Original Article

Flirting with danger: predation risk interacts with male condition to influence sexual display

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Sexual signaling coevolves with the sensory systems of intended receivers; however, predators may be unintended receivers of sexual signals. Conspicuous aerial displays in some species may place males at high risk of predation from eavesdropping predators. There are three different hypotheses to explain how signaling males can deal with increased predation risk: (1) males invest in survival by decreasing signal conspicuousness; (2) males invest in reproduction by increasing signal conspicuousness; and (3) male response is condition-dependent according to his residual reproductive value. Here, we used blue-black grassquits (*Volatinia jacarina*) to test these hypotheses, asking whether males modify leap displays under different levels of predation risk. Grassquit males develop an iridescent nuptial plumage and spend considerable time emitting a multimodal signal: while leaping from a perch, males clap their wings above their heads and emit a high-pitched short song. We exposed males to predator and nonpredator playbacks while video recording their displays. We found interactions between predation risk and 2 male condition variables (ectoparasite infestation and proportion of nuptial plumage coverage) that influenced display behavior. Less parasitized males and those with higher proportion of nuptial plumage showed no change in display behavior, while more parasitized males and those with lower proportion of nuptial plumage increased the vigor of displays under predation risk. In other words, males with low residual reproductive value increased reproductive effort when there was a high risk of extrinsic death. Our study provides some empirical support for the terminal investment hypothesis.

Key words: **asset protection, blue-black grassquit, handicap principle, Neotropical bird, sexual selection, terminal investment.**

Male mating displays may have a high degree of conspicuousness to attract females, but these highly salient signals may also attract unintended receivers (Endler 1992). Conspecific competitors, parasites, and predators may eavesdrop on the signal (Otte 1974, Zuk and Kolluru 1998). Therefore, selection is expected to favor those signalers that can accurately reach intended receptors without suffering a drastic reduction in survival and fitness due to eavesdropping, ultimately affecting the evolution of male signals (Zuk and Kolluru 1998; Lewis and Cratsley 2008). Several hypotheses, with different predictions, have been advanced in the literature to understand mating signal evolution within predator-risk environments. However, these explanations generally lack empirical substantiation, a problem that is especially relevant for hypotheses that involve movement-based signals in natural settings.

Intuitively, we expect that under high predation risk, natural selection should favor males that reduce the conspicuousness of their displays at the cost of decreasing their appeal to females, which may result in lower mating success. Changes in sexual signaling according to predation risk have been observed in several taxa, from katydids (Römer et al. 2010) to fish (Endler 1987), frogs (Tuttle et al. 1982), and lizards (Steinberg et al. 2014). In all these studies, males reduced the conspicuousness or frequency of mating signal emission, altered the sexual display sensory modality to different sensory channels, or even stopped sexual signaling in situations of higher predation risk. Here, we refer to this pattern of adaptively reducing courtship to avoid predation as the survival focused hypothesis (predation avoidance behaviors, Lima and Dill 1990; Magnhagen 1991). Alternatively, some males may tip the scale in favor of reproduction, especially if risk-taking is a sexually selected feature (handicap principle hypothesis, Zahavi 1975). In this context, males should continue or even enhance their display performance under high predation risk. Under these conditions, we would expect that only males of superior inherent quality (e.g., healthier, more elaborate ornaments) would be able to escape predator attacks while signaling and successfully attracting females for

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mating. The reproductive outcome of such behavior should compensate for the higher predation risk costs.

However, the behavioral rules of thumb regarding choice between survival and reproduction may not be as stereotyped as postulated by these more conventional hypotheses (Zahavi 1975; Lima and Dill 1990). Males within the same population may respond differently to predation risk, since individual attributes are variable and mating strategies may be condition-dependent (Dominey 1984; Gross 1996). Therefore, individual variation can result in different risk-taking strategies based upon the individual´s current and future reproductive prospects (Clark 1994). The asset protection hypothesis suggests that the larger the current reproductive value (i.e., expected future lifetime reproduction, Fisher 1930), the stronger the need to protect it (Clark 1994). In other words, animals with high potential for future breeding prospects should take fewer risks with respect to predators. The asset protection hypothesis is akin to the terminal investment hypothesis, a longstanding concept suggesting that iteroparous animals should increase reproductive effort when their residual reproductive value decreases, that is, when their prospects of survival and reproduction decline due to age (Williams 1966; Trivers 1972; Pianka and Parker 1975). Therefore, the terminal investment hypothesis can be considered as a case of the asset protection hypothesis, as both present similar predictions regarding predation risk and the residual reproductive value of a male. In this theoretical scenario, the residual reproductive value should interact with probability of predation to predict how a male should adjust the conspicuousness of his courtship behavior in different levels of predation risk.

