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Original Article

Vigor and skill in the acrobatic mating displays of a Neotropical songbird

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Animal social behaviors are often mediated by signals that provide information about signaler attributes. Although some signals are structurally simple, others are temporally dynamic and multifaceted. In such cases, exaggeration of some display components is likely to curtail the expression of others. We quantified features of the acrobatic, multimodal “leap display” of blue-black grassquits (*Volatinia jacarina*), which appears to entail moderate-to-high performance levels in terms of vigor and skill. We video recorded and quantified leap parameters (height, duration, rotation angle, launch velocity, and number of wing beats) and assessed how these parameters covaried with each other and with vocal parameters, display rates, and body mass index. Our analyses revealed correlations among multiple performance variables: leap height, duration, launch velocity, and number of wing beats. Leap height also correlated positively with song duration. By contrast, no leap parameters covaried with rotation angle. Our analyses also revealed a trade-off in vigor and skill-based leap attributes: birds with a lower body mass index showed a negative relationship between leap heights and the proportion of displays that included leaps (vs. perched vocalizations only). Our results identify directions of display evolution subject to mechanical or timing constraints and provide evidence that display attributes that emphasize vigor and skill may limit one another. Our results also support a key expectation of handicap models of display evolution, which is that costs of display execution should be borne disproportionately by signalers of lower quality.

Key words: birds, motor display, multimodal signal, performance, sexual selection, *Volatinia jacarina*.

Sexual selection often favors signals that are elaborate and conspicuous, such as the long tails of birds, the bright colors of fishes, or the long-duration calls of frogs (e.g., Andersson 1982; Ryan et al. 1990; Petrie 1994). Although many classic studies of sexual selection focused on single traits, attention has recently turned to multimodal signals that stimulate multiple sensorial channels (e.g., vibrational/chemical signals in ants: Hölldobler 1999; visual/acoustic signals in birds: Götmark and Ahlström 1997; Cooper and Goller 2004; and vibrational/visual signals in spiders: Taylor et al. 2006; Elias et al. 2012). Even within given modalities, signals can vary in numerous dimensions, such as in timing, amplitude, and frequency variation within vocal signals or in hue, saturation, and chromatic variation within visual signals (Bradbury and Vehrencamp 2011).

Complex signals are often assessed from a functional perspective, so that questions focus on determining whether different signal

components convey information that is redundant or distinctive (e.g., Doucet and Montgomerie 2003; Gibson and Uetz 2008; McElroy et al. 2007; Wilgers and Hebets, 2011). In the redundant (or backup) signal hypothesis, it is assumed that multiple sexual traits convey information about the same aspect of quality, with some error, and thus allow a more accurate evaluation of mate quality (Møller and Pomiankowski 1993; Johnstone 1997). On the other hand, the multiple messages hypothesis proposes that different signals convey distinctive information about different qualities of the male (Møller and Pomiankowski 1993; Johnstone 1997). Another approach to studying complex signals, which has gained traction in recent years, focuses on display mechanics and performance (e.g., Barske et al. 2011; Reichert and Gerhardt, 2012; Wagner et al. 2012; Irschick et al. 2015). Such an approach can identify constraints on the evolution of signal elaboration that circumscribe or even run counter to selection pressures. For instance, in gray tree frogs (*Hyla versicolor*), the duration of vocal advertisement signals (calls) reliably indicates caller genetic quality and is favored by females (Welch et al. 1998), yet is seen to trade-off with calling rate (Klump and Gerhardt 1987, see also Reichert and Gerhardt 2012). Frogs that maximize one

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parameter are apparently unable to maximize the other, due to timing and mechanical constraints.

Animal mating displays may be difficult to perform in terms of both vigor and skill. The distinction, first made by Darwin (1871), has been highlighted in several recent reviews (Byers et al. 2010; Clark 2012) and provides a useful conceptual framework here. When displays are vigorous, energy budgets can be taxed (e.g., Vehrencamp et al. 1989; Hoglund et al. 1992), and display rates may thus provide reliable indicators of signaler condition and metabolic capacity (i.e., animals' ability to bear "joule costs" of sustained exertion, Clark 2012). This scenario is consistent with handicap theory, wherein animals in comparatively good condition are presumed to be better able to bear the costs of producing elaborate displays (Zahavi 1975; Mappes et al. 1996; Brandt 2003; Clancey and Byers 2014; Wilgers and Hebets 2015). Display skill, by contrast, is defined more in terms of the parameters by which rapid and precisely coordinated movements are executed (Bostwick and Prum 2003; Clark and Dudley 2009; Barske et al. 2011). One common characteristic of high-skill displays is that they are power limited, meaning that the execution of displays is constrained by attributes related to biomechanics, muscle architecture, and metabolic physiology (Clark 2012). High-skill displays might also be limited by the ability to develop the coordination necessary for successful display execution (Podos 1996). Skill-related display attributes likely provide reliable information about signalers' whole-organism performance abilities. In other real-life situations, such abilities may be associated with greater capacity for evading predators and foraging, for example, and may explain female preference for skilled execution of specific display attributes (Byers et al. 2010).

Our study focuses on the mechanics of elaborate mating displays in blue-black grassquits, *Volatinia jacarina* (Linnaeus, 1766), a common Neotropical passerine. During the breeding season, males engage in "leap displays" that include motor and vocal components (Supplementary Material, Video S1; Alderton 1963; Almeida and Macedo 2001; Macedo et al. 2012; Manica et al. 2013). Each leap display comprises a vertical flight and descent, typically starting and ending on the same perch, synchronized with forward body rotation and the exhibition of white wing patches. Male nuptial plumage is iridescent and includes an ultraviolet component, which combined with the white wing patches appears to enhance the conspicuousness of leaps, especially under direct sunlight (Maia et al. 2009; Sicsú et al. 2013). Each leap display also includes a short vocalization, which is frequently produced independently ("perched vocalization") and which varies in acoustic structure across individuals and localities (Fandiño-Mariño and Vielliard 2004). This short vocalization (song) is composed of a single note ranging between 2 kHz and 13 kHz that decreases in frequency modulation from beginning to end (Fandiño-Mariño and Vielliard, 2004) and is repeated at short intervals of about 2 s, whether or not accompanied by the leap display. Bouts of the display (with leap or perched) can vary from just a couple to a dozen or more.

