



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, Rytönen, & 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; Kempaers 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^m) 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^m 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^m. 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^m, 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.

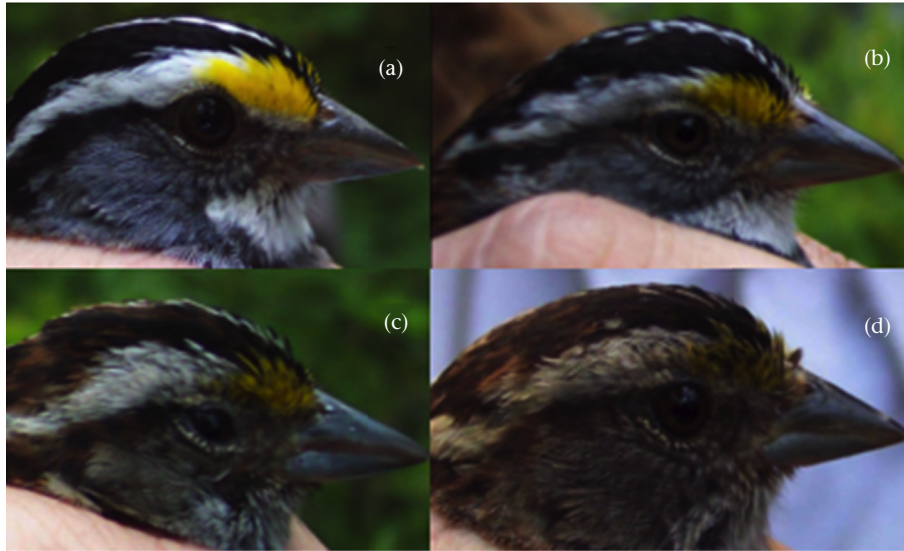


Figure 1. Examples of (a, c) high-contrast and (b, d) low-contrast white-crowned sparrow males of the white morph and the tan morph, respectively. The median crown stripe (MCS) is the white stripe at the centre, top of the head. The lateral crown stripes (LCS) are the brown to black stripes on either side of the MCS. The superciliary stripe contains a patch of yellow, carotenoid-based pigmentation at the front end.

METHODS

Study System

We conducted our study from 2006 to 2014 (May–August), in a population of white-throated sparrows breeding near the Cranberry Lake Biological Station (State University of New York, College of Environmental Science and Forestry, 44°15' N; 74°48' W). Focal birds are banded with U. S. Fish and Wildlife bands bearing unique identification numbers and with colour band combinations that allow visual identification (Master Banding Permit 22296 to E. M. Tuttle). Unbanded birds on the central study site are assumed to be young (first-year) breeders, as the majority of birds on central territories (~90% each year) are banded and adults are highly philopatric. For this study, we used 124 adult male white-throated sparrows (67 white morph, 57 tan morph) that were captured during their first breeding season to measure plumage coloration, and monitored reproductive success within this season. For 98 of these birds (48 white morph, 50 tan morph), we had data on reproductive performance across their entire reproductive life spans. For females, 88 adults (41 white morph, 47 tan morph) were captured during their first breeding season to measure coloration, and reproductive success was monitored within this season. We had lifetime reproductive success from 74 females (33 white morph, 41 tan morph) that were monitored across their entire life spans. Across sexes and morphs, reproductive life span ranges from 1 to 10 years and averages (\pm SE) 2.27 ± 0.11 years. More individuals were used in analyses regarding the relationship between coloration and body condition than for analyses regarding reproductive performance (126 males, 97 females). Some individuals were eliminated from analyses regarding fitness because reproductive success was not accurately determined.

Body Condition, Feather Collection and Spectrometric Analysis

At capture, we weighed birds using a Pesola spring balance (± 0.25 g) and measured tarsus length using digital callipers (± 0.01 mm). We used the residuals of a regression predicting body mass from tarsus length as a metric of body condition. Furthermore, we collected three feathers per plumage patch from the median

crown stripe, lateral crown stripe and superciliaries (Fig. 1). To prevent pigment degradation, we stored feathers in opaque 1.5 ml centrifuge tubes at 4 °C until spectrometric analysis. Before spectrometric analysis, we taped feathers onto blank index cards to create a natural reflectance surface.

We collected reflectance spectra from each plumage patch using a USB4000 Miniature Fiber Optic Spectrometer (Ocean Optics, Dunedin, FL, U.S.A.). We sampled each plumage patch three times and averaged the three readings to obtain a final reflectance spectrum. We repositioned the spectrometer probe between measurements and reset the white reflectance standard approximately every hour (Rathbun et al., 2014).

We used measurements of total brightness from the plumage patches to derive a single metric of plumage contrast, as described below. Brightness is defined as total reflectance (%) summed across all integer wavelengths within the avian visual range (300–700 nm) (Andersson & Prager, 2006; Endler, 1990). Mathematically, total brightness is derived from the formula: $B = \sum_{\lambda=300}^{700} R_{\lambda}$, where R_{λ} is median reflectance at each integer wavelength (nm). To efficiently extract brightness measurements from reflectance spectra, we used CLR version 1.05 (Montgomerie, 2008). Other colorimetric variables extracted from reflectance spectra are discussed elsewhere (Rathbun et al., 2014).

We performed a principal component analysis using R 2.15.2 (R Core Team, 2012), and used scores on the first principal component (PC1) as a metric of overall 'plumage contrast'. We initially intended to use brightness measurements from all three feather patches in the principal components analysis. However, for many birds, we were unable to obtain accurate reflectance measurements from the median crown stripe, because white feathers were highly diaphanous. Thus, to prevent restrictive reductions in sample size, we used data from the black lateral crown stripe and yellow superciliaries alone to extract a plumage contrast score for use in final analyses. Plumage contrast scores derived using brightness measurements from all three feather patches were highly correlated to scores derived from the lateral crown stripe and superciliaries alone (Pearson's correlation: $r_{213} = 0.88$, $P < 0.001$), suggesting that the latter remains a good overall measure of plumage contrast. We used plumage contrast in analyses, rather than brightness measurements on individual plumage patches, because we believe this

composite signal is more relevant to signalling. The receiver most likely evaluates the coloration of different crown plumage patches simultaneously, rather than in isolation. Also, we wanted to avoid an overly complex statistical analysis, involving testing multiple interactions.

