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

PhD thesis

By

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CONTENTS

1. Summary

In most animal signalling systems, reliability of the signals is maintained by their costs payed by the signaller. Plumage colours have long been studied in the contexts of sexual and social signalling, yet our understanding of their honesty-maintaining mechanisms is incomplete. Melanin-based coloration had been hypothesized to be cheap to produce, thereby questioning its potential to reliably signal individual quality in sexual or social competition. In a series of inter- and intraspecific studies I investigated whether melanin-based coloration is related to sexual and social selection, and I tested whether melanin signals may be reliable due to the costs of increased predation risk or to the regulatory effects of elevated testosterone levels.

First, using phylogenetic comparative methods I showed that interspecific variation in the extent of melanin-based black coloration is related to sexual display behaviour in plovers and allies (*Charadriida*) and to reproductive investment in cardueline finches (*Carduelinae*), as predicted by sexual selection theory. Second, using two passerine birds as model species, I demonstrated that melanin ornaments may function in both sexual and social signalling. In penduline tits (*Remiz pendulinus*) the size of the black eye-stripe of males predicts their success in mating but not in male-male competition, suggesting that females prefer more melanized males. In house sparrows (*Passer domesticus*) both the size of the black throat patch and the conspicuousness of the white wingbar predict the males' success in social competition, suggesting that these ornaments act as multiple cues in status signalling. Finally, I studied two possible sources of reliability of melanin ornaments. Using the house sparrow, I experimentally tested whether individual variation in throat patch size and wingbar area and conspicuousness predicts the predator-related risk taken by males and females, and found no support that predation constrains melanization in this species. Using the comparative approach I found that in a wide range of bird species, the extent of black plumage is related to the circulating levels of testosterone in both males and females, supporting that testosterone may regulate the link between melanization and competitiveness.

In sum, my research has provided both inter- and intraspecific evidence that melanin-based ornaments may function in sexual selection and status signalling, and may honestly signal competitive ability through a physiological link. Further studies are important to ascertain the costs of producing and maintaining melanin ornaments, with specific respect to the mechanisms of testosterone-regulation.

2. Introduction

2.1. Theory of honest signals

Signals are behavioural or structural traits that have evolved to alter the receivers' behaviour in a manner that is, on average, beneficial to the signaller individual in terms of increased fitness, i.e. enhanced reproductive success or survival (Maynard Smith & Harper 2003). For a signalling system to be evolutionary stable, the signal should reliably convey some information to the receiver about the signaller or the environment, otherwise it would not pay receivers to perceive and respond to the signal. This information need not be honest in all cases, e.g. as demonstrated by Batesian mimicry, in which an edible species deceivingly signals distastefulness to predators by mimicking the warning signals of a distasteful species. Yet, in order to be effective in eliciting the appropriate response, a signal must be honest most of the time. For example, mimicry systems are usually stable because the mimic is rare relative to the model, so that it pays predators to believe the signal of distastefulness. According to the theory of animal signalling, the reliability of signals can be maintained in three main ways (reviewed by Maynard Smith & Harper 2003).

First, certain signals cannot be faked because the rate of signalling is causally (e.g. genetically or physiologically) linked to the signalled information, i.e. to some aspect of the signaller's quality. These signals are termed indices of quality. A classic example is the pitch of roaring in red deer (*Cervus elaphus*) stags, which reliably signals the body size of males since the longer the vocal tract, the deeper the emitted sound (Fitch & Reby 2001).

Second, in some cases the signaller would not gain by lying because signaller and receiver have a strong common interest in the outcome of their interaction (e.g. to maintain cohesion within a pair or flock) or because cheater individuals are punished and/or remembered by groupmates (e.g. in social groups of primates). In such cases, minimal-cost signals may evolve that only require the costs of efficacy, that is, the expenditure and/or risk that must inevitably be taken by the signaller in order to transmit the signal. For example, many avian contact calls between mates or flockmates are very quiet and plain (Rogers & Kaplan 1998).

However, in many situations the signalling animals would benefit by deceiving the receiver: for example, a male of poor quality would improve its fitness by signalling superior quality to females if females choose mates on the basis of the males' signals. If there is no unfakeable link between the male's quality and its signal, and if no overriding common interest or social punishment prevents cheating, then all males should advertise themselves as perfect, and thus females should cease to select among males because, on average, their investment in mate choice would not be compensated by gaining a truly high-quality mate. The handicap principle (Zahavi 1975, Maynard Smith & Harper 2003) states that in such cases, a signal can be reliable if it is too costly for a low-quality

signaller. Thus, a handicap signal should, in addition to the costs of efficacy, entail some strategic costs that can only be afforded by high-quality signallers. Alternatively, if the signal is equally costly for all individuals, the one in greater need should gain more by signalling. That is, the ratio of the cost of the signal to the benefit gained by signalling should be lower for individuals giving stronger signals. Theoretical analyses of strategic costs support that there are contexts in which the reliability of signals can be ensured by costs, with differential pay-off to individuals signalling at different rates (Enquist 1985, Pomiankowski 1987, Grafen 1990a,b, Maynard Smith 1991).

Signalling often occurs when animals need to resolve conflicts over resources such as food or mating opportunities. Under these circumstances, signaller and receiver are likely to have conflicting interests, as the signaller would do best if he convinced the receivers that he is of superior quality, whereas the receiver would benefit most from learning the exact abilities of the signaller. Therefore, signals of competitive abilities such as sexual attractiveness or social dominance are, if not unfakeable indices of quality, expected to impose some strategic costs to the signallers. Costs may be any loss of fitness resulting from making a signal: for example, the signal may require resources such as nutrients to produce, or it may have costly consequences, such as increased risk of predation or retaliation by competitors. Such costs are of central importance to an understanding of sexual and social signalling.

2.2. Costs of sexual and social signals

For the exaggerated sexual signals such as the peacock's tail that appear to incur a survival cost and thus seemingly contradict the theory of natural selection, Darwin (1871) proposed the idea of sexual selection which became one of the most intensely studied ideas in the last few decades (Andersson 1994, Hill 2002). Sexual selection promotes the maintenance and spread of traits that increase mating success, either through intrasexual competition for mates or through intersexual mate choice. The benefits of increased mating success, however, should be counterbalanced by costs to the trait bearer, as predicted by both main theories of sexual selection by female choice.

First, the Fisherian „runaway process" or self-reinforcing theory (Fisher 1958, Kirkpatrick 1982) states that if females initially prefer males with a specific trait such as a colour patch, then more colourful males as well as females preferring them will have greater reproductive success, because more colourful males will have greater mating success and their females will have more grandchildren since their sons will be attractive too. This process could lead to a continuing elaboration of both the preferred trait and the preference for it, unless further exaggeration of the male trait is hindered by costs that counter its benefits. Note that the preferred trait does not need to invoke any costs initially. The preference may arise, for instance, from some biased preference of the sensory system (i.e. sensory bias) to the given colour that may be adaptive in foraging context,

as has been shown for the yellow tail markings of some fish species (Macías Garcia & Ramirez 2005, Stuart-Fox 2005).

Second, the indicator mechanism theory (Zahavi 1975, Pomiankowski 1987, Grafen 1990a,b) claims that if males vary in some heritable quality that affects their fitness (survival or fecundity), then females choosing fitter males that sire fitter offspring will transfer their genes to more grandchildren. So it may pay females to base their choice of mate on traits that reliably indicate male quality: either because the trait is causally related to quality (i.e. it is an index) or because the trait is too costly for males of low quality to afford (i.e. it is a handicap). Note that the two models are conceptually similar (Kokko et al. 2003) in that they both require preferences for traits that signal male fitness, either in the sense of attractiveness (Fisherian process) or viability (indicator mechanism).

Social signals (Tanaka 1996) are used during disputes over resources other than mates, e.g. over food in wintering flocks of birds. Similarly to sexual signals, a reliable social signal may be either an index or a handicap of individual quality related to resource holding potential such as dominance or fighting ability or aggressiveness. For example, indices of body size are used widely in settling animal contests ranging from spiders vibrating the web of their opponents to tigers marking their territory boundaries by scratching trees as high as they can reach (Maynard Smith & Harper 2003).

There is, however, a third alternative by which contests may be settled. If the value of the disputed resource is low relative to the cost of escalated fight, and thus contestants have a common interest in avoiding serious fights, then the outcome of the contest may be resolved by cheap signals that are not related to fighting ability. These signals have been termed badges of status (Krebs & Dawkins 1984). Colour patches often signal social status in various taxa, with the best examples coming from birds such as the black plumage badges of great tits (*Parus major*) and siskin (*Carduelis spinus*) males (reviewed by Senar 2006). Theory suggests that the stability of such badges requires punishment of cheats, that is, it must be impossible for an individual to dishonestly signal high status but then retreat without costs if challenged by an individual of high status (Maynard Smith & Harper 1988). Thus, although badges of status may be cheap to produce, false signals of high rank should be costly due to the „social control" of cheats.

Up to now, the adaptive value of sexual and social signals has been demonstrated by a vast number of studies (Andersson 1994, Whiting et al. 2003, Hill 2006, Senar 2006). In contrast, the mechanisms maintaining the reliability of these signals remained speculative in most cases, and direct empirical evidence for strategic costs or punishment of cheats is still very scarce (reviewed by Kotiaho 2001).

2.3. Plumage colours as signals

The study of animal coloration, and plumage colours in particular, has played and continues to play a central role in the refinement of our understanding of how evolution works (reviewed by Hill 2002). Although plenty of hypotheses have been developed to explain the evolution of the compelling diversity of animal colour patterns (Savalli 1995), researchers increasingly focused on gaudy ornamental colours and their possible roles in sexual selection and status signalling. Birds are ideal for such studies because a great deal of detailed information has been treasured up on their life history, behavioural ecology and colour diversity. Indeed, a great many empirical studies have corroborated the relationship between various colour traits and the bearer's success in sexual and/or social competition (reviews by Andersson 1994, Senar 1999, Hill & McGraw 2006b). However, the costs ensuring that these colours convey some reliable information about their bearer to potential mates or opponents received much less attention, leaving unclear why females of a certain species should choose more colourful males or why contestants should surrender to opponents with a larger badge. Our understanding of the topic is beginning to accelerate lately as students of animal coloration realized that colours are derived in several different ways that may raise various costs.

Plumage colours are of either structural or pigmentary origin. Structural colours arise by the physical, optical interaction of light waves with the nanometer-scale structure of feathers: mainly by coherent scattering that reinforces specific wavelengths of light, as in the blue plumage of eastern bluebird (*Sialia sialis*) males (Prum 2006). Pigments are biomolecules that incorporate into the growing feathers and create colours by differential absorption and reflection of light, with different pigments having different reflectance spectra (Hill & McGraw 2006a). Most avian pigments belong to either of two main types of pigments: melanins and carotenoids. Melanins are widespread in the animal kingdom from sponges to human skin and hair, producing mainly black, brown or rusty colours such as those in the plumage of zebra finch (*Taeniopygia guttata*) males (McGraw 2006a). Carotenoids are also common sources of integumentary coloration, though in plumage they are restricted to contour feathers, occurring in many bird species with bright yellow, orange or red colours, e.g. in *Carduelis* finches (McGraw 2006b). A major difference between the two pigment types is that animals can synthesize melanins but not carotenoids from basic biological precursors such as amino acids, hence carotenoids must be obtained directly through diet (McGraw 2006a,b).

The facts that melanins are the most prevalent pigments in birds and they can be synthesized seem to argue against their costliness. Besides, melanins often produce colours such as browns that are considered inconspicuous by humans. These facts had led to the assumption that melanin-based coloration is a less promising candidate for sexual signalling than the bright colours based on carotenoids. Consequently, carotenoid-based coloration became the main line of research of colour signals in the last decade of the twentieth century. This research generated a convincing series of

evidence that certain carotenoid ornaments reliably reflect aspects of individual quality such as nutritional or health state due to the costs of carotenoid acquisition and utilization (reviewed by McGraw 2006b). The most thoroughly studied example is the house finch (*Carpodacus mexicanus*) in which females prefer redder males, and plumage redness signals the males' condition at moult because it depends on food and carotenoid intake and is sensitive to endoparasitic infections (Hill 2002). In a few attempts to demonstrate the same costs for melanin-based coloration, however, researchers often failed to find support for the potential of melanin ornaments to signal such qualities honestly (Hill & Brawner 1998, McGraw & Hill 2000, McGraw et al. 2002, Senar et al. 2003, but see Fitze & Richner 2002). These results strengthened the view that melanin and carotenoid ornaments have distinct signalling roles, carotenoids being condition-dependent signals of quality while melanins serving as uncostly badges of status (McGraw & Hill 2000, Badyaev & Hill 2000).

Such generalization is, however, premature given the limited number and scope of studies conducted so far, as suggested also by a recent meta-analysis of melanin and carotenoid ornaments (Griffith et al. 2006). On theoretical grounds, the expression of melanin-based coloration may involve several costs and regulatory mechanisms (reviewed by Jawor & Breitwisch 2003, McGraw 2006a) that may render them honest signals of quality.

2.4. Reliability of melanin signals

Melanin pigments come in two main types: eumelanins which we perceive as black and dark brown, and pheomelanins which are usually light brown, rusty red or dull yellow. Both types of melanins are large biopolymers derived through a complex biochemical pathway called melanogenesis, which takes place in the melanocytes of the skin and hair or feather follicles (reviewed by Jawor & Breitwisch 2003, McGraw 2006a). This process may involve the products of about a hundred different gene loci (Urabe et al. 1993), which may lead to various costs and constraints.

First, melanogenesis demands appropriate precursors and co-factors (Jawor & Breitwisch 2003, McGraw 2006a). Both eu- and pheomelanins are synthesized from tyrosine which is an essential amino acid for birds, i.e. they can obtain it only through diet. Additionally, pheomelanin production requires cysteine which is synthesized from methionine, another essential amino acid. Furthermore, at least three enzymes of melanogenesis use metal co-factors, namely copper, zinc and iron. These trace minerals are typically rare and/or poorly bioavailable in most animal diets, yet they have several critical biological functions (McGraw 2003). If the amino acids and/or trace minerals essential for melanogenesis become limiting during moult, e.g. at low food levels, then a trade-off may occur between plumage melanization and other needs, e.g. the production of proteins such as feather keratin. Thereby melanin ornaments might reflect individual quality such as foraging skills,

only high-quality individuals being able to acquire enough resources for both physiological and ornamental functions.

Second, melanogenesis accumulates cytotoxic byproducts such as oxygen free radicals that are lethal to melanocytes (Jawor & Breitwisch 2003). The very minerals needed for melanogenic enzymes can also be toxic at high concentrations (McGraw 2003). These costs of intense melanin synthesis might only be afforded by individuals with high anti-oxidant and/or chemoprotective capacities, which may be a relevant quality to advertise to females since it may also affect sperm quality and thus fecundity (Blount et al. 2001). Interestingly, melanin pigments have the capacity both to scavenge free radicals (McGraw 2005) and to bind and „store away" toxic metal ions (McGraw 2003), thus they might be needed also for handling oxidative or toxic stress unrelated to their own production.

Third, melanogenesis is influenced by several hormones and regulatory agents (Jawor & Breitwisch 2003, McGraw 2006a) which are also required for other physiological functions. These include thyroxin that regulates metabolic rates, and sex hormones such as testosterone, estrogens and luteinizing hormone that govern sexual and parental behaviours. Some of these hormones may also have costly effects on metabolism or immunocompetence (Folstad & Karter 1992, Roberts et al. 2004). Melanocyte stimulating hormone (α-MSH) also affects both melanin synthesis (Jawor & Breitwisch 2003) and innate host defence (Catania et al. 2000, Haycock et al. 2000), although its role is largely unexplored in birds. These hormones might link the expression of melanin ornaments to individual qualities such as dominance, sexual competitiveness, parental abilities or parasite resistance. Note that, since the production of melanized plumage (moult) usually does not overlap with sexual activities and peak hormone levels (except for thyroxin; McGraw 2006a), a trade-off between the hormone molecules needed for melanization and those for other functions such as breeding behaviour is often unlikely. Rather, these hormones might ensure an unfakeable link between melanin synthesis and other traits regulated by them. In insects for example, melanin ornament expression and immune response to parasites are mechanistically linked because they are produced by the same enzyme cascade (Siva-Jothy 2000, Mackintosh 2001). Therefore such a link should be viewed as an index rather than a handicapping cost.

Furthermore, melanin ornaments may be costly due to not only their complex production but also their optical properties. Although melanins often form cryptic colour patterns such as the eclipse plumage of mallard (*Anas platyrhynchos*) males (Haase et al. 1995), certain melanin ornaments can provide strong contrast against many natural backgrounds and animal colours. For example, a jet-black area reflects very little light, thus it contrasts well with bright surfaces such as a neighbouring orange patch (Brooks 1996) or a light blue sky (Walsberg 1982). Such increased contrast within the signalling animal or with the environment may help the receiver to detect and

evaluate visual signals (Endler 1990, Brooks 1996). For example, female canaries (*Serinus canaria*) prefer males that contrast strongly against the background (Heindl & Winkler 2003), whereas in American goldfinches (*Carduelis tristis*) in which males have yellow ventral plumage, females prefer blue-ringed males over yellow-ringed males (Johnson et al. 1993). However, enhanced contrast may be costly if it increases conspicuousness not only to conspecifics but also to predators. The increased risk of predation is frequently mentioned as a possible maintenance cost of honest signals, assuming that only high-quality individuals are skilful enough in escaping predators to afford the risk of being conspicuous (Andersson 1994, Kotiaho 2001).

Finally, many bird species are ornamented not by the abundance but rather by the scarcity of melanin pigments, such as the light plumage patterns of *Phylloscopus* warblers (MacDougall-Shackleton et al. 2003) or the white forehead patch of collared flycatcher (*Ficedula albicollis*) males (Hegyi et al. 2002, 2006). Such colours are often termed unmelanized or depigmented ornaments and, given that they are found mostly on heavily melanized plumage areas, they are also included in the category of melanin-based ornaments (Török et al. 2003, Amundsen & Pärn 2006, Griffith & Pryke 2006; see also chapter 4.1). The use of these depigmented ornaments in sexual and social signalling appears to be widespread in birds, larger or brighter light patches reflecting better quality (Marchetti 1993, Pärt & Qvarnström 1997, Kose & Møller 1999, Michl et al. 2002, Török et al. 2003, Woodcock et al. 2005, Hanssen et al. 2006, Penteriani et al. 2006, Garamszegi et al. 2006). The reliability of these signals is most puzzling since they lack the aforementioned costs of pigment synthesis, and the structural mechanisms that produce white colour have been suggested to be rather condition-independent (Prum 2006). Therefore the costs of such depigmented ornaments are typically assumed to lie not in their production but instead in their maintenance: conspicuous light patches may increase the risk of predation (Götmark & Hohlfält 1995, but see Palleroni et al. 2005) or the aggressiveness of opponents (i.e. „social control"; Qvarnström 1997, Garamszegi et al. 2006). Also, depigmented feathers may be more susceptible to wear, breakage, chewing lice or bacterial degradation (reviewed by McGraw 2006a). By bearing the least pigmented ornaments, individuals might signal their ability to endure these costs.

Taken together, a handful of mechanisms have been hypothesized to ensure the reliability of melanin-based signals. Most of these mechanisms are poorly or not at all studied, and results so far are controversial (reviews by Griffith et al. 2006, McGraw 2006a). Clearly, the information content of melanin ornaments (including the so-called depigmented ones) stands in the need of detailed study both from ultimate and proximate perspectives. In their candid meta-analytical review of the *status quo* of melanins versus carotenoids, Griffith et al. (2006) called for an increase in the number and depth of case studies, and also for „wide-ranging comparative studies for teasing out general patterns and focusing future experimental work".

3. Thesis objectives

In this thesis I investigate the potential of melanin-based plumage ornaments to function in sexual and social signalling. I use three approaches: (i) I test the relationship between the interspecific variation in melanin-based coloration and sexual selection in comparative studies, (ii) I examine the role of melanin ornaments in sexual and social signalling in two avian model species, and (iii) I investigate two possible reliability-ensuring mechanisms of melanization at the intra- and interspecific level, respectively.

3.1. 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*, Appendix: Fig. 15.3) 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. In chapter 5 I investigate 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*, Appendix: Fig. 15.4) 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 (Hill 2002) that appeared to confirm the functional distinction between „sexy carotenoids" and „cheap melanins" (reviewed in Griffith et al. 2006). In chapter 6 I test whether black melanization in finches relates to components of reproductive effort that are expected to reflect the intensity of sexual selection (Badyaev 1997b).

3.2. Melanin ornaments in model species

I investigate 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*, Appendix: Fig. 15.5) 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 (Persson & Öhrström 1989). Males appear to use multiple signals in sexual advertisement, including complex songs (Menyhárt 2003) and the

building of elaborate nests (Szentirmai et al. 2005). In chapter 7 I examine whether the size of the black eye-stripe may influence the males' success in competing other males and attracting females.

The house sparrow (*Passer domesticus*, Appendix: Fig. 15.7) is highly gregarious, wintering in flocks and breeding colonially (Perrins 1998). The males' black throat patch has a well-established status-signalling function in aggressive interactions among competing flockmates (Liker & Barta 2001). Here I investigate the previously unexplored wingbar of male sparrows, which is a pheomelanin-based ornament. In chapter 8 I test whether the area or conspicuousness of the wingbar predicts the males' success in social competition.

3.3. Reliability of melanin ornaments

Among the various mechanisms proposed to maintain the honesty of melanin-based signals (see chapter 2.4), 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 (Endler 1990), hence they may significantly increase conspicuousness to predators. 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 (throat patch and wingbar). In chapter 9 I investigate whether individual variation in these ornaments is associated with the predator-related risk-taking behaviour of sparrows.

Secondly, many black ornaments predict dominance (Senar 2006); these were often assumed arbitrary badges of status that are under social control. However, as mentioned above, these ornaments may also signal competitiveness through the regulational effects of testosterone, the mediator of many aggressive behaviours (Wingfield et al. 1987). Although a number of studies showed that certain melanin ornaments might be indicative of testosterone levels, this relationship seems to vary with the species and the type of ornament studied (reviews by Jawor & Breitwisch 2003, McGraw 2006a). In chapter 10 I use the comparative approach to test whether interspecific differences in melanization are consistently related to differences in testosterone levels among bird species ranging from ratites to small passerines.

4. General methods

4.1. Defining melanization

Throughout this thesis I focus mainly on a specific type of melanin-based coloration, namely on black plumage ornaments. Black feathers and hair typically contain high concentrations of eumelanins and relatively less pheomelanins (Ito & Wakamatsu 2003, McGraw 2006a). No other pigments are known to produce black plumage, thereby one can confidently study melanin-based coloration using black ornaments without the need for exact identification of the pigments involved. In contrast, the pigment content of several non-black ornaments such as yellows and reds cannot be judged by their appearance because these can result from both melanins and carotenoids or even from other pigments (McGraw et al. 2004a). For example, several studies had assumed that the red throat patch of barn swallows (*Hirundo rustica*) is a carotenoid-based ornament unless a recent biochemical analysis showed that it contains only melanins (McGraw et al. 2004b). Since both eu- and pheomelanin pigments are difficult to isolate and measure (McGraw 2006a), and the pigment content of most avian ornaments is not yet known, I chose black coloration as the main focus of my research. As a measure of melanization I used the extension of black plumage (i.e. ornament size, Appendix: Fig. 15.1), which often shows great variability both within and among species (Appendix: Figs. 15.3–4,6–9) and predicts individual successfulness in various forms of sexual and social competition in several birds (Tarof et al. 2005, Senar 2006, Hill 2006).

Additionally, I also investigate the wingbar of house sparrows, which is a combined type of coloration. It is a depigmented area in a melanized plumage region (Selander & Johnston 1967), appearing mostly white in males and light brownish-yellow in females and some males (Appendix: Figs. 15.9–10). The white colour arises from the nanostructural properties of depigmented feathers (Prum 2006), while the yellowish hue is due to pheomelanins (Appendix: Figs. 15.11–12). Such combination of feather structure and pigments to produce colour displays has been suggested to be widespread in birds (Shawkey & Hill 2005), but we do not yet know to what extent these two components affect the brightness, hue and chroma of a given ornament. On the other hand, the size of an (un)melanized area depends on the number of feather follicles that synthesize melanins or, within a given feather, on the amount and pattern of melanin deposition into that feather (Roulin 2004). Therefore, throughout this thesis I include the house sparrow's wingbar when using the term „melanin-based ornaments" (as done for white patches on black plumage by many authors e.g. Török et al. 2003, Amundsen & Pärn 2006, Griffith & Pryke 2006), although I emphasize here that, at least for the white feather portions of males, it is also affected by structural properties. I also treat the wingbar as a „depigmented ornament" in the sense that less pigmented wingbars appear to be

more ornamental (see chapter 9). I measured both the area and brightness of the wingbars since both aspects are highly variable among sparrows (Appendix: Figs. 15.9–10).

It is important to note here that the visual system of birds is fundamentally different from that of humans, which may confound studies that rely on human judgement of coloration (Endler 1990, Bennett et al. 1994, Cuthill et al. 1999). Due to the presence of a fourth cone cell type in the avian retina that is receptive to short wavelengths of light, birds can see in the ultraviolet (UV) portion of the spectrum and, because of their tetrachromatic vision, they can perceive a greater diversity of hues than do humans (Bennett et al. 1994). Altogether, birds probably see colours in a way that humans cannot even imagine. However, these differences are less likely to affect the studies in the present thesis. First, black arises by strong absorbance of light throughout the entire spectrum, therefore it is achromatic (i.e. has no hue). Second, because of the wide absorbance of melanins, black plumage typically has little or no reflectance in the UV (McGraw 2006a; VB pers. obs.). Therefore, human vision may be sufficient in assessing the size of black ornaments (see page 854 in Bennett et al. 1994). Third, the wingbars of house sparrows also have no increased UV reflectance (Appendix: Fig. 15.11). Although the perception of achromatic brightness is fulfilled by different systems in birds (double cones) and humans (red and green cones), we still can assume that black appears „something very dark" and white as „very bright" to birds, similarly to humans (Bennett et al. 1994).

4.2. Comparative methods

Comparative studies investigate the variation occurring among different species to test evolutionary hypotheses, for example, on the correlated evolution between the species' phenotypic traits or between phenotypic and environmental variables. Raw species values cannot be treated as independent data points for such analyses because species share many characteristics through descent from common ancestors (Harvey & Page 1991). Thus, more closely related species tend to be more similar. This may arise from several constraints (Harvey & Pagel 1991): for example, new species may invade niches that are similar to that of their ancestors, or species with similar phenotypes may respond in similar ways to a given selective pressure. Alternatively, there may not be enough genetic variance for selection to act upon, or there may not have been enough time for new characters to evolve. In any case, the phylogenetic relationships among species should be taken into account in order to distinguish independent evolutionary origins of characters from similarity by descent and to avoid the overestimation of statistical degrees of freedom (Harvey & Pagel 1991).

Several methods have been developed to control for the effects of phylogeny (Harvey & Pagel 1991, Martins et al. 2002). Some of these are applicable to traits that vary on a continuous scale, such as the extension of melanized plumage in many avian taxa. The most widely used of these are

the independent comparisons methods (Harvey & Pagel 1991, Harvey & Nee 1997, Martins et al. 2002) that employ differences among species and/or higher nodes as independent data points. The rationale behind is that differences in a given trait between each pair of sister-taxa evolved independently of the differences between all other pairs of sister-taxa. In this thesis I use the following two types of independent comparisons methods (Appendix: Fig. 15.2).

The independent contrasts method (Felsenstein 1985, Purvis & Rambaut 1995) calculates standardized differences (i.e. contrasts) in each examined trait at each node in the phylogeny. The method estimates the trait values of ancestral nodes assuming a Brownian motion model of evolution for continuous traits, i.e. that increases and decreases in traits occur randomly at each unit of time and independently of the actual value of the trait. Independent contrasts are then calculated for both terminal and reconstructed nodes of the phylogeny, yielding a maximum number of n–1 contrasts for n species (Appendix: Fig. 15.2a). Contrasts in traits X and Y can then be used in parametric tests such as linear regressions. This method performs outstandingly when there are no or weak selection constraints but it gives unreliable results (increased type-1 error) if the traits' evolution deviates strongly from the Brownian motion process (Martins et al. 2002).

The matched-pair comparisons method (Harvey & Nee 1997) does not infer ancestral trait values, restricting comparisons to extant species. Thereby it makes no assumptions about the underlying evolutionary process. It only requires that taxon-pairs be chosen so that the separate evolutionary pathways of sister-taxa traced from a common ancestor should not be shared with other taxa being compared. Paired-samples tests can then be used to test whether sister-species differing in trait X also differ consistently in trait Y (Appendix: Fig. 15.2b). This method has reduced power compared to the independent contrasts method, as it enables only $n/2$ comparisons at best. However, matched-pair comparisons are unlikely to reject a correct null hypothesis due to low expected rates of type-1 error (Harvey & Nee 1997), hence this method exquisitely complements the independent contrasts method.

For each of the three comparative studies in this thesis, I collected all the data excepting testosterone levels, and I did all the phylogenetic and statistical analyses.

4.3. Model species

4.3.1. Penduline tit (Remiz pendulinus)

The penduline tit is a small Eurasian migratory passerine. Males have large black eye-stripes, white-grey crown, chestnut mantle, and pinkish-buff underparts with chestnut feather-centres that show much individual variation in extent (Perrins 1998). Females are similar to males but with less

contrasting colours, and their eye-stripes and chestnut feather-centres are restricted (Appendix: Figs. 15.5–6).

Penduline tits breed by lakes, rivers, swamps, or in moist woodlands (Perrins 1998). Males start building nests to attract females as they arrive to their breeding grounds in April. The nest is an elaborate construction woven by the male for several days (Perrins 1998; Appendix: Fig. 15.5). Parental care is provided by only one parent; either the male or the female deserts the clutch before incubation begins. Biparental desertion is uniquely frequent in penduline tits: about one-third of the clutches are deserted by both parents, indicating strong sexual conflict over parental care (Valera et al. 1997). Deserting parents may remate, so both sexes may have up to six mates over a single breeding season until August (Persson & Öhrström 1989, Szentirmai 2005). The factors influencing individual decisions of mate choice and parental care are largely unexplored in this unique reproductive system (but see Szentirmai 2005). Penduline tits may use multiple cues in sexual signalling, including the size of the nest built by the male (Szentirmai et al. 2005), aspects of the male's song (Menyhárt 2003), and various colour traits. Their plumage ornaments are probably melanin-based since no carotenoids have been detected in the chestnut feathers of males (T. Székely, unpublished data).

The International Penduline Tit Research Group (see *http://people.bath.ac.uk/revd20*) studies the breeding behaviour of penduline tits at Fehér-tó, south-eastern Hungary since 2002. Fehér-tó is an extensively used fishpond system that supports one of the largest penduline tit populations in Hungary. This population is investigated during each breeding season from April to August by locating the nests, capturing the birds on their territories or nests, and measuring and ringing them individually. Then the behaviour and reproductive success of the males or pairs at each nest is followed. I was involved in field work in August 2003, while the majority of field data were collected by many other researchers. In examining the role of the eye-stripe, I took an equal share in photograph measurements with S.A. Kingma, and participated heavily in statistical analyses and preparation of the manuscript.

4.3.2. House sparrow (Passer domesticus)

The house sparrow is a sedentary passerine that has spread worldwide by its successful commensalism with humans (Perrins 1998). Males are boldly patterned with black throat, grey crown, warm brown nape and chestnut mantle contrasting with smoky-white cheeks, white wingbars, and greyish underparts. Females are dull brown with pale supercilium and buff-white wingbars (Appendix: Fig. 15.7).

Throughout the year sparrows live in flocks that can be especially large in autumn and winter. During social activities such as feeding or roosting in flocks, birds competing for resources such as

food or roosting places frequently engage in aggressive interactions with threatening and fighting. Individuals within relatively small flocks usually form a linear or close to linear dominance hierarchy (Møller 1987a, Solberg and Ringsby 1997) in which males and females are equally likely to dominate their flockmates (Liker & Barta 2001). Males use the size of their black throat patch (i.e. bib) to signal their status in aggressive encounters (Møller 1987a, Veiga 1993), while the females' rank is best predicted by their body weight (Liker & Barta 2001).

Sparrows breed in loose colonies in monogamous pairs with some extra-pair matings and occasional polgyny (Griffith et al. 1999a). Males defend nest sites in natural or artificial holes (e.g. on buildings), and sexes share nest-building, incubation and feeding young (Perrins 1998). The males' bib size seems to influence the outcome of sexual competition for nest sites, female choice and reproductive success, although its effect varies among populations (Griffith et al. 1999a).

I studied the behaviour of house sparrows at two sites. To explore the role of the males' white wingbar in social signalling, I investigated sparrows kept in the aviaries of the Zoological Institute of Szent István University, Budapest, Hungary. During this study I participated in capturing and photographing birds, and I did all colour measurements and most statistical analyses. To test the predation costs of melanin ornaments, I observed a free-living population of house sparrows at the Veszprém Zoo, Veszprém, north-western Hungary. This population consists of several hundreds of sparrows, and is being followed continuously since 2004 by the Veszprém University Ornithological Group (see *http://sparrow.elte.hu*, *http://www.allatkertveszprem.hu/Verebek.htm* – the latter only in Hungarian). We capture the birds using mist nets and nest box traps, we measure and ring each bird individually, and we take blood samples for DNA analyses. During the non-breeding season (September–March) we monitor the composition and movement of flocks, while in the breeding season (April–August) we track the reproduction of the pairs nesting in nest boxes provided by us. We investigated the predation risk of the sparrows' ornaments in a field experiment carried out in the first winter months of 2005. I conducted this work in collaboration with other researchers and students, including bird captures, photographing, observations, and colour measurements, and I did all statistical analyses.

5. Melanin-based plumage coloration and flight displays in plovers and allies

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5.1. Introduction

Melanin-based coloration is a common type of plumage ornamentation in birds (Andersson 1994; Savalli 1995). The adaptive significance of interspecific variability in melanin-based plumage coloration, however, is less understood than that of other plumage traits (Jawor & Breitwisch 2003). For instance, sexual dimorphism both in carotenoid-based and structural coloration relates to sexual selection (Owens & Hartley 1998; Badyaev & Hill 2000), whereas the extent of white plumage was found to be associated with flocking behaviour (Brooke 1998; Beauchamp & Heeb 2001). However, previous studies of avian coloration concluded that sexual selection is unlikely to have a strong effect on melanin-based plumage dimorphism (Owens & Hartley 1998; Badyaev & Hill 2000), and no study to our knowledge has specifically addressed the evolution of melanin-based plumage colours.

Plovers and their allies (*Charadriida*, plovers henceforward) are ideal species to study melanin-based coloration, because they exhibit striking interspecific variability in the extent of their black plumage ranging from fully black to completely white. Plovers develop black patches typically on their head and breast when they moult into nuptial plumage during migration to the breeding grounds (del Hoyo et al. 1996). This suggests that the function of melanin-based coloration is related to breeding. The aim of our study was to test three major hypotheses to explain the interspecific variation in melanin-based coloration of plovers.

First, the sexual selection hypothesis predicts that melanin-based colours of males influence their ability to compete for females, or mate choice by females. For example, females prefer males with more extensive black in golden plover (*Pluvialis apricaria*) and dotterel (*Eudromias morinellus*; Edwards 1982, Owens et al. 1994). The sexual displays of males may be amplified by the breast bands (Graul 1973). For instance avocets and thick-knees display on the ground, whereas others such as many lapwings and oystercatchers perform aerial displays (Jehl & Murray 1986, Figuerola 1999, Székely et al. 2000). Since black plumage is particularly conspicuous against the sky (Walsberg 1982), we expect more extensive black plumage in males and greater melanin-based sexual dimorphism in species with display flights than in ground-displaying species.

Second, melanin-based colours may signal competitive ability of birds in territory defence. For example, male golden plovers appeared to use the amount of black on their underparts as a status

signal during competition for territories (Edwards 1982). The black head and breast markings of turnstones (*Arenaria interpres*) were involved in recognition of neighbours, facilitating territory defence against unfamiliar individuals (Whitfield 1986). Social interactions are more frequent at high breeding densities than at low densities (Hötker 2000), thus the territory defence hypothesis predicts that species nesting at high densities should be more melanized than species nesting at low densities.

