

Vocal performance reflects individual quality in male Great Himalayan leaf-nosed bats (*Hipposideros armiger*)

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Abstract

Signals containing parameter trade-offs are likely to be honest indicators of signaler quality because they are difficult to produce. Signals with a trill-rate/bandwidth trade-off have been described for many songbird species, one mouse, and one non-human primate species. However, there were no reports about whether there is a vocal performance trade-off in social calls of bats. This study investigated (1) a possible vocal performance trade-off in territorial calls of male Great Himalayan leaf-nosed bats, *Hipposideros armiger*, recorded from 9 locations in south China, and (2) the relationships between vocal performance (vocal deviation and consistency) and caller's quality (body mass) to determine whether vocal performance honestly indicates a caller's quality. Vocal deviation measures the deviation of a call relative to an extreme call and vocal consistency measures the spectral consistency across a string of syllables. Our results showed a significant negative correlation between syllable repetition rate and frequency bandwidth, suggesting a vocal performance trade-off similar to the one in songbirds. Further, there was a significant negative relationship between body mass and vocal deviation, but no significant correlation between body mass and vocal consistency. This study provides the first empirical evidence for a vocal performance trade-off of social calls in bats, and the potential for the level of performance to indicate caller quality.

Key words: bats, male quality, territorial calls, trade-off, vocal performance

INTRODUCTION

Conflict between opponents occurs when crucial resources, such as food, mating opportunities or territories,

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are limited (Bradbury & Vehrencamp 2011). However, conflict resolution without a fight is common, and often results when communication has played a critical role in resolving the conflict (Briffa 2015). Acoustic signals may provide honest information to adversaries about the competitive quality of the sender and thus allow opponents to assess competitor's fighting ability and avoid costly physical conflicts (Bradbury & Vehrencamp 2011). How is signal honesty maintained when conflicting interests exist? The Index hypothesis predicts that a signal is honest

because its production is constrained by the sender's physical attributes (Maynard Smith & Harper 1995). Attributes correlated with signal production can include body size, age, strength or fighting experiences (Maynard Smith & Harper 1995). The Handicap hypothesis predicts that signal reliability will be maintained by signal production costs because only high quality senders can bear the high signaling cost (Zahavi 1975). Handicap signals can provide information to receivers about a sender's condition, health, and stamina (Zahavi 1975).

One way to evaluate the relative information content of conflict resolution signals is by measuring vocal performance, which is the ability of an animal to produce a physiologically challenging signal (Dinh *et al.* 2020). Two signal properties, "vocal deviation" and "vocal consistency", can be used as measures of vocal performance. These 2 properties have been shown to encode a sender's quality (Janicke *et al.* 2008; Botero *et al.* 2009; de Kort *et al.* 2009).

Vocal deviation is a measure of an animal's ability to excel in the performance of a signal characterized by a trade-off between bandwidth (frequency range) and syllable (or note) repetition rate in a trill, or more generally in a series of stereotypically repeated syllables (Podos 1997). This trade-off has been documented in songbirds, in one mouse species and in one nonhuman primate (Podos 1997; Ballentine *et al.* 2004; Illes *et al.* 2006; Pasch *et al.* 2011; Clink *et al.* 2018). In songbirds, songs with fast trills and broad frequency bandwidths are thought to be difficult to produce because increases in trill rates demand more rapid respiration and more coordinated movements of the vocal tract, and increases in bandwidth demand broader and more rapid modulation of the vocal tract (Podos *et al.* 2004a,b). It is considered to be physically challenging to perform vocal tract modulations rapidly and repetitively while producing a broad range of tonal frequencies (Wilson *et al.* 2014). Thus, plots of syllable bandwidth versus syllable repetition rate are expected to present a triangular distribution where the hypotenuse represents an upper limit to the joint properties of bandwidth and pulse rate (Podos 1997; Wilson *et al.* 2014; Fig. 1). The orthogonal distance from the individual data points to the upper-bound regression line (90%-quantile regression line) can be used as an indicator of an individual's ability to execute the trade-off between syllable bandwidth and syllable repetition rate. This metric is often named vocal deviation (Podos 1997; Wilson *et al.* 2014; Fig. 1). Small vocal deviation values indicate higher vocal performance, and therefore higher individual quality (Podos 2001; Janicke *et al.* 2008; Sprau *et al.* 2013; Wilson *et al.* 2014; Fig. 1).

