



Territorial calls of the bat *Hipposideros armiger* may encode multiple types of information: body mass, dominance rank and individual identity

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Received: 9 July 2020 / Revised: 25 November 2020 / Accepted: 3 December 2020
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Abstract

In highly vocal species, territorial aggression is often accompanied using vocalizations. These vocalizations can play a critical role in determining the outcome of male–male agonistic interactions. For this, vocalizations of contestants must contain information that is indicative of each competitor’s fighting ability as well as its identity, and also contestants must be able to perceive information about the physical attributes, quality and identity of the vocalizer. Here, we used adult male Great Himalayan leaf-nosed bats (*Hipposideros armiger*) to test whether territorial calls encoded honest information about a caller’s physical attributes, quality and individual identity. We did this by exploring the relationships between territorial calls and two potential indices of fighting ability: body mass and dominance rank. Using synchronized audio–video recording, we monitored bat territorial calls and dominance rank of 16 adult male *H. armiger* in the laboratory. Additionally, habituation–dishabituation playback experiments were performed to test for vocal discrimination. Results showed that body mass was negatively related to minimum frequency and positively related to syllable duration. Dominance score was also negatively related to minimum frequency and positively related to peak frequency. Furthermore, a discriminant function analysis suggested that territorial calls encode an individual signature. Therefore, our data show that males have the ability to utilize this vocal individual signature to discriminate between vocalizing males. In short, territorial calls of male *H. armiger* contain information about body mass, dominance rank and individual identity, and contestants are probably capable of perceiving this information and may use it to make appropriate decisions during agonistic interactions.

Keywords Bats · Body mass · Dominance rank · Individual identity · Territorial calls

Congnan Sun, Chunmian Zhang have contributed equally to this work.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10071-020-01455-3>.

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Introduction

Competitors commonly use acoustical signals to indicate their fighting ability and thus resolve contests without costly physical fighting (Briffa 2015). Animal acoustic signals can encode a variety of information such as signaller’s identity, body size, quality (e.g., dominance rank) or external events (Bradbury and Vehrencamp 2011). The exchange of information in the context of a conflict can help both opponents to

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quickly recognize the identity of a competitor and to assess a competitor's fighting ability, and thereby reduce fighting costs by decreasing the number of agonistic interactions or the time and energy spent on a contest (Bradbury and Vehrencamp 2011).

Information flow through spectrally complex signals that convey multiple messages may be constrained by physiological limitations of the receiver (e.g., Henry et al. 2016), or by psychological limitations (e.g., Dukas 2004). Given these limitations, why should complex signals evolve? The multiple messages hypothesis proposes that different signals provide information about different aspects of the signaler's condition, and thus allows signallers to direct different information at different receivers and also allow receivers to more comprehensively assess signallers' quality, which is beneficial for both signallers and receivers (Hebets and Papaj 2005). Correspondingly, different elements of a vocalization contain different information on the vocalizers' attributes (Hebets and Papaj 2005). Most studies on the multiple messages hypothesis in the acoustic domain have focused on vocalizations consisting of different element types (Fischer et al. 2004; Koren and Geffen 2009; Ryan 1983); whether single element types themselves can convey different types of information is not well studied, especially in the context of territorial conflicts.

Acoustical signals containing information about body size have been documented in a wide range of taxonomic groups, such as frogs (Davies and Halliday 1978), birds (Ryan and Brenowitz 1985), primates (Pfefferle and Fischer 2006), and other mammals (Jiang et al. 2017; Wyman et al. 2012). In mammals, the relationship between acoustic characteristics and physical traits can be explained by the source-filter theory (Fant 1960; Titze 1994). The theory asserts that vocalizations are generated by forcing air from the lungs through the larynx to create a source signal (the source) which determines the vocal fundamental frequency, and the source signal is subsequently filtered in the supralaryngeal vocal tract to determine the vocal formant frequency (the filter). Formant frequencies (filter-related vocal parameters) are a good predictor of body size in mammals because the vocal tract length is constrained by the skeletal dimensions (i.e., skull size) and thus tightly associated to overall body size (Fitch 1997). Additionally, temporal parameters such as call and syllable duration are also a good indicator of body size in many species because larger individuals tend to have greater lung volumes and thus produce vocalizations with longer duration (Fitch and Hauser 2003).

Acoustical signals can also convey information about male quality such as dominant rank in many species, e.g., birds (Botero et al. 2009), rock hyraxes (Koren and Geffen 2009), hyenas (Mathevon et al. 2010), deer (Vannoni and McElligott 2008) and baboons (Fischer et al. 2004). For example, high-ranking male fallow deer, *Dama dama*,

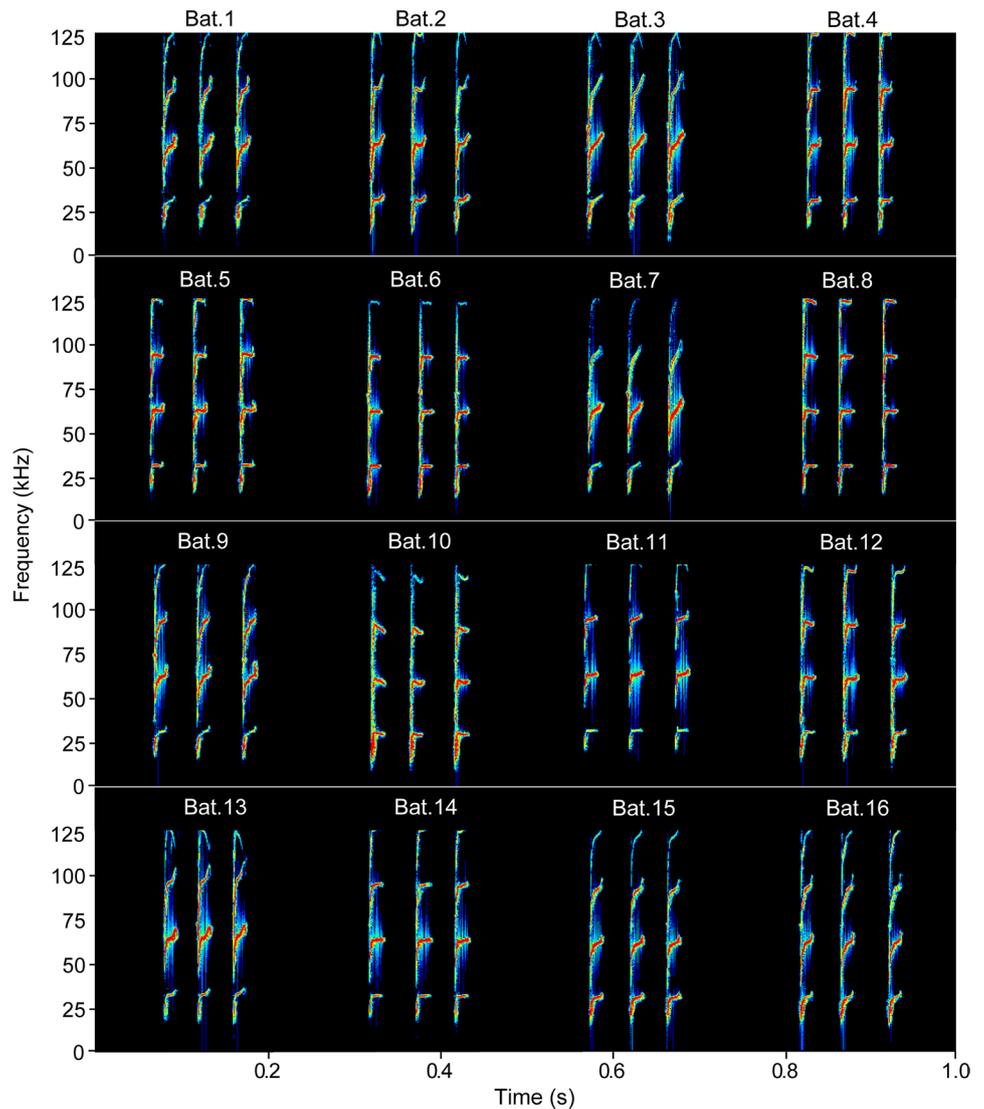
produced lower minimum frequencies than low-ranking males (Vannoni and McElligott 2008). Thus the perception of dominant rank based on acoustical signals by competitors may influence fighting outcomes. Males also fight for high dominance rank through physical conflict between opponents to accrue more resources, such as mating opportunities and food (Drews 1993; Ratchliffe et al. 2007).

