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Sex ratio potentially influence the complexity of social calls in Himalayan leaf-nosed bat groups

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Animals living in a complex social environment emit diverse acoustic signals and thus serve as excellent subjects for understanding the evolution of acoustic communication. Previous studies have focused on the complexity of social calls in some group-living animals, yet the determinants of vocal complexity at the intraspecific level remain unclear. Here, we aimed to assess the influence of group composition on social call complexity in Himalayan leaf-nosed bats (*Hipposideros armiger*) in the non-breeding season. The bats divided into three groups with the same number of individuals but with different sex ratio compositions. We monitored social vocalizations for the all-male group, the all-female group, the mixed group, and also quantified vocal complexity for each group based on multiple acoustic metrics, including vocal repertoire, call sequences, the diversity index, and information capacity. The results showed that there were significant differences in the composition of call sequences among the three bat groups. The number of vocalizations was the highest in the mixed group, while the social call complexity was the highest in the all-male group, followed by the all-female group, and was the lowest in the mixed group. The results suggest that sex ratio potentially influence the vocal repertoire in Himalayan leaf-nosed bats. Our findings might provide a cue for vocalization research to investigate sex ratio in social groups as a potential driver for vocal complexity.

KEYWORDS

sex ratio, vocal complexity, social organization, aggression, bat

Introduction

Acoustic signals play a vital role in transmitting social information and mediating a series of life history events such as foraging and reproduction (Bradbury and Vehrencamp, 2011; Laiolo, 2012; Charlton et al., 2013; Jin et al., 2015; Kalan and Boesch, 2015). Many animals emit complex vocalizations to engage in social interactions, especially in varying ecological and social environments (Freeberg, 2006; Freeberg et al., 2012b; Bhat et al., 2022; Eleuteri et al., 2022; Naguib et al., 2022). For example, territorial meerkats (*Suricata suricatta*) also use contact calls, potentially to maintain social organization during foraging (Townsend et al., 2010). The duet is widely used by Barbets (Capitonidae) in mate guarding

and dominance against subordinate group members (Soma and Brumm, 2020). Despite the long-term attention within the scientific community, how animals have evolved complex and diverse acoustic signals remains an open question.

Vocal complexity in animals often refers to vocalizations containing a large number of structurally and functionally distinct sound elements or possessing a high amount of information (Freeberg et al., 2012a). Vocal complexity can be measured using three indicators, i.e., repertoire size, gradation variation, and information entropy (Oller and Griebel, 2008; Freeberg et al., 2012a; Kershenbaum, 2014). Repertoire size is usually used to characterize the vocal complexity of birdsongs, as it indicates the number of discretely different vocal sequences used by an individual (Catchpole and Slater, 2003; Kershenbaum, 2014). Gradation variation refers to the variety of repertoires that convey information (Marler, 1976). Variability in call structure is another potential way by which the amount of transmitted information can be increased (Davidson and Wilkinson, 2004; Bouchet et al., 2013; Peckre et al., 2019). Moreover, information entropy or uncertainty is an important indicator used to measure the amount of information in information theory (Freeberg and Lucas, 2012). Typically, the greater the diversity of elements within a particular signaling system, the more potential information or complexity in the signaling system (Freeberg and Lucas, 2012).

Acoustic signaling has been predicted to be the result of a combination of several selective pressures, including the social environment (e.g., the number of group members, group composition, and diversity) (McComb and Semple, 2005; Freeberg et al., 2012b; Pougnault et al., 2022), ecology (e.g., predation, habitat environment) (Ouattara et al., 2009; Ord and Garcia-Porta, 2012), morphology (e.g., body size) (Podos, 2001; Charlton and Reby, 2016), and phylogeny (e.g., phylogenetic constraints) (Thin et al., 2011; Luo et al., 2017). Current research mainly focuses on the driving forces of complex social calls in amphibians, birds, rodents, and non-human primates (Ord and Garcia-Porta, 2012; Peckre et al., 2019). Several hypotheses have been proposed, such as the social complexity hypothesis (Freeberg et al., 2012a), the ecological complexity hypothesis (Ord and Garcia-Porta, 2012), and the neutral hypothesis (Grant and Grant, 2009). Among these, the social complexity hypothesis has received widespread attention from researchers. The social complexity hypothesis suggests that complex animal communication is usually associated with the evolution of a complex society (e.g., as individuals interact more frequently in different contexts, the social signals that regulate these interactions tend to be more diverse) (Freeberg et al., 2012a). Blumstein and Armitage (1997) found that the social complexity index of 22 ground-dwelling squirrel species significantly positively correlated with alarm call repertoire size (Blumstein and Armitage, 1997). Similarly, the species experiencing more uncertain social interactions displayed greater vocal diversity and flexibility in macaques (Rebout et al., 2020).

