Experimental confirmation that avian plumage traits function as multiple status signals in winter contests

Alexis S. Chaine [a,*], Allison M. Roth [b,c], Daizaburo Shizuka [b,d], Bruce E. Lyon [b]

[a] Station d'Ecologie Expérimentale du CNRS, USR2936, Moulis, France
[b] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, U.S.A.
[c] Cincinnati, OH, U.S.A.
[d] School of Biological Sciences, University of Nebraska, Lincoln, NE, U.S.A.

ARTICLE INFO

Status signals are thought to reduce costs of overt conflict over resources by advertising social status or an individual's ability to win contests. While most studies have focused on single badges of status, recent empirical work has shown that multiple status signals may exist. To provide robust evidence for multiple badges of status, an experimental manipulation is required to decouple signals from one another and from other traits linked to fighting ability. Such experimental evidence is lacking for most studies of multiple status signals to date. We previously found that two plumage traits in golden-crowned sparrows, Zonotrichia atricapilla, were correlated with social dominance in encounters between unfamiliar individuals. To confirm that each plumage patch functions as an independent status signal, we experimentally augmented the sizes of the gold crown patch and the black crown patch during encounters between unfamiliar individuals with similar premanipulation crown sizes. In nearly all cases, the individual with the artificially augmented gold or black crown was dominant during the trial and manipulations of each colour were equally successful in conferring dominance. The relative differences in crown sizes between manipulated and unmanipulated individuals in a dyad and mismatches in crown sizes of the manipulated bird led to escalation in gold trials, but these same factors were not significant for black trials. This study provides unequivocal evidence for multiple status signals: both black and gold crown patches influence social status per se and they do so independently of the other crown patch.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Physical conflict over limited resources can be costly in terms of both time and health. These costs can favour the evolution of signals that can resolve conflicts without physical aggression, namely 'status signals' or 'badges of status' (Rohwer 1975, 1977; Maynard Smith & Harper 2003). Numerous studies identify traits that function as status signals, in both breeding and nonbreeding contexts, and for a wide diversity of taxonomic groups (Senar 1999, 2006; Whiting et al. 2003; Tibbetts & Safran 2009). Nearly all studies of status signals to date have focused on investigating a single trait or badge that indicates dominance in a given species (Senar 2006; Tibbetts & Safran 2009), in contrast to multiple signals. This may be due to the assumption that status signals should be directly linked to fighting ability and that a single badge should be sufficient to convey this information. In contrast, studies of traits selected through mate choice have focused on multiple signals for the past two decades (Møller & Pomiankowski 1993; Marchetti 1998; Andersson et al. 2002; Uetz & Roberts 2002; Candolin 2003; Doucet & Montgomerie 2003; Chaine & Lyon 2008a; Dunn et al. 2008). In this context, receivers are thought to benefit from attending to a number of different traits that reflect different aspects of individual quality ('multiple messages') in a mate, or if multiple cues aid in more accurate assessment of quality ('backup cues'; Marchetti 1998; Rowe 1999; Candolin 2003). However, signalling in nonmating contexts should entail similar selection pressures as sexual signalling and thus could resemble sexual signals in many respects (West-Eberhard 1983; Lyon & Montgomerie 2012). Indeed, recent evidence from a few species suggests that multiple status signals also occur in contexts other than mate choice (Bókony et al. 2006; Chaine & Lyon 2008b; Chaine et al. 2011) and that they could be more common than previously thought.

Status signals have been particularly well studied in birds, yet studies that investigate the function of multiple status signals are rare. In dark-eyed juncos, Junco hyemalis (Balph et al. 1979), two traits were found to correlate with social dominance, but it was

* Correspondence: A. S. Chaine, Station d'Ecologie Expérimentale du CNRS, USR2936, 09200 Moulis, France.
E-mail address: alexis.chaine@ecoex-moulis.cnrs.fr (A. S. Chaine).

unclear whether the two signals function differently because this was not investigated. Multiple status signals have been identified in studies of two other species, house sparrows, *Passer domesticus* (Bókony et al. 2006) and golden-crowned sparrows, *Zonotrichia atricapilla* (Chaine et al. 2011), and in each study differences were found in the context of use and function of the different signal traits. However, these studies are correlative and experimental manipulation of putative badges is necessary to decouple the influence of the badge itself from that of other correlated traits that might determine dominance (Rohwer & Rohwer 1978; Maynard Smith & Harper 2003). This is especially important for multiple badges of status because the two signal traits might themselves be correlated. With trait correlation, one trait might serve as the badge and the second putative signal trait could show an association with dominance simply because of its phenotypic correlation with the badge. Experimental manipulation of putative multiple status signals to decouple trait correlations is therefore crucial to determine whether more than one signal is actually associated with social dominance.

