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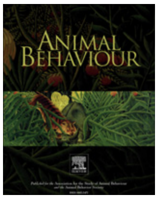

Articles

Androgen-dependent male vocal performance influences female preference in Neotropical singing mice

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Vocalizations used in aggressive and mating contexts often convey reliable information about signaller condition when physical or physiological limitations constrain signal expression. In vertebrates, androgens modulate the expression of vocal signals and provide a proximate link between male condition and signal form. In many songbirds, assessment of males is based on production of trills that are constrained by a performance trade-off between how fast notes are repeated and the frequency bandwidth of each note. In this study, we first recorded trills of male Neotropical singing mice (*Scotinomys*) to examine whether they show a similar performance trade-off, and then manipulated androgen levels to assess their role in modulating vocal performance. Lastly, we broadcast experimentally manipulated trills to females to determine whether they preferred versions resembling those of androgen-treated males. Singing mice showed a vocal performance trade-off similar to that of birds. Males treated with androgens maintained vocal performance, but castrated mice that were administered empty implants produced trills with lower performance. Females approached high-performance trills more rapidly and spent more time near corresponding speakers. Together, our results demonstrate that androgens modulate the production of physically challenging vocalizations, and the resulting signal variation influences female receiver response.

Vocalizations used in aggressive and mating contexts are among the most diverse and elaborate displays in the animal kingdom. Physical or physiological constraints can result in signals that convey information about signaller condition (Maynard Smith & Harper 1995; Vehrencamp 2000; Fitch & Hauser 2003; Hurd & Enquist 2005; Taylor & Reby 2010), and receiver responses to such signals can generate substantial intra- and intersexual selection (Andersson & Simmons 2006). In birds, anurans and mammals, conspicuous features of vocal signals (e.g. duration and fundamental frequency) provide accurate indicators of male quality and size that are attractive to females and threatening to rival males (Clayton & Prove 1989; Welch et al. 1998; Reby et al. 2005). Such displays are thought to transmit honest information because only individuals in better condition are able to afford costs associated with signal production.

In vertebrates, vocal displays associated with reproduction are often mediated by androgens released from the testes (Floody 1981; Ball et al. 2003; Moore et al. 2005; Bass & Remage-Healey 2008). Androgens can influence vocalizations through actions on motivational centres and vocal motor pathways in the central nervous system (reviewed in Yamaguchi & Kelley 2002; Bass & Remage-Healey 2008) or via modulation of peripheral structures involved in signal production. For example, changes in fundamental frequency result from anabolic effects of androgens on the larynx and syrinx, the 'source' of sound production in mammals and birds (Beckford et al. 1985; Beani et al. 1995; Cynx et al. 2005; Evans et al. 2008; Taylor & Reby 2010; Pasch et al. 2011). By modulating signal duration, rate or fundamental frequency, androgens can provide a mechanistic link between male condition and signal form (Remage-Healey & Bass 2007; Charlton et al. 2010).

While androgens influence conspicuous features of vocal signals, little is known about their effects on vocal attributes that reflect male performance. For example, many avian species produce a series of rapidly repeated notes of similar structure, termed trills. Trill production is constrained by a mechanical trade-off between how fast notes are repeated (trill rate) and the frequency bandwidth of each note, resulting in a performance limit (Podos 1997). Males with high vocal performance scores are considered greater threats by rival males and are more attractive to females in a variety of species (Ballentine et al. 2004; Illes et al. 2006). Vocal performance is also correlated with age, social status and reproductive

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success (Janicke et al. 2008; Ballentine 2009; Botero et al. 2009; de Kort et al. 2009). Despite the association between circulating testosterone and these same variables (age: Morton et al. 1990; Vleck & Brown 1999; social status: Wingfield 1985; Wingfield & Moore 1987; reproductive success: Reed et al. 2006), the role of androgens in mediating variation in vocal performance is unclear.

