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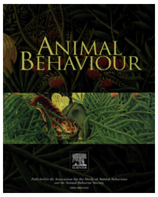

Evidence for vocal performance constraints in a female nonhuman primate

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Trilled vocalizations, wherein notes are repeated in rapid succession, are found in a variety of taxa including oscine birds, singing mice and nonhuman primates. Previous work on birds and singing mice has provided evidence of vocal performance constraints in trills, where there is a trade-off between the rate of the note repetition and the bandwidth (or frequency range) of each note. Here, we investigate vocal performance constraints in the trilled portion of the female contribution to the duet in the Bornean gibbon, *Hylobates muelleri*, recorded from seven sites in Sabah, Malaysia. We used two approaches. First, to ensure that our results were comparable with previous studies on vocal performance constraints, we used a 90% quantile regression to examine the relationship between trill rate and bandwidth. We found that there was a significant negative correlation between bandwidth and trill rate. Second, we formally compared multiple hierarchical models to identify the best predictors of bandwidth and trill rate. Our top model predicting bandwidth showed that trill rate and location within the trill were reliable predictors of bandwidth. With trill rate as the response variable, our top model included location within the trill as well as trill duration. We found that there were no important site-level differences in bandwidth but that trill rate varied predictably among sites. Our analyses provide strong evidence for performance constraints in the production of trills in Bornean gibbon females. Further research is needed to determine whether higher-performance trills provide honest signals of caller quality and whether gibbons respond differently to low- and high-performance calls.

Variation in acoustic signals is influenced by a wide range of factors including physical features of the environment, phylogenetic history of the organism and morphology and physiology of both the caller and the listener (Wilkins, Seddon, & Safran, 2012). The laws of physics and structure of sound-producing organs further constrain the types of signals that animals can produce, and therefore the evolution of acoustic signals and communication systems (Fitch & Hauser, 2003). Like all phenotypic traits, acoustic signals evolve through a combination of neutral and evolutionary mechanisms, and investigating the physical and mechanical limits on signal design can provide insight into the evolution of acoustic communication and diversity more broadly (Podos, Huber, et al., 2004). In addition, understanding the evolutionary constraints on the production of acoustic signals can provide insight into whether signals provide honest information about caller quality to the listener (e.g. Reby & McComb, 2003).

A constraint on the production of acoustic signals that has garnered much interest is a 'vocal performance constraint' on trilled vocalizations where there is a trade-off between the rate of syllable repetition and the bandwidth (or range of frequencies) contained in each syllable (Podos, 1997). In birds and in one mouse species, there is documented evidence that this trade-off exists (Cramer & Price, 2007; Cramer, 2013; Illes, Hall, & Vehrencamp, 2006; Pasch, George, Campbell, & Phelps, 2011; Podos, 1997; Podos, Huber, et al., 2004). Fast trills are predicted to be difficult to produce given the demands for rapid respiration and coordinated movements of the vocal tract (Podos, Huber, et al., 2004, Podos, Southall, & Rossi-Santos, 2004). To produce trills at high bandwidths, animals must broadly and rapidly modulate their

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vocal tracts. Executing modulations of the vocal tract quickly and repetitively while maintaining the tonal frequencies of the vocalizations is physically challenging (Wilson, Bitton, Podos, & Mennill, 2014). This biomechanical trade-off results in a pattern where frequency bandwidths at high trill rates are restricted and relatively narrow, but both narrow and wide bandwidths are possible at lower trill rates (Podos, 1997). Plots of note bandwidth versus trill rate exhibit a triangular distribution that reflects a performance trade-off in trill production, wherein the magnitude of frequency modulation (bandwidth) limits trill rate (or vice versa). The 'performance limit' of trills can be estimated by the upper limit of the regression of trill rate and bandwidth.

Understanding the evolutionary trade-offs in producing high-performance trills has been a topic of interest in the bird literature, with over 26 published studies reporting evidence of vocal performance constraints in birds (Wilson et al., 2014). Experiments on swamp sparrows, *Melospiza georgiana*, showed that hand-reared males that were exposed to artificially elevated trill rates were not able to reproduce trills at these elevated rates, instead producing songs with slower trill rates, omitted syllables or broken syntax (or pauses) between syllables (Podos, 1996). Songbirds learn natural model songs with a high degree of accuracy, so the inability to imitate the artificial models provides evidence of motor constraints on vocal performance. In birds, high fundamental frequencies have been shown to be accompanied by a wide beak opening or gape compared to that at lower fundamental frequencies (Podos, Huber, et al., 2004; Podos, Southall, et al., 2004), but in Neotropical singing mice, high-frequency sounds and gape width were not correlated, although singing mice did show evidence of performance constraints in trill vocalizations (Pasch et al., 2011). Other factors, such as respiratory musculature (Hartley & Suthers, 1989) and motor control of the vocal tract (Riede, Suthers, Fletcher, & Blevins, 2006) are also important in frequency modulation and rate of note production (Hartley & Suthers, 1989), although the relative importance of these factors in shaping performance constraints are probably taxon specific.

