



## Attractive males are less than adequate dads in a multimodal signalling passerine



Pedro Diniz<sup>a, \*</sup>, Desirée M. Ramos<sup>b, 1</sup>, Regina H. Macedo<sup>c, 2</sup>

<sup>a</sup> Programa de Pós Graduação em Ecologia, Universidade de Brasília, Brasília, Brazil

<sup>b</sup> Programa de Pós Graduação em Botânica, Universidade de Brasília, Brasília, Brazil

<sup>c</sup> Laboratório de Comportamento Animal, Universidade de Brasília, Brasília, Brazil

### ARTICLE INFO

#### Article history:

Received 17 July 2014

Initial acceptance 16 September 2014

Final acceptance 12 December 2014

Published online

MS. number: A14-00579R

#### Keywords:

differential allocation

male attractiveness

multiple sexual signals

parental care

sexual selection

Parental attractiveness influences paternal and maternal efforts in a wide range of animals that exhibit biparental care. However, we still lack an understanding concerning the direction of the covariance between attractiveness and parental effort, perhaps because studies typically consider only one or a subset of multiple attractiveness signals. In this study we investigated predictions of four hypotheses about the relationship between attractiveness traits (plumage coloration, song and leap display traits) and parental effort (feeding rates) in a wild population of the blue-black grassquit, *Volatinia jacarina*, a Neotropical sexually dichromatic bird with biparental care. Paternal effort was negatively correlated with male blue-black coloration (UV chroma) and maternal effort was positively correlated with male provisioning rate. Thus, more attractive males relative to the UV chroma are worse fathers relative to less attractive males in this trait. However, female provisioning rate was positively correlated with another male attractive trait: the blue-black plumage coverage. The song, leap display and other features of male coloration were not associated with either male or female parental effort. Taken together, these results support the parental–mating trade-off hypothesis for paternal behaviour, which predicts that attractive males should invest less in current offspring in order to acquire extrapair matings. Also, our results partially support the positive differential allocation hypothesis: although females invested highly in offspring of males with more blue-black plumage coverage, they did not compensate for the low investment of males with UV-shifted blue-black plumage. We highlight the need for future studies to consider multiple sexual traits in order to investigate the relationship between attractiveness and parental investment.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

According to life history theory, parental investment is influenced by trade-offs between the reproductive value of current offspring and the survival and reproductive prospects of a parental individual (Trivers, 1972). In taxa with biparental care, parental attractiveness is an important component that is associated with reproductive value of current offspring (Burley, 1986; Sheldon, 2000). Individual attractiveness may also influence and define the reproductive strategies of both mating partners (Alonso-Alvarez et al., 2012; Osorno et al., 2006; Senar, Figuerola, & Pascual, 2002). However, studies disagree about how parents should allocate their investment in the offspring relative to their own and their

partner's attractiveness (Harris & Uller, 2009; Horváthová, Nakagawa, & Uller, 2012; Kokko, 1998), which has led to a confusing and diverse array of hypotheses.

There are three hypotheses that attempt to explain covariation between self-attractiveness and parental investment in socially monogamous taxa (Table 1): (1) the good parent hypothesis; (2) the parental–mating trade-off hypothesis; and (3) the positive differential allocation hypothesis. The good parent hypothesis predicts that an individual's attractiveness should reliably and positively indicate parental effort (Hoelzer, 1989). In this case, the trade-off between parental and mating efforts may be reduced (Kokko, 1998; Stiver & Alonzo, 2009). On the other hand, the parental–mating trade-off hypothesis predicts that an individual's attractiveness (usually the male's) should be negatively correlated with its parental effort, because the benefits derived from parental care do not compensate the costs of losing extrapair mating opportunities (Magrath & Komdeur, 2003; Schwagmeyer, Parker,

\* Correspondence: P. Diniz, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, 70919-970, Brazil.

E-mail address: [pdadiniz@gmail.com](mailto:pdadiniz@gmail.com) (P. Diniz).

<sup>1</sup> E-mail address: [desibio@gmail.com](mailto:desibio@gmail.com) (D. M. Ramos).

<sup>2</sup> E-mail address: [rhmacedo@unb.br](mailto:rhmacedo@unb.br) (R. H. Macedo).

Mock, & Schwabl, 2012; Stiver & Alonzo, 2009). This prediction is also made by the third explanation, the positive differential allocation hypothesis, but in this case an attractive individual reduces its parental effort because its mate is willing to compensate for it (see below; Burley, 1986).

An individual's attractiveness should also influence its partner's investment in the social parents' offspring (e.g. Mahr, Griggio, Granatiero, & Hoi, 2012). In socially monogamous taxa, there are two hypotheses that suggest how an individual should invest in offspring depending on the partner's attractiveness, leading to opposing predictions (Table 1): (1) the positive differential allocation hypothesis (Burley, 1986; Ratikainen & Kokko, 2009; Sheldon, 2000); and (2) the negative differential allocation hypothesis (Ratikainen & Kokko, 2009; alternatively known as the reproductive compensation hypothesis; Gowaty, 2008). According to the positive differential allocation hypothesis, male attractiveness indicates male quality and is heritable. Therefore, this hypothesis predicts that male attractiveness should positively affect the female's parental effort, because females gain a higher fitness per unit of parental care by investing in offspring sired by high-quality males (Sheldon, 2000). In addition, higher maternal effort could compensate for the possibly lower paternal effort strategy of highly attractive males (Ratikainen & Kokko, 2009). Finally, according to the negative differential allocation hypothesis, ecological and social circumstances may not allow all females to mate with preferred or more attractive males. Offspring from nonpreferred or less attractive males would have low viability and females would compensate for that in terms of parental effort. Therefore, this hypothesis predicts a negative covariation between male attractiveness and maternal effort (Gowaty, 2008).

There is only mixed support for the parental–mating trade-off and the positive differential allocation hypotheses; in addition, few general patterns have emerged, perhaps because it appears that the associations between parental attractiveness and parental effort are species specific (Mazuc, Chastel, & Sorci, 2003; Rutstein, Gilbert, & Tomkins, 2005). Furthermore, recent observational and experimental studies point to patterns that are not predicted by any of the hypotheses mentioned above, such as differences between populations in the covariance patterns between parental effort and parental attractiveness (Limbourg, Mateman, & Lessells, 2013; Mahr et al., 2012), differences between sexes in the same population (Limbourg et al., 2013), or patterns that depend on which male sexual signals are considered (Galeotti et al., 2006). The latter category, for example, is illustrated by female freshwater crayfish (*Austropotamobius italicus*) that lay a few large eggs when paired with small-sized, large-clawed males and lay numerous but smaller eggs when paired with large-sized, small-clawed males (Galeotti et al., 2006).

Few studies have examined the covariation between parental investment and individual attractiveness in the context of multiple

sexual signals. Different secondary sexual traits may convey different, redundant or emergent messages to the same or to different receivers (Bro-Jørgensen, 2010; Hebets & Papaj, 2004). Moreover, different signals in multiple sexual signalling systems may: (1) have different functions or propagation efficiency according to social and environmental contexts (Bro-Jørgensen, 2010), and (2) convey different information about individual quality (Bro-Jørgensen & Dabelsteen, 2008; Freeman-Gallant et al., 2009), including parental quality (Pizzolon et al., 2011). In addition, multiple signals may have greater importance in mate choice and mating success than only one or a subset of multiple signals (Pizzolon et al., 2011; Taylor, Buchanan, & Doherty, 2007). Because most biparental bird species have multimodal sexual traits (Hebets & Papaj, 2004), understanding their adaptive functions and plasticity may generate reliable predictions concerning the covariation between parental effort and parental attractiveness.