Our previous work in golden-crowned sparrows identified multiple signals associated with winning contests over food piles during the nonbreeding season. Prior to arriving at their wintering grounds, golden-crowned sparrows moult into a winter plumage that is highly variable in the sizes of gold and black crown feather patches (they moult again prior to breeding in the spring). We showed that the two signals, the gold crown patch and black crown patch, which originate from carotenoid and melanin pigments, respectively (K. Tjernell, D. Shizuka, B.E. Lyon & A.S. Chaine, unpublished data), played different roles during escalation of a contest (Chaine et al. 2011). Gold crown patch size was associated with winning contests in which no aggressive interactions occurred (e.g. avoidance), given that the two individuals differed greatly in the signal. However, when gold crown size was similar, contests escalated to higher levels of aggression and the winner had a larger black crown patch. We concluded that these two plumage patches each served as a signal and that they function in different contexts. However, the sizes of both the gold and black crown patches are correlated with body size in this species, and bigger body size is associated with winning a contest (Chaine et al. 2011). Therefore, experimental manipulation of each colour patch is necessary to determine whether gold and black crown features both function as badges of status per se. Moreover, a powerful test of the multiple signal hypothesis further requires experimentally demonstrating that each plumage patch influences social dominance independently of the other. In the present study, we experimentally manipulated the two colour patches associated with dominance to test whether multiple status signals occur in this species.

METHODS

Capture and Measurements of Birds

We caught golden-crowned sparrows in January and February 2007–2009 using Potter (cage) traps baited with millet at two natural feeding sites near Pogonip City Park, Santa Cruz, California. Birds were cleared from traps every 5 min and trapping only occurred during good weather so that birds would not get wet. Birds were transported from the trapping site to small aviaries in bird bags to reduce stress and placed in a small cage to prevent escape. For each bird we took standard body size measurements immediately after capture (mass, flattened wing chord, tarsus and beak length) and fitted each bird with a USFWS metal bird band and a unique combination of coloured vinyl leg bands (Hill 1992). Morphological traits excluding mass were simplified into one 'body size' variable using principal components analysis as in past work

(Chaine & Lyon 2008a; Chaine et al. 2011). To estimate crown patch sizes, we took digital photographs perpendicular to the top of the head and included a ruler to scale images. We then used Adobe Photoshop to isolate and calculate the areas (mm^2) of the gold and black portions of each crown by counting pixels. All morphometric and plumage measures are highly repeatable (Chaine et al. 2011).

We measured the colour of the black and gold portions of each crown and manipulated crown colours to ensure that manipulations fell within the natural range of variation. We used an Ocean Optics USB2000 spectrometer and a PX-2 pulsed xenon light source and measured a 2 mm diameter area at a 45° angle (Andersson & Prager 2006; Chaine & Lyon 2008a, b; Chaine et al. 2011).

Tests of the influence of plumage on social dominance should involve birds not previously familiar with each other so that familiarity and information from previous interactions do not confound the influence of status signals. All dominance trials therefore involved dyads of individuals from two different sites; our two sites for capturing experimental birds were over 0.5 km apart, several times farther than the home range size of individual birds (Price 1931; D. Shizuka, B.E. Lyon & A.S. Chaine, unpublished data using telemetry). We did not determine the sex of individuals since previous results showed that social dominance is unrelated to sex (Chaine et al. 2011). Male and female crown sizes in winter show highly overlapping distributions (D. Shizuka, B.E. Lyon & A.S. Chaine, unpublished data). Moreover, the crown manipulations presented here (see below) were well within the range of both male and female natural crown sizes, limiting the possibility that perception of 'sex' was altered during crown manipulation. After the dominance trials were completed, all birds were released at their respective capture sites (natural feeding areas). No birds were kept more than 36 h. Birds settled down in cages in less than 5 min, showed normal behaviour and remained healthy.

Experimental Dominance Trials

After measurement, each bird was transferred to an outdoor aviary with up to three other individuals captured on the same day from the same location and flock (i.e. familiar birds were housed together). We used two holding aviaries to keep individuals from the two populations separate, and these aviaries were placed out of visual and acoustic contact from each other at the University of California Santa Cruz Arboretum. Each aviary measured 1.2 m on each side, was covered with plywood to provide shelter from direct sunlight and precipitation, and contained perches and shelter. Birds were provided with food (millet) and water ad libitum with two feeding trays per cage (10 cm diameter) to ensure that all birds could easily get access to food and to reduce aggression during the pretrial period (Pryke et al. 2002). All birds were allowed to acclimate to their respective housing aviaries without disturbance for 1 day before being observed in the dominance trials.