In birds, vocal performance trade-offs are thought to arise via 'filter' constraints whereby sound frequencies track beak gape, with wide gapes corresponding to high frequencies and small gapes corresponding to low frequencies (Westneat et al. 1993; Hoese et al. 2000). However, other aspects of respiratory and syringeal motor patterns are important in modulating aspects of note rate and frequency modulation (Goller & Suthers 1996; Nelson et al. 2005; Riede et al. 2006). In particular, 'minibreaths' that birds take between each note suggest a potential role for respiratory musculature in limiting temporal aspects of note production (Calder 1970; Hartley & Suthers 1989; Lambrechts 1996). While the influence of androgens on avian respiratory musculature has not been well characterized, the mammalian diaphragm is highly sensitive to androgens that can influence the velocity and force of respiration (Prezant et al. 1997). Similarly, the craniomandibular musculature of rodents is responsive to androgens (Lyons et al. 1986; Eason et al. 2000), which suggests a mechanism by which androgens could influence the rate of gape and frequency modulation. These data suggest that androgens could provide an important yet underappreciated mechanism modulating vocal performance, and highlight the potential for an appropriate mammalian model to inform our understanding of vocal signals.

Neotropical singing mice (genus *Scotinomys*) are diurnal insectivorous rodents that inhabit montane cloud forests throughout Central America (Hooper & Carleton 1976; Wilson & Reeder 2005). Adult males commonly produce stereotyped trills (see Supplementary Material, Audio S1) that are androgen dependent and used in male–male aggression and mate attraction (Pasch et al. 2011; this study). Presentation and subsequent removal of females increases male song rate, and males countersing in response to broadcast songs of intruding males in the field and laboratory (Pasch et al. 2011; B. Pasch & S. M. Phelps, unpublished data). When singing mice trill, they take 'minibreaths' between each note and appear to modulate the fundamental frequency (10–43 kHz) with their mouth gape (Miller & Engstrom 2007; see Supplementary Material, Video S1) in a manner analogous to some bird song (Suthers et al. 1999).

In this study, we first asked whether Alston's singing mouse (*Scotinomys teguina*) shows a vocal performance trade-off between trill rate and frequency bandwidth. We then manipulated androgens in laboratory-reared males to investigate whether they play a role in modulating vocal performance. Finally, we experimentally manipulated trills to determine whether females would respond to versions resembling those of androgen-treated males. We predicted that androgen removal would negatively impact vocal performance, and that females would prefer male mouse trills with higher performance scores over those with lower scores.

METHODS

Generating the Population Performance Limit

To assess variation in male trills, we live-captured animals in Sherman traps baited with peanut butter and oats in four localities throughout Costa Rica and Panamá from 2006 to 2009 (see Campbell et al. 2010). We measured their mass and hindfoot length prior to transferring males to PVC-coated wire-mesh cages (28 × 28 × 28 cm). Cages were placed inside anechoic recording chambers (42 × 42 × 39 cm) made from expanded PVC. Details on song recording can be found in Campbell et al. (2010). We recorded spontaneous trills from 102 males ($N = 3.73 \pm 1.57$ trills/male, range 1–12). Animals were uniquely marked and released at the site of capture. All capture and recording procedures in the field were conducted with approval from the Institutional Animal Care and Use Committee (IACUC) at the University of Florida (No. E436), the Costa Rican Ministerio del Ambiente y Energia and the Panamanian Autoridad Nacional del Ambiente.

We used an automated code in Matlab (available upon request) to quantify the average trill rate and frequency bandwidth for the entire song. Frequency bandwidths were calculated by a threshold routine that identified frequencies at the onset and offset of notes that were eight standard deviations above the average background noise (sampling rate: 96 kHz; fast Fourier transform size: 256; Hann window, time resolution = 50 ms). We plotted an average of each male's songs (see Fig. 2a, filled circles) and calculated vocal performance limits as described in detail elsewhere (Podos 1997; Ballentine et al. 2004). Briefly, we first pooled each male's average trill into bins of one note/s. For each bin, we determined the male with the largest frequency bandwidth (see Fig. 2a, open circles) and calculated a linear regression through these maxima (after Blackburn et al. 1992). This statistical technique attempts to describe biological boundaries by defining theoretical limits to bivariate plots. In this context, the upper-bound regression operationally defines the population performance limit on trill production, with trills closer to the limit being more difficult to produce (Podos 1997).