Here, we investigated whether multimodal sexual signals of male blue-black grassquits, *Volatinia jacarina* (Aves: Thraupidae), a Neotropical socially monogamous species with biparental care, predict paternal and maternal effort in social pairs. We sampled visual (plumage coloration and leap display) and acoustic (song) parameters of male sexual traits, and measured provisioning rates by males and females during the nestling period. We used grassquit social pairs to test predictions of the four hypotheses that suggest explanations for possible relationships between male attractiveness and parental effort (see Table 1). In relation to paternal care, we tested for a positive (good parent hypothesis) or negative (parental–mating trade-off hypothesis and positive differential allocation hypothesis) covariation between male attractiveness and paternal effort. In relation to maternal care, we tested for a positive (positive differential allocation hypothesis) or negative (negative differential allocation hypothesis) covariation between male attractiveness and maternal effort.

## METHODS

### Study Species

The blue-black grassquit is an ideal model for studies involving multiple sexual sensory modalities and parental care. Blue-black grassquits exhibit sexual dichromatism: females have dull brown plumage while males acquire an iridescent blue-black plumage with a white underwing patch during the breeding season. Males vary in expression of the blue-black plumage coverage and their spectral characteristics (Maia, Caetano, Bão, & Macedo, 2009). Males perform an acrobatic display expressed in a vertical flight (leap display), with body rotation, high-speed wing beats and exhibition of white underwing patches (Macedo, Manica, & Dias, 2012). They also have a stereotyped and short song, which is coupled with leap displays (i.e. complete displays) but that can also

**Table 1**  
Hypotheses and predictions regarding the relationship between parental effort and male attractiveness

Hypotheses	Authors	Covariation between male attractiveness and parental effort		Corroborating evidence
		Paternal	Maternal	
Good parent	1	+		7, 8, 9
Parental–mating trade-off	2	–		10, 11
Positive differential allocation	3, 4	–	+	12, 13, 14
Negative differential allocation	4, 5, 6		–	15, 16

Symbols indicate positive (+) or negative (–) covariations.

<sup>1</sup>Hoelzer (1989); <sup>2</sup>Magrath and Komdeur (2003); <sup>3</sup>Burley (1986); <sup>4</sup>Sheldon (2000); <sup>5</sup>Ratikainen and Kokko (2009); <sup>6</sup>Gowaty (2008); <sup>7</sup>Germain, Reudink, Marra, and Ratcliffe (2010); <sup>8</sup>Linville, Breitwisch, and Schilling (1998); <sup>9</sup>Siefferman and Hill (2003); <sup>10</sup>Mitchell, Dunn, Whittingham, and Freeman-Gallant (2007); <sup>11</sup>Sanz (2001); <sup>12</sup>Maguire and Safran (2010); <sup>13</sup>Alonso-Alvarez et al. (2012); <sup>14</sup>Osorno et al. (2006); <sup>15</sup>Bluhm and Gowaty (2004); <sup>16</sup>Gowaty, Drickamer, and Schmid-Holmes (2003).

be produced while the bird is perched (i.e. incomplete displays) (Dias, 2009). Males execute an average of 13 complete leap displays per minute (Carvalho, Macedo, & Graves, 2007). Leap display bouts, defined as periods encompassing consecutive leap displays from the same perch or between nearby perches, may take several minutes.

Blue-black grassquits build cup-shaped nests on grasses or shrubs at a height of approximately 40 cm (Carvalho et al., 2007). Clutch size varies from two to three eggs and nest predation rate is high, averaging around 80% (reviewed in Macedo et al., 2012). Blue-black grassquits have biparental care: both sexes build the nest and feed nestlings and juveniles, while mostly females incubate the eggs (Alderton, 1963).

An important assumption regarding the hypotheses investigated here is that the secondary sexual traits of males reflect the attractiveness and/or some measure of quality of these males. There is indirect evidence across all sexual sensory modalities in grassquit males that the traits selected for evaluation in this study are indicative of some measure of quality. Blue-black plumage reflectance indicates body condition (Doucet, 2002), age (Maia, 2008) and parasite load (Costa & Macedo, 2005), whereas song is related to territorial quality and blue-black plumage coverage in males (Dias, 2009; Manica, Maia, Dias, Podos, & Macedo, 2014). Finally, leap display rate correlates positively with pairing success and negatively with parasite load in male grassquits (Aguilar, Maia, Santos, & Macedo, 2008; Costa & Macedo, 2005).

#### Study Area and General Procedures

Our study was conducted in a savanna fragment (8.91 ha) in an urban matrix located within the Campus of the University of Brasília, Distrito Federal, Brazil (15°44'S, 47°52'W), during two breeding seasons: 2010–2011 (December to March) and 2011–2012 (October to March). We captured adults with mist nets for banding just before and during the breeding seasons. We collected plumage samples from adult males (both breeding seasons), obtained data on leap displays and songs (only the second breeding season), monitored nests and, finally, videorecorded parental care behaviour (both breeding seasons).

#### Plumage Coloration

We estimated coverage and spectral characteristics of male blue-black plumage. Plumage coverage (used to calculate a moult index; Maia & Macedo, 2010) was estimated with a transparent plastic disk, 1.4 cm in diameter, divided into eight segments and placed on different parts of the bird's body (head, chest, rump, back and upper wing coverts). We estimated the proportion of blue-black coverage for each body part by counting how many of the segments coincided completely with blue-black feathers. We averaged measurements of blue-black plumage across body areas (Maia & Macedo, 2010). Blue-black plumage coverage was correlated with day of capture during the breeding season for our grassquit population (Spearman correlation:  $r_s = 0.33$ ,  $P < 0.0001$ ; see Maia & Macedo, 2010); therefore, we constructed a linear mixed model to control for date effect on blue-black plumage using all captured males ( $N = 142$  samples, 125 males). In the model we included the difference between the date of capture and the laying date of the first egg in the breeding season as a fixed variable. We also included year and male identity as fixed and random factors, respectively, because recaptured males had their plumage coverage resampled, mainly between different breeding seasons. To analyse plumage in the context of parental care, we used the residuals from this model as a measurement of blue-black plumage coverage.

We collected three to eight blue-black feathers from the male's back (mode = 4,  $N = 140$  males) and two to six feathers from the underwing patch of the left wing (mode = 3,  $N = 135$  males). We wrapped the feathers in aluminium foil and stored them in dry conditions at room temperature. We analysed the spectral properties of feathers with an Ocean Optics USB4000 spectrometer with a source of pulsed xenon light-PX 2 (Ocean Optics, Dunedin, FL, U.S.A.), which provides illumination in the visible spectrum for birds (315–700 nm), including ultraviolet. We taped the feathers to a black velvet substrate in an overlapping pattern, positioned an optical fibre at a 90° angle relative to the feathers and made four measurements of each sample, removing and repositioning the probe between measures. The 'pavo' package (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013) of the R 3.1.1 software (R Development Core Team, 2014) was used to estimate the following measures of sample coloration (see Montgomerie, 2006): mean brightness (average reflectance over all wavelengths), and blue (only for blue-black feathers) and ultraviolet (UV, for both blue and white feathers) chromas (sum of reflectance values divided by the region of interest) (Fig. 1a).

We estimated the between-year repeatability of plumage coloration traits for 11 recaptured males, according to Nakagawa and Schielzeth (2010). We used the linear mixed-effects model (LMM)-based method for Gaussian data and the rptR package (Schielzeth & Nakagawa, 2013) from R 3.1.1 software. Relative to the white feathers, we found very low repeatability values for mean brightness ( $R \pm SE = 0 \pm 0.17$ ,  $P = 0.48$ ) and UV chroma ( $R \pm SE = 0 \pm 0.17$ ,  $P = 0.53$ ). Relative to the blue-black plumage, we found high repeatability value for UV chroma ( $R \pm SE = 0.81 \pm 0.13$ ,  $P = 0.001$ ), moderate repeatability values for mean brightness ( $R \pm SE = 0.27 \pm 0.23$ ,  $P = 0.18$ ) and blue chroma ( $R \pm SE = 0.22 \pm 0.22$ ,  $P = 0.24$ ), and low repeatability values for blue-black plumage coverage ( $R \pm SE = 0 \pm 0.18$ ,  $P = 0.93$ ). These patterns indicate that most male plumage traits consistently vary within individuals, and may be condition or age dependent in blue-black grassquits. In contrast, UV chroma of blue-black feathers should be a better indicator of intrinsic, genetic male quality in blue-black grassquits.

