

**Szent István University
Postgraduate School of Veterinary Science**

**Melanin-based plumage ornaments as sexual and
social signals: function and evolution.**

Outline of PhD thesis

By

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1. Introduction

Signalling often occurs when animals need to resolve conflicts over resources such as food or mating opportunities. In such signalling systems, reliability of the signals is maintained by either of two ways (Maynard Smith & Harper 2003): the signal should be unfakeably linked to the signalled quality (indices), or it should be too costly for low-quality signallers (handicaps). Therefore, signals of competitive abilities such as sexual attractiveness or social dominance are often expected to impose some fitness-reducing costs to the signallers (Kotiaho 2001).

Colour ornaments have long been studied in the contexts of sexual and social signalling, and many empirical studies have corroborated the relationship between various colour traits and the bearer's success in sexual or social competition (Andersson 1994, Hill & McGraw 2006a). Yet our understanding of the mechanisms ensuring that these colours convey some reliable information about their bearer to potential mates or opponents is incomplete (Hill & McGraw 2006b). The best known case is the carotenoid-based coloration of some species of fish and birds that signals individual condition because animals can obtain carotenoids only through diet by a process that is sensitive to nutritional and health conditions (Houde 1997, Hill 2002). In contrast to carotenoids, melanin pigments are synthesized by the animals. Therefore melanin-based coloration had been assumed cheap to produce, questioning its potential to reliably signal individual quality in sexual or social selection. On theoretical grounds however, the expression of melanin ornaments may involve several costs and regulatory mechanisms that may render them honest signals of quality (Jawor & Breitwisch 2003). These mechanisms are largely unexplored. Hence the information content of melanin ornaments needs detailed investigations both from ultimate and proximate perspectives (Griffith et al. 2006).

2. Thesis objectives and methods

In this thesis I investigated the potential of melanin-based plumage ornaments to function in sexual and social signalling. I used three approaches: (i) I tested the evolutionary effects of sexual selection on the interspecific variation in melanin-based coloration in comparative studies, (ii) I examined the role of melanin ornaments in sexual and social signalling in two avian model species, and (iii) I investigated two possible reliability-ensuring mechanisms of melanization at the intra- and interspecific level, respectively. I focused on black ornaments since the pigmentary origin of other colours cannot be judged by their appearance (McGraw et al. 2004).

2.1. Comparative studies of melanin ornaments

To test whether interspecific differences in melanin-based coloration may be explained by sexual selection, I chose two groups of birds that show great among-species variability in the extent of ornamental black plumage.

Plovers and allies (*Charadriida*) are ground-nesting shorebirds with various black patterns in their breeding plumage. Many plover species seem to display these patterns during courtship and/or territory defence (Perrins 1998), suggesting that they may use them as sexual signals. I investigated whether the extent of melanization in plovers is related to relevant measures of sexual competition, namely to courtship behaviour (the type of sexual display used) and breeding density.

Cardueline finches (*Carduelinae*) are seed-eating passerines that vary greatly in both melanin and carotenoid ornamentation. This avian group is of specific importance since some carduelines became the main model species for studies of carotenoid-based coloration that appeared to confirm the functional distinction between sexually selected carotenoids

and arbitrary melanin badges (Griffith et al. 2006). I tested whether black melanization in finches relates to components of reproductive effort that are expected to reflect the intensity of sexual selection (Badyaev 1997).

I measured the extent of black melanization in the frontal plumage of plovers and finches from digitised colour plate images, and collected data on their behaviour and ecology from literature. I used two alternative comparative methods to control for phylogeny: independent contrasts (Felsenstein 1985) and pairwise comparisons (Harvey & Nee 1997).

2.2. Melanin ornaments in model species

I investigated the sexual and social signalling roles of melanin ornaments in two passerine species that are excellent model organisms to study sexual selection and status signalling.

The penduline tit (*Remiz pendulinus*) has a uniquely diverse breeding system, in which both sexes are sequentially polygamous and parental care is provided by either one of the parents or they both desert the clutch (Szentirmai 2005). Males appear to use multiple signals in sexual advertisement, including complex songs and the building of elaborate nests (Szentirmai 2005). In a field study I examined whether the size of the black eye-stripe may influence the males' success in competing other males and attracting females. The behaviour and reproductive success of individually ringed birds was followed in a breeding population at Fehér-tó, Hungary in collaboration with the International Penduline Tit Research Group in 2003. We measured the aggressivity of males by their response in an intruder-model test, and their attractivity by the time they needed to pair up and the number of females they acquired during the breeding season. We measured eye-stripe size from digital photographs.

The house sparrow (*Passer domesticus*) is highly gregarious, wintering in flocks and breeding colonially (Perrins

1998). The males' black throat patch (bib) has a well established status-signalling function in aggressive interactions among competing flockmates (Liker & Barta 2001). Here I investigated the previously unexplored light wingbar of male sparrows which is a pheomelanin-based ornament, with less pigmented (more white) wingbars appearing more ornamental. I measured the birds' bib size, wingbar area and its achromatic contrast with scapulars from digital photographs, and I tested whether these traits predicted the males' success in social competition in wintering flocks. Birds were observed in two aviaries of the Zoological Institute of Szent István University to determine their success in fighting, attack and defence.

2.3. Reliability of melanin ornaments

Among the various mechanisms proposed to maintain the honesty of melanin-based signals, I chose to examine two candidates that may be especially relevant to black and white ornaments, the focus of my research.