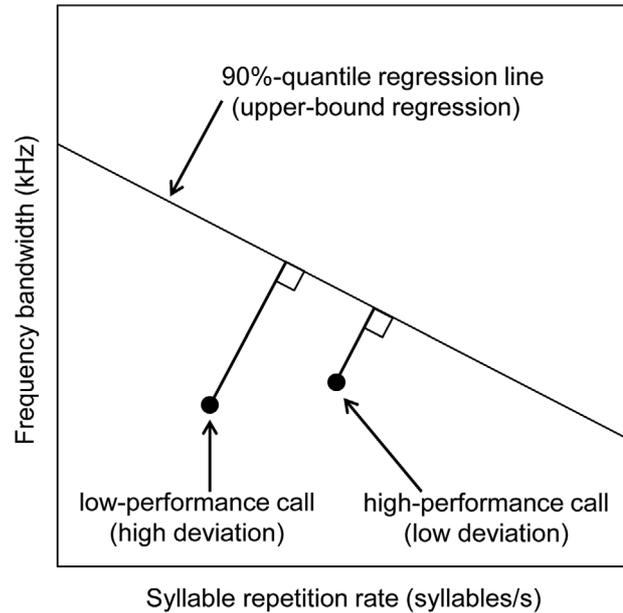


Figure 1 A schematic diagram for vocal deviation. Each call was plotted in an acoustic parameter space of syllable repetition rate and frequency bandwidth (Podos 1997). The hypotenuse represents the 90% quantile regression line (i.e. an upper limit to the joint properties of bandwidth and pulse rate).

Vocal consistency is a measure of an individual's ability to repeat each call or syllable in a series of syllables with a high-consistency (Sakata & Vehrencamp 2012). In songbirds, highly consistent songs are thought to be difficult to produce because they require more accurate coordination of syringeal, respiratory, and vocal tract muscles, as well as integration across the neural control system and syrinx (Lambrechts & Dhondt 1988; Zollinger & Suthers 2004; Sakata & Vehrencamp 2012). Vocal consistency is therefore considered to be an honest indicator of individual quality (Sakata & Vehrencamp 2012). For example, in male tropical mockingbirds (*Mimus gilvus*), syllable types of older individuals are more consistent, and more consistent individuals have higher dominance rank and reproductive success (Botero *et al.* 2009). Similar findings can be found in male banded wrens, *Thryothorus pleurostictus*, where individuals maintain a high degree of trill consistency when they grow older (de Kort *et al.* 2009). Old age could be a sign of high quality because older individuals have proven their viability (by surviving) and tend to be more likely to win fights than younger individuals (e.g. Hyman *et al.* 2004; Hegyi *et al.* 2006).

Bats are a promising mammalian group for studying the vocal performance trade-off between element repetition rate and frequency bandwidth because their

social calls consist of a series of stereotypically repeated elements (sometimes referred to as a trill). Vocalizations consisting of similar elements have been widely reported in many species, such as big brown bat *Eptesicus fuscus* (Gadziola *et al.* 2012), Seba's short-tailed bat *Carollia perspicillata* (Fernandez *et al.* 2014), Brazilian free-tailed bat *Tadarida brasiliensis* (Bohn *et al.* 2009), and Spix's disc-winged bat *Thyroptera tricolor* (Chaverri *et al.* 2010). However, only one study has explored bat vocal performance. Seven species of Southeast Asian rainforest bats were shown to exhibit high-performance echolocation calls by maintaining very high repetition rates at wide frequency bandwidths when approaching to their prey (Schmieder *et al.* 2010). It is unknown whether bats' social calls show a vocal performance trade-off between syllable repetition rate and frequency bandwidth, and therefore whether vocal performance could be an honest indicator of individual quality. This is particularly important given the role of social calls in information transfer between individuals in these social species (Chaverri *et al.* 2018).

