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ORIGINAL PAPER

Are white-crowned sparrow badges reliable signals?

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Abstract Status badges, such as crown plumage, mediate intraspecific interactions. The reliability of crown morphology as a status badge in male mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) is uncertain. We examined morphological and physiological correlates of the proportion of crown that was white ("crown-white") in 178 male mountain white-crowned sparrows during the 2008–2009 breeding seasons. Using a paired experimental design, we presented territory-holding males with white-enhanced and white-reduced decoys and recorded aggressive behaviors. To assess physiological constraints on signal bluffing, a subsample of birds was captured and released after manipulating natural crowns to simulate bluffed white-enhanced or white-reduced crowns; corticosterone concentrations were assayed from blood drawn upon recapture and after a restraint-induced stressor. We found a significant positive association between crown-white and a measure of body size—tarsus length—which is an established indicator of resource-holding potential. In the decoy challenge, males responded more aggressively toward white-enhanced than white-reduced decoys. In the hormone experiment, white-enhanced birds had higher baseline corticosterone levels, whereas white-reduced birds had similar concentrations to controls. Furthermore, white-enhanced birds had an attenuated restraint-induced corticosterone response, while white-reduced birds mounted a significantly larger increase in corticosterone than controls. Taken together, these findings indicate that crown-white is a reliable status badge of resource-holding potential in male mountain white-crowned sparrows during the breeding season.

Keywords Status badge · Corticosterone · Signal reliability · Breeding season · Mountain white-crowned sparrow · Signal bluff

Abbreviations

HPA	Hypothalamic–pituitary–adrenal

Introduction

Status badges (Krebs and Dawkins 1984), such as avian plumage coloration, occur in a wide variety of taxa (Santos et al. 2011) and are often used to signal social status (Rohwer 1975). Information about fighting ability, motivation, and other context-dependent factors is communicated through variation in badge size or intensity (Enquist 1985). Because status badges reflect the signaler's fighting ability (Senar 2006), they facilitate rival assessment though the badge itself has little fighting utility (Tibbetts and Lindsay 2008). Badge conventions are thought to limit the need for excessive wasteful fights during agonistic interactions where the signal sender and signal receiver have opposing interests (Guilford and Dawkins 1995; Hurd and Enquist

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2005). Unlike traditional "handicap signals" (Zahavi 1975) where the quality of information imparted by the signal is maintained by morphological or physiological constraints on the signal sender's ability to produce or perform the signal, status badges often are not limited by inherent production costs (Lachmann et al. 2001; Hurd and Enquist 2005). In this way, status badge signaling systems seem vulnerable to cheating (Johnstone and Grafen 1993; Johnstone and Norris 1993) unless we consider potential costs associated with the receiver's response (Lachmann et al. 2001; Számadó 2011a). Variation in the signal does not need to parallel a variation in cost when the signal is either reliable or bluffed without detection. However, when signal bluffing is detected, it is anticipated to be costly. The subtle point of distinction is that a badge's costs are dependent on the interaction between the signal sender and signal receiver and not inherently fixed. Consequently, researchers have devoted considerable attention to understanding the reliability of and costs associated with status badge signaling.

In a reliable signaling system, status badges convey information that is used to discriminate strong from weak individuals within a population (Senar and Camerino 1998). There are three elements to reliable status badge signaling (Searcy and Nowicki 2005). First, there must be a correlation between the badge and state of the signaler. Variation in badges is correlated with morphology, physiology, or motivational intent, aligning the signal message with underlying content (Enquist 1985; Maynard-Smith et al. 1988). These characteristics are directly related to an individual's resource-holding potential or fighting ability, which is a key component in aggressive interactions (Parker 1974). In a reliable signaling system, the biggest badge owners are also expected to have the highest resource-holding potential (Enquist 1985). Second, there must be evidence of signal discrimination. This has been commonly assessed through behavioral responses of the receiver to badge variation (Studd and Robertson 1985). However, conclusions based solely on behavioral observations can be confounded as there are instances where the receiver may yield to the badge convention without challenge (Rohwer 1985) and instances where the receiver may challenge the badge convention through an aggressive interaction (Møller 1987). An aggressive receiver response, whether a universal reaction to threat or elicited by detection of incongruence between the signal and the signal sender's true state (Rohwer 1977), may result in important costs to signal bluffers (Maynard-Smith et al. 1988). Thus, the final element of badge reliability is a constraint on signal bluffing. The constraint might be related to inherent limitations of the signal sender or could be inflicted by the receiver response (Searcy and Nowicki 2005).

White-crowned sparrows (*Zonotrichia leucophrys*) are small-bodied passerines in which mate choice is determined by male competition and female selection after arrival at the breeding grounds (Morton 2002). Most individuals in this short-lived species have limited breeding opportunity (Morton 2002); thus, territory and mate acquisition are key driving forces of selection pressure among male birds, setting the stage for intense contests during the breeding season. White-crowned sparrows have cryptic brownish plumage, except for a conspicuous black-and-white striped pattern located on the top of the head, termed a "crown" (Fig. 1). In this species, both experimental and observational studies have reported that crown morphology is an important factor that mediates interactions between sexes and age classes (Parsons and Baptista 1980; Fugle et al. 1984; Watt 1986). However, signal bluffers do not appear to experience increased aggression from dominant adult males in wintering flocks, making successful bluffing potentially "cost-free" (Fugle and Rothstein 1987; Keys and Rothstein 1991). This finding contradicts what would be expected from the social-control hypothesis (Rohwer 1977; Slotow et al. 1993). Thus, in the absence of perceived costs, the maintenance of crown signaling reliability in white-crowned sparrows (*Zonotrichia leucophrys gambelii*) is unclear (Fugle et al. 1984; Fugle and Rothstein 1987; Searcy and Nowicki 2005).