Firstly, both black and white ornaments are very suitable for producing high contrast since they are the least and most reflective colours, respectively, hence they may significantly increase conspicuousness to predators (Endler 1990). The increased risk of predation is frequently mentioned as a possible maintenance cost of honest signals, yet this idea is poorly tested for colour traits (Andersson 1994, Kotiaho 2001). The house sparrow is an ideal species for studying such predation costs because it is heavily preyed upon by several raptor species that detect their prey by visual cues (Perrins 1998), and it possesses both black and white ornaments (bib and wingbar). I investigated whether individual variation in these ornaments is associated with the predator-related risk-taking behaviour of sparrows. I studied a free-living sparrow population at the Veszprém Zoo, Hungary in collaboration with the Veszprém University Ornithological Group. We

individually ringed a large number of birds, measured the bill size of males and the wingbar of both sexes, and investigated the risk they took in a field experiment in winter 2005. We manipulated predation risk by moving the feeders between safe and risky positions, i.e. close to and far from bushes used as shelters by foraging sparrows, and we recorded how frequently the birds used the two positions.

Secondly, many black ornaments predict dominance, these were often assumed arbitrary badges of status that are under social control (Senar 1999). However, these ornaments may also be indices of competitiveness due to the regulational effects of the male sex hormone testosterone (T). T mediates many aggressive and sexual behaviours (Wingfield et al. 1987), and it also affects the expression of melanin ornaments in some species (Jawor & Breitwisch 2003). I used the comparative approach to test whether interspecific differences in melanization are consistently related to differences in T levels among bird species ranging from ratites to small passerines. I scored melanization as the extent of black plumage on the whole body on a 0–10 scale using colour plates. Data on T levels were collected from literature. Again, I used both independent contrasts and pairwise comparisons for phylogenetic analyses (Felsenstein 1985, Harvey & Nee 1997).

3. Results and conclusions

We found that in plovers, males were more melanized in species that perform display flights than in ground-displaying species, while breeding density was unrelated to melanization. Display flights are costly signals of male agility and function in female choice (Grønstøl 1996, Blomqvist et al. 1997). Thus we provided the first interspecific comparative evidence for a relationship between the extent of plumage melanization and a proxy for sexual selection, namely courtship display behaviour.

Our results suggest that the conspicuous black markings of plover species evolved to amplify flight displays by increasing the conspicuousness of males against the sky (Walsberg 1982).

We also provided comparative support for the relationship between melanization and sexual selection in a second group of birds, cardueline finches that are known to use carotenoid-based signals in mate choice (Hill 2002). We found that reduced reproductive investment (smaller clutch size in males, and shorter incubation periods in females) was associated with more extended black plumage, indicating a trade-off between parental efforts and melanin ornaments as mating efforts.

In our field study on penduline tits we showed that males with larger black eye-stripes needed less time to acquire mates and paired up with more females than smaller-striped males. This suggests that female penduline tits prefer males with larger eye-stripes. In turn, eye-stripe size did not predict the males' aggressiveness towards other males. These findings underline that the role of melanin ornaments is not confined to intrasexual status signalling but instead needs careful investigation from multiple approaches in each species.

In house sparrows, we found that the conspicuousness of the wingbar of males specifically predicted their defence success in aggressive interactions, even after controlling for the effect of the status-signalling bib size. Males with more contrasting wingbars were more successful in repelling attacks. Using a threat display that exposes the wingbars also increased defence success, suggesting that the wingbar may amplify wing displays that signal motivational levels (Hurd & Enquist 2001). This study was the first to examine the function of the sparrows' wingbar, and also the first to demonstrate the potential of multiple cues in status signalling (Candolin 2003).

Our field experiment with sparrows showed that males and females did not adjust their predator-related risk-taking behaviour to their melanin-based coloration including the size

of the black bib and the area and conspicuousness of the pheomelanin-pigmented/white wingbar. Despite that we successfully manipulated the risk perceived by birds (i.e. they spent less time far than near shelters), more ornamented birds did not use the far positions less often than less ornamented birds. These results argue against the widely accepted yet rarely tested hypothesis that colour signals are maintained by predation costs (Kotiaho 2001).

Finally, we provided comparative evidence that the extent of melanized black plumage is consistently related to increased levels of circulating testosterone in the breeding season among a diverse set of avian taxa. Melanization and T were correlated not only in males but also in females, and sexual dimorphism in melanization was also related to sex differences in T, with highly dichromatic species showing the greatest fall-off in female T relative to male T, and species with equally black sexes being the less dimorphic in T. These results imply that interspecific differences in melanized black plumage may have co-evolved with or evolved in response to differences in T levels. This is the first interspecific study to relate melanization to one of its potential regulatory agents, suggesting that testosterone might provide a link between melanin-based coloration and competitiveness.

In sum, these studies revealed several lines of evidence, both at the inter- and intraspecific level, for the signalling potential of melanin ornaments in sexual and social selection. Our findings suggest that birds widespreadly use melanin ornaments in sexual signalling, and argue against such previous simplifications that melanin ornaments generally are arbitrary badges of status (Senar 1999). Rather, our results concur with the past few years' realization that melanin ornaments are by no means inferior to carotenoid or structural colours in their capacity or prevalence to function in sexual selection, both as status signals as well as mate choice criteria (Hill & McGraw

2006a, Griffith et al. 2006). Our results also highlight that the function of melanin ornaments is complex, varying among species and interacting as multiple cues not only in female choice (Candolin 2003) but also in status signalling. Further studies are important to ascertain the costs of producing and maintaining melanin-based signals, with specific respect to the mechanisms of testosterone-regulation.

4. References

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6. List of own publications

Published papers and manuscripts included in the thesis:

- Bókony V., Liker A., Székely T. & Kis J. 2003. Melanin-based plumage coloration and flight displays in plovers and allies. *Proc. R. Soc. Lond. B* 270, 2491–2497.
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- Bókony V., Liker A., Hirschenhauser K. & Garamszegi L.Z. 2006. Testosterone and melanin-based plumage coloration in birds. Manuscript.

Articles related to the thesis:

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