# Intrasexual selection on multiple plumage ornaments in the lark bunting

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Competition over resources can lead to fights and injury, so many species have evolved badge-of-status signals to settle conflicts without resorting to overt aggression. Most studies of status signals have focused on a single trait, under the assumption that aggression is univariate and therefore multiple signals would be redundant. We examined the relationship between male–male social dominance and several plumage traits (wing patch size and colour, body colour and coverage of black feathers on the body or the rump) in lark buntings, *Calamospiza melanocorys*, using a combination of observation and experimental territorial intrusions. Large body size was correlated with elevated aggression in several assays. Our observational data suggest that some traits function as close-range badges of status, because males with a larger proportion of black feathers on the body and rump win escalated contests, whereas other traits function at longer distances, because males with larger wing patches experience fewer territorial intrusions. Experimental tests of social dominance further suggest that different male plumage traits convey different information: some traits were associated with physical aggression, whereas other traits were associated with the intensity of approach. Together, these results show that selection can favour multiple badges of status to accommodate different levels of escalation or context-dependent dominance interactions.

Competition over limited resources like food, shelter and mates is often intense in social species. Physical resolution of these conflicts can be very costly in terms of injury or even death, and mechanisms that settle conflict without overt physical aggression are expected to be favoured by selection (Maynard Smith 1982; Rohwer 1982; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). For example, status signals (Rohwer 1975) could be used to settle conflicts if these signals accurately predict qualities that determine dominance rank. Such status signalling badges differ from size-assessment traits because badges are not used in actual combat (Geist 1966) and thus could be uncoupled from traits that directly affect physical contests. Such signals should be especially common in birds because feathers obscure muscle mass and make size assessment difficult. Considerable debate still exists over how the honesty of such badges is maintained (e.g. trade-offs, social enforcement; Maynard Smith & Harper 2003; Searcy & Nowicki 2005), but the use of nonweapon signals to settle social conflict has now been supported in studies of a broad variety of taxa (Whiting et al. 2003; reviewed in Senar 2006).

Adding to the complexity is the possibility of multiple independent signals, by which each ornament provides different information to the receiver. A recent focus of sexual selection studies has been the evolutionary benefits of multiple signals (reviewed in Candolin 2003). Most of this work has focused on mate choice of multiple signals (e.g. Doucet & Montgomerie 2003), but the potential for

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multiple signals to be used in the context of male conflict is relatively unexplored (but see Bókony et al. 2006). One might not expect status signalling contexts to favour multiple categories of information because social dominance is expected to be similar in all forms of conflict (West-Eberhard 1983; Sih et al. 2004). However, the social context or the value of the resource being contested could affect social status or motivation to fight (Hansen & Rohwer 1986; Enquist et al. 1990; Hein et al. 2003), providing a benefit to displaying different types of dominance-related information. Indeed, a few studies have found evidence for multiple signals (or components of a signal) used in male contest competition among birds (Balph et al. 1979; Ligon et al. 1990; Mateos & Carranza 1997; Pryke et al. 2001, 2002; Pryke & Andersson 2003; Bókony et al. 2006). It remains unclear from these studies if such traits function in similar forms of male aggression or are associated with different contexts or levels of escalation, as expected if they are multiple badges of status.

We studied the signalling function of multiple sexually selected ornaments in lark buntings, *Calamospiza melanocorys*, in the context of male–male competition for mating territories. Male lark buntings have a number of sexually selected colour patches—several dark body feather regions and white wing patches—each of which is a composite signal based on independent colour and size components (Chaine 2006). We used both observational and experimental methods, together comprising four separate tests, to examine the relationship between male signalling traits, or traits correlated with the actual signal, and social dominance. Lark buntings are ideal for a study of multiple status signals for two reasons. First, males arrive on the breeding grounds a few weeks prior to females, making it possible to measure trait signal functions due to male competition in the complete absence of any direct influence of female mate choice. Second, the rich variety of social interactions in lark buntings suggests that social dominance might be flexible and context-dependent. For example, males frequently forage off territory, and most males tolerate foraging birds on their own territory. Furthermore, male buntings have classic territorial interactions with neighbouring males until they pair with a female, but many paired males are then joined sporadically by groups of males (hereafter 'mobs') seeking extrapair copulations, and males in these groups interact with the paired male and among themselves. Moreover, individual males can interact in all of these contexts: as a territory defender, mate guarder or extrapair mobber. Elsewhere we showed that female mate choice is complex and dynamic across years, but that male traits associated with social dominance do not appear to underlie the mate choice dynamics (Chaine & Lyon 2008).

## METHODS

### Study Area and Basic Techniques

We conducted our study early in each breeding season from 1999 to 2003 on the Pawnee National Grassland, Colorado, U.S.A. We conducted trapping and banding under permits from the U.S. Fish and Wildlife Service and the State of Colorado, and all procedures were approved by the University of California, Santa Cruz, Chancellors Animal Research Committee. We captured most of the males ($\sim$80%) within the first 2 weeks of arrival using potter traps at permanent baited locations on natural communal feeding areas. We monitored the traps continuously and removed birds within 5 min after initial capture. Upon capture, we randomly assigned males a unique colour band combination for individual identification in the field. For each bird we measured standard morphological features (wing chord, tarsus length, exposed culmen length, and length from nares to tip of the beak) as well as a number of plumage traits (described below). We estimated male residual mass, an indication of condition in some species (Brown 1996), as the residual of mass on a principle component of body size. Most males returned to their territory and were displaying within an hour after banding, and the high recapture rates within years suggests no aversion to capture.

