental idea that melanin pigmentation in house sparrows functions as an indicator of aggressive ability (Rohwer 1975; Møller 1987a, 1987b), with those birds that were more similar in badge size and social status behaving more aggressively to resolve finer differences in fighting ability.

Most relevant to the idea that badge expression is linked to the social environment, we found that within-group variability in the size of melanin-based plumage patches grown in captivity was related to the aggressive behavior of individuals during feather growth. First, there was a significant effect of dominance rank during molt on the size of the badge that males developed. A difference in post-molt badge size was not evident between the highest- and lowest-ranked birds, but instead it was the beta males that grew larger badges than gamma individuals. This may have been due to the disproportionately high aggressive activity of beta males, who participated in 75% of all interactions, or to the general level of intensity of each interaction involving a beta male, which we did not score. Second, among-group variation in badge size was predicted best by the degree to which individuals interacted aggressively within a cage at the time of molt. Birds from more aggressive triads grew larger badges on average than males from less aggressive groups. Collectively, these results are consistent with the hypothesis that the expression of melanin-based plumage pigmentation in house sparrows is an honest signal of a male's aggressive behavior and dominance status during the process of feather development. We believe that this

is the first study to demonstrate a relationship between the social environment during molt and the expression of a plumage-based badge of status in birds.

These findings complement past and current work on hormonal control of ornamental melanin pigmentation in birds (reviewed in Hall 1969; Ralph 1969; Owens and Short 1995; Kimball and Ligon 1999; Poiani et al. 2000). Hormones such as testosterone (T) (Witschi 1961; Johns 1964), thyroxine (Miller 1935), and luteinizing-hormone (Okazaki and Hall 1965; Hall and Okazaki 1966) have been shown to influence melanin deposition in the feathers of certain avian species. Evans et al. (2000) and Gonzalez et al. (2001) recently tested the effect of experimentally elevated T on the expression of melanin-based plumage pigmentation in male house sparrows and found that males with high androgen levels grew larger patches of melanin-based plumage. Traditionally, the role of T in sexual signaling systems has been emphasized in light of its link to aggressive behavior (Wingfield et al. 1987). The "challenge" hypothesis (Wingfield et al. 1990) proposes that escalated agonistic encounters among conspecific individuals mediate levels of circulating T, such that birds that compete aggressively will elevate T to win aggressive competitions. Because aggressive behavior in male *P. domesticus* is tied to circulating T levels during periods of social instability (Hegner and Wingfield 1987), which occurred throughout the molt period in our study, and because sparrows in the wild repeatedly renew social status within unstable flocks of birds in the autumn (Lowther and Cink 1992), these results may represent a novel application of the "challenge" hypothesis. The positive feedback loop between aggression and T levels together may mediate the expression of melanin-based ornamental coloration. Our proposed mechanistic pathway demands experimental corroboration in which both aggressive behavior and T levels are manipulated during molt.

In addition to the social predictors of badge size, we considered the potential condition-dependence of melanin pigmentation in our captive male sparrows. In our regression models, we found no significant relationships between the size of a male's badge and his body condition prior to or after molt. This adds to the mounting evidence that melanin-based plumage ornaments develop

independent of the health or nutritional state of individuals. Gonzalez et al. (1999) manipulated protein content in the diet during molt and observed no effect on the growth of plumage badges in captive male *P. domesticus*. Moreover, McGraw and Hill (2000a) found that neither food intake nor endoparasite load experimentally altered the development of melanin-derived ornamental black caps in male American goldfinches (*Carduelis tristis*).

Instead, the observations reported here bring into question the potential costs of elevated aggression as they relate to the signal honesty of melanin pigmentation. Badges of status in house sparrows and other birds are known to incur social costs as individuals repeatedly test the aggressive ability of counterparts throughout the year (Rohwer and Ewald 1981; Rohwer 1982; Møller 1987a). Results from our study suggest that these birds may suffer similar social costs while competing aggressively as they develop ornamental coloration. Only those males who can withstand repeated aggressive attacks at this time of year can grow the largest status badges. Ultimately, by linking badge size to aggressive experiences during feather growth, birds may use their status badge to directly signal their likelihood of winning aggressive competitions throughout the year. Whether melanin displays and status signals in other animals incur similar costs and communicate similar information should be a profitable avenue for future research.