We aimed to investigate whether crown variation in mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) mediates intraspecific communication during the early- to mid-breeding season by testing the three predicted requirements of signal reliability outlined by Searcy and Nowicki (2005). We measured morphological and physiological characteristics to assess the relation between individual state and badge size. We also used a series of decoy challenges to quantify the difference in aggressive response by territory-holding males to intruder crown variation. Finally, we created signal bluffers among free-living males to assess physiological costs associated with badge bluffing.

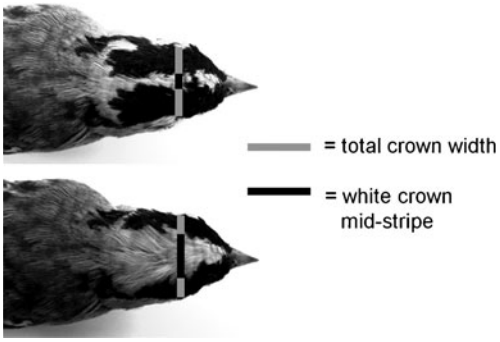


Fig. 1 Mountain white-crowned sparrow crown morphology. Crown-white is defined as the fraction (in percent) of the *black bar* divided by the total *gray bar*. *Top image* shows decoy with white-reduced treatment, whereas *bottom image* shows decoy with white-enhanced treatment

Methods

General field methods

This study was conducted around the Rocky Mountain Biological Laboratory in Gothic, CO (38.9563802° N, -107.0106015° W) in four pre-established study plots (~600 m × 150 m) situated along the East River.

Birds from a free-living study population were captured in Potter traps baited with white proso millet (*Panicum miliaceum*) seed. Trap lines were opened every morning (0600 to 1200 hours) from May through July in 2008 and 2009, during the early- to mid-breeding season. We measured tarsus length, wing cord, tail length, mass, and cloacal protruberance using mechanical calipers or a small ruler, to an accuracy of 0.1 mm. Sex was determined from the cloacal protruberance measurement (males$\geq$4 mm, female <4 mm). In males, the cloacal protruberance is extended during the breeding season to store sperm at a cooler temperature (Morton 2002). When possible, we also looked for the presence of a brood patch found among nesting females. Mass was determined using a spring scale to the nearest 0.1 g. In mountain white-crowned sparrows, the crown consists of a central white band ("stripe") bordered laterally by two black lines (Fig. 1). We measured white stripe and overall crown (i.e., stripe and adjacent eyebrow lines) widths using a caliper across the cranium and between the eyes to the nearest 0.1 mm. We calculated crown-white as the proportion of stripe-to-crown width expressed as a percentage. Our study focused on males because of their territoriality during the breeding season. In this species, once a male arrives at the breeding ground, it settles in a territory that it defends against other males. Active male pursuit of female mates and the presence of unmated "floater" males maintain strong intrasexual competition pressure (Morton 2002). All birds were banded with a sequentially numbered US Fish and Wildlife Service metal band and a unique combination of three colored plastic leg bands facilitating visual identification in the field.

Blood sample collection and corticosterone assays

We obtained blood samples from the brachial vein using a fine-tipped syringe (27 G) and collected blood into heparinized microcapillary tubes. To measure hematocrit, we first centrifuged whole blood in microcapillary tubes. We then estimated percent packed red blood cell volume with the use of a standard hematocrit card reader. Plasma was separated out for corticosterone determinations. To avoid influencing circulating corticosterone concentrations, we followed published recommendations and collected blood samples within 3 min of approaching a trapped bird (Wingfield et al. 1982; Romero and Reed 2005). We checked traps approximately every 15 min to limit the amount of time any bird remained within a trap and to minimize possible stress of detainment (Romero and Romero 2002). For hormone sample collection, we followed the standard passerine stress series protocol requiring collection of two 60–120 μL blood samples, one at baseline and one following a 30-min restraint-induced stressor through confinement in a dark cloth bag (Wingfield et al. 1992; Romero and Reed 2005). Blood samples were stored on ice and centrifuged within 6 h of collection, and plasma samples were frozen at −80 °C (−20 °C at the field station). Plasma corticosterone concentrations were measured using a standardized radioimmunological assay as described previously for this species (Romero et al. 1997). Hormone assays were used to investigate the relation between the naturally occurring crown signal and the sparrow stress response and to determine effects of paint treatment (signal alteration) on corticosterone concentrations (see experiment 2). Interassay and intraassay coefficients of variation were 12 and 7 %, respectively.