Our work with blue-black grassquits has led us to posit that this species' displays are shaped by constraints linked to both vigor and skill. In terms of vigor, grassquits often produce displays over prolonged bouts and in quick succession, at average rates up to 19.8 leaps per minute. For example, during separate observation periods, individual birds were seen to execute 535 leap displays over 30 min (Manica LT, unpublished data), 370 leap displays for 27 min (Manica et al. 2013), and 99 displays for 5 min (data from Sicsú et al. 2013). Few other avian species execute aerial displays at such high intensity (Hedenström 1995). In terms of skill, blue-black grassquit

displays involve a number of motor components (described in the next paragraph) that are rapid, highly coordinated, and consistent in form across display events. Limited data presently available for grassquits provisionally suggest that leap displays reflect variation in male attributes. Most notably, Carvalho et al. (2006) showed that male grassquits who bred successfully leapt higher and at faster rates than grassquits who had failed to breed, suggesting a potential link between display performance and reproductive fitness. Other studies of grassquits described positive correlations between leap parameters (leap rate, leap height, and the duration of leap display bouts) and measures of male condition, including parasite load and plumage condition/molt stage (Doucet 2002; Costa and Macedo 2005; Aguilar et al. 2008; Maia and Macedo 2011). Yet neither the detailed nature of the leap nor the relationships among leap display components have been thoroughly quantified. The first aim of our study was thus to document leap display patterns precisely using a combination of high-speed videography and audio recordings. Secondly, we tested for correlations and trade-offs among display parameters, both within and across modalities, and to assess whether and how display parameters covary with select male attributes.

Inspection of high-speed video clips (Supplementary Material, Video S2; see Methods) allowed us to describe leaps with increased precision. To initiate a leap, a bird crouches down and then springs upward, pushing off from the perch until his legs are extended. While leaving the perch, the bird raises his wings and performs a forceful downstroke, apparently creating rapid upward thrust. The bird continues to flap his wings during the remainder of the display, yet after the first downstroke, he appears to shift speed in subsequent upstrokes. At the end of upstrokes in some males, we observe that the wings make dorsal contact, apparently accounting for "snaps" detectable on audio tracks (analogous to wing snaps in manakin species, e.g., Bostwick and Prum 2003). It would appear that in the latter part of the wingbeat cycle, the strokes do not provide further upward thrust and thus may be nonfunctional and purely skill based. Upward wing strokes are accompanied by forward body rotation, resulting in a head-down orientation at the leap peak. This rotation appears to facilitate presentation of white underwing patches, in part by enhancing plumage iridescence (Sicsú et al. 2013). At the leap peak, the bird's beak opens, suggesting call initiation. Calling and upstrokes continue, and forward body posture is maintained until the bird nears the perch at which time he reduces the magnitude of wing flaps, rotates backward, extends his wings laterally, and alights. The beak typically remains open, and the call is presumed to continue after the bird has landed.

These observations led us to the 4 following predictions about leap mechanics and male attributes. 1) Given the apparent shift in speed from the initial downstroke to subsequent upstrokes, we predicted that leap duration and height are determined by initial launch velocity. 2) Vocal duration or performance (defined here as frequency bandwidth, see Methods) correlate with leap height or forward body rotation angle because of likely shared mechanical elements between the 2 display modalities (Cooper and Goller 2004). 3) Birds leaping with the greatest vigor (i.e., leap rates) experience reductions in the maximal performance of individual leaps (e.g., leap heights or rotation angle) and vocal parameters because of energetic, mechanical, or timing trade-offs between leap quantity and quality (Patricelli and Krakauer 2010). 4) Birds' energy reserves, represented here as a mass to size ratio (see Methods), influence their display performance, with birds with lower reserves having more difficulty maintaining high levels of display vigor or skill.

METHODS

We collected data during 4 breeding seasons (October to February; 2008–2009, 2009–2010, 2010–2011, and 2011–2012) at the campus of Universidade de Brasília (15°44'S 47°52'W) and at Fazenda Água Limpa (15°56'S 47°56'W), in central Brazil. Field sites (ca., 6 ha each) consisted of an abandoned orchard, altered grasslands, and shrubby savanna vegetation.

Study populations

Blue-black grassquits migrate to their breeding grounds in Brasília, typically arriving in October or November. Males quickly establish territories, display, and actively confront and chase territorial intruders. Territories are small, approximately 13–72 m², and often in close proximity to each other (Almeida and Macedo 2001). As in many songbirds, males tend to display most during morning hours, especially under direct sunlight (Sicsú et al. 2013). Females are more difficult to observe but can be seen moving across our study plots, presumably assessing potential mates. Pairing status can be inferred by the consistent presence of females at specific territories and confirmed by nest construction. Blue-black grassquits are socially monogamous, and both parents participate in parental care (Diniz et al. 2015), yet extrapair mating is common (Carvalho et al. 2006; Macedo et al. 2008; Manica, Graves et al. 2016).

Morphological data and body mass index

From October to December in each breeding season, we mist netted birds (0700 h to 1200 h) 3 times weekly and marked them with unique combinations of 3 colored plastic bands and 1 numbered aluminum band supplied by the Brazilian Bird Banding Agency (CEMAVE/ICMBio). From January to March, we mist netted previously unmarked territory holders. For each bird, we measured body mass with a spring scale and tarsus length with calipers.

We calculated a body mass index simply by dividing body mass by tarsus length. This index estimates birds' fat reserves or muscle tissues relative to skeletal size. In the blue-black grassquit, the body mass index has previously been found to correlate negatively with both intestinal parasite load (Costa and Macedo 2005; Aguilar et al. 2008) and social dominance (Santos et al. 2009). Although the utility of body mass indices as measures of quality is a subject of ongoing debate (e.g., Vervust et al. 2008), linking specific biological parameters such as parasite load and social dominance to putative indexes of condition can help justify their use (Clancey and Byers 2014; Wilgers and Heberts 2015).

Behavioral data

We video recorded leap displays of males, for 1 to 3 days, at 30 frames per second (normal-speed videos) with a mini-dv Canon XL1 digital camcorder or a Casio EX-FH25 HD digital camera. From these recordings, we identified a sample of high-quality clips with the bird in focus and at a lateral angle. We analyzed 345 normal-speed video clips from 36 birds (9.6 ± 1.4 clips per bird), all of which also had morphological data. The mean time interval between video recordings and morphological measurement was 31.9 ± 23.0 days. Videos from both camcorders were transferred to a computer and clips for analysis were identified. To measure 2 of the main parameters of interest, leap height and forward body rotation, we identified for each video clip the frames corresponding to 1) the beginning of the leap, that is, the frame before the bird left the perch or flapped its wings to initiate the leap and 2) the maximum height of the leap. We used the program ImageJ®

v. 1.45s (Schneider et al. 2012) to measure leap height, as the distance between the subject's beak at the peak of the leap and a horizontal line at the perch. This distance measure was calibrated to the mean head height, which was visible in video frames and also measured from a sample of grassquit specimens in hand (mean head height = 13.5 ± 0.87 mm, range = 12.35 to 14.45 mm, *n* = 6). Finally, we measured rotation angle as the angle between 2 lines drawn using the bird's longitudinal body axis at the beginning and at the peak of the leap (Figure 1). To connect the base of the upper beak to the distal visible point of the tail, the longitudinal axis was drawn, at each time frame.

