

Condition-dependent resource value affects male–male competition in the blue–black grassquit

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Male–male competition frequently can be resolved without overt aggression through the use of behavioral and phenotypic traits that signal body condition, dominance status, and fighting ability. In this study, we used male blue–black grassquits (*Volatinia jacarina*) to examine the relationship between male dominance status and behavioral, body condition, and ornamental traits in intrasexual agonistic encounters over a food resource. We found an association between body condition and winning, where winners were lighter than losers. This pattern was explained by low amounts of aggression exhibited by losers when they were heavy. In addition to being lighter, winners were, on average, up to 5 times more aggressive than the heavier losers. There were no associations between ornamental characteristics and dominance status, which suggests that male blue–black grassquits do not exhibit a badge signaling body condition and fighting ability, and we propose that such ornamental characteristics may be more functional in mate-choice contexts. However, the amount of male nuptial plumage of winners predicted the aggressiveness of their opponents, suggesting a social cost for sustaining this ornament. *Key words:* body condition, intrasexual selection, male–male competition, sexual selection, structural plumage, UV coloration. [*Behav Ecol* 20:553–559 (2009)]

Competition over limited resources (mates, food, and nesting site) is often vigorous and widespread across bird species. These contests may vary considerably in degree of escalation from ritualized displays to overt physical aggression. When these contests escalate, they can lead to serious injuries or even death, because males have to use physical aggression to settle them. If this is the case, a male's fighting capacity will be directly related to his success in securing the resource. However, mechanisms that lead to the resolution of these conflicts without physical aggression are expected to be selected, because signaling fighting ability is advantageous to both competitors (Rohwer 1982; Searcy and Nowicki 2005). In this scenario, fights that are energetically expensive and with predictable results may be avoided (Maynard Smith 1994). For example, signals of fighting ability could be used to settle conflicts if they accurately predict qualities that determine fighting capacity.

Moreover, the value of the resource in dispute may be different for each opponent, and this, in turn, will affect an individual's willingness to accept escalating and potentially injuring fights (Riechert 1998). A weaker opponent may overthrow a stronger, more dominant one when its willingness or necessity to gain the resource is greater than that of the dominant individual. If this situation occurs, the dominance effect of a reliable signal of fighting ability may be overruled. Although this situation is possible, contest theory proposes that asymmetries in individuals' abilities to defend resources determine the outcome of fights, that is, individuals with the higher resource-holding potential (RHP) win disputes (Parker 1974). Across many taxa, large body size is usually decisive in contest

situations, suggesting that RHP is frequently a function of large body size (Renison et al. 2002).

In birds, plumage brightness or ornamentation may act as a badge of the animal's condition (Rohwer 1982) or status (Rohwer 1975; Mateos and Carranza 1997a, 1997b; Pärt and Qvarnström 1997), which may influence the ability to compete with other males (e.g., *Zonotrichia querula*; Rohwer 1975, 1982). Badges of status (or fighting ability) are more often than not related to body size and age in birds (reviewed by Andersson, 1994). For example, it has been shown that the black bib of house sparrows (*Passer domesticus*) is related to fighting ability and age of males in disputes for resources (reviewed by Searcy and Nowicki 2005; Nakagawa et al. 2007). Another example shows that siskins (*Carduelis spinus*) can avoid the use of overt aggression by assessing fighting ability of their flock companions through plumage badge color and size (Senar and Camerino 1998).

Blue–black grassquits (*Volatinia jacarina*) are small, granivorous birds found in Mexico, Central America, and most of South America (Sick 2001). They are socially monogamous, and during the breeding season, males molt to a blue–black iridescent plumage, whereas females and young males are inconspicuously brown (Sick 2001). Males execute aerial displays by leaping from perches in their territories, which are arranged in lek-like clusters, and obtain high numbers of extrapair matings (Almeida and Macedo 2001; Carvalho et al. 2007). During displays, males expose white underwing patches and vocalize (Sick 2001). The functions of both conspicuous displays and the blue–black plumage are not clear in the context of sexual selection, but they possibly advertise male quality to potential reproductive partners or might be important in male–male competition over territories (Alderton 1963; Murray 1982).