In addition to body size and dominance rank, acoustical signals encode information about individual identity in many vertebrate taxa, such as frogs (Chuang et al. 2017), birds (Elie and Theunissen 2018), primates (Fan et al. 2018), and other mammals (Mumm et al. 2014). Individual discrimination based on acoustic signals plays a critical role in territorial defence (Mackin 2005). For instance, territory holders can discriminate between nearby neighbours and strangers based on individual vocal signatures (Bee and Gerhardt 2002; Chuang et al. 2017), and the ability to discriminate competitors may facilitate subsequent interactions through decreased aggressive competition with individuals with high resource holding potential or high fighting motivation (Bradbury and Vehrencamp 2011).

Bats are an ideal model for studying the multiple types of information contained in social vocalizations because they emit rich social calls in different social contexts (Fenton 2003; Gillam and Fenton 2016). For example, isolation calls of the greater sac-winged bat (*Saccopteryx bilineata*) were composed of three different syllable types (i.e., variable syllables, composite and stereotyped end syllables), and the composite syllables contained information about individual identity and social group affiliation, while the stereotyped syllables conveyed information about age (Fernandez and Knörnschild 2017). The complete advertisement calls of the Nathusius' pipistrelle bat (*Pipistrellus nathusii*) consisted of five different motifs (i.e., A, B, C, D, E), and the motif B and motif C provided information about individual identity, whereas other motifs contained cues relative to behavioural contexts (Jahelková et al. 2008). Nevertheless, in bats, whether syllables in monosyllabic vocalizations convey multiple types of information remains uncertain.

The Great Himalayan leaf-nosed bat, *Hipposideros armiger*, is a highly gregarious species with a polygynous mating system (Yang 2011). Several hundred *H. armiger* commonly roost in a cave sharing day and night roosts with a 10–15 cm minimum spacing between individuals (Cheng and Lee 2004; Sun et al. 2019). Our previous observations in the field and in the laboratory found that when a free-flying male *H. armiger* approaches a roosting male to compete for roosting territory, the roosting male may emit stepped upward frequency modulation calls (sUFM calls; hereafter 'territorial calls'; Fig. 1) to defend its own private roosting territory (Video S1). Therefore, we looked at the specific calls in this specific behaviour. We presume that if sUFM calls serve the function of territorial defence, the sUFM calls

Fig. 1 Example of sUFM calls from sixteen male *Hipposideros armiger*



should be honest signals of body size, dominance rank or individual identity.

In this study, we examine whether territorial calls encode reliable information about individual attributes in the male *H. armiger*. We hypothesized that territorial calls would predict (1) their body size and (2) dominance rank. As a test of these hypotheses, we predicted that: (1) because acoustic attributes such as call frequency and duration can be constrained by individual physiological attributes such as body size (Fitch and Hauser 2003), body size will be negatively related to frequency-related parameters and positively related to syllable duration. (2) Since previous studies on nonhuman mammals have confirmed that high-ranking individuals tend to produce vocalizations with lower frequency than low-ranking individuals (Portugal et al. 2017; Šárová et al. 2013; Vannoni and McElligott 2008), dominance rank in *H. armiger* will be negatively related to frequency-related parameters. Vocal signatures should be expected if signallers

and receivers benefit from mutual recognition, or if vocal signatures are a side-effect of individual differences in the morphology of the vocal organ. Therefore we hypothesized that territorial calls of male *H. armiger* would convey information about a caller's identity to permit discrimination among individuals. We thus made the following predictions: (1) male *H. armiger* territorial calls would encode detectable individual signatures; (2) male *H. armiger* would have the ability to discriminate between two signallers based on territorial calls.

Methods

Ethical approval

Our work adheres to the Guidelines for the Use of Animals in Research (ASAB/ABS 2017), to the National Natural

Science Foundation of China for experiments involving vertebrate animals, and to the Northeast Animal Research Authority of Northeast Normal University China (approval number: NENU-W-2017-101).

Animals and housing

Seventeen adult male Great Himalayan leaf-nosed bats were collected with a mist net from the Shiyan cave in Chongyi County, Ganzhou City, Jiangxi Province, China, on April 30, 2018. Captured bats were housed together in a large flight cage (length \times width \times height: 4.4 \times 1.5 \times 1.8 m) in a husbandry room (length \times width \times height: 6.5 \times 5.5 \times 2.1 m) at a relative humidity around 60% and a temperature at around 23 °C. We use an astronomical light timer to maintain a 12-h dark/light cycle (dark: 1900–0700 h, light: 0700–1900 h). All bats were given ad libitum access to fresh water and *Zophobas morio* larvae. Their diet included vitamins and minerals. All bats were marked with numbered aluminium alloy bands (4.2 mm for the forearm; 2.9 mm for the leg; Porzana Ltd, East Sussex, UK) on either the forearm, leg or a combination of them for individual identification. We validated that the bands could slide loosely on the forearm and the leg, and did not affect the normal behaviour of the experiment individuals (CS, pers. observ.).

Body size measurement

Since our previous study indicated that body mass in *H. armiger* represented a more appropriate proxy for resource holding potential than forearm length (Sun et al. 2019), we used body mass as a proxy for body size. We measured body mass of each male using an electronic balance (\pm 0.01 g; DH-I2000, Diheng Ltd., Shenzhen, China). Since the body mass of a bat changes every day, we measured the body mass of each male for 10 consecutive days between 7 p.m and 9 p.m, and its mean was used for analysis.

Sound and behavioural recording and analysis

After a period of acclimatization, we randomly divided 17 males into two groups. The first group included ten males and the second group included the remaining seven males plus three from the first group. This grouping method allowed us to clearly assign a vocalization to a certain individual. We recorded the vocalizations and monitored the behaviours of each group for ten consecutive days in the large flight cage (length \times width \times height: 4.4 \times 1.5 \times 1.8 m) in the husbandry room. For each group, recordings were performed from 2000 to 0800 h the next day because the majority of social and vocal activities are produced during this period of day. Vocalizations were recorded with an ultrasound recording system (Avisoft UltraSoundGate 116

H, Avisoft Bioacoustics, Glienicke, Germany) with an ultrasound microphone (CM16/CMPA, Avisoft Bioacoustics, Glienicke, Germany). The sampling rate and resolution of the recording system were 250 kHz and 16-bit, respectively. The microphone was positioned two metres from the bats. Simultaneously, two infrared cameras (FDR-AX60, Sony Corp., Tokyo, Japan) were used to monitor vocal behaviours. Camera 1 was mounted 30 cm above the ground to monitor the bats' overall behaviour. Camera 2 was mounted 120 cm above the ground to accurately determine which individuals vocalized. We only recorded the stepped upward frequency modulation (sUFM) syllable calls produced by a roosting male (territorial holder) when a free-flying male (intruder) approached (Fig. 1; Video S1).

Video analyses were conducted with a QvodPlayer (Version 5.0.80, Shenzhen Qvod Technology Co., Ltd., Guangdong, China), and an experimental blinded method was performed to minimize observer bias. Here CMZ was the blind observer. Vocalizations were assigned to signallers if the bats opened their mouth at the time the vocalization was recorded. All vocalizations were analysed using Avisoft SASLab Pro (version 5.1; R. Specht, Avisoft Bioacoustics, Glienicke, Germany). Prior to acoustic measurement, we originally normalized each sound to a peak amplitude of 0.75 V. Spectrograms for measuring frequency parameters were produced using a Hamming window and a 1024-point fast Fourier transform (75% frame size; 93.75% overlap; temporal resolution: 0.256 ms; frequency resolution: 0.244 kHz). We measured temporal parameters from the oscillograms. We applied automatic parameter measurements of the software to measure all frequency parameters at a threshold of 20 dB below the peak spectral amplitude. We only concentrated on the sound harmonics (second harmonic) that contained the highest sound energy. 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 whole vocalization, being comprised of multiple syllables of the different or same types. Since the roosting male only emitted one vocalization consisting of a series of sUFM syllables when a free-flying male approached the roosting male, we defined the vocalization as a call. We randomly measured three high-quality (SNR > 30 dB) syllables in each call (Audio files S1) and their average values were used for statistical analyses.

