

MATING SYSTEM AND SEXUAL CONFLICT IN THE BLUE-BLACK GRASSQUIT (*Volatinia jacarina*, AVES: EMBERIZIDAE): EXTRA-PAIR MATING BEHAVIOR SETS THE SCENE

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ABSTRACT

Here we review several field and laboratory studies with the blue-black grassquit (*Volatinia jacarina*) to show how different aspects of its mating system are inter-related. We discuss previous studies on the negative effects of parasitism upon secondary sexual characters of grassquits and the lack of female choice for healthier males. We also review what is known about the mating patterns of this species and discuss the elevated rates of extra-pair paternity obtained in laboratory experiments with the reactions of males and females towards extra-pair males. From basic breeding biology to complex social and genetic interactions, the present review illustrates how the study of a single species allows for a broader interpretation of many hypotheses and assumptions that are seldom considered with Neotropical birds.

Keywords: Blue-black grassquit, extrapair paternity, mating system, sexual selection, *Volatinia jacarina*.

RESUMO

SISTEMA DE ACASALAMENTO E CONFLITO SEXUAL NO TIZIU (*Volatinia jacarina*, AVES: EMBERIZIDAE): COMPORTAMENTO DE CÓPULA EXTRA-PAR DETERMINA O CENÁRIO.

Aqui revisamos vários estudos sobre o tiziu (*Volatinia jacarina*), usando tanto dados de campo quando obtidos em manipulações experimentais no laboratório, para mostrar diferentes aspectos inter-relacionados do sistema de acasalamento. Discutimos estudos prévios que mostram o efeito negativo do parasitismo sobre caracteres sexuais secundários dos tizius e a falta de escolha das fêmeas por machos mais saudáveis. Também revisamos o que se sabe sobre os padrões de acasalamento da espécie, e discutimos as altas taxas de paternidade extra-par à luz de resultados obtidos em manipulações experimentais em laboratório, nas quais observamos as reações de machos e fêmeas à presença de machos extra-par. Da biologia reprodutiva básica às características fenotípicas e interações complexas sociais e genéticas, essa revisão ilustra como o estudo de uma só espécie permite interpretações abrangentes sobre muitas hipóteses e premissas que têm sido raramente avaliadas para aves Neotropicais.

Palavras-chave: Paternidade extra-par, seleção sexual, sistema de acasalamento, tiziu, *Volatinia jacarina*.

RESUMEN

SISTEMAS DE APAREAMIENTO Y CONFLICTO SEXUAL EN EL SEMILLERITO NEGRO AZULADO (*Volatinia jacarina*, AVES: EMBERIZIDAE): LOS APAREAMIENTOS EXTRAMARITALES DESCRIBEN EL ESCENARIO. Revisamos varios estudios sobre el semillero negro azulado (*Volatinia jacarina*), usando información obtenida en el campo y bajo condiciones experimentales de laboratorio, para mostrar cómo están relacionados los diferentes aspectos de los sistemas de apareamiento.

Discutimos los estudios previos que muestran los efectos negativos del parasitismo sobre los caracteres sexuales secundarios del semillero y la no escogencia de machos saludables por parte de la hembra. También revisamos lo que se conoce sobre los patrones de apareamiento de esta especie y discutimos sobre la alta tasa de paternidad extramarital en relación a los resultados obtenidos en manipulaciones experimentales de laboratorio, en donde se evaluó la reacción de machos y hembras ante la posibilidad de relacionarse con un macho extramarital. Esta revisión ilustra, desde la biología reproductiva básica y las características fenotípicas hasta las interacciones

complejas sociales y genéticas, como el estudio de una única especie permite vastas interpretaciones respecto a muchas hipótesis y supuestos que han sido raramente evaluadas en las aves tropicales.

Palabras clave: semillerito negro azulado, paternidad extramarital, sistemas de apareamiento, selección sexual, *Volatinia jacarina*.