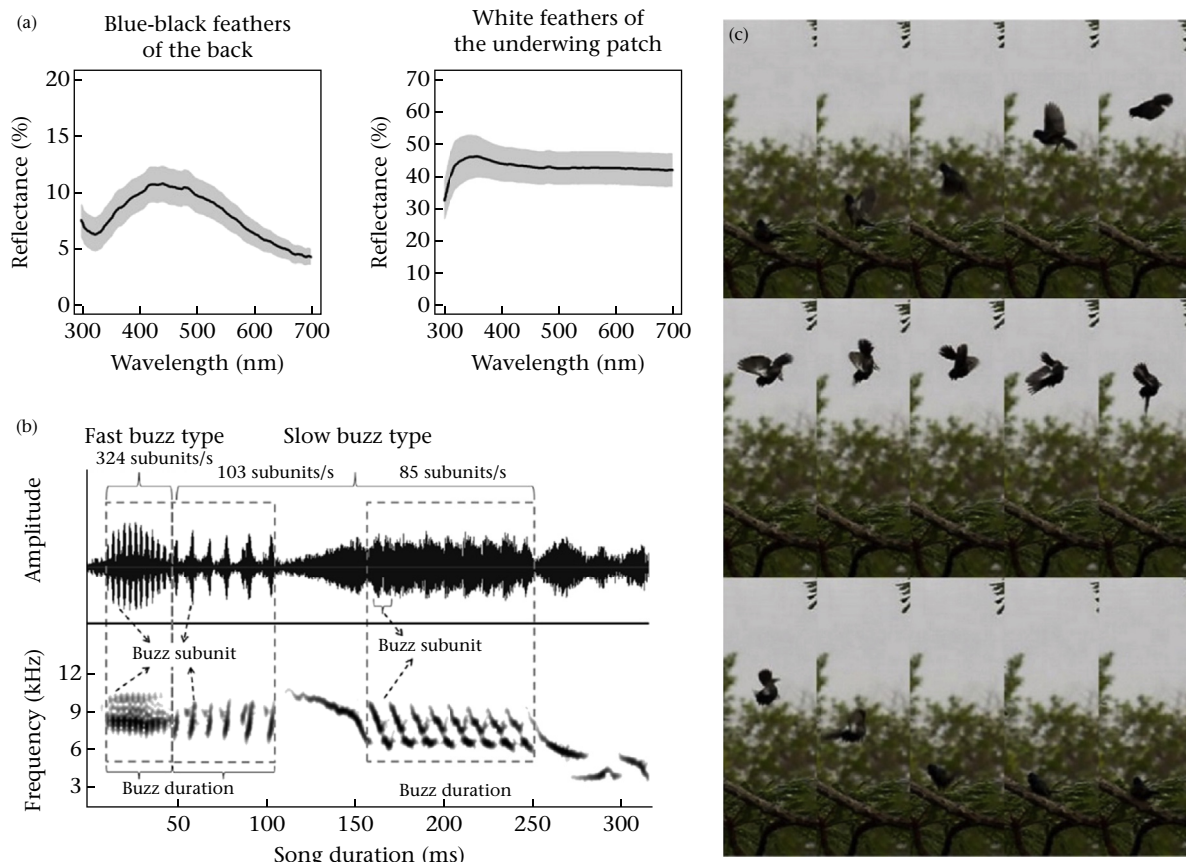
#### Song

Blue-black grassquits produce a trill-like song with a buzzy subunit (Fandiño-Mariño & Viellard, 2004). Buzz subunits are emitted faster than trilled songs and seem to be vocalized only during expiratory bursts, contrasting with the rapid inspiration and expiration pattern of trill units in trilled songs (Hartley, 1990; Podos, 1997). Recent studies suggest that buzz rates can be constrained by trade-offs as usually occurs with trilled songs (Weiss, Kiefer, & Kipper, 2012), which leads to the possibility of buzz songs signalling male quality and influencing mating success (Trillo & Vehrencamp, 2005; Weiss et al., 2012).

We recorded banded male song bouts (mean  $\pm$  SD =  $2.31 \pm 1.55$  bouts, range 1–6,  $N = 22$  males) with a Marantz PMD 660 digital recorder and a Sennheiser K6 microphone before or between nesting attempts during the second breeding season (October 2011 to March 2012). Song bouts lasted  $2.81 \pm 2.62$  min (mean  $\pm$  SD, range 0.43–9.84 min,  $N = 51$  bouts) and contained  $39.75 \pm 32.30$  songs (mean  $\pm$  SD, range 10–135,  $N = 51$  bouts). From recordings of each male we selected up to five high-quality songs (e.g. high signal-to-noise ratio) using Raven Pro<sup>®</sup> 1.4 software (Bioacoustics Research Program, 2011). We estimated vocal deviation for each buzz as a measurement of vocal performance, vocal consistency for each song and vocal output for each song bout.

To estimate vocal deviation and consistency, we excluded introductory low-amplitude notes (Dias, 2009) and used a band-





**Figure 1.** Multiple sexual signals of blue-black grassquit males in central Brazil. (a) Mean reflectance (black line)  $\pm$  SE (grey area) of the blue-black and white feathers ( $N = 42$  males). (b) Oscillogram and spectrogram of a male blue-black grassquit song (i.e. excluding introductory notes) showing the buzz structure. (c) A 0.51 s leap display sample showing the wing beats and body rotation during the flight.

pass filter to remove frequencies lower than 2 kHz to minimize background noise. To estimate vocal deviation, we first looked at the oscillogram (scale = 0.3/line and  $8 \times 10^6$  units/line) and spectrogram (Blackman window, window size = 256, overlap in time grid = 80.1%) of amplitude-normalized male grassquit songs to select buzz bouts with clearly discrete buzz units and containing at least three buzz units (mean  $\pm$  SD =  $2.97 \pm 0.91$  buzz bouts/song, range 1–6,  $N = 899$  buzz bouts). We then counted the number of buzz units in each buzz bout (mean  $\pm$  SD =  $10.55 \pm 6.62$  buzz units/buzz bout, range 4–50,  $N = 9486$  buzz units). All procedures described above were performed in Raven Pro<sup>®</sup> 1.4 software. We identified two buzz types based on buzz rates: a slow buzz type (mean  $\pm$  SD =  $113.70 \pm 45.23$  buzz units/s, range 49.50–217.40,  $N = 426$  buzz bouts) and a fast buzz type (mean  $\pm$  SD =  $336.1 \pm 67.13$  buzz units/s, range 230.80–857.10,  $N = 473$  buzz bouts). We grouped the buzz samples into one of these two buzz types using  $k$ -means clustering analysis in R 3.1.1 software (R Core Team, 2014).

We calculated the frequency bandwidth of each buzz bout as the interquartile range of frequencies (range in frequency between 25% and 75% quartiles, in kHz) using the 'seewave' package (Sueur, Aubin, & Simonis, 2008) from R 3.1.1 software. We found a triangular distribution for the relation between frequency bandwidth and buzz rate for both buzz types, disregarding visually identified outliers ( $N = 7$  for the fastest buzz type,  $N = 2$  for the slowest buzz type). These triangular distributions are similar to those found for several songbirds with trilled songs, which shows a trade-off between frequency bandwidth and trill rate (Podos, 1997). We

conducted an upper-bound regression of frequency bandwidth as a function of buzz rate (Podos, 1997), selecting the maximum value of frequency bandwidth in successive 20 buzzes/s intervals across all the range of frequency bandwidth values, and the correspondent buzz rate values. As expected, we found a negative and significant slope for both buzz types analysed ( $R^2 > 0.42$ ,  $P < 0.02$ ). Finally, we estimated vocal deviation for each buzz type as the orthogonal distance between an upper-bound regression line and each buzz bout. We multiplied vocal deviations by  $-1$  to facilitate interpretation: higher vocal deviation values indicate higher vocal performance. We used the average of the two vocal performance measurements as a final measure of vocal performance.