Experiment 1: behavioral response to decoy challenge

We tested whether crown size affects sparrow interactions by using crown-manipulated decoys to stage territorial challenges to free-living male mountain white-crowned sparrows. Resident males were challenged with one of seven decoys prepared from male sparrows found dead in the area, each mounted in similar neutral perching postures. Taxidermic mounts were made from previously frozen, dead male sparrows. After skinning the specimens, the skins and intact skulls were cleaned before cotton and wire were used to replicate natural shape and provide the mount with structural integrity. The use of a single decoy per study male allowed us to reduce the probability of confounding by inherent differences between the individual decoys (i.e., postural stance and other variations in morphology) and enabled us to isolate and evaluate the role of crown morphology in male–male interactions. We modified decoy crown-white by combing natural crown feathers to either increase (white-enhanced) or reduce (white-reduced) the white area on the decoy's head (Fig. 1). These modifications remained stable throughout the duration of each trial and enabled the same decoy to be presented in consecutive trials as both white-enhanced and white-reduced. We focused on the proportion of crown-white as a possible badge of status because both our own field observations and published studies (Götmark 1993) indicate that black crown plumage is unimportant during male–male interactions. Both white-enhanced and white-reduced crowns fell approximately within the distribution of natural crown widths observed in this population (range 14–53 %). All other aspects of decoy plumage remained unaltered.

To identify territory-holding males (*N*=39), we selected those that were singing or had been observed in territory defense. The trials were administered in random sequence to avoid habituation or order effects. For each trial, a decoy was temporarily clipped onto a branch above a speaker (SONY™ Model SRS-77 G). Decoy and speaker were positioned within 10 m of the singing resident. Focal animal sampling (Altmann 1974) was used during the 7-min decoy presentations, which included a 2-min broadcast (at 4 songs/min rate) of one of four mountain white-crowned sparrow songs, randomly selected and normalized at 85 dB. To reduce unfamiliarity and dialect dissimilarity biases (MacDougall-Shackleton 2001), we broadcast songs of birds singing from the local population. Songs used in the playback were males recorded in previous seasons away from the study plots. In mountain white-crowned sparrows, female song is rarely observed (Baptista et al. 1993); thus, a song playback to initiate each trial further reduces the likelihood of sex confusion. The same song was used for each pair of intrusions. To reduce circadian and seasonal variation in behavior (Breuner et al. 1999; Morton 2002), we conducted both intrusion challenges at approximately the same time of the day and within a span of up to 72 h. Resident bird responses were recorded into an Olympus (VN-5200PC) digital voice recorder by an observer positioned 10 m from the decoy and speaker setup. During territory defense, resident males responded with a number of distinct low-level aggressive behaviors toward the intruder. Interpretation of each acoustic response was derived from Morton's monograph (Morton 2002) and personal observations in the field. Our "chink calls" were the equivalent of Morton's "pink calls," our "strut" was equivalent to Morton's "trill," and songs were similarly named and defined (Morton 2002). We also scored "puffs" (an exaggerated posturing display with fully erected plumage), "flights" (any in air movement greater than 2 m), and "perch changes" (any positional movement less than 2 m). Focal observations were scored using JWatcher 1.0 (Blumstein and Daniel 2007).

Experiment 2: crown painting and corticosterone response

To determine the effects of crown signal bluffing on the glucocorticoid response, we manipulated crown characteristics in 21 free-living male mountain white-crowned sparrows captured on the study plots in 2009. We modified crown morphology by using non-toxic black ZIG Painty® and white Artline® paint markers to paint feathers. We used USB2000 Miniature Fiber Optic Spectrometer (Ocean Optics Inc.) to compare the reflectance of white paint applied to the crown of a dead mountain white-crowned sparrow to that of white crown feathers from four museum specimens. We obtained a total of 4,325 reflectance measurements (87 per bird; 4 birds with natural crowns and 1 bird with a painted white crown using Artline® white paint) across the range of wavelengths from 300–750 nm. Because avian vision is complex and may be sensitive into the ultra-violet wavelengths (Odeen and Hastad 2003), we compared spectral reflectance values of the visible range (400–700 nm) as well as across the ultra-violet range (300–400 nm) (Qvarnstrom 1997; Gottmark and Hohlfat 1995) and found no difference between the painted bird and natural crowns of the museum specimens (Fig. 2). More specifically, we compared the average reflectance across the entire spectrum (300–750 nm), just within the UV range (300–400 nm), and just within the visible range (400–700 nm) between all five birds and between the four natural crowns vs. the painted crown. A comparison of average reflectance across the entire reflectance range using the ANOVA yielded no evidence of a significant difference between the birds (F =1.16, df=4, P=0.33). A further assessment of the average reflectance for all four natural birds vs. the painted bird confirmed that the percent reflectance was not significantly different for the painted bird (chi-square=1.73, df=1, P= 0.19). Likewise, there were no significant differences between the five birds (F=1.66, df=4, P=0.17) or between the natural crowns and painted crown (Wald chi-square=2.62, df=1, P=0.11) in the UV range. For the visible range, there was a significant difference overall between the five birds (F=2.69, df=4, P=0.03); however, further examination of the pairwise comparisons confirmed that none of the significant differences were from the painted bird. Furthermore, the average reflectance of the four natural crowns was not significantly different from that of the painted crown (chi-square=1.26, df=1, P=0.26). Thus, we believe that the paint provided a close approximation to the natural white plumage.