To examine whether the sUFM calls of males encoded individual identity, we measured 23 total acoustic variables to describe territorial calls (for detail, see Tables S1 and S2). To examine whether the sUFM calls of males provided reliable information about the quality (body mass and dominance rank) of the vocalizer, we measured five acoustic variables including syllable rate, syllable duration, peak frequency, minimum and maximum frequency, because previous work has shown that individual quality is correlated to these five

parameters (Davies and Halliday 1978; Fischer et al. 2004; Koren and Geffen 2009; Luo et al. 2017; Vannoni and McElligott 2008; Zhao et al. 2018).

Playback stimuli construction

We constructed playback files following methods outlined by Mumm et al. (2014) and Fernandez et al. (2014). We did not record enough vocalizations (only two calls) from one of the bats and hence the remaining sixteen males were used as stimulus donors (5–24 different calls per male). Nine of sixteen males were tested in playback experiments. We only chose to test nine males because we required at least ten high-quality calls for the habituation stimulus and we wished to avoid using the same bat for two different habituation stimuli. We obtained enough calls from only nine bats, thus we performed only nine playback experiments. We created nine habituation playback files and nine dishabituation playback files (Audio files S2) using Avisoft-SASLab Pro 5.2. The habituation files were created by randomly mixing calls from one stimulus donor (10–19 different calls per sound donor). The calls in the habituation files were separated by silent intervals of 0.51–38.34 s, mimicking the natural intervals between calls produced during approaching encounters. The dishabituation files were created using five randomly mixing calls interspaced by silence from one stimulus donor. Each dishabituation file was 15 s long. After switching playback files from habituation to dishabituation, the bats clearly reacted when they were able to discriminate between the two stimuli. We thus think that the differences between the habituation sample and the dishabituation sample had little impact on the study. All playback files were from different stimulus donors except for two dishabituation files where the same donor was used for both stimulus and habituation files. However, the calls from these donors used for the stimulus trials were different than the calls used from these donors for habituation trials. Each call was used only once. All playback files (250 kHz sampling rate and 16-bit resolution)

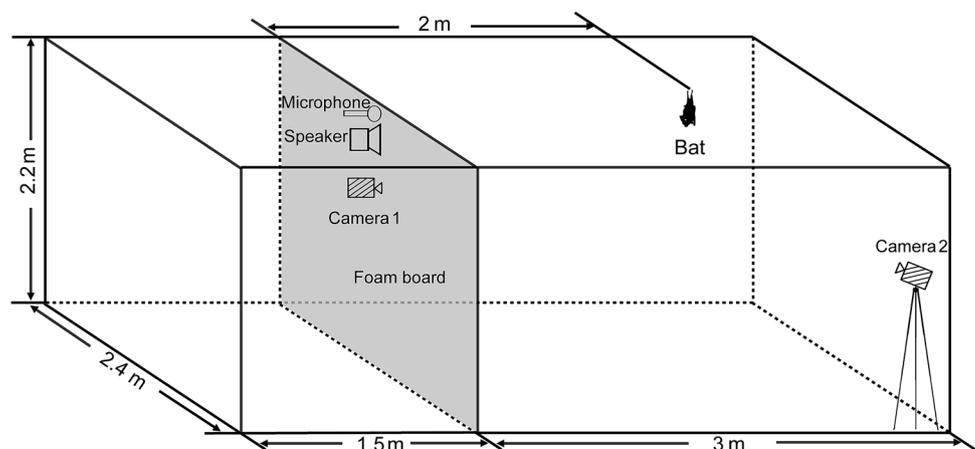
were normalized in order that the maximal peak amplitude of the weakest syllable was about -30 dB (re. to 1 V). All habituation and dishabituation playback files were broadcast at about 85 dB SPL at two metres which was approximately the amplitude of live bat calls (see Supplementary Material for details). We also used a high-pass filter at 2 kHz to avoid the influence of background noise.

Habituation–dishabituation experiments

Playback experiments were performed between 7:00 p.m and 10:30 p.m in a large recording room (length \times width \times height: 4.5 \times 2.4 \times 2.2 m) lined with sound-absorbing foam (Fig. 2). A foam soundproof board separated the recording room into two compartments of different sizes. Bats could fly freely in the large compartment (length \times width \times height: 3 \times 2.4 \times 2.2 m). No sounds produced by the equipment or by the observer in the large compartment were evident in our recordings. Therefore we assume that the bats in the large compartment could not hear sounds produced by the equipment or by the observer (e.g., clicking of the computer). An experimenter could monitor bat behaviour and switch playback files in the small compartment (length \times width \times height: 1.5 \times 2.4 \times 2.2 m). An infrared camera, an ultrasonic microphone, and an ultrasonic loudspeaker (Ultrasonic Dynamic Speaker Vifa) were installed on the foam soundproof board. The microphone and loudspeaker were connected to an ultrasound recording system and an ultrasound playback interface (UltraSoundGate player 116), respectively. Another infrared camera was placed in one corner of the large compartment to monitor the bats' overall behaviour.

Following previous studies (Cheney and Seyfarth 1988; Mumm et al. 2014), we adopted habituation–dishabituation playback experiments to test acoustical discrimination in *H. armiger*. When a bat was positioned in the large compartment and the distance between the bat and the microphone, camera, and speaker was two metres, we broadcast a habituation file from one stimulus donor using

Fig. 2 Schematic of the setup for the habituation–dishabituation experiments



an infinite loop mode. After the bat was habituated to the stimulus for 60 s (i.e., no echolocation for 60 s, no body or head movement), we broadcast another file from a different stimulus donor. Once the bat was dishabituated, we broadcast a control stimulus (i.e., 300 ms pink noise; Audio files S2) to determine if the bat would concentrate on the playback file instead of being otherwise distracted or sleeping. If the testing bat displayed any behavioural activities (i.e., body or leg movements, wing stretching, or echolocation utterances) in response to the dishabituation and control stimuli, we took this as an indication that the bat discriminated between the habituation and the dishabituation file. If the tested bat remained habituated during the dishabituation file but reacted to the control stimulus, we took this as evidence that the bat had not discriminated between the habituation and the dishabituation file. After the playback experiments, all bats were returned to their large flight cage in the husbandry room and were used for agonistic interactions.

Dominance rank determination

Sixteen bats from playback experiments were housed together in the large flight cage to record agonistic interactions among them for 43 consecutive days. We used the same method to quantify agonistic interactions that we used for the vocal recording described above (except for the use of the sound recording device). Following previous studies (Jennings 2007; Jennings et al. 2010), we quantified individual dominance rank using David's scores (DS). The DS is calculated as $DS = w + w_2 - l - l_2$ where w represents the sum of proportion of successes by individual i in his agonistic interactions with all other individuals, w_2 is the weighted w values for all individuals that individual i interacted with, l represents the sum of proportion of failures by individual i in his agonistic interactions with all other individuals, and l_2 is the weighted l values for all individuals that individual i interacted with (David 1987; Gammell et al. 2003). Larger positive values of DS indicate higher dominance rank and larger negative values of DS indicate lower dominance rank. Following the definitions of Sun et al. (2019), we defined the winner was the individual that remained at the position of agonistic interaction after its opponent's retreat, and the loser was the individual that left the interaction position as a consequence of competitor agonistic activity, and did not exhibit any agonistic behaviours and territorial calls after retreat for at least 20 s. The time interval between two consecutive and distinct agonistic interactions was at least one minute. The males either started self-grooming, turned heads accompanied by echolocation or remained motionless during the interval between consecutive interactions.

Statistical analysis

We used individual average values of all acoustic parameters in our analyses, except for the acoustic parameters used for individual signature. We conducted Shapiro–Wilk tests to examine the normality of all of our data, and found that all variables met a normal distribution (Shapiro–Wilk; $0.07 < P < 0.99$).