### Plumage Measurements

Because males complete their partial moult during migration (Shane 2000), all males had already acquired their alternate (breeding) plumage when captured. All measurements are similar to those of previous work in this species (Chaine & Lyon 2008) and will be described only briefly here. We focused on two plumage regions, black body colour and white wing patches, as candidate sexual ornaments and measured both the colour and the size of each trait. The size and colour of each trait are at most weakly correlated, and results suggest they are developmentally uncoupled and are likely to be independent signals (Chaine 2006; percentage black on the body is linked to both percentage black on the rump, $r = 0.50$, and rank body colour, $r = 0.27$; rank body colour is also associated with wing patch size, $r = 0.16$; all other traits show no evidence of developmental coupling, all $r < 0.15$, $N = 624$ for all correlations). We measured the area of wing patches as a rectangle based on length and width in 1999–2000 and using actual area measured in Photoshop 5.5 (Adobe Systems) from digital images taken perpendicular to fully extended wings in 2001–2003. Wing patch size measurements from these two methods were standardized (mean $\pm$ SD $= 0 \pm 1$) to make them comparable across years. We visually estimated the proportion of the body that was covered with black versus brown feathers (patch size) in each of two body regions: the rump and the rest of the body (principal component of head, nape, back, belly). Two lines of evidence suggest that the rump may serve as an independent signal, distinct from the rest of the black body feathers, justifying separate analysis of the proportion of black feathers on the rump. First, the proportion of black feathers on a male's rump was less correlated with the proportion of black on each of the separate components of the rest of the body ($r = 0.31–0.39$, $N = 624$) than the correlations between the other components ($r = 0.44–0.51$, $N = 624$), suggesting it contains variation that could be used

independently as a signal. Second, males frequently display their rump in social interactions, suggesting that it actually plays a unique role in signalling and merits independent treatment (results below support this assertion).

We also measured the colour of a male's black body feathers (excluding brown feathers) and wing patch feathers. We categorized male body colour (four ranks for each body region described above) using a reference colour card in all years and also measured spectral reflectance of colour in 2001–2003. We combined colour estimates of black body feathers using our categorical ranking system in a principal component (including rump because it does not distinguish itself from other regions based on colour of black feathers, as it does for the proportion of black feathers) and called them 'rank colour' to distinguish them from spectrometric measures. We measured spectral reflectance from 300 to 700 nm using an Ocean Optics USB2000 spectrometer with a PX-2 pulsed xenon lamp and acquired it in OOIBase software (Ocean Optics, Dunedin, Florida, U.S.A.). We took three measures on each of four body regions (head, nape, back, rump) at random spots, completely removing the fibre-optic probe from the feathers between measurements, and recalibrated between each measurement on standard white (Labsphere, Inc.) and black surfaces. With the spectrometer data, we calculated tristimulus colour variables (hue, chroma, brightness) using ColoR 1.7 software (Montgomerie 2006). We calculated average absorbance (i.e. the inverse of brightness values) for each black feather region (as described for rank colour above) and combined measures using a principal component (Chaine 2006). This yielded one measure of male body colour for black feathers called 'body blackness'. In 2001–2003 we also measured the colour of wing patches with three samples from each wing patch. We calculated measures of brightness, UV brightness, and UV chroma, because these three measures show the largest coefficient of variation in white signals, and subsequently combined these measures using a principal components analysis. Measures of body feather darkness (rank and spectrometry) are correlated ($r = 0.6$; Chaine 2006), so we used only one in each analysis. We used spectrometer measures in analyses restricted to treatments conducted in 2001–2003, whereas visual estimates were used for analyses involving all years, unless wing patch colour entered into the model thereby restricting the data set. All plumage and body size measures were significantly repeatable (Lessells & Boag 1987) within years (repeatability = 0.63–0.92, $N = 34$–65; Chaine 2006).

### Behavioural Observations

We conducted focal observations on all unmated males during their most active period of the day (0800–1200 hours) throughout the breeding season to record dominance-related interactions among males. We observed all males at least every other day for 15 min on their territories to determine their mating status and to quantify the frequency of male song, aggressive displays, territorial intrusions and dominance interactions. Lark buntings

have two distinct song displays (Shane 2000), which we treated separately in our analyses: (1) display type used only in aggressive contexts with other males (aggressive flight song in Shane 2000), hereafter called 'aggressive song', and (2) primary song displays (Shane 2000) given by territory holders prior to obtaining a social mate, regardless of whether other males are present (hereafter called 'display song'), that may serve in either male–male aggression or mate attraction. For aggressive song, we focused our analysis on unmated males that were individually identified and captured in the focal year and occurrences in which dominance was clear—namely those occurrences in which a display given by a territorial male was not contested by the intruder. During some aggressive interactions we were able to identify both males and clearly determine the dominant and subordinate individual in the interaction based on chasing or supplanting behaviours, allowing us to compare male signalling traits with social dominance in free-ranging birds. Because resource ownership can affect contest outcomes (Davies 1978; reviewed in Kokko et al. 2006), we restricted our analysis to dominance interactions between neighbours at territory boundaries or between pairs of unmated males both of whom were off territory. Although male–male aggression is common (730 observations/year on average during behavioural observations), our selection criteria outlined above for each type of data severely reduced the number of observations used in analyses.