The Great Himalayan leaf-nosed bat (*Hipposideros armiger*) is a gregarious species with a polygynous mating system (Yang 2011). *H. armiger* live in caves with many hundreds of individuals and share roosts maintaining a 10–15 cm minimum spacing between individuals (Cheng & Lee 2002; Sun *et al.* 2019). Adult individuals are involved in daily agonistic encounters to defend their day-roost territories (Sun *et al.* 2019). *H. armiger* are superb subjects for the investigation of performance trade-off in social vocalizations because a previous study showed that social calls of *H. armiger* usually consist of longer series of similar syllables (Lin *et al.* 2016). Our previous work found that male *H. armiger* usually emits territorial calls consisting of bent upward frequency modulation (bUFM) syllables repeated at regular intervals. These calls are used in agonistic interactions over roosting territories (Fig. 2; Sun *et al.* 2018).

In this study, we used male *H. armiger* to examine whether there was a vocal performance trade-off in territorial calls, and whether the vocal performance encoded reliable information about individual quality. First, the trade-off between frequency bandwidth and syllable repetition rate has been shown in several taxa, and this trade-off is the result of physical or physiological constraints on the production of broadband elements repeated in fast succession. Thus, we hypothesized that there would be a trade-off between frequency bandwidth and syllable repetition rate in the territorial calls of *H. armiger*. We predicted that frequency bandwidth would be negatively related to syllable repetition rate. Second, we hypothe-

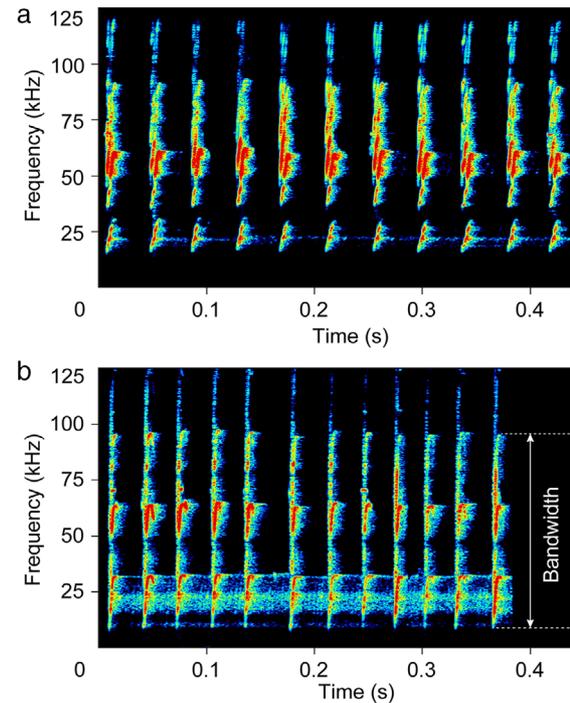


Figure 2 Examples of spectrograms of (a) a low-performance call (syllable repetition rate = 25.99 syllables/s, average bandwidth = 77.73 kHz) and (b) a high-performance call (syllable repetition rate = 32.77 syllables/s, average bandwidth = 88.56 kHz) of *Hipposideros armiger*.

sized that variation in vocal performance will be repeatable within males during a call assuming that the call functions to provide information about the signaler's quality. We therefore predicted that (1) vocal deviation and (2) vocal consistency would be highly repeatable within males, because we expected that males were maximizing their performance of this physically or physiologically constrained call trait. Last, we hypothesized that vocal performance would predict their individual quality. We predicted that (1) vocal deviation would be negatively associated with individual quality and (2) vocal consistency would be positively associated with individual quality.

MATERIALS AND METHODS

Animals and housing

In April–June of 2015–2016, we captured 90 adult male *H. armiger* after sunset using mist nets from 9 locations (10 bats per location) in mainland China (Fig. 3 and Table 1). At each location, we placed each captured adult in a cloth bag and transported it to our field