Using the Casio camera, we also filmed leap displays at 240 frames per second (high-speed videos). These were analyzed from 10 of the 36 birds for which we had normal-speed videos, plus an additional 8 birds for which we did not have morphological measures; across these 18 birds, we analyzed a total of 54 clips (3 clips per bird extracted from videos in which birds were in focus and at a lateral angle). For high-speed video clips, we measured leap height and rotation angle as described above; as expected, values of these 2 parameters closely approximated those calculated from our normal-speed videos (Table 1). Analysis of high-speed video clips enabled us to quantify 3 additional parameters: launch velocity, number of wing beats per leap, and leap duration. Launch velocity was calculated as the distance traversed by the beak between the frame wherein the bird left the perch and the frame wherein the first wing downstroke was completed, divided by the time interval between these 2 frames. The number of wing beats was calculated by counting complete up and down wing flaps after the bird left the perch and before he touched it again with both feet. Leap duration was calculated as the time interval between the frame wherein the bird left the perch and the frame in which he touched it again with both feet. For analysis, we calculated averages of all 5 parameters for each individual, because these parameters are repeatable (see Results). Finally, from high-speed video clips, we calculated leap

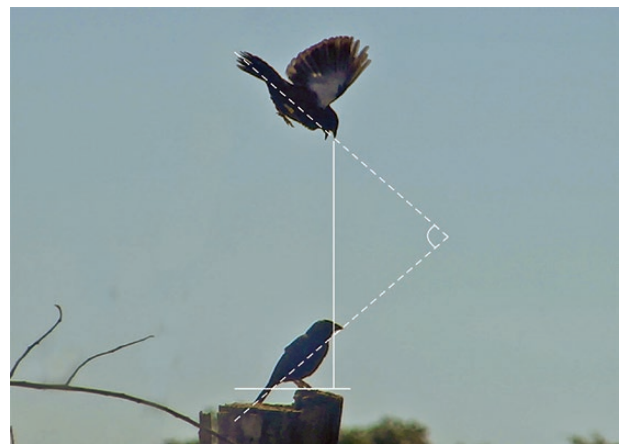


Figure 1

Illustration of measurement of leap height and body rotation angle for a leap display, showing male at the start and then again at the peak of the display leap. Leap height (vertical solid line) was calculated as the perpendicular distance between the perch and the beak tip at the highest point of the leap (horizontal solid line). Leap height thus represents the vertical translation of the lowest part of the bird, which is initially the feet but as the bird rotates forward becomes the beak tip at the leap apex. Body rotation angle was measured as the angle between body axes at the leap start and peak (diagonal dashed lines, extended from tail through base of beak).

Table 1

Leap motor parameters (rows 1–5) and leap display rate (row 6) estimated from normal- and high-speed video recordings, ranges, means, and SD all calculated from per-bird averages. Accurate estimates of leap duration, launch velocity, and number of wing beats could only be obtained from high-speed video samples.

	Normal-speed videos (<i>n</i> = 36)		High-speed videos (<i>n</i> = 18)	
	Range (min–max)	Mean ± SD	Range (min–max)	Mean ± SD
Leap height (cm)	9.8–33.7	19.5 ± 5.5	11.6–34.3	17.6 ± 5.4
Rotation angle (deg)	51.8–128.3	82.7 ± 18.7	62.4–85.4	76.9 ± 7.7
Leap duration (s)	—	—	0.38–0.78	0.49 ± 0.09
Launch velocity (cm/s)	—	—	64.4–114.0	89.3 ± 15.8
Number of wing beats	—	—	2.0–6.7	4.2 ± 1.4
Leap display rate (leaps/min)	0 ^a –15.2	5.8 ± 4.6	1.0–10.4	2.7 ± 2.2

SD = standard deviation.

^aThe 0 value is from a bird who conducted only perched vocalizations (no leaps) during normal-speed videotaped sequences.

display rates as the number of leap displays executed divided by the cumulative leap display bout duration (we define bouts as observed sequences of 2 or more displays).

We conducted focal observations of males from which we also had morphological samples and also videotapes via annotations or narration into a portable audio recorder. Each bird was followed for approximately 30 min, between 0700 h and 1000 h, during 1 to 3 days for periods of up to 2 weeks. These observations were conducted so that there was no overlap with male nesting activities (also monitored), because males reduce display rates when nesting (Alderton 1963, L. Manica and R. Macedo, personal observation). During each focal observation, we noted the occurrence of leap displays and perched vocalizations, from which we calculated 2 variables: display rate (sum of leap displays plus perched vocalizations divided by the cumulative duration of focal observation) and proportion of leap displays relative to total displays (leap displays plus perched vocalizations).

We conducted focal audio recordings of males' vocalizations using a digital Marantz PMD 660 recorder (16-bit precision and 44.1 Hz sampling rate), coupled to a Sennheiser K6/ME66 unidirectional microphone or a Sennheiser K6/ME62 omnidirectional microphone with a Telinga parabola. Recordings were made between 0700 h and 1200 h during 1 to 3 days for each male. We selected for analysis 5 song samples from each bird using Audacity® v. 2.0.0 (<http://audacity.sourceforge.net>). These samples excluded introductory notes that often precede the vocalization and were selected based on the quality of recordings and the absence of background noise. From each sample, in the program Cool Edit Pro® v. 2.1 (Syntrillium Software Corporation 2003), we measured song duration (in milliseconds) from oscillograms and spectrograms and minimum and maximum frequencies from power spectrum using a –24 dB amplitude cutoff criterion (as in Podos 1997). We calculated frequency bandwidth as maximum minus minimum frequency for each song.

Statistical analysis

To assess the relationships among the 5 leap motor parameters calculated from high-speed videos (leap height, rotation angle, leap duration, launch velocity, and number of wing beats, see Table 1, rows 1–5), we calculated Pearson product-moment pairwise correlation scores (Table 2) and Bonferroni's correction for multiple comparisons. Variables were log-transformed when necessary to normalize or to achieve near-normal distributions. We related all the 5 parameters to leap display rates using regression models.

We associated leap height and rotation angle (in 2 different sets of analyses) with the following 5 predictors: song duration, frequency bandwidth, display rate, proportion of leap displays relative to total displays, and the body mass index. For these analyses, we constructed sets of multiple regression models with different combinations of predictors, using only data from normal-speed video recordings, which provided us information from the largest possible sample of individuals. These models included 1) all predictor variables together, 2) each variable independently, 3) all variables within each sensory modality: acoustic (song duration and frequency bandwidth) and motor (display rate and proportion of leap displays), and 4) only the intercept (null model). We also considered in our models the interactions between body mass index and proportion of leap displays or display rate, because previous data exploration indicated possible interactions among these variables. We also related song parameters (song duration and frequency bandwidth) with display rate in 2 separate regression models. To examine whether associations between parameters were influenced by differences among breeding seasons, we also included year as a covariate in all models. Since inclusion of this covariate did not change the relationship between other pairs of variables, except for frequency bandwidth model, the predictor “year” was excluded from all results reported below.

