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Urbanization alters the relationship between coloration and territorial aggression, but not hormones, in song sparrows

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Melanin-based coloration is associated with aspects of phenotype, including conspecific aggression and hormone concentrations. These relationships could arise as a result of genetic and/or biochemical links between melanin production and other traits. Additionally, anthropogenic change, including urbanization, exposes animals to novel conditions that can alter pigmentation, behaviour or hormones, potentially disrupting relationships between coloration and other traits. We examined relationships among the extent and darkness of melanin spotting on the breast of male song sparrows, *Melospiza melodia*, territorial behaviour, plasma testosterone and corticosterone concentrations to determine whether coloration was reliably associated with phenotype in this species. We conducted this study in urban and rural populations to determine whether relationships between coloration, behaviour and hormones varied between habitats. Males in urban habitat had more extensive brown spotting than rural males. The relationship between melanin coloration and territoriality differed in urban and rural habitats. In rural sparrows, territoriality was negatively correlated with spotting area, while in urban sparrows territoriality was positively associated with spotting darkness. Regardless of habitat, males with more extensive spotting increased testosterone secretion more in response to gonadotropin-releasing hormone administration and males with darker spotting had greater handling restraint-induced release of corticosterone. This suggests that plumage coloration is associated with underlying physiology, but the relationship between coloration and behaviour may shift between habitats.

Melanin-based coloration is widespread in vertebrates and can signal aspects of phenotype to conspecifics (Jawor & Breitwisch, 2003; Rohwer, 1975). The size and reflectance of melanin areas are associated with a number of phenotypically plastic traits including behaviour and physiology (Roulin, 2016). Although signal honesty, a reliable association between phenotype and coloration, is essential for the maintenance of stable communication systems, the mechanisms that maintain this association in melanin-based ornaments are unclear (Dawkins & Krebs, 1978; Diep & Westneat, 2013; Wiley, 1994). Recently, it has been proposed that genetic and biochemical links between melanin production and other systems that regulate behaviour and physiology maintain associations between melanin pigmentation and other aspects of phenotype (hypotheses presented in Ducrest, Keller, & Roulin, 2008; Jenkins, Vitousek, & Safran, 2013). There are two predominant types of melanin, eumelanin and pheomelanin, and their production is largely antagonistic such that the genetic and biochemical conditions that produce one inhibit the production of the other (Ducrest et al., 2008; Galvan, Wakamatsu, Camarero, Mateo, & Alonso-Alvarez, 2015), although most melanin ornaments are a mixture of the two pigments. Thus, the type of melanin or relative contribution of each type of melanin to an ornament could be central to generating correct predictions regarding the relationship between coloration and behaviour or physiology (Roulin, Almasi, Meichtry-Stier, & Jenni, 2011).

Much of the work that has addressed relationships between melanin-based coloration, aggression and hormone concentrations has focused on eumelanin-based traits. Individuals with darker and/or larger eumelanin ornaments are predicted to be (1) more aggressive, (2) have greater androgen concentrations and (3) be less responsive to stress. In the case of primarily pheomelanin-based ornaments, the predicted relationships are similar with the exception of reactivity of the hypothalamic–pituitary–adrenal (HPA) axis; more pheomelanic individuals are predicted to have greater baseline and stress-induced release of glucocorticoids than those that are less pheomelanic. In many vertebrates, including

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birds, fish and reptiles, more eumelanic individuals are more aggressive than less eumelanic individuals (Mafli, Wakamatsu, & Roulin, 2011; Schweitzer, Motreuil, & Dechaume-Moncharmont, 2015; Seddon & Hews, 2016; Senar, 2006). Initial testosterone is positively associated with the size of eumelanin-based traits (Buchanan, Evans, Goldsmith, Bryant, & Rowe, 2001; Evans, Goldsmith, & Norris, 2000; Gonzalez, Sorci, Smith, & de Lope, 2001), although some studies found no such relationship (Beziers, Ducrest, Simon, & Roulin, 2017; Laucht, Kempenaers, & Dale, 2010; Seddon & Hews, 2016). In the case of predominantly pheomelanin-based traits, males with darker or larger pheomelanin coloration can have higher androgen levels (Hasegawa, Arai, Sato, & Sakai, 2017; Safran, Adelman, McGraw, & Hau, 2008) while in other cases no relationship was found between coloration and androgens (Grindstaff, Lovern, Burtka, & Hallmark-Sharber, 2012). Animals may transiently increase testosterone during social interactions, and this ability can be assessed by measuring the response to exogenous gonadotropin-releasing hormone (GnRH) (Goymann, 2009; Goymann, Landys, & Wingfield, 2007). Thus, GnRH-induced testosterone concentrations may be more strongly associated with social behaviour and coloration than initial testosterone concentrations (McGlothlin et al., 2008). Relatively few studies have assessed relationships between any type of coloration and GnRH-induced testosterone secretion (Cain & Pryke, 2017; McGlothlin et al., 2008; Spinney, Bentley, & Hau, 2006).

