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Extremely loud mating songs at close range in white bellbirds

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Sexual selection in many animal species favors the evolution of elaborate courtship traits. Such traits might help signalers convey, and receivers discern, information about signaler quality; or they might be favored by perceptual or aesthetic preferences for elaborateness or beauty [1–3]. Under either scenario we expect sexual trait elaboration to be countered by proximate constraints rooted in animals' morphology, physiology and phylogenetic history [3,4]. During expeditions to a montane rainforest in the Brazilian Amazon, we obtained amplitude-calibrated measures of mating songs in two species of cotingas, the white bellbird (*Procnias albus*) and the screaming piha (*Lipaugus vociferans*). The screaming piha sings the loudest songs of any passerine bird previously documented [5]. However, we find that white bellbirds are >9 dB louder, and thus achieve roughly triple the sound pressure levels of pihás. Mechanical constraints on amplitude, and thus limits on the reach of sexual selection, are revealed by trade-offs between maximal sound pressure and song duration. We find that song amplitude in bellbirds is context-dependent: when a female was on the display perch, a male bellbird sang only his louder song type, swiveling his body mid-song to face the female head on. We know of no other species in which such high-amplitude vocal signals are directed to receivers in such close proximity. We propose that bellbird females balance an interest in sampling males at close range with a need to protect themselves from hearing damage.

Birds are known to encounter performance constraints when singing songs with rapid modulations in timing and frequency [6]. By contrast, performance constraints in a third

acoustic domain, amplitude, have been relatively overlooked, and little is known about their potential impact on sexual selection and mate assessment [7]. The few studies published on sexual selection and song amplitude have focused on species with moderate song amplitudes, in the range of 70–90 dB SPL [8]. It is reasonable to expect, however, that constraints on amplitude will be more evident, and associated impacts on signal usage and assessment more likely, in species with exceptionally loud songs.

Cotingas and their close relatives, the manakins, are renowned for intense sexual selection, lek polygyny and the evolution of elaborate courtship ornaments and displays. Recent studies in manakins have characterized high-performance components in males' mating dances and mechanical sounds, showing how these components are enabled by morphological and physiological specializations [4]. As for vocal amplitude, while screaming pihás are known to be exceptionally loud [5], male bellbirds (*Procnias* spp.) have been said to sing “what are probably the loudest of all bird calls” [9]. Yet as far as we know, bellbird song amplitudes have not been previously quantified.

We tracked, observed and recorded birds with a calibrated sound level meter that samples amplitude values 50 times per second, suitable for capturing rapid vocal amplitude modulations. Our analyses focused on two amplitude parameters: *Leq* (equivalent continuous sound level), a root-mean-squared average value, and *Lpeak*, which captures maximal transient amplitude values. Screaming pihás across our site sang a single shared song type, while white bellbirds sang two shared song types, one relatively common (Type 1) and the other relatively rare (Type 2; ~one in every six songs; Figure S1, Video S1). For each song analyzed we constructed calibrated amplitude profiles, corrected all amplitude profiles to account for background noise, and then extrapolated amplitude values to those expected 1 m from the source, by applying a function that accounts for sound energy dissipation via spherical spreading.

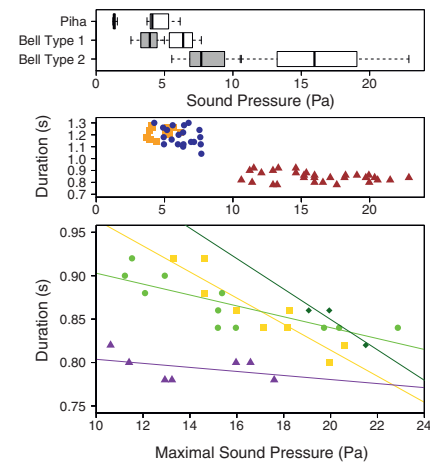


Figure 1 Sound pressure levels of piha and bellbird songs, as they vary by song type and in relation to song duration.