Androgen Manipulation

We experimentally manipulated androgen levels of laboratory-reared offspring (F1) of wild-captured mice from Cerros de la Carpintera, Costa Rica. Sexually experienced adult males were assigned randomly to one of three treatment groups and housed individually in cages for 1 month prior to experimentation. Animals were given cat chow and water ad libitum and maintained on a 12:12 h light:dark cycle at 20 ± 3 °C. Mice were anaesthetized with isoflurane (SurgiVet Isotec T^3 Classic Isoflurane Vaporizer) and castrated (Cast) bilaterally. We placed a 10 mm silastic implant (1.47 mm inner diameter × 1.96 mm outer diameter, Dow Corning Corporation, Midland, MI, U.S.A.) subcutaneously along the dorsal midline. Implants were filled with either 1 mm (15 mg) of testosterone (T; Sigma T1500), 1 mm of dihydrotestosterone (DHT; Sigma A8380), or left empty ($N = 9$ per treatment). The DHT treatment group was included to identify whether androgens were sufficient to cause acoustic changes in the absence of aromatization (Nyby et al. 1992). Implants were sealed with silicon adhesive, sterilized with ethylene oxide, and soaked in 0.1% saline solution at 37 °C for 12 h prior to implantation. Implant concentrations approximated physiological doses of plasma T of field-captured animals (see Pasch et al. 2011).

Fourteen days pre- and postsurgery, we placed mouse cages inside an anechoic recording chamber to record trills ($N = 3$/male) as described above. We then plotted trill rate and frequency bandwidth for all experimental animals pre- and post-treatment and calculated performance scores as the orthogonal deviation (i.e. vocal deviation in Podos 2001) from the performance limit generated from field-captured males. Researchers were blind to animal treatment. All laboratory procedures were conducted with permits from IACUC at the University of Florida (No. 200801939).

Female Phonotaxis

To assess female response to male trills, we live-captured females at Cerros de la Carpintera, Costa Rica in February 2010.

We used only parous females ($N = 18$) as indicated by open pubic symphyses and enlarged nipples, because pregnant and lactating females ($N = 4$) showed no phonotaxis towards male trills in preliminary studies. We isolated females in wire-mesh cages placed inside anechoic chambers for 48 h prior to experimentation. Females were given cat chow and water ad libitum and were released at the site of capture after our experiments.

To synthesize experimentally high-performance scores, we randomly selected six trills recorded from different males from the same population ('Slow'; S) and deleted 70% of gaps of silence between each note using bioacoustics software Raven Pro 1.3 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). Thus for each Slow stimulus we had a corresponding synthetic ('Fast'; F) stimulus that differed only in its trill rate and duration. By increasing trill rate without changing bandwidth, Fast trills were consistently closer to the population performance limit (Slow: -6.8 ± 0.90; Fast: -1.6 ± 0.92; paired t test: $t_5 = 12.16$, $P < 0.0001$; see Fig. 3a). Each Slow–Fast stimulus pair was used to test three different females. Thus, we used a total of six stimulus pairs to test 18 females.

We tested females in a 92 × 8 × 23 cm arena made from translucent white acrylic with a central compartment to house the female subject. The arena was a single runway (8 cm wide, 23 cm tall and 92 cm long), bisected by a central compartment (9 × 8 cm) for housing the subject female. Each sliding door of the central chamber had a 5 cm diameter hole covered with stainless-steel mesh to allow females to hear stimuli. Two speakers (Pioneer TS-250; flat frequency response 6–40 kHz) were mounted at opposite ends (Fig. 1a). Trills were broadcast from a laptop to each speaker via an external soundcard (Edirol FA-66) with a peak amplitude of 50 dB SPL at 1 m, which approximates natural trill amplitudes. Speakers were calibrated daily with a Brüel & Kjær sound level meter (Type 2219) and calibrator (Type 4230). Two days following capture, females were placed in the central chamber of the choice arena between 1500 and 1830 hours. We allowed females to acclimate for 17 min prior to the first test stimulus. Slow and Fast stimuli from the same male were broadcast antiphonally from each speaker beginning 3 min before the doors were lifted. Each stimulus was repeated every 60 s, and the onset of the two stimuli were 30 s out of phase. We then ceased playback, opened the doors and recorded female responses for 5 min. After each trial, the arena was cleaned with water and alcohol and the female was placed in the central chamber for a 17 min intertrial acclimation. The same stimuli were used for a second test, but stimulus order and side were reversed. We calculated the latency to approach (300 s if no approach) and time spent near (within 30 cm of) each stimulus. Researchers blind to treatments scored all trials.

