

# Conspicuous sexual signals in a socially monogamous passerine: the case of neotropical Blue-black Grassquits

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**Abstract** Sexual selection has shaped many traits involving communication, behavior, morphology, and reproductive strategies. Sexual communication in the Blue-black Grassquit *Volatinia jacarina* involves an iridescent, nuptial plumage and the exhibition of a complex motor and acoustic mating display. Blue-black Grassquits breed in small, aggregated territories, are socially monogamous, but have high rates of extrapair fertilization and intensive paternal care. Here, we discuss the evolution of sexually selected ornaments in this species and review some studies that have evaluated their costs and benefits. Our data suggest that females have an active role in obtaining extrapair fertilizations, but appear to be indiscriminate in their choice of extrapair males. However, it remains necessary to evaluate female choice in natural circumstances, and the effects of such on male reproductive success. This is particularly important because, in the field, we found that the male motor display may provide a useful cue for nest predators, and therefore evolution of female choice may be constrained by the probability of higher nest predation associated with choosing males exhibiting high display rates. Our studies also indicate that small males have an advantage in aggressive interactions with larger males. We hypothesize that small male size may be driven by female choice for male motor performance, including aspects of

display agility and acrobatic capacity, leading to better performance by small males in intrasexual interactions involving flight within confined spaces. Alternatively, the food resource may be more valuable to smaller males, resulting in higher aggression to access the food.

**Keywords** Display · Mating system · Neotropical birds · Ornaments · Plumage · Sexual selection

## Introduction: the challenges of interpreting male sexual ornamentation

One of the major challenges in evolutionary ecology and behavior is to understand the selective forces that have shaped the development of complex and costly morphological traits and courtship behaviors in animals. The theory of sexual selection, originally crafted by Darwin (1871), suggests that the evolution of elaborate traits depends upon the existence of variance in male mating success (Arnold 1994), and is based upon the advantages to females of choosing males that differ in value. Female preferences may be based upon male attributes indicating a capacity to supply females or offspring with material benefits, such as food, and other paternal care, such as protection. In other words, elaborate male traits may serve as indicators of males of high parental quality (Heywood 1989; Hoelzer 1989). Another much debated explanation for females favoring elaborate sexual signals is that these potentially costly traits signal high general fitness, that is, they indicate good genes. According to this scenario, only genetically superior males are capable of developing robust and elaborate sexual traits. An explicit prediction of this idea is that offspring of males with the preferred phenotype should be genetically superior to offspring of the non-

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preferred male phenotype. Thus, females that mate with highly ornamented males should increase their own fitness by producing offspring that would inherit the father's superior genome. Many versions of these early indicator models have been developed, including Fisher's runaway selection, the handicap principle, parasite-mediated sexual selection, and the good genes model (Fisher 1915; Williams 1966; Trivers 1972; Zahavi 1975; Hamilton and Zuk 1982).

Males in polygynous species typically exhibit great disparities in mating success, and usually possess elaborate secondary sexual characters. However, many socially monogamous species also exhibit exaggerated male ornamentation and costly sexual courtship signals. This latter evidence suggests that male variance in mating success also occurs in species where the prevailing mating system is social monogamy, but in these cases, less is known about the evolutionary pathways that result in the development of ornamental traits. One likely explanation is that variance in male mating success in monogamous species is achieved through extrapair copulations (Webster et al. 1995).

Despite the intense interest generated by decades of research on sexual selection, and the many relevant empirical findings in this area, our interpretations of the selective mechanisms leading to the evolution of ornaments and behavioral displays remain limited (reviewed in Andersson 1994). A substantial part of the problem rests upon two issues. First, there is the conceptual difficulty of defining male quality and attractiveness to females. A second issue is the actual quantification of male attractiveness using phenotypic traits.