### Model Presentation Experiments

From 1999 to 2002 we used model presentations to quantify the aggressive responses of territorial males to standardized experimental territorial challenges during the period in which each focal male was not yet paired. We were interested in the relationship between a male's own traits and his response to an intruder, as well as the relative response of territory holders to different-coloured intruders. We used freeze-dried models of four different male lark buntings mounted in a standard perched position. These dark models were similar in colour to an average adult male (mean ± SD of absorbance: models: $-0.68 \pm 0.82$, $N = 4$; live birds: $0 \pm 1.00$, $N = 337$; $P = 0.18$). Only unmated males received a presentation and we limited presentations to the first 3 weeks of the breeding season because few males remained unmated after this point. We conducted all model presentations between 0800 and 1100 hours, the period during which males are most active on their territories, and each male received only a single presentation in one day.

We also examined the role of intruder plumage colour by presenting males with both light and dark taxidermic mounts in 2002. We used the same four 'dark' models as in the above experiment but, due to the limited number of salvaged specimens we were able to obtain (all models were road-kills and no birds were killed for this purpose), only one 'light' model was available. The light model was lighter in body colour and had a lower percentage of black feathers than the dark models (mean ± SD of four black models: rank colour $0.80 \pm 0.68$, percentage black

0.39 ± 0.23; brown model: rank colour −1.49, percentage black −1.61; $P < 0.001$ for both traits). We made comparisons of responses to dark and light models using a paired $t$ test to control for differences among males in aggressiveness for individuals presented with both models. All males tested in these experiments were individually identifiable by bands from the previous years or had been captured very early in the same season.

Each presentation consisted of a 10-min observation period with the model perched on a shrub roughly in the centre of the male's display territory. Immediately prior to the start of the trial, we clipped the model to the shrub and played two sequential lark bunting display songs (from *Peterson Audio Guides*) to simulate actual intrusion and to standardize the beginning of the male's focus on the model. Because males often forage on territories that are not their own and are tolerated by territory holders, presenting a model perched on a shrub and playing a song provided a more realistic territorial threat than a silent model. Song itself was not sufficient to elicit a response from the male, as a small number of presentations with a western kingbird (*Tyrannus verticalis*) mount paired with lark bunting song showed absolutely no response by the territory holder (data not shown, $N = 3$). During the 10-min trial period, we recorded display behaviour, song rate, and aggressive response (bill tilt and bill wipe displays, pecks, kicks and how quickly and how closely a male approached the model).

## Statistical Analyses

We transformed all variables to conform to assumptions of normality for parametric statistics and centred them, and all probabilities are two-tailed. We used multiple regression models to examine the relationship between male territorial behaviour and male traits. We performed analyses as stepwise regressions with backwards elimination to determine the best combination of traits that explained the data. We set the significance level for inclusion in the model at $P = 0.1$ to allow inclusion of traits with weak effects on the behaviour but that could interact with other predictor traits. This level also gave the same results as a best subsets analysis using AIC model selection (data not shown). In all cases, tolerance values were high, suggesting that weak correlations among traits were not a concern. We reduced male response to experimental intrusions through principal components analysis of aggressive behaviours based on a correlation matrix of behaviours (see Pearson & Rohwer 2000). We retained the first two components (eigenvalue >1) and rotated components (Varimax) to simplify their interpretation. To compare results across disparate data sets and statistical treatments, we calculated standardized effect size statistics (Fisher transformed correlation coefficients, $Z_r$) and 95% confidence intervals following procedures outlined in Nakagawa & Cuthill (2007). Effect sizes of parameters from a logistic regression were calculated by replacing $t$ values with $z$ values in the standard equations for linear regressions (Nakagawa & Cuthill 2007). To calculate effect sizes for parameters dropped from stepwise elimination

regression models (both linear and logistic), we used the $t$ or $z$ value for that parameter in the step immediately preceding elimination of that parameter (S. Nakagawa, personal communication). All analyses were completed in SYSTAT 10.2 or in spreadsheet software.

## RESULTS

### Observations of Interacting Territorial Males

In aggressive interactions between pairs of banded, unmated territorial males, the dominant male of the pair had a larger proportion of dark feathers on both its rump (paired $t$ test: $t_{46} = 2.84$, $P = 0.007$) and the rest of its body (paired $t$ test: $t_{46} = 2.11$, $P = 0.04$), and it had a larger beak (paired $t$ test: $t_{46} = 1.97$, $P = 0.05$; Fig. 1, Table 1). All other traits showed no difference in size or colour between interaction winners and losers (paired $t$ test: display song: $t_{25} = -0.49$, $P = 0.62$; body size: $t_{45} = 0.74$, $P = 0.46$; rank colour: $t_{45} = 0.27$, $P = 0.79$; wing patch size: $t_{45} = 0.55$, $P = 0.59$; wing patch colour: $t_{25} = 0.90$, $P = 0.38$; residual mass: $t_{45} = 1.03$, $P = 0.31$; Fig. 1, Table 1). Males observed in these interactions were not a random subset of the population (logistic regression final model: $N = 369$, log likelihood $= 4.19$, $P = 0.04$): they had a larger body size than other males in the population (estimate: 0.274, $P = 0.04$), but did not differ in other traits, including morphology, plumage and display song (removed from model, partial $P > 0.1$; Table 1).

