Behavioural Processes 109 (2014) 21–26

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Vocal output predicts territory quality in a Neotropical songbird

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ARTICLE INFO

Article history:
Available online 18 July 2014

Keywords:
Blue-black grassquit
Courtship display
Food abundance
Multimodal display
Ornament
Sexual selection
Song output

ABSTRACT

Females who choose highly ornamented mates may gain resources that improve offspring production and survival. Studies have focused on the relationship between male quality and the complexity of sexual ornaments; however, less is known of the communicative content of courtship displays, and whether they indicate the quality of resources males can provide to mates. Here, we used blue-black grassquits (*Volatinia jacarina*) to test the relationship between male display attributes and territory quality, measured as food availability. Our main hypothesis was that territory quality would be better predicted by dynamic displays than by static ornaments. During four breeding seasons in central Brazil, we quantified display song attributes (output and consistency) and the timing of nuptial molt. We measured territorial seed density, body condition, and ectoparasite infestation. We found a positive relationship between song output and territory seed density, suggesting this attribute provides a reliable indicator of territory quality. However, the timing of molt was unrelated to territory quality. Additionally, no other male attribute was associated with seed density. The link between song output and territory quality might reflect variation in male condition in response to territorial resources, or extra time males on higher quality territories have to invest in territorial defense.

This article is part of a Special Issue entitled: Neotropical Behaviour.

1. Introduction

The theory of sexual selection aims to explain the evolution of elaborate male sexual traits, which are favored either through their influence on male–male competition or female preferences (Darwin, 1871; Andersson, 1994). It is often assumed that elaborate male traits are costly to their bearers, and thus provide females with reliable indicators of male quality (Grafen, 1990; Searcy and Nowicki, 2005). In support of this assumption, numerous studies have linked the complexity of sexual ornaments to variation in male quality traits including condition, genetic constitution, and social status (e.g., McGraw and Ardia, 2003; Grether et al., 2004; Boughman, 2007; Webster et al., 2008). Additionally, other studies have shown that males expressing elaborate ornaments can indeed pay substantial costs, in both trait development (e.g., Cotton et al., 2004; Hunt et al., 2004; Getty, 2006; Rubenstein and Hauber, 2008) and elevated receiver-dependent risks such as retaliation, predation, and parasitism (Tuttle and Ryan, 1981; Rohwer, 1985; Zuk et al., 1993; Bernal et al., 2006).

One major potential benefit for females who choose elaborate males is in obtaining access to superior resources or conditions in which to rear young. This possibility has been assessed most often for sexual ornaments, in tests of relationships between ornament features and the quality of resources males defend and contributions to offspring care. In many such studies, resource quality or, less directly, males' abilities to defend resources, is seen to correlate positively, as expected, with ornament complexity, as with color plumage patches in widowbirds (*Euplectes axillaris*, Pryke et al., 2001; Pryke and Andersson, 2003), UV reflectance in salticid spiders (Lim and Li, 2006), and colored facial bands in mangrove crabs (*Perisesarma eumolpe* and *P. indiarum*; Todd et al., 2011). Yet in other studies, relationships between sexual ornaments and direct benefits from males have proven unclear or difficult to discern (e.g., Gonzalez et al., 1999; Olsson et al., 2008; Butler and McGraw, 2012). A possible reason for these mixed results is that ornament development is often shaped by trade-offs with other resource allocation

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http://dx.doi.org/10.1016/j.beproc.2014.07.004
0376-6357/

priorities that sometimes take precedence, such as parental care and survival, or even with other costly components of sexual signals (Badyaev and Qvarnström, 2002). In species with multiple signals (e.g., songs and elaborate plumage), the discrete properties of each signal component may convey unique messages regarding the bearers' quality ("multiple message hypothesis", Partan and Marler, 2005). Another potential source of information for females about male resources, besides ornaments, is in male courtship displays, i.e., visual, vocal, or tactile mating signals that involve patterned motor output, given that they may be challenging to develop and execute (Byers et al., 2010; see also Barske et al., 2011; Manica et al., 2014).