The first principal component (PC1) from the analysis, including lateral crown stripe brightness and superciliary brightness alone, explained 62% of the variance in coloration and had an eigenvalue of 1.25. Loadings on the first principal component were -0.707 for lateral crown stripe brightness and 0.707 for superciliary brightness. Thus, birds with higher scores on the first principal component had darker black (less bright) lateral crown stripes but brighter superciliary stripes (Fig. 2). This means that birds with more 'contrasting' coloration have crown plumage patches that are more visually distinct from each other. However, our measure of plumage contrast is not completely equivalent to the difference in brightness between plumage patches, because the brightness of the lateral crown stripe is less variable than that of the superciliaries (Fig. 2). Birds can produce darker lateral crown stripes by depositing more melanin in the plumage, and more black eumelanin relative to lighter pheomelanin (McGraw, 2006b; McGraw, Safran, & Wakamatsu, 2005). Birds can produce brighter white median crown stripes by depositing less melanin in this plumage region and by enhancing feather microstructure. Brighter carotenoid-based pigmentation is often associated with less yellow (less saturated) coloration, with lower carotenoid content (Andersson & Prager, 2006). However, in the white-throated sparrow, the deposition of melanins in the superciliary region reduces brightness while masking yellowness. Thus, brighter superciliaries generally contain less melanin but are also yellower (Rathbun et al., 2014).

We also calculated saturation of the carotenoid-based superciliary stripe using the formula $S = (\text{median } R_{700} - \text{median } R_{450}) / (\text{median } R_{450})$ (Andersson & Prager, 2006). Carotenoid saturation indicates the amount of carotenoids deposited in plumage (McGraw, Stoehr, Nolan, & Hill, 2001).

Nest Monitoring and Molecular Analysis

We located white-throated sparrow nests via behavioural monitoring of territories. As white-throated sparrows can rear multiple broods per season, intensive monitoring is required to ensure that all nesting attempts are identified. We checked nests every 2 days to monitor nest fate and contents. When nestlings

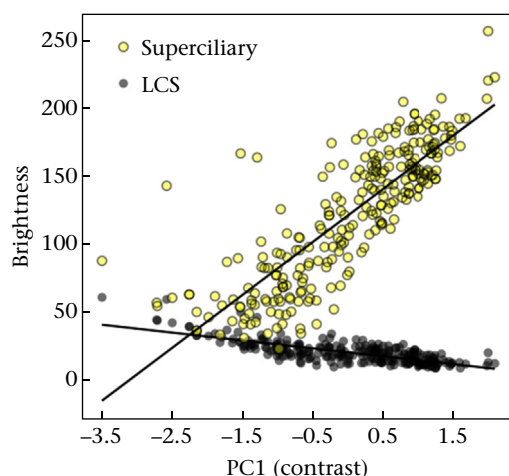


Figure 2. Linear relationships between plumage contrast (PC1) and the brightness of the superciliary patch and lateral crown stripe (LCS).

were banded on day 6–7, we placed an iButton thermochron in the nest. We considered nests depredated if temperature profiles extracted from thermochrons indicated that the nest was empty before day 9, and parents were not seen feeding fledglings. We considered nests successful if thermochron data indicated that nestlings fledged after day 9, and parents were observed with fledglings.

To obtain DNA, we extracted blood (80–200 μl) from adults and 6–7-day-old nestlings. We stored haematocrit in lysis buffer at 4°C (Longmire, Gee, Handenkipf, & Mark, 1992) until extracting DNA using the DNA IQ[®] magnetic extraction system (Promega Corp; Madison, WI, U.S.A.). We conducted parentage analysis using eight microsatellite loci; Gf01 and Gf12 (Petren, 1998), MME1 (Jeffery, Keller, Arcese, & Bruford, 2001), Dp μ 01 and Dp μ 03 (Dawson, Gibbs, Hobson, & Yezerinac, 1997), and ZLC02, ZLC07 and ZLH02 (Poesel, Gibbs, & Nelson, 2009). We used fluorescently labelled primers and ran PCR products on an ABI PRISM 310 Genetic Analyzer[®] (GMI Inc.; Ramsey, MN, U.S.A.) to identify alleles. We used direct comparison of nestling and adult alleles in combination with CERVUS 3.0 (Field Genetics, London, U.K.) to assign paternity to nestlings and determine whether nestlings were within-pair or extrapair offspring. We specified a genotyping error rate of 1%, estimated that 80% of fathers were genotyped, and accepted paternity assignment at 80% certainty (Kalinowski, Taper, & Marshall, 2007). For the microsatellites used, the combined frequency of nonexclusion (probability of considering a male a potential father when he is not the father) was 0.0002 when only the male was genotyped and <0.0001 when both adults were genotyped. We determined the actual reproductive success of males by adjusting apparent reproductive success for extrapair offspring. Females were assumed to be the mother of nestlings in their nests, since rates of intraspecific brood parasitism are low (Tuttle, Jensen, Formica, & Gonser, 2006), and we did not encounter cases in which female and offspring alleles extensively mismatched.

Out of 543 nestlings, 108 (19.8%) were extrapair offspring. We were able to assign relatively few extrapair nestlings (37, 37.2%) to a father, indicating that many nestlings were sired by males whose territories lay beyond our study site. As a corollary, focal males may have obtained extrapair paternity outside of the study site. However, we do not expect the exclusion of these offspring to bias our results.

We determined the sex of adults at capture by the presence of a brood patch (females) or cloacal protuberance (males) and confirmed sex through behavioural observations. We determined the morph of adults at capture using the visual criteria set forth by Lowther (1961), Piper and Wiley (1989) and Tuttle (1993, 2003). We later confirmed the sex (Griffiths, Double, Orr, & Dawson, 1998) and morph (Michopoulos, Maney, Morehouse, & Thomas, 2007; Romanov et al., 2009) of adults using molecular techniques.

All research reported here was in compliance with the current laws of New York State, the State of Indiana, and the U.S. federal government. Indiana State University's Institutional Animal Care and Use Committee approved all methods (protocols 562158-1 and 562192-1). Procedures employed were minimally invasive, and we made extensive efforts to avoid undue distress to birds.

