



## Disruptive selection on plumage coloration across genetically determined morphs



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Sexual selection can drive the evolution of conspicuous visual signals that advertise individual quality to prospective mates. Reproductive strategy can influence the balance between selective pressures and whether sexually selected signals evolve. Alternatively, visual signals can serve other functions, including predator deterrence, species recognition and differentiating genetically determined morphs. In the dimorphic white-throated sparrow, *Zonotrichia albicollis*, we explored how selection on conspicuous coloration changes with reproductive strategy, and whether visual signals of morph identity are discrete from sexually selected signals of individual quality. In this species, white morph birds have more colourful plumage than tan morph birds, and white males are more promiscuous and aggressive than tan counterparts. White females are also more aggressive than tan females. White males with more contrasting coloration achieved higher lifetime fitness, whereas the opposite relationship occurred among tan males. Linear selection gradients indicated strong, positive selection on plumage contrast in white males, but negative selection on contrast in tan males. For both morphs, relationships between female coloration and fitness were weak. Results demonstrate disruptive selection on a visual signalling trait in a colour-polymorphic species and suggest that signals associated with an aggressive morph can also evolve to indicate individual quality within that morph.

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The evolution of striking colour phenotypes has intrigued evolutionary biologists since Darwin. The benefits of expressing these phenotypes are not immediately apparent, whereas costs include increasing predation risk (Fowler-Finn & Hebets, 2011; Gotmark & Olsson, 1997; Huhta, Rytkonen, & Solonen, 2003; Martin & Badyaev, 1996) and expending valuable resources (Galván & Solano, 2009; McGraw, 2006a, b; von Schantz, Bensch, Grahm, Hasselquist, & Wittzell, 1999). Costly visual ornaments, including impressive coloration, can evolve through sexual selection to serve as visual signals that indicate individual quality to prospective mates (Darwin, 1871; Fisher, 1958; Grafen, 1990). Visual ornaments that signal individual genetic or phenotypic quality should positively correlate with mating success and fitness (Balenger, Johnson, & Masters, 2009; Grunst & Grunst, 2014; Hill, 1991; Kempnaers et al., 1992; Safran, Neuman, McGraw, &

Lovette, 2005; Taff et al., 2012; Yezerinac & Weatherhead, 1997) and be under positive, directional sexual selection (Andersson, 1994). However, natural selection against conspicuous visual signals has the potential to counteract sexual selection and maintain genetic variation in sexually selected coloration, especially if selective pressures on coloration vary with alternative reproductive strategies (Jennions, Møller, & Petrie, 2001; Neff, Fu, & Gross, 2003; Robinson, Pilkington, Clutton-Brock, Pemberton, & Kruuk, 2006).

Polymorphic species provide exciting opportunities to assess how selective pressures on visual signals vary with reproductive strategy, as the morphs of these species often display obvious variation in both coloration and reproductive strategy. When morphs display different reproductive strategies, selective pressures on visual signals are also expected to differ between morphs, promoting morph-specific colour patterns, in a fashion analogous to divergent selective pressures acting to generate dichromatism in the two sexes (Badyaev & Hill, 2003; Price & Eaton, 2014). For example, in some species with genetically determined alternative reproductive morphs, one male strategy entails sneak copulation, often through female mimicry (Lank, Smith, Hanotte, Burke, &

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Cooke, 1995; Neff et al., 2003; Sinervo & Lively, 1996). In this case, a compelling hypothesis is that ornamental visual signals are under positive sexual selection, and positively correlate with fitness in displaying, but not sneaking, males. On the other hand, visual signals may positively correlate with fitness metrics (such as reproductive success, offspring quality, or longevity) even in males that do not display or compete intensely for mates, as recently reported for the relationship between melanin-based pigmentation and offspring viability in sneaker male Atlantic salmon, *Salmo salar* (Marie-Orleach et al., 2014).

Polymorphic species also provide a unique opportunity to explore how visual signals can evolve to serve multiple functions, and specifically the extent to which sexually selected coloration is distinct from other visual signals. Visual signals can fulfil functions other than indicating individual quality and attracting mating partners (Dale, 2006), in which case these traits need not be condition dependent, sexually selected or related to fitness. In polymorphic species, discrete differences in coloration commonly indicate morph identity. For example, in the polymorphic Gouldian finch, *Erythrura gouldiae*, alternative head colours signal morph identity and associated behavioural strategies, but show little variation within morphs and do not correlate with measures of individual quality. Rather, other plumage traits, including ultraviolet blue coloration and tail length are directionally selected through female choice (Pryke & Griffith, 2006, 2007). In species with complex social systems, ornamental visual signals can also indicate individual identity (Dale, 2000; Dale, Lank, & Reeve, 2001; Sheehan & Tibbetts, 2010; Tibbetts, 2002, 2004; Tibbetts & Dale, 2007). For instance, plumage coloration in the polymorphic ruff does not display condition-dependent expression or covary with individual fitness, but is rather associated with both morph and individual identity (Dale et al., 2001; Lank & Dale, 2001).