To obtain statistical support for individual vocal signatures, we first conducted a principal components analysis (PCA) using a varimax rotation method for the 23 acoustic variables. We extracted four principal components (PCs; with eigenvalues > 1). They explained 75% of the total variance (Table S3). Both the Bartlett's criteria ($\chi^2_{253} = 12,782.5$, $P < 0.001$) and the KMO index (0.773) indicated that our data were suitable for PCA. Second, we input the four PCs in a discriminant function analysis (DFA). We adjusted the prior probabilities of the DFA according to the observed group sizes because of the unequal numbers of calls per bat. For cross validation, a leave-one-out classification method was performed to assess the percentage of correct classifications, which classified each sUFM call based on the discriminant functions established with all sUFM calls except the call being classified. Subsequently, we conducted a one-tailed binomial test to examine whether the observed percentage of correct DFA classification of territorial calls was higher than the percentage of random DFA classification (mean chance level: $1/16 = 6.3\%$; maximum chance level: $24/224 = 10.71\%$).

A simple linear regression was conducted to test the associations between body mass and dominance rank. To test the associations between the acoustic parameters, body mass and dominance rank of the males, we performed optimized linear models using the function 'glmulti' in the R package 'glmulti' (Calcagno and de Mazancourt 2010). In this model, body mass and dominance rank were used as dependent variables, and five acoustic parameters (i.e., syllable rate, syllable duration, peak frequency, minimum and maximum frequency) were used as independent variables. The model produced a set of 32 candidate models which included five independent variables and all possible combinations of these independent variables based on ordinary least squares (OLS) linear regressions. We compared the competing models using the Akaike information criterion corrected for small sample size (AICc). The model with the lowest AICc value indicates the best-fitting model. We calculated the $\Delta AICc$ values as the AICc value of each model minus the AICc value of the best-fitting model. The difference in AICc value of > 2 ($\Delta AICc > 2$) between the second and the first best models was considered to be a golden rule for model selection (Burnham and Anderson 2002). Additionally, we calculated Akaike weights (w_i) to assess the relative likelihood of a given model, compared with other candidate models in the

set. If differences in AICc value were ≤ 2 ($\Delta\text{AICc} \leq 2$), we conducted multimodel inference using the function ‘model.avg’ in the package ‘MuMIn’ (Bartoń 2017) in R v. 3.5.1 (R Core Development Team 2018). We conducted a hierarchical partitioning method (HP) to estimate the independent contribution of each predictor variable (Chevan and Sutherland 1991). The HP can lessen multicollinearity among predictor variables (Mac Nally 2002) and was performed using the R package ‘hier.part’ (Walsh et al. 2013). In the HP, we assessed the statistical significance for each predictor variable using a randomization method (Mac Nally and Walsh 2004). All statistical tests were conducted in SPSS v20.0 (SPSS Inc., Chicago, IL, U.S.A.) and R v. 3.5.1 (R Core Development Team 2018).

Results

Acoustic characteristics

A total of 224 sUFM calls from 16 bats (mean \pm SD: 14.00 ± 6.28 calls per bat; range 5–24) were obtained. All syllables contained the highest sound energy in the second harmonic. The call and syllable characteristics of male *H. armiger* are shown in Table 1.

Relationships between body mass and acoustic parameters

The body mass of 16 males ranged from 49.51 to 76.22 g (mean \pm SD: 63.36 ± 8.72 g; Table S4).

The top AICc model included three predictor variables, i.e., minimum frequency, maximum frequency and peak frequency (Table 2). Model averaging revealed that both minimum frequency and syllable duration were significantly associated with body mass (Table 3). Males with larger body mass emitted sUFM calls with lower minimum frequency and longer syllable duration (Fig. 3a). Moreover, hierarchical partitioning showed that minimum frequency (38.38%)

and syllable duration (28.51%) contributed significantly more to the correlation with body mass than other acoustic parameters (peak frequency: 17.93%; maximum frequency: 11.03%; syllable rate: 4.16%; Fig. 3b).

Dominance rank

A total of 1657 agonistic interactions from 16 bats (mean \pm SD: 103.56 ± 59.04 interactions per bat; range 37–263) were analysed (Fig. S1). The David’s score for 16 male *H. armiger* are shown in Table S5. There was at least one agonistic interaction between each pair of males. Among the 1657 interactions, the mean \pm standard deviation contest duration was 17.24 ± 20.74 s (range 1–354 s).

Relationships between dominance rank and body mass

There was a significant positive association between body mass and dominance rank (simple linear regression: $t = 4.591$, $R^2 = 0.601$, $P = 0.0004$).

Relationships between dominance rank and acoustic parameters

The best AICc model contained two important predictor variables, i.e., minimum frequency and peak frequency (Table 2). Males with higher David’s scores produced sUFM calls with lower minimum frequency ($t = -4.936$, $R^2 = 0.700$, $P = 0.0003$; Fig. 3c) and higher peak frequency ($t = 4.270$, $R^2 = 0.700$, $P = 0.0009$; Fig. 3c). Moreover, hierarchical partitioning showed that minimum frequency (45.37%) and peak frequency (23.37%) predicted significantly more variation in the dominance rank compared to the other acoustic parameters (syllable duration: 18.27%; maximum frequency: 8.94%; syllable rate: 4.06%; Fig. 3d).

Table 1 Summary of mean \pm standard deviation (SD) and range for acoustic parameters of territorial calls in *Hipposideros armiger*

Parameters	Mean	SD	Minimum	Maximum
Call duration (ms)	263.57	143.86	94.10	1182.60
Number of syllable within a call	5.76	2.72	3	21
Inter-syllable interval within a call (ms)	36.21	13.96	20.05	166.80
Minimum frequency (kHz)	33.62	3.99	23.47	47.63
Maximum frequency (kHz)	65.10	2.88	60.03	75.37
Bandwidth (kHz)	31.48	4.11	20.00	43.20
Peak frequency (kHz)	61.30	1.58	58.00	69.87
Difference between peak and max frequency (kHz)	3.80	2.19	1.13	10.67
Syllable duration (ms)	15.70	1.21	13.20	19.10
Syllable rate (syllables/s)	22.79	3.52	10.29	31.88

Table 2 Results of the Akaike's information criterion (AICc) model selection procedure used to investigate the associations between acoustic parameters and body mass and dominance rank in *Hipposideros armiger*

Model	Predictive variables	df	LogL	AICc	Δ AICc	w_i
Body mass						
1	Min(-), Max(-), Peak(+)	5	-52.99	121.989	0.000	0.293
2	Dura(+)	3	-57.36	122.714	0.725	0.204
3	Min(-)	3	-57.93	123.851	1.862	0.115
4	Min(-), Peak(+)	4	-56.14	123.908	1.919	0.112
5	Min(-), Dura(+)	4	-56.21	124.058	2.069	0.104
6	Min(-), Max(+), Rate(-), Peak(+)	6	-52.39	126.105	4.116	0.037
7	Max(+), Dura(+)	4	-57.25	126.128	4.139	0.037
8	Dura(+), Peak(+)	4	-57.33	126.297	4.308	0.034
9	Rate(-), Dura(+)	4	-57.34	126.307	4.318	0.034
10	Min(-), Dura(+), Peak(+)	5	-55.28	126.559	4.570	0.030
Dominance rank						
1	Min(-), Peak(+)	4	-72.96	157.565	0.000	0.683
2	Min(-), Peak(+), Rate(-)	5	-72.57	161.139	3.574	0.114
3	Min(-), Peak(+), Max(+)	5	-72.84	161.683	4.118	0.087
4	Min(-), Peak(+), Dura(+)	5	-72.96	161.928	4.363	0.077
5	Min(-), Peak(+), Rate(-), Dura(+)	6	-72.49	166.305	8.740	0.009
6	Min(-), Peak(+), Max(+), Rate(-)	6	-72.53	166.391	8.826	0.008
7	Min(-), Max(+)	4	-77.42	166.470	8.905	0.008
8	Min(-), Peak(+), Max(+), Dura(+)	6	-72.80	166.938	9.373	0.006
9	Min(-)	3	-79.98	167.953	10.388	0.004
10	Dura(+)	3	-80.26	168.518	10.953	0.003

Models are ranked based on the AICc values from the best to the worst model. The sign of the regression coefficient of the associations between acoustic parameters and body mass and dominance rank is shown in parentheses ('-': negative; '+': positive)