Third, melanin-based coloration may have evolved by natural selection to camouflage the incubating parent. Plovers nest on the ground and the incubating parents are exposed to visually searching predators. The camouflage hypothesis makes two predictions. First, plovers that nest on dark substrate should be more extensively melanized than species nesting on light substrate. Second, plovers that nest in closed habitats should have more melanized plumage than species nesting in open habitats, since melanized plumage camouflages the incubating parent in closed habitats by providing lower contrast with the environment (Bennett & Owens 2002).

Here we use phylogenetic comparative methods to test the predictions of these three hypotheses. We focus on melanin-based plumage on the head and breast of plovers, because in most species the black plumage is concentrated on the frontal part of the body. The sexual selection hypothesis predicts changes in male melanization across species and differences between male and female melanization (i.e. melanin dichromatism), thus we use both of these response variables. In tests of both territory defence and camouflage hypotheses we use male and female melanization as response variables, since both sexes defend territories and incubate the clutch in vast majority of plovers (Liker & Székely 1997, Reynolds & Székely 1997).

5.2. Methods

5.2.1. Measuring melanization

We measured the extent of melanization in the breeding plumage of plovers using colour plates of three reference books (Hayman et al. 1986, Marchant & Higgins 1993, del Hoyo et al. 1996). We digitised illustrations that showed the birds in lateral view (Appendix: Fig. 15.3). Then we measured the size of black plumage patches on the frontal body region (i.e. head, neck and breast as bordered by the lower edge of the wing and a vertical line drawn from the base of the leg; Appendix: Fig. 15.1) using Scion Image software (Scion Corporation 2000). We restricted our measurements to the head and breast of plovers, since these areas appeared to be highly variable in melanization across species. Although melanin pigments produce a range of colours, we specifically measured black which is produced by eumelanins (Jawor & Breitwisch 2003). If several black patches were found, we calculated the sum of the area of these patches. Melanization was expressed

as the proportion of black area relative to the total area of the frontal body (Appendix: Table 15.1). For sexually monomorphic species, i.e. which the plumage was not illustrated separately for males and females, both sexes were given the same proportion of melanization. Non-iridescent black plumage usually does not reflect ultraviolet light (Bennett et al. 1994). To test the latter assumption we measured the reflectance of black breast badges of Kentish plover (*Charadrius alexandrinus*), and found that these badges did not reflect ultraviolet light (T. Székely & I.C. Cuthill, unpubl. data).

We tested the reliability of our measurements in several ways. First, we estimated the repeatability (Lessells & Boag 1987) by measuring melanization in 15 randomly selected species twice by one observer, and once by another observer. Repeatability was high both within an observer ($r = 0.99$, $F_{14,15} = 15553$, $p < 0.001$), and between the observers ($r = 0.97$, $F_{14,15} = 32.14$, $p < 0.001$). Second, melanization was measured twice for another 15 species using two different books, one figure each from Hayman et al. (1986) and del Hoyo et al. (1996). These two measures were highly correlated (Pearson correlation, $r = 0.89$, $n = 15$ species, $p < 0.001$). Third, we photographed taxidermy mounted specimens of 11 species, and estimated the melanization on these photos. These measures were highly correlated with the measurements we took from colour plates ($r = 0.94$, $n = 11$ species, $p < 0.001$) suggesting that book illustrations represent consistently and accurately the amount of melanized plumage. Fourth, we compared our measurements taken from lateral view to estimates of frontal view. We measured melanization from frontal view using pictures from Hayman et al. (1986) for those species for which the illustrations were available from both perspectives. The measurements were highly correlated between lateral and frontal views ($r = 0.95$, $n = 9$ species, $p < 0.001$). Finally, we measured the melanization from both lateral and frontal view using photographs of taxidermy mounted birds, and these measurements were also highly correlated ($r = 0.83$, $n = 11$ species, $p = 0.002$).

Sexual dimorphism in melanization (dichromatism henceforward) was calculated as log (male melanization + 1) – log (female melanization + 1).

5.2.2. Display behaviour, breeding density and nest site

We collected data on male sexual displays, breeding density, substrate colour and vegetation cover of nest sites using published sources (e.g. Hayman et al. 1986, Marchant & Higgins 1993, del Hoyo et al. 1996, Perrins 1998, Székely et al. 2000, Appendix: Table 15.1). Male sexual displays were scored by Székely et al. (2000) as (1) ground display, (2) non-acrobatic aerial display and (3) acrobatic aerial display. We followed this scoring for an additional set of species. The dotterel was excluded from the analyses of display behaviour because the displays are performed by females. We did not investigate the potential influence of mating system, since nearly all *Charadriida* are socially monogamous (see Székely et al. 2000).

Breeding density was scored as (1) solitary, (2) solitary or in small, loose colonies (often described as semicolonial), (3) typically loose colonies, (4) large, loose or dense colonies, and (5) typically large and dense colonies. We tested the reliability of the breeding density scores for a subset of species by comparing these scores with mean breeding densities (nests/ha; data from Perrins 1998). These two measures of density were strongly correlated (Spearman rank-correlation, $r_s = 0.84$, n = 15 species, $p < 0.001$).

We extracted verbal descriptions of nest sites from literature, and then these descriptions were randomised and scored blindly by three observers. Substrate colour of the nest site was scored as (1) uniform light substrate such as sand; (2) mainly light surface with some dark patches such as dry mud; (3) approximately equal proportion of light and dark patches, for instance shingle; (4) mainly dark surface with some light patches, for instance tundra; and (5) uniform dark substrate e.g. dark rocks. Vegetation cover of the nest site was scored as (1) bare ground, (2) very short and scarce vegetation, (3) short grass cover, (4) continuous grass cover with shrubs and some denser vegetation, and (5) covered nest sites such as forests and cavities. Both substrate colour ($r = 0.71$, $F_{83,168} = 3.32$, $p < 0.001$) and vegetation cover ($r = 0.89$, $F_{82,166} = 6.51$, $p < 0.001$) were highly repeatable between the observers. We used the modal values of the three scores in the analyses (Appendix: Table 15.1).

5.2.3. Phylogenetic analyses

We used a supertree of shorebirds in phylogenetic comparative analyses (Thomas et al. 2004). This supertree included 101 species of plovers (parvorder *Charadriida* excluding *Laroidea*; Monroe & Sibley 1993). Sample sizes were different between statistical analyses, since behavioural and ecological data were not available for some species.

We controlled for the phylogenetic relationships among species in two ways. First, we calculated phylogenetically independent contrasts (Felsenstein 1985) as implemented by the CAIC 2.6 program (Purvis & Rambaut 1995). Melanization was log (x + 1) transformed and male display, breeding density, substrate colour and vegetation cover were log (x) transformed before the calculation of phylogenetically independent contrasts. Unit branch lengths were used, since most branch lengths were not known. Melanin dichromatism was computed as contrasts in male melanization – contrasts in female melanization. We tested the relationships between the contrasts in melanization (or dichromatism, dependent variable) and the contrasts in male display, breeding density, substrate colour and vegetation cover (independent variables) by least square linear regressions forced through the origin (Harvey & Pagel 1991; Garland et al. 1992). Felsenstein's method assumes that the absolute values of the contrasts are independent of their standard deviations (Garland et al. 1992). This assumption was met by all variables. Another assumption of

the method is that the evolution of continuous characters follows Brownian motion, thus the absolute values of the contrasts should be independent of the estimated nodal values for each trait. Although this assumption was not hold in some analyses of melanization, Diaz-Uriarte and Garland (1996) concluded that independent contrasts are robust to violations of this assumption.

Second, we conducted matched-pair comparisons between closely related taxon-pairs using Wilcoxon matched-pairs signed-ranks tests (Harvey & Pagel 1991, Székely et al. 2000; for taxon-pairs see Appendix: Table 15.2). When several species were available for a taxon-pair, we calculated the mean of their melanization. The matched-pair method is restricted to the terminal nodes of the phylogeny, and thus it makes less stringent statistical assumptions than the independent contrasts method. Note that the results of our contrasts analyses are fully consistent with the results of matched-pair analyses. In addition, our conclusions remained unchanged when we used each species as an independent datum (results not shown).

Body size correlates with many life-history and ecological traits (Harvey & Pagel 1991, Reynolds & Székely 1997), thus it may confound the relationships between melanization, breeding behaviour and ecology. We tested the effect of body size on melanization using phylogenetically independent contrasts, and found that body size, as measured by wing length (data from Hayman et al. 1986) was not related to melanization either in males ($r = 0.09$, $F_{1,90} = 0.74$, $p = 0.391$) or in females ($r = 0.11$, $F_{1,92} = 1.20$, $p = 0.277$). Body mass and tarsus length were also unrelated to melanization (results not given). All statistical tests are two-tailed.

5.3. Results

5.3.1. Sexual selection

Melanization was more extensive in males (0.15 median; 0.04 – 0.39 lower and upper quartile, respectively) than in females (0.11; 0.01 – 0.36; Wilcoxon matched-pairs signed-ranks test, $z = -3.94$, $n = 101$ species, $p < 0.001$). Evolutionary increases in male melanization corresponded to changes toward aerial displays (Table 5.1; Fig. 5.1a). The relationship between male melanization and display behaviour remained statistically significant when we excluded species using acrobatic displays, and thus restricted the analysis to species exhibiting ground displays and non-acrobatic aerial displays (Table 5.1). However, the relationship was no longer significant when ground-displaying species were excluded (Table 5.1). The latter results suggest that the key difference in regards to melanization is between aerial versus ground-displaying species. These results were consistent with the results of matched-pair comparisons, since males were more melanized in aerial species than in ground-displaying taxa ($z = -2.40$, $n = 10$ taxon-pairs, $p = 0.017$; Fig. 5.2a).

Table 5.1. Melanization of males and melanin dichromatism in relation to male displays in plovers. Least square linear regressions of independent contrasts were forced through the origin.

	Male melanization			Melanin dichromatism		
Male display	r	F	p	r	F	p
all species[1]	0.48	13.11	0.001	0.33	5.28	0.027
acrobatic species excluded[2]	0.38	5.67	0.023	0.34	4.19	0.049
ground-displaying species excluded[3]	0.21	1.17	0.290	0.10	0.24	0.626

[1] df = 1, 43; [2] df = 1, 33; [3] df = 1, 25

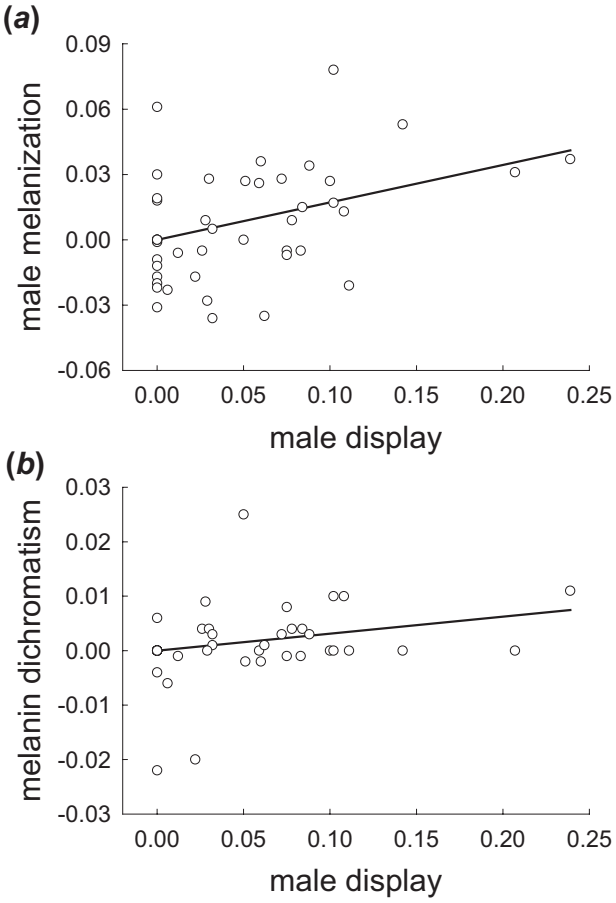

Figure 5.1. Relationships between phylogenetically independent contrasts in display behaviour of male plovers and **(a)** contrasts in male melanization, and **(b)** melanin dichromatism (contrasts in male melanization – contrasts in female melanization). Regression lines are forced through the origin.

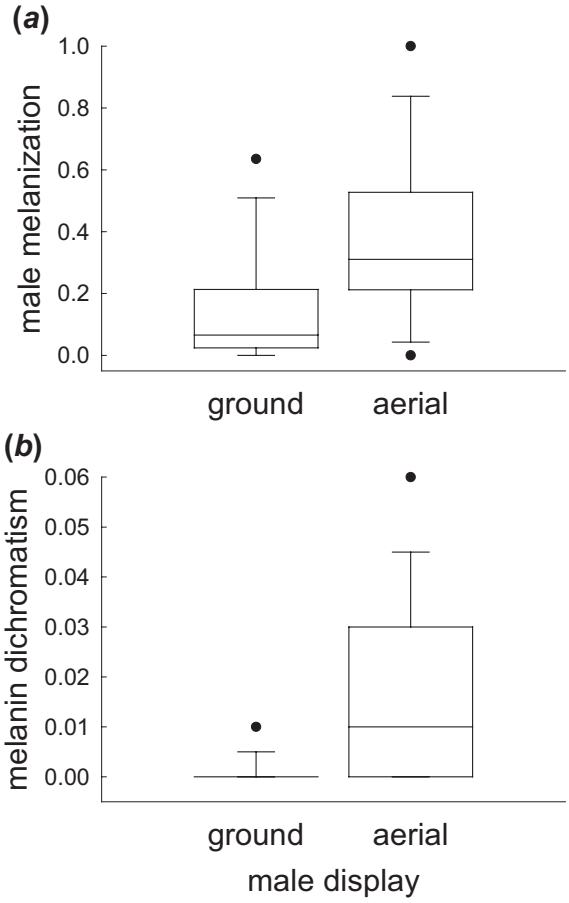

Figure 5.2. Matched-pairs comparisons of **(a)** male melanization, and **(b)** melanin dichromatism between ground-displaying and aerial displaying plovers. Box plots show the medians (horizontal bar), 25th and 75th percentiles (top and bottom of box, respectively), 10th and 90th percentiles (whiskers) and outliers (dots).

Analyses of melanin dichromatism provided similar results to that of male melanization, since evolutionary increases in melanin dichromatism were correlated with changes toward aerial displays (Table 5.1; Fig. 5.1b). The relationship between dichromatism and display behaviour also remained statistically significant when we excluded acrobatic species (Table 5.1), whereas it was no longer significant when ground-displaying species were excluded (Table 5.1). Consistently with these results, aerial displaying species were more dichromatic than ground-displaying ones in matched-pair analysis ($z = -1.99$, $n = 10$ taxon-pairs, $p = 0.046$; Fig. 5.2b).

5.3.2. Territorial defence

Breeding density was unrelated to the melanization of both sexes using phylogenetically independent contrasts (males: $r = 0.16$, $F_{1,71} = 1.88$, $p = 0.174$; females: $r = 0.18$, $F_{1,71} = 2.29$, $p = 0.135$). These results were consistent with the matched-pair analyses (males: $z = -0.32$, $n = 21$, $p = 0.748$; females: $z = -0.24$, $n = 21$, $p = 0.809$).

The territory defence hypothesis also predicts that melanin dichromatism should be greater in species with male-only nest defence than in species with biparental nest defence. We did not find support for this prediction either, since species with male-only defence (0 median; 0 – 0.04 lower and upper quartile, respectively) did not differ in melanin dichromatism from species with biparental defence (0; 0 – 0.02; Wilcoxon matched-pairs signed-ranks test, $z < 0.001$, $n = 6$ species-pairs, $p > 0.999$).

5.3.3. Camouflage

We did not find any evidence that melanization relates to the characteristics of the nest site. First, substrate colour was not associated with melanization using phylogenetically independent contrasts (males: $r = 0.01$, $F_{1,93} = 0.01$, $p = 0.944$; females: $r = 0.06$, $F_{1,93} = 0.30$, $p = 0.588$). Second, vegetation cover was unrelated to melanization using independent contrasts (males: $r = 0.05$, $F_{1,93} = 0.22$, $p = 0.641$; females: $r = 0.03$, $F_{1,93} = 0.10$, $p = 0.758$). These results were fully consistent with that of matched-pair comparisons, since melanization was not different between closely related taxa with different substrate colour (males: $z = -0.71$, $n = 34$, $p = 0.478$; females: $z = -1.02$, $n = 34$, $p = 0.309$) and vegetation cover (males: $z = -0.92$, $n = 34$, $p = 0.357$; females: $z = -0.77$, $n = 34$, $p = 0.443$).

The number of black patches on the head and breast may be a better indicator of crypsis than the total area of black. To test this proposition, we investigated whether the number of patches is related to the characteristics of the nest site using phylogenetically independent contrasts. These analyses

confirmed that the number of black patches was unrelated to substrate colour and vegetation cover both in males and females (results not shown).

5.3.4. Multivariate analyses

Finally we investigated the effects of sexual selection, territorial defence and camouflage using stepwise multiple regression analyses of phylogenetically independent contrasts (Table 5.2). The initial models included male display, breeding density, substrate colour and vegetation cover as explanatory variables. The final models confirmed that display behaviour of males explained a significant proportion of variation in both male melanization and melanin dichromatism (Table 5.2), whereas breeding density, substrate colour and vegetation cover all remained nonsignificant (Table 5.2).

Table 5.2. Multivariate analyses of melanization of males and melanin dichromatism in plovers. Stepwise multiple regressions of independent contrasts were forced through the origin.

	Male melanization[1]		Melanin dichromatism[2]	
	r	p	r	p
Final model:				
male display	0.41	0.009	0.36	0.024
Variables excluded from the final model:				
breeding density	–0.16	0.330	–0.07	0.695
substrate colour	–0.13	0.426	–0.06	0.717
vegetation cover	–0.16	0.338	0.03	0.866

[1] Final model $F_{1,37} = 7.51$; [2] final model $F_{1,37} = 5.55$

5.4. Discussion

Our analyses provided three key results. First, we found that interspecific differences in both male plumage melanization and melanin dichromatism were related to differences in display behaviour. Agility in male displays relates to mating success in shorebirds (Grønstøl 1996, Blomqvist et al. 1997), thus display behaviour appears to be a sexually selected trait. Second, the relationship between melanization and display was specifically due to differences between aerial and ground-displaying species. Third, we did not detect any relationship between proxies of territory defence or camouflage, and plumage melanization. To our knowledge, this is the first avian study that demonstrates a relationship between interspecific variation in melanin-based coloration in males, dichromatism and sexual selection as manifested by display behaviour.

Our results are consistent with the sexual selection hypothesis, and suggest that the frontal melanization of male plovers has evolved to enhance aerial displays. When plovers display in the air the sky provides a contrasting background that makes the displaying bird conspicuous (Walsberg 1982). Recently, the interspecific variation in light environments has been shown to influence plumage colour (Marchetti 1993, Endler & Théry 1996, McNaught & Owens 2002), suggesting that plumage coloration is often adapted to provide maximum contrast against the background of the displays. Species displaying in closed habitats tend to exhibit longer wavelength colours such as orange and red (McNaught & Owens 2002) or more numerous bright patches than species breeding in open habitats (Marchetti 1993). Thus, plovers with ground displays may benefit from exhibiting small black stripes and patches on their light frontal plumage (e.g. many *Charadrius* plovers), whilst extensive black plumage appears to be advantageous for species with display flights (e.g. *Pluvialis* plovers, oystercatchers). Note that in two aerial displaying species, golden plover and dotterel, melanization relates to mating success (Edwards 1982, Owens et al. 1994). An association between aerial displays and frontal melanization was also observed in bustards (*Otitidae*), although this relationship has not been corroborated by phylogenetic comparative analyses (Dale 1992). Thus it appears that the relationship between aerial displays and increased frontal melanization may not only occur in shorebirds.

Székely et al. (2000) showed that the extent and direction of sexual size dimorphism are related to the evolution of male displays in shorebirds, so that sexual selection favoured small males with acrobatic display flights. Here we demonstrate that, in a similar set of species and the same type of display behaviour, sexual selection acts differently on another trait, melanin-based coloration. Unlike in Székely et al.'s (2000) study on sexual size dimorphism, in our study the key difference was between aerial and ground-displaying taxa, and not between acrobatic and non-acrobatic species. Melanization increases the resistance of feathers to abrasion and increases the strength of feathers (Bonser 1995). Thus species that display in the air may gain a twofold benefit from melanized feathers. First, increased conspicuousness against the light background, and second, enhanced resistance to fracture that may be particularly important in aerial displays.

We did not find evidence for the territorial defence hypothesis that higher breeding density selects for more melanized plumage. Furthermore, sexual dimorphism in territory defence was not associated with increased melanin dichromatism. Thus selection for social signalling during territorial encounters does not seem to explain the interspecific variation in melanin-based coloration among plovers. This result is unexpected given that melanin-based ornaments appear to function as social signals of aggression and/or hormonal status in several birds (Jawor & Breitwisch 2003). Although there may be selection for black badges of status or individual markings in shorebirds (Edwards 1982, Whitfield 1986), this may not necessarily result in increased

melanization at high breeding densities. In short distance territorial signalling, conspicuousness may be less important than the individual variability of the signals, which could be maintained by small markings as well as by larger ones.

The predictions of the camouflage hypothesis were not supported by our analyses: neither substrate colour, nor vegetation cover was associated with plumage melanization. However, we did not investigate the plumage patterns of the back and wings that may also be important in camouflaging the incubating birds. The effect of substrate pattern was studied in *Charadrius* and closely related plovers by Graul (1973), who conjectured that black breast bands function as disruptive coloration in species nesting on discontinuous substrates such as dark and light substrate patches. Graul's hypothesis has remained to be tested, although we note that Graul's scores for discontinuous substrate correlate with our substrate colour scores (Spearman rank-correlation, $r_s = -0.51$, $n = 29$ species, $p = 0.005$), and the number of black plumage patches was unrelated to substrate colour in our analyses. There are three important distinctions between Graul's seminal study and our one. Graul was specifically concerned about breast bands, whereas we used the proportion of melanized plumage. Second, Graul scored species according to substrate discontinuity whereas our scores refer to substrate colour. Finally, Graul's study did not control for phylogenetic relationships.

Bearing these caveats in mind, we note that our results are based on a larger set of species and a larger range of melanization than Graul's one. Thus we suggest that even if breast bands may serve disruptive functions in some *Charadrius* plovers, melanin-based coloration is unlikely to be strongly selected for camouflage in *Charadriida*. The relatively open habitats occupied by plovers allow early detection of predators, thus plovers may rather escape from their nest early than stay and rely on crypsis. However, further tests of Graul's hypothesis are still warranted by looking at the number and width of breast bands.

Taken together, we found that the extent of plumage melanization is related to display behaviour in plovers. We suggest that melanized plumage enhances sexual signals under specific ambient light conditions. We found no evidence that selection for territorial defence and cryptic plumage of incubating parents influence the melanin-based coloration in plovers and allies.

6. Melanin-based black plumage coloration is related to reproductive investment in cardueline finches

Veronika Bókony & András Liker – Condor 2005, 107: 775–787.

6.1. Introduction

Recent studies of avian plumage coloration have suggested that the main types of colour ornaments (carotenoid-based, melanin-based, and structural coloration) have distinct signal contents and may evolve in response to different selection pressures (Gray 1996, Owens & Hartley 1998, Badyaev & Hill 2000). For example, several experimental studies have demonstrated the differing functions of carotenoid and melanin ornaments. Carotenoid ornaments are often involved in female choice but not in signaling social status among competing conspecifics (Johnson et al. 1993, Hill 2002), whereas melanin ornamentation usually predicts dominance rank (reviewed by Senar 1999); however, evidence on females preferring more melanized males is equivocal (Møller 1988, Johnson et al. 1993, Senar et al. 2005, Tarof et al. 2005). In addition, careful experiments have shown that the expression of carotenoid but not melanin ornaments was influenced by nutritional condition (Hill 2002, McGraw et al. 2002) and endoparasite load (Hill & Brawner 1998, Brawner et al. 2000, McGraw & Hill 2000), whereas melanin but not carotenoid coloration was affected by ectoparasite infection (Fitze & Richner 2002).

Although these findings suggest that different colour signals should be analyzed separately when studying selective forces influencing interspecific colour variation, most comparative studies have made no such distinction between specific types of coloration (reviewed by Badyaev & Hill 2000). For example, in cardueline finches overall plumage brightness, which encompasses all types of coloration, covaried with ecological factors, as predicted by sexual selection theory, varying with the altitude of breeding (Badyaev 1997a) and nest height (Martin & Badyaev 1996). Furthermore, Badyaev (1997b) demonstrated that plumage brightness and dichromatism were linked to components of fecundity and duration of parental care. The latter result indicated that common mechanisms such as nest predation or adult mortality rates may affect variation in both sexual ornamentation and fecundity, and thus may mediate the relationships between investment in sexually-selected traits and reproductive efforts (Badyaev 1997b).

In one of the first studies that focused on specific types of pigmentation, Gray (1996) showed that overall dichromatism in North American passerines was related to carotenoid-based coloration of males and was unrelated to their melanin-based and structural coloration. Similarly, Badyaev and Hill (2000) demonstrated in cardueline finches that much of the interspecific variation in overall

dichromatism was explained by variation in carotenoid dichromatism, and they found no relationship between overall dichromatism and melanin dichromatism. Thus, Badyaev and Hill (2000) concluded that the relationships between overall plumage coloration and life-history traits in finches may be due to carotenoid rather than melanin ornaments. For other bird species, however, the evolution of melanin-based coloration has been related to parental care (Owens & Hartley 1998) and sexual selection (Bókony et al. 2003).

Our aim here was to expand previous comparative work in cardueline finches by investigating a specific component of plumage ornamentation, melanin-based black coloration. Determining factors that may affect interspecific variation in melanization is particularly important because recent advances in understanding the proximate basis of melanin-based coloration suggest that melanin ornaments may be costly to produce and can reflect individual condition (Jawor & Breitwisch 2003, McGraw 2003). Furthermore, an increasing number of case studies demonstrate that certain melanin ornaments may signal mate quality and predict mating success (Roulin 1999, Roulin et al. 2000, 2001, Parker et al. 2003, Tarof et al. 2005; for nonblack melanization see Siefferman & Hill 2003). This raises the possibility that the evolution of melanin ornaments may be related to variation in life-history traits, as shown for other sexually-selected traits (e.g. plumage brightness). For example, due to a trade-off between sexual and parental investment, in species where males increase their investment in sexual competition they may provide reduced parental care (Verner & Willson 1969, Trivers 1972, Badyaev 1997b). Thus, we hypothesized that if melanin ornaments are used in either form of sexual competition, such trade-offs may lead to a negative association between plumage melanization and reproductive investment (fecundity or parental care). Under this scenario, we predicted that (i) in species with more melanized males, females may lay smaller or fewer clutches or the incubation and nestling period may be prolonged because of decreased male parental care, (ii) in species with more melanized females, both fecundity and duration of care may be reduced because of females' increased investment in sexual competition, and (iii) the more competitive sex will dictate the relationship between melanin dichromatism and reproductive effort; in finches this would probably be the males.

In this study, we first assessed the extent of interspecific variation in melanin-based black coloration and its dichromatism in cardueline finches. We then tested whether melanization is associated with variation in fecundity (i.e. clutch size and number of broods per year) and parental care (i.e. length of incubation and nestling periods) in the same manner as overall plumage brightness in finches (Badyaev 1997b). Although simultaneous investigation of several types of coloration (e.g. both melanin and carotenoid ornaments) would be the most powerful way to clarify their differences with respect to certain evolutionary processes, here we considered only melanin-based coloration because our method for quantifying melanization (Bókony et al. 2003) does not

take into account hue and saturation (Hill 1998, McGraw et al. 2004a). Lastly, we controlled for the possible confounding effects of ecological variables (nest height, breeding altitude, and body size) that are related to coloration and reproductive investment in cardueline finches (Martin & Badyaev 1996, Badyaev 1997a,b,c).

6.2. Methods

6.2.1. Measuring melanization

We measured the extent of melanization in the breeding plumage of male and female finches (n = 125 species) using colour plates of Clement et al. (1993). We digitised illustrations that showed the birds in lateral view (Appendix: Fig. 15.4); in a few cases when no such image was available in Clement et al. (1993), colour plates from Perrins (1998) were used. Using Scion Image software (Scion Corporation 2000), we then measured the area of black plumage patches on the head and breast, as bordered by the lower edge of the nape and the edge of the wing and a vertical line drawn from the base of the leg (frontal body region; Bókony et al. 2003, see Appendix: Fig. 15.1). We restricted our measurements to the head and breast of finches because these areas are highly variable in melanization across species and are likely to be involved in sexual signalling (McNaught & Owens 2002, Bókony et al. 2003). If a species possessed several black patches within the frontal body region, we calculated the sum of the area of all patches. Melanization was expressed as the proportion of black area relative to the total area of the frontal body (Appendix: Table 15.3); both areas were measured in pixels. Note that melanization values are proportions and thus have no unit of measurement. For sexually monomorphic species (i.e. those in which plumage was not illustrated separately for males and females), both sexes were given the same proportion of melanization. Although melanin pigments produce a range of colors (Jawor & Breitwisch 2003), we specifically measured black, which is produced by eumelanins (McGraw & Wakamatsu 2004) and usually does not reflect ultraviolet light (Bennett et al. 1994). See Bókony et al. (2003) for repeatabilities and justification of the method of measuring black plumage ornaments from lateral view on digitised illustrations.

6.2.2. Data on life history and ecology

We collected data on clutch size (average number of eggs per clutch), number of broods per season, and lengths of incubation and nestling periods (in days) using published sources (Badyaev 1997b,c, Perrins 1998, Geffen & Yom-Tov 2000; Appendix: Table 15.3). We also gathered published data on typical nest height relative to ground level (i.e. ground, shrub, or canopy) and altitude of breeding (i.e. average of lowest and highest elevation of breeding range), since these factors were

shown to influence interspecific variation in plumage coloration among finches (Martin & Badyaev 1996, Badyaev 1997a). Because body size correlates with many life-history traits and thus may confound their relationships with coloration (Harvey & Pagel 1991), we collected data from Badyaev (1997a) on tarsus length as a skeletal measure of body size.

6.2.3. Phylogenetic analyses

To control for phylogenetic relationships among species, we used a composite phylogeny of finches that summarizes all recent systematic information available for extant carduelines. This consensus tree is well supported by molecular studies of both basal nodes and within-clade relationships (Badyaev et al. 2002). Since most branch lengths were not known, we set branch lengths to unity. This phylogenetic hypothesis has been used extensively in previous comparative work on cardueline finches (Badyaev 1997a,b,c, Badyaev & Ghalambor 1998, Tobias & Hill 1998, Badyaev & Hill 2000).

We calculated phylogenetically independent contrasts (Felsenstein 1985) as implemented by the CAIC 2.6 program (Purvis & Rambaut 1995). Male and female melanization were arcsine transformed and all other variables were log-transformed before the calculation of independent contrasts. Melanin dichromatism (i.e. the difference in the extent of melanization between sexes) was computed as contrasts in male melanization – contrasts in female melanization (Bókony et al. 2003). We tested the relationships between contrasts in melanization (or dichromatism; dependent variables) and contrasts in clutch size, number of broods per season, and length of incubation and nestling period (predictor variables) by least square linear regressions forced through the origin (Harvey & Pagel 1991, Garland et al. 1992). Although the assumptions of the independent contrast method (Purvis & Rambaut 1995) were not met in some of our analyses, the method is robust to violations of these assumptions (Diaz-Uriarte & Garland 1996, 1998, Martins et al. 2002). Simulation tests showed that the independent contrasts method performs very well when there are no, or weak, constraints on the traits' evolution, and yields biased results only when evolutionary constraints are strong (Martins et al. 2002). In the latter case, however, analyses using raw data without phylogenetic control give reasonable results (Martins et al. 2002). Our results remained qualitatively unchanged when we treated each species as an independent datum (results not shown), so this consistency between the analyses suggests that our results are robust.

We used the information-theoretic approach as described by Burnham and Anderson (2002), based on the second-order Akaike's information criterion corrected for small sample size (AIC_c) to investigate the relative importance of life-history variables and to control for the potential confounding effects of nest height, breeding altitude, and body size. Since the very components of reproductive investment related to melanization were unclear *a priori*, an exploratory approach was

taken and all possible subsets of the seven predictor variables were modelled and considered in the analysis (Gibson et al. 2004), excepting models that only contained confounding variables (i.e., nest height, breeding altitude, and tarsus length). As no single model was clearly superior compared with the others in the model set, we performed model averaging (Burnham & Anderson 2002), where model coefficients were weighted using Akaike weights and inference was based on the entire set of candidate models. We then compared the final sets of predictor variables selected by stepwise regression and AIC_c-based model averaging.

We used the R statistical computing environment (Ihaka & Gentleman 1996, R Development Core Team 2003) and SPSS 11.0 for statistical analyses. Sample sizes are different across statistical analyses, since life history and ecological data were not available for some species. Values of melanization and dichromatism are reported as means ± SE. All statistical tests are two-tailed with a 95% confidence level.

6.3. Results

Melanization of the frontal body (proportion of the black area compared to the whole region) ranged from 0 to 0.97 in males and from 0 to 0.99 in females. Males were more extensively melanized (0.13 ± 0.02) than females (0.04 ± 0.01; paired t-test, $t_{124} = 5.88$, $p < 0.001$), although evolutionary changes in melanization of the sexes was positively correlated (linear regression of independent contrasts through origin; $r = 0.28$, $F_{1,72} = 6.24$, $p = 0.02$). The mean difference between male and female melanization (raw data) was 0.09 ± 0.02, ranging from –0.03 (more extensive female melanization) to 0.82 (more extensive male melanization).

Univariate regression analyses of independent contrasts showed that evolutionary increases in male melanization corresponded to reductions in clutch size (Fig. 6.1a), whereas they were unrelated to the number of broods, incubation length, or nestling period (Table 6.1). In females, evolutionary increases in melanization correlated with decreases in incubation length (Fig. 6.1b), but were not related to other life-history traits (Table 6.1). Increases in melanin dichromatism were strongly correlated with decreases in clutch size (Fig. 6.1c) and increases in nestling stage length (Table 6.1).

Model selection based on the information-theoretic approach confirmed the above results. For each dependent variable (male and female melanization, and melanin dichromatism) we built 120 regression models and ranked them according to their AIC_c values. Table 6.2 shows the maximized log-likelihood values (log[L]), number of estimated parameters (k), differences between the model with the lowest AIC_c value and each candidate model (ΔAIC_c), and relative Akaike weights (ω_i) for models with $\Delta AIC_c < 4.0$ for each dependent variable. Models with ΔAIC_c values ≤ 2 have substantial support (Burnham & Anderson 2002), while ΔAIC_c values of 4–7 show considerably

less support. For both male melanization and melanin dichromatism, the model with the lowest AIC_c included clutch size only, and of the top models 9 of 12 and 14 of 20 contained clutch size as a predictor, respectively. For female melanization, the best model included brood number and incubation length, but the second best included only incubation length, and all 16 top models contained incubation length as a predictor, while only 8 contained brood number.

Because ω_i were similar across candidate models, suggesting substantial model selection uncertainty, we evaluated the relative importance of predictor variables using model averaging (Table 6.3). These results were consistent with the results of stepwise regressions: both male melanization and melanin dichromatism were most strongly related to clutch size, males being more melanized in species with smaller clutches. Female melanization related most strongly to incubation length, females being more melanized in species with shorter incubation periods. The remaining predictor variables explained much less interspecific variation in melanization.

Table 6.1. Melanization of males and females, and melanin dichromatism in relation to life-history traits in cardueline finches. Least square linear regressions of independent contrasts were forced through the origin. Melanin dichromatism was computed as contrasts in male melanization – contrasts in female melanization.