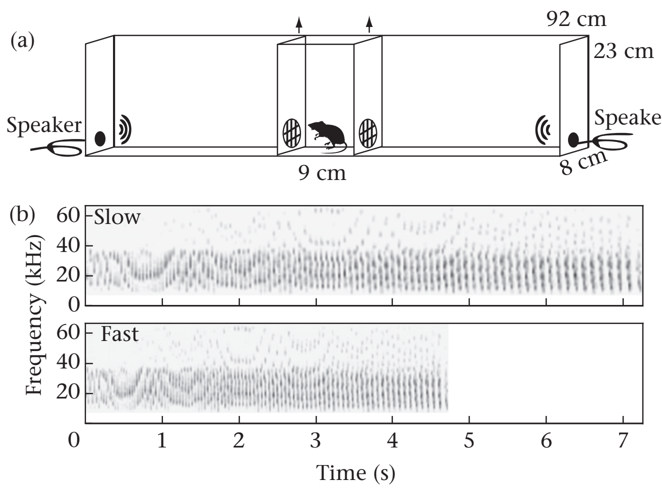

Figure 1. (a) Experimental arena and (b) spectrograms of slow and fast stimuli used in the female preference study. Mouse was redrawn from Reid (1998).

Statistical Analyses

Linear regressions were used to determine the relationship between trill rate and frequency bandwidth, to calculate the performance limit, and to assess how body condition influenced performance scores of male trills recorded in the field. We used model II analysis of variance (ANOVA) to test whether variation in vocal performance was greater among versus within individuals. Variance components were then used to estimate repeatability of vocal performance within males (Lessells & Boag 1987). For experimentally manipulated animals in the laboratory, we used ANOVA to assess variation of pre- and post-treatment performance scores among groups, and paired t tests to assess differences within groups pre- and post-treatment. Significance of post-treatment performance scores among groups was assessed using Bonferroni-corrected alpha values ($\alpha = 0.02$).

To estimate female response to male vocal performance, we identified the speaker that was approached first following playback. The null hypothesis of no preference predicts that females will be equally likely to approach either stimulus in a given test. Expanding that to a two-test paradigm (e.g. Kime et al. 1998), we predicted that 25% of females would initially approach the Fast stimulus twice ('FF', 0.5 × 0.5 = 0.25), 25% would initially approach the Slow stimulus twice ('SS') and 50% would first approach one stimulus in each test ('FS', 0.5 × 0.5 + 0.5 × 0.5 = 0.5). We used a chi-square test to determine deviations from these expectations. To further assess female responses, we calculated the difference in time spent within 30 cm of the speaker broadcasting each stimulus, averaged across the two trials and within each stimulus type, and then performed a paired t test to ask whether females spent more time with Fast or Slow stimuli. We used the same analysis to examine the latency to approach each speaker. Positive values from paired t tests indicated that females showed a preference for Fast stimuli, negative values indicated that females showed a preference for Slow stimuli, and 0 indicated no preference for either stimulus (either moving back and forth to each stimulus or showing place preference after the first trial). In a similar manner, we tested for order effects by assessing differences in approach latencies and time spent near each speaker within and among trials. Lastly, we examined the relationship between female responses to the Fast stimulus and its performance score. We averaged a female's latency to approach the Fast stimulus across the two trials and within each stimulus type and regressed this average against the performance score for the corresponding stimulus. Similarly, we regressed the average time spent near the speaker broadcasting the Fast stimulus against the Fast stimulus' performance score. All statistical analyses were performed in SAS Version 9.2 and JMP, Version 7 (SAS Institute Inc., Cary, NC, U.S.A., 1989–2008). We report means ± SE throughout the text unless otherwise noted.