LogL Log likelihoods, *Min* minimum frequency (kHz), *Peak* peak frequency (kHz), *Dura* syllable duration (ms), *Max* maximum frequency (kHz), *Rate* syllable rate

Table 3 Model-averaged parameter estimates of the best-supported (before and including the null model) linear models used to describe the relationships between acoustic parameters and body mass in *Hipposideros armiger*

	Estimate	SE	Adjusted SE	<i>z</i>	95% CI
(Intercept)	-45.010	102.909	108.625	0.414	(-257.912, 167.892)
Min	-1.460	1.205	1.237	1.181	(-3.904, -0.319)
Max	-0.862	1.383	1.419	0.608	(-5.115, 0.418)
Peak	2.606	3.312	3.378	0.771	(-0.878, 11.177)
Dura	3.539	4.646	4.754	0.745	(0.319, 15.688)
Rate	0.054	0.521	0.560	0.097	(-3.086, 4.612)

Min minimum frequency (kHz), *Peak* peak frequency (kHz), *Dura* syllable duration (ms), *Max* maximum frequency (kHz), *Rate* syllable rate

95% confidence intervals of the parameters that did not overlap zero are indicated in bold

Vocalizer signature and discrimination

Males could be discriminated statistically based on acoustic parameters of their territorial calls (Fig. 1). A linear discriminant function analysis showed that 46.9% of 224 sUFM calls of 16 males were classified to the correct individual (Table 4; Fig. 4). The percent of correct classification was significantly greater than expected by chance (mean chance level: $1/16 = 6.3\%$; one-tailed binomial test: $P < 0.0001$; maximum chance level: 10.71%; one-tailed binomial test: $P < 0.0001$). All nine males showed pronounced responses to the dishabituation files and control stimulus (Video S2). After the playback changed from the habituation files to dishabituation files, only one of nine males flew towards the speakers. The number of calls that were needed for habituation with dominance rank (David's score) of each individual can be found in Fig. S2, with an average of 14.22 ± 3.03 .

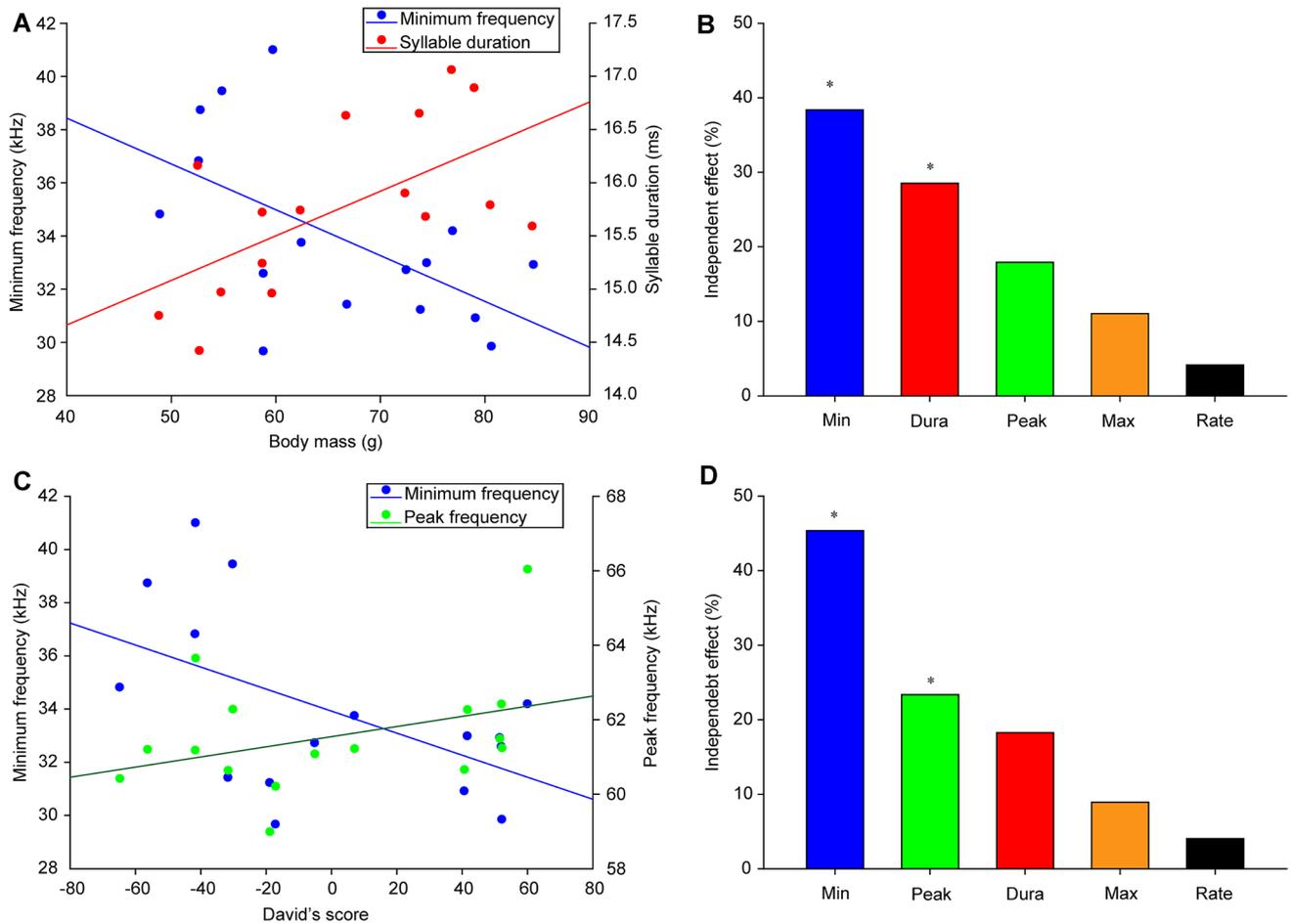


Fig. 3 Relationships between acoustic parameters and **a** body mass and **c** dominance score, and the independent contribution (%) of each predictor (acoustic parameters) for **b** body mass and for **d** dominance rank calculated with hierarchical partitioning in *Hipposideros*

armiger. Min (blue): minimum frequency (kHz). Dura (red): syllable duration (ms). Peak (green): peak frequency (kHz). Max (saffron yellow): maximum frequency (kHz). Rate (black): syllable rate. * $P < 0.05$. $N = 16$

Table 4 Statistical evidence for an individual signature in sUFM calls of *Hipposideros armiger*

Assessment of model fit	DF1	DF2	DF3	DF4
Eigenvalue	3.357	1.416	0.968	0.321
% variance	55.4	23.3	16.0	5.3
Test of functions	DF1–DF4	DF2–DF4	DF3–DF4	DF4
Wilks's λ	0.037	0.159	0.385	0.757
χ^2 (all $P < 0.001$)	704.905	391.431	203.516	59.296
df	60	42	26	12