Determining the exact nature of male quality is complex. Typically, researchers evaluate phenotypic traits that are assumed to be accurate indicators of male genetic quality or parental value. Measuring male quality directly is very complicated, not only because it involves impossibly difficult, long-term studies assessing total number of offspring and grand-offspring produced as well as their viability (total fitness), but most importantly, because the best male genotype in one environment is not necessarily equivalent to the best genotype across all environments (Hunt et al. 2004). Thus, to examine the value of specific ornaments and sexual displays, for comparative purposes it would be important to consider the genetic benefits of these traits for males that vary in their expression, breeding in the same and in different environments. By the same token, to evaluate the pressures that may lead to the evolution of a preferred male phenotype, variation in female choosiness should also be considered, and this is a subject for which there are still relatively little data. The strength of female choice in a particular environment may depend on factors that have been given scant attention. Female choice may vary not only due to the environment itself but also because

choice could be influenced by female age, previous experience, exposure to males, genetic quality, and condition, among other factors (Qvarnström 2001; Burley and Foster 2006; Cotton et al. 2006).

A second problem in considering mechanisms involved in the evolution of male ornaments arises when we consider that many behavioral displays are multicomponent and often present tradeoffs between the different traits, complicating their quantification. Traditionally, studies have focused upon male attributes and ornaments, and their variability among males, but have paid little attention to dynamic mating displays, despite the latter's ubiquity across animal taxa (Byers et al. 2010). Current data have shown that females clearly use male displays as a criterion for choice. For instance, a recent study of Golden-collared Manakins (*Manacus vitellinus*), a piprid species with elaborate and acrobatic displays, showed that females preferred males that exhibited certain display moves at greater speed, sometimes involving differences of only fractions of milliseconds (Barske et al. 2011). Furthermore, variability in display behavior may arise due to dynamic adjustments in response to fluctuating conditions, including habitat variability and physiological or social conditions being experienced by the male (Parker 1974; Payne and Pagel 1996, 1997). Only a few studies have addressed the fitness impact of male flexibility in display behavior (Patricelli et al. 2006), or how males adjust their courtship traits in multicomponent displays, based upon the associated tradeoff costs (Patricelli and Krakauer 2010).

Thus, empirical approaches that seek to understand the evolution of sexual signaling need to consider not only the relationship between male sexual traits and offspring fitness in changing environments but also the occurrence of tradeoffs between traits in multicomponent displays and male behavioral plasticity in displaying. Although it is well known that female preferences for specific phenotypes in sexual ornaments and vocal displays generate variance in male mating success, only a handful of studies have successfully established an association between variation in mating displays and fitness consequences (Gibson and Bradbury 1985; McDonald 1989; Jia et al. 2000; Sheldon 2000; Lawes et al. 2002; Welch 2003; Patricelli and Krakauer 2010). In fact, there is a scarcity of even more fundamental data, such as documentation of variability in conspicuous male traits across different environments for any single species.

### Background scenario and study model

Over 3,000 bird species reside in South America, roughly a third of the world's birds (Ridgely and Tudor 1989). Despite the high diversity of avian species in the

Neotropics, very little is known about their behavioral ecology. This is generally true for tropical birds worldwide. This is regrettable, because tropical birds afford unique opportunities for comparative analyses relative to the much better known avifauna of temperate regions (see Stutchbury and Morton 2001). At present, it remains unclear whether there are genuine differences in life history, ecology, and behavior between tropical and temperate region birds (Martin 2006).

We have addressed many questions tangential to the evolution of sexually selected ornaments by using a model organism, the Blue-black Grassquit *Volatinia jacarina*, during a long-term study involving both a wild population in central Brazil as well as birds kept in captivity. This small passerine has a broad geographic range, extending from Mexico to most of South America (Sick 2001). Blue-black Grassquits migrate into central Brazil, where our field site is located within a farm owned by the University of Brasilia (Fazenda Água Limpa: 15°56'S, 47°56'W), in early November with the beginning of the rainy season. During the non-breeding season, males and females are not easily distinguishable, although males have larger wings and tails but weigh less than females (Carvalho et al. 2007). The sexes become very distinct during the breeding season, when males acquire a nuptial blue-black, iridescent plumage and exhibit a multimodal display composed of vertical leaps ( $25 \pm 9$  cm; Costa and Macedo 2005) from elevated perches, powered by wing beating, in conjunction with a buzzing vocalization. Early natural history descriptions indicated that both sexes cared for the young, and suggested that the species was territorial and monogamous (Alderton 1963). However, later observations of the complex multimodal display behavior and aggregated, small territories also led to speculations that the Blue-black Grassquit could be a lekking species with polygamous mating behavior (Murray 1982; Webber 1985). Recent studies have confirmed that the species has biparental care and is socially monogamous (Almeida and Macedo 2001; Carvalho et al. 2006), and that males defend very small and clustered territories ( $13\text{--}72$  m<sup>2</sup>; Almeida and Macedo 2001). Despite the socially monogamous breeding system, genetic analyses of a small sample of 11 nests revealed an exceptionally high incidence of extrapair fertilizations (63% of broods and 50% of chicks; Carvalho et al. 2006). Nests are small (about 7.5 cm) and placed at heights from 10 to 50 cm above ground in shrubs and grasses, clutch size ranges from 2 to 3 eggs, and the incubation period is 10–11 days (Almeida and Macedo 2001). Like most ground-nesting tropical passerines, predation is extremely high in comparison to temperate regions (Söderström 1999), and in our study site, predation typically averages around 80% of nests.