Sex ratio, an important metric of demographic data, is the ratio of the number of male and female individuals in a population and is one of the most important characteristics that significantly affects the spousal relationship and reproductive potential ability (Kokko and Jennions, 2008; Bookmythe et al., 2017). Polygamous males in nine species of wrens (Troglodytidae) have larger song repertoires compared to monogamous counterparts (Kroodsmma, 1977). However, the sex ratio did not alter the vocal complexity

in Carolina chickadees (*Poecile carolinensis*) (Freeberg, 2006). Whether sex ratio can be used as an indicator of social complexity that affects bird vocal complexity in different species invites further study. In mammals, some studies also suggested the potential influence of sex ratio on vocal complexity. For example, the low number of females in spring increases competition between males and significantly increases the amount and diversity of vocal activity in brown long-eared bats (*Plecotus auritus*) (Furmankiewicz et al., 2013). However, the influence of sex ratio on vocal complexity in mammals also remains unclear.

Bats comprise the second most diverse mammalian order, which are generally gregarious and long-lived. Accordingly, bats have an increased likelihood of social interactions and need to effectively convey more diverse messages (Chaverri et al., 2018). They emit echolocation calls for navigation and localization, as well as highly complex social calls for maintaining social stability (Kanwal et al., 1994; Ma et al., 2006; Kobayasi et al., 2012; Eckenweber and Knörnschild, 2013). Many bat species live in highly clustered populations, and their populations have a complex social structure with dozens to tens of thousands of individuals of different ages, sex, reproductive status, and kinship (Kerth et al., 2011). Therefore, bats serve as an ideal model for testing the social complexity hypotheses, which will ultimately improve our understanding of animal communication (Chaverri et al., 2018). A previous study found a positive relationship between the information content of vocalizations and social group size in 61 Chiroptera species (Knörnschild et al., 2020). However, there is little evidence on whether other aspects of social organization affect social calls that would suggest a relationship between social and vocal complexity in bats.

Several bat species live in fission–fusion societies (Kerth, 2008) in which group dynamics are highly seasonal, and social members interact frequently among different subgroups. In fission–fusion societies, females form summer groups where they give birth and raise their offspring, while males typically live in all-male groups (Ortega, 2016). As a result, a colony consists of multiple social groups that change in sex ratio, group size, and composition (Patriquin et al., 2010; Kerth and Van Schaik, 2012), thereby leading to different social interactions that result in differences in vocal complexity. Because of the unique intraspecies interactions, testing the social complexity hypothesis using bats as a model would likely provide insights into improving our understanding of animal communication.

Populations of the Great Himalayan leaf-nosed bat (*Hipposideros armiger*) have been observed in India and Nepal, central and southeastern China, and in much of peninsular Southeast Asia (Bates et al., 2020). This species typically roosts in caves where hundreds of individuals share day and night roosts (Cheng and Lee, 2004). A previous study found that *H. armiger* has a harem mating system and forms groups that include one male and several females (Yang, 2011). Pregnant females usually give birth to one infant each year between May and early June. The female and infant bats form separate breeding colonies, while the male bats form non-breeding colonies (Chen, 1995). Based on the composition of their colonies, the Himalayan leaf-nosed bats often live in fission–fusion societies in summer (Xiong, 1975; Chen, 1995). Juvenile female bats show higher fidelity to their natal roost than males and bats of other ages (Cheng and Lee, 2004). Moreover, this species is highly gregarious, possessing

active and diverse social vocalizations with 35 distinct syllable types, including 18 simple syllable types and 17 composite types (Lin et al., 2016). They engage in antagonistic interactions daily to defend their day-roost territory through aggressive calls and visually pronounced aggressive displays (Sun et al., 2018). This species clearly exhibits extreme variation in social structure, which makes them excellent subjects for investigating the evolutionary connections between social and vocal complexity.