INTRODUCTION

Avian mating systems can be classified based on variations along two axes, the first axis measuring the number of “social partners” and the second indicating the number of “sexual partners” (Bennett & Owens 2002). In the case of monogamy, the traditional definition focuses on the pair bond, illustrated by biparental care and cooperation during nesting and/or in territory defense. This definition changed greatly with the advent of molecular techniques (reviewed in Griffith *et al.* 2002), and the concept of monogamy is currently partitioned into two components: social and genetic monogamy. While social monogamy is frequent among passerines, genetic monogamy is uncommon, occurring in only 14% of the species examined to date (Griffith *et al.* 2002). Social monogamy is represented by pair bonding during the breeding season, while genetic monogamy is characterized by the absence of extra-pair paternity (EPP), but not necessarily by the absence of extra-pair copulations (EPC; Gowaty 1985). Consequently, the concept of monogamy has been redefined and is considered today to be a complex interaction of conflicting interests between paired males and females (Westneat & Stewart 2003). This new model has generated various interpretations concerning the influence of sexual selection in socially monogamous species, which was traditionally thought to be low, as reproductive success was assumed to be relatively invariable.

Available information on EPP patterns is chiefly derived from studies conducted in temperate regions (Stutchbury & Morton 2001), and yet extra-pair mating is considered to be relatively uncommon in socially monogamous tropical birds (Stutchbury & Morton 2001). Unfortunately, ongoing discussions about the topic are still based on few empirical studies that were not conducted with a broad array of species, thus not representing the vast diversity of life histories and habitat types present in the tropics. Thus, current assumptions about the breeding biology of tropical species are weak (Macedo *et al.* 2008).

In this paper we present a review of the available empirical data on the breeding biology of the socially monogamous blue-black grassquit (*Volatinia jacarina*) in an attempt to contribute to the body of knowledge concerning sexual selection in socially monogamous tropical bird species. We describe the following aspects of this bird’s mating system: 1) the social role of display behaviors and plumage color, and the effects of parasitism upon these; 2) the occurrence of extra-pair courtship behaviors and their implications for sexual selection; 3) behaviors associated with extra-pair mate choice and breeding synchrony; and 4) male-male competition.

THE BLUE-BLACK GRASSQUIT

Blue-black grassquits are Neotropical passerines that occur from southern Mexico to northern Argentina and Chile (Sick 2001). In early November grassquits migrate from the Amazon region to the central region of Brazil, where we conduct our field studies. They exhibit sexual dimorphism: males have larger wings and tails, while females are heavier (Carvalho *et al.* 2007). During the breeding season males acquire a glossy, blue-black nuptial plumage and also start displaying complex vertical flights (25 ± 9 cm; Costa & Macedo 2005) from elevated perches while emitting a buzzing vocalization. The sexual dimorphism of size and plumage may result from sexual selection, as may the elaborate display behavior, since male birds, especially in polygynous species, show a high degree of variance in individual reproductive success (Payne 1979).

The species was considered to be territorial and monogamous, based on observations of parental care by birds of both sexes (Alderton 1963). Later, Murray (1982) reported observations of the vocal and aerial displays of clustered males in Costa Rica that resembled a display arena, typical of lekking behavior suggestive of polygamy. Webber (1985) reported similar observations resembling leks in Mexico, and suggested that this species presents a combination of characteristics, like the presence of a roost with

courtship arena and, possibly, of individual territories. Recent studies confirmed that males provide resources in the form of parental care and nesting sites, and that only one female nests in each male territory, validating the proposal that the blue-black grassquit is socially monogamous (Almeida & Macedo 2001, Carvalho *et al.* 2006). The resemblance to leks results from the extremely small sizes of the clustered territories (13-72m²; Almeida & Macedo 2001) and the aggregated displaying style of the males.