Top panel: Average (grey) and maximal (white) sound pressure levels, converted from noise- and 1 m distance-corrected *Leq* dB(A) (re. 20 μ Pa) values, for a sample of the three song types analyzed. Means, ranges and quartiles are shown. Screaming piha and white bellbird Type 1 songs overlap in maximal sound pressure, yet of the two, bellbird Type 1 songs achieve substantially higher average sound pressures, reflecting these songs' explosive amplitude onsets and sustained high amplitude levels (see Figure S1, lower panels). Both measures are even higher in bellbird Type 2 songs, non-overlapping with the other two types, with maximal sound pressure levels more than three times greater than in pihás. Second panel: Song duration plotted against maximal sound pressure for the three song types (piha songs = orange squares, bellbird Type 1 songs = blue circles, bellbird Type 2 songs = brown triangles). Durations in the bellbird Type 2 songs are substantially briefer than for the other two types, consistent with a potential respiratory constraint on song production. Third panel: The same data for the bellbird Type 2 songs only, plotted on a per-individual basis (differentiated by color/shape). As with the between-type data, three of the four birds individually exhibit decreasing duration with increasing amplitude. The one bird that does not show this trade-off sings with lower overall performance, i.e. with lower maximal sound pressures and shorter durations. This exception is consistent with the supposition that trade-offs tend to occur only when display phenotypes are pushed to maximal values [6]. Bottom panel: male white bellbird singing a Type 2 song. Photo: Anselmo d’Affonseca.

Screaming pihas in our sample achieved maximal vocal amplitudes roughly equivalent to values reported previously [5]: 106.9 ± 0.6 (mean \pm SD) dB(A) *Leq*, and 116.1 ± 0.6 dB(A) *Lpeak*, $n = 3$ birds, all dB values re. 20 μ Pa. White bellbirds were somewhat louder than pihas for their Type 1 songs (108.9 ± 2.3 dB(A) *Leq* and 116.7 ± 1.0 dB(A) *Lpeak*, $n = 8$ birds), and definitively louder for their Type 2 songs (116.6 ± 3.6 dB(A) *Leq* and 125.4 ± 1.7 dB(A) *Lpeak*, $n = 7$ birds). This latter song type is, as far as we know, the highest amplitude vocalization yet documented for any bird, with maximal sound pressure levels exceeding those in the screaming piha by about three-fold (Figure 1, upper panel).

The extreme nature of the vocal display performances documented here imply that pihas and especially bellbirds sing at or near their maximal performance capacities. If so, we might expect to observe trade-offs among display attributes as they approach their upper values [4,6]. We here identify one such trade-off: maximal amplitude is seen to vary negatively with song duration, both across song types (Figure 1, middle panel) and individual bellbirds' renditions of song Type 2 (Figure 1, lower panel). We hypothesize that as birds up-regulate respiratory air flow to elevate song amplitude [10], they deplete their respiratory tidal volumes more quickly, leading to shorter-duration songs. This constraint could presumably limit further evolutionary elaboration in amplitude even in the face of strong and persistent sexual selection.

The effective or realized amplitude of any vocal signal, that is the amplitude experienced by the receiver, is influenced not just by signaler performance but also by how the signal propagates through the environment. Some factors that can influence acoustic signal propagation include distance to receivers, the structure and density of intervening vegetation, abiotic noise such as from wind or rain, and sound interference from other animals [7]. For the three song types in our sample we find that amplitudes declined precisely and steadily with distance, in tight concordance with the prediction of

spherical spreading (Figure S2). This outcome reveals a strong influence of distance, and accordingly a lesser role for other factors, in determining signal amplitudes available to cotinga receivers. The reliability of amplitude as a proxy for distance highlights these signals' potential utility to cotingas for long-distance signaling and localization across their leks [7,9].

On several occasions we observed female white bellbirds joining males on their display perches [9]. In this context, the male first adopted a head-down/tail-down posture, back towards the female, wattle fully distended. He then sang only his higher amplitude (Type 2) song, swiveling dramatically mid-song to face the female head-on for the song's second note (see also [9]). Females in these interactions always retreated as or just before the male sang, yet still experienced songs at very close range, sometimes within four meters or less.

It is curious that one of the world's loudest birds sings only its highest-amplitude song type in such close-range communication. Animals normally reserve loud calls for communication over long distances, and some species are known to vocalize more softly when receivers are nearby [7]. It is also unclear why female white bellbirds willingly stay so close to males as they sing. At four meters, females would experience potentially damaging effective dB values at the ear, of ~ 104 dB(A) *Leq* and ~ 113 dB(A) *Lpeak*. Presumably these risks are offset by benefits females gain in assessing prospective mates. More specifically, as they move around display perches during courtship [9], female bellbirds might actively balance an interest in assessing males at close range while trying to limit hearing damage. Overall, the findings we present for white bellbirds well illustrate sexual selection's power to drive evolution not just in displays themselves, but also in neural and behavioral mechanisms that govern display assessment.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, two figures and one video can be found with this article online at <https://doi.org/10.1016/j.cub.2019.09.028>.

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AUTHOR CONTRIBUTIONS

Both authors contributed equally to the field work and to writing the manuscript. J.P. conducted the analyses and prepared the figures.

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