The goal of this study was to test whether sex ratio affects the complexity of social calls in the Himalayan leaf-nosed bats. We recorded the social calls of three different groups with the same group size but different sex ratios: all-male, all-female, and a mixture of the sexes. The complexity of social calls was measured on multiple levels, including syllables, call sequences, the diversity index (*DI*), and information capacity (ΣH_s). Then, these variables were compared to test whether they significantly differed between groups. We predicted that the mixed group would have the highest vocal complexity, as its members may potentially play more distinct social roles. Additionally, because the complexity of male vocal signals is influenced by sexual selection in many taxa, we also predicted that the all-male group would have higher vocal complexity than the all-female group.

Materials and methods

Study subjects

From July to August 2016, 18 adult *H. armiger* (9 ♀, 9 ♂) were captured from a cave-dwelling population in Shanxi Province, China. The population contained more than 500 individuals by using thermal infrared cameras. Males were considered adult if they had epididymides, enlarged testes, or both; a sealed epiphyseal gap; brown fur; and worn canine cusps (Cheng and Lee, 2002). Females were considered mature if they were pregnant or showed signs of parturition or nursing (i.e., swollen, and elongated nipples,

public nipples, or both) (Racey, 1988). Previous studies found that females gave birth from May to early June (Chen, 1995; Cheng and Lee, 2002). Therefore, the captured females had not given birth or completed lactation after giving birth during the experiment. The bats were captured by using mist nets at the entrance of the cave when the bats flew out of the cave to forage. Captured bats were put in cloth bags and transported to the temporary laboratory near the roosting cave of the bats (a rectangular tent, 2 m × 1.5 m × 1.8 m). The humidity was maintained at ~60%, and the temperature was controlled at ~23°C. To identify different individuals, we used a 4.2 mm-diameter marker ring (Porzana Ltd, Icklesham, UK) to mark the forearm of each bat. Previous studies had shown that marker rings did not alter the behavior of the bats (Kunz and Weise, 2009; Jiang et al., 2017). During the experiment, bats were fed fresh mealworms (*Tenebrio molitor*) with added mineral elements and vitamins and provided with water *ad libitum*. The bats were released in the temporary laboratory and flew freely until they could actively prey on the mealworms and drink water from the dishes on the walls. The acclimatizing process took 3 days.

Data collection

Before the recording experiments, these bats were divided into three groups including the all-male group, the all-female group, and the mixed group, and were placed in three cages (the size of each cage: 80 cm × 60 cm × 70 cm) with a mesh size of 1 cm × 1 cm, respectively. The top of the cage was covered by a cotton cloth to create a dark environment. Each group consisted of six individuals, of which the mixed group consisted of three males and three females. Infrared cameras (HDR-CX 760E; Sony Corp., Tokyo, Japan) and ultrasonic recorders (UltraSoundGate 116; Avisoft Bioacoustics, Berlin, Germany) were arranged in parallel and pointed at the bats to record their behaviors and vocalizations (Figure 1). The distance between the microphone and bats was 1 m in each recording trial to avoid variations in the sound pressure of