Dependent	Predictor	r	F (df)	b ± SE	p
Male melanization	Clutch size	–0.46	14.85 (55)	–1.32 ± 0.34	<0.001
	Number of broods	–0.24	1.96 (32)	–0.52 ± 0.37	0.171
	Incubation length	–0.15	0.90 (38)	–1.64 ± 1.73	0.349
	Nestling period length	0.25	3.29 (49)	1.09 ± 0.60	0.076
Female melanization	Clutch size	–0.03	0.05 (55)	–0.05 ± 0.20	0.816
	Number of broods	–0.06	0.13 (32)	–0.07 ± 0.20	0.720
	Incubation length	–0.57	18.52 (38)	–3.27 ± 0.76	<0.001
	Nestling period length	–0.22	2.44 (49)	–0.46 ± 0.30	0.125
Melanin dichromatism	Clutch size	–0.49	16.90 (55)	–1.27 ± 0.31	<0.001
	Number of broods	–0.23	1.75 (32)	–0.45 ± 0.34	0.195
	Incubation length	0.17	1.13 (38)	1.64 ± 1.54	0.295
	Nestling period length	0.39	8.78 (49)	1.55 ± 0.52	0.005

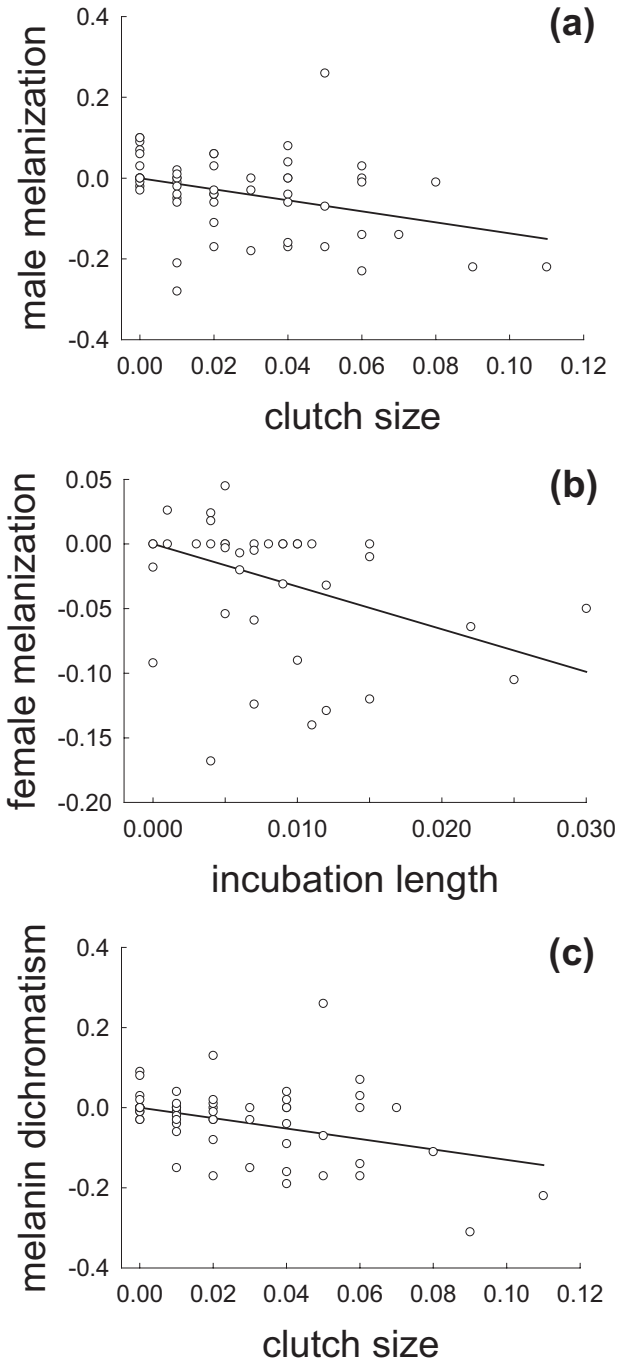

Figure 6.1. Relationship between phylogenetically independent contrasts in **(a)** clutch size and male melanization, **(b)** incubation length and female melanization, and **(c)** clutch size and melanin dichromatism in cardueline finches. Melanization was measured as the proportion of black area to the whole frontal body region; melanin dichromatism was computed as contrasts in male melanization – contrasts in female melanization. On each axis, positive values indicate increases in the given trait between sister taxa, while negative values correspond to decreases. Regression lines are forced through the origin (see Table 6.1 for statistics).

Table 6.2. Results of AIC_c-based model selection: maximized log-likelihood function (log[L]), number of estimated parameters (k), AIC_c differences (ΔAIC_c), and Akaike weights (ω_i) for models with $\Delta AIC_c < 4.0$ for male and female melanization and melanin dichromatism. Predictor variables are clutch size (C), number of broods per season (B), length of incubation (I), length of nestling period (N), nest height (H), breeding altitude (A), and tarsus length (T).

Dependent	Predictors	log[L]	k	ΔAIC_c [1]	ω_i
Male melanization	C	87.22	2	0	0.20
	C, A	89.66	3	1.37	0.10
	C, I	88.48	3	1.96	0.07
	C, B	88.34	3	2.03	0.07
	C, H	87.92	3	2.24	0.06
	C, T	87.90	3	2.25	0.06
	C, N	87.38	3	2.51	0.06
	N	80.74	2	3.24	0.04
	B, N	85.72	3	3.34	0.04
	C, A, T	91.10	4	3.51	0.03
	C, I, A	90.98	4	3.57	0.03
	B	79.34	2	3.94	0.03
Female melanization	B, I	165.52	3	0	0.16
	I	159.22	2	0.55	0.12
	B, I, N	169.08	4	1.08	0.10
	C, I	161.14	3	2.19	0.06
	B, I, T	166.44	4	2.4	0.05
	I, N	160.70	3	2.41	0.05
	I, H	160.60	3	2.46	0.05
	C, B, I	166.16	4	2.54	0.05
	I, A	160.12	3	2.7	0.04
	B, I, H	165.78	4	2.73	0.04
	B, I, A	165.52	4	2.86	0.04
	B, I, N, H	171.80	5	2.88	0.04
	I, N, H	165.24	4	3	0.04
	I, T	159.24	3	3.14	0.03
	C, I, H	164.46	4	3.39	0.03
	B, I, N, T	169.62	5	3.97	0.02
Melanin dichromatism	C	107.50	2	0	0.16
	C, N	110.82	3	0.94	0.10
	C, I	109.68	3	1.51	0.07
	C, A	109.62	3	1.54	0.07
	N	104.38	2	1.56	0.07
	C, B	108.60	3	2.05	0.06
	C, H	108.50	3	2.1	0.06
	C, N, A	113.94	4	2.23	0.05
	N, A	107.76	3	2.47	0.05
	C, T	107.56	3	2.57	0.04
	C, N, H	112.66	4	2.87	0.04
	C, B, A	112.28	4	3.06	0.03
	C, I, A	111.74	4	3.33	0.03
	C, I, N	111.22	4	3.59	0.03
	I	100.16	2	3.67	0.03
	N, H	105.28	3	3.71	0.02
	I, N	105.20	3	3.75	0.02
	C, B, N	110.86	4	3.77	0.02
	C, N, T	110.82	4	3.79	0.02
	B, N	104.84	3	3.93	0.02

[1]Lowest AIC_c values were –39.06, –75.62, and –49.20 for male and female melanization, and melanin dichromatism, respectively.

Table 6.3. Model-averaged regression coefficients (b) and their unconditional standard errors (SE) for each life-history and ecological variable, for male and female melanization and melanin dichromatism. Coefficients of a given predictor were weighted using the Akaike weight of each candidate model containing that predictor.

Predictor	Male melanization	Female melanization	Melanin dichromatism
	b ± SE	b ± SE	b ± SE
Clutch size	–1.58 ± 0.38	–0.03 ± 0.15	–1.37 ± 0.34
Number of broods	–0.13 ± 0.17	–0.13 ± 0.16	0.04 ± 0.14
Incubation length	–0.41 ± 0.34	–1.07 ± 0.44	0.45 ± 0.31
Nestling period length	0.39 ± 0.27	0.12 ± 0.20	0.65 ± 0.27
Nest height	–0.05 ± 0.13	–0.01 ± 0.10	–0.04 ± 0.11
Breeding altitude	0.02 ± 0.06	<0.001 ± 0.03	0.02 ± 0.05
Tarsus length	–0.17 ± 0.23	–0.07 ± 0.16	–0.04 ± 0.19

6.4. Discussion

We found that the extent of melanin-based black coloration and its dichromatism increased in cardueline species with aspects of decreased reproductive investment. Our results are robust since they remained significant after controlling for the possible confounding effects of the most relevant ecological factors known to influence coloration in carduelines. Furthermore, our results are consistent between two alternative multivariate model selection approaches: a conventional frequentist method and an information-theoretic model comparison. This latter finding is also noteworthy in light of the ongoing debate about whether employing information theory should exclusively replace frequentist procedures (Anderson & Burnham 2002) or whether the two approaches may be used in concert to get robust results (Stephens et al. 2005).

Our results suggest that melanization is related to some life-history traits in a similar way as overall plumage brightness (Badyaev 1997b). This finding is interesting given that melanin-based coloration is a minor constituent of sexual dichromatism in finches (Badyaev & Hill 2000), and melanin ornaments appeared not to affect mate choice in cardueline species (Johnson et al. 1993, Senar et al. 2005). Our results further imply that sex differences in melanin-based pigmentation of the head and breast might have contributed to the previously reported association between sexual dichromatism and life-history traits in finches (Martin & Badyaev 1996, Badyaev 1997a,b, Badyaev & Ghalambor 1998).

Although both melanization and overall brightness are related to life-history traits in finches, the mechanisms causing these associations need not be the same for melanization and overall brightness in all instances. On the one hand, Badyaev (1997b) found that male brightness was negatively linked to fecundity (both to the number of broods and to clutch size), and proposed that

this relationship reflects the evolutionary responses of female fecundity to males' trade-off between parental effort and mating effort (i.e. females lay smaller clutches in species with reduced paternal care). Our finding that male melanization varies negatively with clutch size may be explained by a similar logic. Males may use extensive melanin ornaments in intense sexual competition, which is expected to reduce their parental effort (Verner & Willson 1969, Trivers 1972, Qvarnström 1997).

On the other hand, female brightness was positively related to clutch size and strongly negatively associated with incubation length. These relationships were interpreted as a result of multiple effects of nest predation; for example, high nest predation rate may select both for duller females and smaller clutches (Badyaev 1997b). Since male carduelines do not participate in incubation, the rate of nest predation constrains female but not male plumage brightness (Martin & Badyaev 1996). Although we also found a negative relationship between incubation length and female melanization, it is unlikely that nest predation constrains the evolution of frontal black patches of females as it does plumage brightness. Black plumage has very low brightness (i.e. reflects very little light), thus it is expected to be rather inconspicuous in most of the natural nesting habitats of finches (Endler 1990, McNaught & Owens 2002). Accordingly, experimental manipulation of the extent of black patches of incubating females did not alter nest predation rates in the hooded warbler (*Wilsonia citrina*; Stutchbury & Howlett 1995). The lack of an effect of melanization on nest predation may also explain why we did not find associations between either female melanization and clutch size (which is a characteristic prediction of the predation hypothesis; Badyaev 1997b) or between female melanization and nest height (nest height also reflects nest predation rate and is associated with female brightness; Martin & Badyaev 1996). In contrast, the negative association between incubation length and female melanization is consistent with the prediction of sexual selection theory that females may trade off extended parental care for intense sexual competition and sexual signalling.

Finally, Badyaev (1997b) found that overall dichromatism was strongly related to clutch size, and this was ascribed to either sex-specific differences in adult mortality or nest predation rates, both of which affect coloration and fecundity. As for overall dichromatism, we found that melanin dichromatism increased in species with smaller clutch sizes, but it is unclear whether the effects of adult or nest predation rates can explain this relationship (see above). This result may have arisen simply because only male melanization is linked to clutch size. Furthermore, melanin dichromatism is more strongly correlated with male melanization (linear regression of independent contrasts through origin: $r = 0.85$, $F_{1,72} = 191.86$, $p < 0.001$) than with female melanization ($r = –0.26$, $F_{1,72} = 5.24$, $p = 0.025$), which may also explain why melanin dichromatism is negatively related to clutch size but not to incubation length.

We suggest that the relationship between reproductive investment and melanization may be

mediated by levels of sex hormones, particularly testosterone. High levels of plasma testosterone are involved in the regulation of melanization in several vertebrate species, including birds (Haase et al. 1995, Tadokoro et al. 1997, Evans et al. 2000, Buchanan et al. 2001, González et al. 2001, Hill & McGraw 2003, Quinn & Hews 2003). Increased testosterone levels of males have also been shown to reduce paternal care in several species (Hegner & Wingfield 1987, Ketterson et al. 1992, Saino & Møller 1995), including house finches (Stoehr & Hill 2000). These multiple effects of testosterone may result in females laying smaller clutches in species with more melanized males that provide less care. However, the effects of testosterone on the fecundity and behaviour of female birds are not well understood. In one relevant study, experimentally increased testosterone levels of female dark-eyed juncos (*Junco hyemalis*) had no effect on female parental behaviour or clutch size, but prolonged interclutch intervals (Clotfelter et al. 2004). Thus, if melanization is linked to testosterone in female finches, females can afford to develop extensive melanization in those species where the incubation period is relatively short. It is unknown, however, whether interspecific variation in melanin-based coloration of the sexes is related to variation in responsiveness to, or concentration of, sex hormones.

Since we could not measure carotenoid-based coloration in our study, we cannot exclude the possibility that the relationship between melanization and reproductive efforts is a by-product of carotenoid ornaments. However, this is unlikely because there is no known correlation between melanin dichromatism and carotenoid dichromatism in carduelines (Badyaev & Hill 2000). To our knowledge, this is the second study that specifically investigated the factors influencing the interspecific variation of melanin-based coloration in male and female birds. In a former comparative study we demonstrated the role of sexual selection in the evolution of male melanization for a group of shorebirds with no known carotenoid plumage traits (Bókony et al. 2003). Here, we provide additional support for the result that sexual selection may influence melanin ornamentation from finches, which exhibit both types of pigmentation.

In conclusion, we found that melanin-based ornaments in finches, in spite of being a minor constituent of sexual dichromatism, are related to components of reproductive investment in a similar way as overall plumage brightness (Badyaev 1997b), which may be determined mainly by carotenoid ornaments (Badyaev & Hill 2000). This result adds to other recent findings that melanin-based coloration may be a potent means of sexual signalling, its expression being linked to important life-history variables.

7. Sexual selection and the function of melanin-based eye-stripes in promiscuous penduline tits

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7.1. Introduction

Melanin pigments, producing mainly dark colours like black and brown, are common sources of coloration in the skin, hair and plumage of animals (Hill 1992, Jawor & Breitwitsch 2003). Since these colours are often perceived dull or cryptic, much research focused on their non-sexual functions e.g. strengthening feathers to resist abrasion (reviewed by Savalli 1995) or antimicrobial effects in the skin (Mackintosh 2001). Conspicuous melanin ornaments, such as black patches, were traditionally viewed as arbitrary badges of status in social competition among conspecifics, since melanin ornaments signal dominance rank in several birds (reviewed by Senar 1999) and lizards (Zucker 1994, Quinn & Hews 2003). Relatively few studies have investigated the role of melanin ornaments in sexual signalling and particularly female choice, providing equivocal evidence whether females prefer more melanized males (e.g. Møller 1988 *versus* Griffith et al. 1999a, Johnson et al. 1993). Furthermore, experimental studies failed to demonstrate the dependence of melanin ornaments on nutritional condition or health status (Hill & Brawner 1998, McGraw & Hill 2000, McGraw et al. 2002, Senar et al. 2003). These results were consistent with phylogenetic comparative studies that suggested that sexual selection is unlikely to have a strong effect on melanin-based plumage dimorphism in birds (Gray 1996, Badyaev & Hill 2000).

However, melanin-based coloration has received greater interest recently, as researchers realized that melanin ornaments may be costly to produce, and they may honestly reflect individual quality (Jawor & Breitwisch 2003, McGraw 2003). Accordingly, recent studies demonstrated that melanization relates to pairing success (Roulin 1999, Parker et al. 2003, Tarof et al. 2005), to resistance to ectoparasites (Roulin et al. 2000, 2001a, Fitze & Richner 2002) or to parental effort (Roulin et al. 2001b, Siefferman & Hill 2003). Furthermore, recent phylogenetic comparative studies showed that as predicted by sexual selection theory, plumage melanization is related to sexual display behaviour in shorebirds and bustards (Dale 1992, Bókony et al. 2003) and to reproductive investment in cardueline finches (Bókony & Liker 2005).

The role of melanin ornaments in sexual selection may be complicated by the fact that less melanized males may be preferred by females in some species, and these males therefore have higher reproductive success (e.g. Lemon et al. 1992, Griffith et al. 1999a). A reason for this may be

that males with smaller melanin ornaments provide more parental care (Studd & Robertson 1985a,b, Griffith et al. 1999a, but see Voltura et al. 2002), perhaps because they are less dominant or less aggressive (Jawor & Breitwisch 2003). Thus it appears that melanin-based coloration might be involved in intra- and intersexual signalling, and that these functions may differ between species.

In this study we investigate the role of a melanin-based ornament in male-male competition, female choice and parental care in a small passerine bird, the penduline tit (*Remiz pendulinus*). The penduline tit is an excellent model species, due to its uniquely diverse reproductive system. Males build multiple elaborate nests per breeding season to attract females. Competition for females appears to be intense since at about 40% of the nests males are unsuccessful in attracting a female and remain unmated (Hoi et al. 1994, Szentirmai et al. in prep.). After mating, but before incubation either the male or the female deserts the clutch and full care is provided by a single parent (Franz 1991, Franz & Theiss 1983, Persson & Öhrström 1989; I. Szentirmai & T. Székely, unpublished data). One third of clutches, however, are naturally deserted by both parents suggesting intensive sexual conflict over care. Deserting parents can remate and thus both males and females are sequentially polygamous within a single breeding season. Here we focus on the black eye-stripe of male penduline tits and test whether it is involved in male-male interactions, female choice and parental care. Both males and females have conspicuous black eye-stripes that are probably melanin-based, since no other avian pigment is known to produce pitch-black feathers (Jawor & Breitwitsch 2003, McGraw & Wakamatsu 2004).

In this study we have four objectives. First, we investigate whether eye-stripe size reflects the males' quality or age. Second, we test the role of male eye-stripes as an intrasexual signal of aggression and dominance. Third, we explore whether mating success and reproductive success of males are related to eye-stripe size. Finally, we investigate whether eye-stripe size influences parental care of males and females.

7.2. Methods

7.2.1. Study site and morphometric measurements

We investigated the penduline tits at Fehér-tó, southern Hungary (46°19'N, 20°5'E) between April and August in 2003 and 2004. Fehér-tó is an extensive fishpond system (1321 ha), where penduline tits nest mainly on poplar (*Populus spp.*) and willow (*Salix spp.*) trees on the dykes among fishpond units (Szentirmai et al. 2005). We searched for nests nearly every day during the field season, and we found nearly all nests before the male mated (157 out of 163 nests of mated males). Males (n = 90) were caught at their first nest during nest-building using a mist net, a dummy penduline tit and song playback. Females (n = 28) were caught either together with their mate or during incubation in

the nest using a purpose-designed net (Z. Barbácsy, pers. comm.). Each individual was ringed for identification using three colour rings and a numbered metal ring of the Hungarian Ornithological Institute, and weighed using a Pesola spring balance (± 0.1 g). Tarsus length was measured three times using a digital sliding caliper (± 0.1 mm), and the median values were recorded. Digital photographs were taken from each bird at both sides of their head (3 photos from each side) in front of a graph paper (Appendix: Fig. 15.6). All photos were taken in the shade using a Fuji FinePix A203 digital camera (2M pixel) without zoom and flashlight, and at about 15 cm from the bird to create standard conditions. Eight individuals were caught and photographed twice for estimating repeatability (see below).

7.2.2. Eye-stripe measurements

Eye-stripes were measured on the digital photos using Corel Photo-Paint 9 (2001), and eye-stripe size was calculated as the average area of the left and the right eye-stripes (± 0.01 cm^2). Moulting birds were excluded from the analyses, since their eye-stripes could not be measured reliably (n = 4 males and 12 females).

Eye-stripe measurements were conducted blindly to the identity of birds by two observers (SAK, VB). A set of 20 birds was measured by both observers and these measures were highly repeatable between the observers ($r = 0.85$, $F_{19,20} = 18.30$, $p < 0.001$; for methods see Lessells & Boag 1987). In addition, the eye-stripe measurements from different photographs of the same male were highly repeatable both between photographs that were taken at the same capture ($r = 0.93$, $F_{19,20} = 37.49$, $p < 0.001$), and between photographs that were taken at different captures (capture intervals varied between 9 and 36 days; $r = 0.74$, $F_{7,8} = 0.74$, $p = 0.003$). Similarly, there was no difference in eye-stripe size between the first and the second captures of the same male (paired-samples t-test: $t_7 = 1.84$, $p = 0.11$). Therefore we assume that eye-stripe size remains unchanged during the breeding season, so that one measurement is representative for the whole season until moulting starts.

7.2.3. Male condition

We use three indicators of physical condition: body mass, haematocrit value, and presence/absence of buffy coat in blood samples. Haematocrit value (i.e. the proportion red blood cells in blood sample) appears to signal the amount of oxygen consumption and thus work load (Ots et al. 1998, Piersma et al. 2000, Bleeker et al. 2005). Haematocrit value was assessed by taking a 50–100 µl blood sample from the bird's brachial vein which was stored in a heparinized blood capillary. Within one hour the samples were centrifuged for 10 minutes at 9,000 rotations per minute. The

heights of red blood cells and blood plasma in the capillary were measured three times using a sliding caliper (± 0.1 mm). The mean length of each column was used in the analyses. The haematocrit value was calculated as packed red blood cell volume divided by blood plasma volume. Previous studies found that haematocrit values are highly repeatable (90–99 %; Ots et al. 1998, Potti et al. 1999).

The absence/presence of a visible buffy coat layer in the capillary was also noted. Buffy coat represents the presence of white blood cells (Dein 1986) so that high levels of these cells may indicate infection or disease (Ots et al. 1998).

7.2.4. Measuring aggression

Aggressive behaviour of males was assessed in two ways. First, a new male took over the nest from the resident male at seven nests, and the eye-stripe sizes of both males were known. In a paired comparison, we investigated whether usurping males had larger eye-stripe than evicted males.

Second, we challenged resident males using a dummy and song playback, placed about 15 m from the male's nest. During five minutes of observation we recorded (1) the latency (in seconds) as the time between the start of the playback and the arrival of the resident male within 10 m from the dummy; (2) once the resident male had arrived we estimated the distance between the resident male and the dummy every 20 seconds and calculated the mean of these distances; (3) the number of attacks when the dummy was hit or pecked by the resident male; (4) the proportion of time the resident male spent counter-singing the playback.

7.2.5. Mating success

We used two measures of male mating success, (i) whether the male was successful in attracting a female and mate up and (ii) mating time, i.e. the number of days between nest initiation and mating. Nest initiation date was determined for all nests. If a nest was found in an advanced building stage (see figures in Cramp et al. 1993; Appendix: Fig. 15.5), we estimated the nest initiation date using a predictor equation derived from nests that were found at initiation (Szentirmai et al. 2005). Nests were visited every other day for approximately 15 minutes to check the presence and identity of the male at the nest, and to establish whether he paired up. If the male abandoned his nest before mating, the male was considered to be unsuccessful. Since females lay one egg per day, the start of egg-laying was back-calculated from the number of eggs in an incomplete clutch. Since egg-laying starts shortly after pairing, and we had more reliable data on this than on mating date, we defined mating time of males as the number of days between nest initiation and start of egg-laying. We

followed males throughout the breeding season and determined their total number of mates and their mean mating time for all their nests.

7.2.6. Parental care

We checked the nests after mating at least every other day for 15 minutes to establish whether the male, the female or both parents deserted the clutch. Desertion by a parent was recognized if we did not see the parent for at least two consecutive nest checks (Szentirmai et al. 2005). If one of the parents stayed with the clutch we observed incubation and nestling provisioning behaviour.

All observations were carried out with binoculars at 10–20 meters from the nest, using a hide. Between the 7th and 10th days of incubation, three observations of one hour each were conducted between 16:00h and 19:00h to measure the time the parent spent in the nest, or outside the nest feeding or resting. Incubation rate was calculated as the mean proportion of time the parent spent inside the nest during three observation periods. Nestling provisioning was recorded during three observations between the 4th – 6th, 9th – 11th, and 14th – 16th days after the first chick hatched, between 6:00h and 10:00h. Feeding rate was calculated by counting the number of times the parent fed the young during 30 minutes, averaged for the three observations.

7.2.7. Reproductive success

We counted the number of eggs between the 7th and 9th day of incubation, and the number of chicks at hatching (hatchlings), at the age of 10 days (nestlings) and at fledging (fledglings). Nestling survival was calculated as the proportion of hatchlings that survived until the age of 10 days.

Annual reproductive success of males was estimated as the total number of their nestlings produced in all of their nests over the full breeding season. We used the number of nestlings instead of the number of fledglings as a measure of reproductive success, because we had more data on the former and these two variables were highly correlated (Spearman rank-correlation: $r_s = 0.84$, n = 33 nests, $p < 0.001$). At nine nests we suspected that trapping induced nest desertion and we excluded these males from the analyses of annual reproductive success. We also excluded seven other males for which we had no information on the reproductive success in some of their nests. Extra-pair paternity (EPP) appears to be rare in penduline tits (6.9 % of young; Schleicher et al. 1997), although currently we are genotyping offspring to quantify EPP for our population.

7.2.8. Data processing and statistical analyses

Overall body size may confound the relationships between eye-stripe size and behaviour (Green 2001), nevertheless in our study eye-stripe size was unrelated to body size (as measured by tarsus length) both in males (Pearson correlations: $r = 0.12$, $n = 86$, $p = 0.26$) and females ($r = 0.003$, $n = 21$, $p = 0.80$). Hence we use absolute eye-stripe sizes (in cm^2) in all analyses. In the analysis of body mass in relation to male eye-stripe size, tarsus length was also included since body mass might depend on body size.

Aggressive behaviour of males was analyzed using non-parametric correlations between eye-stripe size of males and the four proxy measures of aggression. Date and time of the experiment, breeding stage (number of days between the experiment and the start of the nest building by the male), the distance of the dummy from the nest of the resident male, and wind intensity were all unrelated to the aggression variables (results not reported).

We analyzed the relationship between eye-stripe size and mating success in two ways. First, we chose the first nest of each male and related (i) their successfulness in attracting a female (succesful or unsuccessful) and (ii) their mating time to their eye-stripe size. The analysis of the mating time of successful males may be biased since it did not include those males that did not attract a mate. To incorporate these unsuccessful males in the analyses we used a Cox survival-analysis in which unmated males were entered as censored observations. Second, we calculated the mean mating time and the total number of females attracted over the breeding season for each male and related these two variables to their eye-stripe size. Nest initiation date was included in all analyses of mating success since we expected male mating success to vary over the breeding season (I. Szentirmai & T. Székely, unpublished data). Number of mates was related to the number of days males were present at our study site (number of days between initiation of the first nest and desertion or end of the last nest; $r_s = 0.65$, $n = 83$, $p < 0.001$), therefore we controlled for this confounding effect by partial rank-correlation.

To analyze the influence of eye-stripe size on parental decisions (care or desert), first we used the first nest of each male. We related parental decisions of males and females to the males' eye-stripe size by using binary logistic regressions. In these models we included mating date as a covariate, because previous studies showed that parental decisions may change over the breeding season (Persson & Öhrström 1989, Szentirmai et al. 2005). Second, we related the proportion of those nests of a male that were cared by the male himself and the proportion of those nests that were cared by his females to the male's eye-stripe size. The effects of eye-stripe size on incubation and feeding rates were tested using GLMs. Possible confounding parameters (body mass, date of recordings, breeding stage, time of the day) were included in the initial models, and non-significant effects were excluded by backward elimination (Grafen & Hails 2002).

Components of reproductive success (number of eggs and nestlings, and nestling survival) were averaged for each male, separately for their female-only cared and male-only cared clutches, and analyzed in relation to eye-stripe size. In these analyses we controlled for the potential confounding effect of laying date by partial rank-correlations.

Statistical analyses were performed using SPSS 11.0. For normally distributed variables, we report means with standard errors. Non-normally distributed variables were analyzed using non-parametric methods. Mating times were log (x + 1) transformed. Parameter estimates are given using the slope ± standard error (b ± SE). Probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$. Sample sizes differ between the analyses because we do not have all data for all males and females.

7.3. Results

7.3.1. Eye-stripe size and male quality

Males had larger eye-stripes than females (Fig. 7.1a). The eye-stripes of males and females within a pair were not related to each other ($r = 0.12$, $n = 23$ pairs, $p = 0.54$). Eye-stripe size of yearling males was smaller than that of males older than one year (Fig. 7.1b). Three males were caught both in 2003 and 2004 and the increase in their eye-stripe size was consistent with the latter result (2003: 1.36 ± 0.13 cm^2; 2004: 1.54 ± 0.13 cm^2). Males with larger eye-stripes did not start to breed earlier at our study site than males with smaller eye-stripes ($r = 0.13$, $n = 85$, $p = 0.23$).

Eye-stripe size was related to body condition of males. First, eye-stripe size increased with body mass (multiple linear regression, overall model: $r^2 = 0.08$, $F_{2,83} = 3.81$, $p = 0.03$; body mass: b ± SE = 0.10 ± 0.04, $F_{1,83} = 6.26$, $p = 0.01$; tarsus length: b ± SE = –0.10 ± 0.05, $F_{1,83} = 3.58$, $p = 0.06$). Second, males with buffy coat in their blood had larger eye-stripes than those without buffy coat (Fig. 7.1c). However, eye-stripe size was unrelated to haematocrit values ($r = 0.07$, $n = 42$, $p = 0.67$).

7.3.2. Male-male interactions

Eye-stripe size is unlikely to indicate social dominance or aggressiveness of males. First, eye-stripe sizes of usurping males were not different from eye-stripe sizes of evicted males (paired t-test: $t_7 = 1.39$, $p = 0.21$). Second, eye-stripe sizes were unrelated to all measures of aggression using Spearman rank-correlations (Table 7.1). The results remained unchanged when we analyzed the same data set by multiple linear regression.

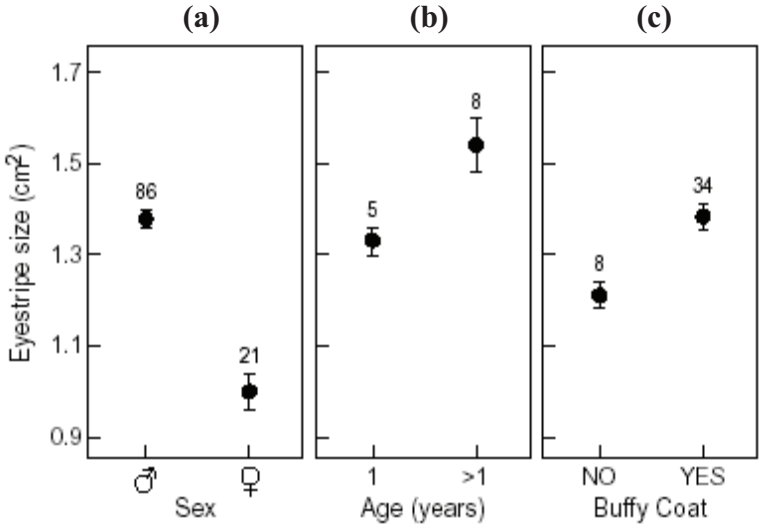

Figure 7.1. Difference between eye-stripe size of **(a)** males and females (t-tests, $t_{106} = 8.42$, $p < 0.001$), **(b)** one year old males and males older than one year ($t_{12} = 2.65$, $p = 0.02$), and **(c)** males without and with buffy coat in their blood sample ($t_{41} = 3.76$, $p = 0.001$). Error bars represent means ± SE and numbers above them denote sample sizes.

Table 7.1. Bivariate relationships between eye-stripe size of males and four proxy measures of aggression.

	r_s	n	p
Latency time	0.12	27	0.56
Average distance to dummy	–0.35	28	0.07
Physical attacks	0.16	28	0.41
Time singing	0.05	28	0.81

7.3.3. Mating success

Mating time of successful males at their first nest decreased with their eye-stripe size (Table 7.2). This result is consistent with the survival analysis of mating time that included unsuccessful males as censored observations (Cox-regression: $\chi^2_2 = 11.31$, $p = 0.003$; eye-stripe size: Wald = 3.81, $p = 0.05$; nest initiation date: Wald = 9.18, $p = 0.002$). However, eye-stripe size did not predict whether a male was successful (n = 65 males) or unsuccessful (n = 21 males) in attracting a female at his first nest (logistic regression: $\chi^2_1 = 0.53$, $p = 0.47$; nest initiation date: $\chi^2_1 = 0.03$, $p = 0.86$).

Mean mating time of males over the full breeding season decreased significantly with male eye-stripe size (Table 7.2, Fig. 7.2). In addition, males with larger eye-stripes attracted more females than males with smaller eye-stripes (Fig. 7.3). This result remained unchanged after controlling for

the number of days that the male spent at our study site (partial rank-correlation: r = 0.26, n = 83, p = 0.02).

Table 7.2. The effect of eye-stripe size of male penduline tits on their mating time at their first nests (overall GLM: $r^2 = 0.21$, $F_{2,63} = 8.25$, $p = 0.001$) and on their mean mating time over the entire breeding season ($r^2 = 0.35$, $F_{2,79} = 20.63$, $p < 0.001$).

	First mating time			Mean mating time		
	b ± SE	F	p	b ± SE	F	p
Eye-stripe size	–0.99 ± 0.26	14.56	< 0.001	–0.33 ± 0.12	6.94	0.01
Nest initiation date	–0.003 ± 0.002	2.84	0.10	–0.01 ± 0.002	32.63	< 0.001

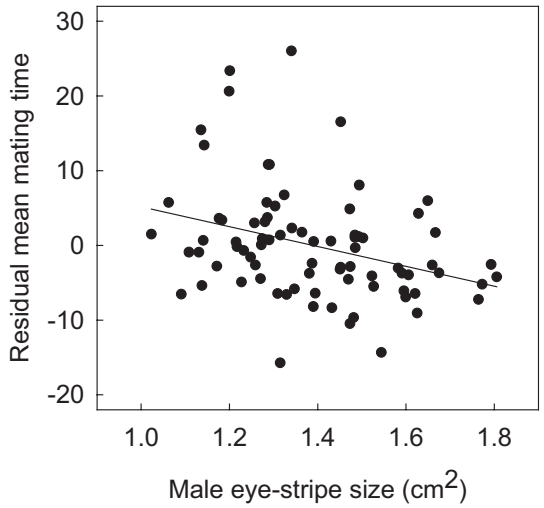

Figure 7.2. Residual mean mating time (obtained from GLM, see Table 7.2) in relation to male eye-stripe size (y = –11.97x + 16.56).

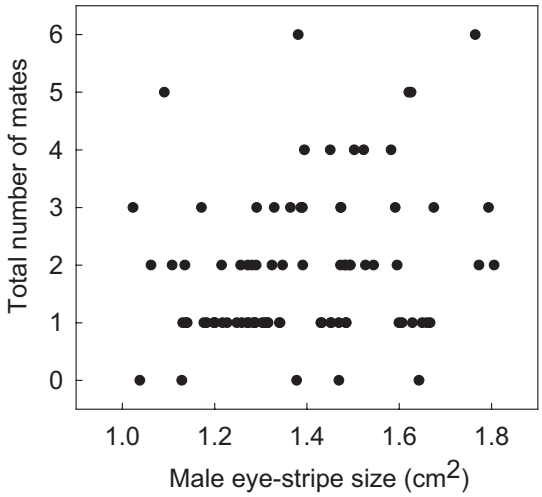

Figure 7.3. Total number of mates attracted by male penduline tits during the entire breeding season in relation to their eye-stripe size ($r_s = 0.26$, n = 86, p = 0.02).