We investigated the trade-off between survival and reproduction by assessing how males of a Neotropical songbird, the blue-black grassquit (*Volatinia jacarina*), coped with predation risk while attempting to attract females. The blue-black grassquit is uniquely suited for testing this trade-off because of 3 specific reasons. First, males have a striking iridescent nuptial plumage and conduct elaborate and highly conspicuous movement-based displays (detailed below). Second, reproductive opportunities for this migratory granivorous bird are limited because they have a short breeding period restricted to the last 3 months of the rainy season in central Brazil (January to March, Sick 1997). Finally, both adults and nests are subjected to very high levels of predation typical of tropical latitudes (Skutch 1985; Macedo et al. 2012; Diniz et al. 2015). At the start of the breeding period, males molt from a cryptic brownish plumage to an iridescent blue-black nuptial plumage (Maia and Macedo 2011). Males then start defending small, clustered territories and perform their typical aerial displays (Manica et al. 2013, 2017), which consist of a stereotyped sequence (Supplementary Videos S1 and S2). First, the male leaps vertically from a perch and claps his wings at high speed behind his head several times. During the leap, the male exposes white underwing plumage patches that sharply contrast to the blue-black coloration. Second, the male emits a high-pitched strident vocalization at the peak of the leap, which adds to the mechanical sound produced by the wing beats, while rotating his body axis and pointing his beak to the ground. Finally, the male returns to the initial perch and most likely leaps again a few seconds later. Blue-black grassquit males may perform this display for hours, especially during sunny days (Sicsú et al. 2013). Experiments with artificial nests showed that this highly conspicuous male display can attract predators (Dias et al. 2010). After pairing, both sexes engage in a social monogamy with biparental care (Almeida and Macedo 2001). However, males continue performing their sexual displays even with active nests in their territories, possibly seeking extrapair copulations, since genetic studies revealed extrapair fertilization rates from 8% to 50% in the species (Carvalho et al. 2006; Manica et al. 2016).

We used predator simulation experiments to assess whether males modulated their mate attraction performances under different predation risk regimes. Specifically, we tested the 3 theoretical scenarios introduced above, each one predicting a different outcome. First, the survival focused hypothesis (Lima and Dill 1990; Magnhagen 1991) predicts that all males should prioritize survival and reduce display rate and/or performance attributes in situations of high predation risk. Second, the handicap principle hypothesis (Zahavi 1975) predicts an interaction between male condition and predation risk by which males in better physical condition (e.g., healthier, less parasitized, more ornamented) should increase display rate and/or performance attributes under high predation risk, in comparison to males in worse condition. Lastly, the asset protection hypothesis (Clark 1994) which comprises the terminal investment hypothesis (Williams 1966; Trivers 1972; Pianka and Parker 1975), predicts a different pattern as a result of the interaction between male condition and predation risk. In this case, males with high residual reproductive value (i.e., males in better physical condition, as described above) should reduce display rate and/or performance attributes under high predation risk, while under these conditions males with low residual reproductive value should present the opposite pattern, that is, increase display rate and/or performance attributes.

METHODS

Study area and subjects

This study took place within savanna vegetation patches in the University of Brasilia campus, Brazil (15°44′S, 47°52′W), during 2 breeding seasons (November to March) in 2015/2016 and 2016/2017. We captured male blue-black grassquits with mist nets (2.5 m × 12 m, 10 mm mesh) and banded them with unique combinations of 4 plastic color bands. Capture took place in the early morning hours; thus, individuals were less likely to exhibit large variations in weight due to foraging or energy expenditure in daily activities. We took different measures to assess their overall body condition and their degree of ornamentation, and afterwards released them in the same locations where they were captured. We measured their body mass to the nearest 0.2 g with a scale and the length of the left tarsus with calipers (accuracy: ±0.01 mm). With these data, we developed a male body condition index (body mass divided by tarsus length; Santos et al. 2009; Magalhães et al. 2014). As a proxy of condition, we also visually counted the number of ectoparasites (feather lice) on both wings (data pooled). A high load of feather-dwelling ectoparasites may incur in several detrimental consequences to birds, such as poor feather quality after molt, increased feather asymmetry, plumage with lower brightness, and depluming (reviewed by Proctor and Owens 2000).

We estimated an index of molting by measuring the proportion of the male body covered by nuptial plumage corrected by the time interval from the beginning of the breeding season (Maia and Macedo 2011, Manica et al. 2014), since these 2 variables are positively correlated (see below). The index consisted of the residuals of a linear regression (nuptial plumage coverage vs. scaled time since the beginning of the breeding season; $\beta = 0.43 \pm 0.06$, degrees of freedom [df] = 309, $P < 0.0001$), using male data from

a different study (2013 to the 2017 breeding seasons; mean ± SD: 78.75 ± 30.18 males/season, N = 315; Diniz et al. 2015). Thus, males captured for the current study were assessed relative to average nuptial plumage coverage of the population from previous breeding seasons. High molting index values indicate a high proportion of nuptial plumage coverage, whereas low values, a lower nuptial plumage coverage. These measurements allow comparisons with other publications that have used the same variable (Maia and Macedo 2011; Diniz et al. 2015).

We used binoculars to monitor the banded males that performed aerial displays in the area and marked the trees and bushes that were used as display perches. Experiments started after we identified display sites for at least 20 banded males. All animal procedures were approved by the Universidade de Brasília animal welfare committee (UnBDoC #92808/2014).

Experimental design

We performed pilot experiments using captive blue-black grassquits to determine whether taxidermized predator models or acoustic predator playbacks would be appropriate options representing predation risk. The taxidermized predator models (Guira cuckoo *Guira guira* and American kestrel *Falco sparverius*) were mobbed and produced such extreme behaviors that this option was considered unsuitable for our intentions. Playing back calls of a local avian predator, the aplomado falcon (*Falco femoralis*), produced changes in grassquit behavior that we interpreted as increased perception of danger by the bird. We observed a reduction in grassquit baseline behavior (e.g., socializing, feeding, and performing aerial displays) and an increase in alarm call emission when falcon vocalization was broadcast to the birds. Captive grassquits resumed their activities a few minutes after the falcon playback emission stopped. Thus, acoustic playbacks of predator vocalizations suggested an increase in predation risk without the perception of an imminent attack by a predator, which was within the context desired for testing our hypotheses.