Before running our models, we checked 1) the normality of response and predictor variables using Shapiro–Wilk tests, 2) the homogeneity of variances by inspecting residuals versus fitted plots, and 3) collinearity by calculating correlations between predictors and the variance inflation factor of each model that included all variables. Based on this assessment, rotation angle and body mass index were log-transformed and proportion of leap displays are sin-transformed. We also excluded 1 outlier (body mass index > 0.70) from the data set of leap height models to reduce heteroscedasticity and improve model fitting. This outlier was strongly influencing the effect of parameters in leap height models by increasing the importance of proportion of leap displays and the interaction between body mass index and display rate as well as decreasing the importance of song duration. Therefore, this outlier was excluded to avoid bias in the results. When repeated measures occurred in different years for the same individual, we used data from the first year.

For normal-speed video samples, we ran regression models using the package AICcmodavg (Mazerolle 2010) in the R environment v. 2.15 (R Development Core Team 2014). With this package, we calculated, for each predictor (input) variable, second-order

Table 2**Correlations (Pearson product-moment scores) among leap parameters estimated from high-speed video recordings (95% confidence interval in parentheses)**

	Sample size	Leap height ^a	Leap duration ^a	Launch velocity	Wing beats
Leap duration ^a	18	0.91 (0.76, 0.96)*	—	—	—
Launch velocity	18	0.80 (0.53, 0.92)*	0.72 (0.38, 0.89)*	—	—
Wing beats	18	0.73 (0.40, 0.89)*	0.81 (0.56, 0.93)*	0.66 (0.28, 0.86)*	—
Rotation angle	9	0.57 (−0.15, 0.90)	0.32 (−0.44, 0.81)	0.09 (−0.61, 0.71)	0.11 (−0.60, 0.72)

^aLog-transformed.* $P < 0.01$ after Bonferroni's correction.

Akaike's Information Criterion (AICc) values and model probabilities (Akaike's weight, w). We also calculated model-averaged estimates, when possible, with unconditional standard errors and 95% confidence interval (CI) for all predictor variables (Burnham and Anderson 2002). From these values, we drew inferences about the relative importance of predictor variables, following steps outlined by Burnham and Anderson (2002): 1) comparison of AICc value rankings among predictor variables and null models; 2) calculation of "evidence ratios," that is, sums of w values of higher-than-null models divided by w values of null models; and 3) inspection of 95% CI among model-averaged estimates, with the degree of skew away from 0 values reflecting the model's predictive strength. We interpreted the structure of 2-way interaction terms by creating a categorical body mass index variable to test and estimate the simple slopes of the regression for males with low and high indexes (Quinn and Keough 2002).

To assess individual consistency in display traits across different focal observations, video and audio recordings, we calculated repeatability (R) for all parameters used in regression models. Repeatability and 95% CI was estimated as the proportion of variance accounted by differences among individuals using the package rptR (Nakagawa and Schielzeth 2010) in the R environment (R Development Core Team 2011).

RESULTS

Analyses revealed strong positive correlations (0.66 to 0.91) among 4 leap parameters estimated from high-speed recordings: leap height, duration, launch velocity, and number of wing beats ($n = 18$, Table 2). Repeatability of these parameters was high ($R_{\text{leap height}} = 0.82$, CI = 0.63 to 0.91; $R_{\text{leap duration}} = 0.81$, CI = 0.60 to 0.90; $R_{\text{launch velocity}} = 0.67$, CI = 0.38 to 0.83; $R_{\text{wing beats}} = 0.88$, CI = 0.75 to 0.94, $P \leq 0.01$ and $n = 18$ in all cases). Similarly, repeatability was high for leap display rate ($R = 0.52$, CI = 0.20 to 0.73, $P = 0.001$, $n = 18$). By contrast, rotation angle correlated only weakly (0.09 to 0.57), with the other 4 leap parameters (Table 2) and repeatability was substantially lower ($R = 0.44$, CI = 0.00 to 0.73, $P = 0.02$, $n = 9$).

Number of wing beats varied negatively with leap display rate, according to AIC analysis outcomes ($n = 18$, Table 3), suggesting that birds that produce the highest number of wing beats also tend to display at lower rates ($\beta = -0.43$, 95% CI = -0.87 to 0.01). We offer this result with 2 caveats: 1) the similarity of AICc values for leap display rate and null models, and the observation that the 95% CI of this result includes 0, suggest the relationship between number of wing beats and rate is only weak to moderate and 2) two birds who performed fewer wing beats yet had the highest display rates drove this relationship. In fact, after excluding these 2 observations, the relationship significantly reduces (leap display rate model

Table 3**Model selection outcomes for linear models of leap motor parameters in relation to leap display rates calculated from high-speed videos ($n = 18$ males).**

Parameter	Model	K	AICc	ΔAICc	w_i
Leap height	Null	2	54.85	0.00	0.682
	Leap display rate	3	56.38	1.53	0.318
Leap duration	Null	2	54.85	0.00	0.642
	Leap display rate	3	56.02	1.17	0.358
Launch velocity	Null	2	54.54	0.00	0.539
	Leap display rate	3	54.85	0.31	0.461
Wing beats	Null	2	54.85	0.73	0.409
	Leap display rate	3	54.11	0.00	0.591
Rotation angle	Null	2	30.48	0.00	0.906
	Leap display rate	3	35.01	4.52	0.094

K = number of parameters, AICc = second-order Akaike's Information Criteria, ΔAICc = difference between model AICc and the minimum AICc, w_i = Akaike's weight.

AICc = 51.02, $w = 0.21$; null model AICc = 48.38, $w = 0.79$). Leap height, leap duration, launch velocity, and rotation angle were also negatively related to leap display rates ($\beta_{\text{height}} = -0.27$, CI = -0.74 to 0.19; $\beta_{\text{duration}} = -0.30$, CI = -0.77 to 0.16; $\beta_{\text{velocity}} = -0.40$, CI = -0.85 to 0.04, $\beta_{\text{angle}} = -0.31$, CI = -1.62 to 1.00, $n = 18$), however the null model outperformed the model including the predictor, suggesting that the relationship is weak.

Repeatability for display parameters calculated from normal-speed videos and song recordings showed a high within-individual consistency ($R_{\text{leap height}} = 0.68$, CI = 0.54 to 0.77; $R_{\text{song duration}} = 0.92$, CI = 0.87 to 0.95 and $R_{\text{frequency bandwidth}} = 0.77$, CI = 0.64 to 0.85, $P = 0.001$ and $n = 36$ in all cases), which is also the case for rotation angle ($R_{\text{rotation angle}} = 0.63$, CI = 0.48 to 0.73, $P = 0.001$, $n = 35$). Repeatability for traits calculated from focal observations was substantially lower ($R_{\text{display rate}} = 0.36$, CI = 0.00 to 0.63 and $R_{\text{proportion of leap displays}} = 0.37$, CI = 0.00 to 0.66, $P = 0.02$ in both cases, $n = 36$). It is worth noting that estimates for repeatability of display rate and proportion of leap displays were calculated based on data from a smaller sample of males ($n = 19$), because for some of them we had only 1 focal observation in different days.