## Ornamentation and behavioral display in male Blue-black Grassquits

Male Blue-black Grassquits molt into a nuptial plumage prior to or early in the breeding season in central Brazil. This black, iridescent plumage contrasts sharply with the inconspicuous plumage of females, juveniles and non-breeding males. The ornamental plumage also includes patches that are evident only during the male display, which reveals the white undersides of both wings during repeated vertical flights from exposed perches. The iridescent plumage color of males results from a thin keratin layer over a single layer of melanin granules; the thickness of the keratin layer and the number of melanine granules and their optical properties determine the resulting color (Maia et al. 2009).

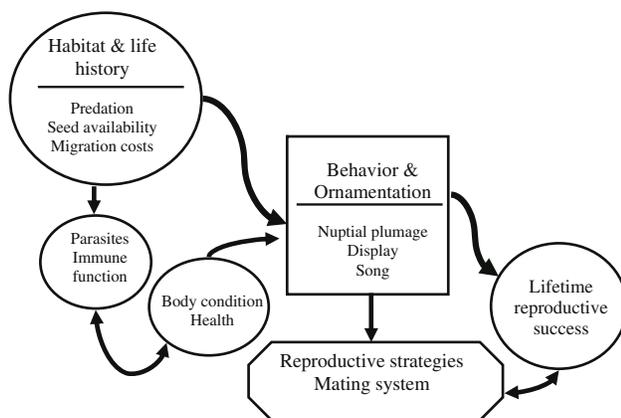
The sexual motor display is very complex and appears to be energetically costly. As mentioned previously, the display consists of leaps powered by several wing flaps, but during this short flight, the male performs a body rotation around the vertical axis, tilting the head down at the highest point of the flight, and on landing, emits a buzzing vocalization. Display leap rates vary from 1.8 to as many as 12.3/min (Almeida and Macedo 2001) and there is high variability among males both in height as well as in frequency of the display (Costa and Macedo 2005). Both density of males as well as height of available perches appear to influence display characteristics: high-density areas lead to increased display frequency (but not height; Costa and Macedo 2005), while display height is inversely related to perch height (Costa and Macedo 2005; Carvalho et al. 2006). These results from past studies suggest that the motor display not only may be costly but also that there are trade-offs between the components of the display, and that males are behaviorally flexible, adjusting components of the display such as rate and height of the leaps according to social or physical parameters of the environment.

## The costs of ornamentation

The Blue-black Grassquit display is clearly important for attracting mates and breeding, since territorial males with higher display flights and rates are more successful in obtaining mates (Carvalho et al. 2006). The display may also play an important role during male–male interactions, though this possibility has not been evaluated. Understanding the tradeoffs that may be involved in the production of the nuptial plumage and display in this species relies upon an assessment of possible costs in developing and exhibiting these attributes, as well as the benefits in mate attraction and competition with other males.

The Blue-black Grassquit ornaments we have described above are necessarily conspicuous, otherwise they would not be useful in transmitting any intended information, whether about male quality or simply as signals of male attractivity. However, the vulnerability of males to both predators and parasites relative to the production and exhibition of these ornaments is possibly the key element that determines their relevance in transmitting information to both females and competitors. Thus, we should expect that males would attempt to optimize performance and conspicuousness while simultaneously decreasing vulnerability whenever possible.