Following initial feather cleaning with 70 % isopropyl ethanol, we assigned birds randomly to one of three treatment groups: white-enhanced (n=5), white-reduced (n=7), and control groups (n=9; Fig. 3). White paint was used to expand the white mid-stripe of the crown laterally for white-enhanced; black paint was used to expand the two black eyebrows for white-reduced. Crown manipulations (crown-white range 10–60 %) were comparable to natural variation (crown-white range 14–53 %). Distributions of black and white areas were not altered in the control group; however, existing white plumage areas were cleaned and painted white.

In the following 1–2 weeks after the paint treatment, we recaptured males. Upon recapture, we measured corticosterone levels at baseline, restraint-induced, and change between baseline and restraint-induced (see above for capture-stress methodology) among painted males.

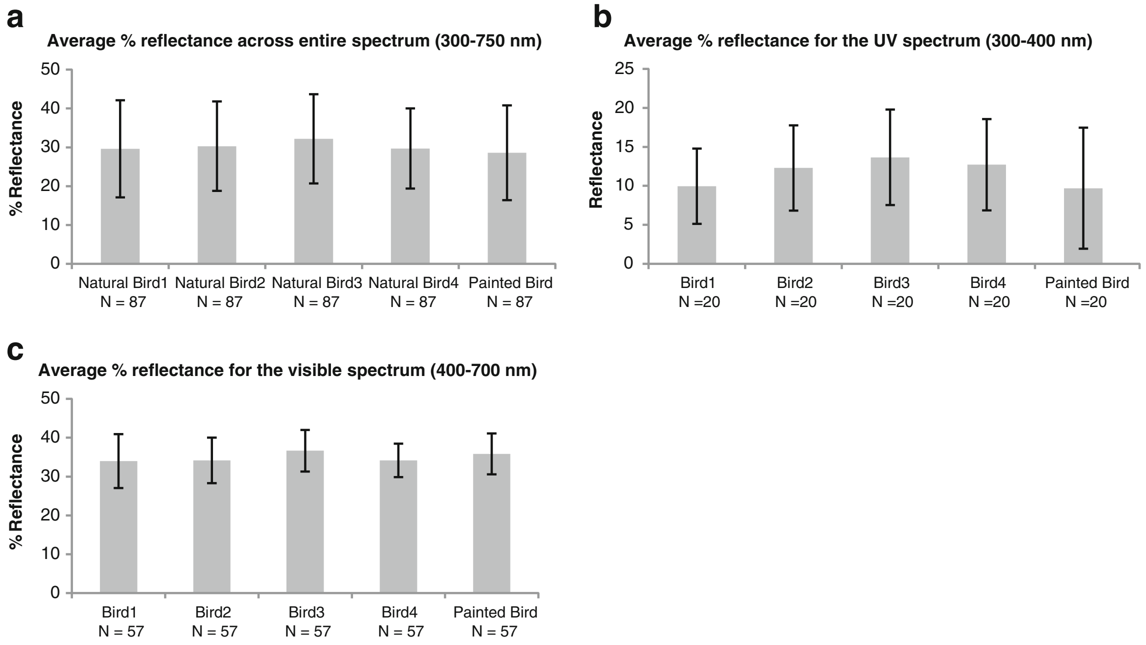


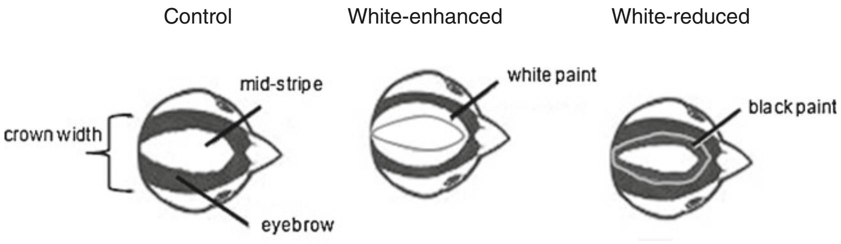
Fig. 2 Average percent reflectance for four natural white crown plumage and one painted bird **a** across the entire spectrum, **b** across the UV spectrum, and **c** across the visible spectrum

Statistical analyses

Morphological characteristics were collected from 178 male mountain white-crowned sparrows over the 2008 and 2009 field seasons. Of the 178 unique birds, 111 were caught in both years. Morphological measurements for birds caught more than once within the same year were averaged, and the data from both field seasons were pooled to maximize power; thus, each bird had the potential of contributing a maximum of two measurements for each morphological trait in the data.

We first examined associations of proportion crown-white, a normally distributed continuous variable, with morphological (tarsus length, wing chord, tail length, and mass) and physiological (hematocrit and corticosterone concentrations) characteristics with use of mixed linear regression models. Each characteristic was entered into the model as a continuous predictor, with crown-white as the outcome. Because some birds contributed morphological measurements in both field seasons, we treated bird ID as a random effect and specified an unstructured covariance matrix to account for correlations between repeated measurements. The unstructured covariance matrix is the most flexible covariance structure and provides the best possible model fit since it does not impose any constraints on variance estimations (West et al. 2007). Because morphology of birds may be inherently different between the two field seasons, we examined the need to control for year as a confounding effect, as well as the need to cluster by year. Including year as a covariate in the models was not necessary since it did not significantly affect the estimates of association for any of the morphological characteristics nor was it a significant predictor in any of the models. We also evaluated the need to cluster by year by including year as random effect in the models. A likelihood ratio test indicated that clustering by year did not improve the model fit. Thus, year was not included as a parameter in any of the models. Of the 178 birds with morphological data, blood specimens were collected from 103 birds for hematocrit determinations, and data on corticosterone concentrations were available for 38 birds from the 2009 field season only. We estimated differences in the proportion of crown-white associated with approximately one standard deviation difference of each

Fig. 3 Crown painting treatments for the signal bluffing prediction (experiment 2)



continuous characteristic (per 1 mm tarsus, per 2 g mass, per 3 mm tail length, per 3 mm wing chord, per 3 % red blood cell volume, and per 10 ng/mL corticosterone).