We conducted 42 paired dominance trials to determine the influence of plumage patch size on social dominance. Birds paired in a given dominance trial were selected from the set of birds captured on the same day to ensure a similar duration of captivity. Food was removed from holding cages at sundown the night before dominance trials and all trials were conducted in the morning between 0800 and 1000 hours. The experimental aviary had the same dimensions as the housing aviaries, but to encourage interactions it contained only a single food dish (4 cm diameter) located centrally and surrounded by a small cluster of branches for perching. Birds for a given experiment were caught in their housing cages with a small sweep net and typically captured within a few minutes of each other. After manipulation (see below), the two individuals were then released simultaneously into the trial cage and observed with binoculars for 30 min from 20 m away. The experimental birds

showed the same suite of behaviours we observe in the field with free-ranging individuals and we observed no signs of stress after less than 1 min of their release into the trial cage.

We conducted two experiments, manipulating (1) the size of the black crown patch and (2) the size of the gold crown patch to determine whether size of either colour patch is used as a badge of status. For both experiments, the two birds for a given trial were chosen so that their focal patch sizes prior to manipulation were as similar to each other as possible, given the variation in the sample of available birds in the cages, and then one was randomly chosen for crown manipulation. Crown patch sizes prior to manipulation did not differ between the manipulated and sham birds (paired t test of natural crown sizes: Black: $t_{41} = -1.25$, $P = 0.22$; Gold: $t_{41} = -0.59$, $P = 0.56$); the birds did not differ in any other traits (colour of gold and black patches, body size, residual mass) either (matched-pair t tests: $N = 42$, all $P > 0.05$). The paired design in this experiment, with one experimental and one sham individual in each trial, leads to an expected 50:50 dominance outcome since crown manipulations were randomly assigned with respect to premanipulation patch size (see Results).

Black patch size was enlarged using a black Sharpie pen and the sham treatment received markings at the edge of the crown using a brown Sharpie pen (a colour that matched background plumage colour). Gold patch size was enlarged using Golden Fluid Acrylic paint that was mixed to match natural gold crown colour (based on spectrophotometry measures) whereas shams received Golden Open thinner on their crown. The manipulated crown colours closely resembled natural coloration of crowns (Fig. 1). The gold manipulation produced UV reflectance that was within the natural range, albeit towards the lower end of the natural distribution. Furthermore, UV reflectance of the gold patch, like total reflectance, was not related to social dominance in our past work (Chaine et al. 2011; paired t test of UV reflectance of dominant versus subordinate: $t_{28} = 0.29$, $P = 0.77$). All manipulations dried in less than 5 min, the birds were photographed, and the size of the manipulated patch was later measured from photographs using the same technique as for natural crowns. However, we do not have size estimates for all experimental birds because some manipulated crown sizes are missing owing to low quality or loss of images (one black and seven gold crowns). Manipulated crown colours were no longer visible after 48 h on birds kept in captivity for a few days during pilot manipulation tests.

Patch size manipulations led to significantly larger patch sizes (paired t test; Black: $t_{18} = 10.08$, $P < 0.0001$, mean before = 46.5 mm², after = 129.6 mm²; Gold: $t_{14} = 6.43$, $P < 0.001$, mean before = 63.9 mm², after = 126.3 mm²). Manipulated crown sizes were within the distribution of natural crown sizes in these populations (mean Natural Black = 83 mm², range Natural Black 2–285 mm², $N = 523$, Manipulated Black 76–180 mm²; mean Natural Gold = 73 mm², range Natural Gold 12–217 mm², $N = 522$, Manipulated Gold 57–178 mm²).

We scored the outcome of two types of interactions related to social dominance, aggression and avoidance (Watt 1986; Chaine et al. 2011). We use these same behaviours to score interactions and social dominance among free-ranging birds at our feeding stations; these behaviours are thus relevant to naturally occurring social interactions in the wild (D. Shizuka, B.E. Lyon & A.S. Chaine, unpublished data). Aggressive behaviour was defined as supplanting, chasing or lunging at the second bird. The bird initiating an aggressive interaction always gained access to the food dish or perch when the interaction was near these resources, or it caused the other bird to move when interactions occurred away from the feeder and perch. Actual physical contact never occurred in these trials and no birds showed any signs of injury as a result of the experiment. Avoidance interactions were scored when an individual failed to challenge the other bird for access to food; avoidance typically entailed the bird perching away from the resource but not approaching it, as has been observed in other studies (Watt 1986; Chaine et al. 2011). In most cases of avoidance interactions, the avoiding bird approached the food or perch only after the dominant individual vacated the resource, as we observe for interactions in the wild (D. Shizuka, B.E. Lyon & A.S. Chaine, unpublished data). During many trials, both aggressive and avoidance behaviours occurred, although aggression usually occurred later in the trial. In each trial we assigned dominance status (dominant or subordinate) based on which bird won the majority of behavioural interactions in the trial (i.e. which bird initiated aggression and was avoided), as in previous work (Chaine et al. 2011). In 10 trials, we were unable to distinguish dominance, owing to either a lack of direct behavioural interactions or a lack of difference in access to food, so these trials were scored as 'ties' for analysis. In 32 trials dominance was clear. No bird was used in more than one dominance trial. All methods were approved by the UCSC IACUC (permit PHS Animal Welfare Number A3859-01 to B.L.) who also checked aviaries with birds in them and complied with Federal and California State banding and research permits (banding licence 10516 to B.L.).