Males that successfully nest do not differ morphologically from those maintaining territories (but that are unable to attract mates). Additionally, the territories of both types of males do not differ in size, composition, or structural vegetation (Almeida & Macedo 2001, Carvalho *et al.* 2006). There seems to be no relationship between the rates of male display and territory characteristics (i.e. size, vegetation structure; Almeida & Macedo 2001), suggesting that females do not rely on territory characteristics when choosing a partner. This way, sexual selection could be based primarily on the complex display behaviors and plumage colors of males, or even on subtle morphological differences.

Nests are small and inconspicuous, with an approximate diameter of 7.5cm and placed 10-50cm above ground on grasses or shrubs (Almeida & Macedo 2001). Typical clutch size is two eggs, laid 24h apart, and with an incubation period of 10-11 days. Egg and nestling predation are high: 14.2% and 12.9%, respectively (Carvalho *et al.* 2007).

ORNAMENTS: BEHAVIORAL DISPLAY AND PLUMAGE

The display behavior of blue-black grassquits can be energetically costly, and therefore likely serve as a reliable indicator of male quality to females choosing mates. Average display rates among males can range from 1.8 to 12.3 displays/min, and this rate varies significantly among individuals in frequency and flight height (Almeida & Macedo 2001, Costa & Macedo 2005). Males in high-density areas execute displays more frequently, but perform lower flights (Costa & Macedo 2005). Flight height is inversely proportional to perch height (Costa & Macedo 2005, Carvalho *et al.* 2006), suggesting that the conspicuousness of a displaying bird depends on the

interplay between perch and flight heights, and that birds with more elevated perches available within their territories would be able to reduce the energetic costs of displaying. A comparison between territorial males revealed that those able to obtain mates had executed significantly higher display flights and had displayed at higher rates than males that failed to reproduce (Carvalho *et al.* 2006). During incubation and nestling periods, nesting males reduced the frequency of displays, but did not cease displaying entirely (Carvalho *et al.* 2007).

The 'handicap principle' suggests that males that produce more exaggerated and costly ornaments signal to females their greater viability and quality as potential mates (Zahavi 1975, 1977). A variation of this principle hypothesizes that parasites can reduce the exuberance of sexually selected ornaments, and females that choose males due to their brighter plumage or more elaborate displays are selecting more parasite-resistant individuals (Hamilton & Zuk 1982). A logical extension of this hypothesis would be that parasite infestations should dull plumage in males and thus affect display ornamentation. We found some support for this hypothesis in a study of the effect of parasites upon blue-black grassquits (Costa & Macedo 2005). Oocyst count had a negative impact upon blue-black plumage coverage, and there was a marginally significant effect of oocysts on the intensity of reflectance of feathers in the breast region. A negative effect upon behavior was also found, and higher counts of oocysts were associated with reduced frequency in display flights.

PARASITE INFLUENCE ON MALE TRAITS AND FEMALE MATE CHOICE

A recent study with the grassquits tested Hamilton and Zuk's (1982) hypothesis by investigating whether parasitism affected male displays and morphology. The study tested whether the effects of parasitism on males would be used by females as cues for choosing mates, and also whether the effects of parasitism on females could lead to different patterns of choice (Aguilar *et al.* 2008). The study -- which was conducted in captivity -- used two groups of birds: birds presenting acute coccidian parasitism and unparasitised birds. The results revealed that the parasites had negative effects on the body condition and behavior of the male birds,

with adverse consequences on male display, leading to less persistence and lower display rates. The results partially corroborate the Hamilton and Zuk hypothesis (1982), showing differences in morphology and behavior between males of the infected and non-infected groups. However, despite these effects, females (both parasitized and non-parasitized) showed no preference for healthy males, suggesting female preferences are not influenced by the level of parasitism (Aguilar *et al.* 2008).

