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Extremely loud mating songs at close range in white bellbirds

Jeffrey Podos¹ and Mario Cohn-Haft²

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 pihas. 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 pihas 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 pihas 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.](image)

Top panel: Average (grey) and maximal (white) sound pressure levels, converted from noise- and 1 m distance-corrected Leq dB(A) (re. 20 µPa) 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 pihas. 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 ± SD) dB(A) $L_{eq}$, and 116.1 ± 0.6 dB(A) $L_{peak}$, $n = 3$ birds, dB values re. 20 µPa. 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 will 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.

**REFERENCES**


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Supplemental Information

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Figure S1. Spectrograms (upper panels), waveforms (middle panels), and calibrated amplitude profiles (lower panels) of representative examples of the screaming piha song type (left column) and the two white bellbird song types (middle and right columns). Amplitude profiles reveal that, of the two species, white bellbird songs are distinguished by explosive amplitude onsets (typically achieving near-peak amplitudes within 20 ms, the temporal resolution of the recording system) and by sustained high amplitudes throughout their songs.
Figure S2. Noise-corrected maximal song amplitudes for $\text{Leq}$ (dB(A) 20 µPa, orange circles) and $L_{\text{peak}}$ (dB(A) 20 µPa, blue triangles) as a function of distance, up to 71 m, between bird and recordist. Data are plotted separately for the single shared song type of the screaming piha (upper panel) and the two shared song types of the white bellbird (middle and lower panels, for the four birds we recorded within 71 m). Orange and blue x-marks indicate grand means of amplitude from our data sets corrected to 1 m distance, and orange and blue curves represent predicted decay functions from 1 m due to spherical spreading. The 1 m amplitude value and decay function from Nemeth’s study on screaming pihas in Venezuela [S6] is included for reference in the top panel (black x-mark and line). The overall tight fit of data points to decay curves illustrates the central importance of distance in determining song amplitudes available to receivers. A similarly tight fit appears for both bellbird song types when data are plotted out to 1250 m; we here show only the nearer recordings to allow closer inspection of these data.
Supplemental Experimental Procedures

Field site. Field work was conducted during two expeditions, 11-15 Dec 2018 and 8-22 Feb 2019, to the Serra do Apiaú in the Mucajai municipality of Roraima state, Brazil. Our field team cleared trails and camping sites from the mountain base, ~100 m elevation, to a series of mountain-top ridges approaching 1500 m elevation. We hiked trails to locate birds of our study species, and recorded birds opportunistically, when we could observe them as they sang. We were able to localize and record screaming pihas (*Lipaugus vociferans*) at distances of 13 to 31 m. Longer-distance recordings of localized pihas were not feasible given that these birds are difficult to observe; they are drab in color and sing in the light-dappled understory, well below the forest canopy. White bellbirds (*Procnias albus*), by contrast, are larger, brighter, and sing and display from dead branches above the canopy, where they present a conspicuous visual contrast to a typically green background. We were able to observe bellbirds and record their songs over a broad range of distances, from 34 m to 1.25 km.

Song recordings. We recorded and made supplemental observations for 3 screaming pihas and 8 white bellbirds. All of the pihas that we recorded were found in forest habitat at the mountain base, ~100 m elevation. Our work with bellbirds featured two individuals at the mountain base and 6 along trails between ~900 and 1100 m elevation. Bellbird males (all four *Procnias* species) are known to return to the same perches within and across days [S2], and we
were able to secure recordings over multiple days for 4 white bellbirds. Our assumption that we were resampling the same males over multiple days was bolstered by two observations: across bouts (and days) we saw birds occupy the same exact perches, from amidst a series of potential perches; and males tend to be widely spaced across the lek, with different birds' favored display perches separated from their nearest neighbors by approximately 150 to 200 m, as estimated from GPS readings.