Statistical Analyses

To determine whether both plumage patches function independently as signals, we first tested whether dominance status would be affected by manipulations of one trait independent of the other. We restricted the data set to the 32 trials for which social dominance could clearly be assigned, and we used matched-pair
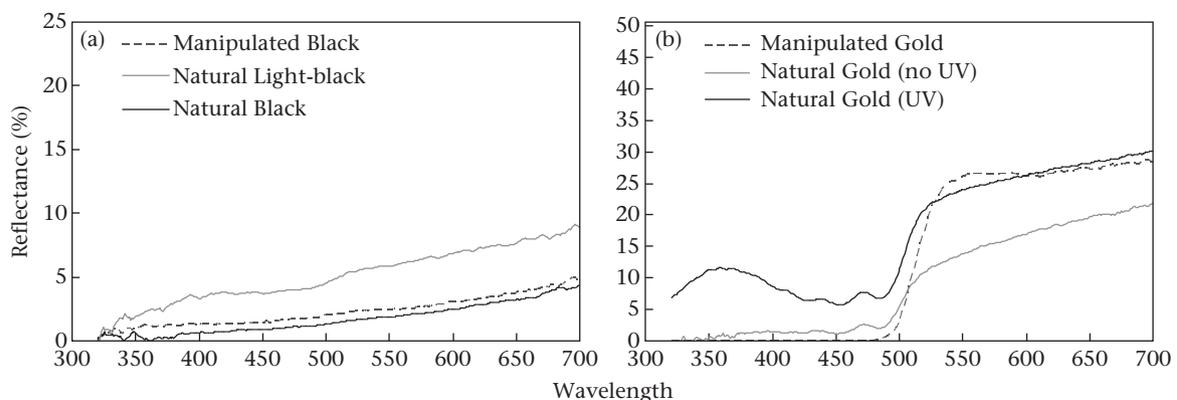

Figure 1. Comparison of manipulated plumage colours and natural crown colours found in the wild. Shown are reflectance curves of individuals that span the extremes of natural colours seen in our local population (solid lines) and the colour of the manipulated badges (dashed line) for both (a) black and (b) gold crown areas.

tests to control for variation in absolute values of traits among trials.

To determine whether the two signals provide different or complementary information, we assessed whether the proportion of trials that escalated to higher levels of aggression (i.e. showed supplants or lunges rather than simply avoidance behaviour) differed according to which crown patch was manipulated or the degree (i.e. size) of the patch manipulation. We included data from the 10 trials for which dominance was not clear so that we could assess when interactions escalated to aggression (total $N = 42$ trials). We then used logistic regression models with multiple predictor variables (described below) to determine which features affected escalation (see also Chaine et al. 2011). We first created a full model with all relevant factors and then compared that model to reduced models that each had one factor removed. A significant change in the predictive ability of the model (deviance) allowed us to determine which factors significantly affected escalation. All tests were conducted in R2.13.0 (R Development Core Team 2009) or GraphPad Software's QuickCalcs applets (http://graphpad.com/quickcalcs/) and two-tailed probabilities ≤0.05 were considered statistically significant.

RESULTS

Multiple Status Signals

In nearly all trials, increasing the size of either the black or the gold crown patch led to a bird being socially dominant. The bird with the experimentally enlarged black patch was dominant in 14 of 15 trials for which dominance was clear (sign test: $N = 15$, $P = 0.001$; Fig. 2a). In the gold plumage experiment, the bird with the enlarged gold patch was dominant in 16 of 17 trials for which dominance was clear (sign test: $N = 17$, $P < 0.001$; Fig. 2b). Therefore, both black and gold crown features per se directly influenced social dominance during initial encounters between socially unfamiliar pairs of birds, and they did so independently of the other plumage trait.

Differences in Signal Function

While both black and gold crown features function independently as badges of status, they may each affect dominance by different behavioural mechanisms or in somewhat different contexts (Bókony et al. 2006; Chaine & Lyon 2008b; Chaine et al. 2011) as would be expected if the two signals contained different

information. We asked whether gold and black patch manipulations differed in (1) the likelihood that the manipulated bird became the dominant or (2) the likelihood that the encounter escalated to higher levels of aggression as was the case in our previous work (Chaine et al. 2011).

Among trials that showed clear dominance, there was no difference in the proportion of trials in which the manipulated individual won the encounter between black (14/15) and gold trials (16/17; Fisher's exact test: $P = 1.0$). There was also no significant difference in the proportion of trials that escalated (aggression versus tolerance + avoidance) between black (11/20) and gold manipulations (8/22; Fisher's exact test: $P = 0.35$).