We used spectrogram cross-correlation analysis in Raven Pro<sup>®</sup> 1.4 software (Blackman window, window size = 256, overlap in time grid = 80.1%) to obtain a measurement of vocal consistency (e.g. Manica et al., 2014). We cross-correlated songs from the same recording for each male, excluding recordings with only one song ( $N = 4$ ). Finally, we estimated vocal output from each recorded song bout. Blue-black grassquit male vocal output (songs/min) correlates with territory quality (Manica et al., 2014), and so may be important in parental allocation strategies. We averaged each of these estimated song parameters (i.e. vocal deviation, consistency and output) within recordings and then within males.

#### Leap Display

The leap display of the blue-black grassquit (see Fig. 1c) encompasses high-speed wing beats, thus we used an Exilim FH-25

video camera to videorecord leap displays performed by territorial banded males before or between nesting attempts during the second breeding season (October 2011 to March 2012). We positioned the camera on a tripod 1.7 m high and 10–20 m from the focal male to produce high-speed (240 frames/s) video recordings. We made one to six video recordings of each male (mean  $\pm$  SD =  $1.91 \pm 1.23$ ,  $N = 22$  males), usually on different days. The recordings lasted  $68.81 \pm 67.42$  s (mean  $\pm$  SD,  $N = 42$  recordings) and contained  $13.60 \pm 15.10$  leap displays (mean  $\pm$  SD,  $N = 42$  recordings). We recorded 5–68 leap displays of each male (mean  $\pm$  SD =  $25.95 \pm 16.07$ ,  $N = 22$  males). We analysed the video recordings with the Cowlog 1.1 software (Hänninen & Pastell, 2009). During a leap display, males beat their wings  $4.83 \pm 1.13$  times (mean  $\pm$  SD, range 2–8,  $N = 441$  displays, 22 males), showing their white underwing patches, and vertically rotate their body in relation to the body axis at the peak height of the flight. The highest point in a leap display is attained by the wings (49.1% of displays) or the tail (50.9% of displays;  $N = 566$  displays, 22 males). In leap displays where the tail is the body part that reaches the highest point in flight, it seems necessary that the male rotate the body vertically at a greater angle than when the wings reach the highest point in flight. We speculate that greater rotation angles performed by males during a leap display may be more difficult to perform, signalling male quality (see Byers, Hebets, & Podos, 2010). For each leap display, we estimated duration (s), number of wing beats and wing beat rate (wing beats/s). We averaged these measurements for each recording and then for each male. We also estimated the proportion of displays of each male where the tail reached the highest point in flight, using pooled data from different recordings of each male.

#### Parental Provisioning Behaviour

Blue-black grassquits breed between December and April, a period that corresponds to the second half of the rainy season in the study area. The incubation and nestling periods last approximately 10 days each (Carvalho et al., 2007). We searched for nests and, once they became active, we monitored them in 3-day intervals. We checked nests every day during egg-laying and hatching periods.

We used an unbalanced design to record parental provisioning behaviour at 85 nests during up to three nestling age classes (0–2, 3–5 and 6–8 days after the first egg hatched) and during up to two periods (morning, 0600–1000 hours, or afternoon, 1500–1800 hours). We used Kodak Zx1 video cameras positioned on a mini tripod approximately 50 cm from nests. The video samples were recorded in VGA at  $640 \times 480$  resolution at a rate of 30 frames/s, and recordings lasted  $2.20 \pm 0.46$  h (mean  $\pm$  SD, range 1.12–2.97 h,  $N = 185$  recordings). Video recordings were occasionally interrupted due to oscillations of the camera's battery life. We conservatively only analysed video samples containing more than 1 h of recording.

We were unable to obtain video recordings for all combinations of age classes and periods for any of the social pairs for several reasons. First, monitoring was frequently interrupted before young fledged due to the high nest predation (~80%, Diniz, Ramos, & Macedo, 2011); second, we only found some nests during the nestling period; and finally, due to logistic constraints (e.g. intense rain, more nests than cameras). When possible, we videorecorded some nests repeatedly in the same sample unit (e.g. during the age class 0–2 during the morning) to increase sample size (see Statistical Analysis about controls to avoid pseudoreplication). We estimated age classes of young in nests that were found during the nestling period based on nestling mass and morphology.

Video recordings of provisioning behaviour were analysed using Cowlog 1.1 and VLC 2.05 software. From each sample, we quantified the number of male and female feeding visits to the nest. We excluded from analyses video samples where there were no parental visits to the nest, or when one or both parents appeared hesitant to visit the nest (e.g. alarm calling, nest feeding visits where the food was not delivered; 8.29% of the recordings). For 81 nests we obtained  $2.28 \pm 1.70$  video recordings of parental provisioning behaviour (mean  $\pm$  SD, range 1–9). Parental provisioning behaviour of each social pair during a nesting attempt was recorded at these same nests for  $5.03 \pm 3.87$  h (mean  $\pm$  SD, range 1.29–18.23) pooling all recordings for each nest. Parental activity of 48 males was recorded in  $1.69 \pm 0.99$  nests (mean  $\pm$  SD, range 1–6), while parental activity of 55 females was recorded in  $1.47 \pm 0.66$  nests (mean  $\pm$  SD, range 1–3).

#### Statistical Analyses

All statistical analyses were performed in R 3.1.1 software. We constructed generalized linear mixed models (GLMMs) using the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2014) to verify the effect of male traits (plumage coloration, song and leap display) on male and female provisioning rates. We assumed a Poisson error distribution and a log-link function. We consider number of feeding visits as the response variable and video duration (in h, log) as an offset in all models. We checked all assumptions (absence of outliers, overdispersion, overfitting, collinearity and inflated or truncated zeros) before analyses (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We included nest within pair identity as a nested random effect in all models. We scaled and centred predictor continuous variables before analyses in order to make  $\beta$  estimates.

We used stepwise backward procedures and log-likelihood ratio tests to progressively simplify and select models. We modelled provisioning rates separately for each sex and each male sexual trait (song, plumage coloration and leap display), because breeding pairs changed during breeding seasons and we did not have a large enough sample size for males with all sexual traits sampled.

We separated models into two phases to avoid model overfitting (similar to Limbourg, Mateman, & Lessells, 2012). First, we added only control variables as fixed effects and selected them. Control variables included brood size (1–3 nestlings), period of the day (0600–1200 hours or 1400–1800 hours), date (difference between dates of parental care video recording and the first egg laid in the population in the corresponding breeding season), breeding season (2010–2011 or 2011–2012), brood age (0–2, 3–5, 6–8 days after first egg hatching) and partner's provisioning rate (number of feeding visits/h) (see Adler & Ritchison, 2011; Goodbred & Holmes, 1996; Karell, Kontiainen, Pietiinen, Siitari, & Brommer, 2008). We did not include broods of singleton nestlings in the models with song and display variables because of the small sample size of such broods ( $N = 3$ ). We added fixed predictors of interest (i.e. variables of plumage coloration, song or leap display) to the most parsimonious model from the first phase, and selected them. We did not include the number of wing beats in the analyses of leap display, since this variable was correlated with display duration. Model selection was conducted until no variable could be removed without significant loss of prediction power ( $P < 0.10$ ). Finally, we reinserted control variables removed in the first phase and selected models for the last time.

We show effects of fixed variables with likelihood ratio tests (approximated  $\chi^2$  error distribution), comparing deviance changes between the final model and the final model plus or minus variables of interest. The effects of control variables are shown with data used in the provisioning rate modelled by plumage coloration, because of the larger sample size obtained for this trait. We also

show  $\beta$  estimates  $\pm$  SE as an effect size measurement of each independent variable.