Although we have addressed several questions relative to the behavior and ornamentation of the Blue-black Grassquit, our overall goal in this ongoing study is to understand how habitat and life history, which include selective pressures such as predation, resource availability and migration costs, may have influenced the evolution of this species' mating system (Fig. 1). Other factors to consider include the cost of parasites and the state of the immune system, both of which can severely affect health and body condition, and thus the development and expression of behavior and ornamentation. We expect that the combination and variation of these characters should vary latitudinally, because selective pressures depend to a large extent upon conditions that vary geographically. Variations in such conditions can include climate, photoperiod, duration of the breeding season, population density, and abundance of resources and predators, among many other possibilities. These divergent



**Fig. 1** Diagram of hypothesized associations among factors that affect the breeding profile of birds. Life history factors (e.g., predation risk, resources, migration cost) can have either a positive or negative impact upon the individual's immune function and capacity for resisting parasites, affecting the individual's health. In turn, this leads to differences in the levels of investment in reproductive traits such as display behavior, nuptial plumage, and song. Ultimately, these factors may determine variance in reproductive success among males and constitute the primary mechanism for the evolution of different mating systems

selective pressures probably have resulted in differences in display behavior, ornamentation and mating strategies for different populations.

We have addressed the issue of information content and costs of the nuptial plumage and sexual display of males to some extent in a few studies. Below, we briefly describe some of the possible costs and tradeoffs associated with the Blue-black Grassquit male ornamentation and display, based on some experimental work conducted using the captive population we maintain in the laboratory as well as some observational and experimental work conducted in the field.

### Vulnerability to nest predators

One recent experimental field study produced suggestive evidence that the leaping displays of male Blue-black Grassquits are costly in terms of nest survival (Dias et al. 2010). This study was developed due to suggestions in the literature that several parental and offspring behaviors may attract predators to the nest, including begging by chicks and feeding trips by parents (Skutch 1949; Haskell 1994; Leech and Leonard 1997; Martin et al. 2000). Additionally, there is evidence that male eye-catching sexual secondary traits that attract females and that are important in male-male competition, which include song, colorful plumage, and conspicuous behaviors, also increase predation risk for the male (Slagsvold et al. 1995; Zuk and Kolluru 1998; Møller et al. 2006). However, prior to our recent study, there was no evidence that conspicuous sexual displays and ornaments may result in higher nest predation rates. Because the Blue-black Grassquit male exhibits such a conspicuous motor display that is frequently executed within meters of its nest, we predicted that predators would be able to use this multi-modal display as a cue to find active nests. To test this hypothesis, we used artificial nests baited with quail eggs introduced into displaying Blue-black Grassquit male territories and compared their rate of predation with similar nests placed in comparable vegetation and heights, but which lacked the presence of a displaying male. We found that predation rate was significantly higher when nests were associated with displaying males (Dias et al. 2010). The results of this experiment bring into sharp focus the tradeoffs associated not only with the display itself but also relative to the female dilemma when choosing a mate.

### Vulnerability to parasites

Zahavi (1975, 1977) suggested that conspicuous secondary sexual ornaments are costly to produce and also constitute

a handicap to the male due to increased vulnerability to predators (the handicap principle). Thus, males that absorb such costs and survive despite the handicap imposed by the conspicuous ornamentation would be favored by females to father their offspring. A variation of the handicap principle suggests that parasites may serve as selective agents affecting the overall condition of the male, and thus his ability to invest in secondary sexual ornamentation. Consequently, females could use the male's ornamentation as an indicator of male resistance to parasites. To test this hypothesis, it would be necessary to show that (1) parasites negatively affect male secondary sexual traits, and (2) that females choose parasite-resistant males due specifically to their increased ornamentation.