Next, we compared behavioral responses of 39 male birds toward a decoy with a white-enhanced vs. white-reduced crown. Paired count data of each behavior were compared using a repeated measures model with a Poisson distribution, a log link function, and an unstructured correlation matrix to account for the paired design. Because count data have no negative values, a Poisson distribution is most appropriate to examine rates as it can account for potential over-dispersion of data. We examined each of the five behaviors separately. In each model, the count of the behavior was the outcome, with predictors that included the binary exposure of interest (presentation with a white-enhanced vs. white-reduced decoy) and the natural log of the amount of time a resident male was present during the trial as the offset.

Finally, we estimated differences in plasma corticosterone concentrations between the white-enhanced treatment group (n=5) and the white-reduced treatment group (n=7) with respect to the control paint treatment group (n=9) upon recapture (baseline) and after a restraint-induced stressor using a linear regression model. In addition, we also examined the difference in change between baseline and restraint-induced corticosterone levels for each group. To validate our control paint treatment group, we also compared baseline corticosterone levels of the control group after recapture to baseline corticosterone concentrations of all natural crown birds with available corticosterone data. A comparison of the mean corticosterone levels provided no evidence of a paint treatment effect for the control birds (mean±SD difference=0.09±0.17 ng/mL; t=0.01, df=6, P=0.99); thus, we believe that our control paint treatment group accurately represented the natural crown of the bird. Additionally, to ensure that the associations we observed were not confounded by underlying physiological or morphological differences between the birds randomly assigned to the three paint treatment groups, we compared baseline physiological characteristics as well as tarsus length and crown-white of these birds prior to paint treatment. There were no significant differences in any of these characteristics; thus, we believe that the associations we observed are related to the crown manipulations.

All analyses were carried out with the use of the Statistical Analyses System software (version 9.2; SAS Institute Inc.).

Results

Morphological and physiological analyses of mountain white-crowned sparrows with natural crowns

In this free-living population of 178 male mountain white-crowned sparrows, mean±SD tarsus length, wing chord, tail length, and mass were 26.7±1.1 mm, 79.0±2.3 mm, 76.9±3.0 mm, and 29.1±2.0 g, respectively. For the subsample of birds from which blood was drawn, the average hematocrit was 51.5±3.5 %. In the subsample of males for which we obtained corticosterone data, the average baseline corticosterone concentration was 10.16±10.81 ng/mL.

When we examined the relation of crown-white with each of the morphological and physiological characteristics, we found a significant positive association between tarsus and crown-white (Table 1). Each 1-mm difference in tarsus length was related to a 2 % higher proportion crown-white (t =3.63, df=45, P=0.0007). There were no associations between crown-white and the other morphological characteristics. We also observed a positive relation of corticosterone and crown-white. Each 10-ng/mL difference in corticosterone was related to a 2 % higher proportion crown-white (Wald chi-square=6.66, df=1, P=0.01).

Experiment 1: behavioral response to decoy challenge

In our decoy experiment, chink and puff rates were significantly higher among territory-holding males when challenged by a white-enhanced decoy as compared to a white-reduced decoy (Fig. 4). When presented with a white-enhanced decoy in comparison to a white-reduced decoy, the rate of chinking was 2.0 times higher (Z=2.07; P=0.04). Similarly, presentation of a white-enhanced decoy elicited a puffing rate that was 2.6 times higher than presentation with a white-reduced decoy (Z=2.32; P=0.02). There were no significant differences by decoy presentation for the other scored behavioral responses. We also compared the rate of all behaviors combined for birds in response to white-enhanced and white-reduced decoys; presentation with a white-enhanced decoy produced a 1.38 times higher rate of all behavior as compared to a white-reduced decoy (Z=1.95; P=0.05).