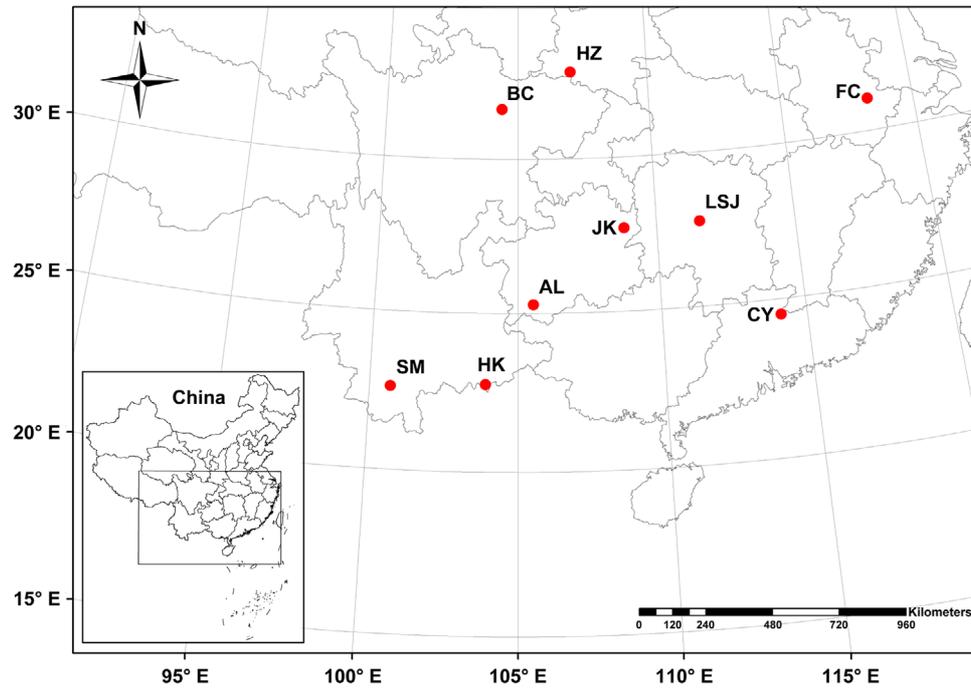


Figure 3 Sampling localities for territorial calls recording of *Hipposideros armiger* in China. Definitions of locality abbreviations are presented in Table 1.

Table 1 Locality name, coordinates, spectrotemporal parameters of syllables, and results of one-way ANOVA tests for each colony of *Hipposideros armiger* in China

Locality	Longitude (°)	Latitude (°)	N_{bat}	N_{call}	N_{syllable}	Mean of calls per male	Range of calls per male	Syllable rate (syllables/s)	Bandwidth (kHz)
Fanchang (FC)	118.30	31.05	8	39	730	4.88 ± 3.09	1–10	31.92 ± 5.33	81.89 ± 5.59
Anlong (AL)	105.54	25.28	8	23	447	2.88 ± 1.46	1–6	30.66 ± 6.10	85.77 ± 2.97
Jiangkou (JK)	108.83	27.68	7	28	443	4.00 ± 2.77	2–8	24.58 ± 5.07	85.63 ± 4.34
Lenshuijiang (LSJ)	111.57	27.75	5	19	272	3.80 ± 2.17	1–7	32.49 ± 5.28	84.73 ± 4.07
Chongyi (CY)	114.10	24.50	5	10	135	2.00 ± 1.00	1–3	23.76 ± 6.75	88.52 ± 3.79
Hanzhong (HZ)	107.03	32.85	8	29	430	3.63 ± 2.97	1–8	27.05 ± 3.45	83.54 ± 6.57
Beichuan (BC)	104.40	31.63	7	26	352	3.71 ± 1.60	2–7	32.54 ± 7.68	85.20 ± 6.87
Hekou (HK)	103.91	22.74	7	26	342	3.71 ± 2.81	1–9	26.87 ± 4.40	85.79 ± 3.40
Simao (SM)	100.71	22.61	9	32	513	3.56 ± 1.81	2–7	29.38 ± 7.68	82.11 ± 4.65
Total			64	232	3664	3.63 ± 2.30	1–10	28.92 ± 6.31	84.55 ± 5.00
One-way ANOVA								$F_{8,55} = 2.049$ $P = 0.057$	$F_{8,55} = 1.180$ $P = 0.325$

N_{bat} , number of sampling bats; N_{call} , number of calls analyzed; N_{syllable} , number of syllables analyzed; bandwidth, difference between the minimum frequency of the first harmonic and the maximum frequency of the third harmonic. All data are given as mean ± SD.

temporary laboratory near the sampling site. Captured males were housed in mosquito nets (length \times width \times height: 2.1 \times 1.5 m \times 1.8 m) in 2 rooms (length \times width \times height: 5 m \times 3 m \times 3 m) at a temperature at around 23°C and a relative humidity around 60%. We marked bats with 4.2 mm numbered aluminium alloy bands (Porzana Ltd, East Sussex, UK) on either the right, left, or both forearms. Larvae of *Zophobas morio* and freshwater were given *ad libitum*.