Doucet (2002) found considerable variation in plumage spectral characteristics among male blue–black grassquits, which was positively correlated to feather growth rate,

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a measure of male condition. Thus, in this species, plumage may function as an honest signal in intrasexual selection. However, Doucet (2002) did not find a relation between plumage characteristics and other measures of body condition (body fat content and body size). Costa and Macedo (2005) found a negative relation between levels of parasite infestation and secondary sexual characters and parasite count and body condition (fat:metric ratio); however, they found no relation between body condition and secondary sexual characters.

In this study, we used blue–black grassquits to examine male–male competition and to evaluate the types of traits that may be involved in determining dominance status. For this, we assessed male dominance status relative to behavioral, body condition and ornamental traits during agonistic encounters over a food resource. First, we asked whether there is a relationship between these traits and dominance status. Second, considering the RHP Hypothesis (Hammerstein 1981), we examined whether dominant males are heavier, exhibit a more exuberant plumage or display a different set of behaviors when compared with subordinate males in disputes over a food resource.

METHODS

Subjects

We mist-netted 24 adult male blue–black grassquits between February and March 2005 within the campus of Universidade de Brasília (15°46'S, 47°51'W) in central Brazil in an area of altered Cerrado vegetation. Of the captured males, 18 were assigned to the experimental group, and 6 were left as replacements. Only adult males were used in the experiment, and this was verified by the presence of at least some nuptial plumage that typically persists throughout the year. Males were kept in visually isolated individual cages (35 × 50 × 40 cm) in an outdoor aviary throughout the experimental period. We banded each male with an aluminum identification band supplied by the Brazilian Bird Banding Agency (CEMAVE, Cabedelo, Brazil). All individuals were treated monthly for endoparasites with a coccidiostatic (sulfamethoxazol and trimetoprim) and an anthelmintic (mebendazol) drug. We provided a mixture of seeds, multivitamin supplemented water, and sterilized sand *ad libitum* in each cage. Trials were only initiated after all individuals had remained at least 2 months in the individual cages.

All experiments were conducted in accordance with the current laws of Brazil, and capturing and banding activities were performed under permit 237 DIFAS/DIREC from the Instituto Brasileiro de Recursos Renováveis—IBAMA.

Experimental procedures

We conducted 65 trials with pairs of males unfamiliar with one another, which were selected on the day prior to the trial. Each pair combination was created *a priori* to ensure that there were no pairing repetitions. Eighteen males were used during the contests, and each participated in an average of 3.6 trials. The repeated use of males in contests may result in pseudoreplication (Milinski 1997), and our statistical treatment of the data addressed this potential problem (see below). Each male was given 3 green or yellow plastic bands to ensure fast identification of individuals during the manipulation. Because band color may affect the result of behavioral manipulations, a focal male wore the 2 band colors in equal proportions throughout the trials. By doing this, we could evaluate if band color was a predictor of dominance status.

On the day of the trial, each pair of males was transferred to a neutral interaction arena inside the laboratory, illuminated overhead by a fluorescent bird lamp (Arcadia Bird Lamp; 2.4% UVB, 12% UVA). Two removable aluminum panels divided the

arena into 3 sections of 50 × 70 × 50 cm, each containing 1 perch. Males were visually isolated from each other in the 2 outer sections, where they were food deprived for a period of 4 h prior to the trial. The intermediate section of the arena contained a feeder on the floor that allowed only 1 male to feed at a time. Trials lasted 11 min and were observed and videotaped from a blind. The trial was initiated when the 2 panels were removed, allowing both males simultaneous access to the intermediate section containing the food.

Behavioral traits

A typical trial involved a male gaining access to the feeder and excluding his opponent whenever the latter tried to feed. During male contests, we recorded 4 types of aggressive interactions that included both displays as well as overt aggression. In 1) “ritualized confrontation,” males faced each other with lowered heads, while maintaining the beak open and tail raised. Overt aggression included 2) “chase,” where the aggressor ran or flew after his opponent; 3) “displacement,” where the aggressor approached his opponent and caused him to move away or out of the feeder; and 4) “pecking,” where the aggressor chased his opponent and pecked him mostly on the head or directed the pecking at the opponent but was not successful in making contact. Chases with and without pecking typically ended when the opponent was displaced to the outer sections of the cage.

We recorded a “win” for a male when he supplanted or successfully dislodged his opponent through ritualized confrontations, displacement, chasing, or pecking. Pecking was rarely observed, and most pecks did not contact the opponent's body. No male was injured in any trial, and these were terminated whenever the observer evaluated that a male could be injured due to overt aggression from his opponent.