Playback trials used vocalizations of the aplomado falcon, which preys on adult birds (Hector 1985; Bó 1999), and for the control treatment, we used the vocalizations of the sayaca tanager (*Tangara sayaca*), a sympatric species that does not engage in aggressive interactions with grassquits. We used 3 different playback stimuli for each treatment, and all vocalizations were taken from an online library of avian songs (Xeno-Canto Foundation©; https://www.xeno-canto.org/—*F. femoralis*: XC53276, XC53277, and XC53279; *T. sayaca*: XC84792, XC116274, and XC215355). Playbacks were broadcast with portable sound-speakers (Kaiyue KY-907 frequency response: 0.15–18 kHz), which were calibrated before each trial with a decibel meter (SEW® 2310 SL; maximum dBA, fast window) positioned at 1 m from the speaker, to a standard of 69 dB (based on the amplitude of the grassquits' breeding song; de Moraes et al. 2019). We performed 2 playback trials daily that coincided with the times of the day when the grassquits were more active (P Diniz, personal observation): the first trial started 1 h after sunrise, and the second trial started 2 h before sunset, thus minimizing confounding effects of variable social context (presence of neighboring males and females). We video recorded all banded males that were displaying near the speaker (up to 10 m from the speaker). Therefore, the experimental trial was composed by the 2 playback trials executed at the same male territory, but one experimental trial may include video recordings of more than 1 male. We controlled for bird identity and possible daily variation

in sexual display intensity during data analysis (see below). There was a habituation period of one hour before each trial (i.e., habituation started at sunrise or 3 h before sunset), so birds could adjust to the presence of the observer. If a male did not perform any sexual displays during the 1-h habituation period, the trial was canceled, and a new attempt was made in the next trial period. Only males that were color-banded were used as experimental subjects. We presented a different experimental treatment to the subjects in each playback trial, and the order of stimuli presentation and the period of the day in which they were presented varied randomly.

Treatment exposure consisted of 5 min period of playback presentation; 30 min period of observations; 5 min period of the same playback presentation; and 30 min period of new observations. During the playback presentations, we placed the speaker 1.5 m above ground facing the focal male's display arenas (3–5 m distance). We video recorded male aerial displays during the 2 observation periods with a single video camera (Casio HD digital camera EX-FH25) set on a tripod for stability, at 2 frame rates: 30 and 240 frames per second (FPS; regular-speed and high-speed videos, respectively). We used 30 and 240 FPSs to allow the measure of both relative display rate and leap duration. We recorded at 240 FPS to obtain the number of wing beats per leap (see below). We switched FPSs during the video recording within each observation period to achieve a balance between the numbers of leaps recorded for each FPS rate. Although we could collect all needed data from 240 FPS videos, we filmed 30 FPS videos to increase sampling effort. Videos recorded in 30 FPS demanded less storage space and their format allowed for faster analysis of individual leaps and display bouts. Given the large number of leaps recorded (see below), the speed of video processing was prioritized. We controlled for FPS and the order of the leap display in a leaping bout in our models (see below). After the treatment ended, we classified weather conditions in one of four categories: 0 = sunny, 1 = partly cloudy, 2 = mostly cloudy, 3 = cloudy. Trials were not run under rain. We used a tape measure to estimate the height of the perches used during male displays. Since leap and perch heights are inversely correlated for grassquit displays (Carvalho et al. 2007), it is important to control for perch height during leap display analysis (see below).

We filmed 33 males during the execution of 839 leaps (details in Appendix Table 1). Grassquit males displayed in long bouts usually starting and ending at the same perch. We estimated the number of leaps per bout for bouts with 3 or more leaps (these bouts contained 91% of the leaps recorded). We used Windows® Movie Maker v. 2012 (Microsoft Corporation 2012) to analyze all recorded leaps. For each leap, we measured: 1) the duration of the leap (using both the regular-speed and high-speed videos) (33 males, 830 leaps); and 2) the number of wing beats performed during the leap (using only the high-speed videos) (29 males, 386 leaps). We have video recorded at least one leap display at each trial (i.e., treatment) for 22 out of the 33 studied males. The remaining 11 males had one or more leap displays recorded at only one trial (control: 7 males, predator: 4 males). Previous studies indicate that the height of the male leaps is positively correlated to leap duration and number of wing beats (Manica et al. 2017), so we did not measure leap height. Grassquit males that perform higher leaps are preferred by females for social pairing (Manica et al. 2016). Therefore, leap duration and number of wing beats, as proxies of leap height, are important cues for mate choice by female grassquits and were the display components used for analysis. Lastly, we calculated 3) relative display rate, computed as the number of leaps performed during a display bout divided by the duration of the display bout. We decided to use duration of the

display bout to calculate a relative display rate because it is unfeasible to track single individuals for long periods of time, as they frequently vanish amid the savanna grassland and bushes.

Data analysis

We analyzed data using R version 3.4.1 (R Core Team, 2017). First, we used a mixed model (package lme4, Bates et al. 2015) to evaluate the relationship between duration of the leap (response variable) and the number of wing beats per leap (predictor), controlling for individual identity (random factor). These 2 variables were correlated (pseudo-R-squared = 0.64, $P < 0.0001$, $N = 384$ leaps from 28 males). A preliminary analysis indicated similar effects of treatment and male condition (ectoparasite count and body condition) upon both display traits (leap duration and number of wing beats per leap). Sample size for number of wing beats per leap was 46% lower in comparison with that of leap duration, thus only leap duration was used in the statistical analyses.