Individual quality measurement

Individual quality can be related to an animal's resource holding potential (RHP) because individual quality is generally associated with strength and the ability to impose injury (Arnott & Elwood 2009). RHP can affect vocal performance because RHP often correlates with individual physiological condition or body size (Arnott & Elwood 2009). Moreover, individuals in better physiological state or larger individuals are more likely to produce higher-performance vocalizations (see Ballentine 2009). Because our previous study showed that body mass in *H. armiger* represented a more appropriate proxy for RHP than forearm length (Sun *et al.* 2019), we used body mass as a proxy for individual quality. Body mass was measured using a portable electronic balance (DH-I2000, Diheng Ltd., Shenzhen, China) (accuracy 0.01 g). The body mass of each individual was measured 3 times, and their average was used for the analysis.

Sound and behavioral recording

Full details on the method for sound and behavioral recording are provided elsewhere (Sun *et al.* 2018). Briefly, for each location, 10 bats were separated into 2 groups of 5 bats per group. Each group was housed in a mosquito net (length \times width \times height: 2.1 m \times 1.5 m \times 1.8 m) in a larger housing room (length \times width \times height: 5 m \times 3 m \times 3 m) where we recorded vocalizations and bat behavior from 2200 to 0800 hours, which includes the main activity periods. Each group was continuously recorded for 6 days, with an infrared camera (HDR-CX 760E; Sony Corp., Tokyo, Japan) and a condenser ultrasound microphone (CM16/CMPA, with a flat frequency response between 10 kHz \pm 3 dB and 200 kHz \pm 3 dB; Avisoft Bioacoustics). Audio was sampled using an ultrasound recording system (Avisoft UltraSoundGate 116 H, Avisoft Bioacoustics, Berlin, Germany), with a sampling rate of 375 kHz and 16-bit resolution. The microphone and camera were placed in the same position on the tripod to standardize recording across trials. A previous study

showed that male *H. armiger* emit bent upward frequency modulated (bUFM) syllables calls, a common social call used during roost territory defense (Fig. 2; Sun *et al.* 2018). Thus, we only recorded the bUFM calls emitted by males during roost territory defense.

Sound and behavioral analysis

Video analysis was performed using a QvodPlayer (Version 5.0.80, Shenzhen Qvod technology Co., Ltd, Guangdong, China) to determine the context of territory defense and the caller identity. All vocalizations were analyzed using Avisoft SASLab Pro (version 5.1; R. Specht, Avisoft Bioacoustics, Glienicke, Germany). Following Kanwal *et al.* (1994) and Gadziola *et al.* (2012), we defined a syllable as the smallest element of a vocalization, and a call as the simplest emission of a whole vocalization, being comprised of multiple syllables. We calculated syllable repetition rate as the number of syllables divided by call duration. Call duration was measured as the time between onset of first syllable in a call and offset of the last syllable in a call, measured from the oscillogram. The calls are composed of 3 main harmonics. The bandwidth was measured as the maximal frequency of the third harmonic minus the minimum frequency of the first harmonic (Fig. 2b). Before the measurement, we normalized each syllable to an amplitude of 0.75 V. We measured the minimum and maximum frequency at -20 dB relative to the peak amplitude frequency from spectrograms (sample rate: 375 kHz; Fast Fourier Transform: 1024; Hamming window; 75% frame size; 93.75% overlap; frequency resolution: 366 Hz; temporal resolution: 0.1707 ms). This protocol allows us to capture variation in frequency bandwidth while excluding the interference of background noise.

Vocal deviation and vocal consistency calculation

A detailed description of vocal deviation values can be found in the Introduction.