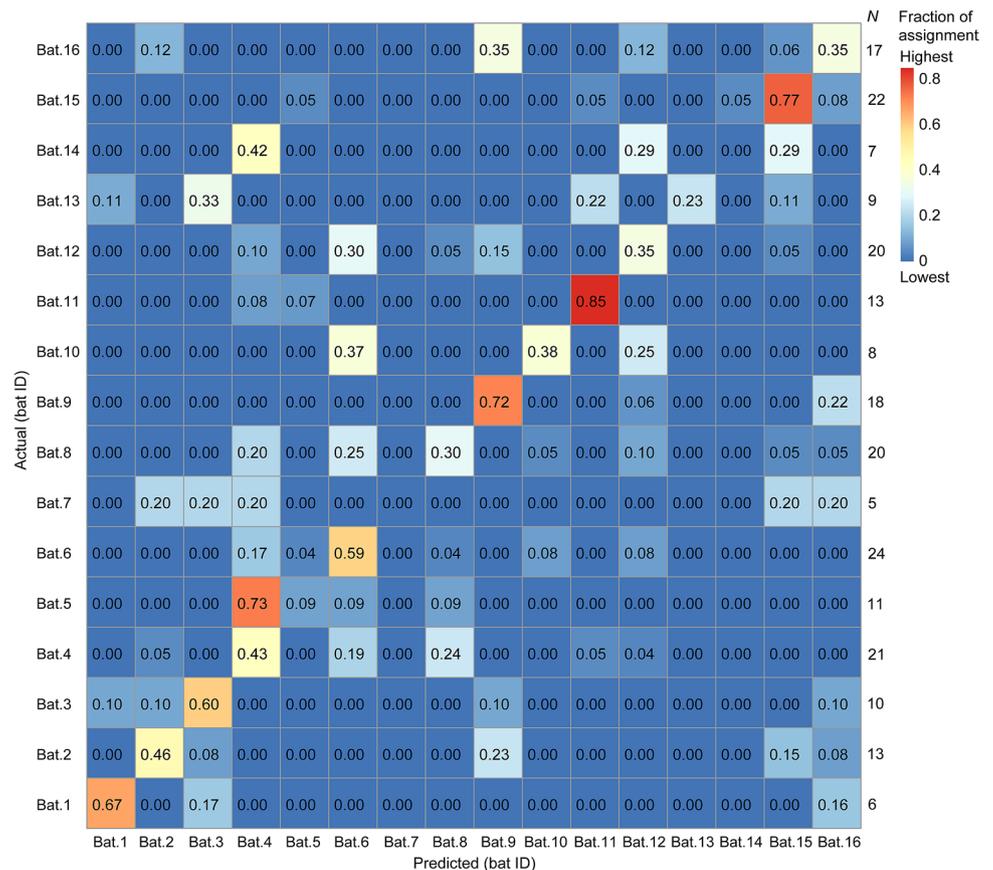
DF discriminant function

Discussion

We found that body mass was negatively correlated with minimum frequency and positively correlated with

syllable duration, which supported our first hypothesis that territorial calls predicted callers' body size. We also found that David's score was negatively correlated with minimum frequency but positively correlated with peak frequency, which partially supported the second hypothesis that territorial calls predicted callers' dominance rank. Additionally, we found an individual signature in male sUFM calls, and all tested bats showed pronounced behavioural responses (i.e., started echolocation utterances, started head or body movements or even flew off) after switching playback files from one stimulus donor to those from a second stimulus donor and from dishabituation files to control stimulus in the habituation–dishabituation experiments. These results supported the first and second prediction of the third hypothesis, respectively.

Fig. 4 A confusion matrix for the prediction of the vocalizers. The number in each cell represents the fraction of each actual class (row) assigned to each predicted class (column). The sum of each row is 1. The total number of calls per class (N) is represented on the right side of the matrix. Blue signifies the lowest value and red signifies the highest value in the matrix



Body mass and acoustic parameters

We found that heavier males emitted sUFM calls with lower minimum frequency. The observed negative relationship between body mass and minimum frequency in the study is similar to the pattern found in other mammals, such as the giant panda *Ailuropoda melanoleuca* (Charlton et al. 2009) and fallow deer *Dama dama* (Vannoni and McElligott 2008). As vocal folds with longer length tend to vibrate at lower frequencies, it is reasonable to suggest that minimum frequency, which is influenced by the length of vocal fold, is prone to be lower in individuals with larger body mass. Additionally, we found that heavier males uttered sUFM syllables with longer duration. Our results echo previous studies of Asian particoloured bats *Vespertilio sinensis* showing that body size scaled positively with syllable duration in aggressive vocalizations (Zhao et al. 2018). Because greater lung volumes have the potential to produce longer vocalizations (Fitch and Hauser 2003), this also suggests why syllable duration, which is physically constrained by lung volumes, tended to be longer in more massive or larger individuals. Taken together, these results show that territorial calls can reliably indicate the body size of male *H. armiger*.

What is the advantage of territorial calls in male *H. armiger* to encode honest signals of body size? One possible

advantage is that territory holders produce territorial calls honestly indicating their large body size to deter potential intruders that are smaller than them, thus limiting physical contests. Because fighting ability is usually positively correlated with body size, large individuals typically have an advantage in fights (Arnott and Elwood 2009). Before escalating to costly physical combat, most animals exchange signals indicating fighting ability to help both opponents decide whether to give up or to continue the contest. Playback results from toads (Davies and Halliday 1978) and red deer (Clutton-Brock et al. 1979) support this view. For example, male toads, *Bufo bufo*, preferred to attack paired males when they heard a high pitched croak indicating small body size than when they heard a deep croak indicating large body size (Davies and Halliday 1978).

Dominance rank and body mass

We found that higher-ranking males tend to be heavier males. Similar results can be found in other species, such as cormorants *Phalacrocorax carbo*, pigeons *Columba livia* (Portugal et al. 2017), fallow deer *Dama dama* (McElligott et al. 2001), and beef cattle *Bos taurus* (Šárová et al. 2013). Dominance rank is usually determined by internal factors such as body size, fighting ability or social skills (Bush et al.

2016; Chase and Seitz 2011). Individuals with larger body size (such as large body mass) prevail in agonistic interactions because body size is generally related to strength and the ability to impose injury (Chase and Seitz 2011). Our previous study showed that *H. armiger* males with larger body mass were more likely to win contests with lighter males (Sun et al. 2019). Therefore, heavier individuals are more likely to acquire dominance status over lighter individuals.

Dominance rank and acoustic parameters

We found that higher-ranking males uttered territorial calls with lower minimum frequency and higher peak frequency. The negative relationships between dominance rank and minimum frequency have been reported in fallow deer *Dama dama* (Briefer et al. 2010; Vannoni and McElligott 2008) and the white-lipped peccary *Tayassu pecari* (Nogueira et al. 2016). Because minimum frequency is typically correlated with body mass of male *H. armiger* and heavier males tend to be higher-ranking males, males thus could use minimum frequency as an auditory signal to indicate their dominance rank. The positive relationships between dominance rank and peak frequency can be found in male baboons *Papio cynocephalus ursinus* (Fischer et al. 2004). One possible interpretation for the rise in peak frequency is that it may be influenced by signal amplitude. Vocalizations that are given with higher amplitude tend to have higher frequencies due to faster air-flow over the vocal membranes and therefore higher vibrating rates (Hsiao et al. 1994). We suggest that higher-ranking male *H. armiger* may give higher amplitude calls than low-ranking males and as a result call with higher peak frequencies. However we cannot test this hypothesis with our data set. The calling direction of each bat and the distance between the bat and the microphone was quite variable making it impossible for us to generate a robust measure of call amplitude for all callers. Future work should be performed to accurately measure the vocal amplitude of high- and low-ranking individuals using on-board microphones (e.g., Danilovich et al. 2015).

Vocal signatures and discrimination

We found a significant individual signature encoded in territorial calls of male *H. armiger*. Similar findings have been found in male greater sac-winged bats *Saccopteryx bilineata* (Eckenweber and Knoernschild 2013), male Seba's short-tailed fruit bat *Carollia perspicillata* (Fernandez et al. 2014), male greater mouse-eared bats *Myotis myotis* (Walter and Schnitzler 2017), and Egyptian fruit bat *Rousettus aegyptiacus* (Prat et al. 2016). The individual signatures in territorial calls of male *H. armiger* could be due to the individual differences in the vocal apparatus such as the vocal organ or body size, given the significant correlation between

acoustic parameters and body mass. Thus, the individual discrimination of male *H. armiger* may also depend on the body-mass effects. Here the differences in acoustic parameters among male *H. armiger* may provide reliable cues to an individual's identification. A similar result has been documented in red deer *Cervus elaphus* (Reby et al. 2006), rhesus monkey *Macaca mulatta* (Rendall et al. 1998) and Japanese macaques *Macaca fuscata* (Furuyama et al. 2016). Vocal signatures are a critical prerequisite for individual discrimination (Pollard and Blumstein 2012; Tibbetts and Dale 2007). The individual signature in territorial calls can facilitate discrimination of male *H. armiger* competitors. Additionally, we found that male *H. armiger* had the ability to discriminate different males based on these territorial calls. Similar findings can be found in male Seba's short-tailed fruit bat *Carollia perspicillata* (Fernandez et al. 2014). Individual discrimination based on territorial calls could be highly useful for male *H. armiger*, especially in dark caves. Male *H. armiger* defend territories against other males during the entire day, especially when they return from foraging to the roost and reoccupy their day-roost territories (Yang 2011). When a free-flying male invades or reoccupies the territories occupied by a roosting male, the free-flying male can discriminate between nearby neighbours and strangers, or more unfamiliar intruders based on the territorial calls emitted by the roosting male. This should allow the free-flying male to decide to persist in fighting or give up, thus reducing unnecessary energy costs.