In our predictive models of leap height, the best predictor parameters are listed in Table 4. These models were, in rank order (and for all models $\Delta\text{AICc} < 4$): 1) song duration; 2) a model that featured 2 predictors—the interaction of body mass index with display rate, and with the proportion of leap displays; 3) song duration and frequency bandwidth; 4) the interaction of body mass index and the proportion of leap displays; 5) the null model; 6) the proportion of leap displays; and 7) frequency bandwidth. These 7 most parsimonious models together accounted for 90% of the accumulated probability. Comparing the different models, we found that

Table 4

Model selection outcomes for linear models of leap height and rotation angle (log-transformed) in relation to input predictor variables: song duration, frequency bandwidth, display rate, proportion of leap displays (“leap”, arcsin-transformed), and BMI

Response	Predictors	K	AICc	Δ AICc	w_i
Leap height ($n = 35$ males)	Song duration	3	93.30	0.00	0.335
	Display rate * BMI + leap * BMI	4	94.71	1.41	0.165
	Song duration + frequency bandwidth	4	95.76	2.47	0.098
	Leap * BMI	3	95.83	2.53	0.095
	Null	2	96.13	2.84	0.081
	Leap	3	96.30	3.00	0.075
	Frequency bandwidth	3	97.20	3.90	0.048
Rotation angle ($n = 36$ males)	Null	2	105.51	0.00	0.250
	Leap	3	106.57	1.06	0.147
	Display rate	3	107.66	2.15	0.085
	Leap * BMI	3	107.66	2.15	0.085
	Display rate * BMI	3	107.70	2.19	0.084
	Song duration	3	107.72	2.21	0.083
	Frequency bandwidth	3	107.74	2.22	0.082
	BMI	3	107.90	2.39	0.076
	Leap + display rate	4	108.36	2.85	0.060

K = number of parameters, AICc = second-order Akaike’s Information Criteria, Δ AICc = difference between model AICc and the minimum AICc, w_i = Akaike’s weight, * = interaction; BMI = body mass index. Models with Δ AICc > 4 are presented in supplementary material (Supplementary Table S1).

the first 2 models in Table 4 showed Δ AICc < 2 and performed better than the null model. The evidence ratio of these 2 models to the null model, 6.16, implies that the first 2 models together offer more than 6 times the explanatory value of the null model. As shown in Table 5 (leap height model column), model-averaged estimates and CIs varied broadly across the 7 parameters that were included in models. CIs for 4 parameters centered around 0, which implies only weak predictive effects. These parameters were frequency bandwidth, display rate, body mass index, and the interaction of these latter 2 parameters. By contrast, CIs for the remaining 3 parameters skewed either negatively (proportion of leap displays) or positively (song duration, interaction of body mass index and proportion of leap displays).

These model outcomes together lead to 2 interpretations. First, we found that leap height was higher for males that sang longer songs (Figure 2; see also Tables 4 and 5 for model outcomes). Second, we identified an interaction between body mass index and the proportion of leap displays. To better describe this interaction, we divided our sample into low and high body mass index groupings, around the sampled population’s central value of the index (0.56), and ran 2 regression models (Figure 3). We found that, for males in the lower body mass group, birds that produced greater proportions of leap displays achieved only lower leap heights ($\beta = -0.45$; 95% CI = -0.82 to -0.07 ; proportion of leap displays model AICc = 74.04, $w = 0.83$; null model AICc = 77.29, $w = 0.17$). This relationship can be considered strong because the CI of the focal predictor is within the negative range, the Δ AICc between the 2 models 3.25, and w values vary substantially between the 2 models. By contrast, for males with higher body mass, birds increased their leap heights even as they increased the proportions of leap displays, although we consider this relationship to be weak ($\beta = 0.17$; 95% CI = -0.71 to 1.05; proportion of leap displays model AICc = 35.03, $w = 0.09$; null model AICc = 30.48, $w = 0.91$).

For our models of rotation angle, we found that rotation angle is predicted only weakly by all display parameters and body mass index (Table 4). The null model proved to be the best predictor of rotation angle, showing from 1.7 to 2.9 times greater evidence ratios than models including proportion of leap displays and display

Table 5

Model-averaged estimates and 95% confidence intervals of predictor variables included in leap height and rotation angle models (see Table 4)

Predictor	Estimate (95% CI)	
	Leap height model	Rotation angle model
Song duration	0.33 (0.04, 0.62)	-0.06 (-0.41, 0.28)
Frequency bandwidth	0.09 (-0.24, 0.42)	-0.06 (-0.41, 0.28)
Display rate	-0.01 (-0.34, 0.31)	0.11 (-0.24, 0.45)
Proportion leap displays	-0.23 (-0.54, 0.08)	0.20 (-0.13, 0.54)
Body mass index	0.08 (-0.31, 0.46)	-0.004 (-0.34, 0.33)
Display rate * body mass index	0.12 (-0.28, 0.53)	-0.06 (-0.33, 0.21)
Proportion leap displays * body mass index	0.49 (-0.009, 0.98)	0.07 (-0.22, 0.36)

rate. Furthermore, model-averaged estimates of all predictors were centered around 0 (Table 5, rotation angle model column). These results, added to the analyses of high-speed videos above (Table 2), suggest that rotation angles during displays were not clearly associated with any other display parameter.

We found a weak relation between song parameters and display rates. Null models of song duration (AICc = 105.51, $w = 0.60$) and frequency bandwidth (AICc = 105.51, $w = 0.86$) outperformed models including display rates as predictor (song duration model: AICc = 106.33, $w = 0.40$ and frequency bandwidth model: AICc = 109.10, $w = 0.14$). Estimates for display rate in both models were low and showed wide CI overlapping 0 ($\beta = -0.21$; 95% CI = -0.53 to 0.12 and $\beta = -0.35$; 95% CI = -0.74 to 0.05, respectively).

DISCUSSION

Grassquit males showed strong positive correlations among 4 leap parameters: leap height, leap duration, launch velocity, and number of wing beats (Table 2). This result supports our prediction that males with greater launch velocity would stay aloft longer and reach higher peaks. Although birds produced more wing beats

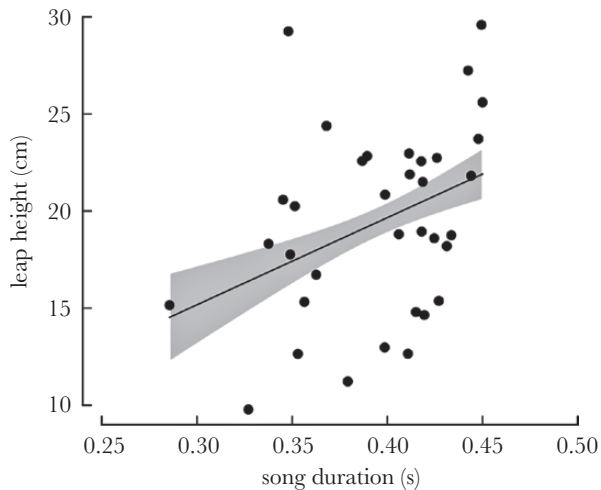


Figure 2
Regression between leap height and song duration (shaded area refers to standard error).