EXTRA-PAIR PATERNITY

Another study with grassquits tested the assumption that tropical birds that breed synchronously have higher rates of EPP than birds that breed asynchronously (Carvalho *et al.* 2006). Parentage of offspring was determined by comparing genotypes using six microsatellite loci (Marshall *et al.* 1998). Each paired couple was evaluated during a single breeding season (the study was conducted over two breeding seasons), and social mates were defined as pairs that attended one nest within their territory, thus each male had only one social mate. Potential parents were assigned with a success rate of 100% with a relaxed confidence level (80%) and 79% using a rigorous confidence level (95%). For 20 chicks from 11 nests, the results indicated that 10 chicks (50%) from seven nests (64%) were genetically

unrelated to one or both of the social parents. In seven cases the chicks could not be assigned to the male attending the nest. In two cases the social mother was genetically unrelated to the chick, and in one case both social parents were unrelated to the chick. Despite the reduced sample size, this exceptionally high rate of EPP may contribute significantly to sexual selection.

Using data from the original study, we generated Bateman gradients to describe the extent of sexual selection (Arnold 1994, Mills *et al.* 2007) by regressing male reproductive success on the number of mates. The actual number of young sired by different males was quite variable (Figure 1), ranging from one individual that produced no genetic offspring to one male that produced four offspring. In contrast, the range of values for the number of social young in nests was more restricted, and all males cared for at least one social offspring in their nests.

The intensity of sexual selection acting on the males is shown by the least-squares regression of reproductive success (number of offspring) on mating success, one of the components of Bateman's principles (Figure 2). This significantly positive Bateman gradient ($y = 0.87x - 0.21$; $R^2 = 0.57$, $n = 10$, $P = 0.01$) indicates that the variance in mating success strongly predicts variance in fitness, and points toward an intense effect of sexual selection in this species.

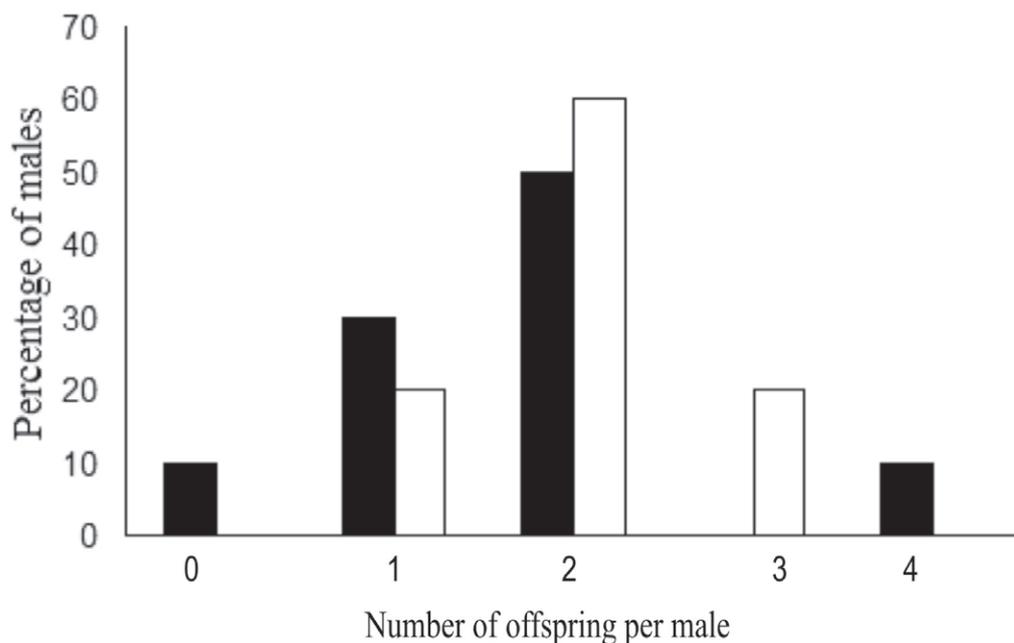


Figure 1. The distribution of social reproductive success (white bars) and actual offspring (full bars) sired by breeding males ($n = 10$ males).