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References

- Andersson M (1982) Sexual selection, natural selection and quality advertisement. *Biol J Linn Soc* 17:375–393
- Andersson M (1986) Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* 40:804–816
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, N.J.
- Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–169
- Dale J (2000) Ornamental plumage does not signal male quality in red-billed queleas. *Proc R Soc Lond B* 267:2143–2149
- Evans MR, Goldsmith AR, Norris SRA (2000) The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 47:156–163
- Fox HM, Vevers G (1960) The nature of animal colours. Sidgwick and Jackson, London
- Gonzalez G, Sorci G, Møller AP, Ninni P, Haussy C, de Lope F (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *J Anim Ecol* 68:1225–1234
- Gonzalez G, Sorci G, Smith LC, de Lope F (2001) Testosterone and sexual signalling in male house sparrows (*Passer domesticus*). *Behav Ecol Sociobiol* 50:557–562
- Grafen A (1990) Biological signals as handicaps. *J Theor Biol* 144:517–546
- Griffith SC, Owens IPF, Burke T (1999) Environmental determination of a sexually selected trait. *Nature* 400:358–360
- Hall PF (1969) Hormonal control of melanin synthesis in birds. *Gen Comp Endocrinol [Suppl]* 2:451–458
- Hall PF, Okazaki K (1966) The action of interstitial cell stimulating hormone upon avian tyrosinase. *Biochemistry* 5:1202–1208
- Hegner RE, Wingfield JC (1987) Social status and circulating levels of hormones in flocks of house sparrows, *Passer domesticus*. *Ethology* 76:1–14
- Hill GE (1999) Mate choice, male quality, and carotenoid-based plumage coloration. In: Adams N, Slotow R (eds) *Proc Int Ornithol Congr* 22:1654–1668
- Hill GE (2000) Energetic constraints on expression of carotenoid-based plumage coloration. *J Avian Biol* 31:559–566
- Hill GE, Montgomerie R (1994) Plumage colour signals nutritional condition in the house finch. *Proc R Soc Lond B* 258:47–52
- Holberton RL, Hanano R, Able KP (1990) Age-related dominance in male dark-eyed juncos: effects of plumage and prior residence. *Anim Behav* 40:573–579
- Johns JE (1964) Testosterone-induced nuptial feathers in phalaropes. *Condor* 66:449–455
- Johnstone RA (1995) Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol Rev* 70:1–65
- Keyser AJ, Hill GE (1999) Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc R Soc Lond B* 266:771–777
- Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav Ecol* 11:202–209
- Kimball RT, Ligon J (1999) Evolution of avian plumage dichromatism from a proximate perspective. *Am Nat* 154:182–193
- Kodric-Brown A, Brown JH (1984) Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat* 124:309–323
- Lowther PE, Cink CL (1992) House sparrow (*Passer domesticus*). In: Poole A, Stettenheim P, Gill F (eds) *The birds of North America*, no. 12. The Birds of North America, Philadelphia, Pa.
- McGraw KJ, Hill GE (2000a) Differential effects of endoparasitism on the expression of carotenoid- and melanin-based ornamental coloration. *Proc R Soc Lond B* 267:1525–1531
- McGraw KJ, Hill GE (2000b) Carotenoid-based ornamentation and status signaling in the house finch. *Behav Ecol* 11:520–527
- McGraw KJ, Vonnegut EA, Dale J, Hauber ME (2002) Different plumage colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental coloration. *J Exp Biol* 205:3747–3755
- Miller DS (1935) Effects of thyroxin on plumage of the English sparrow, *Passer domesticus*. *J Exp Zool* 71:293–309
- Møller AP (1987a) Social control of deception among status signaling house sparrows *Passer domesticus*. *Behav Ecol Sociobiol* 20:307–311
- Møller AP (1987b) Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signaling. *Anim Behav* 35:1637–1644
- Møller AP (1989) Natural and sexual selection on a plumage signal of status and on morphology in house sparrows, *Passer domesticus*. *J Evol Biol* 2:125–140
- Okazaki K, Hall PF (1965) The action of interstitial cell-stimulating hormone upon tyrosinase activity in the weaver bird. *Biochem Biophys Res Comm* 20:667–673
- Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol* 13:510–514
- Owens IPF, Short RV (1995) Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. *Trends Ecol Evol* 10:44–47

- Poiani A, Goldsmith AR, Evans MR (2000) Ectoparasites of house sparrows (*Passer domesticus*): an experimental test of the immunocompetence handicap hypothesis and a new model. *Behav Ecol Sociobiol* 47:230–242
- Ralph CL (1969) The control of color in birds. *Am Zool* 9:521–530
- Rohwer S (1975) The social significance of avian winter plumage variability. *Evolution* 29:593–610
- Rohwer S (1977) Status signaling in Harris' sparrows: some experiments in deception. *Behaviour* 61:107–129
- Rohwer S (1982) The evolution of reliable and unreliable badges of fighting ability. *Am Zool* 22:531–546
- Rohwer S, Ewald PW (1981) The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35:441–454
- Sandell M, Smith HG (1991) Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). *Behav Ecol Sociobiol* 29:147–152
- Senar JC (1999) Plumage coloration as a signal of social status. In: Adams N, Slotow R (eds) *Proc Int Ornithol Congr* 22:1669–1686
- Senar JC, Camerino M (1998) Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proc R Soc Lond B* 265:1515–1520
- Setchell JM, Dixon AF (2001) Changes in secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Horm Behav* 39:177–184
- Veiga JP, Puerta M (1996) Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc R Soc Lond B* 263:229–234
- Wingfield JC, Ball GF, Dufty J, A M, Hegner RE, Ramenofsky M (1987) Testosterone and aggression in birds. *Am Sci* 75:602–608
- Wingfield JC, Hegner RE, Dufty J, A. M., Ball GF (1990) The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am Nat* 130:829–846
- Witschi E (1961) Sex and secondary sexual characters. In: Marshall AJ (ed) *Biology and comparative physiology of birds*, vol 2. Academic Press, New York, pp 115–168
- Zahavi A (1975) Mate selection--a selection for a handicap. *J Theor Biol* 53:205–214
- Zuk M, Johnsen TS (2000) Social environment and immunity in male red jungle fowl. *Behav Ecol* 11:146–153