Our recordings were made using a Larson Davis SoundAdvisor 831C sound level meter (SLM) fitted with a pre-amplifier and free-field omnidirectional condenser microphone. The SLM was calibrated before each expedition using a Larson Davis CAL200 acoustic calibrator. For field recordings, the SLM was configured to measure and save amplitude values in 20 ms time bins, i.e. at a sample rate of 50 Hz. For each time bin the SLM recorded 12 amplitude parameters, as permutations of 3 weighting options (A, C, and Z-weighting) and of 4 calculation algorithms (Leq, Lpeak, Lslow, and Lfast, all dB relative to 20 µPa). We restricted our analyses to 4 of the 12 recorded parameters: the A- and C-weighted values for Leq and Lpeak. Both A- and C-weighting provide for relatively flat amplitude detection across the frequencies of biological interest, and also filter out the amplitude effects of low-frequency noise (more so than Z-weighting). Results from analyses of A- and C-weighted amplitude values were highly comparable. We herein report values only for the former, thus enabling more direct comparison to prior studies on vocal amplitude in birds, most of
which have likewise reported A-weighted amplitude values. \( \text{Leq} \) refers to the average amplitude detected during each time bin. It can thus be considered a root-mean-square (RMS) value, as is often used in studies of animal sound amplitude. \( \text{Lpeak} \) captures the very loudest transient amplitude events within each time bin. Pilot analyses revealed that \( \text{Lslow} \) and \( \text{Lfast} \) algorithms, used in many prior studies of song amplitude in birds, were unsuitable for capturing the rapidly modulated variations in amplitude that characterize our focal species' songs. The SLM was configured to also conduct simultaneous recording of sounds as .wav files, at a 44.1 kHz sample rate.

**Supplemental field data.** For each song bout recorded we measured or estimated 3 spatial variables: linear distance, elevation angle, and bird's orientation. With two exceptions, we measured linear distances between the recordist and the bird using TecTecTec VPRO500 laser range finders. The two exceptions were for birds beyond the capacity of the range finders; for these birds we estimated distance using a combination of the range finder (to measure landmarks) and a GPS contour map.

We used two methods to estimate elevational angles between the bird and recordist, i.e., angles by which the bird was above (+), below (-), or directly horizontal to the recordist. First, for some recordings we measured horizontal distances from the recordist to an object (typically the tree's trunk) directly below where the bird was perched, which when combined with linear distance
measures enabled angle calculation. Second, for other recordings we used a stick with a plumb-line; the recordist visually aimed the stick from eye to the bird's perch, let the plumb line down, and took a photo of the stick and plumb-line in profile. Elevation angles were then estimated using an on-screen protractor application.

Third, we estimated the horizontal orientation of the bird to the recordist, ranging from 0 degrees (directly facing) to 180 degrees (facing away). Estimates were coded in 15 degree intervals. These estimates were made in real time by the recordist or by additional observers using binoculars, or in some cases post hoc from video recordings. Two bellbirds in our sample were too distant (450 m, 1.25 km) to enable clear estimates of horizontal orientation.

**Song sample.** Upon return to the laboratory, we selected songs from our SLM recordings for analysis. For each recorded bout we first listened to and simultaneously perused spectrograms of all songs recorded from the SLM .wav files, using Adobe Audacity and Raven, and eliminated from consideration clips masked by other birds or by our own verbal commentary. We then identified a sample of clips representing a range of birds’ elevation angles, horizontal orientations, and, for white bellbirds, songs from the two described song types. For bellbirds recorded over multiple days, we selected songs from across all days. We analyzed a total of 33 songs from screaming pihas (10, 10, and 13
songs per individual), and a total of 154 songs from white bellbirds (3, 5, 9, 10, 15, 34, 35, and 43 songs per individual).