Following methods outlined by Sprau *et al.* (2013) and de Kort *et al.* (2009), we used similarity coefficients (SC) to quantify individual vocal consistency, that is, the spectral similarity between consecutive syllables within a call. Similarity coefficients were measured using spectral cross-correlations in Avisoft SASLab Pro 5.1. Spectral cross-correlations provide a method of measuring similarity between pairs of syllables by comparing the spectral information in each syllable's spectrogram display (Sprau *et al.* 2013). A SC of 0 means no similarity, while a SC of 1 indicates that the 2 syllables are identical. Each

syllable was compared with all other syllables of the same call. The coefficients of all comparisons were averaged, resulting in a single SC value for each call. A mean of 3.63 (SD: 2.30) calls per bat and a mean of 57.25 (SD: 38.18) syllables per bat were used to estimate SC.

Statistical analyses

We used individual average values for all acoustic and morphological variables, except for the call duration. All variables were normally distributed (Kolmogorov–Smirnov test: $0.24 < P < 1$) except call duration that was log transformed to meet assumptions of normality.

We conducted one-way analysis of variance (ANOVA) for the acoustic parameters to examine whether acoustic parameters differed among locations. There were no significant differences in vocal deviation and consistency among the 9 sites (vocal deviation: one-way ANOVA: $F_{8,55} = 1.007$, $P = 0.442$; consistency: one-way ANOVA: $F_{8,55} = 1.109$, $P = 0.372$), so site was not included as an independent variable in our analyses. In addition, call duration strongly correlated with syllable repetition rate (Pearson correlation: $r_{64} = -0.527$; $P < 0.001$); therefore, we excluded call duration from subsequent analyses.

To determine whether territorial calls showed a vocal performance trade-off, we performed a 90% quantile regression (following Wilson *et al.* 2014) using the function “quantreg” in the R package “quantreg” (Koenker 2013). We then used simple linear regressions to test the associations between individual quality (body mass) and both vocal deviation and vocal consistency.

To quantify repeatability of vocal performance within individuals, we calculated the intraclass correlation coefficient (ICC) based on one-way ANOVA analyses (Wolak *et al.* 2012) using the function “ICCest” in the R package “ICC” (Wolak 2015). The ICC is a measure of variation within versus between individuals in vocal performance. Larger ICC values for vocal performance indicate that each individual shows a similar level of performance (i.e. performs the trade-off between syllable repetition rate and bandwidth) across all the calls we analyzed for that individual. We ran a similar analysis on repeatability of the similarity coefficients. In this case, larger ICC values indicate that the level of similarity of notes within a call was similar across all calls analyzed from a given bat. Note that the similarity coefficient itself measures similarity between notes within a call, and repeatability of the similarity coefficients measures the degree to which within-call note similarity is repeated across calls given by an individual bat. All statistical tests were performed in R v. 3.5.1 (R Core Development Team 2018).

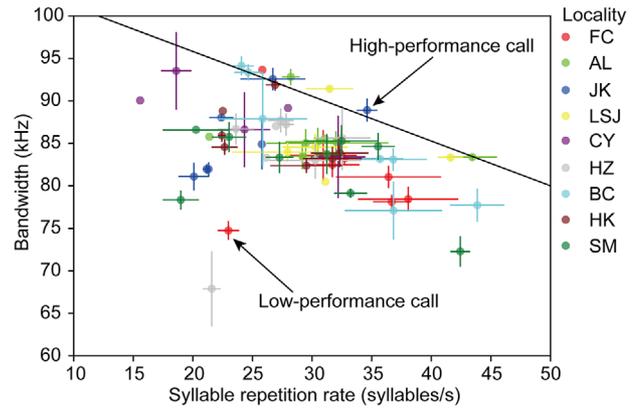


Figure 4 Relationship between syllable repetition rate and bandwidth in *Hipposideros armiger* male territorial calls. Each point represents the mean value \pm standard error for one male. The line represents 90% quantile regression line. The arrow below the regression line shows a male with a low-performance call (spectrogram in Fig. 2a) and the arrow above the regression line shows a male with a high-performance call (spectrogram in Fig. 2b) and. Dots of different colors represent males from different locations (see Table 1 for locality abbreviations).

RESULTS

We analyzed a total of 3021 bUFM syllables belonging to 232 territorial calls produced by 64 different males from 9 localities (see Table 1 and Table S1, Supporting Information). There were no significant differences in syllable rate and bandwidth between the 9 localities (Table 1). Hence, the 90% quantile regressions came from all data points from the 9 localities. The bandwidth correlated negatively and significantly with syllable rate (90% quantile regression: $y = 106.418 - 0.530x$, $P = 0.00066$, Fig. 4).