Statistical Analysis

We performed statistical analyses in R 2.15.2 (R Core Team, 2012). We used zero-inflated generalized linear mixed models (GLMMs) with a negative binomial distribution (R package 'glmmADMB') and first breeding season as a random effect to model the relationship between morph, plumage coloration and lifetime reproductive success. To test whether plumage coloration related differently to reproductive success in the two morphs, we

included two-way interactions between morph and both coloration variables (plumage contrast and carotenoid saturation) in initial models. We specified Helmert contrasts for these models, to facilitate interpretation of main effects when including interactions in the model. For males, we also ran this model using lifetime within-pair reproductive success, excluding extrapair offspring. Furthermore, to assess whether the rate at which individuals accrued reproductive success varied, we used the 'offset' option to add the natural logarithm of the number of breeding years as an exposure variable. In this latter model, we included all birds for which we had determined at least 1 year of reproductive performance (124 males, 88 females). We used an equivalent modelling technique to investigate the relationship between coloration and within-season reproductive success, but used a Poisson rather than negative binomial model, owing to no evidence for overdispersion. We used GLMMs with a Poisson distribution and first year as a random effect to test whether coloration variables and morph interacted to predict reproductive life span (R package 'lme4'; Bates, Maechler, & Bolker, 2012).

For data involving reproductive success, zero-inflated models performed better than standard count models owing to the large number of zeros in our data set. Of the birds for which we measured lifetime reproductive success, 28 (28.5%) of 98 males and 15 (20.2%) of 74 females achieved no reproductive success across their life spans. When including individuals for whom we did not have total reproductive success, 38 (30.6%) of 124 males and 18 (20.4%) of 88 females achieved no reproductive success. Finally, within the year in which coloration was measured, 61 (49.1%) of 124 males and 25 (28.4%) of 88 females achieved no success.

When plumage coloration variables showed significant relationships to lifetime fitness, we derived linear selection gradients to estimate the strength of selection on that trait. To estimate standardized selection gradients, we calculated relative fitness by dividing each individual's lifetime reproductive success by the type- (e.g. white morph male) specific mean and standardized coloration variables (Lande & Arnold, 1983). We then performed univariate linear regressions between relative fitness and the coloration variable. We performed linear regressions within the morphs, as our analyses indicated morph-specific relationships between coloration and fitness. Relative fitness values showed a nonparametric distribution, so we used bootstrapping (function 'Boot' in R package 'car') to obtain beta coefficient estimates (β) and bias-corrected, accelerated (BCa) 95% confidence intervals (CIs) (Fox & Weisberg, 2011).

We used GLMMs with a binomial distribution to model male success in achieving extrapair paternity across a life span (coded 1 or 0), with only males that were monitored across their entire life spans included in the analysis. To model the rate at which males obtained extrapair paternity, we repeated the analysis with breeding years as an offset variable, and all males for which we observed at least one breeding season included. We modelled extrapair paternity as a binary variable because the vast majority of males obtained no extrapair paternity (109 out of 124, 87.9%).

To model male success in avoiding cuckoldry, we used a GLMM with a binomial distribution (R package 'lme4'; Bates et al., 2012). We entered each brood as a separate data point, with number of extrapair young in the brood as the dependent variable and brood size as the binomial denominator. We entered male identity as a random effect and an observation-level random effect (brood identity) to control for overdispersion. We entered brood order (whether the clutch was the first, second, etc., nesting attempt of a given pair) as a covariate. Finally, we used linear models to test for relationships between coloration and body condition.

We removed nonsignificant predictors from models by first removing interaction terms and then always removing the variable

with the highest P value first. After running overall models, we reran analyses within the morphs. We performed separate models for males and females.

RESULTS

Male Plumage Coloration, Longevity and Fitness

Of the 98 males for which we obtained lifetime reproductive success, 50 (51.0%) bred during only one season, 21 (21.4%) during two seasons, 17 (17.3%) during three seasons, 5 (5.1%) during four seasons and 5 (5.1%) during five seasons. Lifetime reproductive success in males ranged from 0 to 15 with a mean \pm SE of 4.27 ± 0.42 . Within white morph males, lifetime reproductive success ranged from 0 to 14 with a mean of 3.93 ± 0.63 , whereas within tan morph males, lifetime reproductive success ranged from 0 to 15 with a mean of 4.15 ± 0.58 .

Plumage contrast tended to interact with male morph to predict number of seasons survived, suggesting that white males with higher contrast survived longer, whereas tan males with higher contrast died younger (Poisson GLMM: $Z = 1.91$, $\beta = 0.18 \pm 0.09$, $P = 0.055$). However, the relationship between plumage contrast and longevity was nonsignificant within both white morph males ($Z = 1.42$, $\beta = 0.21 \pm 0.15$, $P = 0.153$) and tan morph males ($Z = -1.28$, $\beta = -0.16 \pm 0.12$, $P = 0.200$). Carotenoid saturation was not related to longevity ($Z = -0.10$, $\beta = -0.01 \pm 0.10$, $P = 0.917$), irrespective of morph ($Z = -0.49$, $\beta = -0.08 \pm 0.17$, $P = 0.624$, interaction term).

Plumage contrast was related to lifetime reproductive success in opposite fashions in males of the two morphs, as indicated by a significant interaction between morph and plumage contrast in predicting lifetime reproductive success (Table 1). Morph alone was not related to lifetime reproductive success (Table 1). Analyses within the morphs revealed that white morph males with higher plumage contrast achieved higher lifetime reproductive success than white morph males with lower contrast. Conversely, tan morph males with higher plumage contrast achieved lower reproductive success than tan morph males with lower contrast

Table 1
Zero-inflated negative binomial GLMMs predicting lifetime reproductive success from male morph and plumage contrast

Variable	Estimate ($\beta \pm$ SE)	Z	P
Across morphs			
Intercept	1.48 \pm 0.12	11.98	<0.001
Morph ^a	-0.10 \pm 0.11	-0.91	0.36
Plumage contrast	0.04 \pm 0.10	0.43	0.67
Morph * contrast	0.37 \pm 0.10	3.53	<0.001
Zero-inflation	0.25 \pm 0.04		
Dispersion parameter	4.33 \pm 1.67		
Random effects	SD	Variance	N
First year	0.12	0.01	9
Within white morph			
Intercept	1.35 \pm 0.23	5.86	<0.001
Plumage contrast	0.44 \pm 0.18	2.44	0.015
Zero-inflation	0.29 \pm 0.07		
Dispersion parameter	3.70 \pm 2.27		
Random effects	SD	Variance	N
First year	0.25	0.06	7
Within tan morph			
Intercept	1.58 \pm 0.12	12.27	<0.001
Plumage contrast	-0.33 \pm 0.10	-3.04	0.002
Zero-inflation	0.22 \pm 0.06		
Dispersion parameter	7.14 \pm 4.61		
Random effects	SD	Variance	N
First year	0.13	0.01	9

N = 98 males, 48 white morph, 50 tan morph.