7.3.4. Parental care

Males with larger eye-stripes more likely deserted their first clutch than males with smaller eye-stripes (logistic regression, overall model: $\chi^2_2 = 7.01$, n = 5 caring and 60 deserting males, p = 0.03; eye-stripe size: $\chi^2_1 = 5.33$, p = 0.02; mating date: $\chi^2_1 = 3.56$, p = 0.06). However, females' decision to care (n = 23 males) or desert (n = 42 males) was independent of the male's eye-stripe size (overall model: $\chi^2_2 = 0.97$, p = 0.62; eye-stripe size:$\chi^2_1 = 0.73$, p = 0.39; mating date: $\chi^2_1 = 0.05$, p = 0.82).

There was no relationship between the proportion of clutches a male cared for himself and his eye-stripe size (r_s = –0.12, n = 81, p = 0.28). Similarly, the proportion clutches cared for by the male's mates was unrelated to the male's eye-stripe size (r_s = 0.06, n = 81, p = 0.58). Neither incubation nor feeding rate of males was related to their eye-stripe size (Table 7.3). Similarly, female incubation and feeding behaviour did not depend on their partner's eye-stripe size (Table 7.3).

Table 7.3. The effect of male eye-stripe size on incubation rate (final overall GLM: $r^2 = 0.26$, $F_{4,13} = 0.79$, p = 0.56) and feeding rate (final overall GLM: $r^2 = 0.23$, $F_{1,31} = 8.79$, p = 0.01) of male and female penduline tits. Non-significant effects were excluded stepwise, statistics are shown for each excluded variable before its exclusion from the model.

	Incubation rate		Feeding rate	
	F	p	F	p
Sex of caring parent	0.34	0.57	2.61	0.12
Male eye-stripe size	0.85	0.38	0.07	0.79
Sex × Eye-stripe size	0.6	0.46	0.01	0.92
Clutch or brood size	0.04	0.84	8.79	0.01

7.3.5. Reproductive success

Clutches were smaller in male-only cared nests (3.33 ± 0.29 eggs, n = 15 nests) than in female-only cared ones (5.97 ± 0.16 eggs, n = 59 nests; t-test: $t_{73} = 7.39$, p < 0.001). The number of nestlings, however, did not significantly differ between male-only cared (2.36 ± 0.36 nestlings, n = 11 nests) and female-only cared nests (3.27 ± 0.26 nestlings, n = 56 nests; $t_{66} = 1.47$, p = 0.15).

Mean clutch size of males in their female-only cared nests was not correlated with their eye-stripe size (partial rank-correlations controlling for laying date: r = –0.09, n = 39, p = 0.59). However, both mean nestling survival (Fig. 7.4) and mean number of nestlings decreased with eye-stripe size (r = –0.32, n = 40, p = 0.04). In male-only cared nests of males, neither mean clutch size nor mean nestling survival, nor the mean number of nestlings was related to eye-stripe size (clutch size: r = 0.17, n = 13, p = 0.58; nestling survival: r = 0.03, n = 8, p = 0.94; number of nestlings: r = 0.29, n = 9, p = 0.41). Annual reproductive success of males (including nests cared by both the males and their females) was unrelated to their eye-stripe size.

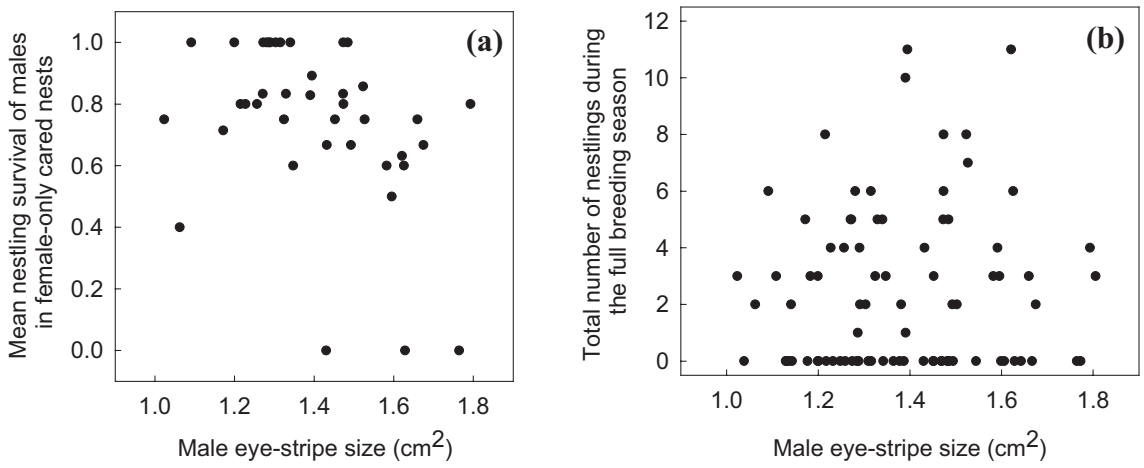

Figure 7.4. (a) Mean nestling survival in female-only cared nests of male penduline tits in relation to their eye-stripe size ($r = –0.41$, $n = 38$, $p = 0.01$). **(b)** Total number of nestlings of male penduline tits produced during the full breeding season in relation to their eye-stripe size ($r_s = 0.01$, $n = 70$, $p = 0.96$).

7.4. Discussion

Our study revealed that black eye-stripes of male penduline tits indicate attractiveness to females rather than social dominance or aggressiveness. By experimentally challenging territorial males, we showed that aggressiveness of nest-building males against intruder males was not related to the size of their eye-stripe. Furthermore, males with larger eye-stripes were not more likely to be usurpers than victims in nest overtakes. We found, however, two lines of evidence suggesting that males bearing larger eye-stripes are more attractive to females and that eye-stripe size is sexually selected. First, males possess larger eye-stripes than females, and eye-stripe size is much more variable among males (coefficient of variation: CV = 13.61) than are non-ornamental morphological traits like tarsus length (CV = 2.36), a pattern typical for sexually selected ornamental traits (e.g. Cuervo & Møller 1999, Kraaijeveld et al. 2004, Komdeur et al. 2005). Second, males with larger eye-stripes were more successful in mating since they needed less time to pair up and they acquired more females during the breeding season than males with smaller eye-stripes. Our results suggest that the black eye-stripes may function in female choice in penduline tits. This finding adds to the growing evidence that melanin-based coloration may be a potent means of sexual signalling as an attractiveness trait (Jawor & Breitwisch 2003, Tarof et al. 2005).

In spite of their higher mating success, males with larger eye-stripe did not obtain higher annual reproductive success than males with smaller eye-stripe. Although more attractive males had more mates and more clutches over a breeding season, survival of their nestlings was lower, and consequently they did not fledge more nestling than less attractive males. This result might suggest

that there is no positive selection on male eye-stripe size in our population, however, several factors may confound this result. For example, attractive males may increase the genetic diversity of their offspring by mating with many females and thus their life-time reproductive success may be still higher than that of less attractive males (Richardson et al. 2004). Also, it is known that short-term fitness consequences of the same male trait may differ among years and populations. For example, in house sparrows (*Passer domesticus*) different studies relating reproductive output to male melanin-based bib size found different results, ranging from males with smaller bib fledging more young (Griffith et al. 1999a), through no effect of bib size (Václav et al. 2002) to males with larger bib fledging more young (Voltura et al. 2002).

Our results indicate that mating to an attractive male includes both costs and benefits for females. First, body mass of male penduline tits increased with eye-stripe size and older males had larger eye-stripes, suggesting that eye-stripe may reflect individual quality (Jawor & Breitwisch 2003, McGraw 2003). Thus females of attractive males might have gained more viable offspring than females of less attractive males as it has been shown in several other species (e.g. Norris 1993, Petrie 1994). However, in contrast to these studies we found that offspring survival decreased with eye-stripe size in penduline tits. Therefore, high offspring viability, at least in the short-term, is unlikely to be an advantage of having an attractive mate. It is still possible that more attractive males sired more attractive offspring and females of these males had higher lifetime reproductive success, although we had no data to test this option (e.g. Gwinner & Schwabl 2005).

Second, the chance that a male had buffy coat in his blood increased with eye-stripe size, which may indicate acute or chronic infection of attractive males (Dein 1986, Gustafsson et al. 1994). This may also contribute to lower offspring survival in the nests of attractive males, if health status of males is transmitted to the offspring. Poorer health status of attractive males may be explained by the immune-suppressive effects of developing exaggerated ornaments. For example, the production of melanization may require high levels of immune-suppressive hormones (e.g. testosterone), therefore males with larger eye-stripes may be more prone to infections (Folstad & Carter 1992, Evans et al. 2000).

Finally, males with larger eye-stripe more likely deserted their clutch than males with smaller eye-stripe. This lower parental investment by attractive male penduline tits is in line with the results of several studies on other species, and may be explained by higher mating opportunities of attractive males (Qvarnström 1997, Kokko 1998, Sanz 2001, Magrath & Komdeur 2003). Our results suggest that having an attractive male is costly for female penduline tits, because reproductive success of females has been shown to decrease with male desertion (I. Szentirmai, T. Székely & J. Komdeur, unpublished data).

In conclusion, our study provides support for female preference for melanin-based eye-stripes of male penduline tits, and suggests that this melanin ornament might have evolved via sexual selection. Although attractive males do not seem to obtain higher short-term reproductive success than less attractive ones, they may gain in the long-term from genetically diverse offspring produced by multiple females. Females pay costs for mating to an attractive male since offspring of these males survive less well and these males are more likely to desert than less attractive ones. The benefits that females may gain from attractive mates and thus the evolutionary basis of female preference remained unclear and needs further investigations.

8. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows

Veronika Bókony, Ádám Z. Lendvai & András Liker – Ethology 2006, 112: in press

8.1. Introduction

The status signalling hypothesis (Rohwer 1975) proposes that conspicuous colour traits have evolved to signal differences in the ability to win agonistic contests. Signalling fighting abilities or aggressiveness should be advantageous for all participants, as they may assess the expected outcome of the fight and may therefore avoid costly and unnecessary interactions (Rohwer 1975). Several studies have found a relationship between coloration and dominance status in diverse vertebrate species including birds (reviewed by Senar 1999) and lizards (reviewed by Whiting et al. 2003). Such colour traits were termed „badges of status" as they were considered cheap to produce and potentially open to cheating. However, recent studies increasingly suggest that certain colour badges are costly to produce and/or to maintain (González et al. 2001, 2002, McGraw et al. 2003, Török et al. 2003, reviewed by Jawor & Breitwisch 2003), so it may only pay high-quality or highly motivated individuals to signal high status (Enquist 1985, reviewed by Johnstone 1995). Although animals often exhibit several conspicuous ornaments, however, previous studies have almost exclusively focused on single badges of status.

Multiple ornaments have received increasing research interest rather in the context of sexual signalling and mate choice (reviewed by Candolin 2003). Most of these studies found multiple ornaments to function either as „multiple messages" that reflect different aspects of individual quality or as „backup signals" that allow a more accurate assessment of a single aspect of quality (Candolin 2003). Evidence also increases for „uninformative cues" that do not indicate qualities *per se* but facilitate the detection and assessment of an indicator trait (Candolin 2003). Such interactions among cues of individual quality may also be advantageous during status signalling in competition for resources other than mates, such as for food in wintering flocks of birds. Although a few studies raised the possibility of multiple status signals (Balph et al. 1979, Zucker 1994, but see Zucker & Murray 1996), these were not of strong support and left the topic open for debate.

One of the best studied species with a status signalling system is the house sparrow (*Passer domesticus*). In winter flocks of house sparrows, the size of males' black throat patch (the bib) predicts their dominance rank (Møller 1987a, Solberg & Ringsby 1997, Liker & Barta 2001, González et al. 2002, Hein et al. 2003). Beside the bib, however, male sparrows exhibit several other contrastingly coloured plumage patches, including a conspicuous wingbar formed by light tips

on the median coverts. The wingbars may be flashed by slightly spreading the wings, or totally hidden by ruffling the flank feathers. When competing for food, sparrows frequently use a threatening posture (wing display henceforward) in which they spread and wiggle their wings (Perrins 1998) that appears to emphasize the wingbars. This behaviour suggests that wingbars may be involved in signalling to opponents during aggressive interactions.

Many other bird species also exhibit light wing patterns (Price & Pavelka 1996), and several functions have been found for such ornaments in various taxa, from distracting prey (Jablonski 1996) or predators (Brooke 1998) through facilitating flock cohesion (Beauchamp & Heeb 2001) to sexual selection by female choice (Senar et al. 2005). Displaying the wings during aggressive encounters is also widespread among birds (Perrins 1998, Hurd & Enquist 2001), and some studies on various avian species have suggested that white wingbars might signal individual quality in intra-sexual competition in males (Jablonski & Matyjasiak 2002, Török et al. 2003) and females (Ruusila et al. 2001). However, the function of the wingbars has not been tested in house sparrows.

In this study we investigated the role of the wingbars and wing displays in aggressive interactions among male house sparrows. Specifically, we asked whether these traits may act as multiple cues in status signalling, that is, do they in addition to bib size predict any aspect of fighting success. First, we tested whether males with larger and/or more conspicuous wingbars are more successful in social competition among conspecifics in winter flocks than less ornamented males. Second, we examined whether the use of wing display is related to success in different aspects of fighting behaviour.

8.2. Methods

8.2.1. Study subjects

We captured 28 house sparrows using mist nets in November 2003 in the Budapest Zoo, Hungary. After capture we immediately measured body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm), and ringed all birds with a numbered metal ring and an individual combination of three colour rings. We then formed two mixed-sex flocks consisting 15 and 13 individuals, respectively (male:female ratios were 9:6 and 10:3). House sparrows live in mixed-sex flocks year-round, and sexes do not differ in dominance rank or aggressiveness (Liker & Barta 2001, Hein et al. 2003). Flocks were housed in two indoor aviaries measuring 3 m (W) × 4 m (L) × 2 m (H) and 2 m (W) × 3 m (L) × 2 m (H), separated so that individuals of different flocks could not interfere with each other. Both aviaries were lit by artificial light (9L:15D) and contained a feeding board for presenting food, artificial roosting trees and small boxes for sleeping and resting. Food, water, sand and fine gravel (to facilitate digestion) were provided *ad libitum*. Food consisted of a mixture of

seeds and occasionally mealworms. After the study we released the birds at the site of capture. Released birds were in good condition and apparently re-established themselves in the local population, as we often re-encountered them after the release (ÁZL, pers. obs.). The study was licensed by the Duna-Ipoly National Park (847/3/2003).

8.2.2. Aggressive interactions

Behavioural observations were conducted between November 2003 and February 2004. During the observations we recorded aggressive encounters between pairs of individuals when both participants were identified and the outcome of the contest was straightforward. We recorded 1050 dyadic fights in which one or both participants were males. An individual was considered to win a fight if it clearly supplanted the opponent. For each male we calculated overall fighting success, i.e. the number of wins divided by the total number of aggressive encounters which the focal bird was involved in (a measure that strongly correlates with dominance rank; Liker & Barta 2001). Then we calculated two additional components of fighting success: (1) attack success, i.e. the proportion of successful attacks out of all attacks launched by the focal bird, and (2) defence success, i.e. the proportion of successful defences out of all attacks received by the focal bird. Measuring success between opponents in established flocks is a standard method to test the relationship between candidate status signalling traits and fighting ability or aggressiveness of individuals (e.g. Møller 1987a, Solberg & Ringsby 1997, Liker & Barta 2001, Hein et al. 2003).

To study wing displays we videorecorded the birds' behaviour in each flock on two occasions during the first feeding in the morning. Before the recordings we placed six clumps of millet seeds on the feeding board. Trials lasted until the food clumps were depleted and the birds left the feeding board. We analysed a total of 32 min video recordings for the two flocks. In these recordings, we identified 116 aggressive interactions in which one or both participants were males. For these interactions we recorded the aggressor and the winner, and noted whether participants used wing display. We defined wing display as flapping or wobbling the wings towards the opponent during fights (we excluded wing movements associated with flight). For all males (n = 19) we calculated attack success and defence success (as above) separately for interactions with and without wing display.

8.2.3. Measuring coloration

Before releasing the birds we took digital photographs from each male to measure their bib size and the conspicuousness and area of their wingbars. Birds were held in standard position and were photographed in a standardized set-up with constant lighting conditions. Bibs were photographed

with the birds' beak held perpendicular to body axis (Appendix: Fig. 15.8) so that we could measure the so-called visible bib (González et al. 2001). Wingbars were photographed on the left wings flattened (Appendix: Fig. 15.9). Photos were converted to grey-scale and measured using the Scion Image software (Scion Corporation 2000). We selected the area of bib or wingbar using the „density slice" and „wand tool" functions. Areas were measured in pixels and converted to cm^2 using a measured standard in the photos. Brightness of the wingbar was measured as the mean density of the pixels constituting the wingbar on the photos (the lighter the pixel, the smaller the density value). We also measured the mean density of the area of brown lesser coverts above the wingbar. This area may serve as a natural background or „standard" against which birds see and judge wingbars, since during threat displays sparrows rotate their wings so that lesser coverts point towards the opponent (Perrins 1998; our pers. obs.). We calculated wingbar conspicuousness by subtracting wingbar density from lesser coverts density, and used this variable as a measure of wingbar conspicuousness (greater values may be interpreted as greater achromatic contrast between the wingbar and the lesser coverts). We preferred wingbar conspicuousness over wingbar brightness because conspicuousness depends not only on the brightness of the plumage patch but also on its visual environment, and within-animal contrast may be a more objective measure of conspicuousness in most natural habitats of sparrows (Endler 1990).

We tested the reliability of our colour measurements in several ways. First, we measured each photograph twice and calculated the repeatability of measurements (Lessells & Boag 1987). Repeatability proved very high for bib size ($r = 0.97$, $F_{18,19} = 64.3$, $p < 0.001$), wingbar area ($r = 0.78$, $F_{18,19} = 8.1$, $p < 0.001$) and wingbar conspicuousness ($r = 0.90$, $F_{18,19} = 19.7$, $p < 0.001$; see also Bókony et al. 2003 for further justification of area measurements from photos). Second, to validate our method using grey-scale density values as a proxy for wingbar conspicuousness, we plucked the 2-5th median coverts with white tips (Appendix: Fig. 15.10) from 25 male sparrows captured at a different site, and measured their reflectances using an USB2000 spectroradiometer with a Mini-DT deuterium-halogen light source (Ocean Optics Europe, Duiven, The Netherlands; methods as in Cuthill et al. 1999). Since these feathers did not reflect in the UV, we calculated total reflectance for the 400–700 nm range of the spectra as an objective measure of wingbar brightness (Marchetti 1993, McNaught & Owens 2002). Before plucking the feathers, we took photographs of the birds' wingbars and measured the density values of these as described above. Wingbar density correlated significantly with total reflectance ($r = –0.49$, $p = 0.013$, $n = 25$; note that a negative correlation is expected since the greater the brightness, the less the density value).

8.2.4. Statistical procedure

To explore the relationships between colour traits and measures of fighting ability in males, we used general linear models (GLM) with flock as a random factor and bib size, wingbar area and wingbar conspicuousness as covariates. Dependent variables (fighting success, attack success and defence success) were arcsine square-root transformed before the analyses. We used stepwise backward elimination of non-significant effects, by removing the predictor with the largest p-value in each step (Grafen & Hails 2002). We do not report flock effects since these were non-significant in all models, and there were no significant interactions between the flock factor and other predictor variables. Since tarsus and wing length and body mass were unrelated to measures of both coloration and fighting ability in our sample (results not shown) and also in other studies (e.g. Møller 1987a, Liker & Barta 2001), we did not control for these biometrical variables in the analyses.

Since the power of our tests was low due to small sample sizes, we did not use any corrections of significance levels for multiple comparisons, as these would only exacerbate the problem of low power by increasing the risk of neglecting existent small effects (Nakawaga 2004). Instead, to prevent our conclusions from being based purely on the significance of each test, we also evaluated our results using a different analytical approach, the information-theoretic model comparison (Anderson et al. 2000), where inference is based on the entire model set. We evaluated all possible subsets of the three initial GLM models based on the second-order Akaike's information criterion corrected for small sample size (AIC_c). As no single model was highly superior compared with the others in our model sets, we performed model-averaging (Anderson et al. 2000) where model coefficients were weighted using Akaike weights. We also examined the relative importance of predictors by summing the Akaike weights for each predictor across all sub-models that contained that predictor. Then we compared the final sets of predictor variables selected in each approach (i.e. stepwise GLM and AIC_c-based model-averaging).

We analyzed the data on display behaviour using the independent sample derived from video recordings. Here we used non-parametric tests because the distribution of these variables did not allow for parametric tests. Using Wilcoxon matched-pairs signed-ranks tests we tested whether the males' attack success and defence success was greater when displaying than when not displaying. Since the power of these tests were low due to the small number of males performing attacks and defences both with and without wing display in our sample, we also checked for the associations between success and display using fights as data points in χ^2-tests. Since these data points are not independent **(**each male participated in several fights**)**, in this latter case we used a full permutation procedure to calculate the exact level of significance for the tested associations.

All statistical tests were two-tailed with a 95% confidence level. We used the R statistical computing environment (R Development Core Team 2003) and SPSS 11.0 for statistical analyses.

8.3. Results

Wingbar area and wingbar conspicuousness were not correlated (Pearson correlation, $r = –0.05$, $p = 0.828$, $n = 19$). Bib size was not correlated with wingbar area ($r = 0.37$, $p = 0.120$, $n = 19$) or wingbar conspicuousness ($r = 0.24$, $p = 0.324$, $n = 19$). Defence success and attack success were significantly correlated ($r = 0.68$, $p = 0.001$, $n = 19$).

8.3.1. Coloration and fighting ability

Bib size was the strongest predictor for each measure of fighting ability both in stepwise GLMs (Table 8.1) and AIC_c-based model comparison (Table 8.2, Table 8.3). For fighting success and defence success, both the final GLM (Table 8.1) and the models with the lowest AIC_c included bib size (Table 8.2). For attack success, the best model contained bib size again, but its relative importance was similar to that of the other coloration variables (Table 8.3), and its effect was non-significant in GLM (Table 8.1).

Wingbar conspicuousness was significantly related to defence success only; both the final GLM (Table 8.1) and the model with the lowest AIC_c (Table 8.2) for defence success included wingbar conspicuousness in addition to bib size. Both traits were of similar importance in explaining defence success, as indicated either by effect size in GLM (Table 8.1) or the sum of Akaike weights (Table 8.3).

Wingbar area was not related to any measures of fighting ability in GLMs (Table 8.1) and proved of minor importance in AIC_c-based model selection (Table 8.3).

Table 8.1. Relationships of plumage colour traits with measures of fighting ability in male house sparrows using stepwise general linear models. Predictor variables are bib size (B), wingbar conspicuousness (C), and wingbar area (A). Asterisks (*) indicate predictors included in the final models. For these variables, regression coefficients (b) ± SE and effect sizes (η^2) are given for the final models. For predictors not included in the final models, estimates are given for the initial models.

	Fighting success[a]		Attack success		Defence success[b]	
Predictor	b ± SE	η^2	b ± SE	η^2	b ± SE	η^2
B	0.10 ± 0.04	0.274*	0.04 ± 0.04	0.055	0.09 ± 0.03	0.416*
C	0.01 ± 0.01	0.189	0.01 ± 0.01	0.098	0.01 ± 0.004	0.381*
A	-0.01 ± 0.24	< 0.001	0.01 ± 0.24	< 0.001	-0.20 ± 0.16	0.096

[a] Final model: $F_{1,17} = 6.42$, $p = 0.021$; [b] final model: $F_{2,16} = 13.97$, $p < 0.001$.

Table 8.2. Results of model selection based on Akaike's information criterion corrected for small sample size (AIC_c): AIC_c values, number of estimated parameters (k), AIC_c differences between the best model and each candidate model (Δ_i), and Akaike weights (ω_i) of the candidate models are given for measures of fighting ability. Predictor variables are bib size (B), wingbar conspicuousness (C), wingbar area (A), and flock (F).

Dependent	Model	Predictors	AIC_c	k	Δ_i	ω_i
Fighting success	1	B	1.04	3	0	0.41
	2	B+C	1.98	4	0.94	0.26
	3	C	3.15	3	2.10	0.14
	4	B+A	4.23	4	3.19	0.08
	5	A+C	5.72	4	4.67	0.04
	6	B+A+C	5.74	5	4.70	0.04
	7	A	6.99	3	5.94	0.02
	8	B+F	15.01	4	13.97	0
	9	A+F	16.56	4	15.52	0
	10	B+A+F	19.66	5	18.62	0
	11	C+F	20.69	4	19.65	0
	12	B+C+F	24.77	5	23.73	0
	13	A+C+F	24.91	5	23.87	0
	14	B+A+C+F	30.18	6	29.14	0
Attack success	1	B	0.27	3	0	0.36
	2	C	1.08	3	0.81	0.24
	3	A	1.74	3	1.47	0.17
	4	B+C	3.12	4	2.85	0.09
	5	B+A	3.53	4	3.26	0.07
	6	A+C	4.08	4	3.81	0.05
	7	B+A+C	6.87	5	6.60	0.01
	8	A+F	12.08	4	11.80	0
	9	B+F	13.93	4	13.65	0
	10	C+F	17.81	4	17.54	0
	11	B+A+F	18.72	5	18.45	0
	12	A+C+F	22.59	5	22.31	0
	13	B+C+F	25.06	5	24.78	0
	14	B+A+C+F	30.49	6	30.22	0
Defence success	1	B+C	–13.83	4	0	0.71
	2	B+A+C	–11.59	5	2.24	0.23
	3	B	–6.85	3	6.98	0.02
	4	B+A	–6.58	4	7.25	0.02
	5	C	–5.21	3	8.62	0.01
	6	A+C	–2.02	4	11.82	0
	7	B+F	6.90	4	20.73	0
	8	B+A+F	10.2	5	24.03	0
	9	C+F	11.73	4	25.56	0
	10	B+C+F	11.75	5	25.58	0
	11	A	11.99	3	25.82	0
	12	A+F	12.49	4	26.33	0
	13	B+A+C+F	16.51	6	30.34	0
	14	A+C+F	16.97	5	30.80	0

Table 8.3. Model-averaged regression coefficients (b) and their unconditional standard errors (SE) for bib size (B), wingbar conspicuousness (C), and wingbar area (A) in relation to measures of fighting ability. Coefficients of a given predictor were weighted using the Akaike weight of each candidate model containing that predictor. Σ shows the sum of Akaike weights for each predictor across all models that contain that predictor, reflecting the relative importance of predictors in explaining variation in the dependent variable. The effect of flock as a random factor was not estimated.

	Fighting success		Attack success		Defence success	
Predictor	Σ	b ± SE	Σ	b ± SE	Σ	b ± SE
B	0.79	0.08 ± 0.17	0.53	0.03 ± 0.10	0.99	0.09 ± 0.09
C	0.48	0.01 ± 0.05	0.39	0.00 ± 0.03	0.96	0.01 ± 0.07
A	0.18	0.01 ± 0.11	0.31	0.02 ± 0.13	0.25	–0.05 ± 0.10

8.3.2. Wing displays

In the video samples, defence success tended to be greater when the defender's wingbar was displayed than when it was not (Wilcoxon matched-pairs signed-ranks tests, $z = -1.49$, $p = 0.068$, $n = 8$ males, Fig. 8.1), while attack success was not improved by wing displaying ($z < 0.001$, $p > 0.999$, $n = 7$ males). When we used fights as data points, success was significantly associated with the use of wing display in defences ($\chi^2_1 = 16.36$, $n = 63$ defences, exact $p < 0.001$) but not in attacks ($\chi^2_1 = 1.06$, $n = 91$ attacks, exact $p = 0.388$).

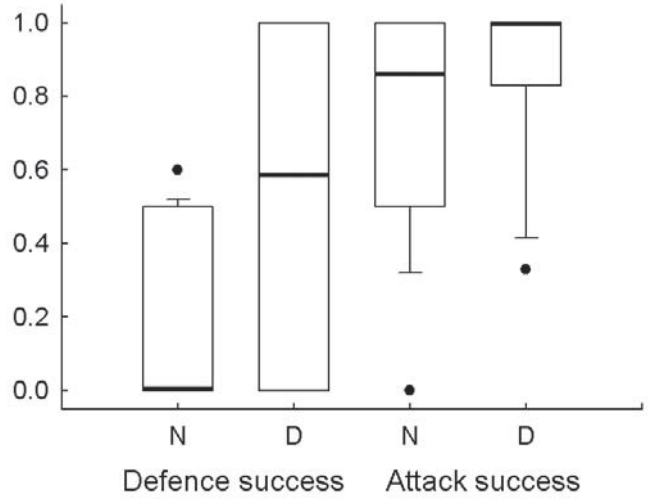

Figure 8.1. Defence success and attack success of male house sparrows in aggressive interactions without wing display (**N**) and with wing display (**D**); n = 8 and 7 males for defence and attack, respectively (see the text for statistics). Box plots show the medians (horizontal bar), 25th and 75th percentiles (top and bottom of box, respectively), 10th and 90th percentiles (whiskers) and outliers (dots).

8.4. Discussion

In this study we demonstrated that male house sparrows may use multiple cues in status signalling during social competition. First, we found that bib size of males was related to their fighting success. This finding agrees with other observations and experimental studies showing that bib size functions as a status signal during aggressive interactions of sparrows (Møller 1987a, Solberg & Ringsby 1997, Liker & Barta 2001, González et al. 2002, Hein et al. 2003). Second, we showed that beside bib size, the conspicuousness of the wingbar also explained a significant proportion of variation in defence success. This relationship was independent of the effects of bib size because (1) wingbar conspicuousness was unrelated to bib size in our sample, and (2) we controlled for the effects of bib size in multivariate analyses. Furthermore, we found that the use of wing displays also tended to improve the sparrows' success in defence but not in attack. Thus, our results suggest that conspicuous wingbars may function in aggressive interactions of male sparrows by increasing the defence success of their bearer.

Since bib size and wingbar conspicuousness were not correlated, it is unlikely that the wingbar is merely a back-up signal that serves to reinforce the signal of the bib. Furthermore, wingbar conspicuousness was related to defence but not overall fighting success, suggesting that the bib and the wingbars may have different functions in signalling during aggressive interactions. First, they may signal slightly different aspects of fighting ability. Namely, bib size may be important for assessing the opponents' overall aggressiveness or fighting ability (including both attacks and defences), whereas wingbar conspicuousness may specifically signal their ability to defend their already occupied resources (e.g. a food patch or resting site). In line with this idea, it has been shown in great tits (*Parus major*) that males selected for „fast" exploratory behaviour attack their opponents more vigorously, but „slow" individuals use more threat displays and they recover sooner after a defeat (Groothuis & Carere 2005), suggesting that attack and defence may involve different behavioural mechanisms. If such differences also exist in sparrows, it may pay for males to signal these different aspects of their fighting ability by different ornaments. Under this scenario, bib size and wingbar conspicuousness may act as „multiple badges of status" in sparrows.

Alternatively, wingbars may not signal specific information about defending potential, but may serve as signal amplifiers (Hasson 1989, Candolin 2003) to facilitate the detection and/or assessment of the birds' wing displays. Avian wing displays probably signal aggressive motivation or willingness to escalate fights (Hurd & Enquist 2001). Since sparrows can regulate the visibility of their wingbars either by exposing them in wing display or by hiding them with the neighbouring feathers, wingbars may function as „coverable badges" (Hansen & Rohwer 1986) that are exposed when birds are highly motivated to defend their resources but not displayed when birds are not willing to engage in an escalated fight. Although sparrows use the wing display during both

launching and withstanding attacks, it may be especially useful during defence because the level of motivation may be more variable among defenders than among attackers. Attackers may usually be willing to fight (otherwise they would not attack), and accordingly, the majority of attacks result in wins in sparrows (Jawor 2000, this study: Fig 8.1). Contrarily, defenders cannot help being attacked, and they should only risk fighting if they are motivated enough to defend their resources. This may explain our finding that wing displays increase defence success but do not affect attack success in sparrows. Birds may uncover their wingbars to amplify the signal of wing display, with more conspicuous badges being more effective threats (Hansen & Rohwer 1986).

We have found that the conspicuousness but not the area of wingbars was associated with defence success. This may reflect the fact that different characteristics of an ornament may differ in developmental constraints and/or selection pressures (Badyaev et al. 2001). For example, different aspects of a single plumage ornament in house finches (the hue of the red breast patch, its area and the symmetry of both) are partially independent of each other and differ both in proximate control and in fitness consequences (Badyaev et al. 2001). In sparrows, it is also possible that wingbar conspicuousness is a more reliable signal of defending ability or is more effective in amplifying rapid wing displays than the area of the wingbars (Endler 1990, Marchetti 1993).

In sum, we have found that in addition to the well known bib size, the conspicuousness of the wingbar also relates to success in social competition in male house sparrows. Wingbar conspicuousness is specifically related to defence success, which is also improved by actively displaying the wingbars. We propose that the bib and the wingbar may convey multiple messages on aspects of fighting abilities or, alternatively, wingbars may serve as amplifiers for aggressive wing displays. To our knowledge, this is the first one to demonstrate a possible use of colour traits as multiple cues in non-sexual status signalling.

9. Plumage coloration and risk taking in foraging house sparrows

Veronika Bókony, András Liker & Anna Kulcsár – Manuscript

9.1. Introduction

The costs of sexual signals are of central importance to the theory of sexual selection, since sex traits that increase mating success are expected to be constrained by costs that reduce the fitness of the trait bearer (reviewed by Kotiaho 2001). While many studies have corroborated the relationship between mating success and the expression of various sexual traits (Andersson 1994, Hill & McGraw 2006b), the costliness of these traits has received much less attention until recently (Kotiaho 2001). One of the most frequently cited costs of sexual signals is the increased conspicuousness to predators (reviews by Andersson 1994, Kotiaho 2001), but despite its wide acceptance, direct evidence for this idea is scarce (Kotiaho 2001, Godin & McDonough 2003, Lindström et al. 2006). Studies examining predation in relation to sexual traits focused mainly on auditory signals (Kotiaho 2001, Lindström et al. 2006). Despite the recent years' intensive research interest in the signalling potential of different types of avian coloration (Griffith et al. 2006, Hill & McGraw 2006a,b), empirical support for the predation costs of plumage colour traits is limited and controversial (but see Godin & McDonough 2003, Stuart-Fox et al. 2003, and Husak et al. 2006 for coloration in guppies and lizards).

Maintenance costs such as predation are especially often assumed for plumage signals that presumably have low physiological production costs. These include depigmented ornaments that are devoid of all known costs of pigment production (Török et al. 2003), and melanin-based coloration that is often considered condition-independent (although whether melanins are indeed cheap to produce has been questioned by some recent work, see Jawor & Breitwisch 2003, McGraw 2004, Griffith et al. 2006). Thus, predation costs of melanized and depigmented ornaments are in special need of study, yet experimental evidence up to now is scarce and inconclusive. Enlargement of the black plumage patches reduced the survival of house sparrow (*Passer domesticus*) males (Veiga 1995), but did not alter nest predation rates for incubating hooded warbler (*Wilsonia citrina*) females (Stutchbury & Howlett 1995). A recent experimental study showed that the white rump patch of feral pigeons (*Columba livia*) actually decreases their vulnerability to raptor attacks (Palleroni et al. 2005). Although some studies indicated that males with more pronounced black and/or white ornaments suffered greater predation than less ornamented males (Møller 1989, Slagsvold et al. 1995), these observations might have been confounded by among-male differences in dominance or reproductive effort (Veiga 1995). In a series of experiments to test whether prey

selection by raptors was affected by gross colour differences between species and sexes of prey birds, Götmark (1999) concluded that predation might select against conspicuous plumage in some cases, but his results were often confounded by sex-differences in prey behaviour, density-dependent prey selection, novelty-avoidance and other (not coloration-based) preferences of raptors (reviewed by Götmark 1999). He even suggested certain black-and-white species to be cryptic rather than conspicuous (Götmark 1999). Comparative studies specifically concerning melanin ornaments did not support that selection for crypsis influenced the interspecific variation of black plumage in shorebirds (Bókony et al. 2003) or finches (Bókony & Liker 2005). Thus, although predation may influence the overall plumage brightness of prey species (Martin & Badyaev 1996, Huhta et al. 2003), it is unclear to what extent melanized and depigmented ornaments contribute to this effect.