The total number of wins per male was used to produce a winner–loser matrix, with rows labeled as wins and columns as defeats. During each trial, any given male could score several to no “wins,” based on the types of interactions explained above. We calculated individual ranks with David's score (DS) ranking method (David 1987; Gammell et al. 2003; Hemelrijk et al. 2005). The DS ranking method was appropriate for our analyses for it is possible to calculate individual scores based on an unbalanced winner–loser matrix. Also, by using a dominance score that summarizes the outcome of all interactions of a given male, we avoided pseudoreplication by considering a single value for each male and not including each trial outcome separately, unless when such effects were the focus of our questions.

Body condition

Morphological traits and ornamentation were measured just prior to each trial and several more times for each male throughout the experimental period, and these measures were averaged for each individual for statistical analyses. Morphological measures included mass and tarsus length (± 0.1 mm). From these, we calculated a body-condition index: weight/tarsus length. This body-condition index was used because it has been previously shown in the blue–black grassquit that parasitism significantly decreases this index (Aguilar et al. 2008) and that it is negatively correlated with oocyst levels (Costa and Macedo 2005). In order to avoid multicollinearity issues, we did not include other morphological variables in the analyses.

We used data from 493 free-living male blue–black grassquits for comparative purposes with reference to body condition, in order to evaluate the effects of captivity on males used in the experiment. We conducted an analysis of variance to evaluate whether there was an effect of captivity on winners' and losers'

body condition. To avoid pseudoreplication in using repeated measures from winners and losers, we used the DS to classify individuals as dominants or subordinates, insuring that each individual was included only once in the analysis. Males that presented DS rank above the median were classified as dominants, whereas individuals below the median were considered subordinates. This classification only took effect for this comparison and was not considered for the analyses presented in the results section. There was no significant effect of captivity on the weight of dominants or subordinates ($F_{2,506} = 0.25, P = 0.78$). This result assured us that maintenance of the birds in captivity did not affect the weight of individuals, which did not differ from that observed in a natural population.

Ornamental traits

The ornamental traits assessed included measures of structural plumage reflectance and a subjective estimate (taken by E.S.A.S.) of percentage of blue–black plumage covering the male's body (0–100%) as proposed by Keyser and Hill (1999). It is important to point out that all males used in the experiment exhibited a high percentage (>67%) of blue–black plumage coverage.

For the analyses of structural plumage reflectance, we collected feathers at 2 distinct moments: before trials initiated (May 17, 2005) and after all trials were concluded (July 30, 2005). We removed 3–5 feathers with forceps from the central part of the rump and from the wing coverts and arranged them on a black paper card replicating their position on the male's body. Reflectance measurements were taken separately from feathers collected at both points in time, and the color characteristics were averaged for each individual.

Reflectance was measured using an Ocean Optics USB4000 spectrometer and a pulsed xenon light source (Ocean Optics PX-2; 220–800 nm range). All reflectance measurements were taken in relation to a WS-1-SS white standard (Ocean Optics, Dunedin, FL). For all measurements, we used 2 bifurcated probes (UV–VIS, core diameter 400 μm) where both the emission and reception probes were positioned at a 45° angle at approximately 6 mm from the sample surface. Both surplus ends were protected to prevent light entry, and all ambient light was excluded.

We used SpectraSuite software (Ocean Optics) to conduct all spectrometric measurements. For each body region, we collected 3 measurements that consisted of the average of 50 individual readings (integration time = 20 ms; boxcar correction = 30). For analyses, we used the region between 300 and 700 nm of the obtained spectra, which corresponds to the visible spectra of birds (Cuthill 2006; Mullen and Pohland 2008). We also reduced the number of data points by interpolating to a step width of 1 nm.

We report the spectral properties of the reflectance of the rump by calculating 4 indexes—brightness, hue, intensity, and UV chroma—and then averaging these across the 3 replicate spectra and later across the feathers collected before and after the trials. Brightness was the average reflectance between 300 and 700 nm, hue was the wavelength of maximum reflectance, and intensity was the maximum reflectance reached. UV chroma was the sum of reflectance between 300 and 400 nm, divided by the sum of reflectance between 300 and 700 nm (Montgomerie 2006). We only used measures from 1 body region in the analyses because both body regions' spectral properties were interrelated.