In summary, this study demonstrates that territorial calls of male *Hipposideros armiger* contain reliable information about body mass, social dominance and individual identity in individual syllable types. This encoding of multiple types of information is particularly likely when the difference types are highly correlated. The reliable information encoded in the male *H. armiger*'s territorial calls is likely to play seminal roles during territorial agonistic interactions. Further playback experiments will need to examine whether males can both perceive and use the spectral properties of an opponent's territorial calls reflecting different body size or dominance rank to make decisions.

Data availability statements

The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Acknowledgements We would like to thank Yossi Yovel for his valuable comment on the manuscript. This research was supported by the National Natural Science Foundation of China (Grant nos. 31872680, 31922050, 31670390 and 31872681) and the Fund of the Jilin Province Science and Technology Development Project (Grant no. 20180101024JC).

Author contributions CNS, TLJ and JF participated in study design. CNS and CMZ collected and analysed the data. AQL assisted with experiments. CNS drafted the manuscript. TLJ and JRL revised the manuscript. All authors read and approved the final version.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

References

- Arnott G, Elwood RW (2009) Assessment of fighting ability in animal contests. *Anim Behav* 77:991–1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>
- ASAB/ABS (2017) Guidelines for the treatment of animals in behavioural research and teaching. *Anim Behav* 123:I–IX. [https://doi.org/10.1016/S0003-3472\(16\)30351-7](https://doi.org/10.1016/S0003-3472(16)30351-7)
- Bartoń K (2017) MuMIn: Multi-model inference. <http://R-Forge.R-project.org/projects/mumin/>
- Bee MA, Gerhardt HC (2002) Individual voice recognition in a territorial frog (*Rana catesbeiana*). *Proc R Soc B Biol Sci* 269:1443–1448. <https://doi.org/10.1098/rspb.2002.2041>
- Botero CA, Rossman RJ, Caro LM, Stenzler LM, Lovette IJ, de Kort SR, Vehrencamp SL (2009) Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Anim Behav* 77:701–706. <https://doi.org/10.1016/j.anbehav.2008.11.020>
- Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer Associates, Sunderland
- Briefer E, Vannoni E, McElligott AG (2010) Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. *BMC Biol* 8:35. <https://doi.org/10.1186/1741-7007-8-35>
- Briffa M (2015) Animal signaling: integrating analysis of functions and mechanisms. In: Irschick DJ, Briffa M, Podos J (eds) Animal signaling and function: an integrative approach. Wiley, Hoboken, pp 141–173
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Bush JM, Quinn MM, Balreira EC, Johnson MA (2016) How do lizards determine dominance? Applying ranking algorithms to animal social behaviour. *Anim Behav* 118:65–74. <https://doi.org/10.1016/j.anbehav.2016.04.026>
- Calcagno V, de Mazancourt C (2010) Glmulti: an R package for easy automated model selection with (generalized) linear models. *J Stat Softw* 34:1–29. <https://doi.org/10.18637/jss.v034.i12>
- Charlton BD, Zhang Z, Snyder RJ (2009) The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. *Anim Behav* 78:893–898. <https://doi.org/10.1016/j.anbehav.2009.06.029>
- Chase ID, Seitz K (2011) Self-structuring properties of dominance hierarchies: a new perspective. *Adv Genet* 75:51–81. <https://doi.org/10.1016/B978-0-12-380858-5.00001-0>
- Cheney DL, Seyfarth RM (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim Behav* 36:477–486. [https://doi.org/10.1016/S0003-3472\(88\)80018-6](https://doi.org/10.1016/S0003-3472(88)80018-6)
- Cheng HC, Lee LL (2004) Temporal variations in the size and composition of Formosan leaf-nosed bat (*Hipposideros terasensis*) colonies in central Taiwan. *Zool Stud* 43:787–794
- Chevan A, Sutherland M (1991) Hierarchical partitioning. *Am Stat* 45:90–96
- Chuang MF, Kam YC, Bee MA (2017) Territorial olive frogs display lower aggression towards neighbours than strangers based on individual vocal signatures. *Anim Behav* 123:217–228. <https://doi.org/10.1016/j.anbehav.2016.11.001>
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE (1979) The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225. [https://doi.org/10.1016/0003-3472\(79\)90141-6](https://doi.org/10.1016/0003-3472(79)90141-6)
- Danilovich S, Krishnan A, Lee W-J, Borrisov I, Eitan O, Kosa G, Moss CF, Yovel Y (2015) Bats regulate biosonar based on the availability of visual information. *Curr Biol* 25:R1124–R1125. <https://doi.org/10.1016/j.cub.2015.11.003>
- David HA (1987) Ranking from unbalanced paired-comparison data. *Biometrika* 74:432–436. <https://doi.org/10.1093/biomet/74.2.432>
- Davies NB, Halliday TR (1978) Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683–685. <https://doi.org/10.1038/274683a0>
- Drews C (1993) The concept and definition of dominance in animal behaviour. *Behaviour* 125:283–313. <https://doi.org/10.1163/156853993X00290>
- Dukas R (2004) Causes and consequences of limited attention. *Brain Behav Evolut* 63:197–210. <https://doi.org/10.1159/000076781>
- Eckenweber M, Knörnschild M (2013) Social influences on territorial signaling in male greater sac-winged bats. *Behav Ecol Sociobiol* 67:639–648. <https://doi.org/10.1007/s00265-013-1483-z>
- Elie JE, Theunissen FE (2018) Zebra finches identify individuals using vocal signatures unique to each call type. *Nat Commun* 9:4026. <https://doi.org/10.1038/s41467-018-06394-9>
- Fan P, Liu R, Grueter CC, Li F, Wu F, Huang T, Yao H, Liu D, Liu X (2018) Individuality in coo calls of adult male golden snub-nosed monkeys (*Rhinopithecus roxellana*) living in a multilevel society. *Anim Cogn* 22:71–79. <https://doi.org/10.1007/s10071-018-1222-y>
- Fant G (1960) Acoustic theory of speech production. Mouton, Hague
- Fenton MB (2003) Eavesdropping on the echolocation and social calls of bats. *Mamm Rev* 33:193–204. <https://doi.org/10.1046/j.1365-2907.2003.00019.x>
- Fernandez AA, Fasel N, Knörnschild M, Richner H (2014) When bats are boxing: aggressive behaviour and communication in male Seba's short-tailed fruit bat. *Anim Behav* 98:149–156. <https://doi.org/10.1016/j.anbehav.2014.10.011>
- Fernandez AA, Knörnschild M (2017) Isolation calls of the bat *Sacopteryx bilineata* encode multiple messages. *Anim Behav Cogn* 4:169–186. <https://doi.org/10.12966/abc.04.05.2017>
- Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behav Ecol Sociobiol* 56:140–148. <https://doi.org/10.1007/s00265-003-0739-4>
- Fitch WT (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *J Acoust Soc Am* 102:1213–1222. <https://doi.org/10.1121/1.421048>
- Fitch WT, Hauser MD (2003) Unpacking “honesty”: vertebrate vocal production and the evolution of acoustic signals. In: Simmons A, Fay RR, Popper AN (eds) Acoustic communication. Springer, New York, pp 65–137
- Furuyama T, Kobayashi KI, Riquimaroux H (2016) Role of vocal tract characteristics in individual discrimination by Japanese macaques (*Macaca fuscata*). *Sci Rep*. <https://doi.org/10.1038/srep32042>
- Gadziola MA, Grimsley JMS, Faure PA, Wenstrup JJ (2012) Social vocalizations of big brown bats vary with behavioral context. *PLoS ONE* 7:e44550. <https://doi.org/10.1371/journal.pone.0044550>
- Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ (2003) David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Anim Behav* 66:601–605. <https://doi.org/10.1006/anbe.2003.2226>