In the present study we manipulated the risk of predation perceived by the prey, and measured the responses of differently coloured individuals to test the predation costs associated with the expression of plumage ornaments in house sparrows. Being the principal prey of several raptors (Sodhi & Oliphant 1993, Götmark & Post 1996), the house sparrow is an ideal species for investigating predation costs. The role of the males' black throat patch (the bib) in both intra- and intersexual signalling is well studied (Møller 1987a, Møller 1988, Veiga 1993, Solberg & Ringsby 1997, Griffith et al. 1999a, Liker & Barta 2001, González et al. 2002, Hein et al. 2003), and males and females also possess a light wingbar that appears to be used, at least by males, in dominance signalling (Bókony et al. 2006). The partial concealment of the bib by white feather tips outside the breeding season has been interpreted as a mechanism to avoid the costs of predation (González et al. 2001). Accordingly, Møller (1989) demonstrated increased mortality and, in particular, increased predation for males with larger bibs in autumn and winter, although in a small sample. In contrast, in a thorough analysis of lifetime reproductive success of house sparrows, Jensen et al. (2004) found that lifespan was unrelated to bib size. No previous study has investigated the predation cost of the sparrows' wingbar. Here we tested whether the size of the black bib and the area and conspicuousness of the depigmented wingbar are related to the predation risk taken by foraging house sparrows. We predicted that, if larger or more conspicuous ornaments really pose a significant predation cost on their bearers, more ornamented birds should show a greater response to increased predation risk by decreasing their use of the more risky feeding places. Furthermore, all other things being equal, males may show a stronger preference for safer feeding sites than females because male sparrows are more ornamented than females.

9.2. Methods

9.2.1. Study site and subjects

We conducted the study in the Zoo of Veszprém, northwest Hungary. Several hundreds of house sparrows live year-round at this study site. During winter, sparrows are highly gregarious and in the Zoo they usually can be found in flocks of up to ca. 100 birds. Sparrowhawks (*Accipiter nisus*) and goshawks (*Accipiter gentilis*) regularly visit the Zoo, and we often observed sparrowhawks attacking foraging sparrow flocks and taking victims. Feral cats also hunt in the Zoo, and even captive predators such as the lynx (*Felis lynx*) occasionally take house sparrows.

We captured house sparrows in the Zoo between 16 September and 10 December 2004 using mist-nets. We ringed all birds with a numbered metal ring and an individual combination of three colour rings, and measured body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm). Body condition at capture was calculated by dividing body mass by tarsus length. The repeatability of both body mass and condition was highly significant between recaptures (using recaptures with the minimum and maximum values of each individual; mass: $r = 0.64$, $F_{207,208} = 4.48$, $p < 0.001$, condition: $r = 0.53$, $F_{199,200} = 3.25$, $p < 0.001$). By the start of the study, we individually colour-ringed and measured 410 sparrows.

9.2.2. Measuring coloration

Upon capture we measured the length (L) and width (W) of the males' bib using a ruler (± 1 mm). Then we calculated bib size assuming the shape of a circular sector with radius L and chord W (Veiga 1993). We also took digital photographs from each bird (males and females) in a standardized indoor set-up with constant lighting conditions. We photographed bibs with the males' beak held perpendicular to body axis, and wingbars on the left wings flattened (Appendix: Figs. 15.8–9). Photos were converted to grey-scale and measured using the Scion Image software (Scion Corporation 2000). We selected the area of bib or wingbar using the „density slice" and „wand tool" functions. Areas were measured in pixels and converted to cm^2 using a measured standard in the photos. Brightness of the wingbar was measured as the mean density of the pixels constituting the wingbar on the photos (the lighter the pixel, the smaller the density value). We also measured the mean density of the area of brown lesser coverts above the wingbar, and calculated wingbar conspicuousness by subtracting wingbar density from lesser coverts density (greater values may be interpreted as greater achromatic contrast between the wingbar and the lesser coverts, see Bókony et al. 2006). Coloration was not measured for moulting birds.

We tested the reliability of our colour measurements in several ways. First, we measured a number of photographs three times and calculated the repeatability of measurements (Lessells &

Boag 1987). Repeatability proved very high for all colour traits (bib size: $r = 0.99$, $F_{124,250} = 283.0$, $p < 0.001$; wingbar area: $r = 0.99$, $F_{198,398} = 766.0$, $p < 0.001$; wingbar conspicuousness: $r = 0.99$, $F_{198,398} = 388.0$, $p < 0.001$). Second, we assessed repositioning error by repositioning (i.e., taking from the photo set-up, putting back again, and re-photographing) a number of birds three times. Repeatability among these photos was also high (bib size: $r = 0.74$, $F_{25,52} = 9.7$, $p < 0.001$; wingbar area: $r = 0.87$, $F_{37,76} = 20.2$, $p < 0.001$; wingbar conspicuousness: $r = 0.68$, $F_{37,76} = 7.5$, $p < 0.001$). All these measurements were done by AK. Additionally, some photos were also measured by VB. Inter-personal repeatability was high for bib size ($r = 0.90$, $F_{15,16} = 18.2$, $p < 0.001$), wingbar area ($r = 0.88$, $F_{34,35} = 15.0$, $p < 0.001$) and wingbar conspicuousness ($r = 0.81$, $F_{34,35} = 9.3$, $p < 0.001$). Finally, to validate our method using grey-scale density values as a proxy for wingbar conspicuousness, we plucked the wingbar feathers from 25 male sparrows and measured their reflectance using a spectroradiometer (for details see Bókony et al. 2006). Wingbar density correlated significantly with total reflectance ($r = –0.49$, $p = 0.013$, $n = 25$; note that a negative correlation is expected since the greater the brightness, the less the density value).

Although the visible area of the bib increases as the season progresses due to the abrasion of white feather tips, this increase typically accelerates after the end of winter (Møller & Erritzøe 1992). In our sample, both measures of bib size remained similar within males recaptured between September and January (paired t-tests, bib size measured by ruler: $t_{30} = –0.74$, $p = 0.465$, bib size measured from photo: $t_{14} = 0.30$, $p = 0.771$), and the change in their bib size was unrelated to the time elapsed between measurements (Pearson correlations, bib size measured by ruler: $r = 0.002$, $p = 0.994$, $n = 31$, bib size measured from photo: $r = 0.16$, $p = 0.512$, $n = 19$). Ruler and photograph measures of bib size were highly correlated ($r = 0.36$, $p < 0.001$, $n = 93$), and we obtained qualitatively identical results using these two alternative measures. For brevity we only report results with bib sizes measured from photos.

9.2.3. Experimental procedure

Risk taking by sparrows was studied using two artificial feeding platforms established at two distant sites (platform sites hereafter) in the Zoo in late December 2004 and early January 2005, respectively. The platforms were made of fibreboard sheet (80 x 80 cm) and placed on the ground near bushes that were regularly used by sparrow flocks for resting. From the installation of the platforms until the beginning of the experiment, we regularly provided seed mixture (sunflower seed, wheat, millet, corn grit) on the platforms to familiarize sparrows with feeding there. Before the start of the experimental protocol (see below), the nearest edge of the platforms was always 1 m from the nearest bush. Sparrows readily fed on the platform at both sites, and used the nearest bushes as shelter.

Foraging sparrows were also studied at a third site (container site henceforward), where the birds were accustomed to feed from three plastic food containers (diameter 15 cm, height 20 cm) in which food was provided for the Zoo's racoons. The containers were simultaneously placed on the top of 1.2 m high wooden pillars that were ca. 0.5, 1.5, and 2 m away, respectively, from the nearest bush used by sparrows. All three containers were filled with a food mixture (minced meat, carrots, apples, boiled eggs, and jam) each morning.

The experimental protocol was as follows. We divided the day (between 08:00 – 15:00) into three equal observation periods. The two experimenters (AL and VB) observed feeding sparrows at the container site in one period, and at the platform sites in two periods. The order of these observations was chosen randomly each day, fulfilling the constraint that each order-combination must have occurred equal times during the study.

Each platform was observed two times on each day, by each experimenter conducting one observation per day at both sites (i.e. they changed sites between the two observation periods). At the beginning of each observation period, we added food on both platforms, and shifted the position of the platforms according to a randomly selected treatment (see below). We then left the platforms and returned after 30-60 min to start the observation. We observed the feeding sparrows from remote locations by scopes and identified as many colour-ringed individuals on the platforms as possible for 60 min. During each observation period, a video camera recorded the whole surface of the platform for 30 min at either one of the two sites (note that colour-ringed individuals could not be identified in these recordings). The camera was fixed on a tripod 1.5 m above ground and 10-30 m from the platforms (depending on the availability of suitable cover for the camera). At the end of the one-hour of observation we shifted the platforms either according to the next treatment or, at the end of the day, to the 1 m position.

To manipulate predation risk, we shifted the platform either near the shelter (the edges of the bush and of the platform were 0.5 m apart; low predation risk) or far from the shelter (the edges were 2.0 m apart; high predation risk). Positioning a feeder relative to cover is a frequently used method for manipulating predation risk in birds (e.g. Slotow & Rothstein 1995, Barta et al. 2004), and house sparrows are known to prefer foraging sites close to shelter (Horn et al. 2003). We allocated treatments such that both treatments were used at both sites on each day.

At the container site, observations were done simultaneously by the two experimenters from a remote location. Two containers were observed by the experimenters and at the third container feeding birds were recorded by a video camera placed on a tripod 2.5 m above ground and 5 m from the containers. After 30 min of observation and recording, we switched the order of experimenters and the camera such that each recorded a different container for another 30 min. The order was chosen randomly, fulfilling the constraint that each container-observer/camera combination must

have occurred equal times during the study. We identified colour-ringed individuals on the containers during observations by scopes. Birds were also reliably sexed and identified from the video recordings at the containers.

Platform manipulations were carried out on 7, 11, 13, 18, 19, 21 January and 1, 2, 4, 11 February 2005. Container observations were done on 5, 7, 18, 19, 21 January and 1, 2, 4, 9, 11 February 2005. In total, we conducted 62 hours of observation and analysed 16 hours of video-recording.

9.2.4. Data analysis

To measure the effect of treatment (near or far condition) on perceived predation risk, we analysed the video-recordings as follows. First, we defined a feeding bout as each occasion when at least one sparrow stayed on the feeder (n = 256 for the platforms and n = 276 for the containers). Then we recorded the length of bouts (from the landing of the first sparrow until the departure of the last one, in sec), and the maximum number of sparrows observed on the feeder as a surrogate of group size. We also noted the number of males, females and unsexable sparrows at the time when the maximum number of sparrows stayed on the feeder. For each bout we also recorded whether other species (mostly great tits *Parus major* and rock doves *Streptopelia decaocto* on the platforms, and blackbirds *Turdus merula* and jays *Garrulus glandarius* on the containers) stayed on the feeder. At one of the platform sites, tree sparrows (*Passer montanus*) often fed on the platform, and were sometimes difficult to distinguish from house sparrows on the video recordings. These latter bouts were excluded from the analyses. We also noted weather conditions (sunny, cloudy, or snowy) for each observation period.

Bout length and group size were $\log_{10}$ transformed to meet the assumptions of parametric tests. Sex ratio (expressed as the proportion of females) was $\log_{10}(x+1)$ transformed for the platform sites. Platform sites were analysed separately from the container site. We tested the effect of distance from shelter (fixed factor) on bout length, group size and sex ratio using general linear models (GLM). We also tested the effect of potentially confounding variables by including date, time of day (covariates), weather, and platform site (random factors) into the GLMs.

We observed 186 ringed individuals at the feeding sites during the study, with a total of 3650 recordings (1 – 121 records per individual, mean ± SE = 19.62 ± 1.54). To test for associations between their predator-related risk taking and coloration, we quantified risk-taking by the following variables. First, we counted the total number of observations an individual was seen to feed near and far from shelter (multiple recordings of the same individual in a single observation period were treated as independent observations). We then calculated the proportion of near feedings to all feedings (proportion of near feedings hereafter). Second, since individuals might have differed in

the probability of being observed (e.g. if different birds consistently fed on different parts of the feeders, making themselves more or less easy to identify), we also applied a more strict measure of risk taking by counting the one-hour observation periods in which we identified a given individual at least once (multiple recordings of the same individual during a single observation period were treated as a single observation). We then calculated the proportion of near observation periods to all observation periods (proportion of near periods hereafter). These measures of risk taking were calculated separately for the platforms and the container site. Finally, at the container site we could identify colour-ringed individuals from the video-recordings. For these individuals, we also measured the duration of their feeding bouts on the respective containers (in sec). We calculated the mean time spent on the respective containers for each individual by averaging the duration of its feeding bouts separately for the three containers. We excluded bouts in which blackbirds or jays were present on the containers, since these species often chased sparrows away. Then we expressed the proportion of time spent on the near container relative to all time spent on containers (proportion of near time hereafter) as a third measure of risk taking.

The proportions of near feedings and near periods had bimodal distributions, because birds that we identified only a few (e.g. one or two) times were often observed at only one feeder condition (near or far). For these measures of risk taking we conducted all analyses in two ways. First, we tested the relationships between risk taking and coloration variables by bivariate Spearman rank-correlations using all individuals (including those with few observations). Second, we restricted the analyses to those individuals for which we had at least ten feedings, or five observation periods, respectively. This enabled normal distributions and the calculation of more realistic proportions. Here we tested the relationships between risk taking and coloration variables by bivariate Pearson correlations. The proportion of near time was normally distributed, thus here we applied parametric analyses only.

Since risk-taking may be affected by environmental and individual factors such as time of day or body condition (Stankowich & Blumstein 2005), we used multivariate statistical models to control for such confounding effects. We tested the multiple effects of coloration and possible confounding variables on risk-taking in multivariate mixed GLMs. Because environmental factors such as weather or time of day varied across observation periods, as dependent variable we used the number of occasions (bouts) a bird was identified in each observation period (i.e. we used observations periods instead of individuals as measurement units), and included individual as random factor. Initial full models included date, time of day (covariates), and the interaction of feeder position (fixed factor) with all colour variables, body condition and wing length (covariates). Additionally, platform models included weather as fixed factor, and container models included observation period as random factor (because both near and far positions were available

simultaneously within a given period at this site). We eliminated non-significant effects stepwise by removing the predictor with the largest p-value in each step (Grafen & Hails 2002), but never excluding the random factors and feeder position.

All tests were two-tailed with a 95% confidence level. We report means ± SD followed by range (min – max). We provide t-values for independent samples t-tests throughout. We used the R statistical computing environment (R Development Core Team 2003) and SPSS 11.0 for statistical analyses.

9. 3. Results

Among all the birds measured by the start of the study, bib size ranged 0.11 – 2.30 cm^2 (0.86 ± 0.41, n = 161). Wingbar area was significantly larger in males (1.03 ± 0.30, 0.13 – 1.69 cm^2, n = 157) than in females (0.36 ± 0.13, 0.14 – 0.81 cm^2, n = 117; $t_{272} = 24.99$, $p < 0.001$). Wingbar conspicuousness was also significantly greater in males (83.10 ± 13.25, 52 – 113) than in females (64.10 ± 9.39, 37 – 86; $t_{272} = 13.89$, $p < 0.001$).

9.3.1. Effect of treatment on perceived predation risk

9.3.1.1. Platforms

Sparrows spent significantly less time on the platforms in the far than in the near condition ($t_{158} = 4.32$, $p < 0.001$; Fig. 9.1), and group size was also significantly smaller far than near shelter ($t_{149} = 2.30$, $p = 0.023$; Fig. 9.2). These results remained unchanged when we included several potentially confounding variables in GLMs (site, date, time of day, weather; Table 9.1), or when we excluded bouts in which other species (tits or doves) were present (not shown). Sex ratio on the platforms did not differ between the far and near conditions ($t_{160} = 0.72$, $p = 0.471$), even when controlling for the above variables (Table 9.1). The latter results should be treated with caution, however, because 8 ± 22 % (0 – 100 % in respective feeding bouts) of the sparrows could not be sexed from the platform videos.

9.3.1.2. Containers

Sparrows spent significantly more time feeding on the container nearest to shelter than on the two farther containers ($F_{2,273} = 6.32$, $p = 0.002$; Fig. 9.3). Group size did not differ on the three containers ($F_{2,273} = 1.23$, $p = 0.295$), note however that group size was limited to a maximum number of 10 sparrows crowding on a single container, while up to 28 sparrows could conveniently fed on the platforms. These results were not altered when we included date and time of day in the GLMs (Table 9.1; weather was constant during container observations), or when we excluded bouts

in which other species (blackbirds or jays) were present (not shown). We observed a significantly greater proportion of female sparrows on the nearest than on the farthest container ($F_{2,273} = 3.19$, $p = 0.043$; Fig. 9.4), even when controlling for date and time of day (Table 9.1).

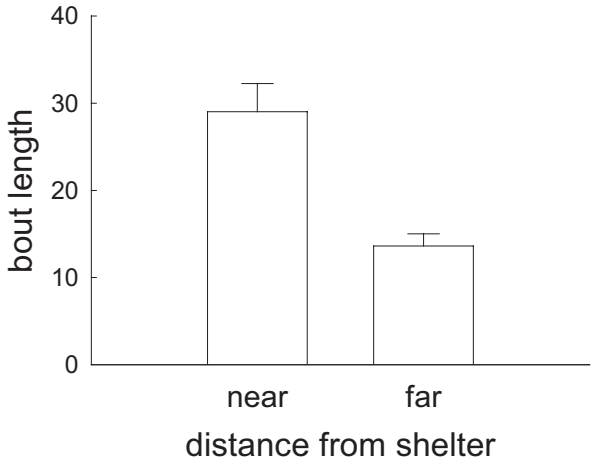

Figure 9.1. Feeding bout length (in sec, mean + SE) of sparrow flocks on the platforms near and far from shelter (data from the two platform sites combined).

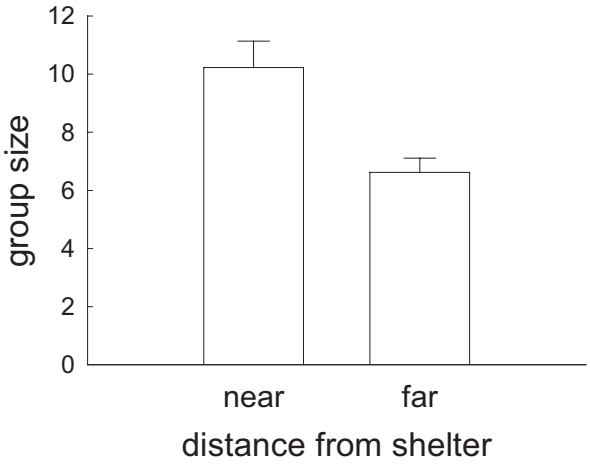

Figure 9.2. Group size (maximum number of sparrows per feeding bout; mean + SE) on the platforms near and far from shelter (data from the two platform sites combined).

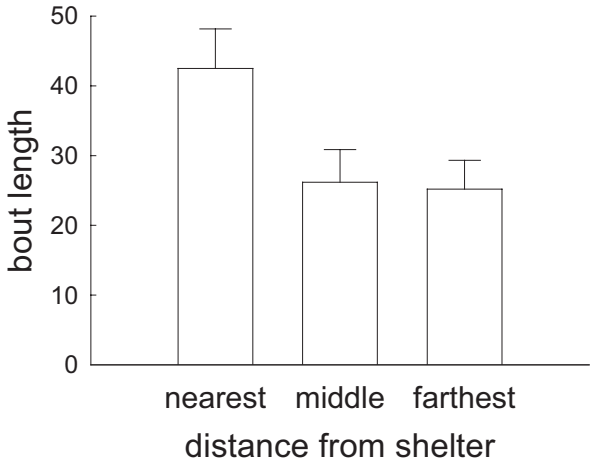

Figure 9.3. Feeding bout length (in sec, mean + SE) of sparrow flocks in relation to distance from shelter on the three containers.

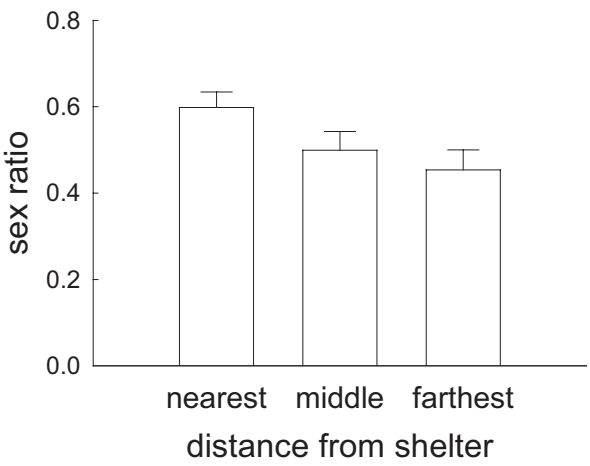

Figure 9.4. Sex ratio (proportion of females, mean + SE) of sparrow flocks in relation to distance from shelter on the three containers.

Table 9.1. Feeding bout length (sec), maximal group size (no. birds), and sex ratio (proportion of females) of sparrow flocks feeding on two types of feeders, in relation to the feeder's distance from shelter and possible confounding variables. Effect sizes (η^2) are given for the initial full GLMs. Asterisks (*) mark the predictors included in the final models obtained by stepwise backward elimination of non-significant effects.

	Feeding bout length		Maximal group size		Sex ratio	
	Platforms	Containers	Platforms	Containers	Platforms	Containers
Distance from shelter	0.088*	0.049*	0.098*	0.014	0.014	0.031*
Date	< 0.001	0.006	0.050*	0.019*	0.074*	0.003*
Time of day	0.095*	0.034*	0.009	0.001	0.002	0.031
Platform site	0.145*	–	0.018	–	0.114*	–
Weather	0.039*	–	0.068*	–	0.038	–

9.3.2. Coloration and risk taking

Of the 186 colour-ringed individuals identified during observations, 83 were seen at both types of feeders (platform and container). For these birds, the proportion of near feedings was not correlated between the two feeder types (for all birds: $r_s = 0.10$, $p = 0.353$, $n = 83$; for individuals with at least ten feedings: $r = 0.05$, $p = 0.724$, $n = 65$), neither was the proportion of near periods (for all birds: $r_s = 0.09$, $p = 0.404$, $n = 83$; for individuals with at least five observation periods: $r = –0.02$, $p = 0.879$, $n = 66$).

9.3.2.1. Platforms

On the platforms, neither the proportion of near feedings nor the proportion of near periods was related to bib size, wingbar area, or wingbar conspicuousness in males and females (Table 9.2). The sexes did not differ in either measure of risk taking (Table 9.3). The two platform sites did not differ in the proportions of near feedings (for all birds: $t_{147} = 0.60$, $p = 0.549$; for individuals with at least ten feedings: $t_{84} = –1.34$, $p = 0.185$) and near periods (for all birds: $t_{147} = 1.72$, $p = 0.089$; for individuals with at least five observation periods: $t_{80} = 0.86$, $p = 0.391$), hence we pooled data from the two platform sites in the above analyses. Note however that we obtained identical results when platform site was included as a factor in the stepwise models (not shown).

In multivariate analyses, the effects of all colour variables remained non-significant. The final model for males included time of day ($F_{1,338} = 16.14$, $p < 0.001$) and wing length (feeder position * wing length interaction: $F_{1,338} = 5.60$, $p = 0.019$). The final model for females contained time of day ($F_{1,274} = 10.47$, $p = 0.001$) and date ($F_{1,274} = 7.11$, $p = 0.008$).

Table 9.2. Relationships between measures of risk taking and coloration in male and female sparrows feeding on two types of feeders. Bivariate Pearson correlations were restricted to individuals with at least ten feedings or five observation periods, respectively. Results of bivariate Spearman rank-correlations for all birds are given in parentheses.

		Platforms			Containers		
		r (r_s)	p	n	r (r_s)	p	n
Proportion of near feedings, with:							
bib size		–0.05	0.766	47	–0.11	0.544	36
		(–0.09)	(0.407)	(84)	(–0.19)	(0.155)	(55)
wingbar area							
	males	0.04	0.803	48	–0.15	0.373	37
		(0.04)	(0.692)	(85)	(0.11)	(0.431)	(54)
	females	–0.10	0.541	37	–0.06	0.731	34
		(–0.15)	(0.250)	(58)	(0.05)	(0.724)	(47)
wingbar conspicuousness							
	males	0.26	0.070	48	0.20	0.230	37
		(0.07)	(0.520)	(85)	(0.12)	(0.394)	(54)
	females	–0.13	0.454	37	–0.04	0.821	34
		(0.002)	(0.991)	(58)	(0.01)	(0.962)	(47)
Proportion of near periods, with:							
bib size		–0.08	0.648	38	–0.07	0.642	47
		(–0.11)	(0.323)	(84)	(–0.18)	(0.192)	(55)
wingbar area							
	males	–0.06	0.706	48	0.01	0.941	39
		(0.03)	(0.767)	(85)	(0.18)	(0.203)	(54)
	females	–0.14	0.431	34	0.06	0.721	34
		(–0.16)	(0.237)	(58)	(0.08)	(0.612)	(47)
wingbar conspicuousness							
	males	0.18	0.220	48	0.16	0.347	39
		(0.07)	(0.542)	(85)	(0.13)	(0.369)	(54)
	females	–0.18	0.318	34	0.02	0.915	34
		(0.003)	(0.984)	(58)	(0.07)	(0.628)	(47)

9.3.2.2. Containers

On the containers, the proportions of near feedings and near periods were unrelated to bib size, wingbar area and wingbar conspicuousness in both sexes (Table 9.2). The proportion of near time on the containers was not related to bib size (r = 0.11, p = 0.764, n = 10), wingbar area (males: r = 0.02, p = 0.957, n = 11; females: r = 0.11, p = 0.665, n = 17) and wingbar conspicuousness (males: r

< 0.001, p > 0.999, n = 11; females: r = 0.03, p = 0.908, n = 17). Males and females did not differ in any of the three measures of risk taking (Table 9.3).

In multivariate analyses, the effects of all colour variables remained non-significant again. The final model for males included only the time of day ($F_{1,109} = 5.45$, p = 0.021), while the final model for females contained time of day ($F_{1,146} = 5.68$, p = 0.018) and wing length (feeder position * wing length interaction: $F_{1,146} = 9.56$, p = 0.002).

Table 9.3. The effect of sex on measures of risk taking in house sparrows feeding on two types of feeders. For the tests marked by asterisks (*) z values of Mann-Whitney U-tests are given instead of t.

	Platforms			Containers		
	t (or z)	p	n	t (or z)	p	n
Proportion of near feedings:						
all individuals*	–0.79	0.430	154	–0.12	0.906	115
birds with ≥ 10 feedings	–0.13	0.896	90	–0.28	0.782	75
Proportion of near periods:						
all individuals*	–0.57	0.567	154	–0.86	0.391	115
birds with ≥ 5 obs. periods	–0.03	0.975	86	–0.17	0.869	77
Proportion of near time:						
all individuals	–	–	–	1.13	0.270	30

9.4. Discussion

In this study we tested whether individual variation in predator-related risk taking during foraging was associated with the elaborateness of melanin-based and depigmented plumage ornaments in house sparrows. We successfully manipulated the predation risk perceived by sparrows, as shown by their shorter feeding time and smaller flock size at the more risky (farther) feeder conditions. Yet, the birds' risk taking was not related to their coloration. First, the use of the more risky feeders was unrelated to either the males' bib size or to the area and conspicuousness of the wingbars in both sexes. Second, despite that males are more ornamented than females, they did not use the more risky feeders less than females. Third, although a number of sparrows were observed at both platform and container sites, their proportions of near feedings and near periods were not correlated between the two feeder types, suggesting that they had no consistent preferences for particular feeder locations (near or far). These results imply that sparrows do not adjust their predator-related

risk taking to the degree of their ornamentation. Thus we found no support that individual variation in black and depigmented ornaments of sparrows influence their predation risk significantly.

How can these results be explained? First, although the black bib of male sparrows contrasts strongly with the surrounding light breast feathers at close view, yet when viewed at longer distances by predators, it may blend in with the brown and grey patterns of the bird and its background (Endler 1978, 1990), providing a relatively inconspicuous appearance. Furthermore, sparrows typically feed on the ground where their bibs seem to be hidden rather than exposed to any observer (e.g. a raptor) viewing from above. Second, although the light wingbar is displayed pronouncedly by sparrows during aggressive interactions (Bókony et al. 2006), it can be totally covered by the neighbouring feathers, and we often observed sparrows to stay on the feeders with completely hidden wingbars (VB, pers. obs.). Similarly, male chaffinches (*Fringilla coelebs*) expose their white wing patch, which promotes their detectability to humans, only during social and sexual displays and hide it while foraging (Götmark & Hohlfält 1995). Thus, whereas the presence or absence of some additional square millimetres of melanized plumage or slight differences in its brightness may well be conspicuous and informative to sparrows during sexual and non-sexual interactions (Møller 1988, Veiga 1993, Griffith et al. 1999a, Liker & Barta 2001, Hein et al. 2003, Bókony et al. 2006), it seems unlikely that this variation is relevant to, and constrained by, predators.

Alternatively, more ornamented birds might have better escape abilities that compensate for increased conspicuousness. For example, Moreno-Rueda (2003) reported that bib size was correlated with the capacity to escape from a predator that hunts by chasing sparrows (not by surprise attacks). However, the main predictor of chase-escaping ability was wing length (Moreno-Rueda 2003), which did not influence the relationship between coloration and risk-taking in our study. Also, we controlled for individual differences in body condition that may affect escape ability and/or risk-taking (Stankowich & Blumstein 2005), and still found no effect of coloration. It is also noteworthy that coloration is not correlated with either wing length or body condition within age groups in our population (not shown). Finally, although dominant birds may outcompete subordinates from safer feeding sites (Slotow & Rothstein 1995), it is unlikely that such effects masked the relation between coloration and risk-taking in our study. First, dominant males have larger bibs and more conspicuous wingbars (Møller 1987a, Liker & Barta 2001, Hein et al. 2003, Bókony et al. 2006), which would predict even less predation risk taken by more ornamented males. Second, dominant females are heavier (Liker & Barta 2001), yet body mass did not influence risk-taking or its relation with female coloration (not shown).

If the predation costs of sparrow ornaments are minimal, then how can the honesty of these signals be maintained? For bib size, there is convincing evidence that males with larger bibs are

more dominant and do better in social competition than males with smaller bibs (Møller 1987a, Solberg & Ringsby 1997, Liker & Barta 2001, González et al. 2002, Hein et al. 2003, Bókony et al. 2006). Frequent aggression among males with similarly sized bibs was reported to control cheats (Møller 1987b), however, both theoretical (Johnstone & Norris 1993) and empirical work (González et al. 2001) suggested that such social control alone is not sufficient to maintain the reliability of the status signalling system. Alternatively, bib size may be linked to the competitiveness of males through the regulatory effect of testosterone, since both bib size (Evans et al. 2000, González et al. 2001, Buchanan et al. 2001) and aggressive and sexual behaviours (Hegner & Wingfield 1987) are enhanced by elevated testosterone levels. According to this idea, males that interact more aggressively with conspecifics during moult grow larger bibs (McGraw et al. 2003). Furthermore, testosterone may handicap the immunocompetence of males (reviewed by Roberts et al. 2004), although the evidence is still inconclusive whether this cost can mediate the link between bib size and male quality in house sparrows (Buchanan et al. 2003, Greenman et al. 2005).

The wingbar's significance in sparrows' social interactions has only been investigated recently (Bókony et al. 2006), showing that males may use the wingbars in signalling defensive aggression. The function of the females' somewhat darker wingbars has not been studied, but these might have a similar signalling role because females display them as frequently and successfully as males during aggressive interactions (V. Bókony, Á. Lendvai & A. Liker, unpublished results). Interestingly, two recent studies indicate that the white wingbars of male sparrows may reflect some aspects of their quality, namely their ability to obtain high-protein food at the time of moult (Poston et al. 2005) or their resistance to ectoparasites (Moreno-Rueda 2005). These findings warn us that even depigmented plumage badges might be condition-dependent through significant production costs.

Taken together, we have found no evidence that house sparrows with more conspicuous melanin-based and depigmented plumage ornaments respond more strongly to increased predation risk than less ornamented individuals. We propose that other mechanisms such as hormonal regulation and condition-dependent production are more plausible ways than predation costs to maintain the reliable signalling function of the sparrows' colour badges.

10. Testosterone and melanin-based plumage coloration in birds

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10.1. Introduction

Conspicuous coloration has long been the focus of research on sexual selection, and plenty of studies have demonstrated the adaptive function of colour traits in both intrasexual competition and mate choice (Andersson 1994, Hill 2006, Senar 2006). Research on the proximate control of coloration has lagged behind until the last decade, despite the crucial importance of understanding the mechanisms that regulate the expression of coloration. For example, it is difficult to see why female house finches (*Carpodacus mexicanus*) would prefer to mate with males with more red in their plumage (Hill 1990) unless we understand that the red colour is derived from carotenoid pigments by a process that is sensitive to both nutritional condition (Hill & Montgomerie 1994, Hill 2002) and endoparasitic infections (Brawner et al. 2000, McGraw & Hill 2000). Thus, redness signals individual quality through its condition-dependence.

For melanin-based coloration such as the black bib of house sparrows (*Passer domesticus*), the signalled information proved more complex to understand. Although several hypotheses have been put forward regarding the proximate control of melanization (Jawor & Breitwisch 2003, McGraw 2003), empirical evidence is few and controversial. For instance, the expression of certain melanin ornaments are under strong genetic control (Roulin & Dijkstra 2003), while others are determined by environmental effects (Griffith et al. 1999b). Experimental studies up to now barely found any effect of nutrition or endoparasitism on melanization (Hill & Brawner 1998, McGraw & Hill 2000, McGraw et al. 2002, Poston et al. 2005), whereas resistance to ectoparasites was shown to be related to melanin-based coloration in some species (Roulin et al. 2001a, Fitze & Richner 2002). These results hardly explain the overall picture that melanin ornaments seem to signal dominance rank and competitive ability in a wide range of bird species (reviews by Hill 2006, Senar 2006).

One promising candidate for the regulation of melanization is the level of sex hormones, most importantly androgens. Testosterone (T) appears to be involved in regulating melanin pigmentation in skin, scales, feathers, hair, and fur in several vertebrate taxa (Haase et al. 1995, Tadokoro et al. 1997, 2003, Evans et al. 2000, Peters et al. 2000, Buchanan et al. 2001, González et al. 2001, Hill & McGraw 2003, Quinn & Hews 2003, but see Roulin et al. 2004). Increased T levels of male birds have also been shown to enhance aggressive and sexual behaviour (Wingfield et al. 1987, Goodson et al. 2005). Thus, T may mediate the frequently observed relationship between melanization and

aggression in male birds. Furthermore, a similar relationship may be expected for females, because intra-sexual aggression among females is significant in many species, often involving plumage ornaments (Amundsen & Pärt 2006), and several studies suggest that female T may be under direct selection, especially in monogamous and colonial species where females are expected to compete more intensely for territories and/or mates (Garamszegi et al. 2005, Ketterson et al. 2005).

In this study we investigated the relationship between T and melanin-based coloration at the interspecific level. Such a comparative approach has successfully been used previously to identify factors influencing the evolution of T levels (Hirschenhauser et al. 2003, Goymann et al. 2004, Garamszegi et al. 2005, Ketterson et al. 2005, Møller et al. 2005) and melanization (Owens & Hartley 1998, Bókony et al. 2003, Bókony & Liker 2005). Although the latter studies demonstrated the adaptive value of melanin ornaments in sexual selection and parental care, no comparative study has attempted to test interspecific associations between this specific type of coloration and its proposed regulating factors such as nutrients, parasites or sex hormones (Griffith et al. 2006), as has been done for carotenoid ornaments (Mahler et al. 2003, Olson & Owens 2005). Here we examined whether plumage melanization is consistently related to any measures of T in a taxonomically diverse set of avian species. We tested the predictions that (i) species with more melanized males should have higher male T levels, (ii) species with more melanized females should have higher female T levels, and (iii) species with greater sexual dimorphism in melanization (henceforth melanin dichromatism) should also exhibit greater sex differences in T levels (henceforth T dimorphism). The latter prediction is expected since selection for increased T in males was found to be associated with a relative decrease in females, possibly because of the costs of high T levels in females (Møller et al. 2005).