In territorial observations, other males frequently intruded on a male's territory to contest resources, to forage or potentially in search of extrapair opportunities. We examined the association between the territory holder's traits and the average rate of male intrusions on territory (intrusion pressure: number of intrusions onto a male's territory scaled for minutes observed). Intrusion pressure on territorial males was associated with the territory holder's traits (multiple regression full model: $F_{3,193} = 3.45$, $P = 0.02$). Larger males (partial $P = 0.03$, coefficient $= -0.121$) and males with larger wing patches (partial $P = 0.056$, coefficient $= -0.140$) were intruded upon less frequently than small males with small wing patches (Table 1). Males with darker body feathers were intruded upon more frequently than lighter males (partial $P = 0.02$, coefficient $= 0.170$; Table 1). No other male traits (plumage, morphology, display song) of the territory holder entered into the model (all partial $P > 0.1$; Table 1). Territorial males frequently used aggressive flight displays to repel intruders. Males who showed a higher aggressive song rate had larger beaks (multiple regression model: $F_{1,263} = 5.16$, $P = 0.024$, partial coefficient $= 0.139$), but did not differ in other traits, including morphology, plumage and display song (all partial $P > 0.1$ and removed from final model; Table 1).

### Model Presentation Experiment

To examine whether a male's traits were correlated with the degree of his aggressive response towards a standard intruder, we presented territorial males with a dark-plumaged
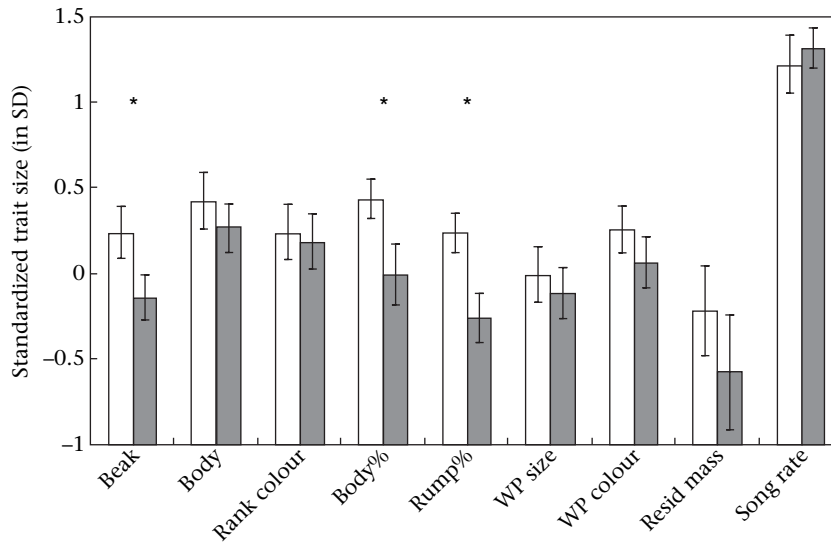
**Figure 1.** Trait size or colour for dominant and subordinate individuals seen in pairwise aggressive interactions among free-ranging birds. Bars present the mean ± standard error of winners (white) and losers (dark). Significant differences between winners and losers were established by paired *t* test and are designated as *$P < 0.05$.

taxidermic model. There was no significant difference among male responses to the four dark male models (ANOVA, $F_{3,43} = 0.46$, $P = 0.63$), suggesting that individual characteristics of the models did not influence aggression towards the model. There was no significant difference in average response to the models across years, so we combined data for all years (ANOVA, $F_{3,43} = 0.53$, $P = 0.66$). Furthermore, presentation date within each year had no effect on male response (linear regression: $N = 85$, $P > 0.30$). Principal components reduction of

response variables yielded two orthogonal variables (eigenvalue >1). The first component represented the speed and proximity of approach to the model, or 'approach intensity', and the second component represented physical attacks on the model (pecks, kicks, beak wipes), or 'aggression' (Table 2).

Most of the male traits we examined (except wing patch colour and display song) were correlated with degree of aggressive response towards the experimental model (Figs 2, 3, Table 1). Interestingly, different traits were

**Table 1.** Result summary and effect size values of associations between male traits and dominance indexes from observational and experimental portions of the study