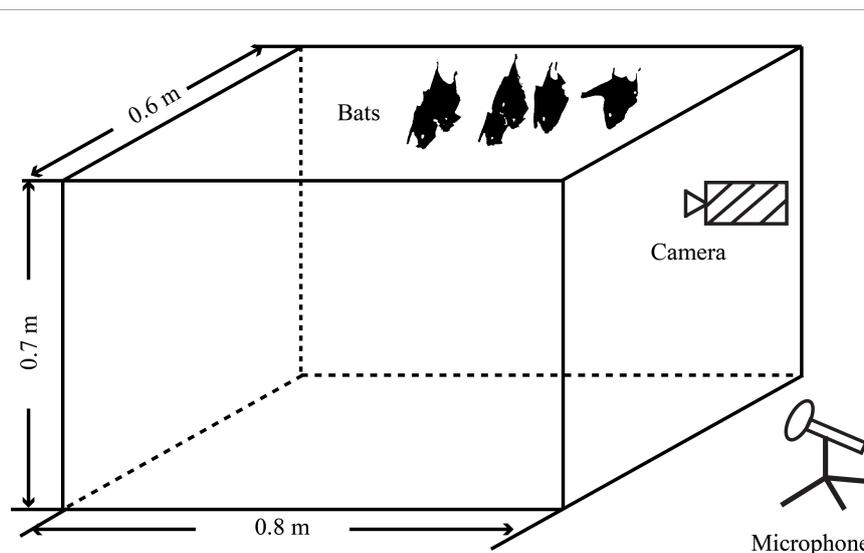


FIGURE 1
Schematic diagram of the bat vocalization sound recordings.

the recorded calls. Sound recordings were set at a sampling rate of 375 kHz and 16 bits resolution. Each recording file was 60 s long. Previous studies have found that this species vocalizes most actively approximately 2 h before they leave the cave to nightly forage and during the early morning hours after they return to the cave from foraging (Lin et al., 2016; Sun et al., 2020). Therefore, recording sessions were scheduled from 19:30 in the evening to 8:30 on the next morning to include the active vocal period of the bats. Each group was recorded for the same amount of time for 10 days until no new syllables were found. After the experiment, the bats were released in their original cave.

Social calls were analyzed using the software Avisoft SASLab Pro (version 5.1; R. Specht, Avisoft Bioacoustics, Berlin, Germany). Behavioral videos were analyzed using Qvod-Player with a resolution of 25 frames/s (version 5.0.80, Shenzhen Qvod Technology Co., Ltd, Guangdong, China). We looped each individual bat, and then recorded the social calls and behaviors of the bats simultaneously. According to our observations, social calls of bats are often accompanied by body vibrations and mouth movements, and the calls are generally audible. Therefore, the individual vocalizations were determined by matching the time of the sound wave and the behavioral video, as the pattern of body or mouth movements on the video corresponded to the pattern of sounds appearing on the real-time spectrogram of the sonograph (Sun et al., 2018; Zhang et al., 2019).

Classification of syllable types

The syllable is the basic unit of social calls. A simple syllable typically consists of a single element, while a composite syllable consists of different elements with no interval between any two elements. In a previous study, Lin et al. (2016) demonstrated the structural diversity of communicative vocalizations in *H. armiger* and classified sounds into 35 distinct syllable types. We classified the types of syllables following the methods proposed by Kanwal et al. (1994) and Lin et al. (2016). In general, composites were named according to the combination of simple syllables without any intervening silence interval (separated by a dash) and abbreviated accordingly. We also defined some new composites that had not been previously described (Supplementary Figures 1–3). Most of the individuals emitted aggressive social calls when they were disturbed by others, either one bat approached another, or potential opponents faced each other, but did not approach (Sun et al., 2018). In addition, the calls in mild behavioral contexts were often emitted individually. Therefore, although temporal overlap occurred frequently in the recordings, there were a considerable number of calls without temporal overlap (approximately 75.34% of the call sequences had no temporal overlap). In our study, only calls with no overlap and a high signal-to-noise ratio (>40 dB) were retained for further analyses. Syllables were classified by visual inspection of the spectrograms using Avisoft-SASLab Pro (version 5.2, R. Specht, Avisoft Bioacoustics, Berlin, Germany) with a fast Fourier transform (FFT: 1024; Hamming window: 75%; frame size: 75% overlap; temporal resolution: 1.024 ms; frequency resolution: 0.244 kHz). We identified sounds based on the maximum frequency, minimum frequency, duration, number of harmonics, noisiness, spectrographic patterns, and temporal composition of constant frequency (CF), frequency modulation

(FM), and noise bursts (NBs). Finally, the syllable types of each individual bat were counted. We calculated the Sorensen index of the same syllables in three groups. The formula is as follows:

$$SI = \frac{2c}{a + b}$$

Where, *SI*: the Sorensen index; *a*, *b*: the number of syllables of the two groups; *c*: The number of syllables shared by the two groups.