^a White morph contrasted to tan morph.

(Table 1, Fig. 3a,b). Model results were qualitatively equivalent when using within-pair lifetime reproductive success as the dependent variable ($Z = 3.17$, $\beta = 0.29 \pm 0.09$, $P = 0.001$, morph*plumage contrast interaction). Similarly, white morph males with greater contrast showed a nonsignificant tendency to accrue reproductive success at a faster rate, whereas tan morph males with lower contrast accrued reproductive success more rapidly (Table 2). On the other hand, carotenoid saturation was not associated with lifetime reproductive success ($Z = -0.97$, $\beta = -0.08 \pm 0.09$, $P = 0.334$), regardless of morph ($Z = -0.76$, $\beta = -0.06 \pm 0.09$, $P = 0.444$, carotenoid saturation*morph), or with the rate at which males accrued reproductive success ($Z = -1.27$, $\beta = -0.08 \pm 0.06$, $P = 0.200$), regardless of morph ($Z = 0.08$, $\beta = 0.004 \pm 0.06$, $P = 0.940$, carotenoid saturation*morph).

When including number of breeding seasons as a covariate in the model predicting male lifetime reproductive success, breeding seasons had a highly significant positive effect on lifetime reproductive success ($Z = 7.05$, $\beta = 0.33 \pm 0.04$, $P < 0.001$). However, the interaction between crown plumage contrast and morph remained highly significant ($Z = 2.56$, $\beta = 0.20 \pm 0.08$, $P = 0.011$), suggesting independent effects of coloration and longevity on lifetime reproductive success.

There were also opposing relationships between within-year reproductive success and plumage contrast in the two morphs, with crown plumage contrast and male morph interacting to predict reproductive success ($Z = 2.44$, $\beta = 0.22 \pm 0.09$, $P = 0.015$). Crown plumage contrast was not significantly related to within-year reproductive success within white morph males ($Z = 1.47$, $\beta = 0.22 \pm 0.15$, $P = 0.150$), but tan morph males with higher contrast had lower within-season success ($Z = -2.04$, $\beta = -0.23 \pm 0.11$, $P = 0.041$). As for lifetime reproductive success,

Table 2

Zero-inflated negative binomial GLMMs predicting rate of accrual of reproductive success (per season) from male morph and feather contrast (number of breeding years included as an exposure variable)

Variable	Estimate ($\beta \pm \text{SE}$)	Z	P
Across morphs			
Intercept	0.79 \pm 0.09	8.79	<0.001
Morph	-0.17 \pm 0.08	-2.03	0.042
Plumage contrast	0.002 \pm 0.07	0.03	0.972
Morph*contrast	0.20 \pm 0.08	2.58	0.009
Zero-inflation	0.23 \pm 0.04		
Dispersion parameter	17.17 \pm 14.66		
Random effect	SD	Variance	N
First year	0.001	0.04	9
Within white morph			
Intercept	0.58 \pm 0.18	3.20	0.001
Plumage contrast	0.23 \pm 0.15	1.54	0.124
Zero-inflation	0.25 \pm 0.08		
Dispersion parameter	4.93 \pm 3.23		
Random effect	SD	Variance	N
First year	>0.001	>0.001	8
Within tan morph			
Intercept	0.95 \pm 0.08	11.29	<0.001
Plumage contrast	-0.20 \pm 0.08	-2.51	0.012
Zero-inflation	0.19 \pm 0.05		
Dispersion parameter	>403.43 \pm 2.40		
Random effect	SD	Variance	N
First year	>0.001	>0.001	9

$N = 124$ males, 67 white morph, 57 tan morph.

the interaction between morph and carotenoid saturation was not related to within-season success ($Z = 0.23$, $\beta = 0.02 \pm 0.10$, $P = 0.818$), nor was carotenoid saturation related to within-year reproductive success across the morphs ($Z = 0.38$, $\beta = 0.03 \pm 0.10$, $P = 0.707$).

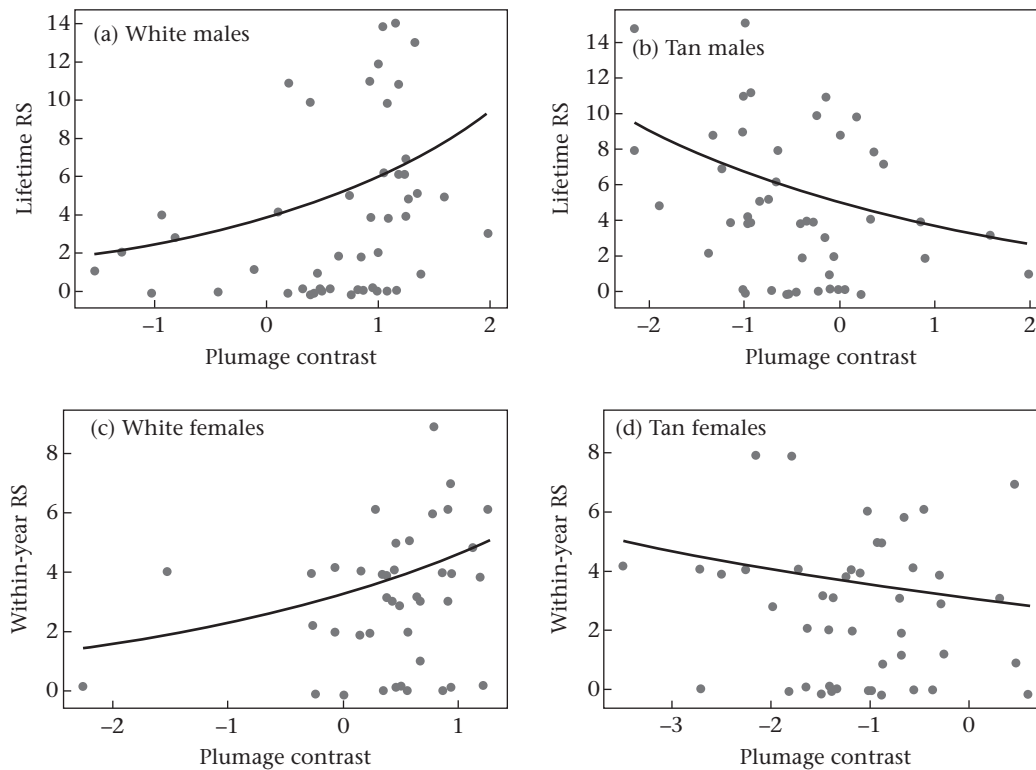


Figure 3. Relationship between lifetime reproductive success and plumage contrast in (a) white morph and (b) tan morph males, and between within-year reproductive success and plumage contrast in (c) white morph and (d) tan morph females. Lines represent predicted values from GLMs.