We inserted the 4 calculated indexes in a principal components analysis in order to reduce the influence of the correlations between the indexes. The values of the 1st 2 components were used for subsequent analyses. PC1 was interpreted as a measure of brightness, because it was strongly and positively

influenced by brightness and intensity and was weakly influenced by UV chroma and hue (loadings: 0.68, 0.70, 0.17 and -0.13 , respectively). PC2, on the other hand, was interpreted as a measure of spectral saturation, because it was heavily and positively influenced by UV chroma and negatively by hue, with little influence of brightness and intensity (loadings: 0.68, -0.69 , -0.19 , and -0.11).

Statistical analyses

We used R statistical software (ver. 2.7.1, R Development Core Team 2008) for all computations. All tests were 2-tailed, and the null hypothesis was rejected at $P < 0.05$. Unless noted otherwise, data are presented as absolute mean \pm standard error (SE).

We used a multiple regression to determine if individual DS rank was associated with body condition and ornamental plumage traits (arcsine-transformed percentage of plumage cover, PC1 and PC2). After the transformation of plumage cover, none of the variables included in these models deviated from normality (Shapiro–Wilk test of normality, all $P > 0.05$). Model simplification was achieved by a backwards stepwise procedure, in which variables were removed from the final model if they did not approach significance ($P > 0.1$).

To investigate the relationship between access to the resource (expressed in terms of feeder visits), aggressiveness and conflict outcome (winner/loser), generalized linear mixed models (GLMM, “lmer” in R package “lme4”) were fitted considering a Poisson error distribution and log link function. Aggressiveness (number of aggressive acts) was “ $\log(x + 1)$ ” transformed in order to log-linearize the relationship between the 2 count variables. This GLMM framework was applied to account for the repeated usage of individuals in different trials, by including the identity of the individual and of its opponent as crossed random effects. To evaluate the relationship between male characteristics and the number of aggressive acts they displayed in each experiment, we fitted GLMM with frequency of aggressive acts of winners and losers as response variables in separate models; body condition and plumage traits of both the individual and its opponent were included as fixed factors, and winner and loser identities were included as crossed random effects. Because we computed a single value of color score for each individual, they could not be included in any mixed-effects model.

Parsimonious models were achieved by sequentially removing the variables with lowest explanatory power and comparing nested models by likelihood ratio tests (LRT), using the change in deviance as a chi-square approximation. If removing a variable caused no significant decrease in model fit, the simplified model was preferred. Therefore, significance of parameters in GLMM analyses reflects an increase in deviance and thus a decrease in model fit. Furthermore, the removal of all explanatory variables with no significant increase in deviance implied failure to reject the null hypothesis (i.e., that none of the variables considered has any predictive value). Parameter estimates and SEs are reported in log scale for the GLMMs. When necessary, we estimated a variance inflation factor (\hat{c}) to account for overdispersion, which was used to adjust model log-likelihood and parameter estimated SEs (Anderson 2008).

RESULTS

General results

During the experimental trials, no aerial displays or vocalizations were executed. Total lack of aggression was observed in only 1 trial, and losers retaliated in 49 (77%) of 64 trials. Access to the feeding resource was positively associated with

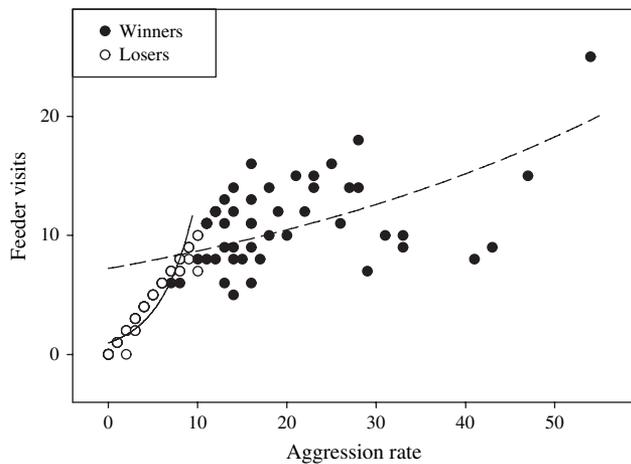


Figure 1
Association between number of aggressive acts and number of feeder visits by male blue-black grassquits (winner = black dots, dashed line; loser = white dots, solid line) during experimental trials.

individual aggressiveness and dominance status, with winners being considerably more aggressive (winner = 16.9 ± 1.33 ; loser = 3.43 ± 0.36) and feeding with greater frequency (winner = 10.09 ± 0.48 ; loser = 3.29 ± 0.35 ; Figure 1). There was also an interaction between these 2 terms, with a stronger association between aggressiveness and feeder visits for losers than for winners (Table 1).