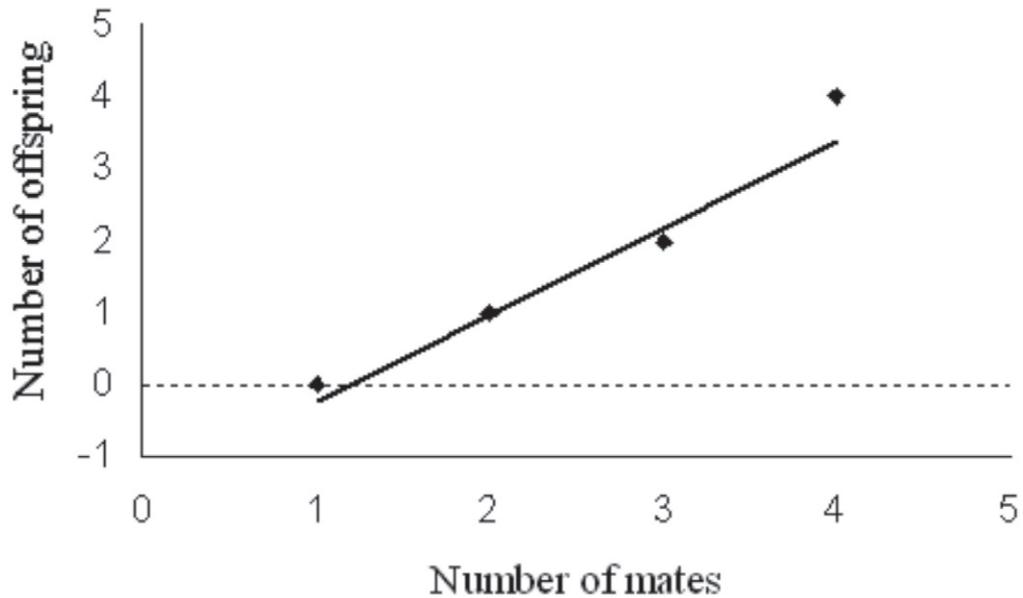


Figure 2. The relationship between number of mates and number of offspring sired ($F_{1,8} = 128.1$, $P < 0.001$; $N = 10$ males).

SEARCH FOR EXTRA-PAIR COPULATIONS – CHOICE AND PERCEPTION

Despite relatively good data on the levels of EPP among species, little is known about whether extra-pair mating is driven by males or females (Eliassen & Kokko 2008). Several hypotheses have been proposed to explain possible adaptive advantages for females to engage in EPC, however, contrary to obvious benefits gained by males that engage in EPC, the suggested benefits gained by females through EPC remain controversial.

A recent study conducted in captivity revealed that female grassquits are not particularly choosy when engaging in extra-pair courtship (Dias *et al.*, in prep.). For this study, socially paired females had the opportunity to interact with extra-pair males without the presence of their social mates. Although the social mate was positioned out of the female's field of vision, he could observe his mate interacting with an extra-pair male. The results showed that social males did not respond to the possibility of being cuckolded, either behaviorally or physiologically. On the other hand, females were not selective with respect to phenotypic characteristics of the extra-pair males or even to the level of attractiveness of their social partner. These results may partly explain the high levels of EPP found for this species, given that there appear to be few costs associated with female

extra-pair copulatory behavior, and both males and females may benefit from the high rates of EPP in the population.

BREEDING SYNCHRONY

The indirect genetic benefits hypothesis (reviewed by Jennions & Petrie 2000) suggests that females seek extra-pair copulations with males of higher quality to increase the genetic benefits to their offspring. Based upon this assumption, the breeding synchrony hypothesis predicts that females will have a better opportunity to compare males and carry out EPC in synchronously breeding populations where several males will be displaying simultaneously (Stutchbury & Morton 1995). A latitudinal trend in breeding synchrony has been recorded for some tropical and temperate species (Moore *et al.* 1999) and through meta-analyses of data in the literature, but has also been challenged in several cases (Verboven & Mateman 1997, Weatherhead 1997, Weatherhead & Yezerinac 1998).