Male Plumage Coloration, Extrapair Paternity and Cuckoldry

Our capacity to analyse the relationship between extrapair success and coloration was limited by the low number (37) of extrapair offspring assigned to fathers. Fifteen males in our data set obtained extrapair paternity, and all were white morph males. The number of extrapair offspring sired ranged from 1 to 5, with a mean \pm SE of 0.36 ± 0.10 . Within white morph males, plumage contrast ($Z = 1.29$, $\beta = 0.65 \pm 0.50$, $P = 0.196$) and carotenoid saturation were both unrelated to the probability of obtaining extrapair paternity across a life span ($Z = 0.08$, $\beta = 0.48 \pm 5.83$, $P = 0.934$). When modelling the rate at which males obtained extrapair paternity, results were qualitatively equivalent.

Plumage coloration was not related to the number of extrapair young in a male's social broods. Plumage contrast ($Z < 0.001$, $\beta = -0.0001 \pm 2.25$, $N = 159$ clutches, 82 males, $P = 0.999$) and carotenoid saturation ($Z = 0.59$, $\beta = 1.16 \pm 1.97$, $P = 0.556$) did not interact with morph to predict the number of extrapair young in broods. Furthermore, in a model excluding interaction terms, plumage contrast ($Z = -0.39$, $\beta = -0.36 \pm 0.91$, $P = 0.697$), carotenoid saturation ($Z = 1.23$, $\beta = 1.19 \pm 0.96$, $P = 0.215$) and clutch number ($Z = -1.16$, $\beta = -1.20 \pm 1.02$, $P = 0.243$) were unrelated to the number of extrapair young. White morph males had more extrapair young in their broods than tan morph males ($Z = 2.04$, $\beta = 2.67 \pm 1.30$, $P = 0.040$).

Female Plumage Coloration, Longevity and Fitness

Of the 74 females for which we obtained lifetime reproductive success, 44 (59.4%) bred during only one season, 17 (22.9%) during two seasons, 5 (6.7%) during three seasons, 6 (8.1%) during four seasons and 2 (2.7%) during five seasons. Lifetime reproductive success in females ranged from 0 to 19 with a mean of 5.13 ± 0.54 . Within white morph females, lifetime reproductive success ranged from 0 to 19 with a mean of 6.15 ± 0.87 , whereas within tan morph females, lifetime reproductive success ranged from 0 to 15, with a mean of 4.31 ± 0.67 .

Plumage coloration was not related to female survival. Plumage contrast did not interact with morph to predict seasons survived (Poisson GLM: $Z = -0.25$, $\beta = -0.03 \pm 0.13$, $P = 0.799$), and neither plumage contrast ($Z = -0.33$, $\beta = -0.04 \pm 0.12$, $P = 0.736$) nor morph ($Z = 0.85$, $\beta = 0.13 \pm 0.15$, $P = 0.393$) were independently related to seasons survived. In parallel, carotenoid saturation was not related to seasons survived ($Z = -0.20$, $\beta = -0.02 \pm 0.11$, $P = 0.839$), irrespective of morph ($Z = -0.64$, $\beta = -0.07 \pm 0.12$, $P = 0.520$, interaction term). However, longevity was positively related to lifetime reproductive success in females ($Z = 7.27$, $\beta = 0.38 \pm 0.05$, $P < 0.001$).

In females, plumage coloration was not related to lifetime reproductive success. The interactions between morph and both coloration variables were highly nonsignificant ($P > 0.40$). In a reduced model, plumage contrast ($Z = -0.55$, $\beta = -0.07 \pm 0.13$, $P = 0.59$), carotenoid saturation ($Z = -0.62$, $\beta = -0.06 \pm 0.10$, $P = 0.54$) and morph ($Z = 1.24$, $\beta = 0.20 \pm 0.16$, $P = 0.22$) were all unrelated to lifetime reproductive success. Results were qualitatively equivalent when modelling the rate at which females accrued reproductive success.

Female reproductive success within the year in which coloration was measured (the first breeding season) was related to crown plumage contrast in opposite fashions in females of the two morphs, as indicated by a significant interaction between plumage contrast and morph; (Table 3). White morph females with greater plumage contrast tended to achieve higher within-season reproductive success (Table 3), whereas among tan morph females there

Table 3

Zero-inflated Poisson GLMMs predicting within-year reproductive success from female morph and plumage coloration

Variable	Estimate ($\beta \pm$ SE)	Z	P
Intercept	1.15 \pm 0.12	9.04	<0.001
Morph	0.04 \pm 0.11	0.37	0.713
Plumage contrast	0.10 \pm 0.11	0.87	0.385
Morph * contrast	0.23 \pm 0.11	2.06	0.039
Zero-inflation	0.23 \pm 0.04		
Random effect	SD	Variance	N
First year	0.15	0.02	8
Within white morph			
Intercept	1.17 \pm 0.15	7.86	<0.001
Plumage contrast	0.35 \pm 0.19	1.81	0.070
Zero-inflation	0.21 \pm 0.06		
Random effect	SD	Variance	N
First year	0.08	0.007	
Within tan morph			
Intercept	1.12 \pm 0.19	5.80	<0.001
Plumage contrast	-0.14 \pm 0.11	-1.19	0.230
Zero-inflation	0.25 \pm 0.06		
Random effect	SD	Variance	N
First year	0.19	0.03	8

N = 88 females, 41 white, 47 tan.

was a nonsignificant negative relationship between within-season success and plumage contrast (Table 3, Fig. 3c,d).