For many songbirds, male resource quality can be defined largely as territory quality, which has been quantified with respect to food abundance (Howard, 1974; Nystrom, 1997), territory size (Buchanan and Catchpole, 1997; Conner et al., 1986), vegetation cover (Conner et al., 1986; Hoi-Leitner et al., 1995), and territory tenure (Møller, 1983; Hiebert et al., 1989; Beecher et al., 2000). Abundant evidence in songbirds suggests that females can enhance their reproductive output by choosing mates on high-quality territories (e.g., Bensch and Hasselquist, 1992; Pribil and Searcy, 2001), which implies that selection should favor the evolution of male traits that honestly indicate territory quality. One class of such traits are vocal displays, prominent in nearly all songbird species, which are expected to provide particularly reliable indicators of various male attributes including developmental history, condition, vigor, and skill (Nowicki et al., 1998; Gil and Gahr, 2002; Podos et al., 2009). A song feature often discussed as a possible signal of territory quality is vocal output, i.e., the quantity of song a given bird produces per unit time. Males who defend higher-quality territories might sing with greater vigor for at least two reasons. First, males with ability to maintain a good territory in the face of male–male competition might be in better overall condition; and second, males on high-quality territories may need less time for foraging, which can free up time for singing (Davies and Lundberg, 1984; Gottlander, 1987; Alatalo et al., 1990; Arvidsson and Neergaard, 1991; Hoi-Leitner et al., 1995; Nystrom, 1997). Other aspects of song that may also provide reliable indicators of male quality include frequency and timing features related to song copying accuracy and vocal performance, or the consistency of song structure across renditions (e.g., Nowicki et al., 2002; Byers, 2007; Podos et al., 2009).

In this study we focused upon the potential relationship between territory quality and song, in a Neotropical grassland species, the blue-black grassquit (*Volatinia jacarina*). This species produces short (~0.5 s) songs in two contexts: while perched, or in conjunction with an acrobatic visual/behavioral display, the "leap display". Both the leap display and the perched song are produced intermittently through the day, although at greater rates in the early morning and late afternoon, and typically the bird uses the same perches at the edges of his territory. In the leap display, males crouch down and then leap upwards while flapping their wings, rotate their bodies forward (displaying white shoulder and underwing patches), begin to vocalize at the peak of the leap, and continue vocalizing while descending and after landing (Carvalho et al., 2006; Manica et al., 2014). Songs emitted while perched or during the leap appear to have the same structure: a single note ranging between 2 and 13 kHz that decreases in frequency from beginning to end (Fandiño-Mariño and Vielliard, 2004). Each male sings a unique song, the structure of which is highly stereotyped and retained with fidelity both within and across years (Fandiño-Mariño and Vielliard, 2004; Dias, 2009).

Here we test the potential information content of both song output and song consistency, as they may relate to territory quality. We postulate that males who sing at higher rates and/or with greater inter-song consistency will occupy superior territories, as in the Grava et al.'s (2012) study of black-capped chickadees (*Poecile atricapillus*). In addition, the multimodal nature of the grassquit leap display offers us an opportunity to compare the potential information content of dynamic (i.e., traits likely to modulate instantaneously) versus static (i.e., ornaments) display attributes. We hypothesize that dynamic acoustic display attributes, characterized in this paper as vocal output and vocal consistency, will prove more informative about territory quality than will static display attributes, characterized here as the timing of nuptial plumage molt. Our postulation is based upon the assumption that dynamic displays should reflect with greater accuracy the current condition of the male and his resources. Such information would be potentially very important to females as they seek a site for rearing offspring. Additionally, as proposed by Byers et al. (2010), patterned motor output may provide precise cues about males' current condition, given that some types of dynamic displays may be unusually difficult to execute. It is not known, however, if and how display (including vocal) output maps onto natural variation in territory quality, defined herein as seed availability. Finally, we also assess possible relationships between acoustic display features and three putative measures of male quality: ectoparasite load, body condition index, and nuptial plumage coverage.