- Gillam EH, Fenton MB (2016) Role of acoustic social communication in the lives of bats. In: Fenton MN, Grinnell GA (eds) *Bat bioacoustics*. Springer, New York, pp 117–139
- Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. *Behav Ecol Sociobiol* 57:197–214. <https://doi.org/10.1007/BF00606371>
- Henry KS, Gall MD, Vélez A, Lucas JR (2016) Avian auditory processing at four different scales: variation among species, seasons, sexes, and individuals. In: Bee MA, Miller CT (eds) *Psychological mechanisms in animal communication*. Springer, New York, pp 17–55
- Hsiao TY, Solomon NP, Luscher ES, Titze IR, Liu K, Fu T-C, Hsu M-M (1994) Effect of subglottic pressure on fundamental frequency of the canine larynx with active muscle tensions. *Ann Otol Rhinol Laryngol* 103:817–821. <https://doi.org/10.1177/000348949410301013>
- Jahelková H, Horáček I, Bartonička T (2008) The advertisement song of *Pipistrellus nathusii* (Chiroptera, Vespertilionidae): a complex message containing acoustic signatures of individuals. *Acta Chiropterol* 10:103–126. <https://doi.org/10.3161/150811008X331144>
- Jennings DJ (2007) The effect of chemical immobilization on dominance rank in the fallow deer. *Anim Behav* 74:1107–1110. <https://doi.org/10.1016/j.anbehav.2007.01.011>
- Jennings DJ, Carlin CM, Hayden TJ, Gammell MP (2010) Investment in fighting in relation to body condition, age and dominance rank in the male fallow deer, *Dama dama*. *Anim Behav* 79:1293–1300. <https://doi.org/10.1016/j.anbehav.2010.02.031>
- Jiang T, Huang X, Wu H, Feng J (2017) Size and quality information in acoustic signals of *Rhinolophus ferrumequinum* in distress situations. *Physiol Behav* 173:252–257. <https://doi.org/10.1016/j.physbeh.2017.02.025>
- Kanwal JS, Matsumura S, Ohlemiller K, Suga N (1994) Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats. *J Acoust Soc Am* 96:1229–1254. <https://doi.org/10.1121/1.410273>
- Koren L, Geffen E (2009) Complex call in male rock hyrax (*Procavia capensis*): a multi-information distributing channel. *Behav Ecol Sociobiol* 63:581–590. <https://doi.org/10.1007/s00265-008-0693-2>
- Luo B, Lu G, Chen K, Guo D, Huang X, Liu Y, Feng J (2017) Social calls honestly signal female competitive ability in Asian particoloured bats. *Anim Behav* 127:101–108. <https://doi.org/10.1016/j.anbehav.2017.03.012>
- Mac Nally R (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers Conserv* 11:1397–1401. <https://doi.org/10.1023/A:1016250716679>
- Mac Nally R, Walsh CJ (2004) Hierarchical partitioning public-domain software. *Biodivers Conserv* 13:659–660. <https://doi.org/10.1023/B:BIOC.0000009515.11717.0b>
- Mackin WA (2005) Neighbor-stranger discrimination in Audubon's shearwater (*Puffinus l. lherminieri*) explained by a “real enemy” effect. *Behav Ecol Sociobiol* 59:326–332. <https://doi.org/10.1007/s00265-005-0055-2>
- Mathevon N, Koralek A, Weldele M, Glickman SE, Theunissen FE (2010) What the hyena's laugh tells: sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta*. *BMC Ecol* 10:9–10. <https://doi.org/10.1186/1472-6785-10-9>
- McElligott AG, Gammell MP, Harty HC, Pains DR, Murphy DT, Walsh JT, Hayden TJ (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* 49:266–272. <https://doi.org/10.1007/s002650000293>
- Mumm CAS, Urrutia MC, Knörnschild M (2014) Vocal individuality in cohesion calls of giant otters, *pteronura brasiliensis*. *Anim Behav* 88:243–252. <https://doi.org/10.1016/j.anbehav.2013.12.005>
- Nogueira SSC, Caselli CB, Costa TSO, Moura LN, Nogueira-Filho SLG (2016) The role of grunt calls in the social dominance hierarchy of the white-lipped peccary (mammalia, tayassuidae). *PLoS ONE* 11:e0158665. <https://doi.org/10.1371/journal.pone.0158665>
- Pfefferle D, Fischer J (2006) Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. *Anim Behav* 72:43–51. <https://doi.org/10.1016/j.anbehav.2005.08.021>
- Pollard KA, Blumstein DT (2012) Evolving communicative complexity: insights from rodents and beyond. *Proc R Soc B Biol Sci* 367:1869–1878. <https://doi.org/10.1098/rstb.2011.0221>
- Portugal SJ, Sivess L, Martin GR, Butler PJ, White CR (2017) Perch height predicts dominance rank in birds. *Ibis* 159:456–462. <https://doi.org/10.1111/ibi.12447>
- Prat Y, Taub M, Yovel Y (2016) Everyday bat vocalizations contain information about emitter, addressee, context, and behavior. *Sci Rep*. <https://doi.org/10.1038/srep39419>
- R Core Development Team (2018) R: a language and environment for statistical computing, 3.5.1 edn. Vienna (Austria): R Foundation for Statistical Computing. Retrieved from: <http://www.R-project.org>
- Ratcliffe LM, Mennill DJ, Schubert KA (2007) Social dominance and fitness in black-capped chickadees. In: Otter KA (ed) *The ecology and behavior of chickadees and titmice; an integrated approach*. Oxford University Press, Oxford, pp 131–146
- Reby D, Andre-Obrecht R, Galinier A, Farinas G, Cargnelutti B (2006) Cepstral coefficients and hidden markov models reveal idiosyncratic voice characteristics in red deer (*Cervus elaphus*) stags. *J Acoust Soc Am* 120:4080–4089. <https://doi.org/10.1121/1.2358006>
- Rendall D, Owren MJ, Rodman PS (1998) The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *J Acoust Soc Am* 103:602–614. <https://doi.org/10.1121/1.421104>
- Ryan MJ (1983) Frequency modulated calls and species recognition in a neotropical frog. *J Comp Physiol A* 150:217–221. <https://doi.org/10.1007/s00265-008-0693-2>
- Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am Nat* 126:87–100. <https://doi.org/10.1086/284398>
- Šárová R, Špinka M, Stěhulová I, Ceacero F, Šimečková M, Kotrba R (2013) Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Anim Behav* 86:1315–1323. <https://doi.org/10.1016/j.anbehav.2013.10.002>
- Sun C, Zhang C, Gu H, Jiang T, Feng J (2019) Self-assessment strategy during contest decisions between male Great Himalayan leaf-nosed bats. *Behav Ecol Sociobiol*. <https://doi.org/10.1007/s00265-019-2657-0>
- Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. *Trends Ecol Evol* 22:529–537. <https://doi.org/10.1016/j.tree.2007.09.001>
- Titze IR (1994) *Principles of vocal production*. Prentice-Hall, Englewood Cliffs
- Vannoni E, McElligott AG (2008) Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PLoS ONE* 3:e3113. <https://doi.org/10.1371/journal.pone.0003113>
- Walsh C, Mac Nally R, Walsh MC (2013) Package ‘hier.part’. <http://www.cranr-project.org/web/packages/hierpart/index.html>
- Walter MH, Schnitzler H-U (2017) Spectral call features provide information about the aggression level of greater mouse-eared bats (*Myotis myotis*) during agonistic interactions. *Bioacoustics* 28:1–25. <https://doi.org/10.1080/09524622.2017.1359798>
- Wyman MT, Mooring MS, McCowan B, Penedo MCT, Reby D, Hart LA (2012) Acoustic cues to size and quality in the vocalizations of male North American bison, *Bison bison*. *Anim Behav* 84:1381–1391. <https://doi.org/10.1016/j.anbehav.2012.08.037>

Yang (2011) Mating system and kinship of the formosan leaf-nosed bat, *Hipposideros armiger Terasensis* (Chiroptera, Hipposideridae). Dissertation. National Chung Hsing University.

Zhao X, Jiang T, Gu H, Liu H, Sun C, Liu Y, Feng J (2018) Are aggressive vocalizations the honest signals of body size and quality in female Asian particoloured bats? Behav Ecol Sociobiol. <https://doi.org/10.1007/s00265-018-2510-x>

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