Linear Selection Gradients

As we found a significant relationship between lifetime reproductive success and plumage contrast in males, we calculated linear selection gradients for plumage contrast. Bootstrapping of the regression model yielded a beta estimate \pm SE (BCa 95% CI) of 0.26 ± 0.09 (0.12, 0.48) for the relationship between relative lifetime fitness and plumage contrast within white morph males. In tan morph males, the beta estimate for this relationship was -0.30 ± 0.12 (-0.57, -0.07). Thus, our analysis indicated that selection on plumage contrast acts in opposing directions within males of the two morphs (Fig. 4). For comparison to males, we also calculated linear selection gradients to assess the strength of selection on plumage contrast in females. In white morph females, the beta estimates for the relationship between relative lifetime fitness and plumage contrast was near zero (0.005 ± 0.02 (-0.04, 0.04)). Similarly, in tan morph females the beta estimate was also

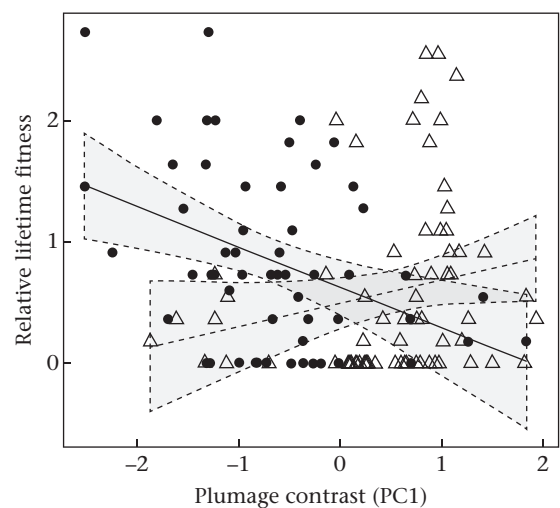


Figure 4. Linear relationships between relative fitness and crown plumage contrast (standardized) within tan morph males (●) and white morph males (△). Shaded regions represent 95% confidence intervals.

near zero (-0.02 ± 0.11 ($-0.23, 0.21$)) and associated with much uncertainty.

Body Condition and Plumage Coloration

Males with higher plumage contrast had higher residual mass, with this effect being particularly pronounced in the tan morph and nonsignificant in the white morph (Table 4, Fig. 5). The relationship between plumage contrast and residual mass partially encompassed an effect of morph, since when alone in the model with capture time, white morph males tended to have higher residual mass than tan morph males ($F_{1,131} = 3.58$, $\beta = 0.39 \pm 0.20$, $P = 0.060$). However, plumage contrast better predicted residual mass, due to the strong relationship between plumage contrast and residual mass within tan morph males. Furthermore, carotenoid saturation was related to male residual mass in a morph-specific fashion (significant interaction term, Table 4). White morph males with greater carotenoid saturation were in better condition (Table 4), whereas carotenoid saturation and condition showed a nonsignificant negative association in tan morph males (Table 4, Fig. 5). Capture date was not related to residual mass ($F_{1,118} = -1.00$, $\beta = -0.005 \pm 0.005$, $P = 0.318$), but males caught later in the day were in better condition (Table 4). In females, residual mass was significantly related only to time of capture ($F_{1,96} = 8.13$, $\beta = 0.37 \pm 0.13$, $P = 0.005$). Female coloration, morph and interaction terms were all unrelated to residual mass ($P > 0.40$ in all cases), and date was also unrelated to residual mass ($F_{1,95} = 1.21$, $\beta = -0.01 \pm 0.01$, $P = 0.273$).

DISCUSSION

Our study shows that divergent selective pressures act on conspicuous coloration within genetically determined morphs of the white-throated sparrow, providing a rare example of disruptive selection on a visual signalling trait. Results agreed with our prediction that plumage contrast should be under positive selection in white morph males owing to the actions of sexual and social selection, but under negative selection in the tan morph. White morph males with higher plumage contrast achieved higher lifetime reproductive success, whereas the opposite was true of tan morph males. Furthermore, linear selection gradients suggested

that selection acts in opposite directions in males of the two morphs, generating disruptive selection on plumage coloration across the morphs. The beta estimate for the relationship between relative fitness and plumage contrast was 0.26 ± 0.09 in white morph males and -0.30 ± 0.12 in tan morph males. In a review of studies of phenotypic selection, Kingsolver et al. (2001) found a median selection gradient estimate of 0.16. Within males of both morphs, the estimated directional selection gradient is well above this median value, suggesting strong selection within both morphs.

Other examples of disruptive selection on visual signalling traits are rare. In first-year male lazuli buntings, *Passerina amoena*, Greene et al. (2000) found disruptive selection on plumage coloration, with the most colourful and the least colourful males achieving higher within-season reproductive success than males with intermediate coloration. Older male buntings better tolerate young males with dull coloration as territorial neighbours, increasing the fitness of these males. Disruptive selection on sexually selected visual signals is also expected in the context of speciation. For instance, studies in *Heliconia* butterflies (Naisbit, Jiggins, & Mallet, 2001) and sticklebacks (McKinnon & Rundle, 2002) demonstrate disruptive sexual selection against hybrids, probably due to female avoidance of intermediate colour patterns (Gray & McKinnon, 2007). However, to our knowledge, no study has directly demonstrated disruptive selection on coloration in a species with a stable, genetically determined colour polymorphism. In the white-throated sparrow disruptive selection on plumage coloration across the two morphs should help to maintain morph-distinctive colour phenotypes, while dissortative mating by morph prevents speciation and maintains the polymorphism.

More contrasting plumage in white morph males could be selected through female choice, intrasexual competition for mates or social selection generated through competition over resources. We did not find a significant relationship between extrapair paternity or cuckoldry and plumage coloration. Moreover, the relationship between plumage contrast and lifetime within-pair reproductive success was the same as for lifetime success, including extrapair young, suggesting a strong role for within-pair reproductive success in driving the pattern we observed. White morph males with more contrasting plumage may obtain higher-quality social mates and be more aggressive and successful in intrasexual disputes over territories, as in the congeneric white-crowned sparrow, *Zonotrichia leucophrys* (Fugle, Rothstein, Osenberg, & McGinley, 1984; Laubach, Blumstein, Romero, Sampson, & Fofopoulos, 2013), thus elevating within-pair reproductive success. Both carotenoid saturation and plumage contrast positively correlated with body condition in white morph males, also suggesting that plumage coloration could serve as a reliable sexually or socially selected indicator of individual quality within white males.