| | Observational | | | | Experimental | |
|---|---|---|---|---|---|---|
| | Interaction winner | Seen interacting | Number of intrusions | Uncontested displays | Approach intensity | Physical aggression |
| Beak size | **+** | | | **+** | | **+** |
| | 0.204±0.200 | −0.012±0.102 | −0.072±0.141 | 0.139±0.121 | −0.086±0.475 | 0.336±0.327 |
| Body size | | **+** | **−** | | | **+** |
| | 0.078±0.200 | 0.108±0.102 | −0.121±0.141 | 0.025±0.121 | −0.106±0.475 | 0.285±0.327 |
| Body colour | | | **+** | | **−** | **+** |
| | 0.029±0.200 | 0.021±0.102 | 0.170±0.141 | −0.035±0.121 | −0.465±0.475 | 0.276±0.327 |
| Body percentage black | **+** | | | | **−** | |
| | 0.218±0.200 | 0.098±0.102 | −0.037±0.141 | 0.028±0.121 | −0.682±0.475 | −0.237±0.327 |
| Rump percentage black | **+** | | | | **+** | |
| | 0.292±0.202 | −0.023±0.102 | −0.015±0.141 | 0.072±0.121 | 0.535±0.475 | 0.158±0.327 |
| Wing patch size | | | **−** | | | **−** |
| | 0.058±0.200 | −0.096±0.102 | −0.140±0.141 | 0.002±0.121 | 0.071±0.475 | −0.342±0.327 |
| Wing patch colour | 0.127±0.263 | −0.002±0.141 | 0.021±0.146 | −0.012±0.172 | −0.137±0.475 | −0.109±0.475 |
| Residual mass | | | | | **−** | |
| | 0.108±0.201 | 0.015±0.102 | 0.101±0.141 | −0.108±0.121 | −0.553±0.475 | −0.053±0.327 |
| Display song | −0.069±0.263 | 0.032±0.193 | −0.093±0.149 | 0.016±0.172 | −0.107±0.475 | −0.220±0.327 |

Bold plus or minus symbols indicate the direction of the effect for significant parameters only (see text) to facilitate comparison across different data sets. Effect sizes are presented for all traits as Fisher's corrected $Z_r$ ± 95% confidence interval. A lower 'number of intrusions' reflects increased social dominance whereas for all other measures a higher value reflects increased dominance.

**Table 2.** Principal component factor loadings (Varimax rotated) of behavioural responses to experimental territorial intrusions using taxidermic mounts

| | Approach intensity | Physical aggression |
|---|---|---|
| Time until first approach | −0.875 | −0.033 |
| Distance of first approach | −0.692 | −0.276 |
| Time until closest approach | −0.739 | −0.198 |
| Distance of closest approach | −0.813 | −0.075 |
| Pecks | 0.110 | 0.704 |
| Kicks | 0.072 | 0.709 |
| Wing tilt display | 0.055 | 0.736 |
| Bill tilt display | 0.328 | 0.575 |
| Bill wipe display | 0.111 | 0.471 |

Traits fall onto two orthogonal axes that describe the speed and proximity of approach (called approach intensity) and the number of aggressive behaviours directed at the model (physical aggression).

associated with each of the two response variables and no trait was correlated with both approach intensity and aggression. Males with more black feathers on their rump approached models much more quickly and closely, as did males that also had lighter body feathers, lower residual mass, and a lower proportion of black feathers on the nonrump portion of their body (Fig. 2, Table 1). Males who were larger, by both beak size and body size, showed more intense attacks on the model (Fig. 3, Table 1). These more physically aggressive males also tended to have smaller wing patches and darker body feathers (Fig. 3).

To examine the association between a male's aggressive response and variation in the perceived threat due to variation in the plumage colour of the intruder, we used a matched-paired design whereby 13 males were sequentially tested with both a dark and a light model. We randomized the order of presentation to control for habituation; repeated-measures ANOVA of the order of presentation did not reveal evidence of habituation on any of the response categories measured (both $N = 25$, $P > 0.05$). Males approached dark models faster and closer than the light model (t test: $t_{13} = 2.09$, $P = 0.023$; effect size $\pm 95\%$ CI $Z_r = 0.415 \pm 0.373$) and attacked dark models more than the light one (t test: $t_{13} = 2.60$, $P = 0.059$; effect size $\pm 95\%$ CI $Z_r = 0.509 \pm 0.379$; Fig. 4). There was no difference in the display song rate of territory holders in response to dark or light models (t test: $t_{13} = -0.71$, $P = 0.49$; effect size $\pm 95\%$ CI $Z_r = -0.144 \pm 0.360$).
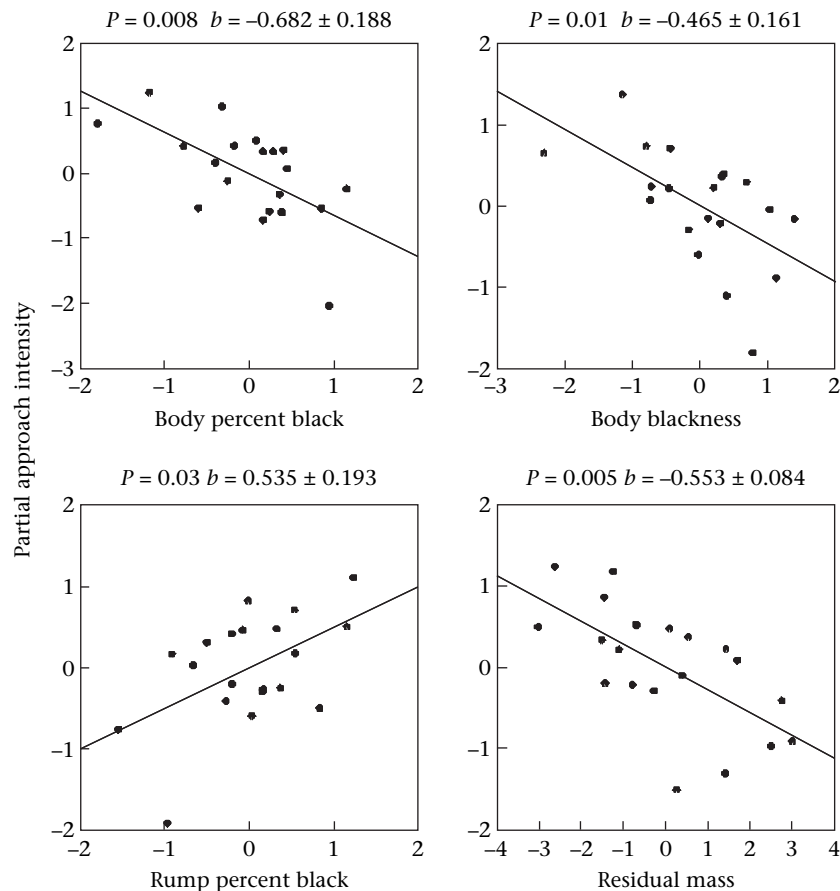