Experiment 2: crown painting and corticosterone response

From the 2009 population of recaptured males, neither tarsus length nor crown-white differed between paint treatment groups (Table 2). Likewise, baseline, restraint-induced, and change in corticosterone levels were similar between the treatment groups prior to crown manipulations. On the other hand, after the experimental crown manipulations, the baseline corticosterone concentration for birds with the white-enhanced crown treatment was 10.24 ng/mL higher than that for the control group birds (Wald chi-squared=3.75, df=1, P=0.05). In contrast, white-reduced treatment did not differ from control birds in their baseline corticosterone levels (Table 3). After the restraint-induced stressor, birds in the white-reduced treatment group had an average corticosterone concentration that was marginally significantly

Table 1 Proportion crown-white by morphological and physiological characteristics of 178 male mountain white-crowned sparrows in May–July 2008 and 2009

	Number[a]	Mean ± SD	Difference in proportion crown-white[b] β (95 % CI)	*P*
Morphological characteristics				
Tarsus length (mm) per 1 mm increase	222	26.7±1.0	0.02 (0.01, 0.02)	0.0007
Mass (g) per 2 g	213	29.1±2.0	0.00 (−0.01, 0.01)	0.90
Wing chord (mm) per 3 mm	220	78.7±2.3	0.00 (−0.01, 0.01)	0.71
Tail length (mm) per 3 mm	218	76.9±2.8	0.00 (−0.01, 0.01)	0.80
Physiological characteristics				
Hematocrit (%) per 3 % red cell volume	151	51.4±3.2	0.00 (−0.01, 0.01)	0.51
Corticosterone (ng/mL)[c] per 10 ng/mL	38	10.16±10.81	0.02 (0.01, 0.04)	0.01

[a] Totals are >178 due to repeated measurements

[b] Calculated as the ratio of white crown width to total crown width

[c] From 2009 only

11.45 ng/mL higher than the control group (Wald chi-square= 3.26, df=1, *P*=0.07), and white-enhanced group birds had restraint-induced corticosterone concentration that was 3.48 ng/ mL lower than the control birds; however, the latter difference was not statistically significant (Wald chi-square=0.27, df=1, *P* =0.60). We also calculated the change in corticosterone concentrations between the baseline and restraint-induced measurements (the difference between baseline and restraint-induced corticosterone). The changes in corticosterone for the white-enhanced, white-reduced, and control groups were significantly different (chi-square=9.73, df=1, *P*=0.008). White-reduced birds experienced on average a 17.26-ng/mL larger magnitude of increase than the control group (Wald chi-square=5.04, df=1, *P*=0.02). On the other hand, the white-enhanced treatment group experienced a marginally statistically significant increase in corticosterone that was 13.71 ng/mL smaller in magnitude than the control group (Wald chi-square=3.18, df=1, *P*=0.07).

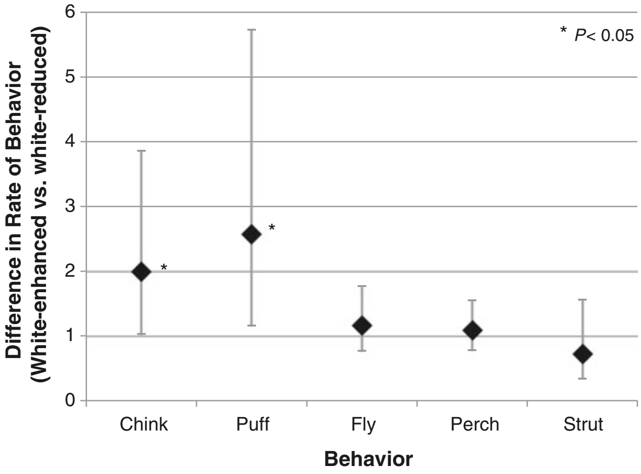


Fig. 4 Rate ratio of behavioral responses of 39 male mountain white-crowned sparrows to white-enhanced in comparison to white-reduced decoys

Discussion

A reliable status badge should satisfy three requirements: (1) it must be correlated with some aspect of the signal sender, (2) signal discrimination is demonstrated by variation in receiver response, and (3) there have to be constraints on signal bluffing (Searcy and Nowicki 2005). Our results confirmed each of these requirements in a free-living population of male mountain white-crowned sparrows during the early- to mid-summer breeding season.

Signal correlates of resource-holding potential

We found a significant positive correlation between proportion crown-white in male mountain white-crowned sparrows and tarsus length, an indicator of frame size (Senar and Pascual 1997) and resource-holding potential. The positive association between size and resource-holding potential is a well-documented phenomenon across many taxa (Andersson 1994). For example, studies of aggressive male–male interactions among Gambel's quail (*Callipepla gambelii*) and scaled quail (*Callipepla squamata*) reported that larger frame size and, in particular, longer tarsi were dependable proxies for resource-holding potential and dominance due to the inherent advantage of being larger during aggressive interactions (Hagelin 2002). Furthermore, longer tarsi may be indicative of higher resource-holding potential as it reflects prior access to resources invested in this energetically expensive trait (Sears and Hatch 2012). Positive associations have also been observed between the largest or most elaborate badges and factors related to resource-holding potential in other species: size in paper wasps (*Polistes dominulus*) (Tibbetts and Dale 2004), nutritional condition in mangrove crabs (*Perisesarma eumolpe* and *Perisesarma indiarum*) (Todd et al. 2011), age and physical

Table 2 Baseline characteristics of birds that received the paint treatment

	Paint treatment group			P^a
	Control (N=9)	White-enhanced (N=5)	White-reduced (N=7)	
Proportion crown-white[b]	0.25±0.02	0.30±0.07	0.29±0.09	
	Reference	0.04 (−0.02, 0.11)	0.03 (−0.02, 0.09)	0.33
Tarsus (mm)	26.67±0.69	26.98±0.65	26.97±0.57	
	Reference	0.31 (−0.34, 0.96)	0.30 (−0.28, 0.89)	0.51
Corticosterone (ng/mL)				
Baseline	13.39±11.96	18.10±0.35	8.54±9.27	
	Reference	4.71 (−9.85, 19.27)	−4.84 (−14.55, 4.87)	0.37
Restraint-induced	38.34±20.91	51.62±34.82	36.60±24.88	
	Reference	13.28 (−12.91, 39.48)	−1.73 (−25.41, 21.94)	0.53
Change[b]	28.07±16.06	35.11±60.00	28.06±16.58	
	Reference	7.04 (−26.40, 40.49)	−0.01 (−25.91, 25.90)	0.91