We used a linear mixed model (LMM; Zuur et al. 2013) to test the effect of predation risk treatment, body condition index, nuptial plumage coverage (molting index), and ectoparasite count (main effects) on relative display rate and leap duration. Sample sizes to run the models were the number of display bouts (for relative display rate) and the number of leap displays (for leap duration), while controlling for individual identity (Appendix Table 1).

To test the handicap principle and the asset protection hypotheses, we added the following interactions (and associated main effects): playback treatment × nuptial plumage coverage, playback treatment × ectoparasite count, and playback treatment × body condition index. The handicap principle and the asset protection hypotheses predict, respectively, positive and negative interactions between predation risk and the variables reflecting variation in relative display rate and leap duration.

We also included possible confounding variables as predictor factors: date, breeding season (2015/2016 or 2016/2017), weather category, day time (morning or afternoon), FPS (30 or 240; only for leap duration), perch height, and sequence number (i.e., the order) of the leap within the display bout (only for leap duration). Finally, we added the identity of males, the identity of playback stimuli, and experimental trial as random intercepts in all models to avoid pseudo-replication.

We performed backward stepwise model selection based on likelihood ratio tests (and Wald tests for main effects of variables with significant interaction terms) to simplify the models and test for predictor effects (Zuur et al. 2013). We used the "stepwise-reintroduction for parameter estimation" (SRPE) method, which consists in adding removed terms one by one for the final model and checked their fitting and effect sizes (Hegyi and Garamszegi 2011). Although stepwise modeling has some drawbacks (Whittingham et al. 2006), the SRPE method mitigates the main issue of extreme parameter estimation bias, and even increases estimation accuracy compared with full models (Hegyi and Laczi 2015). Results were checked using an AIC model selection procedure (dredge function), and results remained qualitatively unchanged. All continuous variables were scaled before the analyses to obtain standardized (β) coefficients for predictors. In cases where we found an effect of an interaction between a continuous and a categorical variable, we reran the best-fitting model for each class of each categorical variable to help interpret the relationship between the response variable and the continuous variable involved in these interactions.

RESULTS

Predation risk affected leap duration ($\chi^2 = 12.10$, df = 1, $P < 0.001$), but this effect varied with 2 male traits: ectoparasite load and molting index (i.e., nuptial plumage coverage corrected by date). First, we found a significant interaction between wing ectoparasite count and predation risk explaining variation in leap duration (predation risk × wing ectoparasite count; likelihood-ratio test: $\chi^2 = 7.30$, df = 1, $P < 0.01$; Appendix Tables 2 and 3), though model predictor lines overlapped in their 95% confidence intervals (Figure 1), suggesting a weak effect of this interaction. Highly parasitized males increased leap duration when subjected to the predation treatment (Figure 1). In contrast, leap duration of males with a low ectoparasite count did not vary with predation risk (Figure 1).

We also found that the interaction between molting index and predation risk affected leap duration (likelihood-ratio test: $\chi^2 = 15.91$, df = 1, $P < 0.0001$; Appendix Tables 2 and 3). Males with a low molting index produced longer leaps in the predation treatment when compared with the control treatment (Figure 2). In
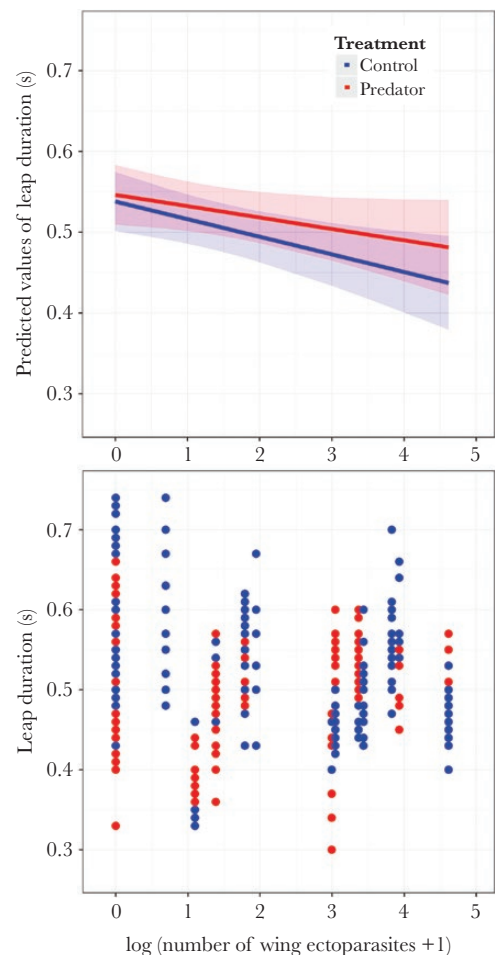

Figure 1
Interaction between predation risk (control = no-risk control; predator = predator simulation treatment) and wing ectoparasite count explains the variation in leap duration. We show predicted values (and 95% CI) by the linear mixed models (upper image) and the corresponding raw data (lower image, $N = 578$ leaps from 24 males; control = 324 leaps from 21 males, predator = 254 leaps from 17 males).

contrast, males with a high molting index presented similar leap duration in both treatments (Figure 2).