In tan morph males, social or predation costs of expressing conspicuous coloration may outweigh potential signalling benefits, leading to selection against conspicuous plumage. Tan morph males with lower plumage contrast could avoid predation and conspecific aggression (Horton, Hauber, & Maney, 2012; Laubach et al., 2013), be less likely to attract predators to nests (Martin & Badyaev, 1996) and be more readily tolerated by white morph males as territorial neighbours, and thus establish better territories (Greene et al., 2000). However, there was not a statistically significant relationship between plumage coloration and body condition either across or within the morphs, and we found a positive correlation between plumage contrast and residual body mass in tan morph males, arguing against strong viability costs of plumage contrast. Furthermore, past work suggests that tan and white morph males prefer territories in different areas, which do not differ in habitat productivity (Formica, Gonser, Ramsay, & Tuttle, 2004; Formica & Tuttle, 2009).

Table 4

LMs predicting body condition from male plumage contrast, carotenoid saturation and morph

Variable	Estimate ($\beta \pm SE$)	R^2	F	df	P
All males					
Intercept	-1.78 ± 0.68	—	—	—	—
Morph	-0.04 ± 0.28	—	1.93	1, 120	0.166
Plumage contrast	0.38 ± 0.12	—	6.26	1, 120	0.013
Carotenoid saturation	-0.24 ± 0.16	—	0.91	1, 120	0.339
Time	0.15 ± 0.06	—	6.09	1, 120	0.014
Morph * carotenoid saturation	0.59 ± 0.26	—	5.10	1, 120	0.025
Full model		0.10	3.88	5, 120	0.001
White morph males					
Intercept	0.07 ± 0.19	—	—	—	—
Plumage contrast	0.20 ± 0.18	—	1.26	1, 70	0.263
Carotenoid saturation	5.60 ± 2.63	—	4.06	1, 70	0.047
Full model		0.04	2.66	2, 70	0.076
Tan morph males					
Intercept	0.28 ± 1.78	—	—	—	—
Plumage contrast	0.54 ± 0.18	—	6.52	1, 54	0.013
Carotenoid saturation	-3.18 ± 2.08	—	1.79	1, 54	0.185
Time	0.20 ± 0.09	—	4.70	1, 54	0.034
Full model		0.14	4.34	3, 54	0.009

All P values are from type III F tests.

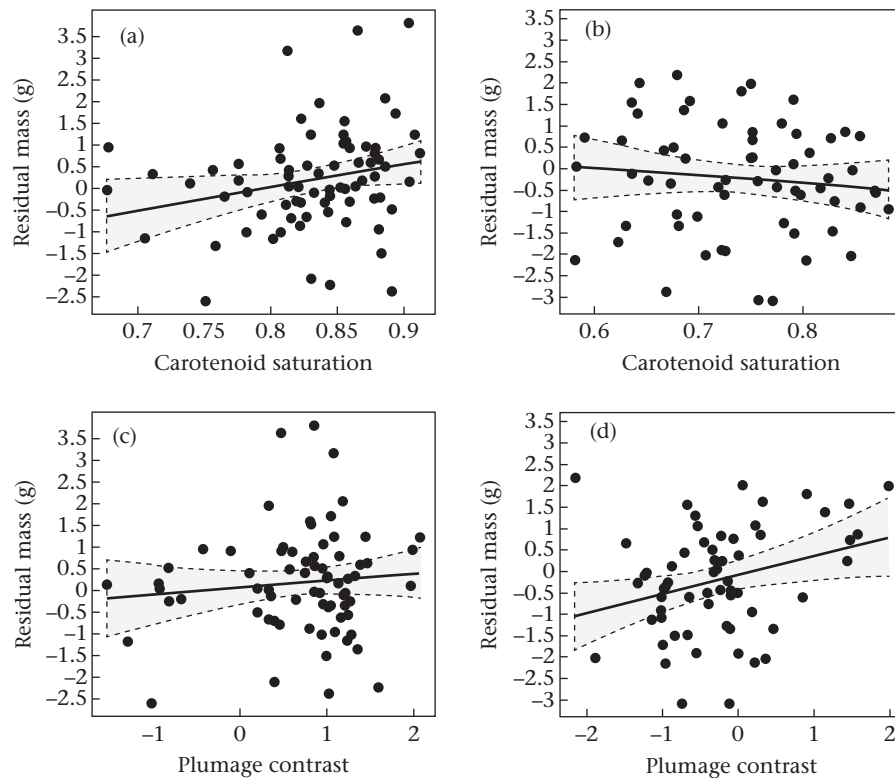


Figure 5. Linear relationships between carotenoid saturation, plumage contrast and body condition (residual mass) in (a, c) white morph males and (b, d) tan morph males. Shaded regions represent 95% confidence intervals.

Alternatively, if white morph females prefer males with lower plumage contrast, tan morph males with lower plumage contrast could attract higher-quality social mates. Examples of female preference for less elaborate visual signals are uncommon. However, in some populations of the house sparrow, *Passer domesticus*, females prefer males with smaller plumage badges, seemingly because of a testosterone-mediated trade-off between plumage badges and aggressiveness versus paternal care (Griffith, Owen, & Burke, 1999). Similarly, plumage contrast and paternal behaviour may negatively correlate within tan morph males, as also observed across the morphs, owing to pleiotropic genetic effects or physiological controls (Ketterson & Nolan, 1994; Lindsay, Webster, & Schwabl, 2011; McGlothlin, Jawor, & Ketterson, 2007). Mate choice for paternal benefits are likely to be highly important for white morph females, which are less parental than tan morph counterparts. In fact, mate choice trials suggest that females of both morphs may prefer tan males over white males, perhaps due to parental benefits, in which case tan males more similar to white males in coloration could be disfavoured (Houtman & Falls, 1994; Tuttle, 1993). Furthermore, if paternal care is critical for fitness in tan morph males independent of female choice, selection on paternal care could also exert correlational selection for reduced plumage contrast. Indeed, in species with polymorphisms, correlational selection involving suites of traits may enforce linkage disequilibrium between alleles that confer favoured trait combinations, and be crucial to explaining patterns of selection on individual traits (Sinervo & Svensson, 2002).