[a] From an ANOVA

[b] Calculated as the difference between restraint-induced and baseline corticosterone concentrations

condition in house sparrows (*Passer domesticus*) (Veiga 1993), and size in Augrabies flat lizards (*Platysaurus broadleyi*) (Whiting et al. 2006).

We did not find significant associations between the other morphological and physiological characteristics and crown-white. However, we unexpectedly found a slight positive relation of circulating corticosterone levels with natural crown-white. This trend could be due to the nature of agonistic interactions during the breeding season (Goymann and Wingfield 2004) and warrants further investigation in other contexts and species.

Receiver response

In our first experiment, the paired decoy challenges confirmed that territory-holding males are able to discern and respond to variation in crown-white. Under the hypothesis that higher crown-white communicates elevated resource-holding potential, we modified decoys to signal high (white-enhanced) and low (white-reduced) resource-holding potentials, respectively. We found that territory-holding males exhibited higher rates of "chink" calls and "puffing" of feathers when presented with a white-enhanced as compared to a white-reduced decoy. A variation in these aggressive behaviors (Morton 2002) directed toward the decoys confirms status badge discrimination; furthermore, the direction of aggression was consistent with the social control hypothesis, which states that individuals displaying the most dominant signals will experience increased levels of aggression (Rohwer 1977). Elevated receiver aggression toward more conspicuous badges has also been found in territory-holding male red-winged blackbirds (*Agelaius phoeniceus)* (Hansen and Rohwer 1986; Yasukawa et al. 2009). Yet, the opposite trend has also been observed. In a study of male red-collared widow birds (*Euplectes ardens)*, territory-holding males were less aggressive toward decoys with more intense collar display badges (Pryke et al. 2001). Such discrepancies may be explained by the fact that aggressive responses are

Table 3 Associations of paint treatment crown manipulations with baseline and restraint-induced corticosterone levels

	Corticosterone (ng/mL)					
	Baseline		Restraint-induced		Change[a]	
	Mean ± SD	Difference β (95 % CI)	Mean ± SD	Difference β (95 % CI)	Mean ± SD	Difference β (95 % CI)
Paint treatment group						
Control (N=9)	12.77±6.47	Reference	31.12±7.46	Reference	18.35±10.24	Reference
White-enhanced (N=5)	23.01±17.02	10.24 (−0.12, 20.59)	27.65±6.14	−3.48 (−16.62, 9.67)	4.64±16.54	−13.71 (−28.77, 1.35)
White-reduced (N=7)	12.46±7.78	−0.31 (−10.10, 9.48)	42.57±21.42	11.45 (−0.97, 23.87)	35.61±20.46	17.26 (2.19, 32.32)
P^b		0.13		0.11		0.008

[a] Calculated as the difference between post-stressor corticosterone levels and baseline corticosterone levels

[b] From the ANOVA

elicited by a constellation of factors: the similarity of signal expression between the sender and receiver (Midamegbe et al. 2011), how well a signal matches the sender's behavior (Parker and Ligon 2002), value of the contested resource (Tibbetts 2008), and the interaction between resource value and contestants' resource-holding potential (Tibbetts and Shorter 2009). While we were not able to evaluate resource value in this study, mountain white-crowned sparrow life history suggests that the summer breeding conditions constitute a high stake context for intense territorial competition among males, a process further exacerbated by a male-biased sex ratio (Morton et al. 1972). The frequency or intensity of male–male competition during the breeding season may reflect commitment to defend a highly valuable resource (Számadó 2011b). In this manner, receiver responses to badge variation underpin signal reliability, whereby signal bluffers will receive the most social aggression and suffer the greatest cost (Számadó 2011b). Thus, without directly quantifying resource value, the differential behaviors we observed in response to the decoys are evidence of signal discrimination and provide insight on context-dependent aggression.

Cost of signal bluffing

Our second experiment provided evidence of physiological costs associated with signal bluffing in a free-living population of male mountain white-crowned sparrows. Although decoy challenges isolate behavioral responses to discrete status badge signals (Chaine and Lyon 2008), a major shortcoming of decoy designs is the inability to ascertain costs associated with signal bluffing. Altering the badge of live birds allows the quantification of both somatic (Nakagawa et al. 2008) and reproductive (Qvarnstrom 1997) tradeoffs related to signal bluffing. For example, bluffing a signal affords the individual poorer control over their social environment and can be physiologically costly (Lindström et al. 2005). Because physiological responses vary across individuals, manipulating badges of live birds is better suited to capture the range of costs associated with signal bluffing. We found that white-enhanced signal bluffs had elevated levels of baseline corticosterone, while baseline corticosterone concentrations of the white-reduced group did not differ from the control. After the restraint-induced stressor, white-reduced males had higher corticosterone levels than the control group, whereas the corticosterone concentration of white-enhanced birds did not differ from the controls. However, the stressor induced a significantly larger rise in corticosterone from baseline in white-reduced birds in comparison to the control group, while the white-enhanced birds had a smaller magnitude of change than controls.