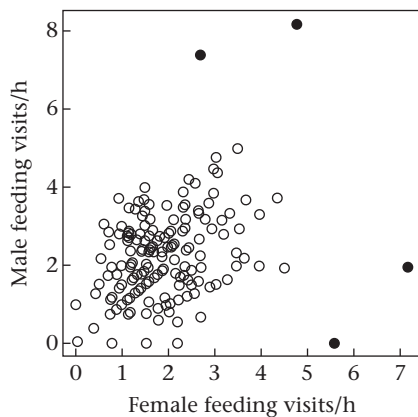
### Ethical Note

All birds were handled and banded with permission from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – IBAMA (permission no. 31601-1) and the Brazilian bird banding agency CEMAVE (no. 3469/1). All procedures were performed in accordance with the ASAB/ABS Guidelines for the treatment of animals used in scientific research. We collected three to eight blue-black feathers from the male's back and two to six feathers from the underwing patch of the left wing. Birds were handled for 15 min on average and individuals showed no discernable negative impacts after release. No territorial bird abandoned its territory after manipulation. Male song and leap displays were recorded at distances greater than the bird's flight initiation distance and did not alter individuals' behaviour. Finally, we covered video cameras with green and brown paper sheeting to avoid disturbance to individuals' provisioning behaviour and nestlings. We found no sign of disruption of nesting behaviour due to our observations at the most studied nests.

## RESULTS

### General Pattern of Provisioning Rate

Both male and female provisioning rates were positively influenced by brood size (likelihood ratio test: male,  $\chi^2_2 = 16.62$ ,  $P = 0.0002$ ; female,  $\chi^2_2 = 11.85$ ,  $P = 0.0027$ ). Only male provisioning rate was positively correlated with brood age (male,  $\chi^2_2 = 18.52$ ,  $P < 0.0001$ ; female,  $\chi^2_2 = 1.39$ ,  $P = 0.50$ ) and differed between periods of the day (male,  $\chi^2_1 = 5.94$ ,  $P = 0.015$ ; female,  $\chi^2_1 = 1.96$ ,  $P = 0.16$ ). Female provisioning rate differed marginally between breeding seasons (male,  $\chi^2_1 = 0.11$ ,  $P = 0.74$ ; female,  $\chi^2_1 = 3.12$ ,  $P = 0.078$ ). Neither male nor female provisioning were affected by date within the breeding season (male,  $\chi^2_1 = 0.63$ ,  $P = 0.43$ ; female,  $\chi^2_1 = 1.36$ ,  $P = 0.24$ ). Although male and female provisioning rates were positively correlated (Pearson correlation:  $r_{162} = 0.35$ ,  $P < 0.0001$ ; Fig. 2), when we look at the final and most parsimonious model for each sex (i.e. controlling for other variables), only female provisioning rate was influenced by the partner's provisioning rate (male,  $\chi^2_1 = 1.17$ ,  $P = 0.28$ ; female,  $\beta = 0.11 \pm 0.04$ ,  $\chi^2_1 = 6.23$ ,  $P = 0.013$ ).



**Figure 2.** Correlation between male and female blue-black grassquit nest provisioning rates ( $N = 164$  video recordings, 39 males, 44 females) (Pearson correlation:  $r_{162} = 0.35$ ,  $P < 0.0001$ ) for a population in central Brazil. The four black circles indicate removed outliers.

### Provisioning Rates and Male Plumage Coloration

Socially paired male and female provisioning rates were influenced by different spectral properties of the male blue-black plumage coloration (Fig. 3). The UV chroma of male blue-black feathers negatively influenced male provisioning rates ( $\beta = -0.12 \pm 0.05$ ,  $\chi^2_1 = 5.78$ ,  $P = 0.016$ ) whereas female provisioning rates were not influenced by this male trait ( $\chi^2_1 = 1.05$ ,  $P = 0.31$ ). On the other hand, female provisioning rates were positively influenced by their partner's blue-black plumage coverage ( $\beta = 0.12 \pm 0.04$ ,  $\chi^2_1 = 7.73$ ,  $P = 0.005$ ), whereas males did not alter their provisioning rates as a function of their blue-black plumage coverage ( $\chi^2_1 = 0.38$ ,  $P = 0.54$ ). Also, male provisioning rates tended to be negatively influenced by the blue chroma of their feathers ( $\beta = -0.09 \pm 0.05$ ,  $\chi^2_1 = 3.35$ ,  $P = 0.067$ ) whereas female provisioning rates were not influenced by this male trait ( $\chi^2_1 = 0.47$ ,  $P = 0.49$ ). Neither male nor female provisioning rates were influenced by the mean brightness of male blue-black feathers (male  $\chi^2_1 = 1.84$ ,  $P = 0.18$ ; female,  $\chi^2_1 = 0.03$ ,  $P = 0.85$ ) or by the white underwing patch mean brightness (male,  $\chi^2_1 = 0.07$ ,  $P = 0.79$ ; female,  $\chi^2_1 = 0.26$ ,  $P = 0.61$ ) and UV chroma (male,  $\chi^2_1 = 0.65$ ,  $P = 0.42$ ; female,  $\chi^2_1 = 0.08$ ,  $P = 0.78$ ).

### Provisioning Rates and Male Song

Neither male nor female provisioning rates were predicted by male song features we measured: vocal performance (male,  $\chi^2_1 = 2.34$ ,  $P = 0.13$ ; female,  $\chi^2_1 = 0.34$ ,  $P = 0.56$ ), vocal consistency (male,  $\chi^2_1 = 1.40$ ,  $P = 0.24$ ; female,  $\chi^2_1 = 0.63$ ,  $P = 0.43$ ) and vocal output (male,  $\chi^2_1 = 0.42$ ,  $P = 0.52$ ; female,  $\chi^2_1 = 0.46$ ,  $P = 0.50$ ).

### Provisioning Rates and Male Leap Display

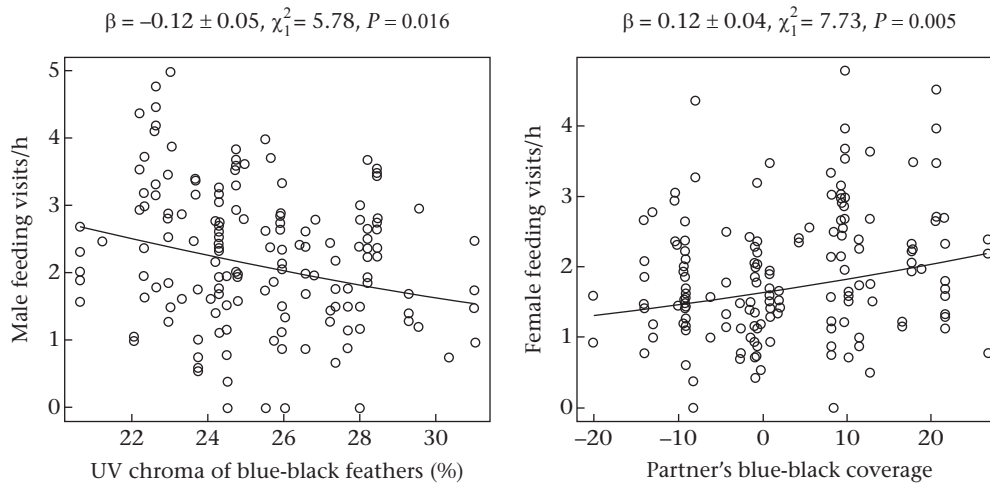
Neither male nor female provisioning rates were influenced by male leap display parameters: display duration (male,  $\chi^2_1 = 0.26$ ,  $P = 0.61$ ; female,  $\chi^2_1 = 0.03$ ,  $P = 0.86$ ), wing beat rate (male,  $\chi^2_1 = 0.02$ ,  $P = 0.88$ ; female,  $\chi^2_1 = 0.01$ ,  $P = 0.91$ ) and the proportion of displays where the tail reached the highest point in flight (male,  $\chi^2_1 = 1.55$ ,  $P = 0.21$ ; female,  $\chi^2_1 = 0.41$ ,  $P = 0.52$ ; Tables 2, 3).