It has been suggested that blue-black grassquits may have high breeding synchrony due to their intracontinental migratory pattern and dependence on ephemeral grain resources for feeding, which could explain the high EPP and lek-like aggregations (Carvalho *et al.* 2006), though this relationship has not been quantified. To evaluate this possibility, we

determined the breeding synchrony of two populations breeding from Oct. 2005 to March 2006, located 25km apart in central Brazil. We predicted that these nearby populations, breeding within the same season, should exhibit similar breeding synchrony measures. One population was located in a native savanna fragment within an urban matrix (“Urban”) near the University of Brasilia campus; the second population (“Rural”) was located in a more rural setting of native savanna within an orchard. Female breeding synchrony was calculated using Kempnaers’ (1993) breeding synchrony index (SI) by considering the fertile period from five days before the laying of the first egg until the day prior to laying the last egg. We estimated the fertile period in nests found with eggs by backdating from the hatching date. Nest predation was considered when all eggs disappeared and the nest was damaged.

The synchrony indices of the two populations were strikingly different (Table I). At both sites the birds arrived during the first week of November, but subsequent breeding events progressed differently in each population. Male displays started almost one month later in the Rural population, although active nests were found only one week later at this site compared to the Urban site. Predation rate was much higher in the Rural site, and female breeding synchrony in this area was almost twice that exhibited by the Urban population. This suggests that female fertile periods in this species may be influenced by very localized ecological and/or social pressures that differ widely even across very short distances.

In the Rural population, ecological constraints, such as indicators of food abundance and/or availability, may have prevented early breeding. The reproductive period of both populations ended at roughly the same time, and this may be regulated by physiological factors associated with migration. One possible explanation leading to the variance in breeding synchrony between these two populations

is the observed difference in rates of nest predation (Westneat 1992). The Urban population experienced a much lower predation rate (40%) compared to the Rural population (67%). In areas of high predation it may benefit females to breed more synchronously, thus diluting individual predation chances (Turner & Pitcher 1986).

Another interesting interpretation of these data concerns the overall low SI for these populations relative to what is expected given the high rate of EPP reported for this species and according to the predictions of the breeding synchrony hypothesis. The SI for the Rural population (27.9%) is one of the highest reported for a tropical monogamous species to date (Table II). However, it is still very low compared to monogamous temperate birds with similar EPP rates.

The breeding synchrony hypothesis suggests that the number of displaying males and their display efforts are modulated by fertile female availability. Although this may happen, we suggest three scenarios where there is no *a priori* reason for this assumption, all of which may apply to the blue-black grassquit mating system.

First, females may choose extra-pair mates based upon phenotypic characteristics not temporally restricted to their fertile period, such as social status (Otter *et al.* 1998), or traits related to intra-sexual competition (Berglund *et al.* 1996, Mennill *et al.* 2002). This may be especially relevant for tropical species where social interactions are pervasive year-round. This may provide an explanation for blue-black grassquits, since their migrating plumage includes some nuptial plumage patches that could reflect male condition (Doucet 2002). Thus, these vestiges of nuptial plumage may have some importance during dominance challenges in flocks earlier in the breeding season, before males establish territories. Another possibility is that multimodal displays, such as the acoustic-and-visual display

Table I. Breeding characteristics of two blue-black grassquit populations 25km apart in central Brazil.

Site	No. of nests	Arrival Date	Display Initiation Date	Nest Activity Period	Predation (%)	Breeding Synchrony (%)
Rural (FAL)	23	1-7 Nov	02 Jan	15 Jan-01 Mar	67	27.9
Urban	26	1-7 Nov	06 Dec	07 Jan-01 Mar	40	16.5

Table II. Some reported values for extrapair fertilization rates (EPF) in broods and breeding synchrony index (SI) of birds from tropical and temperate regions with EPF rates above 40% (see Macedo *et al.* 2008 for further detail).