We also examined whether degree of trial escalation (no escalation beyond avoidance versus escalating to aggression) was related to the relative difference in crown features after manipulation of crown sizes. We constructed general linear models to examine the relationship between trial escalation (binomial, logit link) and three measures of crown features that could influence dominance interactions based on the receiver's (i.e. sham bird since the manipulated bird is not aware of the manipulation) perception of plumage signals. (1) We compared the difference in postmanipulation patch sizes between the manipulated and sham birds since relative crown size influences dominance in contests between unmanipulated birds (Chaine et al. 2011). (2) We measured the difference in patch sizes of the trait that was not augmented (i.e. gold patch in 'black trials' and black patch in 'gold trials') between the experimental and sham individuals. Since the trait that was eventually augmented was matched in our experiments, the difference in the other trait could affect dominance interactions. (3) We asked whether escalation might increase if the receiver perceives an inconsistency in the two plumage traits (Rohwer 1977; Rohwer & Rohwer 1978; Järvi et al. 1987) of the manipulated bird since these traits are weakly correlated in the wild ($r = 0.23$ in Table 1 of Chaine et al. 2011). Thus we measured the mismatch in size of the gold and black crowns of the manipulated bird (manipulated−unmanipulated crown patch sizes of the experimental individual) as a measure of inconsistency in information.

In gold plumage manipulation trials ($N = 15$), higher levels of escalation were associated with a larger contrast between the postmanipulation crown sizes of the experimental and sham individuals (log-likelihood = −11.59, $P < 0.001$; Fig. 3a). Higher levels of escalation were also associated with a smaller mismatch in sizes of the manipulated and unmanipulated patches of the experimental individual (log-likelihood = −12.15, $P < 0.001$; Fig. 3b). Escalation was unrelated to the difference in sizes of the
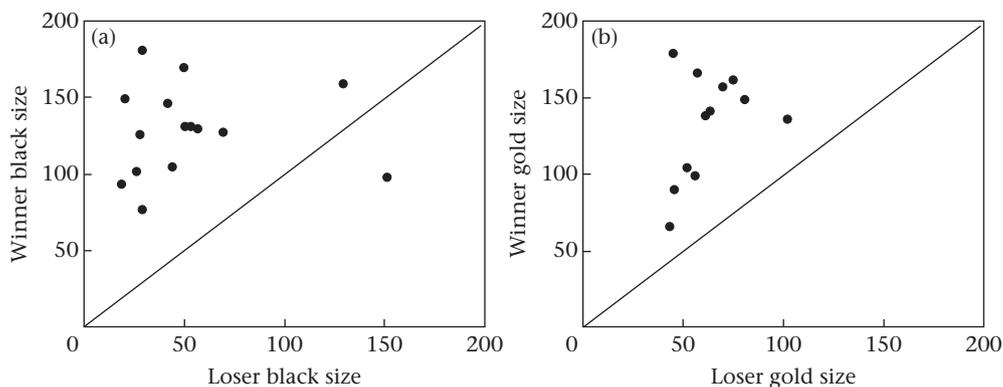

Figure 2. Comparisons of postmanipulation patch size between winners and losers of a trial. If points lie above the diagonal of equal crown size, then the individual with the larger crown size (i.e. manipulated bird in this case since premanipulation sizes were very similar) was dominant in the interaction. (a) Black patch manipulation trials. (b) Gold patch manipulation trials. Trials are included only if dominance was clear. For each manipulation, there was one trial in which the sham individual was dominant, although only the black trial had postmanipulation crown size data available for this interaction (the one point below the diagonal) whereas the gold trial in which the sham was dominant was missing postmanipulation crown size (photo too blurry).

unmanipulated patches of the experimental and sham individuals (log-likelihood = −0.71, P = 0.40).

In black patch manipulations (N = 19), we did not find any significant relationships between crown features and the probability that aggression escalated in a trial. The probability of escalation was not associated with a difference in crown sizes between the manipulated and sham individuals in either the manipulated patch (log-likelihood = −0.10, P = 0.76) or unmanipulated patch (log-likelihood = −1.40, P = 0.24) nor was it associated with the mismatch in size between the manipulated and unmanipulated patches of the experimental individual (log-likelihood = −2.67, P = 0.10).

DISCUSSION

While a number of correlative studies suggest that multiple badges of status are used to determine dominance in nonbreeding birds (Balph et al. 1979; Bókony et al. 2006; Chaine et al. 2011), we provide here the first experimental confirmation that multiple badges directly and independently affect social dominance. We found that experimentally increasing the size of either the black or the gold patch was sufficient to establish dominance among unfamiliar individuals with similar-sized natural crowns. Two implications of this experiment are critical. First, the experiment confirms that the plumage patches per se act as badges of status and determine the outcome of a contest. Second, by experimentally decoupling the two traits, we showed that each trait is linked to social dominance independently of body size and the other patch. This result confirms our previous correlational findings that both traits serve as badges of status and provides unequivocal evidence for multiple badges of status in a nonbreeding bird.