## DISCUSSION

We have shown that multimodal sexual signals of male blue-black grassquits convey information about paternal effort and are associated with female parental effort. In the first part of our study we examined evidence that might be used to verify three hypotheses that are linked to how the male phenotype might be indicative of paternal effort: the good parent hypothesis, the parental–mating trade-off hypothesis and positive differential allocation hypothesis (which also predicts maternal effort). Paternal effort was negatively correlated with UV and tended to be negatively correlated with blue reflectance of blue-black feathers. However, paternal effort was not correlated with partner's provisioning rate. In contrast, female parental effort was positively correlated with their partner's provisioning rate and blue-black plumage coverage.

We found that bluer males (plumage shifted towards higher levels of UV and blue reflectance) provide less food to their offspring. Previous studies of blue-black grassquits have found that older males and males with greater coverage of blue-black plumage are brighter in terms of UV reflectance (Maia, 2008; Maia & Macedo, 2010). Moreover, males with better body condition have brighter, more contrasting and highly saturated plumage in both the UV and blue spectrum (Maia, 2008). Finally, the UV reflectance of blue-black plumages is highly repeatable across years (see Methods), which may signal intrinsic male quality. These





**Figure 3.** Variation in male and female provisioning rates as a function of male blue-black grassquit plumage coloration ( $N = 164$  video recordings, 67 nests, 39 males and 44 females) in central Brazil.

observations, taken together, suggest that males with highly attractive plumages invest less effort in parental care of offspring in their nest in comparison with their drabber peers, which supports the parental–mating trade-off hypothesis (Magrath & Komdeur, 2003) and the positive differential allocation hypothesis (Burley, 1986; Ratikainen & Kokko, 2009) (Table 1). We hypothesize that very attractive grassquit males may derive more fitness benefits by investing in extrapair courtship instead of taking care of their social offspring, which may or may not be their genetic offspring, given the high rates of extrapair fertilization in the species.

Given our results about male attractiveness and paternal effort, we suggest that male blue-black grassquits use conditional mating strategies dependent on their plumage coloration. Assuming that there is a trade-off between parental and mating efforts, less attractive blue-black grassquit males (with lower UV reflectance) may have fewer chances of gaining extrapair copulations, compared with more attractive males. Thus, males with duller plumage should opt for investing heavily in caring for their social offspring. On the other hand, attractive males with UV-shifted plumage should invest in pursuing extrapair copulations and, consequently, invest less in parental duties. A similar pattern, but concerning only social reproductive success, is well documented for house finches, *Haemorhous mexicanus*, where more attractive redder males breed earlier in the breeding season and have lower parental effort compared to yellow males (Badyaev & Hill, 2002). Future studies with blue-black grassquits should verify whether the two male strategies have equivalent fitness.

The second part of our study focused on examining whether male attractiveness might influence maternal parental investment. We sought evidence to test the positive differential allocation

versus the negative differential allocation hypotheses, which have contrasting predictions. We found that female parental effort was positively correlated with their partner's blue-black plumage coverage. The blue-black plumage coverage is a parasite-mediated trait in male blue-black grassquits: males with lighter loads of intestinal parasites (coccidial oocysts) exhibit higher blue-black plumage coverage (Costa & Macedo, 2005). Blue-black coverage also predicts UV reflectance and brightness in grassquit plumage (Maia & Macedo, 2010). Structural and iridescent bird plumages may be costly to produce (Fitzpatrick, 1998) and maintain (Eliason & Shawkey, 2011), thus indicating several aspects of male quality: nutritional condition (McGraw, Mackillop, Dale, & Hauber, 2002), parasite resistance and immune response (Hill, Doucet, & Buchholz, 2005; Møller, Petrie, & Curie, 2002) and body condition (Doucet & Meadows, 2009). Uniformity in the distribution of structural coloration may reflect developmental stability of the plumage (Fitzpatrick, 1998). Therefore, female grassquits should invest more heavily in parental care of offspring sired by males that have greater blue-black plumage coverage, which supports the positive differential allocation hypothesis (Ratikainen & Kokko, 2009).

Although females invested heavily in offspring of males with higher blue-black plumage coverage, female provisioning rate was positively correlated with their partner's provisioning rate, indicating that females do not compensate for lower parental investment of males with high UV-reflecting blue-black feathers. Additionally, male provisioning rate was not predicted by male blue-black coverage. Therefore, these results do not support the prediction of the positive differential allocation hypothesis that highly attractive males should provide low parental care because females are willing to compensate for it (Burley, 1986). Perhaps

**Table 2**  
GLMM final models assuming a Poisson error distribution showing the effect of male plumage colour, song and leap display on male and female provisioning rates

Male trait	Parent	Final model	N	Random effects (SD)	
				Parent	Nest within parent
Plumage coloration	Male	Brood size+brood age+period of day+male UV chroma+male blue chroma	164/67/39	0.18	0.0003
	Female	Brood size+breeding season+partner's provisioning rate+male blue-black plumage coverage	164/67/44	<0.01	0.04
Song	Male	Brood age+partner's provisioning rate	45/30/19	0.08	<0.01
	Female	Brood size+partner's provisioning rate	45/30/19	<0.01	<0.01
Leap display	Male	Brood age+partner's provisioning rate	49/33/21	0.13	<0.01
	Female	Partner's provisioning rate	49/33/21	<0.01	<0.01

N = video recordings per nest per parent (male or female).

**Table 3**  
GLMM final models  $\beta$  estimates  $\pm$  SE for predictors of male and female blue-black grassquit provisioning rates

Male traits and model predictors	Male		Female	
	$\beta$	SE	$\beta$	SE
<b>Plumage coloration</b>				
Intercept	0.74	0.08	0.28	0.12
Breeding season			-0.16	0.09
Brood size (1)	-0.52	0.15	-0.04	0.14
Brood size (3)	0.14	0.10	0.34	0.09
Brood age (0–2)	-0.26	0.09		
Brood age (6–8)	0.15	0.09		
Partner's provisioning rate			0.11	0.04
Period of day (1400–1800)	0.21	0.09		
Blue-black coverage			0.12	0.04
UV chroma	-0.12	0.05		
Blue chroma	-0.09	0.05		
<b>Song</b>				
Intercept	0.30	0.23	0.005	0.18
Brood age (0–2)	-0.18	0.18		
Brood age (6–8)	0.27	0.18		
Brood size (3)			0.32	0.16
Partner's provisioning rate	0.26	0.10	0.16	0.06
<b>Leap display</b>				
Intercept	0.34	0.22	0.36	0.15
Brood age (0–2)	-0.10	0.18		
Brood age (6–8)	0.35	0.16		
Partner's provisioning rate	0.20	0.09	0.13	0.05

Predictors include male secondary sexual traits (plumage coloration, song and leap display) and life history and environmental traits (period of the day, brood size and age, breeding season and date within the breeding season).

blue-black grassquit females are behaving according to the positive differential allocation hypothesis, but show phenotypic plasticity in response to the male's parental effort strategy. To disentangle the magnitude of these effects upon female provisioning rate, future studies should experimentally manipulate both the blue-black plumage coverage (e.g. Limbourg, Mateman, Andersson, & Lessells, 2004) and provisioning rates (e.g. Schwagmeyer, Mock, & Parker, 2002) of blue-black grassquit males, to observe the parental effort response of their social partners. In conclusion, our results provide only partial support for the positive differential allocation hypothesis (Burley, 1986; Ratikainen & Kokko, 2009) (Table 1).