**Figure 2.** Partial correlations between male badges and the intensity of approach towards experimental intrusion with a taxidermic male model. Lines represent regression trend lines for each effect. Partial effects are indicated above each graph (partial $P$, partial coefficient $\pm$ SE). Higher values of approach intensity reflect a faster and closer approach to the model intruder. Whole model: $F_{4,15} = 5.92$, $P = 0.005$.
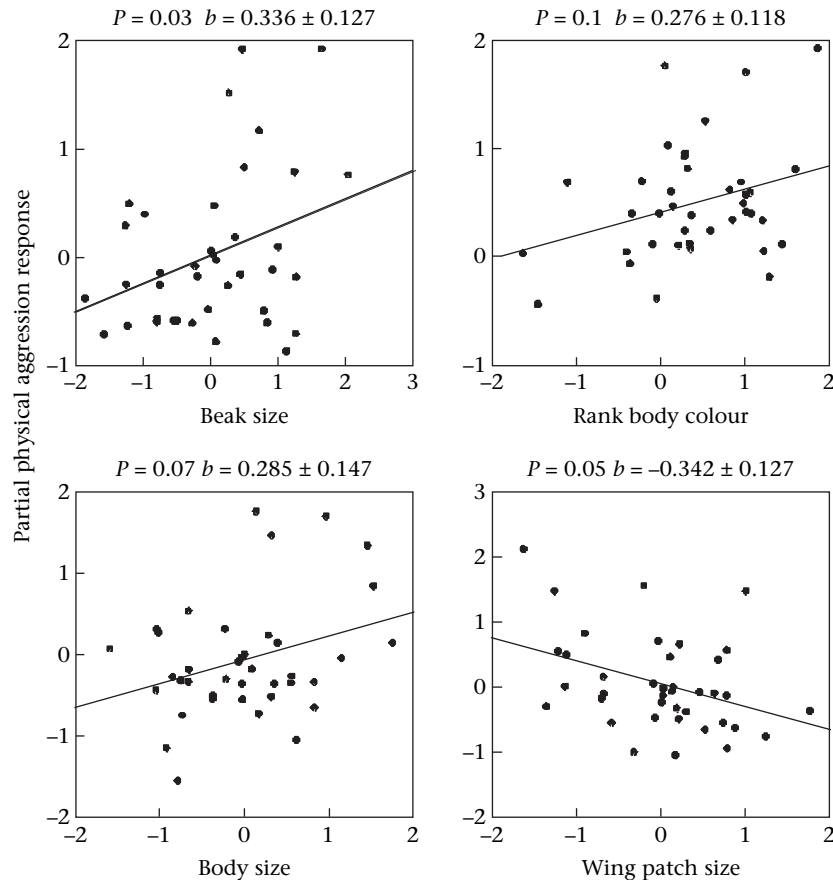
**Figure 3.** Partial correlations between male badges and the aggression reaction towards experimental intrusion with a taxidermic male model. Lines represent regression trend lines for each effect. Partial effects are indicated above each graph (partial $P$, partial coefficient $\pm$ SE). Higher values of aggression reflect more kicks, pecks and bill tilts towards the model. Whole model: $F_{4,34} = 2.81$, $P = 0.04$.

## DISCUSSION

### Badges of Status and Levels of Escalation

A powerful way to identify badges of status is to compare ornamental traits that differ between winners and losers of pairwise competition, an approach used in both captive studies (Eckert & Weatherhead 1987; McGraw & Hill 2000; Pryke et al. 2002; Pryke & Andersson 2003; Tibbetts & Dale 2004; Tarof et al. 2005) and studies of free-living individuals (Geist 1966; Järvi & Bakken 1984; Evans & Hatchwell 1992; Greene et al. 2000; Mennill et al. 2003). In lark buntings, winners of paired contests had a larger proportion of black feathers on both their rump and the rest of their body, suggesting that these plumage traits do serve as badges of status, but no other plumage traits differed significantly between winners and losers. However, relying solely on the outcome of interacting individuals can provide an incomplete picture of all of the signals and cues used to assess social dominance—many males may never interact simply because other traits allow them to determine dominance asymmetries at a distance. In lark buntings, males seen in pairwise contests were a nonrandom subset of the population because they were larger than males not seen interacting.