RESULTS

Population Performance Limit

We found a negative relationship between trill rate and frequency bandwidth from Costa Rican and Panamanian field populations ($Y = -466.8X + 30080$, $R^2 = 0.10$, $F_{1,101} = 11.45$, $P = 0.001$; Fig. 2a). Regression of maximum bandwidth against trill rate revealed a negative relationship, operationally defined as the performance limit ($Y = -1191.4X + 42692$, $R^2 = 0.72$, $F_{1,8} = 20.12$, $P = 0.002$). We found greater among- versus within-individual variation in vocal

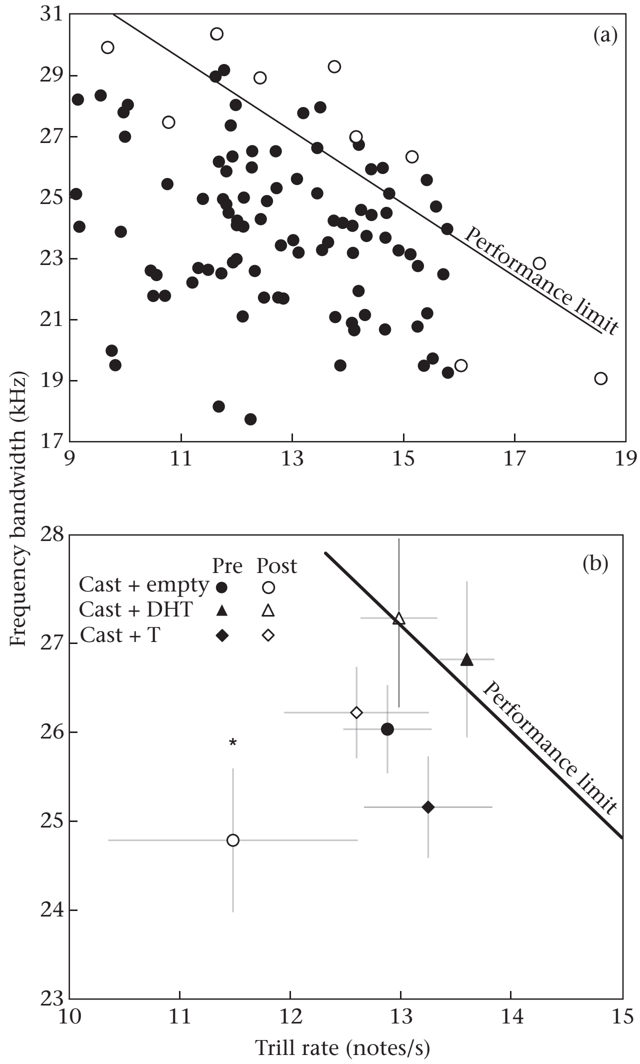

Figure 2. Vocal performance in male singing mice. (a) Average trill rate (notes/s) versus frequency bandwidth (kHz) of male *S. teguina* from Costa Rican and Panamanian field populations (filled circles; $N = 102$). The upper-bound regression on trills with the largest frequency bandwidth per one note/s bin (open circles) represents a performance limit on trill production. (b) Trill rate (notes/s) versus frequency bandwidth (kHz) of male *S. teguina* pre- and post-treatment ($N = 9$ per group) plotted against performance limit of males from Costa Rican and Panamanian field populations from (a). Error bars are ± 1 SD. $^{*}P < 0.05$ for deviation of performance score (orthogonal distance from upper-bound regression).

performance ($F_{101,280} = 4.80$, $P < 0.0001$), which showed a moderate level of repeatability (0.52). Body condition showed a significant but weak positive association with performance scores of field-captured animals ($R^2 = 0.05$, $F_{1,96} = 5.01$, $P = 0.027$).