2. Methods

2.1. Study species and field methods

The blue-black grassquit is a seed-eating songbird with a broad geographic range extending from Mexico to most of South America. The population in central Brazil, where we conducted the study, is migratory, with individuals arriving in October, breeding, and departing in April for northern regions of South America (Sick, 2001). The study site is located in Fazenda Água Limpa (15°56′S 47°56′W), a rural property of the University of Brasília within the Federal District. Ecologically the field site is classified within the *Cerrado* biome, a tropical savanna ecosystem where grasses of approximately 300 species have been identified (Almeida, 1995). The blue-black grassquit breeding season coincides with the peak period of grass seeding in the region (Carvalho et al., 2006). Grass species in the *Cerrado* exhibit a staggered pattern of flowering and seeding through the rainy season (Sarmiento, 1992; Almeida, 1995; Ramos et al., 2014). The study area encompasses an abandoned orchard in initial stages of succession, as well as a denser grassland area sparsely covered with small trees within a tropical savanna matrix. It appears that the peak period of seeding for numerous grass species occurs in March (Ramos et al., 2014), when the rains are ending in central Brazil. Despite the diversity of grasses, behavioral observations at our study site indicate that the grassquits prefer to exploit *Urochloa* sp. (signalgrass; Poaceae) seeds. These become available from January to April in the region (Batalha and Mantovani, 2000; Tannus et al., 2006), and may constitute up to 90% of all grass culms in some grassquit territories (P. Diniz, unpubl. data). *Urochloa* seed availability overlaps the growth period of the grassquit offspring and these seeds constitute a major part of their diet (P. Diniz, unpubl. data).

Males typically begin to display in November and start building nests in early December, although there is much variability in this timing depending on climatic conditions (R.H. Macedo, unpubl. data). Males execute displays throughout the breeding season (December–March), with peak rates typically seen at the end of January (Carvalho et al., 2007). Such displays are executed during uninterrupted periods or bouts that vary greatly in duration. Focal male observations indicate that individual males decrease the frequency of display bouts, but do not cease displaying, when they have an active nest (Manica et al., unpubl. data). Nests are built in bushes or grasses within the male's territory, and both parents feed nestlings (Almeida and Macedo, 2001). Males molt into an alternate, nuptial, plumage at the onset of the breeding season, and are then easily distinguished from brownish females and juveniles by their iridescent black plumage and white wing underparts. After breeding, males molt into a basic plumage with duller black feathers edged with white (Sick, 2001).

As mentioned above, each male sings a unique and highly complex song of a single syllable (Fandiño-Mariño and Vielliard, 2004), which is usually coupled with a characteristic motor display consisting of a short vertical leap (approximately 32 cm) with repeated wing flaps (Carvalho et al., 2006, 2007). This song and motor display can be repeated as quickly as every 3–5 s, during bouts performed throughout long periods of the day (Sick, 2001).

We collected data for this study from October to March during four breeding seasons (October 2006–March 2010). Because of the shifting nature of the migratory population, not all attributes of individual birds and territories were sampled each year, and sample sizes in our analyses reflect these differences. We captured males with mist nets, marked them with unique combinations of three colored plastic bands and one numbered metallic band (Brazilian bird-banding agency – CEMAVE), measured phenotypic and territorial attributes, and recorded their songs (see below).

2.2. *Song sampling*

During morning hours (between 0700 h and 1000 h) we recorded 69 banded males (eight in 2006–2007, 22 in 2007–2008, 24 in 2008–2009, 15 in 2009–2010), with either an analog (SONY TC-D5 PRO II, 2006–2007) or digital audio recorder (Marantz PMD 660, sampling rate 44.1 kHz, .wav files, 2007–2008, 2008–2009, 2009–2010), coupled to either a Sennheiser K6/ME66 unidirectional or Sennheiser K6/ME62 omni-directional microphone with a Telinga parabola. We digitized analog recordings at a sampling rate of 44.1 kHz and 16-bits in non-compressed .wav files. Each focal male was recorded in bouts of up to 11 min, and songs were included whether or not they were part of a leap display, as they appear to be structurally identical. Considering that males can often produce up to 19 consecutive displays (leap with song) per minute (Manica et al., submitted for publication), recordings of long bouts encompassed many songs, up to a maximum of 130 songs in sequence. For each bird we identified five song samples for our calculations of vocal consistency, after cropping introductory notes and applying a 1 kHz high-pass filter. Introductory notes are distinguishable from the song itself due to their unique spectrogram shape, while the song itself is an overall continuous "buzz" (Fandiño-Mariño and Vielliard, 2004). Recordings with low background noise and that did not overlap other songs were favored. We used Cool Edit v.2.1 software for all acoustic measurements and filters, except where noted otherwise.