We evaluated the interactions between parasite load (coccidian parasitism), ornamentation and body condition in wild Blue-black Grassquits in central Brazil (Costa and Macedo 2005). Relative to ornamental traits, we considered the percentage of nuptial plumage coverage and spectral color properties of feathers, and display characteristics. We also assessed body condition using mass and size and two physiological parameters (haematocrit and total plasma protein levels). Results of this study showed that as parasite load increased, males exhibited decreased nuptial plumage coverage and a lower display leaping frequency. Additionally, we found that the coccidian infection was associated with lower mass and size of males. However, we did not find any association between body condition and secondary sexual traits, leading us to conclude that our data supported parasite-mediated but not condition-dependent sexual selection.

These correlation-based results led us to develop a more controlled experimental manipulation to examine the interdependency between coccidian parasitism, body condition, and ornamentation, and assess these factors in the context of female choice (Aguilar et al. 2008). For this experiment, we randomly assigned 45 males and 29 females to one of two groups, healthy or parasitized (control), for a duration of 5 months. Males and females for each treatment were housed separately in an outside aviary. Individuals in the healthy group were treated monthly with a coccidiostatic drug, a vermifuge, and an insecticide talcum to maintain them free of coccidian parasites and ectoparasites. The control group was not treated with any medications. The first question we asked was whether parasitism influenced the expression of ornamentation, including the sexual display, and body condition. The second question we had was whether females might use cues based on male ornamentation, body condition, and/or displays to choose healthy males over parasitized ones.

To measure the impact of coccidian parasites upon male attributes, we assessed parasite loads monthly for all

individuals, as well as body condition parameters, morphological measures, and ornamentation, which included plumage traits as well as specific characteristics of the motor display (see below). To answer whether females favored healthier males, we used 20 fixed male dyads, consisting of a parasitized and a healthy male, and presented these randomly to females during mate-choice trials. A total of 165 mate-choice trials (120 min each) were conducted, 83 using parasitized females and 82 using healthy females. We assessed male display behavior during the mate-choice trials, and parameters measured included persistence of the display, leap height, duration of leaping, and relative leap rate.

During the months of this study, we found that coccidian parasitism remained close to zero for the healthy group but rose steadily for the parasitized group, peaking in the fifth month at a mean intensity of 739.45 (total number of parasites/number of host individuals). Thus, we verified that our experimental manipulation successfully resulted in different intensities of coccidian oocysts between the two groups.

We did not find an effect of coccidian parasites upon the plumage ornamentation attributes we measured (percentage nuptial plumage coverage and patch/wing area). However, our data showed that parasitized males developed a lower body condition (weight/tarsus indices and mass) relative to healthy males, and they also exhibited deficient displays. In fact, all specific display attributes were lower for parasitized males, except for absolute leap rate. It is thus clear that a high infestation of coccidian parasites not only has negative effects upon physical condition but also profoundly decreases the male's vitality during sexual motor displays. However, we did not find that female Blue-black Grassquits, whether healthy or parasitized, preferred the healthy males over the parasitized ones with poor displaying capacity.

### **Intrasexual or intersexual signaling?**

Despite the possible costs that may be associated with producing and maintaining ornaments, the fact that they have evolved strongly suggests the existence of advantages. Determining the exact mechanisms and functions of ornaments within different contexts, however, remains a challenge. Ornaments may have multiple functions, serving as signals of quality and dominance in both inter- as well as intrasexual contexts. We addressed this issue through two recent experiments with captive Blue-black Grassquits.

In the first study, we considered male–male competition to determine how dominance hierarchies develop and how this may be associated with ornamentation, body size, and behavior (Santos et al. 2009). We conducted 65 agonistic