Analysis of call sequences

A call sequence usually consists of several syllables (the number of syllables ≥ 2). The interval between syllables is defined as the time from the end of one syllable to the start of the next. We measured the inter-syllable intervals of 5,667 syllables and obtained a distribution graph (Figure 2), which was used as the basis for identifying call sequences. The trough between peaks at an inter-syllable interval of 80 ms was used to divide the call sequences (Figure 2). If the inter-syllable interval between two adjacent syllables was more than 80 ms, the separated call sequences were identified (Figure 3). Call sequences were divided into “Single” (consisting of one syllable, inter-syllable interval > 80 ms), “Repeated” (consisting of single syllable repetition, the number of syllables ≥ 2), and “Combined” sequences (consisting of a variety of different syllable types). We counted the number and proportion of different types of call sequences in the three groups. For the three types of call sequences in each group, we analyzed the proportion of intra-individual variation (the mean of the individual standard deviations of the proportions of the three types of call sequences) and presented the proportion of each type of call sequence versus all call sequences, which includes call sequences more than 1% (Some call sequences have low emitted rates, but the number of types of sequences is shown).

Analysis of vocalization diversity

To estimate the diversity of social vocalizations in bats, we calculated the diversity index following the method of Shannon and Weaver (1949). For each individual, we classified the call sequences as “Single,” “Repeated,” or “Combined” and then computed their occurrence frequency following previously described methods (Bouchet et al., 2013). We calculated the diversity index (*DI*) values at the group and inter-individual levels as follows:

$$DI = \frac{H_i}{H_{i\max}} = \frac{-\sum_{i=1}^n P_i \log_2(P_i)}{\log_2(n)}$$

where H_i max represents the value of all signal types uttered at the same frequency, H_i represents the actual observed values (Bouchet et al., 2013), P_i represents the occurrence frequency of each call sequence, and n represents the number of call sequence types.

Measurement of information capacity

We quantified the potential ability of coding information by measuring information capacity based on the information

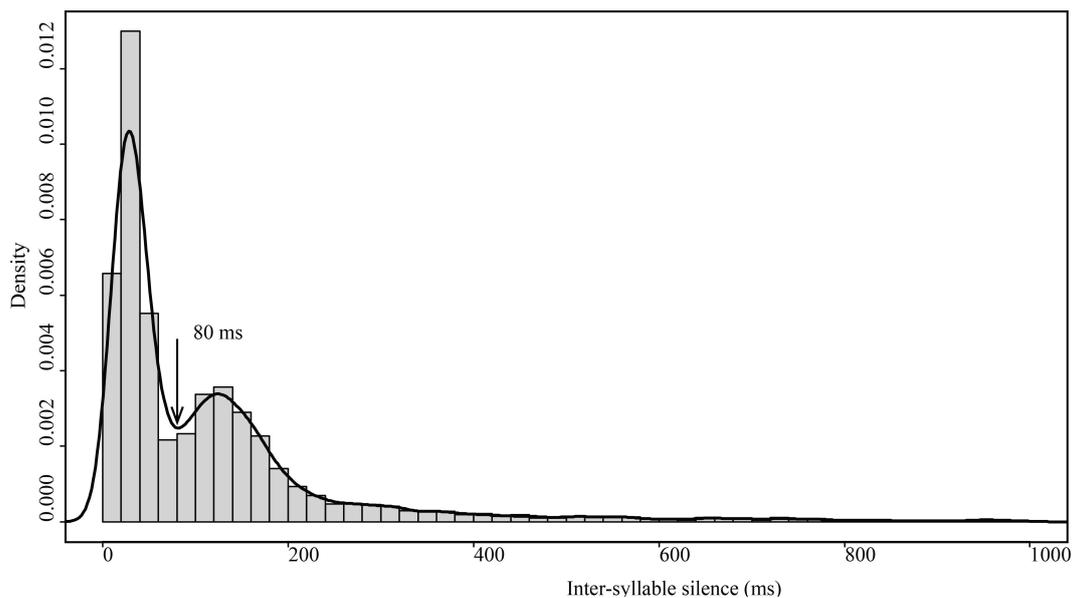


FIGURE 2

The distribution of inter-syllable intervals of *H. armiger* social calls. The solid line represents the smooth curve of the histogram. The arrow indicates the inter-syllable intervals at 80 ms, which was the threshold used to identify call sequences.