10.2. Methods

The primary selection criterion of bird species for the study was the availability of T data, without any taxonomic restrictions (Appendix: Table 15.4). We collected data on breeding baseline T (level B *sensu* Wingfield et al. 1990), breeding peak T (level C *sensu* Wingfield et al. 1990), and non-breeding baseline T (level A *sensu* Wingfield et al. 1990) of male birds from Hirschenhauser et al. (2003), Goymann et al. (2004), Garamszegi et al. (2005) and Møller et al. (2005). Female breeding peak T data were obtained mainly from Møller et al. (2005; see Appendix: Table 15.4 for data sources), breeding and non-breeding baseline T levels were unavailable for females. We used T concentrations measured from blood plasma only, not fecal equivalents. In sum, we gathered T data on 141 species. When more than one T value was available for a species, we used the most recent one of the above compilations. From these sources we also gathered data on the following potentially confounding variables that has been shown to affect T levels and/or melanization: social

mating system (polyandrous, monogamous, polygynous, or lekking), mean latitude of distribution, testes mass, extra-pair paternity (% of offspring being extra-pair offspring), parental care (paternal, biparental, helpers or maternal/none), paternal incubation (% of male contribution to incubation) and paternal feeding (% of male contribution to feeding offspring in altricial species), and coloniality (solitarily or colonially breeding). In some cases these data were obtained from Perrins (1998). Relative testes mass was expressed as residuals from regressing testes mass on body mass. T values and confounding variables (except mating system and parental care) were $\log_{10}$ transformed to obtain normal distributions. We calculated residual T levels (*sensu* Garamszegi et al. 2005) as the residuals from regressing peak T on non-breeding baseline T, which depicts the difference between T levels within and outside the breeding season. Note that this measure is not comparable to androgen responsiveness (*sensu* Wingfield et al. 1990, Hirschenhauser et al. 2003) which describes T variability within the breeding season. Both the absolute values of baseline and peak T and their residuals have previously proved relevant in investigating interspecific variation of T levels (Goymann et al. 2004, Garamszegi et al. 2005, Møller et al. 2005), and species measures of baseline and peak T are both repeatable among different studies (Garamszegi et al. 2005). Sexual dimorphism in T was calculated as the residulas from regressing independent contrasts (see below) in female peak T on contrasts in male peak T.

We evaluated melanization, defined as the extension of black on the whole breeding plumage (not bare parts), using colour plates and detailed descriptions in Perrins (1998), del Hoyo et al. (1992–2003), and various field guides. We did not consider non-black melanization, since the pigmentary basis of such colours cannot be judged by their appearance (McGraw et al. 2004). We measured melanization (Appendix: Table 15.4) on a scale from zero (no black) to ten (all black) using a scoring method adapted from Owens & Hartley (1998). Total melanization was the sum of scores from the five main body regions (head; upperparts i.e. nape, back and rump; underparts i.e. throat, chest and belly; wings; and tail), where each body region was scored separately: 0, no black present; 1, partially black; and 2, completely black plumage region. We also defined frontal melanization as the sum of head and underparts scores (with maximum value of 5), because these body regions are highly variable in melanization across species, and are most likely to function in intraspecific signalling (Bókony et al. 2003, Bókony & Liker 2005, Senar 2006). Using one source of colour plates (Heinzel et al. 1995), both total and frontal melanization were repeatable (Lessels & Boag 1987) between two scorers (VB and LZG, total melanization: $r = 0.74$, $F_{32,33} = 6.64$, $p < 0.001$, frontal melanization: $r = 0.75$, $F_{32,33} = 6.85$, $p < 0.001$). However, because scoring depends on the source of illustration for some species, scores used in our analyses were obtained by one observer (VB) using as many sources as possible for each species, assigning melanization only to regions that are consistently illustrated black. We measured total melanin dichromatism as the sum

of scores from the five main body regions, where each body region was scored separately as 0 if sexes did not differ in black, 1 if males had more black, and –1 if females had more black on a given plumage region. We also defined frontal melanin dichromatism similarly to frontal melanization. Note that species may have non-zero dichromatism score even if the sexes have identical melanization scores when both sexes are partially melanized on the scored body region. We did not score melanization for domesticated species in which coloration and possibly also hormonal patterns have been changed by artificial selection.

We obtained phylogenetic information from Sibley and Ahlquist (1990), augmented by recent data from Kimball et al. (1999) and Dimcheff et al. (2002) for *Galliformes*, Geffen & Yom-Tov (2001) for *Anseriformes*, Friesen et al. (2002) for *Sula*, Nunn et al. (1996) for *Diomedea*, Klicka et al. (2005) for *Turdus*, James (2004) for *Drepanidini*, Badyaev (1997) for *Carduelinae*, Sato et al. (2001) and Yuri & Mindell (2002) for *Thraupini*, Webster & Webster (1999) for *Atlapetes*, Patten & Fugate (1998) and Klicka et al. (2000) for other *Emberizini*, and Searcy et al. (1999) for *Icteridae*. Our composite phylogeny is shown in the Appendix (Fig. 15.13).

We used two alternative approaches to control for phylogenetic relatedness among species. First, we calculated phylogenetically independent contrasts (Felsenstein 1985) as implemented by the CAIC 2.6 program (Purvis & Rambaut 1995). We tested the relationships between the contrasts in melanization or dichromatism as dependent variables and the contrasts in T levels and confounding variables as predictors by least square linear regressions forced through the origin (Harvey & Pagel 1991). We investigated (i) the relation between T and melanization for males and (ii) for females separately, and (iii) the relation between T dimorphism and melanin dichromatism. We generated branch lengths according to either a gradual model of evolution (the ages of taxa are proportional to the number of species they contain), or a punctuational model of evolution (unit branch lengths; Purvis & Rambaut 1995). Since the two models yielded the same conclusions, we present the results for the gradual model only. The assumptions of the independent contrast method (Purvis & Rambaut 1995) were not in all cases met, thus we repeated these analyses using each species as an independent datum. Simulation tests showed that the independent contrast method yields biased results only when evolutionary constraints are very strong, in which case analyses using raw species data should give reasonable results (Martins et al. 2002). Our conclusions remained unchanged when we analyzed species without phylogenetic control, thus we report the CAIC results only.

Second, we conducted matched-pair comparisons between closely related taxon-pairs (Harvey & Nee 1997). This method restricts comparisons to the terminal nodes of the phylogeny, thus it makes less stringent statistical assumptions than the independent contrast method. We chose pairs of species that clearly differed in the extension of black on their plumage (Appendix: Table 15.5).

To enable a reasonable sample size, we also considered sister-species that had the same melanization scores but apparently differed greatly in the amount of black (e.g. the two *Parus* species; for a short description of differences within pairs see Appendix: Table 15.5). Note that species categorized as „more melanized" had significantly greater scores for total (mean ± SE = 4.63 ± 0.52) and frontal (2.06 ± 0.20) melanization than their „less melanized" sister-taxa (total: 1.43 ± 0.27, frontal: 0.74 ± 0.15; Wilcoxon matched-pairs signed-ranks tests: total melanization: $z = -4.69$, $p < 0.001$, $N = 34$; frontal melanization: $z = -4.09$, $p < 0.001$, $N = 34$). Taxon-pairs were chosen so that sister-species do not differ in social mating system that is known to influence interspecific differences in breeding baseline T (Hirschenhauser et al. 2003) and peak T (Garamszegi et al. 2005). Matching mating systems also led to matching parental care systems in all but two of our species-pairs (*Aix–Tadorna*, *Tetrao–Lagopus*; excluding these pairs did not alter our results qualitatively). When several species were available for a taxon-pair, we used the mean of their respective T values. Using paired t-tests, we investigated whether species with more melanized males have higher T levels. We also tested whether sister-species differed in the relevant potentially confounding variables. Since female T data were limited, and interspecific variation in melanization was much less in females than in males, only males could be tested in the paired comparisons. We used the R statistical computing environment (R Development Core Team 2003) and SPSS 11.0 for statistical analyses. All tests were two-tailed with a 95% confidence level. Sample sizes differ across statistical analyses, since various data were not available for some species.

10.3. Results

10.3.1. T and melanization in males

In males, breeding baseline T was significantly positively related to both total melanization ($r = 0.34$, $F_{1,69} = 8.79$, $p = 0.004$; Fig. 10.1a) and frontal melanization ($r = 0.39$, $F_{1,69} = 12.20$, $p = 0.001$; Fig. 10.1b). In paired tests, species with more melanized males tended to have higher breeding baseline T than less melanized species ($t_{11} = 2.13$, $p = 0.057$). Breeding peak T was significantly positively related to both total melanization ($r = 0.30$, $F_{1,122} = 12.29$, $p = 0.001$; Fig. 10.1c) and frontal melanization ($r = 0.34$, $F_{1,122} = 16.39$, $p < 0.005$; Fig. 10.1d). Consistently, more melanized species had higher peak T than less melanized species ($t_{32} = 2.45$, $p = 0.020$; Fig. 10.2a). Also, residual T correlated significantly with both total melanization ($r = 0.25$, $F_{1,96} = 6.30$, $p = 0.014$; Fig. 10.1e) and frontal melanization ($r = 0.40$, $F_{1,96} = 18.38$, $p < 0.005$; Fig. 10.1f). Consistently again, residual T levels were greater in more than in less melanized species ($t_{24} = 2.09$, $p = 0.048$; Fig. 10.2b).

We checked the effects of potentially confounding variables in several ways. First, we tested whether they related to melanization scores in bivariate linear regressions of independent contrasts. In our sample, both total and frontal melanization were unrelated to mating system, latitude, extra-pair paternity, parental care, and paternal incubation (Table 10.1). However, both melanization variables related positively to relative testes mass (i.e. residuals from regressing testes mass on body mass) and paternal feeding (Table 10.1). Second, we included respective T levels, relative testes mass and paternal feeding as predictors in multiple regression models (including all confounders would have decreased sample size seriously). In these analyses, the effects of all measures of breeding T on both melanization variables remained significant, as was the effect of relative testes mass in most cases, while paternal feeding was non-significant in all models (Table 10.2). Third, we tested whether more and less melanized sister-species differed in any of our confounders using paired t-tests. We found no such differences in latitude ($t_{33} = –0.59$, $p = 0.556$), relative testes mass ($t_{16} = –0.25$, $p = 0.809$), paternal incubation ($t_{20} = 1.30$, $p = 0.209$) and paternal feeding ($t_{15} = 0.65$, $p = 0.528$; extra-pair paternity data were not available for most of our species-pairs). Thus the T differences between more and less melanized species were not mere by-products of differences in these confounders.

Table 10.1. Bivariate relationships between melanization and ecological traits in male birds. Least square linear regressions of independent contrasts were forced through the origin.

Dependent	Predictor	r	F (df)	p
Total melanization	Mating system	< –0.005	< 0.005 (1,128)	0.971
	Latitude	< –0.005	0.11 (1,121)	0.735
	Relative testes mass	0.25	5.62 (1,86)	0.020
	Extra-pair paternity	0.04	0.05 (1,34)	0.817
	Parental care	–0.07	0.41 (1,96)	0.523
	Paternal incubation	0.05	0.20 (1,91)	0.658
	Paternal feeding	0.21	4.13 (1,92)	0.045
Frontal melanization	Mating system	0.01	0.01 (1,128)	0.924
	Latitude	0.11	0.11 (1,121)	0.739
	Relative testes mass	0.20	3.75 (1,86)	0.056
	Extra-pair paternity	0.01	< 0.005 (1,34)	0.958
	Parental care	–0.11	1.11 (1,96)	0.294
	Paternal incubation	0.06	0.32 (1,91)	0.572
	Paternal feeding	0.22	4.52 (1,92)	0.036

In turn, non-breeding baseline T was not related to total melanization ($r = –0.02$, $F_{1,102} = 0.06$, $p = 0.804$) or frontal melanization ($r = –0.08$, $F_{1,102} = 0.67$, $p = 0.414$). Consistently, non-breeding baseline T levels did not differ between pairs of more and less melanized species ($t_{25} = 1.08$, $p = 0.289$). In some species, however, melanization differs in breeding and non-breeding plumage due to pre-nuptial moult, which may erase the relationship between non-breeding baseline T and breeding melanization. Thus we scored total and frontal melanization in non-breeding plumages in the same way as breeding melanization. None of these measures were related to non-breeding baseline T (total non-breeding melanization: $r < 0.005$, $F_{1,99} < 0.005$, $p = 0.952$; frontal non-breeding melanization: $r = –0.05$, $F_{1,99} = 0.24$, $p = 0.626$). Among our taxon-pairs, some sister-species did not differ in non-breeding melanization (*Aix–Tadorna, Phalaropus–Actitis, Malurus spp.*). After excluding these pairs, more and less melanized species still did not differ in non-breeding baseline T ($t_{23} = 1.37$, $p = 0.185$).

Table 10.2. Multivariate analyses of breeding measures of T and melanization, controlling for the effects of relative testes mass and paternal feeding, in male birds. Multiple linear regressions of independent contrasts were forced through the origin.

		Male total melanization[1]		Male frontal melanization[2]	
	Predictors	r	p	r	p
Breeding baseline T model:					
$^1F_{3,48} = 3.56$, $p = 0.021$					
$^2F_{3,48} = 4.72$, $p = 0.006$					
	Breeding baseline T	0.26	0.070	0.44	0.012
	Relative testes mass	0.26	0.067	0.26	0.149
	Paternal feeding	0.02	0.869	0.20	0.330
Breeding peak T model:					
$^1F_{3,60} = 3.95$, $p = 0.012$					
$^2F_{3,60} = 7.60$, $p < 0.005$					
	Breeding peak T	0.26	0.044	0.44	< 0.005
	Relative testes mass	0.31	0.016	0.26	0.043
	Paternal feeding	0.03	0.801	0.20	0.126
Residual T model:					
$^1F_{3,58} = 4.68$, $p = 0.005$					
$^2F_{3,58} = 8.77$, $p < 0.005$					
	Residual T	0.32	0.014	0.49	< 0.005
	Relative testes mass	0.31	0.018	0.26	0.041
	Paternal feeding	0.01	0.869	0.15	0.239

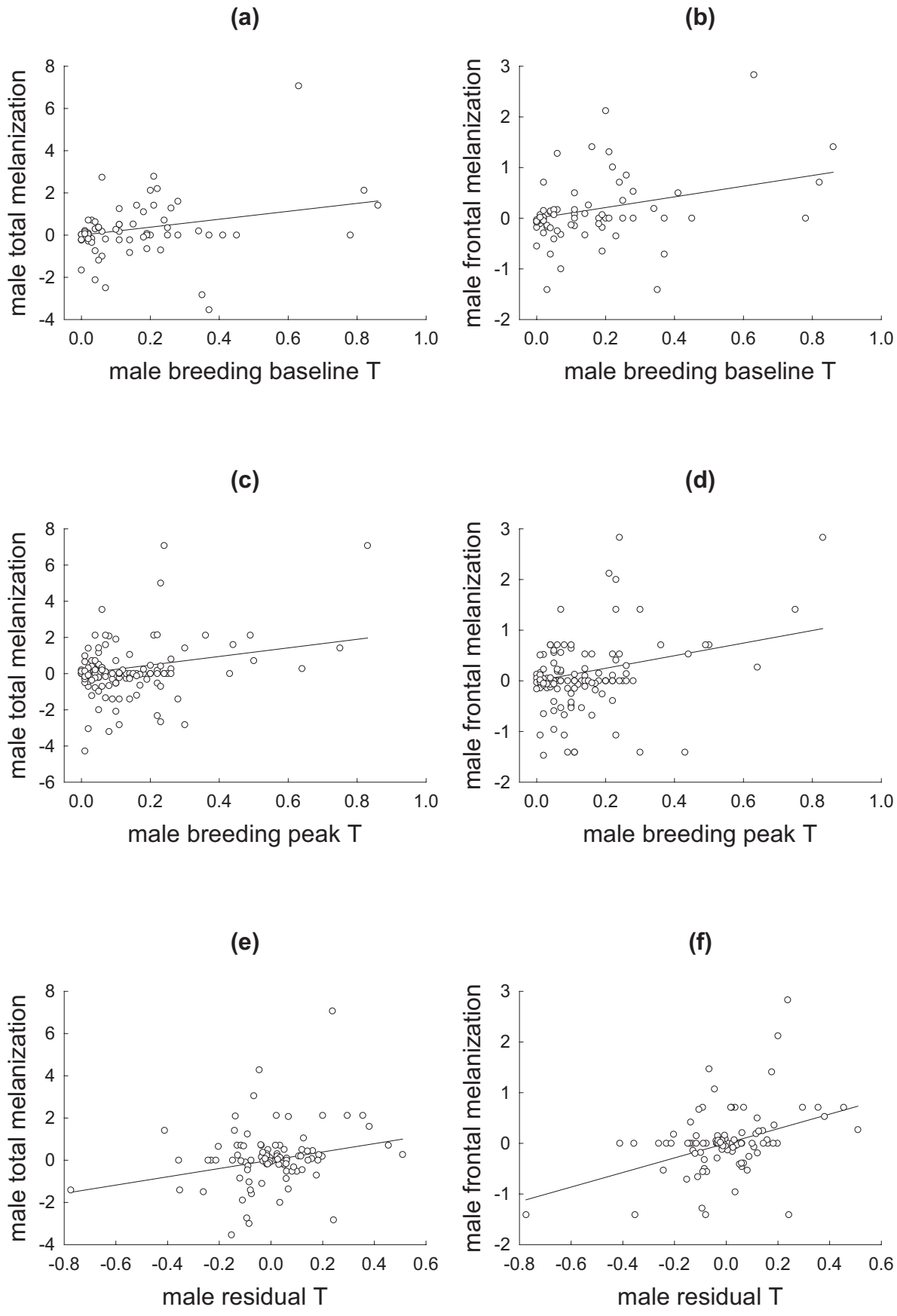

Figure 10.1. Relationships between phylogenetically independent contrasts in breeding measures of T and in melanization among male birds. Regression lines are forced through the origin.

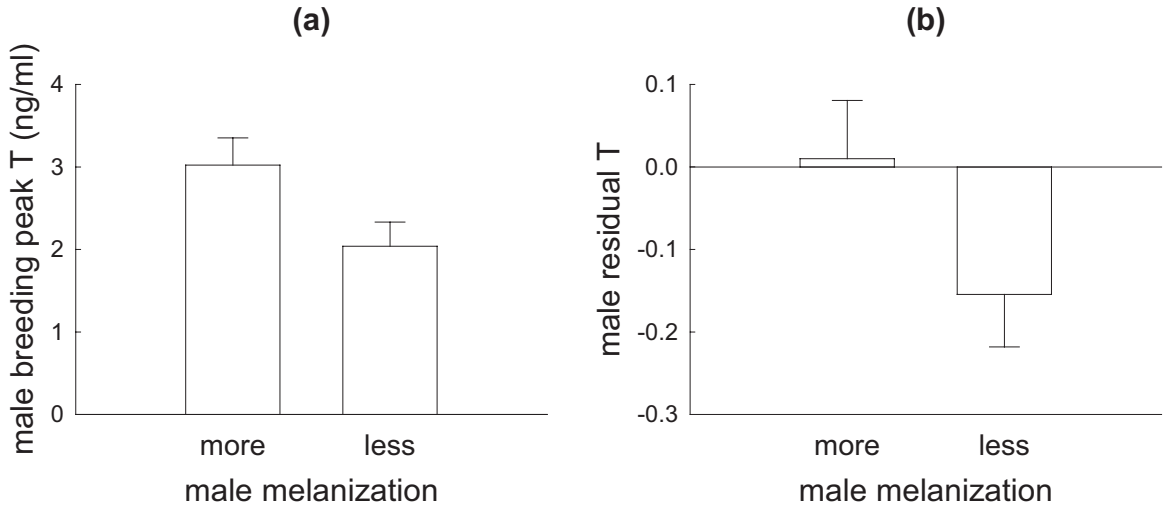

Figure 10.2. (a) Male breeding peak T (mean ± SE, n = 33) and **(b)** residual T (residuals from the regression of breeding peak T on non-breeding baseline T; mean ± SE, n = 25) in pairs of closely related bird species that differ in male melanization (extension of black on the whole plumage) but not in social mating system.

10.3.2. T and melanization in females

In females, breeding peak T was significantly positively related to both total melanization ($r = 0.42$, $F_{1,58} = 12.60$, $p = 0.001$; Fig. 10.3a) and frontal melanization ($r = 0.33$, $F_{1,58} = 7.01$, $p = 0.010$; Fig. 10.3b). Females of colonial species have higher T levels than females of solitarily breeding species (Møller et al. 2005), and using bivariate linear regressions of independent contrasts we found that colonial females were more melanized than solitary females (total melanization: $r = 0.63$, $F_{1,58} = 37.21$, $p < 0.005$; frontal melanization: $r = 0.59$, $F_{1,58} = 31.07$, $p < 0.005$). After controlling for the effect of coloniality in multiple linear regressions, the relationship between total melanization and female T remained significant, whereas frontal melanization tended to increase with female T (Table 10.3).

10.3.3. T dimorphism and melanin dichromatism

As expected, T dimorphism significantly negatively correlated with total melanin dichromatism ($r = –0.30$, $F_{1,58} = 5.75$, $p = 0.020$, Fig. 10.4), and showed a similar trend with frontal melanin dichromatism ($r = –0.25$, $F_{1,58} = 3.71$, $p = 0.059$). This means that female T (relative to male T) is smaller than expected in highly dichromatic species with more melanized males, while females have higher than expected relative T levels in species where sexes are equally melanized. We also controlled for the effects of relative testes mass and coloniality, since these were the significant confounders for male and female melanization, respectively. In multiple regression analyses, the

effect of T dimorphism was significant on both total and frontal melanin dichromatism, whereas relative testes mass and coloniality were all non-significant (Table 10.4).

Some species in our data set have reversed sex roles, with females being more aggressive and more ornamented than males (*Actitis*, *Dromaius*, *Phalaropus* spp.). It has been suggested that these phenomena are caused not by increased T levels but possibly by changes in androgen receptivity in females (Fivizzani et al. 1986). Thus we repeated all our analyses after excluding these species (results not shown). All results remained qualitatively similar and did not alter our conclusions.

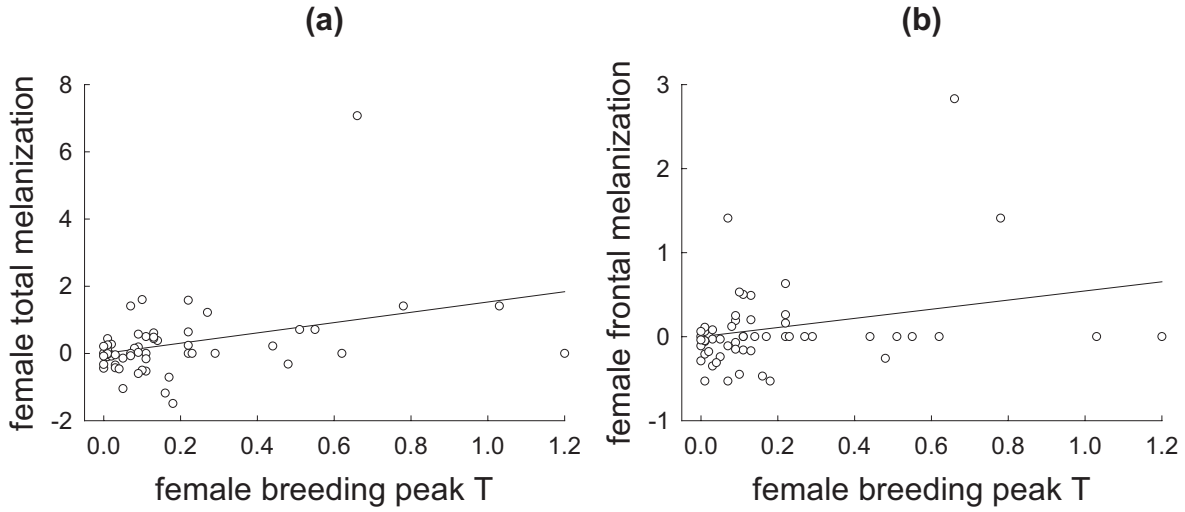

Figure 10.3. Relationships between phylogenetically independent contrasts in breeding peak T and in melanization among female birds. Regression lines are forced through the origin.

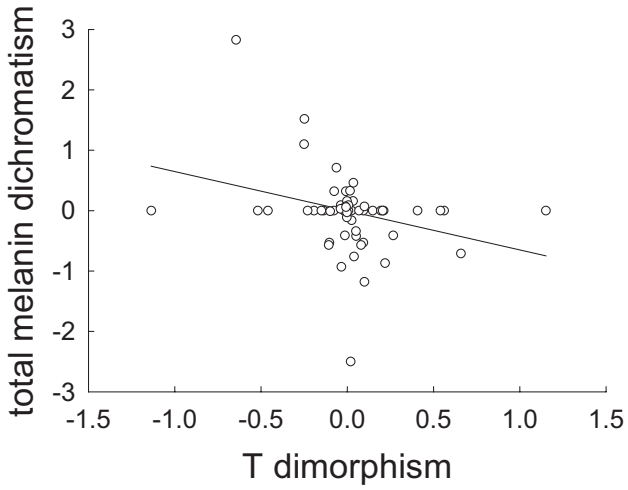

Figure 10.4. Relationship between T dimorphism (residulas from regressing independent contrasts in female peak T on contrasts in male peak T) and independent contrasts in total melanin dichromatism (sexual dimorphism in the extent of black plumage). The regression line is forced through the origin.

Table 10.4. Multivariate analyses of T dimorphism (residulas from regressing female peak T on male peak T) and melanin dichromatism (sexual dimorphism in black melanization), controlling for the effects of residual testes mass and coloniality. Multiple linear regressions of independent contrasts were forced through the origin.

	Total melanin dichromatism (Model $F_{3,35} = 3.90$, $p = 0.017$)		Frontal melanin dichromatism (Model $F_{3,35} = 1.65$, $p = 0.195$)	
	r	p	r	p
T dimorphism	–0.49	0.002	–0.33	0.043
Residual testes mass	0.03	0.870	< 0.005	0.997
Coloniality	0.18	0.291	0.07	0.669

10.4. Discussion

Our study has provided three key results. First, evolutionary increases in the extent of black plumage have paralelled the increases in all breeding measures of T in male birds. These results are likely to be robust, since they were consistent between two alternative phylogenetic approaches, and were not altered by the effect of several measures of mating competition and parental behaviour. Second, similarly to males, evolutionary increases in female melanization corresponded to increases in peak breeding T, indicating that a common mechanistic link might exist between melanization and T. Third, sex differences in T and in melanization were correlated, in a manner that species with equally black sexes showed the smallest fall-off in female T relative to male T. Our findings thus suggest that interspecific differences in black melanization may have co-evolved with or evolved in response to differences in T levels. We propose three alternative explanations for these relationships.

First, melanization may have evolved in response to T, as T may be involved in the regulation of melanogenesis. This idea is in concordance with the findings of several intraspecific studies that demonstrated the effect of T on melanocyte function or melanogenesis (Tadokoro et al. 1997, 2003, Hill & McGraw 2003) and on plumage or skin melanization (Haase et al. 1995, Evans et al. 2000, Peters et al. 2000, Buchanan et al. 2001, González et al. 2001, Quinn & Hews 2003). To our knowledge, the present study is the first to provide comparative support for the hypothesis that T may be a widespread mediator of melanization in birds. If so, increased levels of aggression or fighting activity for acquiring higher rank or greater mating success should lead to elevated T and thereby to increased melanization. Thus, T-regulation could enable melanin ornaments to honestly reflect the competitive ability of individuals.

Second, T levels may have evolved in response to melanization, as melanin ornaments may expose males to social challenges that increase T. Since melanin ornaments are frequently involved in dominance signalling and intrasexual competition (Senar et al. 1999, Jawor & Breitwisch 2003), extensive melanization may increase T levels by stimulating opponents' aggressive behaviour (Wingfield et al. 1990, Hirschenhauser et al. 2003). Such „social testing" has been hypothesized to ensure the costs of bearing melanin ornaments that signal high rank (Rohwer 1977). However, both theoretical (Johnstone and Norris 1993) and empirical work (González et al. 2001) suggest that social testing alone is not sufficient to maintain the honesty of the status signalling system, hence we need additional mechanisms to explain the link between aggression and melanization (such as T). It is also possible that a „positive feedback loop between aggression and T levels together may mediate the expression of melanin-based ornamental coloration" (McGraw et al. 2003).

Third, the evolutionary relationship between melanization and T may have arisen due to a third, unmeasured variable that influences both. Although in our study we controlled for the effect of several relevant ecological traits that are known to influence T, we could not measure potential confounders that act at the infra-individual level. Importantly, many behavioral effects of T are in fact mediated by the action, at the cellular level, of estrogens derived from local aromatization of androgens in the brain (Goodson et al. 2005). When the testes are regressed and circulating T levels are low, birds are still able to express similar aggressive behaviours by delivering steroid precursors (such as dehydroepiandrosterone, produced by the adrenals and the regressed testes) to the brain and converting them into T and estrogens, or by synthesizing steroids *de novo* in the brain (Goodson et al. 2005). Thus, different levels of aggression are possibly regulated by differences in the activity of aromatase (the enzyme that converts androgens into estrogens) both at the intraspecific and interspecific level (Silverin et al. 2000, 2004). Aromatase activity in the brain regions regulating male sexual behaviours is correlated with plasma T levels during social challenges in the breeding season (Silverin et al. 2000). Interestingly, the same aromatization of T into estrogens has been suggested to mediate the effect of T on melanin pigmentation (Haase et al. 1995). For example, in chicken with a henny feathering mutation, increased aromatization of androgens to estrogens takes place in the skin and causes more heavily eumelanized plumage (Carefoot 2002). Cells in the skin and feather follicles are able to bind, metabolize and produce sex steroids, and estrogens are also known to affect melanocytes (Jee et al. 1994, McLeod et al. 1994, Carefoot 2002, Zouboulis 2004). Thus, melanogenesis may be influenced either by estrogens produced and released to circulation by the brain or other tissues (Silverin et al. 2000), or by the local aromatization of T and other sex steroids in the skin (Carefoot 2002, Zouboulis 2004).

We have found an association between melanization and levels of breeding but not non-breeding T. This may seem confusing since many bird species develop melanin ornaments during

the post-breeding moult when the testes are regressed and T levels are typically low (Goodson et al. 2005). However, two lines of evidence are worth considering here. First, as detailed above, aromatase activity may link the intensity of melanogenesis to the level of aggression expressed at any time of the year, including T-mediated aggression during breeding. Second, since the levels of non-breeding baseline T are typically low (i.e. less detectable by measuring techniques) and less repeatably measured across species than breeding peak T (Garamszegi et al. 2005), it is also possible that we have failed to detect an otherwise existing relationship between melanization and non-breeding baseline T simply because variation in T levels is better captured by breeding measures of T. Notably, non-breeding baseline T is correlated with breeding peak T among species ($r = 0.32$, $F_{1,96} = 11.29$, $p = 0.001$, see also Garamszegi et al. 2005). According to the social challenge hypothesis, species with low breeding baseline T remain hormonally responsive to social challenges, while androgen responsiveness is typically low in species that maintain high breeding baseline T (Wingfield et al. 1990, Hirschenhauser et al. 2003). Although this hypothesis was originally proposed and supported for breeding measures of T (Wingfield et al. 1990, Hirschenhauser et al. 2003), it has been extended to year-round aggressive behaviour in tropical birds (Wikelski et al. 1999), and it might also hold for the social challenges during moult (McGraw et al. 2003). In house sparrows for example, males that interact more aggressively during moult grow larger bibs (McGraw et al. 2003). The subtle differences among male sparrows in T levels during the post-breeding period (when moult occurs) are enough to determine their bib size, and non-breeding T is correlated with breeding T within individuals (Buchanan et al. 2001).

Taken together, we have provided the first phylogenetic comparative evidence that melanin-based black coloration is related to circulating levels of T in both male and female birds. Demonstrating the causality of this relationship is not possible at the interspecific level, thus more case studies are needed to ascertain the underlying mechanisms, with specific respect to the role of aromatase.

11. Conclusions

The studies presented in this thesis revealed several lines of evidence, both at the inter- and intraspecific level, for the signalling potential of melanin ornaments in sexual and social selection. First, phylogenetic comparative studies support the role of sexual selection in the evolution of black plumage in two distantly related avian groups, shorebirds and cardueline finches. Second, black melanization is evolutionary related also to the breeding levels of male sex hormone (T) in a hundred of bird species ranging from ratites to small passerines. Third, we showed that mating success but not aggressiveness of male penduline tits is related to the size of their black eye-stripe. These 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 (e.g. McGraw & Hill 2000). 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, not only as status signals but also as mate choice criteria (Tarof et al. 2005, Griffith et al. 2006, Hill 2006). Although different colour traits may convey information on different aspects of male quality, the information that females are looking for may well vary among species or even among populations of a given species (Griffith et al. 1999a, Hegyi et al. 2002). Finally, we demonstrated that both wingbar conspicuousness and bib size of male house sparrows is related to their success in defensive aggression, indicating that different colour badges may communicate multiple messages to conspecifics not only in mate choice but also in status signalling. Since we did not find support for the predation costs of these ornaments, our results also highlight the urging need for exploring the possible mechanisms that maintain the reliability of melanin signals. In the following sections I discuss these possibilities and their current evidence, and propose directions for future research.

11.1. Indices of quality

As detailed in chapter 10, melanin-based coloration may be uncheatably linked to aggressiveness or sexual competitiveness by the regulatory effects of testosterone. Although the present-day bunch of case studies implies that the effect of T on melanization varies among species (McGraw 2006a) and even among plumage regions within a given species (Haase et al. 1995), our wide-ranging comparative study indicated that a specific type of melanin ornaments, namely the extent of black plumage is consistently associated with increased T levels (chapter 10). This finding parallels the well-documented case of the size of the black bib in male house sparrows, which is influenced by intraspecific variation in T (Evans et al. 2000, Buchanan et al. 2001, González et al. 2001). Despite these promising relationships detected both at the inter- and intraspecific level, the cellular or

molecular mechanisms by which T may affect melanogenesis are poorly known. The few studies up to now have provided controversial results. For example, the activity of tyrosinase (the enzyme responsible for the first step of melanogenesis and several following steps of eumelanin synthesis) was stimulated by T in human genital melanocytes (Tadokoro et al. 1997) but was inhibited in normal human melanocytes (Tadokoro et al. 2003). No such studies have been conducted on birds, to which the results of mammalian studies cannot be automatically extrapolated (McGraw 2006a). Recent research has also discovered intriguing alternative pathways in the hormonal regulation of aggressive behaviour, involving the effects of estrogens, dehydroepiandrosterone and aromatase (reviewed by Goodson et al. 2005, see also chapter 10), yet their relevance to melanin pigmentation is just speculative. Future studies should establish whether such mechanisms may provide a link between the expression of melanin-based coloration and aggression.

Additionally, recent studies on barn owls (*Tyto alba*) indirectly support another possibility, namely that melanization might be an index of immunocompetence. The area covered by black spots on the ventral plumage of females (i.e. spottiness) signals their resistance to ectoparasites, and both spottiness and parasite resistance are inherited by offspring without any sign of environmental effects (Roulin et al. 2000, 2001a). Roulin (2004) proposed a possible explanation that the genes responsible for variation in the amount of eumelanin pigments may have pleiotropic effects on the immune system, for example through α-MSH. This hormone is produced from the large precursor molecule proopiomelanocortin along with several agents of innate host defence and stress response (Catania et al. 2000). The role of α-MSH is poorly studied in birds because they lack the hypophysial lobe that manufactures this hormone in mammals, yet some recent evidence cautions that birds do synthesize α-MSH in their brain, eyes or skin for physiological purposes including the regulation of pigmentation (Boswell & Takeuchi 2005). Thus a genetic link between melanization and immunity might exist and deserves further research.