2.3. *Song output and consistency*

We quantified two acoustic variables: song output and the consistency of song structure across multiple renditions. Song output was calculated as the number of songs sung per minute during the segment of the longest bout recorded for each male, which varied from 0.2 to 10.8 (mean ± SD = 3.1 ± 2.14) min per bird. Song consistency was calculated for each bird using spectrogram cross-correlation analyses, among the five song samples chosen for analysis. Samples were normalized to 0 dB peak amplitude and cross correlation analyses were carried out with Raven Pro 1.3. Cross correlation analysis compares the structure of spectrogram pairs and generates a score between 0 and 1, with 0 indicating spectrograms that are completely dissimilar and 1 spectrograms with identical structure (e.g., Clark et al., 1987).

2.4. *Territory quality*

We estimated territory seed density as the number of seed stalks per m^2 for 30 of the recorded males shortly after the end of three breeding seasons (2007–2008, 2008–2009 and 2009–2010) in which they were recorded. The end-of-the-season measurement using counts of both grass stalks bearing seeds as well as those with empty culms should offer a reliable window into seed density within the breeding season, given the continuous crop throughout the season. Territories are very small in this species (13–72 m^2; Almeida and Macedo, 2001), and we endeavored to sample each male's territory in a uniform though random manner. In the first breeding season (2007–2008), we delineated these males' territories by marking their display perches relative to the study area grid points, and then constructing minimum-area polygons. We used five equally-spaced 1 m × 1 m quadrats (method 1) placed on the longest transect of each polygon and estimated seed density by counting the number of grass stalks with seeds or vestiges of production within each quadrat. The counts from the five quadrats were averaged for each territory. In the last two breeding seasons (2008–2009 and 2009–2010), we used a similar seed density estimation method, but did not delineate territory boundaries and used four 0.5 m × 0.5 m quadrats instead, placed at a very short distance (5 m) from each territory's nest, one in each cardinal direction (method 2). Seed estimation methods 1 and 2 yielded similar and significant repeatable measurements of seed density across plots within territories (method 1: $r = 0.33$, $F_{12,52} = 3.49$, $P < 0.001$; method 2: $r = 0.31$, $F_{14,43} = 2.7$, $P = 0.006$; combined and considering breeding season effects: $r = 0.38$, $F_{26,95} = 3.54$, $P < 0.001$; method by Lessells and Boag, 1987).

2.5. *Male plumage and quality attributes*

We measured the length of the left tarsus (0.1 mm precision) and body mass (Pesola^{TM} 0.25 g precision) of captured birds and assessed ectoparasite load by visually inspecting feathers in both wings against the light and counting ectoparasites (Aguilar et al., 2008). To estimate the average percentage of nuptial plumage coverage, we overlaid a 1.4 cm transparent plastic disk (subdivided in eight sections) over four body areas (back, head, rump and chest) and then counted the number of sections that completely coincided with black plumage (Maia and Macedo, 2011). These measures taken from captured males were used to generate three parameters: (1) body condition, calculated as body mass divided by tarsus length ($n = 59$) (Costa and Macedo, 2005; Maia and Macedo, 2011); (2) molt index, which indicates how early in the season a male acquired nuptial plumage (see below) ($n = 62$); and (3) number of wing ectoparasites ($n = 55$ males). Since individuals either lacked ectoparasites ($n = 29$) or were heavily infested (47.15 ± 44.82 parasites; $n = 26$), this trait was expressed as a binary (presence/absence) variable.