If some signals of social status are used at longer ranges to avoid conflict, such traits should be associated with a lower rate of intrusion onto a male's territory, as we found for male lark buntings with larger wing patches. The observation that wing patch size predicts rate of intrusion, but not the outcome of pairwise aggressive interactions (see Table 1), suggests that wing patch size may serve primarily as a long-range signal, but that at close range other signals are a better metric of fighting ability. This may be particularly appropriate because white wing patches are visible against the black body from a considerable distance. Associations between social dominance and some traits at long distance (wing patches) and others at close range (percentage black body and rump plumage) suggest that multiple signals function in lark buntings to avoid interactions in some cases and settle escalated interactions in others. Alternatively, some traits may be important in offense (pairwise contests), whereas others are only used in defence (intrusions), as has been suggested in other species (Bókony et al. 2006). Finding that different traits indicate different levels of aggression is novel for plumage-based badges of status (see Zucker 1994 for an example in lizards), but this effect is known for behavioural traits.

Large body size confers an advantage in many animal contests and is often associated with winning fights (Geist
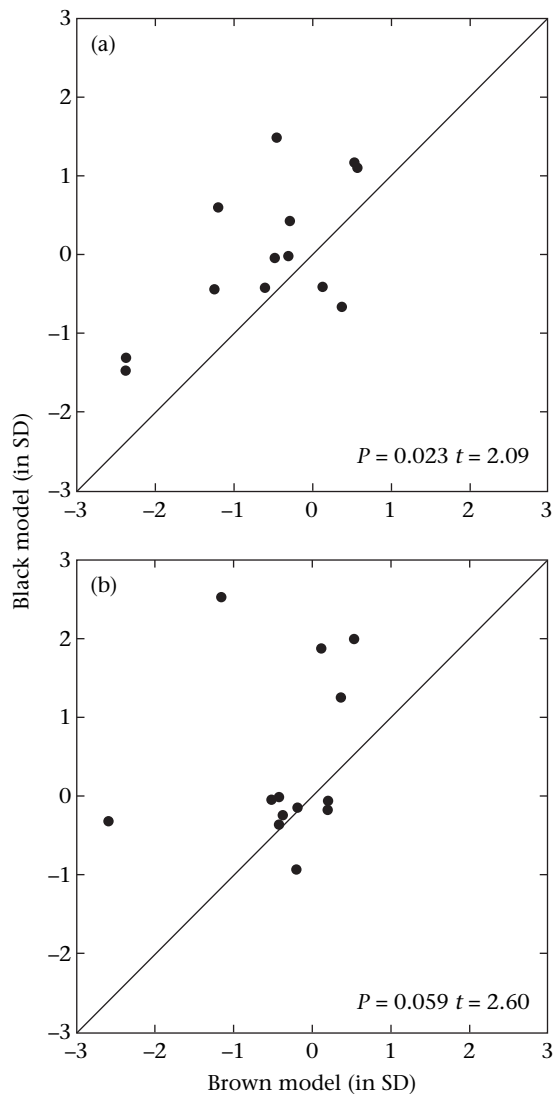
**Figure 4.** Relative male responses towards a dark and light experimental intruder for (a) intensity of approach and (b) aggression. Higher values of approach intensity reflect a faster and closer approach to the model and higher values of aggression reflect more pecks, kicks, bill wipes and bill tilts towards the model. Each point is one male presented with both model types. Points above the diagonal (1:1 line) reflect a greater response towards the dark model than the light model. $N = 13$.

1966; Kodric-Brown & Brown 1984; Andersson 1994). Depending on the context of the social interaction, this pattern can reflect the effect of physical strength on the outcome of physical combat or the influence of body size as a cue for predicting social dominance without resorting to physical combat. Body size in lark buntings appears to be particularly important, as it was associated with virtually all our measures of social dominance (Table 1). Similarly, beak size, an indication of body size and in rare cases a weapon, was also associated with some measures of aggression (Table 1). However, in lark buntings no male plumage traits were directly linked to body or beak size (Chaine 2006), suggesting that associations between plumage traits and aggression provide

information above and beyond that conveyed by body size. Whereas some studies have shown associations between body size, putative badges and dominance (Järvi & Bakken 1984; Maynard Smith & Harper 1988; Ligon et al. 1990), these patterns are certainly not universal (e.g. Evans & Hatchwell 1992; Senar et al. 1993; McGraw & Hill 2000; Pryke et al. 2001).

## Badges of Status Assessed by Model Presentations

Simulating territorial intrusions with taxidermic models provides an excellent complement to observational studies, for two reasons. First, it enables an investigation of the link between plumage signals and aggression in all individuals, not just the subset that engages in direct social conflict. This is particularly important where the individuals that actually interact comprise a nonrandom subset of the population, as we found. Second, the use of model presentations enables the traits of one of the interacting individuals (the model) to be held constant and provides a measure of the link between the plumage traits of a focal animal and its aggressive response to a standardized stimulus (e.g. Pryke et al. 2001). We presented a standardized intruder to territorial, unmated males and measured two aspects of their response: aggression and approach. Because approach intensity and aggression are often correlated in model presentation studies (e.g. Muehter et al. 1997; Pearson & Rohwer 2000), it is intriguing that they were virtually uncoupled in our study, evidenced by the distinct principal components for each of the two measures. Moreover, the plumage and size characteristics correlated with degree of aggression differ completely from those associated with approach intensity (Table 1) and suggest multiple signal functions of male traits, whereby each suite of traits provides different information to the receiver (multiple messages).