We found a significant negative effect of body condition index on leap duration (likelihood-ratio test: $\chi^2 = 5.09$, df = 1, $P = 0.024$), which is independent of predation risk (predation risk × body condition index; likelihood-ratio test: $\chi^2 = 0.007$, df = 1, $P = 0.93$). In other words, males with high body condition index values exhibited shorter leaps compared with males with a lower body condition index (Figure 3). Finally, we found no direct effect of predation risk treatment on relative display rate (likelihood-ratio test: $\chi^2 = 0.62$, df = 1, $P = 0.43$; Appendix Table 4).

DISCUSSION

We predicted 3 possible scenarios for how varying levels of predation risk would influence the sexual displays of blue-black grassquit males. Our findings partially supported the combined predictions of the asset protection and the terminal investment hypotheses (Williams 1966; Trivers 1972; Pianka and Parker 1975; Clark 1994). We found that lower quality males (i.e., those with high ectoparasite

load and low molting index) increased leap duration when predation risk was high. These lower condition males could have reduced chances of future breeding and therefore could be willing to suffer higher risks to gain mating opportunities at a given breeding season. According to this hypothesis, we expected that higher quality males (i.e., those more highly ornamented and with a lower parasite load), would protect their reproductive assets, and decrease display performance under high predation risk because of greater chances of future breeding. However, our findings did not support this second prediction since higher quality males did not differ in display performance in high versus low predation risk contexts.

Parasites decrease their hosts' residual reproductive value by consuming resources that are otherwise used for host development and maintenance (Sheldon and Verhulst 1996), and also for investment in the expression of secondary sexual traits (Gustafsson et al. 1994; Magalhães et al. 2014). Depending on the costs of parasitism, infested males may delay reproduction due to the damaging effects of parasites on nuptial ornaments (review by Proctor and Owens 2000) or they may not even survive to the next breeding season (Brown et al. 1995; Richner and Tripet 1999). Furthermore, males may advertise a healthy and parasite-resistant profile by exhibiting fully developed sexual ornaments and performing dynamic sexual displays (Hamilton and Zuk 1982; Andersson 1994). The expression of these honest secondary sexual traits is typically associated with higher reproductive success (Sheldon et al. 1997), ultimately influencing a male´s residual reproductive value (Clark 1994). Our results showed that less ornamented and more parasitized grassquit males (i.e., low residual reproductive value) were able to perform sexual displays that are as intense as those performed by fully ornamented and healthier males in high predation risk contexts. Therefore, our data agree with one of the key predictions of the terminal investment hypothesis (Williams 1966; Trivers 1972; Pianka and Parker 1975): individuals with low residual reproductive value (i.e., reduced expectations of future reproduction) should increase their current reproductive effort when facing a high perceived risk of extrinsic mortality (Velando et al. 2006, 2014; Copeland and Fedorka 2012; Nielsen and Holman 2012).

A relevant question is why the predation risk treatment did not affect the sexual display of males with fewer ectoparasites and greater nuptial plumage coverage. Given that parasites may
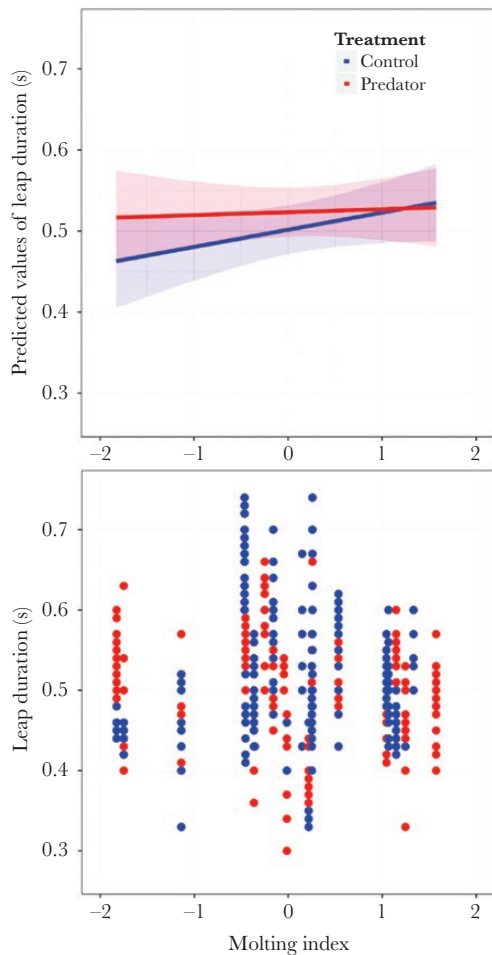

Figure 2

Interaction between predation risk (control = no-risk control; predator = predator simulation treatment) and molting index (nuptial plumage coverage corrected by date) explains the variation in leap duration. We show predicted values (and 95% CI) by the linear mixed models (upper image) and the corresponding raw data (lower image, $N = 578$ leaps from 24 males; control = 324 leaps from 21 males, predator = 254 leaps from 17 males).
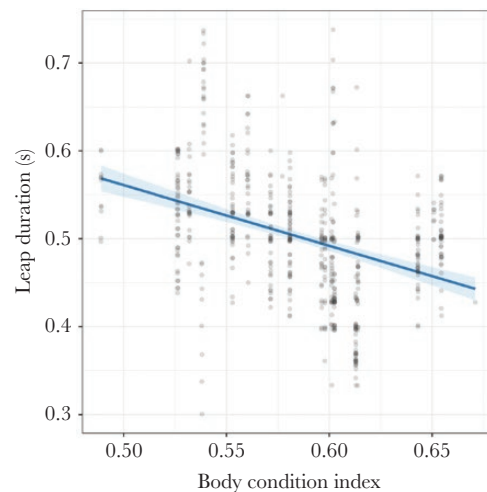