theory method (Shannon and Weaver, 1949; Beecher, 1989). The information content of one parameter, H_s , is a standard measure used to quantify individuality (Medvin et al., 1993; Wilkinson, 2003; Blumstein and Munos, 2005; Pollard et al., 2010). This parameter expresses a signal's ability to reduce a receiver's initial uncertainty about the identity of the signaler down to a minimum level (Pollard and Blumstein, 2011). Bent upward frequency modulation (*bUFM*) is the syllable most frequently emitted in an antagonistic context and plays an important role in *H. armiger* territory defense (Sun et al., 2018; Sun et al., 2020). Significant differences of the acoustic parameters of *bUFM* have been observed between individuals, suggesting that *bUFM* may encode discriminable signatures (Sun et al., 2018). Therefore, we selected *bUFM* as the representative syllable type for measuring information capacity. Ten *bUFM* syllables were randomly selected from different call sequences and measured with a standardization of 75% for each individual. Twenty-seven acoustic parameters, including the maximum frequency, minimum frequency, and bandwidth, of the second harmonic *bUFM* syllables were measured (Supplementary Table 1). Then, a principal components analysis (PCA) was conducted to calculate the contribution of these 27 acoustic parameters. We obtained six principal components (PCs) for the all-female and mixed groups and five PCs for the all-male group (Supplementary Table 2). Prior to statistical analysis, we tested the normal distribution of the data. If the data were not normal, we added 10 to the factor scores and then performed a \log_{10} transformation until the data were normally distributed. A one-way analysis of variance (ANOVA) was conducted using the factor scores to obtain the F values ($P < 0.05$). Then, the H_s information was calculated using the following formula (Beecher, 1989; Sebe et al., 2010):

$$H_s = \log_2 \left(\sqrt{\frac{F \times n(k-1)}{k(n-k)}} \right)$$

where F is the ANOVA result, n is the number of syllables, and k is the number of bats. The higher the H_s value, the greater the coding potential of the individual.

Statistical analysis

Kolmogorov-Smirnov tests were used to confirm whether all variables were normally distributed ($P > 0.05$). A one-way ANOVA was used to test whether the total number of call sequences and the number of each call sequences type of "Single," "Repeated," and "Combined" differed among the three groups. Chi-square tests were conducted to compare the proportion of each type of "Single," "Repeated," and "Combined" sequences in the three groups. A one-way ANOVA was used to test significant differences between the diversity index (DI) values across the three groups. The basic sample units of all the ANOVA analysis were individual bats. Fisher's least significant difference (LSD) post-hoc multiple comparison tests were employed to examine whether the diversity index (DI) values significantly differed between any two groups. All statistical analyses were conducted using SPSS version 20.0 (SPSS Inc., Chicago, IL, USA).

Results

A total of 1718 min of sound wave files were obtained from three groups (nine females and nine males). The sounds were divided into syllables, and call sequences were based on the distribution of inter-syllable intervals (Figure 2). We obtained a total of 1,552 call sequences from the all-male group (mean \pm SD: 258.7 ± 136.6), 1,453 from the all-female group (242.2 ± 129.2), and 4,419 from the mixed group (736.5 ± 290.9). Then, the syllable