The above examples suggest that visual signals related to morph or individual identity are sometimes distinct from those that signal individual quality, with sexually selected signals of individual quality particularly distinguished by condition dependence (Tibbetts & Curtis, 2007). However, a single ornamental trait can evolve to serve multifaceted functions, although the contexts in which this occurs remain poorly understood. For instance, aposematic coloration that signals toxicity to predators has been co-opted as a sexual signal in *Heliconius* butterflies (Finkbeiner, Briscoe, & Reed, 2014) and strawberry poison frogs, *Oophaga pumilio* (Crothers & Cummings, 2013; Cummings & Crothers, 2013). In the colour polymorphic strawberry poison frog, bright aposematic coloration indicates differences in toxicity between morphs, but also signals male territorial aggressiveness within some morphs (Crothers & Cummings, 2015). Furthermore, aposematic coloration is preferred by females and sexually dimorphic in at least one *O. pumilio* population, suggesting the action of sexual selection (Maan & Cummings, 2009). Similarly, colour patterns associated with genetically determined morphs that differ in aggressiveness could evolve to also signal variation in competitive ability and fitness within a morph.

The dimorphic white-throated sparrow, *Zonotrichia albicollis*, is an excellent species in which to investigate whether selective pressures on visual signals vary with reproductive strategy, and whether visual signals associated with morph identity also serve as sexually selected signals of individual condition and fitness. In this species, males and females occur as one of two alternative morphs: white-striped or tan-striped, which show clear differences in plumage coloration and reproductive strategy. White morph birds display more colourful plumage than tan morph birds, with darker black lateral crown stripes, brighter white median crown stripes and brighter yellow superciliaries (Fig. 1;

Rathbun et al., 2014). Morph is genetically determined, with white morph birds heterozygous for a >100 Mb inversion-based supergene on the second chromosome (ZAL2<sup>m</sup>) and tan morph birds homozygous for the version of chromosome 2 without the inversion (ZAL2) (Lowther, 1961; Thorneycroft, 1966, 1975; Tuttle et al., 2016). White morph males are more aggressive, sing at higher rates (Falls & Kopachena, 2010; Kopachena & Falls, 1993a) and have higher testosterone levels and larger testes than tan morph males (Maney, 2008; Spinney, Bentley, & Hau, 2006; Swett & Breuner, 2009). Furthermore, white morph males engage in more extrapair mating, but also lose more within-pair paternity and provide less paternal care. Similarly, white morph females are more aggressive and less parental than tan morph counterparts, and sometimes sing and engage in territoriality (Knaption & Falls, 1983; Kopachena & Falls, 1993b; Tuttle, 1993, 2003). White-throated sparrows pair disassortatively by morph (Houtman & Falls, 1994). In addition to potential behavioural reasons, disassortative mating may be favoured because being homozygous ZAL2<sup>m</sup> is deleterious (Falls & Kopachena, 2010; Romanov et al., 2009; Tuttle et al., 2016). Selection for disassortative mating may thus promote a conspicuous plumage marker for ZAL2<sup>m</sup>. Therefore, differences in plumage coloration may have evolved as a signal of the distinct genetic make-up and behavioural strategies of each morph. As morph identity is defined by the presence of ZAL2<sup>m</sup>, and closely associated with well-documented behavioural differences, we hereafter refer to differences in plumage coloration as a signal of morph identity.

In white-throated sparrows, crown plumage coloration clearly signals morph identity. However, variation in coloration also occurs within the morphs. Females have less conspicuous coloration than males (Rathbun et al., 2014), suggesting that sexual selection may act on males, leading to sexual dichromatism (Maan & Cummings, 2009). Birds of the same sex also vary in coloration within the morphs, with some birds having more contrasting crown plumage coloration than others (Fig. 1). Here we address whether this within-morph variation in coloration is related to fitness and under phenotypic selection. Variation in coloration in the white-throated sparrow could solely indicate morph identity, with within-morph variation largely unrelated to fitness. On the other hand, white morph males, in particular, may be under sexual selection for ornamental plumage to indicate individual quality to prospective mates and competitive ability to territorial rivals. Conspicuous plumage in white morph females could arise through nonadaptive genetic correlation (Kirkpatrick, Price, & Arnold, 1990; Lande, 1980), leading to sexually antagonistic selection on coloration within the white morph, especially given the potential survivorship cost associated with conspicuous coloration. However, conspicuous coloration in white morph females could also be favoured by social or sexual selection to indicate individual quality and facilitate competition over high-quality territories and mates (Amundsen, 2000; Doutrelant et al., 2008; Griggio, Devigili, Hoi, & Pilastro, 2009; LeBas, 2006; Tobias, Montgomerie, & Lyon, 2013). In contrast, more highly parental, monogamous and less aggressive tan morph birds may be under natural and social selection against conspicuous plumage signals, to avoid detection by predators and prevent misdirected aggression from white morph birds (Fowler-Finn & Hebets, 2011; Martin & Badyaev, 1996).

Most studies of phenotypic selection quantify fitness components (Kingsolver & Pfennig, 2007). Our data set derives from an intensive, long-term field study, which allowed us to determine the lifetime reproductive success of individuals. Using this data set and the unique context provided by a polymorphic species, our study grants new insights into how phenotypic selection on visual signals can change depending on reproductive strategy, and how visual signals can evolve to serve multiple functions.

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