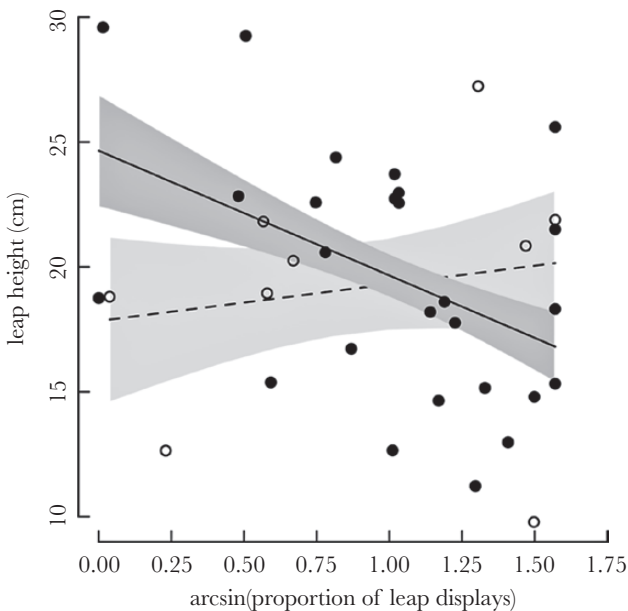


Figure 3
Regression between leap height and proportion of leap displays (arcsin-transformed) of males with lower body mass indexes (<0.56 , filled circles, solid line) and higher body mass indexes (≥ 0.56 , open circles, dashed line); statistical analysis described in text (shaded areas refer to standard error).

during longer and higher leaps, rotation angle was not correlated with any leap trait. The correlations we have identified between leap height and song duration might enhance receivers' abilities to assess overall leap performance. This is because receivers could presumably extract reliable information about leap performance from any of these predictor parameters independently or through the simultaneous assessment of multiple parameters (as per the redundant signal hypothesis).

Our next main finding was that body mass appears to influence the relationship of 2 leap display parameters, leap height and the proportion of leap displays (Figure 3). More specifically, birds with a higher body mass index showed a slightly positive (although weak) relationship between leap height and the proportion of

displays that included leaps (Figure 3, dashed lines); whereas birds with a lower body mass index showed a strong negative relationship between these 2 parameters. This relationship in birds with lower body mass relative to skeletal size suggests a quantity–quality trade-off, in which birds achieving high leaps tended to produce fewer displays with leaps in them. Birds with lower body mass index might be expected to suffer disproportionately from mechanical or timing constraints, possibly due to reduced fat reserves or decreased muscle tissue. Relatively thin birds may have overall reduced ability to invest in and execute displays versus other metabolically costly activities, such as those related to survival or growth. Greater costs in signal production and expression for low-quality individuals, as suggested by our data, are a fundamental prediction of handicap models (e.g., Zahavi 1975; Johnstone 1997; reviewed by Searcy and Nowicki 2005). Evidence for this prediction has typically been garnered in studies of morphological traits (e.g., Hill and Montgomerie 1994; David et al. 2000; Emlen et al. 2012), yet may also apply in the evolution of complex behavioral displays (Brandt 2003). We present our interpretation with the caveat that we have no corroborating data on if and how birds' condition affects other organismal attributes related to whole-organism performance, relationships that would be central to discussions of male quality (Vervust et al. 2008).

Our third finding was that number of wing beats correlated negatively with leap display rate. This supports our prediction for a trade-off between display skill (quality) and vigor (quantity). This result should be considered with caution, because only 2 of 18 males expressed extreme values of leap display rate and presumably pushed the relationship toward negative slopes. Nonetheless, this finding points toward the possibility that birds augmenting rates of leaping should endure compromises in the execution of individual leaps: the more rapidly an action is repeated, the more untenable it becomes to devote time and high-performance output to each individual rendition of that action.

We emphasize that the trade-off in behavioral traits, such as those identified here (Figure 3) might arise from limits in either vigor or skill. In terms of vigor, unhealthy or resource-deprived individuals likely suffer disproportionately from energetic constraints; life-history allocations that enhance survival may diminish signal expression. Energetic costs of courtship displays are likely especially high for species whose displays are rapid, stereotyped, and repeated vigorously (Vehrencamp et al. 1989; Gibson 1996; Patricelli and Krakauer 2010; Barske et al. 2011; Clark 2012). Skill-related constraints, on the other hand, can be attributed to biomechanical, musculoskeletal, or nervous system features. Such constraints can drive trade-offs among related features, such as within-trill production in songbirds (Podos 1997; Ballentine et al. 2004) or between rapid strike and crushing foraging strategies in turtles (Herrel et al. 2002). Animals who display with high degrees of precision and fine motor control might show similar levels of skill in organismal functions more directly related to survival such as foraging and predator evasion (Byers et al. 2010). Skill in the blue-black grassquit leap display could presumably also be achieved and improved through the repeated performance of this motor task, similarly to what has been shown for high-achievement athletes (Nielsen and Cohen 2008).

An emerging challenge in studies of display evolution is to parse the relative impacts of constraints related to vigor versus skill. This challenge is illustrated in a series of recent studies on male golden-collared manakins (*Manacus vitellinus*). Barske et al. (2011) found that males achieve twice their normal heartbeat rate as they perform complex display movements (up to 1300 beats per minute; see also Fusani and

Schlinger 2012), suggesting a role for metabolic constraints on signaling endurance. Yet these birds' displays are sufficiently rare over the course of a day that they impose no substantial effect on daily energy expenditure (Barske et al. 2014). Display attributes that distinguish male golden-collared manakins are thus skill related and power limited; indeed, females prefer males who execute complex display maneuvers at the greatest speeds (Barske et al. 2011). Compared with golden-collared manakins, display bouts in grassquits appear to be much more prolonged and intense, with display rates approaching 20 displays per minute (Manica et al. 2013; Sicsú et al. 2013). High energetic expenditure associated with long and intense display bouts might degrade the efficacy of mechanisms responsible for the execution of specific signal components (e.g., wing beats) and thus contribute to degradation in overall display performance, especially for birds with restricted fat reserves or muscle tissue volume. One goal of further studies on grassquits could be to explain the interaction of vigor and skill-associated constraints in shaping display form. One puzzling result of our study is the fact that body forward rotation carried out at the peak of the leap did not covary with any other leap parameter measured. For specific attributes such as this one, the role of experience in acquiring and shaping its final form may be important and could be targeted by female choice. In these cases, no trade-off constraints may necessarily apply.

Returning to the trade-off between leap height and proportion of leap display rates for males with lower body mass index, we note that leap height has been shown to predict mating success in this population (Carvalho et al. 2006; Manica, Graves et al. 2016); by contrast, we have no data on the potential signal value of proportion of leap displays. The role of females as receivers and assessors of male displays thus becomes especially intriguing. Do females discriminate among males based on their performance of either parameter separately, or do they conduct a combined assessment? Would females favor males who maximize both parameters relative to each other? Furthermore, how informative are each of these components about male breeding value for offspring performance?