Body mass had a significantly negative effect on vocal deviation (simple linear regression: $t = -2.535$, $R^2 = 0.094$, $P = 0.014$, Fig. 5), while had no effect on vocal consistency (simple linear regression: $t = 1.133$, $R^2 = 0.020$, $P = 0.261$).

Repeatability for vocal deviation was 0.71 (95% confidence interval for mean 0.60–0.81; one-way ANOVA: $F_{55,168} = 10.722$, $P < 0.001$). Repeatability for vocal consistency was 0.29 (95% confidence interval for mean 0.14–0.44; one-way ANOVA: $F_{55,168} = 2.657$, $P < 0.001$).

DISCUSSION

We found that frequency bandwidth was negatively correlated with syllable repetition rate, which supported

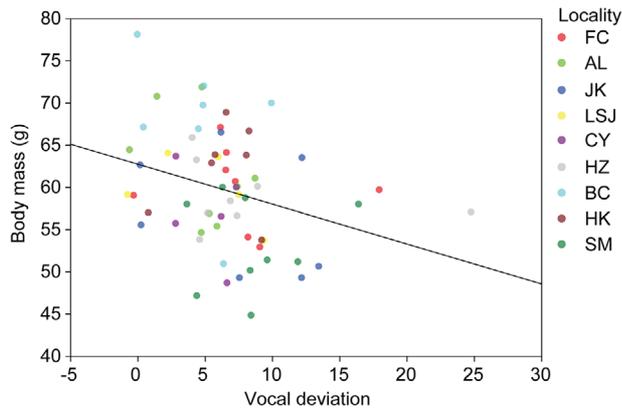


Figure 5 Relationship between body mass and vocal deviation in *Hipposideros armiger*. Dots of different colors represent males from different locations (see Table 1 for locality abbreviations).

our first hypothesis that vocal performance limits exist for territorial calls. We found that there was significant variation within versus between individuals in vocal performance, which supported our second hypothesis that variation in vocal performance was repeatable within males during a call. We also found that vocal deviation was negatively correlated with body mass, which supported the first prediction of our third hypothesis that a negative relationship between vocal deviation and individual quality would be detected. No relationship between vocal consistency and body mass was detected. This did not support the second prediction of our third hypothesis.

Vocal performance limits

We found that territorial calls of male *H. armiger* exhibited a negative correlation between syllable repetition rate and frequency bandwidth, indicating a vocal performance trade-off analogous to that reported in a wide range of songbirds (Podos 1997; Ballentine *et al.* 2004; Janicke *et al.* 2008), in a rodent, the neotropical singing mouse (Pasch *et al.* 2011), and in a nonhuman primate (Clink *et al.* 2018). In some bird species, vocalizations with quickly repeated syllables are thought to be quite difficult to emit because fast trills require more rapid respiration and more coordinated movements of the vocal tract (Westneat *et al.* 1993; Zollinger & Suthers 2004), whereas vocalizations with broad frequency bandwidth are considered to require large beak gape (Hoese *et al.* 2000; Podos *et al.* 2004b). In one bird and one mouse species, vocal performance trade-offs may not depend on gape width, but arise from motor constraints of the respiratory musculature

and the vocal tract (Janicke *et al.* 2008; Pasch *et al.* 2011). The above examples indicate that the biological mechanisms of the trade-off between syllable repetition rate and frequency bandwidth are possibly taxon specific. In our study, frequency bandwidths (first harmonic) of the territorial calls in male *H. armiger* are much wider (14–28 kHz) than in birds (1–14 kHz; Podos 1997; Ballentine *et al.* 2004; Podos *et al.* 2004a; Cramer 2013) and in a nonhuman primate (1 kHz; Clink *et al.* 2018), suggesting different biological mechanisms of vocal production (Fitch & Hauser 2003). Territorial calls of male *H. armiger* are produced with mouths wide open (long-term personal observations by CNS). This observation may indicate that the trade-off between syllable repetition rate and frequency bandwidth may rely on the motor activity of the respiratory musculature and the vocal tract, but not on gape width. Further research should be performed to elucidate the biological mechanisms on setting upper constraints of vocal performance in *H. armiger*.