Traits and dominance hierarchy

A decrease in body condition resulted in a higher dominance hierarchy ranking indicating that lighter males were dominant to heavier ones (adjusted $R^2 = 17.16\%$, $\beta = -0.47 \pm 0.22$, $t = 2.13$, $P = 0.04$, $n = 18$; Figure 2). Plumage traits, which included the 2 color components and blue-black plumage cover, were excluded from the model because they did not improve model fit ($P > 0.05$).

None of the considered parameters significantly predicted the number of aggressive acts by winners (GLMM, all LRT $P > 0.05$). However, the number of aggressive acts performed by losers during trials decreased significantly relative to their own body condition (Figure 3a) and significantly increased with the percentage of blue-black plumage coverage (Figure 3b) exhibited by winners (Table 2).

DISCUSSION

We evaluated whether males use behavioral, body condition or ornamental traits in intrasexual interactions over a food re-

source. The main objective of our study was to investigate if any of these traits could predict dominance status in male-male competitions. Male-male dominance was assessed through the computation of a dominance hierarchy based on aggressive behaviors. The multiple regression model indicated that male body condition decreased with dominance ranking. None of the other traits included in the analysis predicted male status. This result suggests that the outcome of male-male competition in grassquits is context dependent, where only amount of aggression and body condition of a male predict the result of an interaction.

Several bird species use plumage characteristics as status signals. One of our expectations was that males with more exuberant blue-black plumage would dominate males with less exuberant plumage. Our results suggest, however, that none of the plumage structural coloration components are associated with dominance status. It is possible that plumage traits function strongly in intersexual contexts but are not used in male-male contests. A recent study of the blue-black grassquit found that coccidian oocyst count was negatively correlated to the percentage of blue-black plumage coverage, which suggests that parasite infestation affects this sexually selected trait; furthermore, less infected individuals displayed more exuberant plumage (Costa and Macedo 2005). Because in our study we treated all males for endoparasitic infestations, they possibly exhibited healthier plumage than if they had not been medicated. This treatment may have concealed the status-signaling capacity of this sexually selected trait, resulting in a higher frequency of aggressive acts to settle competitive contests than would have occurred otherwise. Two recent studies with blue tits (*Cyanistes caeruleus*) agree with our results that structurally based UV plumage does not signal social status (Korsten et al. 2007; Vedder et al. 2008). Both studies suggest that UV plumage might be a signal used only in mate choice, as an attractiveness enhancer.

Male mating success variance in socially monogamous birds may result from extrapair fertilizations (EPF), leading to the evolution of secondary sexual characters (Webster et al. 1995; Albrecht et al. 2007), and sexually dimorphic structural plumage coloration may be one such ornament (Korsten et al. 2007; Vedder et al. 2008). Blue-black grassquits are socially monogamous and present high rates of EPF (50% chicks and 60% nests, Carvalho et al. 2006); however, females do not have any structural coloration (Macedo RH, unpublished data). Thus, the structural coloration of male grassquits could be a signal used strictly by females when selecting extrapair mating partners, instead of a signal of social status in male-male competition for resources. Males possibly establish social hierarchies based on aggressive disputes.

We expected that more dominant males would be heavier, which is typical for most birds (Andersson 1994). However, we observed a significant negative relationship between rank and

Table 1
Analysis of deviance table for the significant predictors in the GLMM for feeder visiting rate

Model	Terms	Estimate (SE)	Change in df	Change in deviance	<i>P</i>
Feeder visits ~ aggression × outcome	Intercept	-1.22 (0.28)			
	-Aggression ^a	1.51 (0.15)	1	282.97	<0.001
	-Outcome ^b	2.21 (0.35)	1	130.1	<0.001
	-Aggression:outcome	-1.04 (0.16)	1	43.76	<0.001

GLMMs fit by Laplace approximation, considering individual and opponent identities as crossed random effects. Random effects variance: individual 0.007 ± 0.005 ; opponent $< 0.001 \pm 0.001$.

^a “log($x + 1$)” transformed.

^b Estimate relative to losers.