Production of melanins may be associated with glucocorticoid concentrations as well. Biochemical links between the production of melanins and the HPA axis lead to the predictions that pheomelanin-based coloration is positively associated with glucocorticoids while eumelanin coloration is indicative of lower initial and stress-induced corticosterone release (Ducrest et al., 2008; Jenkins et al., 2013). A few studies have found that more eumelanic individuals have lower baseline corticosterone profiles (Kittilsen et al., 2009; Saino et al., 2013), although in other cases, no relationship has been found between initial corticosterone and either melanin pigment (Almasi, Jenni, Jenni-Eiermann, & Roulin, 2010; Corbel et al., 2016; Grindstaff et al., 2012; Jenkins et al., 2013). Similarly, stress-induced corticosterone concentrations can be negatively (Almasi et al., 2010; Kittilsen, Johansen, Braastad, & Overli, 2012; Saino et al., 2013) or positively (Corbel et al., 2016) associated or unassociated with both melanins.

Melanin coloration, behaviour and physiology could be influenced by environmental conditions, including human alteration of habitats. Urbanization produces novel ecological conditions that influence melanin coloration (Giraudeau et al., 2015; Senar, Conroy, Quesada, & Mateos-Gonzalez, 2014), behaviour (Bokony, Kulcsar, Toth, & Liker, 2012; Davies & Sewall, 2016; Lowry, Lill, & Wong, 2013; Shochat, 2004; Yeh, Hauber, & Price, 2007) and physiology (Atwell, Cardoso, Whittaker, Price, & Ketterson, 2014; Bonier et al., 2007; Partecke, Schwabl, & Gwinner, 2006). Examining populations in urban and rural habitats may provide novel insights into the mechanisms, including physiological linkages, ecological factors and selective pressures, that maintain associations between plumage coloration and other phenotypic traits. Given the widespread nature of urbanization, such research is increasingly important.

Song sparrows, *Melospiza melodia*, provide an ideal system for exploring relationships between melanin coloration, phenotype and urbanization. Both sexes display brown, melanin-based spotting on the breast, which is likely a mixture of eumelanin with some pheomelanin based on the reflectance spectra (Galvan & Wakamatsu, 2016), but to date no studies have determined whether the breast spotting is a signal used in conspecific interactions. The first step towards determining whether melanin plumage pigmentation is a signal in song sparrows is to determine whether it is reliably associated with behaviour or physiology. We focused on the breast spotting because the pattern is conspicuous on the chest (dark brown spots on a white background), particularly when males sing, and there is obvious variation among individuals in the size and colour of the spotting (Fig. 1). This spotting is also similar to plumage traits that are related to physiology and behaviour in other avian species, including sparrows (Grunst & Grunst, 2015; Rohwer, 1975, 1977). One goal of our study was to determine whether the darkness and/or area of spotting predicted a bird's level of territorial aggression in response to a simulated territorial challenge, and we focused on males because females are not territorial. Previous research found that urban song sparrows were more aggressive than rural males (Davies & Sewall, 2016; Evans, Boudreau, & Hyman, 2010; Foltz et al., 2015). Based on these results, we predicted that urban birds would possess more extensive and/or darker spotting (i.e. be more melanic) than rural birds. We also predicted that males with darker plumage and/or greater spotting would respond more aggressively during a simulated territorial intrusion, independent of habitat type. Additionally, we predicted that male song sparrows with larger and/or darker spotting would have greater initial and GnRH-induced release of testosterone as this is the general pattern for both eumelanin- and pheomelanin-based traits. Because greater eumelanin production is associated with greater resistance to stressors, we predicted that males with darker spotting would have lower initial and stress-induced corticosterone than males with lighter spotting. Finally, we examined all of these relationships in urban and rural habitats, thereby testing the hypothesis that urbanization influences pigment–phenotype relationships.

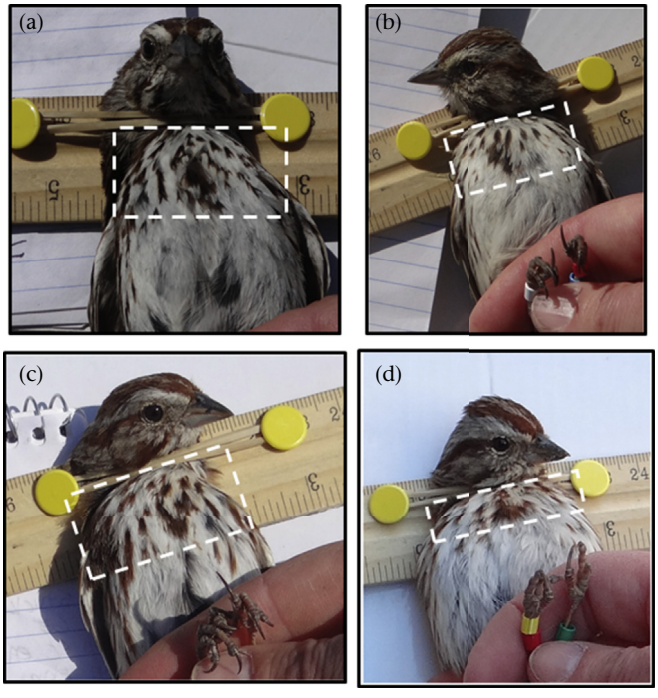

Figure 1. Variation in song sparrow chest pigmentation. The two male song sparrows depicted in (a) and (b) have rather darker brown, more eumelanic chest pigmentation compared to the two redder, more pheomelanic males depicted in (c) and (d). The amount of chest pigmentation also varies, with some males having a greater area of their chest covered (a, c) or a relatively smaller area covered (b, d).