The ability to repeatedly perform energetic displays (i.e. vigour) and to mechanically perform difficult motor tasks well (i.e. skill) may be better indicators of male genetic quality than static ornaments (Byers et al., 2010). For instance, the display performance of the golden-collared manakin, *Manacus vitellinus*, male predicts female attraction to male courtship arenas (Barske, Schlinger, Wikelski, & Fusani, 2011), and the ability to perform vocal signals close to the physical limit influences mate choice in swamp sparrows, *Melospiza georgiana* (Ballentine, Hyman, & Nowicki, 2004). In our study, we considered how females might respond in terms of offspring provisioning to male display measurements reflecting vigour and skill: display duration, wing beat rate and vertical rotation during flight. However, we found no evidence for the hypothesis that leap display skills modulate either male or female parental effort. In addition, we did not find any effect of our measurements of male song (vocal performance, consistency and output) on male or female parental effort. Our results thus do not conform well to the predictions of current hypotheses that suggest explanations for the covariation between secondary sexual traits and parental effort in socially monogamous birds.

Clearly, the association between male attractiveness and parental effort in males and females is not easily understood when one considers multiple male secondary sexual signals. Particularly, it is challenging to explain why some male ornamental traits predict

parental effort by males or females, whereas other traits do not, even when considering parental effort in an opposite direction. For instance, both song and plumage coloration of male pied flycatchers, *Ficedula hypoleuca*, are attractive to females, but only plumage coloration seems to affect female parental effort (Lampe & Sætre, 1995; Osorno et al., 2006; Rinden, Lampe, Slagsvold, & Espmark, 2000; Sætre, Dale, & Slagsvold, 1994). Untangling the content and temporal relevance of messages conveyed in multiple secondary sexual signals will not be an easy task. Presently, we believe our study is the only one that has investigated the relation between parental effort and sexual attractiveness in a multimodal signal context. Therefore, we strongly urge future studies to consider the effects of multiple signals on breeding strategies to understand fully the role of secondary sexual signals in parental investment strategies.

## Acknowledgments

We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarship granted to P.D., the fellowship for R.H.M. and for research financial assistance. We thank Fundação de Empreendimentos Científicos e Tecnológicos (FINATEC) for funding part of the research and the Universidade de Brasília for logistic support. We also thank Fernanda de Lacerda, Guilherme Marques and Jaqueline Menezes for help with field work. Finally, we are grateful to Eduardo Santos, Glauco Machado and two anonymous referees for suggestions that improved this manuscript. This study was carried out with permission from IBAMA (permission no. 31601-1) and license from CEMAVE (no. 3469/1).

## References

- Adler, J., & Ritchison, G. (2011). Provisioning behavior of male and female grasshopper sparrows. *Wilson Journal of Ornithology*, 123, 515–520.
- Aguilar, T. M., Maia, R., Santos, E. S. A., & Macedo, R. H. (2008). Parasite levels in blue-black grassquits correlate with male displays but not female mate preference. *Behavioral Ecology*, 19, 292–301.
- Alderton, C. C. (1963). The breeding behavior of blue-black grassquit. *Condor*, 65, 154–162.
- Alonso-Alvarez, C., Pérez-Rodríguez, L., Ferrero, M. E., García de-Blas, E., Casas, F., & Mougeot, F. (2012). Adjustment of female reproductive investment according to male carotenoid-based ornamentation in a gallinaceous bird. *Behavioral Ecology and Sociobiology*, 66, 731–742.
- Badyaev, A. V., & Hill, G. E. (2002). Paternal care as a conditional strategy: distinct reproductive tactics associated with elaboration of plumage ornamentation in the house finch. *Behavioral Ecology*, 13, 591–597.
- Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: an experimental test. *Behavioral Ecology*, 15, 163–168.
- Barske, J., Schlinger, B. A., Wikelski, M., & Fusani, L. (2011). Female choice for male motor skills. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3523–3528.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4*. Retrieved from <http://CRAN.R-project.org/package=lme4>.
- Bioacoustics Research Program. (2011). *Raven Pro: Interactive Sound Analysis Software (Version 1.4) [Computer software]*. Ithaca, NY: Cornell Lab of Ornithology. Retrieved from <http://www.birds.cornell.edu/raven>.
- Bluhm, C. K., & Gowaty, P. A. (2004). Reproductive compensation for offspring viability deficits by female mallards, *Anas platyrhynchos*. *Animal Behaviour*, 68, 985–992.
- Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, 25, 292–300.
- Bro-Jørgensen, J., & Dabelsteen, T. (2008). Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. *BMC Biology*, 6, 1–8.
- Burley, N. (1986). Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, 127, 415–445.
- Byers, J., Hebets, E., & Podos, J. (2010). Female mate choice based upon male motor performance. *Animal Behaviour*, 79, 771–778.
- Carvalho, C. B. V., Macedo, R. H. F., & Graves, J. A. (2007). Reproduction of blue-black grassquits in central Brazil. *Brazilian Journal of Biology*, 67, 275–281.
- Costa, F. J. V., & Macedo, R. H. F. (2005). Coccidian oocyst parasitism in the blue-black grassquit: influence on secondary sex ornaments and body condition. *Animal Behaviour*, 70, 1401–1409.