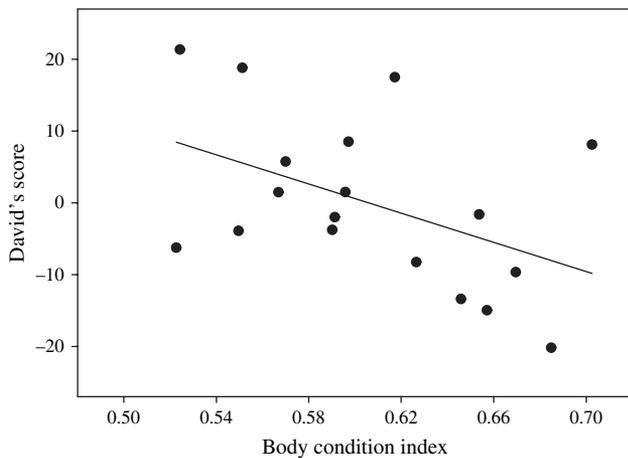


Figure 2
Association between body-condition index (mass/tarsus length) and DS dominance index for male blue-black grassquits in experimental trials.

the body-condition index. All other measured traits were not significantly related to dominance rank. This lighter winner pattern was unexpected, in light of existing information in the literature. Where size and weight differences have been detected between winners and losers, winners generally are larger and heavier than their adversaries (Andersson 1994). There are 2 possible explanations for the pattern we observed. First, lighter males may be favored by increased agility (McLachlan and Allen 1987) or some context-specific advantage of smallness per se. Male agility may be a sexually selected characteristic in the blue-black grassquit. If the aerial display of the blue-black grassquit is a trait selected through mate choice, females possibly favor males that exhibit a specific component of the display, for example, display rate. In that case, female choice for display rate would drive selection for small male size and mass, as these may be crucial for aerial agility. Smaller size may increase acrobatic agility, particularly with regard to a smaller turning radius (McLachlan and Cant 1995; Blomqvist et al. 1997). As a by-product of mate choice, lighter and more agile males may be more capable of maintaining a higher frequency of aggressive acts and aerial chases in intrasexual agonistic encounters. In support of this explanation, we observed 199 aerial chases in our experiment, all of which were initiated by the winner. This positive feedback mechanism, which involves intersexual and intrasexual selection, should favor more agile males over heavier, less nimble ones.

Alternatively, our results may be explained through evolutionary game theory. It may be advantageous for a much stronger opponent to give way to a weaker one when small individuals have more to gain and less to lose than adversaries

with greater RHP (Hammerstein 1981). Our results indicated that the amount of aggression that a loser used against his opponent is inversely related to his own weight. Thus, lighter losers are more aggressive toward winners than are heavier losers. This pattern is also informative when considering the negative relation between body condition and dominance ranking. It is possible to infer that, aside from benefits conferred due to small size, heavier males do not engage in severe contests. Heavier males are probably more satiated, or have higher energy reserves than lighter males; thus they may have a lower motivation to fight when compared with nimbler, hungrier individuals. Possibly, the value of the resource is much lower for a heavier individual than for a lighter one when both are competitors for a food resource after a period of food deprivation (see Hammerstein 1981).

Our results further support this hypothesis by demonstrating that winners are more aggressive than losers in order to gain access to the feeding station. Winners use an amount of aggression that is sufficient to determine dominance and from this point on do not escalate any further, because this is not necessary to maintain feeding access. On the other hand, the amount of feeding access gained by losers is strictly related to their aggressiveness, which demonstrates the reluctance of winners to give up such a valuable resource. The aggression exhibited by losers, in turn, is strongly linked to their own body weight (resource necessity) and the amount of nuptial plumage shown by their opponent.

With the exception of the body-condition index, all other traits measured were uncorrelated with winning agonistic encounters. The absence of a status badge may explain the high levels of aggression observed: Winner blue-black grassquits were on average 5 times more aggressive than losers. Asymmetries in quality between competitors may affect aggression levels, such that when degree of asymmetry in quality decreases, there is an increase in the intensity of aggression (Riechert 1998). Our results are consistent with this concept in terms of plumage ornamentation. In our experiment, the degree of asymmetry among individuals in blue-black plumage coverage was small, because all of the males had at least 67% nuptial plumage coverage. Thus, it is possible that males had to use higher rates of aggression to establish dominance than would have been observed if opponents had a higher degree of asymmetry in this trait. For example, a study of blue tits showed that males became less aggressive toward other males when the latter had their UV reflectance experimentally reduced, thus increasing the degree of plumage asymmetry between them (Alonso-Alvarez et al. 2004).