We calculated the molt index as the residuals of a linear regression model of the nuptial plumage percentage (arcsine-transformed) on date of capture, using breeding season as a covariate (date: $F_{1,55} = 28.27$, $P < 0.01$, breeding season: $F_{3,55} = 3.96$, $P = 0.01$, model: $R^2 = 0.43$, $F_{7,55} = 5.88$, $P < 0.01$; Maia and Macedo, 2011). High molt index scores indicate males in a relatively advanced stage of prenuptial molt, which also have a more saturated and UV-shifted plumage color (Maia and Macedo, 2011). High scores can be interpreted as a higher investment by the male in the growth of new feathers or an earlier onset of molting, and thus could indicate a male in good condition. Molting may impose a conflicting energetic demand with other physiological processes, such as thermoregulation (Nilsson and Svensson, 1996), thus only individuals in good condition may be able to handle such trade-offs. In addition, the molting speed of a male blue-black grassquit could have substantial impact on breeding success since this is a migratory species and males that acquire a nuptial plumage earlier or faster are more likely to establish a territory or to form a pair bond with a female (e.g., *Malurus cyaneus*, Mulder and Magrath, 1994; *Empidonax minimus*, Tarof et al., 2004).

2.6. Statistical analyses

We tested for associations between the two measures of males' individual acoustic performance, output and consistency, using a Pearson's correlation test. To assess if song parameters were indicative of territory or individual quality, we built linear models of male song output and consistency with four predictor variables of interest: seed density, body condition, molt index, and ectoparasite load. We also used a linear model to test if any male morphological attributes were indicative of territory quality, defined here by seed density. We tested the significance of predictors using a forward selection approach, adding one variable at a time and comparing the change in model fit using *F* tests. Selection procedure started from the model including breeding season (2007–2008, 2008–2009 and 2009–2010) as a covariate (fixed factor), despite its significance, to control for variation due to any differences between years, and also to account for changes in recording and seed density estimation between field seasons. Song output and song consistency did not vary among breeding seasons ($F_{2,20} = 1.82$, $P = 0.19$ and $F_{2,20} = 0.34$, $P = 0.71$, respectively), while seed density did ($F_{2,20} = 35.27$, $P < 0.01$). For song output and consistency models, we initially tested the interaction between breeding season and seed density to check if annual variation (and hence, the difference between methods of food availability estimation) could bias our estimates for seed density. As we did not find a significant effect of this interaction term (song output model: $F_{2,17} = 1.40$, $P = 0.27$; consistency model: $F_{2,17} = 1.50$, $P = 0.25$), it was excluded from model selection.

We checked the homogeneity of variances by inspecting plots of the residuals versus fitted values, and checked the normality of residuals using quantile–quantile plots. Based on these inspections, three outliers were identified, all were individuals with song output values lower than 7 songs/min. Though maintaining these individuals did not affect the significance of predictors, they influenced parameter estimates and were therefore excluded. Thus, our final sample size in the correlational analysis between song output and consistency was of 66 males, and sample sizes in linear models of song output, consistency and seed density, which also included only complete observations (all predictors measured), were of 23 males in each model. Song output and seed density were log-transformed in all analyses. All statistical analyses were performed with R software (v. 2.13.2; R Development Core Team, 2011).

3. Results

Male song output varied broadly, ranging from 5.0 to 20.8 songs/min (mean ± SD; 14.2 ± 3.2). Song consistency also varied across individuals, with spectrogram cross-correlation scores ranging from 0.34 to 0.89 (0.66 ± 0.12). Song output and consistency were not significantly correlated with each other ($r = 0.14$, $t_{64} = 1.1$, $P = 0.28$). Male plumage and quality attributes also exhibited wide variation among individuals: the body condition index (weight/tarsus length ratio) ranged from 0.43 to 0.84 (0.57 ± 0.07); molt index, from −1.06 to 0.52 (−0.08 ± 0.30); and among sampled individuals, 47.3% were infected with wing feather ectoparasites. Regarding male territory quality, seed density per territory varied from 12 to 168 stalks/m^2 (92.8 ± 47.6).

Table 1
Standardized estimates (β) and ANOVA results of linear models for song output and song consistency in relation to male phenotypic attributes and territory quality. Breeding season was included as covariate to control for among-year variation due to change in methods ($n = 23$).