Vocal performance repeatability

We found significant differences in vocal performance between individuals and significant repeatability of performance (both vocal deviation and vocal consistency) within individuals. According to a study on the repeatability of male signal production from different taxonomic groups, repeatability values typically range from 0.21 to 0.85 (Boake 1989). Our result showed that the repeatability for vocal deviation (0.71) was at the high end of this range, indicating that differences among calls within a male in vocal deviation were significantly greater than differences between males. These results suggested a great ability for *H. armiger* to consistently produce individual-specific calls, and that vocal deviation potentially provides honest information about individual quality. Indeed, a high degree of stereotypy is an index of the ability of a call to convey information, and more generally an index of the evolution of signal design (Bradbury & Vehrencamp 2011). The significantly negative relationship between vocal deviation and individual quality in male *H. armiger* supports this view.

In contrast, we found that the repeatability for vocal consistency (0.29) was at the low end of this range of repeatability values, indicating a low level of repeatability for *H. armiger* to perform repetitive versions of a syllable, suggesting that vocal consistency may not reliably signal individual quality. Weak repeatability within males for vocal consistency may be explained by differences in vocal practice among individuals (see review in Sakata & Vehrencamp 2012). Vocal practice can help adults refine

and maintain vocal consistency. Individuals with lower vocal rates can have less vocal practice and thus emit their calls with lower consistency. Further experimental investigation is needed to clarify the potential role of vocal practice in vocal consistency.

Individual quality and vocal performance

Our results showed that males with higher body condition produced territorial calls of higher performance (specifically vocal deviation). A similar result can be found in male swamp sparrows *Melospiza georgiana* (Ballentine 2009). One possible interpretation of this result was that the production of higher performance calls requires more rapid respiration and more precise movements of the vocal tract (Podos 1997; Podos *et al.* 2004a), and therefore only individuals in better quality (such as larger body mass) should be able to give higher-performance vocalizations. Taken together, these results indicated that vocal deviation can serve as an honest index of quality in male *H. armiger*.

What is the benefit of territorial calls in male *H. armiger* encoding reliable information about individual quality (specifically body mass)? One possible benefit is that territory holders produce territorial calls reliably indicating their larger body mass to repel potential intruders that are smaller than them, thus avoiding unnecessary escalation of costly physical contests (e.g. boxing or wrestling in bats (Sun *et al.* 2019)). Since fighting ability is usually positively associated with body mass, individuals in greater body mass were more likely to win contests than individuals with smaller body mass (reviewed in Arnott & Elwood 2009). Our previous studies showed that *H. armiger* males with larger body mass were more likely to win fights with lighter males and heavier males had higher dominance status (Sun *et al.* 2019, 2021). Before escalating to costly physical fights, male *H. armiger* may exchange signals indicating fighting ability to help both competitors decide whether to retreat or to continue the impending conflict.

Vocal consistency honestly signaling individual quality has been documented in a number of animals (Botero *et al.* 2009; de Kort *et al.* 2009; Węgrzyn *et al.* 2010). In the study, however, we found no relationship between vocal consistency and body mass in males, indicating that vocal consistency failed to function as a reliable signal of individual quality in bats. One possible reason for the difference is the nature of the calls in these studies. The cited works all studied avian systems in which vocal signals all had frequencies below 14 kHz, whereas the bat calls range from 25–100 kHz. We suggest that there are

constraints on the precision of production of such high frequency calls that may limit consistency between calls emitted by a given sender, although we are unaware of validation of this possibility in the literature. In addition, the fact that signal performance does seem to encode this information in the bats reduces the fitness consequences of vocal consistency providing a redundant source of information about caller quality (Hebets & Papaj 2005).

In summary, this study demonstrated that there was a trade-off between syllable repetition rate and frequency bandwidth for territorial calls in male *H. armiger*, and that male body mass was potentially predicted by vocal performance. To our knowledge, this was the first investigation of vocal performance constraints in social vocalizations produced by a bat species. Further playback experiments will need to determine whether males can both perceive and use the differences in vocal performance of a rival's territorial calls indicating different body condition to make decisions.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Table of all parameters measured in territorial calls

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