encounters (11 min each) between paired males over a food source, after a 4-h food deprivation period. We filmed interactions and recorded aggressive behaviors. A male was considered the winner of an interaction when he successfully displaced his opponent. A winner–loser matrix was generated based upon the total number of wins per male, and we then calculated individual ranks with David's score (DS) ranking method (David 1987; Gammell et al. 2003; Hemelrijk et al. 2005). We evaluated structural plumage reflectance and nuptial plumage coverage as well as a body condition index (weight/tarsus length). Our results showed that males did not use any aerial displays or vocalizations during the experimental trials, but other aggressive behaviors were exhibited and included ritualized confrontations, chases, displacements, and pecking. Aggression rate was positively associated with access to the feeder and individual aggressiveness was correlated with dominance status. Curiously, the multiple regression model applied to the data indicated that male body condition decreased with dominance ranking. However, none of the structural plumage coloration properties were associated with dominance status. Our expectations were that heavier males would be dominant to lighter ones, but we found instead that lighter birds were dominant and won more disputes over food. There are two interpretations of these results. First, female choice for display rate and acrobatic performance may have driven selection for small male size and mass. Thus, as a by-product of female choice, lighter males may perform better during male–male interactions that involve chases and short flights, especially within confined spaces such as within the arena used in the experiment. A possible better explanation is that there is an asymmetry relative to resource value between individuals: lighter individuals engage in more aggressive behavior and win more encounters because they more urgently need the resource in comparison to heavier individuals. In other words, the value of the resource depends upon the condition of the individual contestant, each of which is willing to invest aggressively in gaining access to the food in proportion to their relative need (see Hammerstein 1981).

In a second study, we addressed the role of plumage ornamentation in the context of mate attraction. With the advent of molecular tools, it has become clear that socially as well as genetically monogamous birds are the exception and not the rule (Griffith et al. 2002). There is also evidence that in many species females actively seek copulations with extrapair males (Smith 1988; Gray 1997), although it remains unclear what may be the advantages or motivations that induce females to do so. In this experiment, we wanted to investigate whether socially paired females used visual cues provided by ornamentation that would induce them to engage in courtship with unfamiliar males (Dias and Macedo, unpublished data). The first step

of the experiment involved pairing males and females for a period of 5 months, monitoring their behavior to determine whether they developed a socially paired status (e.g., mutual preening, displaying by the male, copulations, etc.). We then tested whether females demonstrated an interest for extrapair males and whether such an interest was associated with the quality of this new male's phenotype by separating the female from her social mate and presenting her with unfamiliar males in an adjacent cage. We kept the paired male in a darkened cage where he could see his female interacting with the extrapair male but could not be seen. We then monitored the interest of the female for the extrapair male by recording the amount of time she spent in proximity to the extrapair male's cage as well as the ritualized courtship behaviors she exhibited. After the experimental test, we evaluated the ornamental traits of the extrapair male relative to the social male and also monitored the behavior of the social pair after they were placed back in their home cage. Details and full results of this experiment are still unpublished, but briefly we summarize here one of the more important outcomes of this study. We found that females responded indiscriminately to extrapair males and engaged in courtship behavior whether the unfamiliar male's plumage ornamentation was more or less exuberant in comparison to that of her social pair.

### Conclusions and future research

Our studies to date point to some consolidated conclusions as well as a few paradoxical results that need further investigation. The foremost message based on our results is that females in this species play a crucial role in sexual conflict and appear to determine the stability of the pair-bond, which may greatly depend on whether or not they have opportunities for matings with other males. Females do not appear to be particularly selective relative to the ornamental attributes we measured. This has suggested to us that looking at the ornamental attributes in a more integrated fashion may be very important. It is possible that the complete display, with the males performing the leap coupled with the song (in captivity the song is often lacking), is vitally important for female choice. As suggested by Byers et al. (2010), empirical evidence indicates that male motor performance within mating displays may be crucial to female choice over a wide range of taxa. Alternatively, other aspects of the natural context of male ornamentation and behavior in the field that were not replicated in the laboratory environment, may also weigh heavily. For instance, females that choose particularly active males in terms of their displays may be selecting for traits associated with robust health and possibly, a viable genotype, while at the same time incurring a cost of

increased probability of nest predation, as suggested by the experiment conducted with artificial nests. Thus, we speculate that females socially paired with less actively displaying males may attempt to obtain extrapair copulations from vigorously displaying males, thus combining two sets of desired components in their reproduction: low probability of nest predation (social partner) with good genes from more energetic males (extrapair mate). This possibility remains to be tested in a field context. Our studies also suggest that the established paradigm of large body advantage may not apply to species such as the Blue-black Grassquit, where being lighter may confer a greater ability in the execution of aerial displays.