Model terms	β (SE)	*F* (df)	*P* value
Song output			
Body condition	−0.16 (0.22)	0.58 (1,19)	0.45
Molt index	−0.26 (0.21)	1.56 (1,19)	0.23
Ectoparasites	0.06 (0.21)	0.09 (1,19)	0.76
Seed density	1.06 (0.38)	7.98 (1,19)	0.01
Song consistency			
Body condition	−0.17 (0.23)	0.54 (1,19)	0.47
Molt index	0.29 (0.22)	1.64 (1,19)	0.22
Ectoparasites	−0.05 (0.23)	0.05 (1,19)	0.82
Seed density	−0.24 (0.48)	0.26 (1,19)	0.62

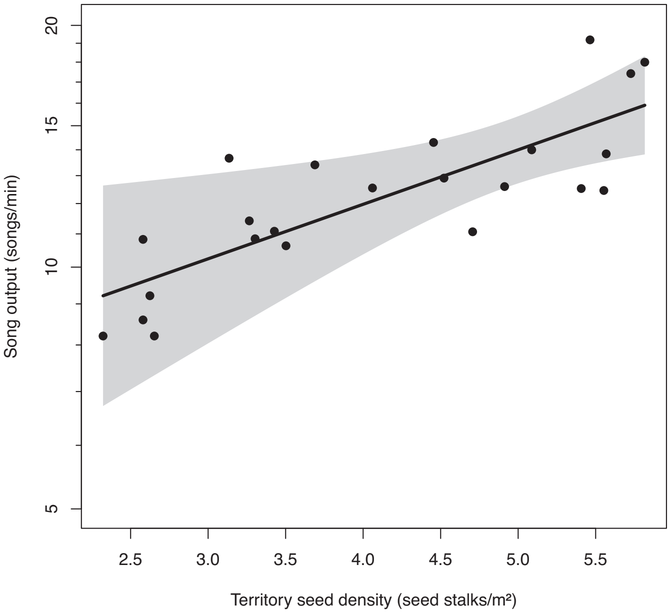

Fig. 1. Relationship between partial residuals of song output (centered by accounting for median year effects) and territory seed density of 23 blue-black grassquit males (note *y*-axis is log-scaled).

Table 2
Standardized estimates (β) and ANOVA results of linear models for territory seed density in relation to male phenotypic attributes. Breeding season was included as covariate to control for among-year variation due to change in methods ($n = 23$).

Model terms	β (SE)	*F* (df)	*P* value
Body condition	0.002 (0.11)	>0.001 (1,19)	0.98
Molt index	−0.09 (0.11)	0.69 (1,19)	0.42
Ectoparasites	−0.01 (0.21)	0.004 (1,19)	0.95

We found a positive relationship between song output and territory seed density (Table 1 and Fig. 1). By contrast, song output was not significantly associated with any of the male attributes (Table 1). Additionally, song consistency was not associated with any of the tested male or territory attributes (Table 1), and none of the male morphological traits, including molt index, were significant predictors of territory quality (Table 2).

4. Discussion

Our study yielded two significant findings. First, we found that song output was positively and significantly associated with territory seed density. Thus, song output, or any correlated parameter such as the leap display, should be a useful cue for female grassquits choosing prospective mates that occupy high quality territories, measured in terms of seed abundance. Second, no other male phenotypic attribute, including nuptial plumage molt index, was associated with territory quality or with the two vocal performance measures evaluated. Thus, our results accord with our central hypothesis, that male dynamic attributes should indicate territory quality more accurately than at least some static ornaments. In contrast to song output, vocal consistency was not associated with territory attributes and is probably not an important signal of male ability to hold a resource-rich territory. This result, added to the lack of relationship between song output and consistency, could mean that these components of the grassquit song are non-redundant attributes of a multicomponent signal (sensu Partan and Marler, 2005, see also Doucet and Montgomerie, 2003).

There are at least three possible explanations for the positive association between song output and territory quality. First, males' ability to sing at high rates might depend on the amount of food they can access. This explanation is consistent with a recent study of black-capped chickadees (*Poecile atricapillus*), in which males who received supplemental food on their territories sang more frequently and for longer periods during the dawn chorus, as compared to males without food supplementation (Grava et al., 2009). In the case of blue-black grassquits, we can speculate that males residing on territories with higher food abundance may have more ready daily access to a constant energy source that translates immediately into higher song rates, although in a way that was not reflected in other phenotypic attributes in our study. As a caveat, we note that both males and females do not forage exclusively within the boundaries of their territories (R.H. Macedo, unpubl. data). However, easy and fast access to a plentiful amount of seeds could still translate into reductions in energy expenditure, especially during the nestling growth period where parents may need to remain relatively close to the nest.