Figure 3

Relation between body condition index (male body mass divided by tarsus length) and leap duration ($N = 578$ leaps from 24 males).

enhance host susceptibility to predator attacks (Hudson et al. 1992; Gehman and Byers 2016), and that blue-black grassquit males with more ornaments have a lower ectoparasite load (Magalhães et al. 2014), we presume that less parasitized and more ornamented males would be less sensitive to variations in predation risk. Thus, we speculate that although all males in the study faced the same predatory stimulus, males probably were intrinsically different relative to their perception of predation risk, with increased risk perception by low-quality males (leading to terminal investment strategies) and attenuated risk-perception by high-quality males (no response to predation treatment).

An alternative explanation might be that mating displays performed by male grassquits in high predation risk scenarios change to a pursuit-deterrent function directed toward potential predators (Caro 1995). However, a core assumption for pursuit-deterrent signal evolution is that this signal should be costly and only individuals of higher inherent quality and with greater escape capabilities would be able to emit the signal (Nur and Hasson 1984; Vega-Redondo and Hasson 1993). In our data, low-quality grassquit males increased leap display intensity under high predation risk to levels comparable to those of high-quality males. Given the uncertainty of an aerial predatory threat associated only with acoustic cues, the lack of information about the predator's location and the high cost of pursuit-deterrent signal emission (Bergstrom and Lachmann 2001), we can assume that it would be easier for grassquit males to just move closer to the ground and hide in the vegetation until the predation risk is lower. Thus, based on these observations, we cannot suggest that pursuit-deterrence is a plausible explanation for the behavioral patterns found in our data. Another alternative explanation is that low-quality males may be exploiting the moment of silence right after the exposure to the predator stimuli, when high-quality males possibly stop displaying. In these specific moments of low male competition, low-quality males may produce intense displays that equal high-quality male displays but for a shorter period. Unfortunately, we were not able to test for this because it was not possible for us to visually track as well as video record the birds during the whole observation period.

Going further, we found that males with lower body condition performed more intense displays (i.e., longer leaps) relative to those with better body condition. This was surprising since males in better condition are expected to perform sexual displays more vigorously (Morales et al. 2003; Hunt et al. 2004). Santos et al. (2009) found a similar pattern where grassquit males with lower body condition scores were more likely to win aggressive interactions over food compared with males with better body conditions. One possible explanation is that lighter males might be sexually selected since their aerial displays may be easier to perform because of the greater agility to leap. These lighter males may signal better inherent quality to females (Barske et al. 2011). This is an interesting finding given that the typical pattern is for sexual selection to favor males with larger and heavier bodies as they usually prevail in intrasexual competition (Andersson 1994).

The female perspective in this predator–prey system is also of critical importance. If males enhance or sustain display performance under high predation risk and females are the target audience, why should females put themselves at risk by choosing a mate in this situation? Even while hidden from predators, females can still evaluate nearby males through acoustic cues, since the acoustic components of the mating display correlate with leap height: the higher (and longer) the leap, the higher the wing beat count and the longer the song duration (Manica et al. 2017). Therefore, once predation risk is lower, females can choose a male based on the information collected during high predation risk moments or continue mate-sampling for better males.

In conclusion, our results suggest that predation risk affects blue-black grassquit sexual displays according to the male's residual reproductive value. The fact that low-quality grassquit males were able to exhibit sexual signals as intensely as high-quality males, specifically in the context of high levels of predation risk, provides support for the idea of a terminal investment, based upon the perception of imminent death (Williams 1966; Trivers 1972; Pianka and Parker 1975). Our results also suggest that the perception of predation risk varies among males, so that those in poorer condition have a more acute sensitivity to threatening situations. One major premise of sexual selection theory is that all sexual signals are honest displays of signaler health and parasite resistance (Andersson 1994). Our study provides evidence that this may not always be the case. Therefore, this tropical songbird deviates from classical evolutionary assumptions, and highlights the importance of considering the influence of ecological and life-history factors, such as predation risk and residual reproductive value, on signal evolution.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

Data Accessibility: Analyses reported in this article can be reproduced using the data provided by de Moraes et al. (2019). The data used in this study has been uploaded in DRYAD (doi: 10.5061/dryad.fc37vr6).

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APPENDIX

Appendix Table 1

Sample sizes and descriptive statistics for leap displays recorded for blue-black grassquit males

Experimental treatment	Number of males	Number of display bouts	Number of leap displays	Mean (±SD) number of leap displays/display bout (range)	Mean (±SD) number of leap displays/male (range)
Control	29	53	461	7.89 ± 3.15 (3–14)	15.90 ± 7.53 (1–29)
Predator	26	42	378	8.31 ± 3.02 (3–12)	14.54 ± 7.20 (2–22)

Appendix Table 2

Backward stepwise model selection with SRPE method for explaining variation in leap duration

Predictor variables	Likelihood ratio test (df = 1)	P
Date	0.77	0.38
Order of the leap on the leap bout	0.0002	0.99
Playback treatment × body condition index	0.007	0.93
Breeding season	2.87	0.09
Playback treatment × wing ectoparasite count (log)	7.30	0.007
Playback treatment × nuptial plumage coverage index	15.91	<0.0001
Playback treatment	12.10	0.0005
Wing ectoparasite count (log)	8.65	0.003
Nuptial plumage coverage index	1.61	0.20
Body condition index	5.09	0.024
FPS	9.38	0.002
Weather	11.00	0.0009
Perch height during leaping (log)	13.39	0.0003
Daytime	14.65	0.0001

Variables highlighted in bold were kept in the final model. All models contain the identities of males, playback stimuli, and experimental trial as random effects. Main effects for variables involved in meaningful interactions accessed by Wald tests. Sample size: 24 males (578 leap displays), 21 in control treatment (324 leap displays), and 17 in the predator treatment (254 leap displays).