Androgenic Effects on Performance Scores

We found no significant group differences in presurgery performance scores, as expected given random assignment of treatments (ANOVA: $F_{2,24} = 1.71$, $P = 0.20$). However, performance scores of empty-implanted males fell significantly away from the population performance limit following castration (paired *t* test: $t_8 = -3.01$, $P = 0.01$; Fig. 2b). Conversely, performance scores of DHT-treated and T-treated animals remained at precastration levels (DHT: $t_8 = -0.49$, $P = 0.63$; T: $t_8 = 0.47$, $P = 0.64$). The influence of androgens was reflected in a significant treatment effect on postcastration performance (ANOVA: $F_{2,24} = 3.89$, $P = 0.03$). Both T-treated and DHT-treated animals differed marginally from empty-implanted controls (T versus empty: $t_{17} = 3.27$, $P = 0.09$; DHT versus empty: $t_{17} = 6.72$, $P = 0.02$), but did not differ from one another ($t_{17} = 1.05$, $P = 0.34$).

Female Phonotaxis

Three females did not approach either stimulus during the trials. The remaining 15 females responded in both trials. For the 15 responsive females, we found FF:FS:SS = 8:4:3. This differed significantly from the null expectation of no preference ($\chi^2_2 = 6.6$, $P = 0.037$). In general, females were twice as likely to approach the Fast stimulus as the Slow stimulus (F:S = 20:10). Females also had shorter latencies to approach Fast speakers and spent more time near Fast stimuli than Slow stimuli (latency$_{\text{Fast}}$: 135.8 ± 20.48 s; latency$_{\text{Slow}}$: 189.4 ± 20.17 s; Wilcoxon signed-rank test: $t_5 = -10.5$, $P = 0.03$; time$_{\text{Fast}}$: 105.9 ± 18.09 s; time$_{\text{Slow}}$: 29.9 ± 6.75 s; paired *t* test: $t_5 = 6.71$, $P = 0.001$; Fig. 3b). Order of stimulus presentation did not influence approach latency or time spent near speakers (Wilcoxon signed-rank tests: $t_5 = 0.86$, $P = 0.43$ and $t_5 = -1.4$, $P = 0.22$, respectively). Time spent near Fast stimuli was positively correlated with variation in performance scores among trials ($R^2 = 0.69$, $F_{1,4} = 9.12$, $P = 0.04$; Fig. 3c), whereas latency to approach Fast speakers showed a negative association ($R^2 = 0.57$, $F_{1,4} = 5.24$, $P = 0.08$).

DISCUSSION

We documented a vocal performance trade-off in the trills of male Neotropical singing mice and found that androgens play an important role in modulating performance scores. In turn, females showed shorter latencies and spent more time near speakers broadcasting high-performance trills that resembled vocalizations of androgen-treated males. These results demonstrate that androgens influence both the structure and efficacy of mouse vocalizations.

Singing mice showed a negative relationship between trill rate and frequency bandwidth, suggesting a trade-off similar to that documented in a variety of birds (Podos 1997; Janicke et al. 2008; Podos et al. 2009). Frequency bandwidths are much higher in mice (17–30 kHz) than in birds (1–8 kHz; Podos 1997; Ballentine et al. 2004; Illes et al. 2006; Janicke et al. 2008), reflecting divergent mechanisms of vocal production (Fitch & Hauser 2003). Notably, high-frequency sound production did not seem to correspond to large gape widths (Supplementary Material, Video S1), suggesting gape width functions differently across taxa. Indeed, vocal performance trade-offs may not arise from gape width per se, but from additional motor constraints governing sound-producing organs (i.e. syrinx and larynx) and surrounding musculature (Nowicki et al. 1992; Suthers & Goller 1997; Podos & Nowicki 2004; Nelson et al. 2005). While the origin of the trade-off in mice remains to be elucidated, such convergence across taxa suggests fundamental constraints on mechanisms of trill production.