**Song Analysis I: calibration for noise.** Background noise artificially inflates estimates of signal amplitude. We therefore corrected all of our recorded amplitude values for this artifact. To do so we first quantified the amplitude of noise floors of each clip in the absence of song, calculated for most of our clips as mean amplitude captured during 1 second (50 time bins) prior to each song. For a small number of clips in which other sounds such as researcher narrations were captured just before the focal song began, we took measures of the noise floor after the focal song was complete. Next we subtracted noise floor values from signal amplitude values within-song 20 ms time bin, applying a standard equation \[ S7 \].

The effects of noise on many of our clips were negligible. This is because noise floors for song clips analyzed were typically modest, ranging from 33.9 to 52.7 dB(A) Leq (43.6 ± 5.3 mean and SD), and because our focal birds are exceptionally loud (see results). By happenstance one clip with very low background noise (35.1 dB(A)) was of the bellbird recorded at 1250 m; the low background noise allowed us to detect this bird's maximal amplitudes. These might be the longest-distance calibrated measures of song amplitude yet achieved for any non-aquatic animal. At the other extreme, the clip with the highest background noise, for which the recordist was positioned adjacent to a
running stream, was made sufficiently close to the bird (130 m) to allow maximal amplitudes to be detected. The only subject for which some song amplitude profiles could not be detected at all against background noise was of a white bellbird who was both relatively distant (450 m) and at a locality with moderate background noise (mean value of 44.5 dB(A)) in the form of wind across an intervening valley. The clips we could analyze for this bird were obtained primarily during lulls in the wind.

**Song Analysis II: amplitude by distance.** We next standardized all noise-corrected amplitude values, again on a 20 ms bin basis, to estimate what those values would have been at 1 meter from the bird. This is another typical correction that allows comparison of data recorded across different distances. Towards this end we applied a standard equation that accounts for sound energy dissipation via spherical spreading, a process expected to result in 6 dB losses for every doubling of distance, all other factors remaining equal [S7]. Maximal noise- and distance-corrected amplitude values were determined for each song and then each bird, and grand mean and standard deviation values (on a per-bird basis) were identified for our three song types. For these grand means, the predicted degradation of amplitude values from 1 m outwards were then plotted, out to 71 m (Figure S2) and for our entire data set, out to 1250 m (not shown), using the *attenuation* function in the R package *Seewave* [S8].
**Song Analysis III: maximal and average amplitude, song duration.** We conducted additional acoustic analyses on a subset of song clips, up to 5 songs per bird for pihas and bellbird song Type 1, and for all clips of bellbird song Type 2. We could not work with our entire song sample because obtaining meaningful measures of average amplitude and song duration requires robust signal-to-noise ratios (see below).

Our first step for these analyses was to identify, on a per-song basis, the sequential block of time bins from onset to offset that contained energy equal to or above a standard dB threshold relative to the peak amplitude. We used a standard threshold so that we could extract measures of song onset and offset timing equivalently and objectively across the entire sample. Based on an examination of waveforms of a subset of our sample, we chose a threshold value of -18 dB, which allowed us to capture most of a given song's sound energy (98.4%) while also not crossing into the noise floor. For bellbirds, only our recordings at 71 m or closer featured peak amplitudes that exceeded their corresponding noise floors by at least 18 dB. Accordingly, we excluded from these analyses the four bellbirds recorded at greater distances. We also note that bellbird song Type 2 includes a silent gap between its two notes, for which amplitude always dipped below the -18 dB threshold. These time bins were retained for the calculations described below, and thus contributed to our calculations of song duration and average amplitude.
Having identified sample bins with amplitudes exceeding the specified dB threshold, we were able to calculate song duration to a time resolution of 20 ms. We next transformed the retained noise- and distance-corrected dB values to sound pressure units (Pascals), thus converting a logarithmic scale to a linear scale. For each clip we then identified maximal and average sound pressure levels. Average sound pressure levels, and their comparison to maximal sound pressure levels, provide an indication of a song’s onset and overall sustained amplitude output, not just peak amplitude.

**Supplemental references**

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