Appendix Table 3

Beta coefficients for predictors to explain variation in leap duration

Fixed effects	β ± SE
Playback treatment (predator)	0.29 ± 0.08
Nuptial plumage coverage index	0.28 ± 0.14
Wing ectoparasite count (log)	−0.48 ± 0.14
Body condition index	−0.31 ± 0.13
Weather	0.23 ± 0.05
Perch height during leaping (log)	−0.16 ± 0.04
Daytime (1600–1710)	−0.31 ± 0.08
FPS (240)	−0.17 ± 0.05
Playback treatment (predator) × Nuptial plumage coverage index	−0.24 ± 0.06
Playback treatment (predator) × Wing ectoparasite count (log)	0.17 ± 0.06
Date	0.17 ± 0.19
Order of the leap on the leap bout	0.00 ± 0.03
Playback treatment × Body condition index	0.007 ± 0.08
Breeding season (2016/2017)	−0.72 ± 0.39

Variables highlighted in bold were kept in the final model.

Appendix Table 4

Backward stepwise model selection with SRPE method for explaining variation in leap rate

Predictor variables	Likelihood ratio test (df = 1)	P
Perch height during leaping (log)	0.49	0.48
Daytime	0.97	0.32
Playback treatment × Body condition index	0.84	0.66
Date	0.09	0.76
Breeding season	0.61	0.43
Playback treatment × Wing ectoparasite count (log)	0.40	0.82
Wing ectoparasite count (log)	0.21	0.64
Body condition index	0.82	0.36
Playback treatment × Nuptial plumage coverage	0.93	0.63
Playback treatment	0.62	0.43
Nuptial plumage coverage index	0.13	0.72
Weather	2.77	0.10

Variables highlighted in bold were kept in the final model. All models contain the identities of males, playback stimuli, and experimental trial as random effects. Sample size: 22 males (19 in the control treatment and 15 in the predator treatment).

REFERENCES

Almeida JB, Macedo RH. 2001. Lek-like mating system of the monogamous blue-black grassquit. The Auk. 118:404–411.

Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press.

Barske J, Schlinger BA, Wikelski M, Fusani L. 2011. Female choice for male motor skills. Proc Biol Sci. 278:3523–3528.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67:1–48.

Bergstrom CT, Lachmann M. 2001. Alarm calls as costly signals of antipredator vigilance: the Watchful Babbler game. Anim Behav. 61:535–543.

Bó MS. 1999. Dieta del halcón plomizo (*Falco femoralis*) en el sudeste de la província de Buenos Aires, Argentina. Ornitol Neotrop. 10:95–99.

Brown CR, Brown MB, Rannala B. 1995. Ectoparasites reduce long-term survival of their avian host. Proc R Soc B. 262:313–319.

Caro TM. 1995. Pursuit-deterrence revisited. Trends Ecol Evol. 10:500–503.

Carvalho CBV, Macedo RH, Graves JA. 2006. Breeding strategies of a socially monogamous neotropical passerine: extra-pair fertilizations, behavior, and morphology. Condor. 108:579–590.

Carvalho CBV, Macedo RH, Graves JA. 2007. Reproduction of blue-black grassquits in central Brazil. Braz J Biol. 67:275–281.

Clark CW. 1994. Antipredator behavior and the asset-protection principle. Behav Ecol. 5:159–170.

Copeland EK, Fedorka KM. 2012. The influence of male age and simulated pathogenic infection on producing a dishonest sexual signal. Proc Biol Sci. 279:4740–4746.

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.

Dominey WJ. 1984. Alternative mating tactics and evolutionary stable strategies. Am Zool. 24:385–396.

Endler JA. 1987. Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim Behav. 35:1376–1385.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. Am Nat. 139:S125–S153.

Fisher RA. 1930. The genetical theory of natural selection. Oxford, UK: Clarendon Press.

Gehman ALM, Byers JE. 2016. Non-native parasite enhances susceptibility of host to native predators. Oecologia. 183:919–926. doi:10.1007/s00442-016-3784-1

Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol. 11:92–98.

Gustafsson L, Nordling D, Andersson MS, Sheldon BC, Qvarnström A. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. Philos Trans R Soc Lond B Biol Sci. 346:323–331.

Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites? Science. 218:384–387.

Hector P. 1985. The diet of the Aplomado Falcon (*Falco femoralis*) in eastern Mexico. Condor. 87:336–342.

Hegyi G, Garamszegi LZ. 2011. Using information theory as a substitute for stepwise regression in ecology and behavior. Behav Ecol Sociobiol. 65:69–76.

Hegyi G, Laczi M. 2015. Using full models, stepwise regression and model selection in ecological data sets: Monte Carlo simulations. Ann Zool Fennici. 52:257–279.