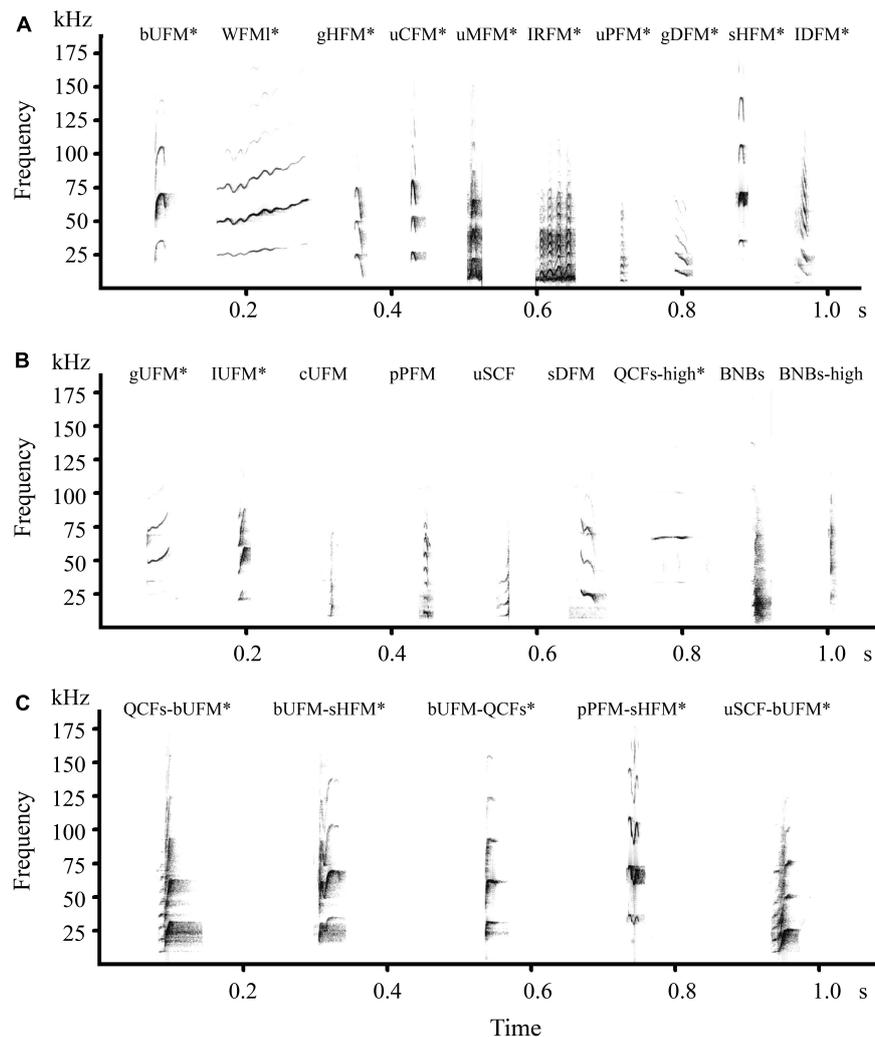


FIGURE 4

Sound spectrograms of syllable types of *Hipposideros armiger*. (A,B) All the single syllables in the vocal repertoire of the three groups; (C) composites shared in the three groups; *Syllable types shared by the three groups. Other composites are shown in the [Supplementary Figures 1–3, Supplementary Table 3](#). bUFM, bent upward FM; WFMI, long duration, wrinkled FM; gHFM, gliding humped FM; uCFM, upward chevron FM; uMFM, upward mexican-hat FM; IRFM, linear rippled FM; uPFM, upward paraboloid FM; gDFM, gliding downward FM; sHFM, single humped FM; IDFM, linear downward FM; gUFM, gliding upward FM; IUFM, linear upward FM; cUFM, checked upward FM; pPFM, plateaued paraboloid FM; uSCF, upward short CF; sDFM, stepped downward FM; QCFs-high, short duration, high-frequency quasi-CF; BNBs, short broadband noise burst; BNBs-high, short broadband, high-frequency noise burst; QCFs-bUFM, quasi CF-bent upward FM; bUFM-sHFM, bent upward FM-single humped FM; bUFM-QCFs, bent upward FM-quasi-CF; pPFM-sHFM, plateaued paraboloid FM-single humped FM; uSCF-bUFM, upward short CF-bent upward FM.

syllables, call sequences, diversity index and information capacity among the three groups with different sex ratios. The results suggest that the sex ratio potentially affects the vocal complexity of *H. armiger*. Most previous studies that investigated the correlation between the vocal complexity and social structure have focused on different social organizations at the interspecies level (Kroodsmá, 1977; Baker, 1984; Bouchet et al., 2013; Rebout et al., 2020). Our study verifies that sex ratio, as a representative metric of social organization, plays an important role in animal communication at the intraspecies level. The study invites future studies on the driving forces of vocal complexity in mammals to consider both common key metrics (e.g., social size and density) and social organization.