We emphasize that constraints on display expression should not always manifest as trade-offs but might sometimes lead to signal redundancies. One such redundancy concerns the positive relationship we observed between leap height and song duration (Figure 2). Studies with other birds have suggested a linked expression of visual and acoustic display parameters, due to shared morphological and physiological (especially respiratory) mechanisms (e.g., Williams 2001; Cooper and Goller 2004). For example, in brown-headed cowbirds (*Molothrus ater*), a lowered wing posture appears to inhibit vocal production by favoring respiratory inhalations rather than exhalations (Cooper and Goller 2004). Although it is unknown whether a similar mechanism occurs in grassquits, it certainly does seem like a viable possibility.

Another caveat worth emphasizing is that grassquit display features are undoubtedly shaped by factors other than mechanical constraints. Such factors could include social and environmental characteristics such as presence of potential mates, predation risk, and light and climatic conditions (Roberts et al. 2006). Displays in blue-black grassquits are thought to attract nest predators (Dias et al. 2010), and reductions in leap height might conceivably reduce this risk. Yet there is a specific context in which grassquits enhance their conspicuousness: in direct sunlight, they tend to produce greater proportions of leap displays (vs. vocalizations only), which enhance plumage visibility (Sicsú et al. 2013). Males likely also adjust display strategies and intensity with varying social situations. Such modulations have been observed in numerous species, such as

the satin bowerbird (*Ptilonorhynchus violaceus*), in which males adjust display intensity to female behavior (Patricelli et al. 2002).

To conclude, recent studies on courtship displays are emphasizing the role of performance limits in display expression. Most such studies have been conducted with birds using high-speed and traditional video recordings and have revealed detailed information about displays, emphasizing variations in flight velocity as well as mechanical sounds produced by wing feather specializations (Bostwick and Prum 2003; Clark 2009; Patricelli and Krakauer 2010; Barske et al. 2011, 2014). Of particular interest are trade-offs between the expression and quality of distinct components of multimodal displays. Our results suggest that trade-offs among parameters related to both vigor and skill occur in the multimodal courtship display of the blue-black grassquit, and it seems probable that similar sorts of trade-offs characterize courtship displays of other species as well. The signal value of these aspects of display variation remains largely unknown.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Manica, Macedo et al. (2016).

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REFERENCES

- Aguilar TM, Maia R, Santos ESA, Macedo RH. 2008. Parasite levels in blue-black grassquits correlate with male displays but not female mate preference. *Behav Ecol.* 19:292–301.
- Alderton CC. 1963. The breeding behavior of the blue-black grassquit. *Condor.* 65:154–162.
- Almeida JB, Macedo RH. 2001. Lek-like mating system of the monogamous blue-black grassquit. *Auk.* 118:404–411.
- Andersson M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature.* 299:818–820.
- Ballentine B, Hyman J, Nowicki S. 2004. Vocal performance influences female response to male bird song: an experimental test. *Behav Ecol.* 15:163–168.
- Barske J, Fusani L, Wikelski M, Feng NY, Santos M, Schlinger BA. 2014. Energetics of the acrobatic courtship in male golden-collared manakins (*Manacus vitellinus*). *Proc Biol Sci.* 281:20132482.
- Barske J, Schlinger BA, Wikelski M, Fusani L. 2011. Female choice for male motor skills. *Proc R Soc B Biol Sci.* 278:3523–3528.
- Bostwick KS, Prum RO. 2003. High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *J Exp Biol.* 206:3693–3706.
- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd ed. Sunderland (MA): Sinauer Associates.