We did not find a difference between the two colour patch manipulations in the frequency of trials in which the manipulated bird won the contest nor in the frequency with which a contest escalated to higher levels of aggression. The overall lack of differences between the two manipulations may not be surprising since the manipulation greatly altered patch size (see Methods) and could have overwhelmed any more subtle differences in badge function of the two patches. This pattern and the experimental design we used prevent us from distinguishing between alternative hypotheses for the evolution and function of multiple signals (reviewed in Marchetti 1998; Candolin 2003).

In line with our previous study (Chaine et al. 2011), we found that the difference in gold, but not black, patch size between individuals was linked to the probability that a trial escalated in aggression over food. However, the way in which the manipulated gold patch influenced escalation was different from our previous study. When the plumage patches are not manipulated, individuals that are closely matched in gold patch sizes are more likely to interact aggressively (Chaine et al. 2011). In this study, we found the opposite pattern: when the gold plumage patch was manipulated, larger differences between the manipulated (larger patch) and sham (natural patch size) individuals increased the probability of aggression (Fig. 3a). Our results suggest that gold plumage has an important role in determining the type of interaction the birds engage in, but that role is more complex than we might have predicted.

There are at least two ways to reconcile the differences in the role of gold plumage in generating escalation between the correlative and experimental studies. One possible explanation for the difference between the effects of gold plumage in the observational study (smaller difference between manipulated and sham individual leads to more aggression) and the current experimental study (larger difference leads to more aggression; Fig. 3a) is that the increased aggression relates to behavioural signals exchanged between the signaller and receiver. For example, if the receiver

(sham bird) displays more submissive behaviour in response to the signaller's (manipulated bird) enlarged plumage patch than the signaller typically experiences, the signaller may respond with increasing aggression. Such a dynamic would only occur in experimental manipulations, because the signaller does not have direct access to information about its current signal size and responds aggressively to unexpectedly submissive behaviour displayed by the receiver.

A second possible explanation for the observed increase in aggression with an increasing difference in gold patch size in the present study (Fig. 3a) is provided by the 'incongruence hypothesis' (Rohwer 1977; Rohwer & Rohwer 1978; Järvi et al. 1987). Under this hypothesis, experimentally altering a badge creates a mismatch between the manipulated patch and behaviour (Järvi et al. 1987) of the experimental bird which leads to conflicting signals about their dominance status. As a result, the receiver may increase aggression towards the signaller to 'test' its dominance status and enforce signal honesty by social means (Rohwer 1975; Rohwer 1982; Tibbetts & Dale 2004). The results of our experimental manipulation are consistent with both of the above hypotheses. The identity of the individuals that instigated escalated interactions, which we did not record, would be necessary to distinguish between these alternatives.

In theory, we can apply the same logic that underlies the incongruence hypothesis to a multiple-signalling context that does not include behaviour. If multiple signals show some correlation (e.g. Chaine et al. 2011) and only one of the signals is manipulated, the resulting mismatch in traits could result in increased aggression. In other words, a trait manipulation could generate an extreme combination of phenotypic traits and such individuals might experience more testing in general. Our results were not consistent with the prediction that mismatches in multiple signals lead to increased testing. Instead, we found that a larger mismatch in the sizes of the gold manipulated and black unmanipulated patches of the experimental bird led to lower levels of escalation in gold manipulations (Fig. 3b). Likewise, the mismatch between the black manipulated and gold unmanipulated patches of the experimental bird were unrelated to escalation in black manipulations. One possible reason that we did not find increased escalation could be that our manipulations may not have produced sufficiently unusual or extreme phenotypes, counter to the assumptions of the multiple signal mismatch hypothesis. Future tests should employ manipulations that produce unusual combinations of traits. Alternatively, it is possible that the enlarged patches produced an unusual combination of patch sizes, but that the assumption that mismatches lead to testing is incorrect for golden-crowned sparrows. Despite this, we believe that the logic of the multiple-signalling mismatch hypothesis for maintaining signal honesty is sound and should be tested in other systems.