Androgens played a strong role in modulating vocal performance in singing mice and appear to be necessary for the proper performance of trills. Both trill rate and frequency bandwidth decreased following castration and administration of empty implants, whereas T and DHT implants maintained both measures. The ability of DHT, a nonaromatizeable androgen, to maintain vocalizations suggests that androgens act directly on androgen receptors rather than being aromatized to oestrogens. However, administration of aromatase inhibitors would help to clarify the possible contributions of extragonadal (e.g. adrenal) sources of aromatizeable androgens. To our knowledge, this is the first study

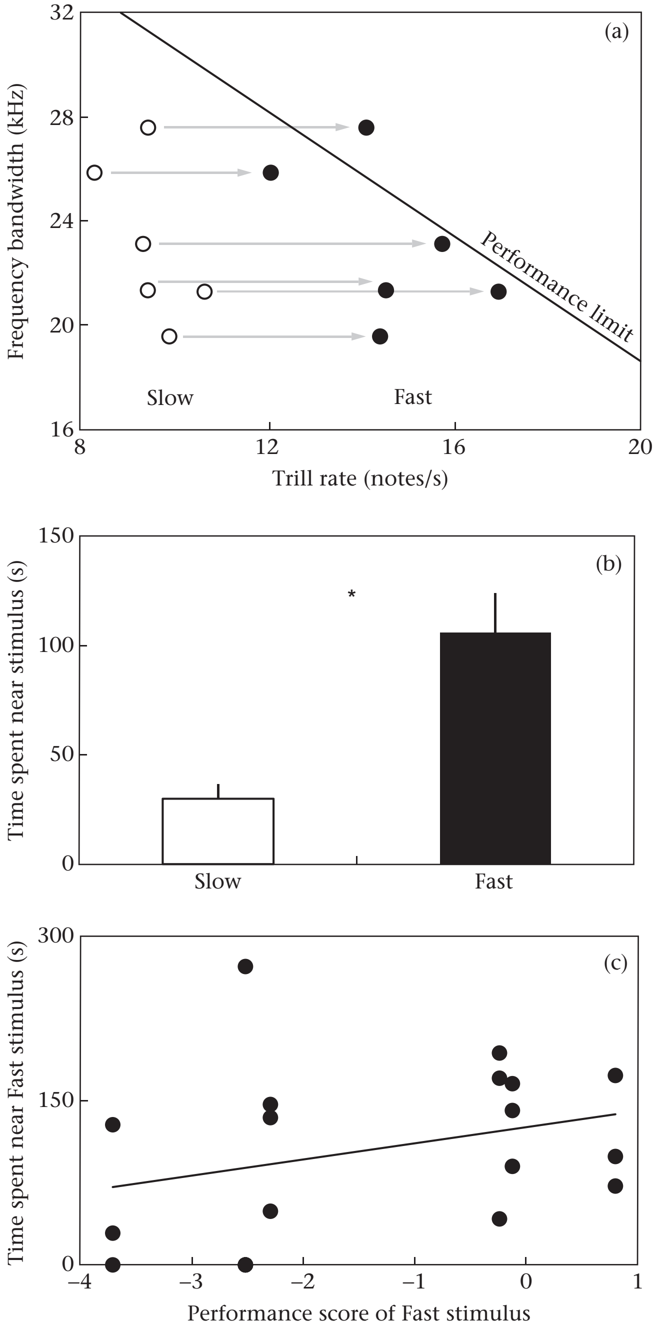

Figure 3. Female response to experimentally manipulated male trills. (a) Trill rate (notes/s) versus frequency bandwidth (kHz) of male *S. teguina* from Cerros La Carpintera males ($N = 6$). Arrows illustrate the experimental manipulation of vocal performance from Slow (open circles) to Fast (filled circles) stimuli. (b) Mean time spent near Slow and Fast stimuli ± SE. $^*P < 0.05$. (c) Time that females spent near Fast stimuli against male performance score among trials.