Second and relatedly, song output may be condition-dependent, and males that were able to secure territories with more food might have been in better condition a priori, and thus able to invest more time and energy in displays than they could have otherwise. That is, we might expect that higher quality males will be better able to defend superior territories, and to invest more in song given their superior condition. This possibility is not, however, consistent with our male quality measurements, which showed no relationship with either song output or seed density. Notably, previous studies on this species showed that levels of endoparasitism, particularly in terms of the presence of coccidian oocysts, correlated negatively with leap display rates (all of which are coupled with song). This suggests that at least some types of parasites and/or the severity of deleterious effects may influence acoustic expression, rendering it an important signal of male quality (Costa and Macedo, 2005; Aguilar et al., 2008). It will be useful in future work to determine if territory quality predicts endoparasite load, as we might expect combining our present results with those of Costa and Macedo (2005) and Aguilar et al. (2008).

A third possible explanation for the observed correlation between song output and seed density concerns the function of song between males in territorial defense. If males can assess the quality of other males' territories, then we might expect males on higher-quality territories to invest more time and energy in defending those territories from male rivals. One way to test this possibility in future work will be to determine whether males who sing more, or who are protecting higher quality territories, indeed engage in higher rates of territorial interactions.

In many taxa, male sexual ornaments and displays have been linked with mate choice by females (Andersson, 1994). The benefits females may gain for choosing good singers as mating partners can be indirect (e.g., good genes for the offspring) (Fisher-Zahavi hypothesis, Kokko et al., 2006) or direct (e.g., food resources) (Andersson, 1994). While associations have frequently been found between male sexual traits and physical or physiological indicators of health or quality (e.g., male dominance status; reviewed in Andersson, 1994), relatively few studies have examined whether male sexual traits reliably indicate the quality of tangible resources males can provide. One such recent study found that the size of melanin plumage patches in American redstarts *(Setophaga ruticilla)* predicted the quality of territories males occupied (Germain et al., 2010). Associations between resources and display parameters such as song, however, are even less well documented. Our study not only suggests a link between a dynamic display parameter and resource quality, but also that this link is stronger than that between resource quality and a static ornamental attribute, nuptial plumage molt index. This finding is consistent with the expectations laid out by Byers et al. (2010). The possibility remains that resource quality could potentially influence other static ornamental attributes not evaluated in this study, such as plumage color variation, or size and reflectance properties of the white patches, but this remains to be tested.

To conclude, our data provide new insight into how displays might mediate sexual interactions in blue-black grassquits. In this species, males that leap at higher rates have been shown to be more successful in obtaining mates (Carvalho et al., 2006). The current data set extends this finding by suggesting that if females prefer higher singing output, which may be associated or not with the motor part of the display, mate choice should be biased toward males that can provide a higher quality foraging territory. A link between male reproductive success and singing rate, however, has not yet been established in our study species, both because we do not know if females actually prefer mates with higher singing rates, and also because within-pair mating success may not reflect genetic paternity given the high rates of extra-pair fertilization (Carvalho et al., 2006). Hence, it remains to be seen whether mating success in this species is indeed influenced by song output, and also if other aspects of male display prove even more reliable as predictors of territory quality.

Acknowledgments

This work was funded by the National Geographic Society, Fundação de Apoio à Pesquisa – DF, CAPES/CNPq and University of Brasília. We thank Marina Anciães, Juan Reboreda, Braulio Dias, Melissa Hughes, and Denise Pope for valuable discussion or comments on earlier versions of our manuscript. We thank two anonymous reviewers for their suggestions and corrections. For help with field work, we thank David Cho, Wanner Medeiros, Marcelo Moraes, Sofia Bethlem, Leonardo Castilho, Luiza Brasileiro and Raphael Igor Dias. JP's contribution to the project was supported by National Science Foundation grant IOS-1028964.

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