11.2. Costly signals (handicaps)

As reviewed in chapter 2.4, the production and maintenance of melanin ornaments may involve various costs that may ensure their condition-dependent expression. Although some previous studies concluded that „carotenoid-based coloration is more vulnerable to the effects of diet, parasitism, and overall condition than is melanin-based coloration" (Hill & Brawner 1998), these studies appreciated the mechanisms of carotenoid expression much more mindfully than those of melanins. For example, while they demonstrated that endoparasitic infections injuring the intestinal epithelium seriously hamper the uptake of carotenoids but not melanins (Hill & Brawner 1998, McGraw & Hill 2000), they did not attempt to explore any specific mechanisms by which endoparasites may influence melanization. By contrast, utilizing the knowledge that melanins are

synthesized from specific amino acids, Poston et al. (2005) found experimental support for the condition-dependence of two melanin-based ornaments, the brightness of the black bib and the width of the pheomelanin-based/white wingbar in male house sparrows. By manipulating the amount of proteins and melanogenic amino acids in the diet, they showed that these ornaments are sensitive to nutritional conditions and thereby may reflect the males' ability to acquire proteins or particular amino acids. However, diet manipulations did not affect bib size (McGraw et al. 2002, Poston et al. 2005), suggesting that different aspects of melanin-based coloration may be differentially prone to certain environmental stressors. Hence, studies that carefully delve into the mechanistic basis of melanization are required so that we can assess how it may signal specific components of individual quality. If melanization appears to be costly in certain cases, it should be tested whether these costs are indeed strategic costs of signalling that differ between individuals displaying low and high quality (Kotiaho 2001, Maynard Smith & Harper 2003).

11.3. Badges of status

Even when a melanin ornament is virtually uncostly to produce and unlinked to individual quality, it may be used to reliably signal social status if costs are paid by individuals that give false signals (Maynard Smith & Harper 1988, 2003). This means that cheaters should be punished by truly dominant individuals, a postulate that has proved quite difficult to demonstrate in non-primate animals. For the status badges of birds, the social control hypothesis has been proposed (Rohwer 1977), predicting that cheaters are exposed to increased risk of fighting with truly high-quality opponents because of greater aggression among similarly ranked individuals. Experimental tests up to now did not provide unambiguous evidence for this hypothesis in any species (reviewed by Senar 2006), thus it remains a challenge to take. Still, there are some promising results at hand. In Hungarian collared flycatchers for example, territorial males respond more aggressively to intruders with larger white wing patches (Garamszegi et al. 2006), indicating that bearing a large wing patch should be costly for weak males. Furthermore, the owners' wing patch size is not related to their aggressivity, suggesting that the wing patch is an arbitrary badge of status rather than a signal of fighting ability *per se* (Garamszegi et al. 2006). Future experimental studies should consider the badges and behaviour of both participants (i.e. signallers and receivers) of status signalling systems (Garamszegi et al. 2006, Senar 2006).

11.4. „Uninformative cues"

Although the currently favoured paradigm of sexual selection is that sexual traits are indices or costly signals of individual qualities (reviewed by Kotiaho 2001), it is important to bear in mind

that, theoretically, mate-choice cues need not be functionally designed to signal specific components of male fitness (Candolin 2003, Kokko et al. 2003), unless we think of fitness in conventional terms such as viability or fecundity. The use of „uninformative" or „unreliable" cues seems to be common in mate choice (reviewed by Candolin 2003), including arbitrary attractiveness traits and signal amplifiers.

Arbitrary attractiveness traits (also called „Fisherian traits", although the Fisherian theory is not confined to arbitrary cues) are misleadingly termed uninformative because they do indicate an important fitness component: heritable attractiveness that increases the reproductive value of offspring (Candolin 2003, Kokko et al. 2003). If a preference exists for any heritable male trait, indirect benefits arise inevitably to females choosing the preferred trait since their sons will be attractive too (i.e. sexy sons). Therefore females may prefer such traits even if mate choice is costly and attractive males sire offspring of poor viability (Kokko et al. 2003). Eye-stripe size in penduline tits might provide an example for this case. As shown in chapter 7, females do not seem to benefit from mating to males with large eye-stripes, since their nestlings survived worse than those of males with small eye-stripes. The low nestling survival was not due to larger brood size or less parental care (chapter 7), thus it may indicate poor nestling quality. Furthermore, males with larger eye-stripes deserted more often, which reduces their females' reproductive success (Szentirmai 2005). These results suggest that the males' eye-stripes might have evolved as a manipulative tool through an antagonistic coevolution between sexes, to seduce females even at their expenses (Holland & Rice 1998). However, if eye-stripe size is heritable, as are several melanin-based ornaments (Møller 1989, Hegyi et al. 2002, Roulin & Dijkstra 2003, Török et al. 2003), then the sexy-sons benefit to females might exceed the aforementioned costs of mating with males with large eye-stripes. In our study we could not examine such indirect benefits, hence further investigations should clarify this issue.

Signal amplifiers are traits that that do not convey any information about the signaller's quality but instead facilitate the detection and assessment of its other signal(s) (Hasson 1989, Candolin 2003). Such an effect may be advantageous not only for the signaller but also for the receiver, e.g. by increasing the accuracy or speed of estimating the signaller's quality. In two spider species for example, males display their black ventral markings to rivals and females, so that it can be easier to assess their condition signalled by the plumpness of their abdomen (Taylor et al. 2000, Moya-Larato et al. 2003). Our comparative studies (chapters 5-6) provided two lines of indirect evidence that black melanization may be especially suitable to amplify visual signals. First, by contrasting strongly with the background of blue sky, black plumage may amplify the flight displays of plover species (chapter 5), a costly signal of male agility (Grønstøl 1996, Blomqvist et al. 1997). Second, the extent of black melanization follows a similar trend with reproductive investment among

cardueline finches as overall plumage brightness (chapter 6, Badyaev 1997b) which is largely determined by carotenoid-based coloration (Badyaev & Hill 2000). This seems to imply that finch species with reduced parental efforts couple melanin and carotenoid ornaments in sexual signalling, although carotenoid- but not melanin-based coloration is preferred by females in the two carduelines tested so far (Johnson et al. 1993, Senar et al. 2005). The coupled signalling role of the two types of pigmentation may be explained by the fact that black ornaments provide strong contrast with the bright yellow or orange carotenoid colours, thus melanization might function as an amplifier for the costly signals of carotenoids, such as it does in guppies (Brooks 1996).

Both arbitrary attractiveness traits and signal amplifiers may be selected for by biases of the receiver's sensory system or psychology (i.e. sensory drive; Endler & Basolo 1998). These biases could have evolved in contexts other than sexual selection, such as natural selection to detect predators or prey (Endler & Basolo 1998). In water mites for instance, the male stimulates the predatory response of the female by „courtship trembling" that mimics the vibration of prey to manipulate her orientation to favour the uptake of his spermatophores (Proctor 1991). Although such sensory traps may be costly to females in some cases, for example if the prey-mimicking male signals reduce the foraging efficiency of females, there is evidence that deceiving sensory traps can evolve into honest signals of quality (Macías Garcia & Ramirez 2005, Stuart-Fox 2005). Alternatively, sensory biases may be non-functional innate properties of the sensory system or results of genetic drift (Endler & Basolo 1998). Birds have been shown to have „latent" preferences for non-existent male traits, e.g. two non-crested grassfinch species prefer mates with artificial white crests but not other colours, and this preference seems to lack any adaptive function (Burley & Symanski 1998). Up to now, sensory drive and amplifiers have received interest almost exclusively in the context of mate choice, yet both may be relevant in social signalling too. The study presented in chapter 8 provides a possible example for this case: the conspicuous wingbar of male house sparrows might have evolved as an amplifier to promote the motivational signal of wing displays. Birds may well have a sensory preference for contrasting stimuli (e.g. Johnson et al. 1993, Heindl & Winkler 2003), thus black and white ornaments offer excellent opportunities to study the role of sensory biases in the evolution of sexual and social signals.

11.5. Final remarks

The studies presented in this thesis have paralleled the emerging research interest in the signalling function of melanin-based coloration. Here we focused mainly on the size of eumelanin-based black ornaments, as done by the majority of previous case studies of melanin signals (Hill 2006, Senar 2006). However, recent advances in the methodologies of quantifying colours and pigments, coupled with a developing comprehension of the proximate control of coloration (Hill & McGraw

2006a) enable researchers to move away from handy black patches to more elaborated studies of melanization. First, melanins produce a wide range of colours depending on the amount and ratio of eu- and pheomelanin pigments deposited into the coloured parts (McGraw 2006a). Apart from the first step of synthesis, the two kinds of melanins are derived through separate pathways that have different regulatory agents (Jawor & Breitwisch 2003). Therefore, eu- and pheomelanin ornaments may have the potential to reveal different types of information about their bearer, which would be most interesting to examine in species that exhibit both kinds of melanization. Second, melanin ornaments often vary not only in size but also in brightness, hue and saturation (Jawor & Breitwisch 2003, Siefferman & Hill 2003), symmetry (Swaddle & Cuthill 1994), immaculateness (Ferns & Lang 2003), or their fine-scale patterning even within feathers that is unique to melanin-based coloration (McGraw 2006a). Each of these aspects may have its own signalling function. Considering colour ornaments as complex traits is essential not to miss their „multiple messages" (Badyaev et al. 2001, Candolin 2003), not only the ones they signal to conspecifics but also the ones we can learn from them.

11.6. New scientific results

To summarize, the following new results have been achieved in this thesis:

1. 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, while they are unlikely to be selected for camouflage.
2. We also provided comparative support for the relationship between melanization and sexual selection in a second group of birds, finches that are known to use carotenoid-based signals in mate choice. We found that reduced reproductive investment was associated with more extended black plumage, indicating a trade-off between parental efforts and melanin ornaments as mating efforts.
3. In a field study we showed that the size of the black eye-stripe of male penduline tits predicts their attractiveness to females in terms of mating time and number of mates, but it does not predict their 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.
4. We demonstrated that the conspicuousness of the wingbar of male house sparrows predicts specifically their defence success in aggressive interactions, even after controlling for the effect of the status-signalling bib size. 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.
5. In a field experiment we found that male and female house sparrows do 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. These results argue against the widely accepted yet rarely tested hypothesis that colour signals are maintained by predation costs.
6. 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. This is the first interspecific study to relate melanization to one of its potential regulatory agents, suggesting that testosterone might unfakeably link melanization to competitiveness.

12. References

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14. 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.

Bókony V. & Liker A. 2005. Melanin-based black plumage coloration is related to reproductive investment in cardueline finches. *Condor* 107, 775–787.

Bókony V., Lendvai Á. & Liker A. 2006. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows. *Ethology* 112, in press.

Kingma S.A., Szentirmai I., Székely T., Bókony V., Bleeker M., Liker A. & Komdeur J. 2006. Sexual selection and the function of melanin-based plumage coloration in promiscuous penduline tits (*Remiz pendulinus*). Manuscript, submitted to *Anim. Behav*.

Bókony V., Liker A. & Kulcsár A. 2006. Plumage coloration and risk taking in foraging house sparrows. Manuscript.

Bókony V., Liker A., Hirschenhauser K. & Garamszegi L.Z. 2006. Testosterone and melanin-based plumage coloration in birds. Manuscript.

Articles related to the thesis:

Bókony V. 2004. Csábító erejű színek. A hódító fekete. *National Geographic Magyarország* 2, 10.

Bókony V., Liker A., Székely T., Kis J. & Szentirmai I. 2005. A melanin alapú színezet funkciója madaraknál: a hódító fekete? *Állattani Közlemények* 90, 17–28.

Bókony V. 2006. A tollazat színének funkciói I. Költséges díszekkel a szerelemért. *Élet és Tudomány* 61(34): 1066–1068.

Bókony V. 2006. A tollazat színének funkciói II. Költséges melaninok. *Élet és Tudomány* 61(35): 1101–1103.

Conference presentations related to the thesis:

Bókony V., Liker A., Székely T. & Kis J. 2003. Melanin-based plumage coloration and flight displays in plovers and allies. *Wader Study Group Annual Conference*, Cádiz, Spain.

Bókony V., Liker A., Székely T. & Kis J. 2004. Melanin-based plumage coloration and flight displays in plovers and allies. *10th International Behavioral Ecology Congress*, Jyväskylä, Finland.

Kingma S.A., Szentirmai I., Bókony V., Liker A., Bleeker M., Székely T. & Komdeur J. 2004. Men in black: girls just love them. The function of melanin-based plumage pigment in promiscuous penduline tits. *10th International Behavioral Ecology Congress*, Jyväskylä, Finland.

Bókony V., Liker A., Székely T., Kis J., Szentirmai I. & Lendvai Á.Z. 2004. A melanin alapú színezet funkciója madaraknál: a hódító fekete? *Magyar Madártani és Természetvédelmi Egyesület VI. tudományos ülése*, Debrecen, Hungary.

Bókony V., Lendvai Á.Z. & Liker A. 2005. Swords and shields differ: multiple ornaments reflect different aspects of fighting ability in male house sparrows. *XXIX. International Ethological Conference*, Budapest, Hungary.

Bókony V. & Liker A. 2006. A tesztoszteronszint és a melanin alapú színezet kapcsolata. *A Magyar Tudományos Akadémia Állatorvos-tudományi Bizottsága és a Szent István Egyetem Állatorvos-tudományi Doktori Iskola Akadémiai Beszámolói,* Budapest, Hungary.

Bókony V., Liker A., Hirschenhauser K. & Garamszegi L.Z. 2006. Testosterone and melanin-based plumage coloration in birds. *11th International Behavioral Ecology Congress*, Tours, France.

Bókony V., Liker A. & Kulcsár A. 2006. Plumage coloration and risk taking in foraging house sparrows. *11th International Behavioral Ecology Congress*, Tours, France.

Bókony V., Liker A. & Kulcsár A. 2006. A színezet kapcsolata a predációs kockázat-vállalással házi verebeknél. *7. Magyar Ökológus Kongresszus*, Budapest, Hungary.

15. Appendix

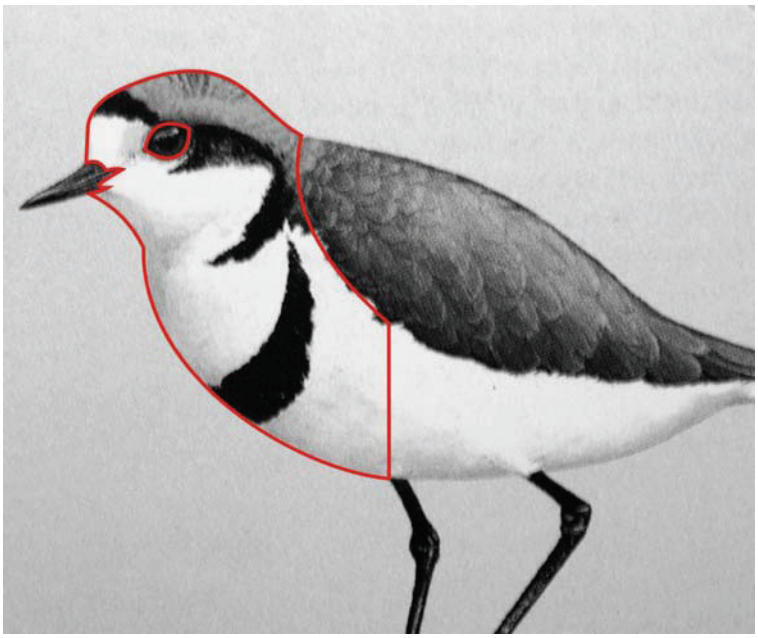

Figure 15.1. Definition of the frontal body region on colour plate images and photographs. Melanization of plovers and finches was measured as the proportion of black area relative to the total area of the frontal body (i.e. head, neck and breast bordered by the lower edge of the wing and a vertical line drawn from the base of the leg; as indicated by the red line). The picture was taken from del Hoyo et al. (1996).

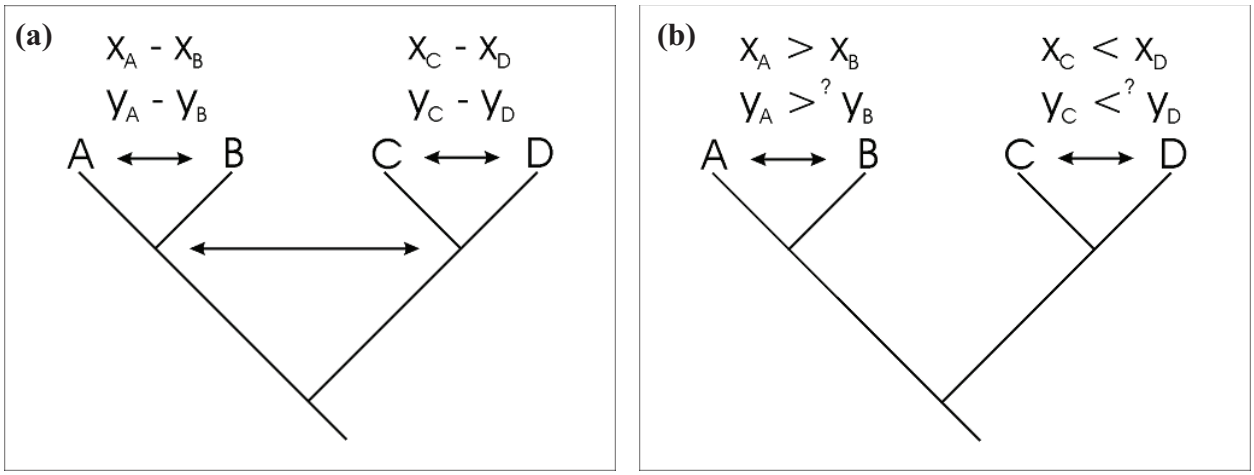

Figure 15.2. Schematic illustrations of the two comparative methods used in the thesis. **(a)** Phylogenetically independent contrasts are calculated as standardized differences between sister-taxa, including reconstructed internal nodes of the phylogeny. **(b)** Matched-pair comparisons are restricted to the terminal nodes of the phylogeny, comparing sister-taxa that do not share evolutionary pathways from their common ancestor with other pairs of taxa compared (e.g. here a comparison of species B–C would preclude the comparison of A–D).

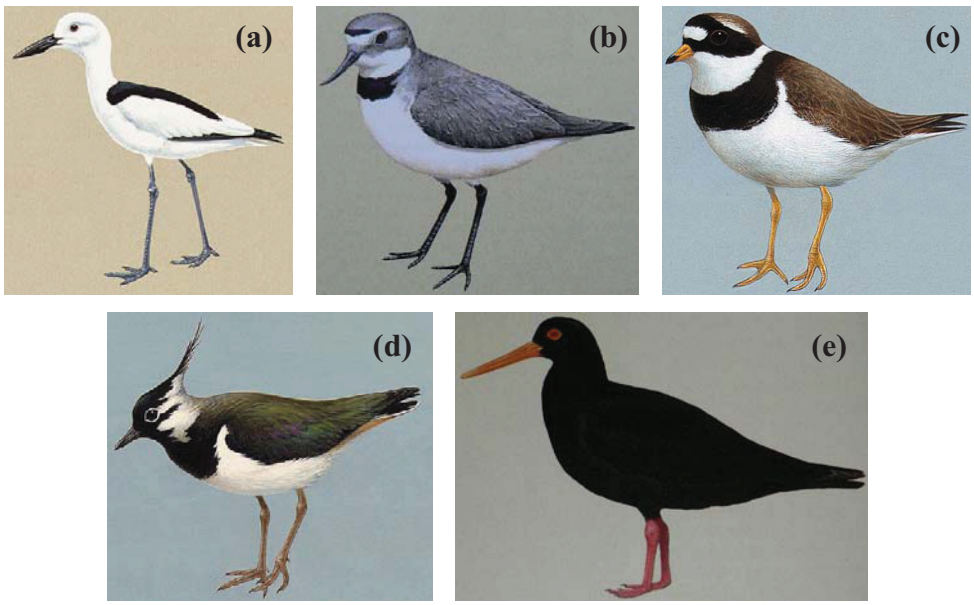

Figure 15.3. Interspecific variation in frontal melanization in the breeding plumage of male plovers (*Charadriida*). **(a)** Crab plovers (*Dromas ardeola*) and **(b)** wrybills (*Anarhynchus frontalis*) display on the ground, while **(c)** ringed plovers (*Charadrius hiaticula*) **(d)** lapwings (*Vanellus vanellus*), and **(e)** African black oystercatchers (*Haematopus moquini*) perform display flights, the latter two being acrobatic. Pictures **a**, **c**, **d** were taken from Perrins (1998) and pictures **b**, **e** from del Hoyo et al. (1996).

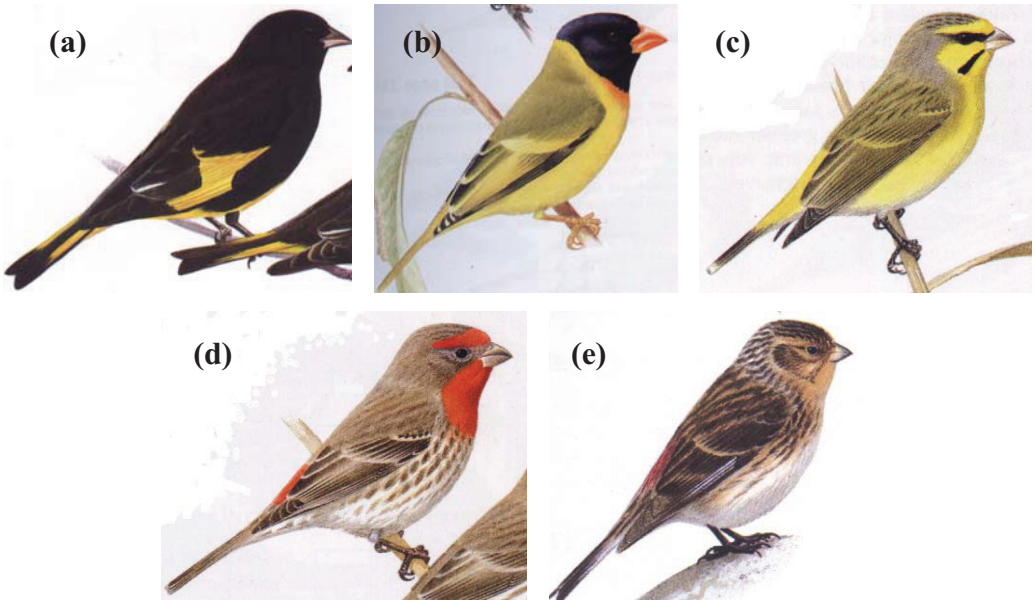

Figure 15.4. Interspecific variation in frontal melanization in the breeding plumage of male finches (*Carduelinae*): **(a)** black siskin (*Carduelis atrata*; clutch size not known), **(b)** oriole finch (*Linurgus olivaceus*; with smallest mean clutch size: 2 eggs), **(c)** yellow-fronted canary (*Serinus mozambicus*; 3 eggs), **(d)** house finch (*Carpodacus mexicanus*; 4.2 eggs), **(e)** twite (*Carduelis flavirostris*; with largest mean clutch size: 5.7 eggs). Note also the variation in carotenoid-based (yellow, red) coloration. Pictures were taken from Clement et al. (1993).

Figure 15.5. Penduline tit male (left, on its partially built nest) and female (right, at the entrance of a fully built nest). Photos by Gyula Molnár.

Figure 15.6. Male penduline tits with small (left, 0.59 cm^2) and large (right, 1.80 cm^2) eye-stripes. Photos by the International Penduline Tit Research Group.

Figure 15.7. House sparrow male (left, in breeding plumage) and female (right). Note that both birds partially hide their wingbars by their scapulars and flank feathers. Photos by Tamás Kaljuste and Dénes Gáspár.

Figure 15.8. Male house sparrows with the smallest (0.13 cm^2, left) and largest (2.30 cm^2, right) visible bibs measured in our free-living study population during the non-breeding season. Both pictures were taken on 18. November 2004. Note the light feather tips partially concealing the black area. Photos by the Veszprém University Ornithological Group.

Figure 15.9. Wingbar of a male (left) and a female (right) house sparrow, representing the average area and conspicuousness of wingbars in our free-living study population (area: male 1.03 cm^2, female 0.36 cm^2; conspicousness, i.e. difference in pixel density between the wingbar and the lesser coverts: male 84, female 66). Photos by the Veszprém University Ornithological Group.

Figure 15.10. Typical wingbar feather (median covert) of a male (left) and a female (right) house sparrow. Note that the distal non-black portion is larger and lighter on the male than on the female feather, and only the male feather exhibits a fully depigmented white area. Photo by the author.

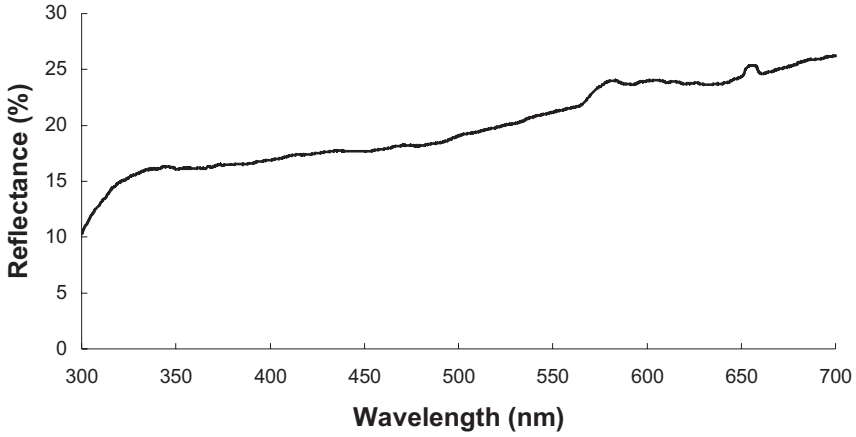

Figure 15.11. Spectral reflectance curve of the wingbar of male house sparrows (averaged for 25 males). The steadily increasing line is characteristic for melanin-containing feathers. Note that if carotenoid pigments were present, the reflectance curve should show fall(s) and peak(s) between 400–500 nm, such as those of the white belly feathers with yellowish wash in male and female sparrows (see Figure 4 in Selander & Johnston 1967). Spectra taken by the author.

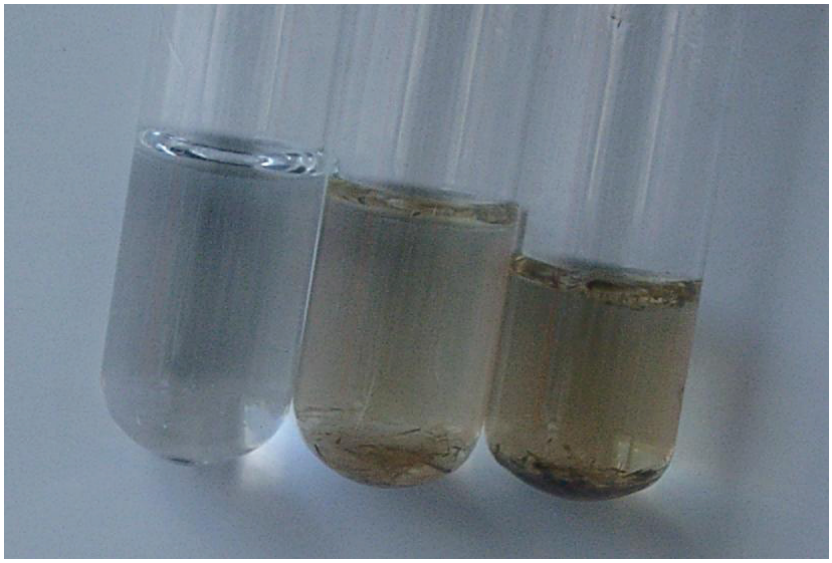

Figure 15.12. Pheomelanin content of the wingbar feathers was confirmed by the extraction technique suggested by McGraw (2006a). I cut the distal non-black feather portions of the median coverts of 25 male and 25 female house sparrows, respectively (2 feathers from each bird). Male (8 mg) and female (6 mg) feather portions were separately added to 4 mg/ml NaOH and the solutions were placed in a 60ºC water bath for an hour (along with a control NaOH solution). After treatment, the control solution (on the left) remained colourless, while both feather-containing solutions (male sample in the middle, female sample on the right) became yellowish, indicating the release of pheomelanin pigments from the feathers. The solutions did not fluoresce under UV light, so the presence of pterin pigments can be ruled out. Photo by Nóra Vili and the author.

Figure 15.13. Topology of the composite phylogeny used in the analyses of T levels (see chapter 10). **(a)** Phylogeny for non-passeriform birds, **(b)** phylogeny for Passeriformes.

Table 15.1. Data used in the analyses of melanization in plovers, and data sources. See Figure 15.1 and chapter 5.2 for explanations of the variables.

	Melanization		Display	Breeding	Substrate	Vegetation	References[1]	
Species	Male	Female	type	density	colour	cover	Image	Data
Anarhynchus frontalis	0.08	0.06	1	1	3	1	2	5, 6, 9
Burhinus bistriatus	0.04	0.04	–	1	2	4	1	5, 9
Burhinus capensis	0.00	0.00	–	1	2	4	3	5, 8, 9
Burhinus giganteus	0.11	0.11	–	1	2	2	3	5, 9
Burhinus grallarius	0.00	0.00	1	1	3	4	1	5, 6, 9, 11
Burhinus oedicnemus	0.00	0.00	1	1	2	2	1	5, 9, 10
Burhinus recurvirostris	0.09	0.09	–	2	3	2	3	5, 9
Burhinus senegalensis	0.00	0.00	1	2	1	1	1	5, 9, 10
Burhinus superciliaris	0.02	0.02	–	1	4	2	3	5, 9
Burhinus vermiculatus	0.00	0.00	–	1	2	4	3	5, 8, 9
Charadrius alexandrinus	0.10	0.00	2	2	1	1	1	9, 10, 11
Charadrius alticola	0.08	0.03	–	1	2	2	1	5, 9
Charadrius asiaticus	0.02	0.00	2	2	2	2	1	9, 10
Charadrius bicinctus	0.10	0.06	2	1	3	2	1	5, 6, 9
Charadrius collaris	0.16	0.09	–	–	1	1	1	5, 9
Charadrius dubius	0.24	0.24	2	2	3	1	1	5, 9, 10, 11
Charadrius falklandicus	0.21	0.15	3	1	2	2	1	5, 9
Charadrius forbesi	0.10	0.10	–	1	3	1	3	5, 9
Charadrius hiaticula	0.29	0.21	2	2	3	1	1	5, 7, 9, 10
Charadrius javanicus	0.01	0.00	–	–	–	–	3	10, 9
Charadrius leschenaultii	0.09	0.03	2	1	1	2	1	5, 8, 9
Charadrius marginatus	0.03	0.00	–	1	1	1	3	5, 9
Charadrius melodus	0.15	0.00	–	2	2	2	1	9
Charadrius modestus	0.09	0.09	–	1	3	2	1	9
Charadrius mongolus	0.14	0.00	–	–	3	1	1	5, 9
Charadrius montanus	0.02	0.02	1	2	3	2	1	2, 5, 7, 9
Charadrius novaeseelandiae	0.33	0.26	3	–	3	5	1	6, 9
Charadrius obscurus	0.00	0.00	1	1	2	2	1	5, 6, 9
Charadrius pallidus	0.03	0.00	–	1	1	1	1	9, 10
Charadrius pecuarius	0.11	0.11	1	2	2	1	1	5, 9
Charadrius peronii	0.11	0.00	–	1	1	1	3	5, 9
Charadrius placidus	0.13	0.13	–	–	3	1	1	5, 9
Charadrius rubricollis	0.38	0.38	1	1	2	1	1	5, 6
Charadrius ruficapillus	0.06	0.06	2	2	2	1	1	5, 6, 9
Charadrius sanctaehelenae	0.07	0.07	–	1	2	3	1	9, 10
Charadrius semipalmatus	0.29	0.29	–	2	3	1	1	5, 9
Charadrius thoracicus	0.16	0.16	–	2	2	2	3	5, 8, 9
Charadrius tricollaris	0.15	0.15	–	1	3	1	3	6, 9
Charadrius veredus	0.03	0.00	–	1	2	2	1	5, 9, 10
Charadrius vociferus	0.16	0.06	–	–	3	2	3	5, 9
Charadrius wilsonia	0.17	0.00	–	3	2	2	1	9
Chionis alba	0.00	0.00	1	1	2	5	3	6, 9, 11
Chionis minor	0.00	0.00	1	1	2	5	3	6, 9
Cladorhynchus leucocephalus	0.04	0.04	1	5	1	1	1	5, 6
Dromas ardeola	0.00	0.00	1	5	1	5	1	5, 9, 11
Elseyornis melanops	0.19	0.19	2	1	3	1	1	5, 6, 9
Erythrogonys cinctus	0.68	0.68	2	2	1	5	1	5, 6, 9
Eudromias morinellus	0.04	0.08	–	1	3	2	3	9, 10, 11
Haematopus ater	1.00	1.00	–	–	3	1	1	5, 9
Haematopus bachmani	1.00	1.00	–	2	5	1	1	5, 9
Haematopus finschi	0.64	0.64	3	–	3	2	1	5, 6
Haematopus fuliginosus	1.00	1.00	3	–	3	1	1	5, 6, 9

Haematopus leucopodus	0.63	0.63	1	–	2	2	1	5, 9
Haematopus longirostris	0.53	0.53	3	–	3	2	1	5, 6, 9
Haematopus maedewaldoi	1.00	1.00	–	–	–	–	1	5, 9
Haematopus moquini	1.00	1.00	3	5	3	1	1	5, 9
Haematopus ostralegus	0.68	0.68	3	1	3	2	1	5, 9, 10, 11
Haematopus palliatus	0.64	0.64	–	–	2	1	1	5, 9
Haematopus unicolor	1.00	1.00	–	–	2	1	3	5, 6, 9
Himantopus himantopus	0.00	0.01	2	3	2	2	1	5, 6, 9, 10, 11
Himantopus leucocephalus	0.06	0.06	–	3	2	2	3	9
Himantopus melanurus	0.12	0.19	–	3	2	2	1	9
Himantopus mexicanus	0.26	0.27	–	3	2	2	3	9
Himantopus novaezelandiae	1.00	1.00	–	1	3	4	3	5, 9
Ibidorhyncha struthersii	0.21	0.21	1	1	3	1	1	5, 9
Oreopholus ruficollis	0.01	0.01	–	–	1	1	1	6, 9
Peltohyas australis	0.16	0.16	–	2	2	2	1	6, 9
Phegornis mitchellii	0.41	0.41	–	1	3	3	1	6, 9
Pluvialis apricaria	0.26	0.06	2	1	3	3	3	4, 5, 10, 11
Pluvialis dominica	0.69	0.69	–	–	4	2	1	1, 9, 10
Pluvialis fulva	0.49	0.49	–	–	4	3	1	9, 10
Pluvialis squatarola	0.43	0.18	2	1	4	2	3	1, 9, 10
Pluvianus aegyptius	0.35	0.35	–	1	1	1	3	5, 9
Recurvirostra americana	0.00	0.00	1	4	3	2	1	9, 10
Recurvirostra andina	0.00	0.00	–	–	2	2	1	9
Recurvirostra avosetta	0.15	0.15	1	3	2	1	1	9, 10, 11
Recurvirostra novaehollandiae	0.00	0.00	1	2	2	2	1	6, 9
Vanellus albiceps	0.01	0.01	–	1	2	1	1	8, 9
Vanellus armatus	0.77	0.77	2	1	2	2	1	5, 9, 10
Vanellus cayanus	0.36	0.36	–	–	1	1	1	9
Vanellus chilensis	0.40	0.40	–	3	3	3	1	3, 5, 9
Vanellus cinereus	0.07	0.07	–	–	4	4	1	5, 9
Vanellus coronatus	0.15	0.15	3	3	3	4	1	5, 8, 9
Vanellus crassirostris	0.49	0.49	–	1	4	3	1	5, 8, 9
Vanellus duvaucelii	0.19	0.19	–	–	2	1	1	5
Vanellus gregarius	0.36	0.17	–	3	2	3	1	5, 9, 10
Vanellus indicus	0.44	0.44	3	1	4	4	1	5, 10
Vanellus leucurus	0.00	0.00	–	3	3	3	1	5, 9, 10
Vanellus lugubris	0.03	0.03	2	3	4	4	1	5, 8, 9
Vanellus macropterus	0.42	0.42	–	–	–	–	3	9
Vanellus malabaricus	0.14	0.14	–	–	2	3	1	5, 9
Vanellus melanocephalus	0.18	0.18	–	–	2	4	3	5, 9
Vanellus melanopterus	0.07	0.07	–	1	3	2	1	5, 8, 9
Vanellus miles	0.28	0.28	2	1	3	3	1	5, 6, 9
Vanellus resplendens	0.00	0.00	–	–	3	3	1	5, 9
Vanellus senegallus	0.04	0.04	–	1	2	3	1	8, 9
Vanellus spinosus	0.64	0.64	2	2	2	2	1	5, 9, 10, 11
Vanellus superciliosus	0.05	0.05	1	–	3	2	1	5, 9
Vanellus tectus	0.31	0.31	–	2	2	4	1	9, 10
Vanellus tricolor	0.49	0.49	2	1	2	3	1	5, 6, 9
Vanellus vanellus	0.40	0.32	3	3	3	3	3	9, 10, 11

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Table 15.2. Taxon-pairs of plovers that differ in **(a)** male display, **(b)** breeding density, **(c)** substrate coloration, and **(d)** vegetation cover of the nest site.