These findings are salient as they bring to light both acute and persistent physiological constraints associated with signal bluffing. As mentioned earlier, the breeding season may represent a period of heightened male–male aggression. This is observed in many songbirds, as evidenced by high plasma steroid concentrations during the early breeding season (Romero 2002; Goymann et al. 2007) and rapid increases in plasma corticosterone levels following aggressive interactions (Hirschenhauser and Oliveira 2006; Goymann et al. 2007). The release of glucocorticoids, including corticosterone, is an adaptive mechanism of the hypothalamic–pituitary–adrenal (HPA) cascade to counter stressful events (Sapolsky et al. 2000), yet prolonged stimulation can be physiologically costly (Awerman and Romero 2010). The changes in corticosterone levels observed in the white-reduced group likely correspond with increased HPA activity in response to the acute stressor (McEwen and Wingfield 2003). On the other hand, the elevated baseline corticosterone followed by a blunted response to the acute stressor observed in the white-enhanced group is indicative of an attenuated reactive scope, which is defined as the range between homeostasis and homeostatic overload (Romero et al. 2009). The reactive scope buffers the adaptive glucocorticoid response and the onset of pathophysiological changes (Romero et al. 2009). Challenges of chronic stress, such as those associated with falsely signaling via an enlarged badge, have been related to a narrowed reactive scope (Cyr and Romero 2009) which may dampen the glucocorticoid response to an acute stressor (Cyr et al. 2007). This pattern has been previously observed in other subspecies of white-crown sparrows; stimulation of the HPA axis through repeated corticosterone administration was related to elevated baseline corticosterone and a down-regulated adrenocortical response to an acute stressor (Busch et al. 2008). On the other hand, no association was observed between signal bluffs and glucocorticoid levels in a study of house sparrows, suggesting that signal bluffers do not necessarily suffer increased costs while enjoying the benefits of an enlarged badge (Gonzalez et al. 2002). A potential explanation for the discordant literature is that physiological responses function in association with the social atmosphere and competitive context in which status is signaled and maintained. This is supported by a recent review of experiments conducted in free-living animals, which reported that the glucocorticoid response was modified by the maintenance of social status (Goymann and Wingfield 2004).

Conclusions

In a large sample of male mountain white-crowned sparrows, we were able to show that a well-documented morphological correlate of resource-holding potential was significantly associated with crown-white. We demonstrated that free-living birds are able to discriminate between different badge sizes through a paired decoy design experiment that minimized confounding extraneous factors. Finally, we manipulated badges of live birds and were able to quantify physiological costs associated with signal bluffing using a highly reproducible assay. Together, these findings indicate that crown-white is a reliable badge of status in male mountain white-crowned sparrows during the summer breeding season.

The implications of our findings for the individual bird, as well as for the reliability of the overall signaling system, should still be interpreted with caution. First of all, our study was conducted in the context of the early- to mid-summer breeding season, so the findings may not be applicable to late- or non-breeding life history stages. Secondly, although we observed increased rates of aggressive behaviors toward more conspicuous badges, behavioral responses are subject to other factors that we were not able to quantify, such as resource value. Furthermore, in spite of the fact that we observed a physiological cost associated with signal bluffing through badge manipulation, we did not have a large sample size for this experiment, and the observed corticosterone stress response could also be attributable to unmeasured heritable and environmental factors (Evans et al. 2006). Additionally, our study design did not enable us to determine whether the elevated baseline corticosterone concentrations in the white-enhanced birds were the result of heightened social aggression toward a more threatening badge or a result of bluff detection and subsequent social punishment (Rohwer 1977). In a free-living population of house sparrows, the costs associated with signal bluffs were not directly correlated with the badge display alone, but in relation to the degree of individual bluffing that was detected (Nakagawa et al. 2008). Finally, it is important to consider that corticosterone and testosterone are ligands to the same binding site on the plasma-carrying protein (Deviche et al. 2001); the availability of these binding sites depends on physiological state and is influenced by aggressive interactions (Charlier et al. 2009). Although an analysis of these physiological relationships is beyond the scope of this study, it does warrant future investigation. Due to the complexity of interactions between social status, signaling context, and homeostatic mediators that underlie status badge reliability, a longitudinal study design with a larger sample size would be appropriate. Further research is required to identify and understand thresholds of reactive scope and HPA sensitivity and to improve understanding of the associated deleterious effects at the individual level.

Future studies should consider resource value and commitment to resource defense while obtaining morphological, behavioral, and physiological information about both signal senders and signal receivers. Additionally, consideration of a non-breeding season context and the role of status signaling among females would further improve understanding of this study system. Using the example of our experimental design, coupled with suggestions made here, we hope that future studies will build upon current knowledge of status badge reliability.

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Ethical standards The methods for this study were approved by the University of Michigan's University Committee on the Use and Care of Animals and complied with the United States Fish and Wildlife Regulations.

Conflict of interest The authors declare that they have no conflict of interest.

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