Gibbons (Hylobatidae) are pair-living, territorial primates that occur throughout Southeast Asia. All of the approximately 20 species of gibbons produce species- and sex-specific vocalizations, and most species engage in coordinated duets with unique male and female components (Geissmann, 2002). In contrast to many bird species, the species-specific vocalizations are not learned, as shown in captive hybrid studies wherein hybrids produce calls that contain aspects from both parental species, despite only hearing the sex-specific call from one of the parental species (Brockelman & Schilling, 1984; Geissmann, 1984). Female gibbons generally call along with their mothers as juveniles (Koda, Lemasson, Oyakawa, Rizaldi, Pamungkas, & Masataka, 2013) or as adults in mated pairs (Brockelman & Srikosamatara, 1993), with the exception of a few nonduetting gibbon species (e.g. Javan gibbons, *Hylobates moloch*: Ham, Hedwig, Lappan, & Choe, 2016). The function of the female portion of the duet in gibbons appears to be related to territory defence, as females show a stronger response to playbacks at the centre of their territories (Mitani, 1985), and playbacks of female solos and duets often elicit female calling whether broadcast from the centre or boundary of their territory (Mitani, 1984). Unlike male birdsong, there is little evidence that the female contribution to the duet is the result of intersexual selection; rather, it appears to be the result of intrasexual competition among females.

Gibbons lack specialized amplifier organs such as the enlarged hyoidlaryngeal complex in howler monkeys (Schön, 1971), or the laryngeal airsac found in the siamangs (Riede, Tokuda, Munger, & Thomson, 2008). Rather, gibbons produce their loud calls through dynamic control of their vocal tract, analogous to that of human soprano singers, where precise tuning of the supralaryngeal vocal tract results in the amplification of the fundamental frequency (Koda et al., 2012). This 'source-filter tuning' requires active control by the animal to produce loud vocalizations, and allows for gibbon calls to broadcast information to conspecifics in neighbouring territories over distances greater than 1 km (Mitani, 1985). In a few gibbon species, the female contribution to the duet contains trills, which are defined as vocalizations wherein frequency-modulated syllables are repeated in rapid succession (Podos, 1997). If the trade-off between trill rate and bandwidth is in fact the result of physical limitations on the production of broadband notes repeated in rapid succession, then this trade-off should be observed across taxa, regardless of taxonomic group or call function.

Here, we evaluate the evidence for vocal performance constraints in the trill portion of the great calls of Bornean gibbon, *Hylobates muelleri*, females. To our knowledge this study is one of the first to investigate performance constraints on female trills in any taxon, and one of the first to investigate performance constraints in vocalizations of a nonhuman primate (but see Terleph, Malaivijitnond, & Reichard, 2016). Our study had two main objectives. First, we evaluated evidence for performance constraints in the trills of Bornean gibbon females using 90% quantile regression, so that our results are comparable to previous studies on vocal performance constraints (Wilson et al., 2014). And second, given the long duration of gibbon calls (up to 15 s; Clink, Bernard, Crofoot, & Marshall, 2017) and the tendency of trill rate to increase over the course of a single call, we used multilevel models and model selection to determine which were the best predictor(s) of trill note bandwidth: trill rate (Hz), placement within the trill sequence, placement of the call within the calling bout, or whether the calling bout was spontaneous or produced in response to artificially broadcast calls of conspecifics (playbacks). We also used multilevel models to test for the best predictor of trill rate and to investigate site-level variation in both bandwidth and trill rate.

METHODS

Study Sites and Subjects

We visited seven different sites across Sabah, Malaysia (Fig. 1, Table 1). Recordings were collected from January 2013 to August 2015 using a Marantz PMD 660 flash recorder equipped with a RODE NTG-2 directional condenser microphone. We recorded with a sample rate of 44.1 kHz and a sample size of 16 bits and saved each file as a Waveform Audio (WAV) file. Our research focused on the female contribution to the duet, known as the great call (Geissmann, 2002). Bornean gibbon great calls consist of a combination of long (up to 1.8 s), frequency-modulated notes as well as shorter, broadband trill notes, so we arbitrarily designated a cutoff duration of less than or equal to 0.135 s for trill notes. Calling bouts consist of alternating male and female contributions, and can last from a few minutes up to a few hours (D. J. Clink, personal observation), with a mean bout length of approximately 15 min (Mitani, 1985). Gibbon trills are distinct from most bird trills as they tend to be of a relatively long duration (3.5–15 s). Given the variable duration of gibbon trills and the typical gradual change in trill rate over the course of a trill, the fundamental unit of analysis for our study focuses on 1 s bins within trills that contain multiple trill notes (see Fig. 2).

Recording distances ranged from directly under the tree where the individual was calling to approximately 250 m away. In some cases, individuals moved over the course of a calling bout. Recording distance can influence bandwidth measures (Kroodsma, 2017), so we calculated the signal-to-noise ratio (a proxy for distance) for each 1 s bin used in our analysis; we only used 1 s bins where the signal-to-noise ratio was greater than 10 dB (see below