- Brandt Y. 2003. Lizard threat display handicaps endurance. *Proc R Soc B Biol Sci.* 270:1061–1068.
- Burnham K, Anderson D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York (NY): Springer-Verlag.
- Byers J, Hebets E, Podos J. 2010. Female mate choice based upon male motor performance. *Anim Behav.* 79:771–778.
- Carvalho CBV, Macedo RH, Graves JA. 2006. Breeding strategies of a socially monogamous Neotropical passerine: extra-pair fertilizations, behavior, and morphology. *Condor.* 108:579–590.
- Clancey E, Byers JA. 2014. The definition and measurement of individual condition in evolutionary studies. *Ethology.* 120:845–854.
- Clark CJ. 2009. Courtship dives of Anna's hummingbird offer insights into flight performance limits. *Proc Biol Sci.* 276:3047–3052.
- Clark CJ. 2012. The role of power versus energy in courtship: what is the “energetic cost” of a courtship display? *Anim Behav.* 84:269–277.
- Clark CJ, Dudley R. 2009. Flight costs of long, sexually selected tails in hummingbirds. *Proc R Soc B Biol Sci.* 276:2109–2115.
- Cooper BG, Goller F. 2004. Multimodal signals: enhancement and constraint of song motor patterns by visual display. *Science.* 303:544–546.
- Costa FJV, Macedo RH. 2005. Coccidian oocyst parasitism in the blue-black grassquit: influence on secondary sex ornaments and body condition. *Anim Behav.* 70:1401–1409.
- Darwin C. 1871. The descent of man, and selection in relation to sex. London (UK): John Murray.
- David P, Bjorksten T, Fowler K, Pomiankowski A. 2000. Condition-dependent signalling of genetic variation in stalk-eyed flies. *Nature.* 406:186–188.
- Dias RI, Castilho L, Macedo RH. 2010. Experimental evidence that sexual displays are costly for nest survival. *Ethology.* 116:1011–1019.
- Diniz P, Ramos DM, Macedo RH. 2015. Attractive males are less than adequate dads in a multimodal signalling passerine. *Anim Behav.* 102:109–117.
- Doucet SM. 2002. Structural plumage coloration, male body size, and condition in the blue-black grassquit. *Condor.* 104:30–38.
- Doucet SM, Montgomerie R. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behav Ecol.* 14:503–509.
- Elias DO, Maddison WP, Peckmezian C, Girard MB, Mason AC. 2012. Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). *Biol J Linn Soc.* 105:522–547.
- Emlen DJ, Warren IA, Johns A, Dworkin I, Lavine LC. 2012. A mechanism of extreme growth and reliable signaling in sexually selected ornaments and weapons. *Science.* 337:860–864.
- Fandiño-Mariño H, Viellard JM. 2004. Complex communication signals: the case of the Blue-black Grassquit *Volatinia jacarina* (Aves, Emberizidae) song. Part I—a structural analysis. *An Acad Bras Cienc.* 76:325–334.
- Fusani L, Schlinger BA. 2012. Proximate and ultimate causes of male courtship behavior in golden-collared manakins. *J Ornithol.* 153:119–124.
- Gibson JS, Uetz GW. 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. *Anim Behav.* 75:1253–1262.
- Gibson RM. 1996. Female choice in sage grouse: the roles of attraction and active comparison. *Behav Ecol Sociobiol.* 39:55–59.
- Götmarm F, Ahlström M. 1997. Parental preference for red mouth of chicks in a songbird. *Proc R Soc B Biol Sci.* 264:959–962.
- Hedenström A. 1995. Song flight performance in the Skylark *Alauda arvensis*. *J Avian Biol.* 25:337–342.
- Herrel A, O'Reilly J, Richmond A. 2002. Evolution of bite performance in turtles. *J Evol Biol.* 15:1083–1094.
- Hill G, Montgomerie R. 1994. Plumage colour signals nutritional condition in the house finch. *Proc R Soc B Biol Sci.* 258:47–52.
- Höglund J, Kålås JA, Fiske P. 1992. The costs of secondary sexual characters in the lekking great snipe (*Gallinago media*). *Behav Ecol Sociobiol.* 30:309–315.
- Hölldobler B. 1999. Multimodal signals in ant communication. *J Comp Physiol A.* 184:129–141.
- Irschick DJ, Briffa M, Podos J. 2015. Animal signaling and function: an integrative approach. Hoboken (NJ): John Wiley & Sons.
- Johnstone RA. 1997. The evolution of animal signals. In: Krebs JR, Davies N, editors. *Behavioural Ecology*. Oxford (UK): Blackwell Publishing. p. 155–178.
- Clump GM, Gerhardt HC. 1987. Use of non-arbitrary acoustic criteria in mate choice by female gray tree frogs. *Nature.* 326:286–288.
- Macedo RH, Karubian J, Webster MS. 2008. Extrajoint paternity and sexual selection in socially monogamous birds: are tropical birds different? *Auk.* 125:769–777.
- Macedo RH, Manica L, Dias RI. 2012. Conspicuous sexual signals in a socially monogamous passerine: the case of neotropical blue-black grassquits. *J Ornithol.* 153:15–22.
- Maia R, Caetano JVO, Bão SN, Macedo RH. 2009. Iridescent structural colour production in male blue-black grassquit feather barbules: the role of keratin and melanin. *J R Soc Interface R Soc.* 6:S203–S211.
- Maia R, Macedo RH. 2011. Achieving luster: prenuptial molt pattern predicts iridescent structural coloration in blue-black grassquits. *J Ornithol.* 152:243–252.
- Manica L, Podos J, Graves J, Macedo RH. 2013. Flights of fancy: mating behavior, displays and ornamentation in a neotropical bird. In: Macedo R, Machado G, editors. *Sexual Selection. Perspectives and Models from the Neotropics*. San Diego (CA): Academic Press. p. 391–407.
- Manica L, Macedo RH, Graves JA, Podos J. 2016. Data from: Vigor and skill in the acrobatic mating displays of a Neotropical songbird. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.g16gv>
- Manica LT, Graves JA, Podos J, Macedo RH. 2016. Multimodal flight display of a neotropical songbird predicts social pairing but not extrajoint mating success. *Behav Ecol Sociobiol.* doi: 10.1007/s00265-016-2208-x
- Mappes J, Alatalo RV, Kotiaho J, Parri S. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proc R Soc B Biol Sci.* 263:785–789.
- Mazerolle MJ. 2010. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.25. Available from: <http://CRAN.R-project.org/package=AICcmodavg>.
- McElroy EJ, Marien C, Meyers JJ, Irschick DJ. 2007. Do displays send information about ornament structure and male quality in the ornate tree lizard, *Urosaurus ornatus*? *Ethology.* 113:1113–1122.
- Møller AP, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments? *Behav Ecol Sociobiol.* 32:167–176.
- Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev.* 85:935–956.
- Nielsen JB, Cohen LG. 2008. The Olympic brain. Does corticospinal plasticity play a role in acquisition of skills required for high-performance sports? *J Physiol.* 586:65–70.
- Patricelli GL, Krakauer AH. 2010. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. *Behav Ecol.* 21:97–106.
- Patricelli GL, Uy JA, Walsh G, Borgia G. 2002. Male displays adjusted to female's response. *Nature.* 415:279–280.
- Petrie M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature.* 371:598–599.
- Podos J. 1996. Motor constraints on vocal development in a songbird. *Anim Behav.* 51:1061–1070.
- Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution.* 51:537–551.
- Quinn GP, Keough MJ. 2002. *Experimental design and data analysis for biologists*. New York (NY): Cambridge University Press.
- R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited 2014 October 4]. Available from: <http://www.R-project.org/>.
- Reichert MS, Gerhardt HC. 2012. Trade-offs and upper limits to signal performance during close-range vocal competition in gray tree frogs *Hyla versicolor*. *Am Nat.* 180:425–437.
- Roberts JA, Taylor PW, Uetz GW. 2006. Consequences of complex signaling: predator detection of multimodal cues. *Behav Ecol.* 18:236–240.
- Ryan MJ, Fox JH, Wilczynski W, Rand AS. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature.* 343:66–67.
- Santos ESA, Maia R, Macedo RH. 2009. Condition-dependent resource value affects male-male competition in the blue-black grassquit. *Behav Ecol.* 20:553–559.
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods.* 9:671–675.

- Searcy WA, Nowicki S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton (NJ): Princeton University Press.
- Sicsú P, Manica LT, Maia R, Macedo RH. 2013. Here comes the sun: multimodal displays are associated with sunlight incidence. *Behav Ecol Sociobiol.* 67:1633–1642.
- Taylor P, Roberts J, Uetz G. 2006. Compensation for injury? Modified multi-modal courtship of wolf spiders following autotomy of signalling appendages. *Ethology Ecol Evol.* 18:79–89.
- Vehrencamp S, Bradbury J, Gibson R. 1989. The energetic cost of display in male sage grouse. *Anim Behav.* 38:885–896.
- Vervust B, Lailvaux SP, Grbac I, Van Damme R. 2008. Do morphological condition indices predict locomotor performance in the lizard *Podarcis sicula*? *Acta Oecologica.* 34:244–251.
- Wagner WE Jr, Beckers OM, Tolle AE, Basolo AL. 2012. Tradeoffs limit the evolution of male traits that are attractive to females. *Proc Biol Sci.* 279:2899–2906.
- Welch AM, Semlitsch RD, Gerhardt HC. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science.* 280:1928–1930.
- Wilgers D, Hebets EA. 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. *Curr Zool.* 57:175–186.
- Wilgers D, Hebets EA. 2015. Functional approach to condition. In: Irschick DJ, Briffa, M, Podos J, editors. *Animal Signaling and Function: An Integrative Approach.* Hoboken (NJ): John Wiley & Sons. p. 229–252.
- Williams H. 2001. Choreography of song, dance and beak movements in the zebra finch (*Taeniopygia guttata*). *J Exp Biol.* 204:3497–3506.
- Zahavi A. 1975. Mate selection—a selection for a handicap. *J Theor Biol.* 53:205–214.