Hudson PJ, Dobson AP, Newborn D. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. J Anim Ecol. 61:681–692.

Hunt J, Brooks R, Jennions MD, Smith MJ, Bentsen CL, Bussière LF. 2004. High-quality male field crickets invest heavily in sexual display but die young. Nature. 432:1024–1027.

Lewis SM, Cratsley CK. 2008. Flash signal evolution, mate choice, and predation in fireflies. Annu Rev Entomol. 53:293–321.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:619–640.

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:S15–S22.

Magnhagen C. 1991. Predation risk as a cost of reproduction. Trends Ecol Evol. 6:183–186.

Magalhães RB, Diniz P, Macedo RH. 2014. Plumage coverage is related to body condition and ectoparasitism in blue-black grassquits. Wilson J Ornithol. 126:581–584.

Maia R, Macedo RH. 2011. Achieving luster: prenuptial molt pattern predicts iridescent structural coloration in blue-black grassquits. J Ornithol. 152:2243–2252.

Manica LT, Graves JA, Podos J, Macedo RH. 2016. Multimodal flight display of a neotropical songbird predicts social pairing but not extrapair mating success. Behav Ecol Sociobiol. 70:2039–2052.

Manica LT, Macedo RH, Graves JA, Podos J. 2017. Vigor and skill in the acrobatic mating display of a Neotropical songbird. Behav Ecol. 28:164–173.

Manica LT, Maia R, Dias A, Podos J, Macedo RH. 2014. Vocal output predicts territory quality in a Neotropical songbird. Behav Processes. 109(Pt A):21–26.

Manica LT, Podos J, Graves J, Macedo RH. 2013. Flights of fancy: mating behavior, displays and ornamentation in a neotropical bird. In: Macedo RH, Machado G, editors. Sexual selection. perspectives and models from the Neotropics. Sandiego, CA: Academic Press. p. 391–407.

de Moraes PZ, Diniz P, Fernández-Juricic E, Macedo RH. 2019. Data from: flirting with danger: predation risk interacts with male condition to influence sexual display. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.fc37vr6.

de Moraes PZ, Diniz P, Macedo RH. 2019. Dangerous love? Predation risk does not affect female mate choice in blue-black grassquits. Ethology. 1–9. doi:10.1111/eth.12866.

Morales MB, Alonso JC, Martín C, Martín E, Alonso J. 2003. Male sexual display and attractiveness in the great bustard *Otis tarda*: the role of body condition. J Ethol. 21:51–56.

Nielsen ML, Holman L. 2012. Terminal investment in multiple sexual signals: immune-challenged males produce more attractive pheromones. Funct Ecol. 26:20–28.

Nur N, Hasson O. 1984. Phenotypic plasticity and the handicap principle. J Theor Biol. 110:275–297.

Otte D. 1974. Effects and functions in the evolution of signaling systems. Annu Rev Ecol Evol Syst. 5:385–417.

Pianka ER, Parker WS. 1975. Age-specific reproductive tactics. Am Nat. 109:453–464.

Proctor H, Owens I. 2000. Mites and birds: diversity, parasitism and coevolution. Trends Ecol Evol. 15:358–364.

R Development Core Team. 2017. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/.

Richner H, Tripet F. 1999. Ectoparasitism and the trade-off between current and future reproduction. OIKOS. 86:535–538.

Römer H, Lang A, Hartbauer M. 2010. The signaller's dilemma: a cost-benefit analysis of public and private communication. PLoS One. 5:e13325.

Santos ESA, Maia R, Macedo RH. 2009. Condition-dependent resource value affects male-male competition in the blue-black grassquit. Behav Ecol. 20:553–559.

Sheldon BC, Merilö J, Qvarnström A, Gustafsson L, Ellegren H. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. Proc R Soc B. 264:297–302.

Sheldon BC, Verhulst S. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends Ecol Evol. 11:317–321.

Sick H. 1997. Ornitologia Brasileira. Rio de Janeiro, RJ: Editora Nova Fronteira.

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.

Skutch AF. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithol Monogr. 36:575–603.

Steinberg DS, Losos JB, Schoener TW, Spiller DA, Kolbe JJ, Leal M. 2014. Predation-associated modulation of movement-based signals by a Bahamian lizard. Proc Natl Acad Sci U S A. 111:9187–9192.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago, IL: Aldine Press. p. 136–179.

Tuttle MD, Taft LK, Ryan MJ. 1982. Evasive behavior of a frog in response to bat predation. Anim Behav. 30:393–397.

Vega-Redondo F, Hasson O. 1993. A game-theoretic model of predator–prey signaling. J Theor Biol. 162:309–319.

Velando A, Beamonte-Barrientos R, Torres R. 2014. Enhanced male coloration after immune challenge increases reproductive potential. J Evol Biol. 27:1582–1589.

Velando A, Drummond H, Torres R. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. Proc Biol Sci. 273:1443–1448.

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP. 2006. Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol. 75:1182–1189.

Williams GC. 1966. Natural selection, the cost of reproduction and a refinement of Lack´s principle. Am Nat. 100:687–690.

Zahavi A. 1975. Mate selection—a selection for a handicap. J Theor Biol. 53:205–214.

Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. Q Rev Biol. 73:415–438.

Zuur AF, Hilbe JM, Ieno EN. 2013. A beginner's guide to GLM and GLMM with R: A frequentist and Bayesian perspective for ecologists. Newburgh, NY: Highland Statistics Ltd.