The Blue-black Grassquit study system provides us with an opportunity to investigate the cost–benefit equation relative to plumage ornamentation and multimodal displays. Several studies are currently in progress to tease apart the tradeoffs of ornamentation, how each component contributes to the overall message being exhibited, and the intended audience for the signal. Lines of investigation include the following. First, integration of the data concerning phenotypic attributes and display behavior of males with the successful siring of offspring within the study population; this would allow us to evaluate ornamental attributes relative to reproductive success in nature, providing some measure of male quality. Second, assessment of the tradeoffs involving displaying behavior, paternal investment, and within-brood and extra-brood paternity. In this case, we will be able to interpret the decision-making and energy investment process of males relative to their own attributes in order to gain the highest reproductive success. Males with more attractive phenotypes possibly invest less in paternal care of their own broods and more in displaying, thereby gaining access to a higher number of extrapair fertilizations. And third, the relationship between social context, testosterone production, and production of plumage ornamentation. In a species with such highly clustered territoriality, the frequent interactions among individuals of both sexes should play a critical role in determining behavior, which, in turn, is highly integrated with the individual's physiology.

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## References

- Aguilar TM, Maia R, Santos EA, Macedo RH (2008) Parasite levels in blue-black grassquits correlate with male displays but not female mate preference. *Behav Ecol* 19:292–301
- Alderton CC (1963) The breeding behavior of the Blue-black Grassquit. *Condor* 65:154–162
- Almeida JB, Macedo RH (2001) Lek-like mating system of the monogamous blue-black grassquit. *Auk* 118:404–411
- Anderson MA (1994) *Sexual selection*. Princeton University Press, Princeton
- Arnold SJ (1994) Bateman's principles and the measurement of sexual selection in plants and animals. *Am Nat* 144(Suppl):S126–S149
- Barske J, Schlinger BA, Wikelski M, Fusani L (2011) Female choice for male motor skills. *Proc R Soc Lond B* 278:3523–3528
- Burley NT, Foster VS (2006) Variation in female choice of mates: condition influences selectivity. *Anim Behav* 72:713–719
- Byers J, Hebets E, Podos J (2010) Female mate choice based upon male motor performance. *Anim Behav* 79:771–778
- Carvalho CBV, Macedo RH, Graves JA (2006) Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior, and morphology. *Condor* 108:579–590
- Carvalho CBV, Macedo RH, Graves JA (2007) Reproduction of blue-black grassquits in central Brazil. *Braz J Biol* 67:275–281
- Costa FJV, Macedo RH (2005) Coccidian oocyst parasitism in the blue-black grassquit: influence on secondary sex ornaments and body condition. *Anim Behav* 70:1401–1409
- Cotton S, Small J, Pomiankowski A (2006) Sexual selection and condition-dependent mate preferences. *Curr Biol* 16:R755–R765
- Darwin C (1871) *The descent of man, and selection in relation to sex*. John Murray, London
- David HA (1987) Ranking from unbalanced paired-comparison data. *Biometrika* 74:432–436
- Dias RI, Castilho L, Macedo RH (2010) Experimental evidence that sexual displays are costly for nest survival. *Ethology* 116:1011–1019
- Fisher RA (1915) The evolution of sexual preference. *Eugenics Rev* 7:184–192
- Gammell MP, Vries HD, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Anim Behav* 66:601–605
- Gibson RM, Bradbury JW (1985) Sexual selection in lekking sage grouse—phenotypic correlates of male mating success. *Behav Ecol Sociobiol* 18:117–123
- Gray EM (1997) Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations? *Anim Behav* 53:605–623
- Griffith SC, Owens IPF, Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol Ecol* 11:2195–2212
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Hammerstein P (1981) The role of asymmetries in animal contests. *Anim Behav* 29:193–205
- Haskell DG (1994) Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proc R Soc Lond B* 257:161–164
- Heywood JS (1989) Sexual selection by the handicap mechanism. *Evolution* 43:1387–1397