(a)	Ground display	Aerial display
	Charadrius obscurus	*Charadrius leschenaultii*
	Charadrius pecuarius	*Charadrius hiaticula*
	Charadrius montanus	*Charadrius falklandicus*
	Charadrius rubricollis	*Charadrius dubius*
	Anarhynchus frontalis	*Elseyornis melanops*
	Vanellus superciliosus	*Erythrogonys cinctus*
	Cladorhynchus leucocephalus	*Himantopus himantopus*
	Haematopus leucopodus	*Haematopus fuliginosus*
	Ibidorhyncha struthersii	*Haematopus longirostris*
	Chionis alba, Chionis minor	*Charadrius novaeseelandiae*

(b)	Less colonial	More colonial
	Charadrius falklandicus	*Charadrius montanus*
	Charadrius bicinctus	*Charadrius asiaticus*
	Charadrius veredus, C. alticola, C. palliatus	*Peltohyas australis*
	Charadrius tricollaris	*Charadrius hiaticula*
	Charadrius rubricollis	*Charadrius pecuarius*
	Charadrius peronii	*Charadrius dubius*
	Charadrius modestus	*Charadrius wilsonia*
	Anarhynchus frontalis	*Erythrogonys cinctus*
	Vanellus armatus	*Vanellus spinosus*
	Vanellus indicus	*Vanellus leucurus*
	Vanellus albiceps	*Vanellus vanellus*
	Vanellus senegallus	*Vanellus coronatus*
	Vanellus tricolor	*Vanellus tectus*
	Recurvirostra novaehollandiae	*Recurvirostra avocetta*
	Recurvirostra americana	*Cladorhynchus leucocephalus*
	Ibidorhyncha struthersii	*Himantopus mexicanus*
	Haematopus ostralegus	*Haematopus moquini*
	Burhinus oedicnemus	*Burhinus senegalensis*
	Himantopus novaezelandiae	*Himantopus himantopus*
	Burhinus capensis	*Burhinus recurvirostris*
	Chionis alba, Chionis minor	*Dromas ardeola*

(c)	Lighter substrate	Darker substrate
	Charadrius alexandrinus	*Charadrius ruficapillus*
	Charadrius asiaticus	*Charadrius bicinctus*
	Charadrius collaris	*Charadrius rubricollis*
	Charadrius falklandicus	*Charadrius montanus*
	Charadrius leschenaultii	*Charadrius obscurus*
	Charadrius marginatus	*Charadrius tricollaris*
	Charadrius melodus	*Charadrius semipalmatus*
	Charadrius palliatus	*Charadrius alticola*
	Charadrius thoracicus	*Charadrius hiaticula*
	Charadrius sanctahelenae	*Charadrius vociferus*
	Charadrius peronii	*Charadrius dubius*
	Charadrius wilsonia	*Charadrius modestus*
	Erythrogonys cinctus	*Anarhynchus frontalis*
	Oreopholus ruficollis	*Elseyornis melanops*
	Peltohyas australis	*Charadrius forbesi*
	Pluvialis apricaria	*Pluvialis squatarola*
	Vanellus albiceps	*Vanellus vanellus*
	Vanellus armatus, V. spinosus	*Vanellus cinereus*
	Vanellus cayanus	*Vanellus superciliosus*

Vanellus gregarius	*Vanellus lugubris*
Vanellus malabricus	*Vanellus melanopterus*
Vanellus miles	*Vanellus crassirostris*
Vanellus senegallus	*Vanellus coronatus*
Burhinus giganteus	*Burhinus superciliaris*
Burhinus bistriatus	*Burhinus recurvirostris*
Burhinus senegalensis	*Burhinus oedicnemus*
Haematopus ater	*Haematopus bachmani*
Haematopus leucopodus	*Haematopus fuliginosus*
Haematopus palliatus	*Haematopus finschi*
Haematopus unicolor	*Haematopus ostralegus*
Himantopus mexicanus	*Ibidorhyncha struthersii*
Recurvirostra andina	*Recurvirostra americana*
Himantopus himantopus	*Himantopus novaezelandiae*
Dromas ardeola	*Chionis alba, Chionis minor*

(d)	More open nest site	Less open nest site
	Charadrius mongolus	*Charadrius bicinctus*
	Charadrius alexandrinus, C. ruficapillus	*Charadrius falklandicus, C. montanus*
	Charadrius palliatus	*Charadrius veredus*
	Charadrius placidus	*Charadrius obscurus*
	Charadrius marginatus	*Charadrius leschenaultii*
	Charadrius hiaticula	*Charadrius thoracicus*
	Charadrius vociferus	*Charadrius sanctahelenae*
	Charadrius semipalmatus	*Charadrius melodus*
	Charadrius dubius	*Charadrius wilsonia*
	Eudromias morinellus	*Phegornis mitchelli*
	Anarhynchus frontalis	*Charadrius modestus*
	Oreopholus ruficollis	*Erythrogonys cinctus*
	Vanellus melanopterus	*Vanellus malabricus*
	Vanellus gregarius	*Vanellus lugubris*
	Vanellus armatus, V. spinosus	*Vanellus cinereus*
	Vanellus leucurus	*Vanellus indicus*
	Vanellus albiceps	*Vanellus vanellus*
	Vanellus senegallus	*Vanellus coronatus*
	Vanellus tricolor	*Vanellus tectus*
	Vanellus cayanus	*Vanellus superciliosus*
	Pluvialis dominica	*Pluvialis fulva*
	Pluvialis squatarola	*Pluvialis apricaria*
	Elseyornis melanops	*Charadrius novaeseelandiae*
	Himantopus himantopus	*Himantopus novaezelandiae*
	Recurvirostra avocetta	*Recurvirostra novaehollandiae*
	Himantopus mexicanus	*Cladorhynchus leucocephalus*
	Ibidorhyncha struthersii	*Haematopus longirostris*
	Haematopus unicolor	*Haematopus ostralegus*
	Haematopus palliatus	*Haematopus finschi*
	Haematopus fuliginosus	*Haematopus leucopodus*
	Burhinus senegalensis	*Burhinus oedicnemus*
	Burhinus recurvirostris	*Burhinus capensis*
	Burhinus superciliaris, B. giganteus	*Burhinus bistriatus*
	Pluvianus aegyptius	*Chionis alba, Chionis minor*

Table 15.3. Data used in the analyses of melanization in cardueline finches. See Figure 15.1 and chapter 6.2 for explanations of the variables and for data sources.

Species	Melanization		Clutch size	Number of broods per season	Incubation period (days)	Nestling period (days)	Nest height	Breeding altitude	Male tarsus
	Male	Female							
Callacanthis burtoni	0.41	0.00	2.0	–	–	–	3	2800	19.0
Carduelis ambigua	0.23	0.00	4.0	–	12.5	18.5	2	2900	11.0
Carduelis atrata	0.97	0.99	–	–	–	–	–	3300	–
Carduelis atriceps	0.21	0.17	–	–	–	–	–	2700	–
Carduelis barbata	0.18	0.00	–	–	–	–	–	750	13.0
Carduelis cannabina	0.00	0.00	4.7	2.0	12.6	13.4	2	1100	15.6
Carduelis carduelis	0.15	0.12	4.9	2.0	12.0	14.7	3	2125	14.7
Carduelis chloris	0.01	0.01	4.8	2.0	12.9	15.1	2	700	17.3
Carduelis crassirostris	0.33	0.00	–	–	–	–	–	3900	–
Carduelis cucullata	0.44	0.00	4.0	1.0	12.0	15.0	3	790	–
Carduelis dominicensis	0.36	0.00	–	–	–	–	–	750	15.0
Carduelis flammea	0.03	0.03	4.8	2.0	10.7	11.5	2	175	14.5
Carduelis flavirostris	0.00	0.00	5.7	2.0	12.5	11.5	1	500	15.8
Carduelis hornemanni	0.02	0.02	4.8	2.0	11.5	11.0	1	200	15.0
Carduelis johannis	0.01	0.01	–	–	–	–	–	1800	13.0
Carduelis lawrencei	0.16	0.00	4.5	–	12.5	12.0	3	0	–
Carduelis magellanica	0.47	0.00	–	–	–	–	–	2500	9.0
Carduelis monguilloti	0.39	0.25	–	–	–	–	–	500	11.0
Carduelis notata	0.54	0.38	–	–	–	–	–	1875	–
Carduelis olivacea	0.45	0.00	–	–	–	–	–	2100	–
Carduelis pinus	0.00	0.00	3.5	2.0	13.0	14.5	3	–	14.3
Carduelis psaltria	0.47	0.00	4.5	2.0	12.0	15.0	3	1550	11.5
Carduelis siemiradzkii	0.40	0.00	–	–	–	–	–	400	–
Carduelis sinica	0.00	0.00	5.0	2.0	12.5	14.5	3	1200	16.0
Carduelis spinescens	0.10	0.00	–	–	–	–	–	2950	–
Carduelis spinoides	0.19	0.00	4.0	1.0	13.0	–	3	3000	15.0
Carduelis spinus	0.13	0.00	4.3	2.0	12.5	14.0	3	900	13.7
Carduelis tristis	0.10	0.00	5.2	2.0	13.0	14.0	3	–	14.4
Carduelis uropygialis	0.71	0.63	–	–	–	–	–	3250	12.0
Carduelis xanthogastra	0.68	0.00	2.5	–	–	–	3	2550	13.5
Carduelis yarrellii	0.17	0.00	–	–	–	–	–	250	9.0
Carduelis yemenensis	0.00	0.00	–	–	–	–	–	2730	14.4
Carpodacus cassinii	0.00	0.00	4.5	2.0	13.0	14.0	3	2250	18.3
Carpodacus edwardsii	0.00	0.00	–	–	–	–	–	3645	23.5
Carpodacus eos	0.00	0.00	–	–	–	–	–	4625	–
Carpodacus erythrinus	0.00	0.00	4.9	1.0	12.1	11.6	2	1000	19.0
Carpodacus mexicanus	0.00	0.00	4.2	–	13.5	15.0	3	750	17.2
Carpodacus nipalensis	0.00	0.00	–	–	–	–	–	3915	21.5
Carpodacus pulcherrimus	0.00	0.00	3.0	–	–	–	2	4300	20.0
Carpodacus puniceus	0.00	0.00	4.0	–	–	–	1	4350	23.5
Carpodacus purpureus	0.00	0.00	4.5	2.0	13.0	14.0	3	0	17.8
Carpodacus rhodochlamys	0.00	0.00	4.0	1.0	15.0	16.5	2	3810	21.0
Carpodacus rhodochrous	0.00	0.00	4.5	–	–	–	3	3395	19.5
Carpodacus rhodopeplus	0.00	0.00	–	–	–	–	–	4000	23.0
Carpodacus roborowskii	0.02	0.00	–	–	–	–	–	4950	21.0
Carpodacus roseus	0.00	0.00	4.0	–	–	–	3	1515	20.5
Carpodacus rubescens	0.00	0.00	–	–	–	–	–	4000	18.0
Carpodacus rubicilla	0.00	0.00	4.8	1.0	16.0	17.0	1	4050	23.7
Carpodacus rubicilloides	0.00	0.00	5.0	–	–	–	–	4750	24.5
Carpodacus synoicus	0.00	0.00	4.5	2.0	13.5	15.0	1	2675	19.9
Carpodacus thura	0.00	0.00	3.7	–	–	–	2	4100	25.0
Carpodacus trifasciatus	0.11	0.00	–	–	–	–	–	2590	21.5
Carpodacus vinaceus	0.00	0.00	–	–	–	–	–	2735	20.0

Coccothraustes coccothraustes	0.09	0.08	4.4	1.0	12.0	12.5	3	1500	21.4
Eophona migratoria	0.26	0.00	4.5	–	–	–	3	1000	–
Eophona personata	0.21	0.21	–	–	–	–	3	0	–
Haematospiza sipahi	0.00	0.00	–	–	–	–	–	2478	20.5
Hesperiphona abeillei	0.46	0.21	–	–	–	–	–	2175	–
Hesperiphona vespertinus	0.09	0.01	3.0	1.0	13.4	14.1	3	1000	21.2
Leucosticte arctoa	0.00	0.00	4.0	1.0	–	15.0	1	4000	–
Leucosticte brandti	0.07	0.07	3.5	–	–	–	1	4975	21.0
Leucosticte nemoricola	0.00	0.00	4.8	1.0	14.0	17.5	1	3800	20.5
Linurgus olivaceus	0.44	0.00	2.0	–	–	–	2	2286	20.0
Loxia curvirostra	0.00	0.00	3.7	2.0	15.0	23.0	3	2250	18.3
Loxia leucoptera	0.00	0.00	4.0	3.0	14.5	23.0	3	0	16.1
Loxia pytyopsittacus	0.00	0.00	3.8	2.0	15.0	22.0	3	0	19.2
Loxia scotica	0.00	0.00	3.7	2.0	13.2	21.0	3	0	18.3
Mycerobas affinis	0.41	0.00	–	–	–	–	–	3750	27.5
Mycerobas carnipes	0.78	0.00	3.2	2.0	16.0	21.0	2	3700	27.5
Mycerobas icterioides	0.40	0.00	2.5	–	–	–	3	2650	24.0
Mycerobas melanozanthos	0.54	0.40	2.5	–	–	–	3	3000	23.5
Neospiza concolor	0.00	0.00	–	–	–	–	–	–	20.0
Pinicola enucleator	0.00	0.00	3.8	1.0	13.5	14.0	3	1000	22.2
Pinicola subhimachala	0.00	0.00	–	–	–	–	–	3850	23.0
Pyrrhoplectes epauletta	0.82	0.00	–	–	–	–	–	3800	19.5
Pyrrhula aurantiaca	0.09	0.09	3.5	–	–	–	3	3650	18.0
Pyrrhula erythaca	0.05	0.05	3.0	–	–	–	2	3500	17.0
Pyrrhula erythrocephala	0.07	0.05	3.5	–	–	–	–	3450	18.5
Pyrrhula leucogenys	0.15	0.18	–	–	–	–	–	1500	19.0
Pyrrhula nipalensis	0.02	0.02	–	–	–	–	–	3100	17.0
Pyrrhula pyrrhula	0.18	0.12	4.7	2.0	13.0	16.0	–	1450	18.0
Rhodopechys githaginea	0.00	0.00	5.0	2.0	13.5	13.5	1	1175	18.1
Rhodopechys mongolica	0.00	0.00	5.0	2.0	–	18.0	1	2575	17.4
Rhodopechys obsoleta	0.02	0.00	4.8	2.0	13.8	13.5	2	750	17.3
Rhodopechys sanquinea	0.05	0.00	4.5	1.5	14.0	14.0	1	2600	20.5
Rhynchostrustus socotranus	0.34	0.13	–	–	–	–	–	2080	16.0
Serinus alario	0.46	0.00	–	–	–	–	2	–	14.0
Serinus albogularis	0.00	0.00	3.5	–	–	15.0	2	0	21.0
Serinus ankoberensis	0.00	0.00	3.0	–	–	14.0	1	3090	16.0
Serinus atrogularis	0.00	0.00	3.0	–	12.5	16.5	3	450	12.0
Serinus burtoni	0.00	0.00	–	–	–	–	–	2250	19.0
Serinus canaria	0.00	0.00	3.8	2.0	13.5	16.0	3	850	17.2
Serinus canicollis	0.00	0.00	3.5	–	13.0	17.0	3	3150	15.0
Serinus capistratus	0.10	0.00	3.0	–	–	–	3	750	–
Serinus citrinella	0.00	0.00	4.5	2.0	13.5	16.5	3	2000	14.6
Serinus citrinelloides	0.08	0.00	2.5	–	–	–	2	2000	14.8
Serinus citrinipectus	0.00	0.00	3.0	–	13.0	16.8	2	375	13.5
Serinus donaldsoni	0.00	0.00	–	–	–	15.0	–	650	–
Serinus dorsostriatus	0.00	0.00	3.0	–	–	19.5	3	1500	18.0
Serinus estherae	0.10	0.04	–	–	–	–	–	2400	13.5
Serinus flavigula	0.00	0.00	–	–	–	–	–	1450	–
Serinus flaviventris	0.00	0.00	4.0	–	–	15.0	3	0	18.0
Serinus gularis	0.00	0.00	3.0	–	13.5	15.5	3	1600	15.5
Serinus koliensis	0.00	0.00	–	–	–	–	–	1250	–
Serinus leucopterus	0.00	0.00	–	–	–	–	2	–	18.0
Serinus leucopygius	0.00	0.00	3.5	–	–	19.5	3	500	13.0
Serinus menachensis	0.00	0.00	–	–	–	14.0	1	2833	–
Serinus mennelli	0.07	0.03	3.0	–	13.0	17.0	3	1275	13.5
Serinus mozambicus	0.03	0.00	3.0	–	13.5	20.5	3	900	13.0
Serinus nigriceps	0.55	0.00	2.5	–	–	16.5	2	2950	–
Serinus pusillus	0.62	0.21	3.7	1.0	12.0	14.0	2	3300	14.3

Serinus rothschildi	0.00	0.00	–	–	–	15.5	–	1900	–
Serinus rufobrunneus	0.00	0.00	–	–	–	–	–	450	18.5
Serinus scotops	0.07	0.00	3.5	–	–	18.0	3	900	15.0
Serinus serinus	0.04	0.06	3.8	2.0	12.7	14.6	3	650	13.6
Serinus striolatus	0.00	0.00	3.5	–	–	15.0	3	2800	20.0
Serinus sulphuratus	0.00	0.00	3.0	–	–	15.0	3	1700	18.0
Serinus symonsi	0.00	0.00	3.5	–	–	–	2	1200	16.5
Serinus syriacus	0.00	0.00	4.0	2.0	13.0	15.0	2	1350	14.8
Serinus thibetanus	0.02	0.05	–	–	–	–	–	3400	14.5
Serinus totta	0.00	0.00	–	–	–	–	1	–	14.5
Serinus tristriatus	0.00	0.00	3.5	–	–	14.0	3	2195	16.5
Serinus xantholaema	0.01	0.01	–	–	–	–	–	0	15.0
Uragus sibiricus	0.00	0.00	4.5	1.0	–	–	2	1700	15.8
Urocynchramus pyzlowi	0.00	0.00	–	–	–	–	–	4025	–

Table 15.4. Data on T and melanization used in the analyses of chapter 10. Circulating T levels were categorized as A: non-breeding baseline, B: breeding baseline, and C: breeding peak T (*sensu* Wingfield et al. 1990). The extension of black on the whole breeding plumage was scored as total melanization, while that on the head and underparts was scored as frontal melanization. The sex difference in the extension of black plumage were scored as melanin dichromatism. See chapter 10.2 for further details.

	Testosterone (ng/ml)				Melanization				Dichromatism		
Species	male A	male B	male C	female C	male total	male frontal	female total	female frontal	total black	frontal black	Source[1]
Acanthagenys rufogularis	–	–	0.90	–	4	2	4	2	0	0	3
Acrocephalus scirpaceus	1.10	0.50	1.34	–	0	0	0	0	0	0	3
Actitis macularia	0.15	2.05	6.10	0.61	3	1	3	1	-1	-1	3,4
Agelaius phoeniceus	0.41	3.32	3.77	–	9	4	0	0	5	2	3
Aix sponsa	0.03	–	0.71	–	4	1	0	0	4	1	3
Alectoris rufa	0.01	0.56	5.34	–	2	2	2	2	0	0	1
Amphispiza bilineata	0.20	0.69	4.65	–	2	2	2	2	0	0	3
Anas platyrhynchos	0.25	1.51	3.44	0.35	2	0	0	0	2	0	3,4
Anser indicus	0.19	0.62	3.21	0.55	3	1	3	1	0	0	3,4
Aphelocoma coerulescens	0.19	0.17	1.56	0.09	0	0	0	0	0	0	3,4
Aptenodytes forsteri	2.40	1.00	13.30	–	8	2	8	2	0	0	3
Aptenodytes patagonicus	0.03	0.44	7.26	0.77	8	2	8	2	0	0	3,4
Apteryx australis	0.18	0.06	2.30	0.10	0	0	0	0	0	0	3,4
Atlapetes pallidinucha	–	–	1.70	–	1	1	1	1	0	0	2
Branta canadensis	0.20	1.01	3.10	–	4	1	4	1	0	0	1
Calcarius lapponicus	0.45	1.10	8.91	–	2	2	2	2	2	2	3
Calidris mauri	0.18	–	1.59	0.40	3	0	3	0	0	0	3,4
Calidris pusilla	0.14	0.32	2.99	1.03	3	0	3	0	0	0	3,4
Campylorhynchus brunneicapillus	0.13	0.40	1.03	–	2	2	2	2	0	0	3
Carduelis flammea	1.33	–	4.50	0.15	1	1	1	1	0	0	3,4
Carpodacus mexicanus	0.09	0.12	0.30	–	0	0	0	0	0	0	1
Catamenia inornata	–	–	2.10	–	0	0	0	0	0	0	2
Centropus grillii	–	–	2.80	–	6	4	6	4	0	0	2
Ceryle rudis	0.50	0.51	1.22	–	5	2	5	2	0	0	3
Cettia diphone	0.15	1.65	2.97	–	0	0	0	0	0	0	3
Chionis minor	0.12	0.67	1.67	0.90	0	0	0	0	0	0	3,4
Chlamydotis macqueenii	1.62	3.32	10.30	–	2	2	2	2	0	0	1
Chlamydotis undulata	1.20	3.10	9.06	–	1	1	1	1	0	0	3
Ciconia ciconia	0.60	–	2.40	–	1	0	1	0	0	0	3
Colinus virginianus	0.13	0.14	2.68	–	2	2	2	2	0	0	3
Columba livia domesticus	0.59	–	1.24	–	–	–	–	–	–	–	3
Corvus frugilegus	0.20	1.32	3.40	0.76	10	4	10	4	0	0	3,4
Coturnix japonica	0.20	0.33	7.85	0.60	0	0	0	0	0	0	3,4
Cyphorhinus phaeocephalus	0.40	–	–	–	0	0	0	0	0	0	3
Diglossa humeralis	–	–	0.40	–	8	2	8	2	0	0	2
Diomedea chrysostoma	0.07	–	1.96	1.53	2	0	2	0	0	0	3,4
Diomedea exulans	1.04	1.12	5.12	2.45	1	0	1	0	0	0	3,4
Diomedea melanophris	0.08	–	2.03	1.50	2	0	2	0	0	0	3,4
Dolichonyx oryzivorus	–	–	1.40	0.30	7	4	0	0	5	2	4
Dromaius novaehollandiae	0.07	0.98	6.05	1.27	2	2	2	2	-1	-1	3,4
Epthianura tricolor	–	–	1.30	–	0	0	0	0	0	0	3
Eudocimus albus	0.36	–	1.05	–	0	0	0	0	0	0	3
Eudyptes chrysolophus	0.75	5.98	3.20	0.01	7	2	7	2	0	0	3,5
Euplectes orix	–	–	1.70	–	2	2	0	0	2	2	2
Falco tinnunculus	0.50	0.68	2.55	–	4	1	5	2	-5	-2	3
Ficedula hypoleuca	0.10	0.20	2.20	0.08	5	1	0	0	4	1	3,6
Fregata magnificens	–	–	1.03	0.30	10	4	7	3	3	1	4

Gallirallus philippensis	0.08	–	0.62	–	1	1	1	1	0	0	3
Gallus gallus	0.84	–	7.83	1.20	–	–	–	–	–	–	3,4
Geospiza fuliginosa	–	–	3.00	–	10	4	0	0	5	2	2
Gymnopithys leucaspis	1.10	–	–	–	2	2	2	2	0	0	3
Gymnorhina tibicen	0.14	–	1.51	–	6	3	6	3	0	0	3
Hemignathus virens	–	–	4.81	0.35	3	1	3	1	0	0	4
Himatione sanguinea	–	–	2.94	0.57	3	0	3	0	0	0	4
Hirundo rustica	0.90	–	1.90	–	8	2	7	1	1	1	3
Hylophylax naevioides	0.30	0.43	1.60	–	2	1	2	1	0	0	3
Junco hyemalis	1.12	1.77	6.75	–	2	2	0	0	2	2	3
Lagopus lagopus	0.17	0.18	1.91	0.13	5	2	5	2	5	2	3,4
Lagopus mutus	0.10	0.45	1.41	–	5	2	5	2	5	2	1
Lamprotornis chalybaeus	–	0.55	1.24	–	0	0	0	0	0	0	3
Lamprotornis purpuropterus	0.50	–	0.91	–	2	2	2	2	0	0	3
Laniarius funebris	0.27	–	2.94	–	10	4	0	0	5	2	3
Lanius collaris	0.50	–	1.50	–	5	1	5	1	0	0	3
Lanius collurio	0.50	0.46	2.40	–	3	1	0	0	3	1	3
Larus occidentalis	0.30	0.37	0.41	0.30	1	0	1	0	0	0	3,4
Larus ridibundus	0.20	–	4.66	0.38	3	2	3	2	0	0	3,4
Lichenostomus penicillatus	–	–	1.50	–	1	0	1	0	0	0	3
Lonchura striata var. domestica	0.10	0.09	1.54	0.22	–	–	–	–	–	–	3,4
Loxia leucoptera	0.71	–	2.35	–	2	0	2	0	0	0	3
Malurus cyaneus	0.11	0.36	3.30	–	4	2	0	0	4	2	3
Malurus lamberti	–	–	5.11	–	3	2	0	0	3	2	3
Malurus leucopterus	–	–	4.10	–	0	0	0	0	0	0	3
Manacus vitellus	1.10	–	–	–	5	1	0	0	4	1	3
Manorina flavigula	–	–	0.50	–	2	1	2	1	0	0	3
Manorina melanophrys	0.57	–	–	–	2	1	2	1	0	0	3
Megadyptes antipodes	0.13	0.47	4.94	0.65	7	2	7	2	0	0	1,7
Meleagris gallopavo	0.60	2.27	5.60	–	–	–	–	–	–	–	3
Melospiza melodia	0.12	1.01	7.87	1.45	2	2	2	2	0	0	3,4
Mimus polyglottos	0.70	–	2.30	0.38	0	0	0	0	0	0	3,4
Molothrus ater	0.33	1.74	1.92	0.22	6	1	0	0	4	1	3,4
Nesomimus parvulus	–	–	1.30	–	0	0	0	0	0	0	2
Pachycephala rufiventris	0.06	0.15	4.00	–	2	2	2	2	0	0	3
Parabuteo unicinctus	0.02	0.05	0.52	0.08	1	0	1	0	0	0	3,4
Parus caeruleus	–	–	2.32	–	2	2	2	2	0	0	3
Parus major	0.17	0.24	1.05	0.13	2	2	2	2	0	0	3,4
Parus montanus	0.30	–	1.33	0.35	2	2	2	2	0	0	3,4
Passer domesticus	0.41	1.48	5.65	0.41	2	2	0	0	2	2	3,4
Passer motitensis	0.18	0.68	1.09	–	1	1	0	0	1	1	3
Perdix perdix	0.28	0.13	1.80	–	0	0	0	0	0	0	3
Phaeton rubricauda	0.11	0.25	0.91	0.50	2	1	2	1	0	0	1,8
Phalacrocorax capensis	0.19	0.24	0.42	–	10	4	10	4	0	0	3
Phalaropus fulicarius	0.45	–	6.00	1.55	4	1	4	1	-3	-1	3,4
Phalaropus lobatus	0.04	0.08	5.46	0.26	3	1	3	1	-3	-1	3,4
Phalaropus tricolor	0.42	0.63	4.91	0.58	3	1	3	1	-3	-1	3,4
Phasianus colchicus	0.20	1.63	2.40	–	–	–	–	–	–	–	3
Phylidornyris albifrons	–	–	2.00	–	2	2	2	2	0	0	3
Picoides borealis	0.16	0.30	2.06	0.38	5	2	5	2	0	0	3,9
Pipilo erythropthalmus	0.20	–	5.72	0.18	7	3	0	0	5	2	3,4
Plectrophenax nivalis	0.17	1.19	4.20	0.15	3	0	4	1	2	-1	3,4
Plocepasser mahali	0.02	0.08	0.33	0.17	1	1	1	1	0	0	3,4
Ploceus baglafecht	0.20	0.51	0.80	–	1	1	0	0	1	1	3
Ploceus jacksoni	–	–	1.00	–	3	3	0	0	2	2	2
Ploceus philippinus	0.36	0.82	1.55	0.21	2	2	0	0	2	2	3,4
Pomatostomus ruficeps	–	–	1.30	–	0	0	0	0	0	0	3
Pomatostomus superciliosa	–	–	2.10	–	0	0	0	0	0	0	3

Pooecetes gramineus	0.70	–	4.40	1.00	0	0	0	0	0	0	3,4
Psittacula krameri	0.20	0.54	0.93	0.67	2	2	2	2	0	0	3,4
Ptilonorhynchus violaceus	0.20	5.30	5.70	–	0	0	0	0	0	0	3
Pygoscelis adeliae	0.11	1.27	9.62	–	9	3	9	3	0	0	3
Pygoscelis papua	0.10	1.45	2.97	0.27	6	2	6	2	0	0	3,4
Saxicola torquata	0.50	0.69	1.84	0.60	0	0	0	0	0	0	3,4
Serinus canaria	0.45	–	3.20	–	0	0	0	0	0	0	3
Somateria mollissima	0.10	0.48	1.31	–	6	2	3	0	4	2	1
Spheniscus humboldtii	0.16	–	3.32	1.15	7	2	7	2	0	0	3,4
Spheniscus magellanicus	0.55	–	2.75	0.66	8	2	8	2	0	0	3,4
Spizella arborea	0.05	0.18	0.57	–	1	1	1	1	0	0	3
Streptopelia decaocto	0.27	0.46	2.09	0.28	2	0	2	0	0	0	3,4
Streptopelia risoria	0.20	1.08	0.70	0.17	–	–	–	–	–	–	3,4
Struthio camelus domesticus	1.35	2.61	3.63	–	–	–	–	–	–	–	3
Sturnella neglecta	1.00	–	4.00	0.50	1	1	1	1	0	0	3,4
Sturnus vulgaris	0.30	0.40	2.78	1.80	5	2	5	2	0	0	3,4
Sula capensis	0.26	–	0.85	0.85	2	0	2	0	0	0	3,4
Sula dactylatra	0.01	0.08	1.15	0.02	3	1	3	1	0	0	1,8
Sula nebouxii	0.10	0.16	0.46	0.47	5	1	5	1	0	0	1,4
Sula sula	0.01	0.03	0.11	0.06	1	0	1	0	0	0	1,8
Tadorna ferruginea	0.32	–	3.65	1.60	4	1	3	0	1	1	3,4
Taeniopygia guttata	0.01	–	3.48	–	–	–	–	–	–	–	3
Tetrao tetrix	0.29	1.15	1.15	–	8	4	5	2	5	2	3
Tetrao urogallus	0.20	–	1.00	–	5	3	4	2	4	2	3
Thraupis episcopus	–	–	0.20	–	0	0	0	0	0	0	2
Threskiornis melanocephalus	–	–	2.80	–	0	0	0	0	0	0	3
Thryothorus nigricapillus	0.50	–	–	–	5	2	5	2	0	0	3
Toxostoma curvirostre	0.11	1.23	3.19	–	0	0	0	0	0	0	3
Turdus fuscater	–	–	0.90	–	0	0	0	0	0	0	2
Turdus grayi	1.90	–	–	–	0	0	0	0	0	0	3
Turdus merula	0.04	0.56	2.56	0.05	10	4	0	0	5	2	3,4
Vestiaria coccinea	–	–	2.05	0.40	3	0	3	0	0	0	4
Xanthocephalus xanthocephalus	0.90	–	5.70	–	7	2	0	0	5	2	3
Zonotrichia albicollis	0.40	–	2.79	2.23	2	1	2	1	0	0	3,4
Zonotrichia capensis	–	–	1.70	–	2	2	2	2	0	0	3
Zonotrichia leucophrys	0.30	0.67	2.99	0.43	1	1	1	1	0	0	3,4

[1]Sources for T data:

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Table 15.5. Pairs of closely related bird species that differ in male melanization but not in social mating system. Extension and distribution of black plumage on the body surface (not considering feathers that are only seen during flight) is described shortly.

More melanized species	Less melanized species
Dromaius novaehollandiae: whole head plumage	*Apteryx australis*: none
Ceryle rudis: head, wings, breast heavily patterned	*Psittacula krameri*: collar, chin
Branta canadensis: anterior half of head, whole neck, tail	*Anser indicus*: stripes on head and neck, primaries
Aix sponsa: large patches on head and wings, tail	*Tadorna ferruginea*: collar, primaries, tail
Tetrao urogallus: whole plumage except wings and back	*Lagopus mutus*: mottled with brown and white
Alectoris rufa: eye-stripe, breast stripes	*Perdix perdix*: none
Phalaropus, 3 spp.: patches on head, back, wings	*Actitis macularia*: small spots on underparts
Larus ridibundus: whole head, primaries	*Larus occidentalis*: primaries
Falco tinnunculus: spots on underparts and upperparts	*Parabuteo unicinctus*: none
Sula nebouxii: back, wings, stripes on head	*Sula dactylatra*: wings
Phalacrocorax capensis: whole plumage	*Sula capensis*: wings, tail
Ciconia ciconia: wings, tail	*Eudocimus albus*: none
Fregata magnificens: whole body plumage	*Diomedea*, 3 spp.: wings
Corvus frugilegus: whole body plumage	*Aphelocoma coerulescens*: none
Lanius collaris: head, back, wings, tail heavily black	*Lanius collurio*: eye-stripe, tail, primaries
Laniarius funebris: whole plumage	*Gymnorhina tibicen*: majority of plumage
Phylidornyris albifrons: large breast patch, head patterns	*Lichenostomus penicillatus*: primaries
Malurus lamberti: throat, breast, nape, rump all black	*Malurus leucopterus*: none
Turdus merula: whole body plumage	*Turdus fuscater*: none
Ficedula hypoleuca: head, back, wings, tail heavily black	*Saxicola torquata*: none
Lamprotornis purpuropterus: whole head plumage	*Lamprotornis chalybaeus*: none
Thryothorus nigricapillus: cap, stripes on underparts, wings and tail	*Campylorhynchus brunneicapillus*: cap, spots on throat
Parus major: cap, collar, breast stripe	*Parus montanus*: cap, chin
Hirundo rustica: head, back, wings, tail, breast patch	*Acrocephalus scirpaceus*: none
Ploceus jacksoni: whole head, throat	*Ploceus philippinus*: face, chin
Passer domesticus: throat and breast patch	*Plocepasser mahali*: small area between bill and eye
Loxia leucoptera: wings, tail	*Carpodacus mexicanus*: none
Carduelis flammea: throat patch	*Serinus canaria*: none
Geospiza fuliginosa: whole plumage	*Thraupis episcopus*: none
Atlapetes pallidinucha: majority of head	*Zonotrichia capensis*: stripes on head and breast
Junco hyemalis: head, breast	*Spizella arborea*: one spot on breast
Pipilo erythropthalmus: head, whole upper body, breast	*Pooecetes gramineus*: none
Amphispiza bilineata: throat, breast, eye-stripe	*Melospiza melodia*: stripes on head and breast
Xanthocephalus xanthocephalus: whole body excepting head and breast	*Sturnella neglecta*: breast band