A few other systems have found multiple badges of status and comparisons among these studies provide insights into the contexts in which we might be more likely to find multiple status signals. For example, evidence for multiple status signals comes from both breeding (male—male competition; Ligon et al. 1990; Mateos & Carranza 1997; Pryke et al. 2001, 2002; Pryke & Andersson 2003; Chaine & Lyon 2008b) and nonbreeding (Balph et al. 1979; Järvi & Bakken 1984; Bókony et al. 2006; Chaine et al. 2011) contexts, which suggests that multiple status signals are not restricted to one part of the life cycle. A subset of these studies sought to identify how multiple status signals might differ in function. In house sparrows, one signal (bib) appears to be linked to aggression, whereas the other (wing bars) is associated with the ability to defend against an intrusion (Bókony et al. 2006). In great tits, *Parus major*, one signal (breast stripe; Järvi & Bakken 1984; Maynard Smith & Harper 1988) appears to provide longer term information on dominance whereas the other (missing cheek patch feathers; Galván & Sanz 2008, 2009) conveys more recent dominance history. Finally, in lark buntings,
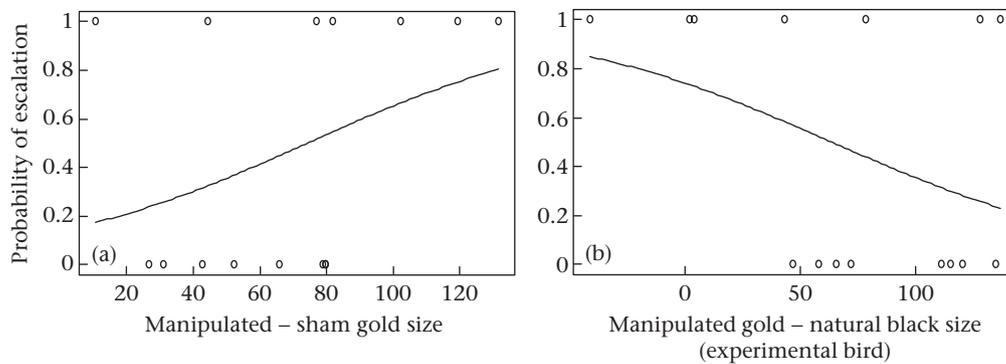
Figure 3. The probability that a trial escalated from low aggression (avoidance) to higher aggression (supplant) in relation to the relative size of colour patches postmanipulation for gold manipulation trials. (a) Escalation in relation to the difference in gold patch size between the manipulated and sham individuals. (b) Escalation in relation to the difference in size of the two colour patches of the manipulated individual.

Calamospiza melanocorys (Chaine & Lyon 2008b) and golden-crowned sparrows (Chaine et al. 2011) one signal seems to function primarily at a distance prior to overt aggression whereas the other is important in escalated encounters. From these examples, it is clear that a seemingly simple competitive interaction for food (or mates) may actually entail multiple, subtle levels of interactions. If this is the case, a number of badges might be important to fine-tune the assessment of social status in natural populations.

Despite the dearth of studies investigating multiple signals in the nonbreeding season, we suggest that there are several contexts in which such multiple signals would be favoured by selection. For example, multiple 'redundant' signals could evolve as psychological 'amplifiers' (Rowe 1999; Rowe & Skelhorn 2004; Rowe 2013) or as a means to prevent cheating. Deception (Dawkins & Guilford 1991) that requires 'cheating' in a number of signals could be much more difficult or costly than manipulation of just one trait: a notion not yet investigated in empirical studies of multiple signals. In turn, complexity in social dynamics could lead to the evolution of 'multiple messages', as suggested in some of the empirical examples given above (Bókony et al. 2006; Chaine et al. 2011). One possibility not yet investigated is that some signals may target familiar individuals while others target strangers (but see Tibbetts & Dale 2004; Sheehan & Tibbetts 2011). Likewise, dominance interactions in different contexts (e.g. over food piles versus over central roosting positions) may entail different forms of conflict and thus require different types of social signals. Specific attention to signalling contexts in the wild and the intended receivers will be important for understanding the social factors that favour multiple badges of status.

Acknowledgments

References

Andersson, S. & Prager, M. 2006. Quantification of coloration. In: *Bird Coloration 1: Mechanisms and Measurements* (Ed. by G. Hill & K. McGraw), pp. 41–89. Cambridge, Massachusetts: Harvard University Press.

Andersson, S., Pryke, S. R., Ornborg, J., Lawes, M. J. & Andersson, M. 2002. Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, **160**, 683–691.

Balph, M. H., Balph, D. F. & Romesburg, H. C. 1979. Social status signaling in winter flocking birds: an examination of a current hypothesis. *Auk*, **96**, 78–93.

Bókony, V., Lendvai, A. Z. & Liker, A. 2006. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows. *Ethology*, **112**, 947–954.

Candolin, U. 2003. The use of multiple cues in mate choice. *Biological Reviews*, **78**, 575–595.

Chaine, A. S. & Lyon, B. E. 2008a. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science*, **319**, 459–462.

Chaine, A. S. & Lyon, B. E. 2008b. Intrasexual selection on multiple plumage ornaments in the lark bunting. *Animal Behaviour*, **76**, 657–667.

Chaine, A. S., Tjernell, K. A., Shizuka, D. & Lyon, B. E. 2011. Sparrows use multiple status signals in winter social flocks. *Animal Behaviour*, **81**, 447–453.