Species	Breeding region	EPP (%)	Synchrony index (%)	Source
<i>Volatinia jacarina</i>	Tropical	64	27.9; 16.5	Present study; Carvalho <i>et al.</i> 2006
<i>Turdus grayi</i>	Tropical	53	25	Stutchbury <i>et al.</i> 1998
<i>Tachycineta bicolor</i>	Temperate	47	46	Reviewed in Stutchbury & Morton 1995
<i>Delichon urbica</i>	Temperate	60	73	Reviewed in Stutchbury & Morton 1995
<i>Luscinia sivevica</i>	Temperate	44	66	Reviewed in Stutchbury & Morton 1995

of the blue-black grassquit, may have numerous, non-redundant signaling functions (Partan & Marler 2005). Thus, the displays may occur in a social context unrelated to female courtship, such as territory maintenance, therefore dissociating male displays from the female fertile period, while still conveying reliable information on male quality to females as an epiphenomenon. Finally, females may base their choice upon extremely persistent male displaying (Payne & Pagel 1997), selecting males that begin displaying much earlier than the overall female fertile period, again dissociating male display period from female fertile period, without reducing the intensity of sexual selection.

MALE-MALE COMPETITION

Signaling fighting ability during intra-sexual competition may be advantageous to both competitors involved in a dispute over a resource, since this may avoid energetically and physically expensive agonistic conflicts (Maynard Smith 1994). Thus, some species possess badges of status, which honestly indicate an individual's quality or fighting ability to its opponent (Rohwer 1982). We have seen that grassquits might be under strong sexual selection from extra-pair matings, thus it is possible that males engage in intra-sexual conflicts to defend or gain access to females or to inflict damage to possible extra-pair competitors. We have frequently observed aggressive interactions among territorial males in the field.

We conducted a laboratory experiment wherein pairs of unfamiliar grassquit males competed for a food resource. The aim of this study was to identify possible badges of status used by males in intra-sexual competition. To stimulate interactions, all males were food deprived for four hours before each trial. We evaluated whether body condition and plumage characteristics could predict male

dominance status. Our results suggest that male grassquits do not possess a badge of status. All trials were resolved through physical aggression. Thus, we can infer that intra-sexual competition in grassquits is context dependent, and the winner of a trial seems to be the bird that is in greater need of the resource being disputed. The results indicate that heavier individuals do not fight fiercely for the food resource, and end up losing the trials. In other words, the value of the food resource might be more important for lighter individuals than for heavier, more satiated ones. Food deprivation might be more costly to lighter individuals that have less energy reserves (Santos *et al.*, unpublished results).

CONCLUSIONS

Data from studies performed in our group have shown that both behavioral displays and plumage coloration of male grassquits are affected by parasitism. Thus, both of these characteristics are costly to maintain and could be used as honest signals by females to choose mates. However, contrary to expectations, there is puzzling evidence that female choice may not be based on these direct indications of male quality, at least under laboratory conditions. Other studies have revealed that grassquits exhibit high levels of extra-pair paternity and that females are keen to engage in extra-pair courtship when presented with the opportunity. This genetic mating system opens the possibility for strong sexual selection pressures that could explain the polygynous behavior observed in grassquits as well as the maintenance of ornaments that may carry a social cost, a possibility that is currently under investigation.

This review concerning the breeding biology and mating system of blue-black grassquits, together with other studies of tropical birds, suggest that extra-pair mating systems may be more closely associated with

social and localized ecological contexts than with broad climatic and biogeographical patterns. Thus, it is conceivable that similar social and ecological patterns observed for both tropical and temperate species lead to converging mating systems. However, only more data on tropical species can reveal whether this prediction is correct.

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