- Hemelrijk CK, Wantia J, Gygas L (2005) The construction of dominance order: comparing performance of five methods using an individual-based model. *Behaviour* 142:1037–1058
- Hoelzer GA (1989) The good parent process of sexual selection. *Anim Behav* 38:1067–1078
- Hunt J, Bussière LF, Jennions MD, Brooks R (2004) What is genetic quality? *Trends Ecol Environ* 19:329–333
- Jia FY, Greenfield MD, Collins RD (2000) Genetic variance of sexually selected traits in waxmoths: maintenance by genotype X environment interaction. *Evolution* 54:953–967
- Lawes M, Slotow R, Andersson S (2002) Male nest building but not display behaviour directly influences mating success in the polygynous Red Bishop, *Euplectes orix*. *Ostrich* 73:87–91
- Leech SM, Leonard ML (1997) Begging and the risk of predation in nestling birds. *Behav Ecol* 6:644–646
- Maia R, Caetano JVO, Bao SN, Macedo RH (2009) Iridescent structural colour production in male blue-black grassquit feather barbules: the role of keratin and melanin. *J R Soc Interface* 6:S203–S211
- Martin TE (2006) Life history evolution in tropical and south temperate birds: what do we really know? *J Avian Biol* 27:263–272
- Martin TE, Scott J, Menge C (2000) Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc R Soc Lond B* 267:2287–2293
- McDonald DB (1989) Correlates of male mating success in a lekking bird with male–male cooperation. *Anim Behav* 37:1007–1022
- Møller AP, Nielsen JT, Garamszegi LZ (2006) Song post exposure, song features, and predation risk. *Behav Ecol* 17:155–163
- Murray BG Jr (1982) Territorial behavior of the blue-black grassquit. *Condor* 84:119
- Parker GA (1974) Courtship persistence and female-guarding as male time investment strategies. *Behaviour* 48:157–183
- Patricelli GL, Krakauer AH (2010) Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. *Behav Ecol* 21:97–106
- Patricelli GL, Coleman SW, Borgia G (2006) Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their display intensity in response to female startling: an experiment with robotic females. *Anim Behav* 71:49–59
- Payne RJH, Pagel M (1996) When is false modesty a false economy? An optimality model of escalating signals. *Proc R Soc Lond B* 263:1545–1550
- Payne RJH, Pagel MD (1997) Why do animals repeat displays? *Anim Behav* 54:109–119
- Qvarnström A (2001) Context-dependent genetic benefits from mate choice. *Tree* 16:5–6
- Ridgely RS, Tudor G (1989) *The Birds of South American*, Vol. I. The Oscines Passerines. Oxford University Press, Oxford
- Santos ESA, Maia R, Macedo RH (2009) Condition-dependent resource value affects male–male competition in the blue-black grassquit. *Behav Ecol* 20:553–559
- Sheldon BC (2000) Environmental dependence of genetic indicator mechanisms. In: Espmark Y, Amundsen T, Rosenqvist G (eds) *Animal signals: signalling and signal design in animal communication*. Tapir Academic Press, Trondheim, pp 195–207
- Sick H (2001) *Ornitologia Brasileira*, 3rd edn. NovaFronteira, Rio de Janeiro
- Skutch AF (1949) Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455
- Slagsvold T, Dale S, Kruszewicz A (1995) Predation favours cryptic coloration in breeding male pied flycatchers. *Anim Behav* 50:1109–1121
- Smith SM (1988) Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour* 107:15–23
- Söderström B (1999) Artificial nest predation rate in tropical and temperate forests: a review of the effects of edge and nest site. *Ecography* 22:455–463
- Stutchbury BJ, Morton ES (2001) *Behavioral ecology of tropical birds*. Academic, San Diego
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man, 1871–1971*. Heinemann, London, pp 136–179
- Webber T (1985) Songs, displays, and other behavior at a courtship gathering of blue-black grassquits. *Condor* 87:543–546
- Webster MS, Pruett-Jones S, Westneat DF, Arnold SJ (1995) Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* 49:1147–1157
- Welch AM (2003) Genetic benefits of a female mating preference in gray tree frogs are context-dependent. *Evolution* 57:883–893
- Williams GC (1966) *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton
- Zahavi A (1975) Mate selection—a selection for a handicap. *J Theor Biol* 53:205–214
- Zahavi A (1977) The cost of honesty (further remarks on the handicap principle). *J Theor Biol* 67:603–605
- Zuk M, Kolluru GR (1998) Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol* 73:415–438