to experimentally manipulate androgens levels to assess their impact on vocal performance. Circulating levels of testosterone are correlated with the number of notes in avian ‘rattles’, a phrase type similar in structure to trills and used in aggressive contexts (Galeotti et al. 1997). In singing mice, androgens also modulate aggressive behaviour, spontaneous song rate and dominant frequency of trills (Pasch et al. 2011). These extensive effects on a suite of behavioural phenotypes suggest that androgens act on motivational centres in the brain as well as in the larynx and its surrounding musculature. In anurans, androgens alter the expression of laryngeal myosin heavy chain isoforms that influence the velocity and force of muscular contractions (Fischer et al. 1993). In addition, musculature of both the diaphragm and the jaw are known to be androgen responsive in mammals (Lyons et al. 1986; Prezant et al. 1997; Eason et al. 2000), providing additional possible routes for androgen influences over vocal performance. Future studies that disentangle central and peripheral targets of androgens will be valuable in understanding their dynamic effects on vocal signals that reflect performance.

While androgens had a strong influence on vocal performance in experimental animals in the laboratory, field-captured males showed a significant but weak relationship between body condition and performance score. Such weak correlations between condition and performance are often found in birds (Ballentine et al. 2004; Beebee 2004; Janicke et al. 2008). We speculate that this weak correlation emerges because males modulate vocal effort based on their standing relative to competitors, rather than based on their absolute body condition. In contrast to residual mass, androgen levels have a strong influence over vocal performance because they more accurately reflect a male’s resource holding potential (RHP, Parker 1974). Our reasoning draws heavily on the well-established ability of sexual and aggressive success to elicit testosterone surges in many taxa (Wingfield 1987; Wingfield et al. 1990; Oliveira 2004). Such successes provide a male with direct measures of his ability to monopolize access to resources such as mates, space or food. Androgen responses to success may then act on androgen-responsive tissues in the brain and body to translate individual differences in RHP into an appropriate level of reproductive investment. To assess whether androgens are indeed signalling individual differences in RHP to the body’s tissues, it will be useful to correlate circulating levels of androgens with vocal performance measures in the field. In practise, however, the episodic release of androgens may make it difficult to detect relationships between plasma titres and behaviour, and measures such as faecal metabolites may prove more stable predictors. It will also be necessary to manipulate both social experience and testosterone surges (e.g. Oyegbile & Marler 2005) to observe the impact each has over vocal performance.

The fact that females showed preference for trills that had higher performance scores provides preliminary evidence that vocal performance may be used in mate choice, although we cannot distinguish among preferences for duration, trill rate or vocal performance per se. We speculate that trill duration may not be as informative as other measures because female birds and frogs tend to prefer longer vocalizations (not shorter ones, as found herein; e.g. Clayton & Prove 1989; Ryan & Keddy-Hector 1992; Neubauer 1999; Gerhardt et al. 2000). Decoupling the importance of vocal performance from trill rate will require additional playback experiments that manipulate frequency bandwidth while holding trill rate constant. Nevertheless, our experiment mirrors avian studies that demonstrate female preference for high-performance songs (Draganoiu et al. 2002; Ballentine et al. 2004; Caro et al. 2010) and recent work in laboratory mice (*Mus*) showing female approach to male vocalizations used in sexual contexts (Hammerschmidt et al. 2009). More generally, our results add to a growing body of literature suggesting that female mate choice is based upon assessment of male motor performance (reviewed in Byers et al. 2010; Barske et al. 2011). The correlation between female responses and performance scores among trials suggests that females not only attend to variation between two given trills, but increase their response to high-performance trills independent of the stimulus against which it is compared (Ballentine et al. 2004). Understanding how such preferences contribute to reproductive success under more natural conditions will provide important insight into the evolution of male trills.

Our study highlights links between hormones coordinating reproductive behaviours and trade-offs inherent to the production of physically challenging displays. Collectively, our findings support the classification of vocal performance as an index signal, with performance scores putatively reflecting the combination of social and physiological factors that contribute to androgen release (Vehrencamp 2000; DuBois et al. 2008). In turn, females attend to variation in male vocal performance and use it to guide their behaviours. These findings elucidate how male reproductive status can be translated into biologically meaningful variation in signal form.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.04.018.

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