The patterns revealed by the model presentations overlapped somewhat with the observational data (e.g. size consistently reflected dominance), but there were striking differences as well (Table 1; e.g. proportion of black feathers on the rump and rest of the body). The differences between the two assays may reflect the difference between a naturally escalated fight and a reaction to an individual for which no information has yet been acquired. Wing patch size showed a surprising pattern: larger patches were associated with less aggression in the experiment but with fewer territorial intrusions in the observational component. Two factors might account for some of the differences between the experimental and the observational aspects of the study. First, the males that engage in real interactions comprise a nonrandom subset of the population, and different factors may determine dominance for more equally matched contestants than when representatives of the entire population are tested with experimental intrusions. Second, the responses assayed in the model presentation are not necessarily those used by birds to determine dominance in real social interactions, which are more often based on

behavioural interactions like supplanting than on direct physical aggression. In either case, signals that denote social dominance are likely to be meaningful under certain contexts—some signals may be used when no other information exists about a rival (e.g. model presentations), whereas others are used when the activity, behaviour and motivation of an individual can be observed. A complete resolution to the conflicting associations between wing patch size and social dominance in lark buntings will require experimental manipulations under different social contexts.

It is particularly surprising that two traits, the proportion of black feathers on the rump and that on the rest of the body, showed opposite relationships with approach intensity because these traits are correlated (Chaine 2006) and both are associated with social dominance in escalated contests (although the pattern is particularly strong for rumps). A key difference between the rump and the rest of the body is that the feathers on the rump are often concealed, and then quickly exposed in particular social contexts. For example, many males who join the mobs of males that follow and harass mated pairs drop their wings and expose their rump while perched (personal observation), a pattern that prompted us to examine this trait separate from the rest of the body. A glance at any avian field guide reveals that distinct colour patches on the rump are taxonomically widespread, which may suggest that rump signals might generally serve as flexible, coverable badges. In lark buntings, the ability to conceal rump feathers appears to provide males with the flexibility to adjust their perceived dominance rank or degree of threat when dominance depends on the social context, as has been suggested for species with coverable badges (Hansen & Rohwer 1986; Metz & Weatherhead 1992; Jablonski & Matyjasiak 1997; Hurd & Enquist 1998). However, more frequent testing or misjudgements by other males may be a cost of having a flexible or less informative badge of status (Dawkins & Guilford 1991) and may more often require responses by territory holders, similar to the rapid response of males with more black rump patches observed in our study.

The second experiment, in which each male was presented sequentially with a lighter and a darker model, focused on how male aggressive response varies in relation to the plumage colour of the intruder, rather than the link between aggression and the male's own colour (focus of experiment 1). Territorial males all responded more intensively towards the darker model than the lighter model, although this effect was more striking for approach intensity than for physical aggression. This faster, more intense, response suggests that darker models are perceived as a greater threat (Røskaft & Rohwer 1987) due to increased risk of either territorial usurpation or future extrapair sirings by the darker males.

## Multiple Badges of Status

Multiple signals—traits that provide information and are uncorrelated with one another—have recently received considerable theoretical and empirical interest, but most attention has focused on signals that function in the context of female mate choice. By showing that lark bunting plumage ornaments function in different social contexts and levels of escalation, we provide some of the first clear evidence that multiple signals can function in badge-of-status contexts, not just mate choice. Our results are similar in some respects to a recent finding that both bib size and wing bars provide information in contests among captive house sparrows, *Passer domesticus* (Bókony et al. 2006). Most traits we examined are associated with some form of male social dominance, but it is notable that different traits are associated with different contexts or levels of escalation (Table 1). In addition, unlike some other taxa with multiple signals (Hill 1994; Andersson et al. 2002), the lack of phenotypic correlations between different traits or trait components in lark buntings means that these traits could function in independent signalling contexts, including both intrasexual and intersexual selection. Whereas the difference in response to dark and light models suggests that plumage colour acts as a signal, manipulative studies will be required to determine if the traits studied here are the true signals used in social dominance or if they are simply correlated with the true, unmeasured signal trait.

In lark buntings, multiple badges of status appear to provide information at different distances and different levels of escalation. Some traits, such as wing patch size and body colour, appear to function as long-distance signals but play no role in escalated conflicts. In contrast, other traits appear to be assessed at close proximity, such as the proportion of black feathers on the rump or body, and these may provide more accurate or nuanced information (Dawkins & Guilford 1991). Thus, these multiple signals may be used in sequential assessment of fighting ability between individuals as contests escalate (Andersson 1980; Enquist et al. 1990). Similar long- and short-range visual signals have also been suggested for multiple badges of status in a lizard (Zucker 1994). This proposed mechanism for the evolution of multiple badges of status is akin to the 'multiple-messages' hypothesis for intersexual ornaments (Johnstone 1995, 1996). In general, contrasting colour patches (e.g. wing patches, epaulettes or bibs) could provide easy metrics of coarse-grained dominance from a distance, whereas other more precise signals (Andersson 1980; Dawkins & Guilford 1991), such as the proportion of black feathers on the rump or the colour of the badge (Mennill et al. 2003), may provide better estimates of dominance at closer ranges. Further tests of such a distinction would improve our understanding of information content provided by badges of status.

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