- Dias, A. F. S. (2009). *Comparação e descrição de parâmetros acústicos do canto de Volatinia jacarina (Aves: Emberizidae) no contexto de seleção sexual*. Brasília, Brazil: Universidade de Brasília (Master's thesis).
- Diniz, P., Ramos, D. M., & Macedo, R. H. (2011). [Nest predation rate for a subset of nests monitored in the present study]. Unpublished raw data.
- Doucet, S. M. (2002). Structural plumage coloration, male body size, and condition in the blue-black grassquit. *Condor*, *104*, 30–38.
- Doucet, S. M., & Meadows, M. G. (2009). Iridescence: a functional perspective. *Journal of the Royal Society Interface*, *6*, 115–132.
- Eliason, C. M., & Shawkey, M. D. (2011). Decreased hydrophobicity of iridescent feathers: a potential cost of shiny plumage. *Journal of Experimental Biology*, *214*, 2157–2163.
- Fandiño-Mariño, H., & Viellard, M. E. (2004). Complex communication signals: the case of the blue-black grassquit *Volatinia jacarina* (Aves, Emberizidae) song. Part I: a structural analysis. *Anais da Academia Brasileira de Ciências*, *76*, 325–334.
- Fitzpatrick, S. (1998). Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici*, *35*, 67–77.
- Freeman-Gallant, C. R., Taff, C. C., Morin, D. F., Dunn, P. O., Whittingham, L. A., & Tsang, S. M. (2009). Sexual selection, multiple male ornaments, and age- and condition-dependent signaling in the common yellowthroat. *Evolution*, *64*, 1–11.
- Galeotti, P., Rubolini, D., Fea, G., Ghia, D., Nardi, P. A., Gherardi, F., et al. (2006). Female freshwater crayfish adjust egg and clutch size in relation to multiple male traits. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1105–1110.
- Germain, R. R., Reudink, M. W., Marra, P. P., & Ratcliffe, L. M. (2010). Carotenoid-based male plumage predicts parental investment in the American redstart. *Wilson Journal of Ornithology*, *122*, 318–325.
- Goodbred, C. O. N., & Holmes, R. T. (1996). Factors affecting food provisioning of nestling black-throated blue warblers. *Wilson Bulletin*, *108*, 467–479.
- Gowaty, P. A. (2008). Reproductive compensation. *Journal of Evolutionary Biology*, *21*, 1189–1200.
- Gowaty, P. A., Drickamer, L. C., & Schmid-Holmes, S. (2003). Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer. *Animal Behaviour*, *65*, 95–103.
- Hänninen, L., & Pastell, M. (2009). CowLog: open source software for coding behaviors from digital video. *Behavior Research Methods*, *41*, 472–476.
- Harris, W. E., & Uller, T. (2009). Reproductive investment when mate quality varies: differential allocation versus reproductive compensation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 1039–1048.
- Hartley, R. S. (1990). Expiratory muscle activity during song production in the canary. *Respiration Physiology*, *81*, 177–188.
- Hebets, E. A., & Papaj, D. R. (2004). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, *57*, 197–214.
- Hill, G. E., Doucet, S. M., & Buchholz, R. (2005). The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Animal Behaviour*, *69*, 387–394.
- Hoelzer, G. A. (1989). The good parent process of sexual selection. *Animal Behaviour*, *38*, 1067–1078.
- Horvátová, T., Nakagawa, S., & Uller, T. (2012). Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 163–170.
- Karell, P., Kontiainen, P., Pietinen, H., Siitari, H., & Brommer, J. E. (2008). Maternal effects on offspring Igs and egg size in relation to natural and experimentally improved food supply. *Functional Ecology*, *22*, 682–690.
- Kokko, H. (1998). Should advertising parental care be honest? *Proceedings of the Royal Society B: Biological Sciences*, *265*, 1871–1878.
- Lampe, H. M., & Sætre, G. (1995). Female pied flycatchers prefer males with larger song repertoires. *Proceedings of the Royal Society B: Biological Sciences*, *262*, 163–167.
- Limbourg, T., Mateman, A. C., Andersson, S., & Lessells, C. M. (2004). Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 1903–1908.
- Limbourg, T., Mateman, A. C., & Lessells, C. M. (2012). Parental care and UV coloration in blue tits: opposite correlations in males and females between provisioning rate and mate's coloration. *Journal of Avian Biology*, *43*, 1–10.
- Limbourg, T., Mateman, A. C., & Lessells, C. M. (2013). Opposite differential allocation by males and females of the same species. *Biology Letters*, *9*, 1–4.
- Linville, S., Breitwisch, R., & Schilling, A. (1998). Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*, *55*, 119–127.
- Macedo, R. H. F., Manica, L., & Dias, R. I. (2012). Conspicuous sexual signals in a socially monogamous passerine: the case of neotropical blue-black grassquits. *Journal of Ornithology*, *153*, 15–22.
- Magrath, M. J. L., & Komdeur, J. (2003). Is male care compromised by additional mating opportunity? *Trends in Ecology & Evolution*, *18*, 424–430.
- Maguire, S. E., & Safran, R. J. (2010). Morphological and genetic predictors of parental care in the North American barn swallow *Hirundo rustica erythrogaster*. *Journal of Avian Biology*, *41*, 74–82.
- Mahr, K., Griggio, M., Granatiero, M., & Hoi, H. (2012). Female attractiveness affects paternal investment: experimental evidence for male differential allocation in blue tits. *Frontiers in Zoology*, *9*, 1–8.
- Maia, R. (2008). *Coloração estrutural iridescente do tiziu (Volatinia jacarina, Aves: Emberizidae): mecanismos de produção, variação e função* (Master's thesis). Brasília, Brazil: Universidade de Brasília.
- Maia, R., Caetano, J. V. O., Bão, S. N., & Macedo, R. H. (2009). Iridescent structural colour production in male blue-black grassquit feather barbules: the role of keratin and melanin. *Journal of the Royal Society Interface*, *6*, 203–211.
- Maia, R., Eliason, C. M., Bitton, P. P., Doucet, S. M., & Shawkey, M. D. (2013). pavo: an R package for the analysis, visualization and organization of spectral color data. *Methods in Ecology and Evolution*, *4*, 906–913.
- Maia, R., & Macedo, R. H. (2010). Achieving luster: pre-nuptial molt pattern predicts iridescent structural coloration in blue-black grassquits. *Journal of Ornithology*, *152*, 243–252.
- Manica, L. T., Maia, R., Dias, A., Podos, J., & Macedo, R. H. (2014). Vocal output predicts territory quality in a neotropical songbird. *Behavioural Processes*, *109*, 21–26.
- Mazuc, J., Chastel, O., & Sorci, G. (2003). No evidence for differential maternal allocation to offspring in the house sparrow (*Passer domesticus*). *Behavioral Ecology*, *14*, 340–346.
- McGraw, K. J., Mackillop, E. A., Dale, J., & Hauber, M. E. (2002). Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, *205*, 3747–3755.
- Mitchell, D., Dunn, P., Whittingham, L., & Freeman-Gallant, C. (2007). Attractive males provide less parental care in two populations of the common yellowthroat. *Animal Behaviour*, *73*, 165–170.
- Møller, A. P., Petrie, M., & Curie, M. (2002). Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behavioral Ecology*, *13*, 248–253.
- Montgomerie, R. (2006). Analyzing colors. In G. E. Hill, & K. J. McGraw (Eds.), *Bird coloration: Mechanisms and measurements* (pp. 90–147). Cambridge, MA: Harvard University Press.
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*, 935–956.
- Osorno, J. L., Morales, J., Moreno, J., Merino, S., Tomás, G., & Vázquez, R. A. (2006). Evidence for differential maternal allocation to eggs in relation to manipulated male attractiveness in the pied flycatcher (*Ficedula hypoleuca*). *Journal of Ornithology*, *147*, 605–611.
- Pizzolon, M., Locatello, L., Warner, R. R., Chimento, N., Finos, L., & Rasotto, M. B. (2011). Linking male qualities to multiple display traits: an example in a fish with exclusive male care. *Behavioral Ecology and Sociobiology*, *66*, 497–504.
- Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution*, *51*, 537–551.
- R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>.
- Ratikainen, I. I., & Kokko, H. (2009). Differential allocation and compensation: who deserves the silver spoon? *Behavioral Ecology*, *21*, 195–200.
- Rinden, H., Lampe, H. M., Slagsvold, T., & Espmark, Y. O. (2000). Song quality does not indicate male parental abilities in the pied flycatcher *Ficedula hypoleuca*. *Behaviour*, *137*, 809–823.
- Rutstein, A. N., Gilbert, L., & Tomkins, J. L. (2005). Experience counts: lessons from studies of differential allocation. *Behavioral Ecology*, *16*, 957–960.
- Sanz, J. J. (2001). Experimentally reduced male attractiveness increases parental care in the pied flycatcher *Ficedula hypoleuca*. *Behavioral Ecology*, *12*, 171–176.
- Sætre, G., Dale, S., & Slagsvold, T. (1994). Female pied flycatchers prefer brightly coloured males. *Animal Behaviour*, *48*, 1407–1416.
- Schielzeth, H., & Nakagawa, S. (2013). *rptR: Repeatability for Gaussian and non-Gaussian data*. Retrieved from <http://R-Forge.R-project.org/projects/rprr>.
- Schwagmeyer, P. L., Mock, D. W., & Parker, G. A. (2002). Biparental care in house sparrows: negotiation or sealed bid? *Behavioral Ecology*, *13*, 713–721.
- Schwagmeyer, P. L., Parker, G. A., Mock, D. W., & Schwabl, H. (2012). Alternative matings and the opportunity costs of paternal care in house sparrows. *Behavioral Ecology*, *23*, 1108–1114.
- Senar, J. C., Figuerola, J., & Pascual, J. (2002). Brighter yellow blue tits make better parents. *Proceedings of the Royal Society B: Biological Sciences*, *269*, 257–261.
- Sheldon, B. C. (2000). Differential allocation: tests, mechanisms and implications. *Trends in Ecology & Evolution*, *15*, 397–402.
- Siefferman, L., & Hill, G. E. (2003). Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology*, *14*, 855–861.
- Stiver, K. A., & Alonzo, S. H. (2009). Parental and mating effort: is there necessarily a trade-off? *Ethology*, *115*, 1101–1126.
- Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*, 213–226.
- Taylor, R. C., Buchanan, B. W., & Doherty, J. L. (2007). Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. *Animal Behaviour*, *74*, 1753–1763.
- Trillo, P. A., & Vehrencamp, S. L. (2005). Song types and their structural features are associated with specific contexts in the banded wren. *Animal Behaviour*, *70*, 921–935.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. G. Campbell (Ed.), *Sexual selection and the descent of man 1871–1971* (pp. 136–179). Chicago, IL: Aldine.
- Weiss, M., Kiefer, S., & Kipper, S. (2012). Buzzwords in females' ears? The use of buzz songs in the communication of nightingales (*Luscinia megarhynchos*). *PLoS One*, *7*, e45057.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models an extensions in ecology with R*. New York, NY: Springer.