Dawkins, M. S. & Guilford, T. 1991. The corruption of honest signalling. *Animal Behaviour*, **41**, 865–873.

Doucet, S. M. & Montgomerie, R. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behavioral Ecology*, **14**, 503–509.

Dunn, P. O., Whittingham, L. A., Freeman-Gallant, C. R. & DeCoste, J. 2008. Geographic variation in the function of ornaments in the common yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.

Galván, I. & Sanz, J. J. 2008. The cheek plumage patch is an amplifier of dominance in great tits. *Biology Letters*, **4**, 12–15.

Galván, I. & Sanz, J. J. 2009. Cheek plumage uniformity as a social status signal in great tits. *Annales Zoologici Fennici*, **46**, 271–282.

Hill, G. E. 1992. An inexpensive source of colored leg bands. *Journal of Field Ornithology*, **63**, 408–410.

Järvi, T. & Bakken, M. 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). *Animal Behaviour*, **32**, 590–596.

Järvi, T., Walsø, Ø. & Barken, M. 1987. Status signalling by *Parus major*: an experiment in deception. *Ethology*, **76**, 334–342.

Ligon, J. D., Thornhill, R., Zuk, M. & Johnson, K. 1990. Male–male competition ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Animal Behaviour*, **40**, 367–373.

Lyon, B. E. & Montgomerie, R. 2012. Sexual selection is a form of social selection. *Philosophical Transactions of the Royal Society B*, **367**, 2266–2273.

Marchetti, K. 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Animal Behaviour*, **55**, 361–376.

Mateos, C. & Carranza, J. 1997. The role of plumage in male-male interactions in the ring-necked pheasant. *Animal Behaviour*, **54**, 1205–1214.

Maynard Smith, J. & Harper, D. G. C. 1988. The evolution of aggression: can selection generate variability? *Philosophical Transactions of the Royal Society B*, **319**, 557–570.

Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. New York: Oxford University Press.

Møller, A. P. & Pomiankowski, A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, **32**, 167–176.

Price, J. B. 1931. Some flocking habits of the crowned sparrows. *Condor*, **33**, 238–242.

Pryke, S. R. & Andersson, S. 2003. Carotenoid-based status signalling in red-shouldered widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition. *Behavioral Ecology and Sociobiology*, **53**, 393–401.

Pryke, S. R., Lawes, M. J. & Andersson, S. 2001. Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Animal Behaviour*, **62**, 695–704.

Pryke, S. R., Andersson, S., Lawes, M. J. & Piper, S. E. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behavioral Ecology*, **13**, 622—631.

R Development Core Team. 2009. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rohwer, S. A. 1975. The social significance of avian winter plumage variability. *Evolution*, **29**, 593—610.

Rohwer, S. 1977. Status signaling in Harris' sparrows: some experiments in deception. *Behaviour*, **61**, 107—129.

Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531—546.

Rohwer, S. & Rohwer, F. C. 1978. Status signalling in Harris' sparrows: experimental deceptions achieved. *Animal Behaviour*, **26**, 1012—1022.

Rowe, C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, **58**, 921—931.

Rowe, C. 2013. Receiver psychology: a receiver's perspective. *Animal Behaviour*, **85**, 517—523.

Rowe, C. & Skelhorn, J. 2004. Avian psychology and communication. *Proceedings of the Royal Society B*, **271**, 1435—1442.

Senar, J. C. 1999. Plumage coloration as a signal of social status. In: *Proceedings of the International Ornithological Congress* (Ed. by N. Adams & R. Slotow), pp. 1669—1689. Durban: BirdLife International.

Senar, J. C. 2006. Color displays as intrasexual signals of aggression and dominance. In: *Bird Coloration 2: Function and Evolution* (Ed. by G. Hill & K. McGraw), pp. 87—136. Cambridge, Massachusetts: Harvard University Press.

Sheehan, M. J. & Tibbetts, E. A. 2011. Specialized face learning is associated with individual recognition in paper wasps. *Science*, **334**, 1272—1275.

Tibbetts, E. A. & Dale, J. 2004. A socially enforced signal of quality in a paper wasp. *Nature*, **432**, 218—222.

Tibbetts, E. A. & Safran, R. J. 2009. Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *Journal of Evolutionary Biology*, **22**, 2376—2386.

Uetz, G. W. & Roberts, J. A. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain Behaviour and Evolution*, **59**, 222—230.

Watt, D. J. 1986. A comparative study of status signalling in sparrows (genus *Zonotrichia*). *Animal Behaviour*, **34**, 1—15.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, **58**, 155—183.

Whiting, M. J., Nagy, K. A. & Bateman, P. W. 2003. Evolution and maintenance of social status signalling badges: experimental manipulations in lizards. In: *Lizard Social Behavior* (Ed. by S. F. Fox, J. K. McCoy & T. A. Baird), pp. 47—82. Baltimore, Maryland: Johns Hopkins University Press.