Past studies have suggested that signalling traits indicative of morph might be inexpensive and unrelated to condition and fitness (Pryke & Griffith, 2007; Tibbetts & Dale, 2007). However, our findings suggest that elaborate visual signals can evolve to simultaneously indicate morph and individual condition and quality. Social costs are often critical to maintaining reliable signalling of

individual quality (Martín & Forsman, 1999; Safran, Adelman, & Hau, 2009; Tibbetts, 2014) and might particularly allow visual signals associated with a highly aggressive morph to also reliably indicate individual quality within that morph. In the white-throated sparrow, white morph males respond more aggressively to territorial intruders that are also of the white morph (Horton et al., 2012). White morph males with the most contrasting plumage may analogously receive the highest levels of aggression, enforcing reliable signalling of individual quality via plumage contrast. Costs of producing highly contrasting plumage could also contribute to maintaining signal reliability. For instance, deposition of metabolically expensive melanin molecules in the lateral crown stripe and carotenoids in the supercilii could occur at the expense of antioxidant status or immune defence (Alonso-Alvarez, Perez-Rodriguez, Mateo, Chastel, & Viñuela, 2008; Catoni, Peters, & Schaefer, 2008; McGraw, 2006b; von Schantz et al., 1999). However, given the relatively small size of plumage badges in the white-throated sparrow and because territorial interactions vary strongly with morph identity (Horton et al., 2012; Tuttle, 2003), we find social costs to be a more compelling explanation for why plumage coloration associated with white morph identity could also effectively signal individual quality and evolve through sexual selection.

Furthermore, the version of chromosome 2 found in tan morph birds appears ancestral (Romanov et al., 2009; Thomas et al., 2008; Tuttle et al., 2016), suggesting that highly contrasting plumage evolved only after the emergence of morphs. Thus, a shift in behavioural strategy could have promoted social selection for conspicuous coloration within the white morph, and conspicuous coloration could have subsequently become related to individual quality within white morph birds as a result of social costs. Given that genes controlling colour phenotype are located on the inversion, the presence of the inversion-based rearrangement would

have prevented antagonistic effects in the tan morph and facilitated divergence of colour phenotype in the white morph. Similarly, sex linkage of male-advantageous alleles can limit sexually antagonistic selection and facilitate evolution of traits that benefit males, including elaborate visual signals (Tripathi, Hoffman, Weigel, & Dreyer, 2009).

Plumage contrast is a composite metric of coloration, which increases with the darkness of melanin-based pigmentation in the lateral crown stripes and the brightness of the white median crown stripe and yellow superciliaries. Thus, selection could act to increase plumage contrast in white morph males by favouring birds that deposit more melanin in the lateral crown stripe and birds that increase the brightness of white and yellow coloration, either by enhancing feather microstructure (Kennedy, Lattin, Romero, & Dearborn, 2013) or depositing less melanin in these latter areas (Rathbun et al., 2014). In contrast, tan morph males that deposit relatively less melanin in the lateral crown stripe and more melanin in the median crown stripe and superciliaries could be favoured. In addition, selection could favour tan morph males that deposit more pheomelanin rather than eumelanin in the lateral crown stripes, as pheomelanin produces lighter brown coloration (McGraw, 2006b; McGraw et al., 2005).

Importantly, the pattern of disruptive selection observed across males of the two morphs could be generated through selection against males with phenotypes atypical of their morph, or occur because, within each morph, individuals with more extreme phenotypes (i.e. more contrasting in white morphs, duller in tan morphs) are favoured. These mechanisms are not mutually exclusive, and in either case, an overall pattern of disruptive selection is generated and coloration relates differently to fitness in the two morphs. Nevertheless, underlying selective forces could differ in some respects in the two cases. For instance, in the case of selection against morph-atypical individuals, one could argue that especially highly contrasting plumage need not be a socially selected indicator of individual quality in white morph males (although dull plumage could still be an indicator of poor quality). Based on our data, we cannot conclusively disentangle the above interpretations, which would require a more specific knowledge of selective mechanisms and threshold effects. However, in addition to the pattern reported for lifetime fitness, body condition in white morph males showed a linear, positive relationship to both carotenoid saturation and plumage contrast, suggesting that increasing coloration has the potential to signal condition and quality in white morph males.

In contrast to males, we found weak evidence for contrasting associations between plumage coloration and fitness in females of the two morphs. Within the first breeding season, white morph females with higher plumage contrast achieved higher reproductive success than duller white morph females (but $P = 0.058$), whereas there was a nonsignificant negative relationship between plumage contrast and reproductive success in tan morph females. Thus, white morph females may benefit by expressing higher plumage contrast, perhaps by acquiring better mates or territories (Tobias et al., 2013), whereas tan morph females may benefit from expressing dull plumage, perhaps by avoiding nest predation (Martin & Badyaev, 1996) or misdirected aggression (Coady & Dawson, 2013; Horton et al., 2012). However, female plumage coloration was not related to lifetime fitness, linear selection gradients suggested negligible selection on plumage contrast, and female coloration was not correlated with residual mass. Given these results, it is possible that highly contrasting plumage in white morph females arose through genetic correlation with white morph males (Kirkpatrick et al., 1990; Lande, 1980). However, in white morph females, relatively high plumage contrast is probably also favoured to signal morph identity and avoid maladaptive pairing patterns (Rathbun et al., 2014). The least contrasting white

morph female in our data set was observed to pair with different white morph males during two of three breeding seasons, anecdotally supporting this possibility. However, white–white pairs are rare, suggesting that selection has reduced variation in coloration that might lead to confusion of morph identity.

We only measured plumage coloration once within the lifetime of focal birds, within the first breeding season. Thus, the relationships between fitness and coloration that we identified might apply only to young breeders, and patterns could differ among older birds. Indeed, age-dependent relationships between phenotype and fitness are common (Freeman-Gallant et al., 2010; Grunst, Rotenberry, & Grunst, 2014; Potti, Canal, & Serrano, 2013). However, most white-throated sparrows on our study site have short lives. Thus, selection acting early in life is likely to have the strongest effect on fitness.

In summary, our study provides direct evidence of disruptive selection acting on a visual signalling trait in a colour-polymorphic species, and suggests that signals associated with morph identity need not be discrete from signals of individual condition and fitness. Furthermore, we found stronger current selection on male coloration than on female coloration, perhaps due to sexual and social selective pressures acting differentially on males. Disruptive selection on the plumage coloration of white versus tan morph males may facilitate the maintenance of distinctive colour phenotypes, and has the potential to exert correlational selection on associated suites of traits, such as aggressiveness and paternal care.

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