Although none of the ornamental traits predicted dominance, winners sustained more aggression from their opponents when they exhibited a higher amount of nuptial plumage. This pattern suggests that darker adversaries are perceived as a greater threat. Recent studies have revealed that structural plumage may be used by females in mate choice

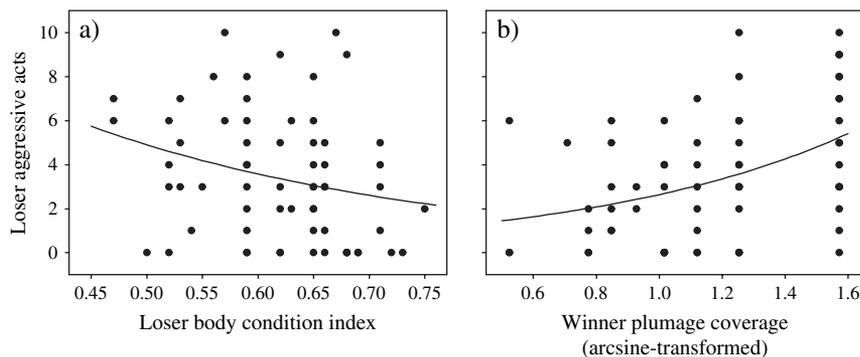


Figure 3
(a) Negative effect of loser body weight on its own number of aggressive acts during experimental trials. (b) Positive effect of the amount of blue-black plumage of winner blue-black grassquits on the amount of aggressive acts exhibited by losers during experimental trials.

Table 2
Analysis of deviance table for the significant predictors in the GLMM of the amount of aggression brandished by losers

Model	Terms	Estimate (SE)	Change in df	Change in deviance	<i>P</i>
Loser aggression ~ loser weight + winner plumage	Intercept	1.99 (1.19)			
	-Loser weight	-3.69 (1.87)	1	4.34	0.037
	-Winner plumage ^a	1.17 (0.36)	1	12.43	<0.001

GLMMs fit by Laplace approximation, considering winner and loser identities as crossed random effects. Random effects variance: winner 0.039 ± 0.049 ; loser 0.095 ± 0.073 ; variance inflation factor ($\hat{\rho}$) of final model: 1.57.

^a Arcsin(x) transformed.

(Korsten et al. 2007; Vedder et al. 2008). For a male grassquit, another male with more blue-black plumage coverage may be seen as a possible threat in terms of loss of paternity; possibly, this signal influences intrasexual dispute for other kinds of resources. In a field experiment conducted with lark buntings (*Calamospiza melanocorys*), resident males presented with model males that varied in plumage coloration were more reluctant to approach darker models, but when doing so reacted more aggressively than when approaching duller ones (Chaine and Lyon 2008). Therefore, even when plumage acts as a badge of status used to avoid confrontation, it may also provide information about the response needed to challenge a dominant intruder. This may result in an escalation of aggressiveness to evict an opponent that poses a clear threat for loss of paternity or resource access. In our experimental procedure, where there was little opportunity for avoiding conflict, an increase in aggression by subordinates under the threat posed by ornamented males may have led directly to such escalation.

To conclude, we have shown that male blue-black grassquits use overt aggression to settle dyadic encounters over a food resource in the context of relatively symmetric plumage characteristics. We have also shown that contrary to the established paradigm of the larger body size advantage, being lighter may confer advantages in species where males execute aerial displays. Small size may be valuable not only in the execution of the display itself, but also because it appears to provide greater agility in competitions where aerial chases play a significant role. Thus, small size may grant a competitive edge in physical encounters and also result in higher hierarchical status in birds that execute aerial displays. Also, the value of the resource may not be as important to heavier males, so that it is not beneficial for these males to risk being injured in aggressive disputes. Alternatively, the resource is valuable to lighter individuals, which was demonstrated by their extreme aggressiveness. The male's body weight affected motivation to fight over the resource, so that lighter losers were more aggressive in order to increase their access to the feeding station. Finally, we have shown a social cost associated with the nuptial plumage of males. Individuals are more aggressive toward opponents that exhibit more nuptial plumage coverage, likely perceiving them as potential extrapair threats.

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