Interestingly, our results demonstrated that the all-male group had the highest diversity index values and information capacity of the vocal repertoires, while the mixed group had the lowest

for both variables. This supported that the all-male group emits the most complex social calls. The diversity index (*DI*) represents the uniformity and variation of social vocalization. Our results confirmed that the proportions of the three types of call sequences in the all-male group were more uniform than those of the other groups, where the intra-individual variation values of the proportions of the three types of call sequences were 0.3489 in the mixed group, 0.2759 in the all-female group, and 0.2515 in the all-male group. Along with complex vocalizations, the male bats showed many territorial and aggressive behaviors. Previous studies indicated that bats in a male-male combination exhibited more aggressive and territorial behaviors for territorial competition or to establish a dominance hierarchy, along with a display of diverse and complex vocalizations. For example, *H. armiger* males were observed to use various and multiple vocalizations in antagonistic

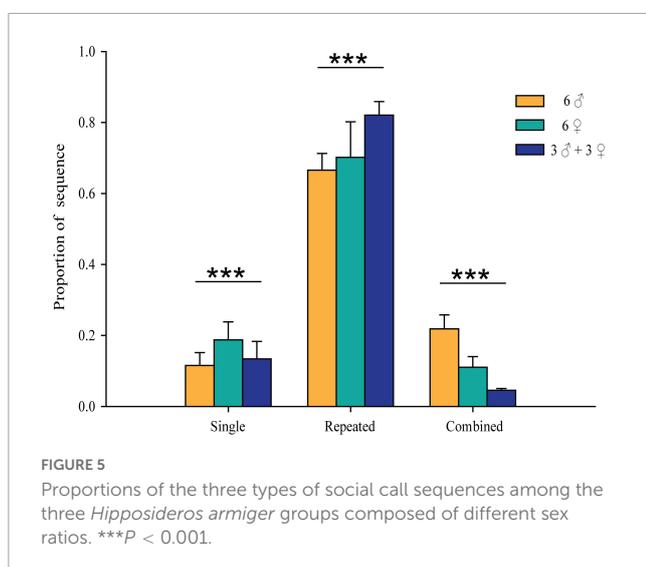
TABLE 1 Number of types of calls sequences of *Hipposideros armiger* in three groups.

	Single sequence	Repeated sequence	Combined sequence	Total
All-male				
Bat1	4	3	18	25
Bat2	3	3	7	13
Bat3	5	3	21	29
Bat4	5	5	11	21
Bat5	4	3	4	11
Bat6	5	5	43	53
Group	14	7	84	105
All-female				
Bat1	2	2	7	11
Bat2	1	5	17	23
Bat3	3	3	28	34
Bat4	3	2	9	14
Bat5	5	2	10	17
Bat6	4	4	13	21
Group	8	7	74	89
Mixed group				
Bat1	5	2	8	15
Bat2	4	4	17	25
Bat3	4	4	12	20
Bat4	4	2	12	18
Bat5	3	2	8	13
Bat6	14	4	37	55
Group	16	7	68	91

In the mixed group, the first three individuals were females and the last three were males.

interactions (Sun et al., 2018). Similarly, Seba’s short-tailed fruit bat (*Carollia perspicillata*) males used different vocalization types with sufficient variation to encode individual signatures during

aggressive displays (Fernandez et al., 2014). These phenomena were also detected in two *Oreobates* species (Akmentins, 2011). In addition, individual signatures of acoustic signals as a type of informational capacity have been studied in several bat species, such as the territorial trills and courtship calls of Seba’s short-tailed bat (*C. perspicillata*) (Fernandez et al., 2014; Knörnschild et al., 2014), the territorial songs of *S. bilineata* (Davidson and Wilkinson, 2002), and the inquiry calls and response calls of Spix’s disk-winged bat (*Thyroptera tricolor*) (Chaverri and Gillam, 2013). In general, the information encoded by acoustic parameters is related with the individual characteristics and emotional state of the sender (Morton, 1977; Morton, 1982; Elie et al., 2011). It was discovered that *bUFM* encoded different information potentials in aggressive circumstances, i.e., *H. armiger* increased the frequency bandwidth but reduced the minimum frequency within the syllable as aggression intensity increased (Sun et al., 2018). Moreover, there is experimental evidence that *bUFM* calls may serve the function of territorial defense (Zhang et al., 2021). In this study, we found that the all-male group had the highest information capacity, and it has been speculated that the emotional state of the vocalizers may play an important role, as the all-male group showed more frequent aggressive behaviors such as boxing and pushing than the other two groups. This is consistent with group membership of



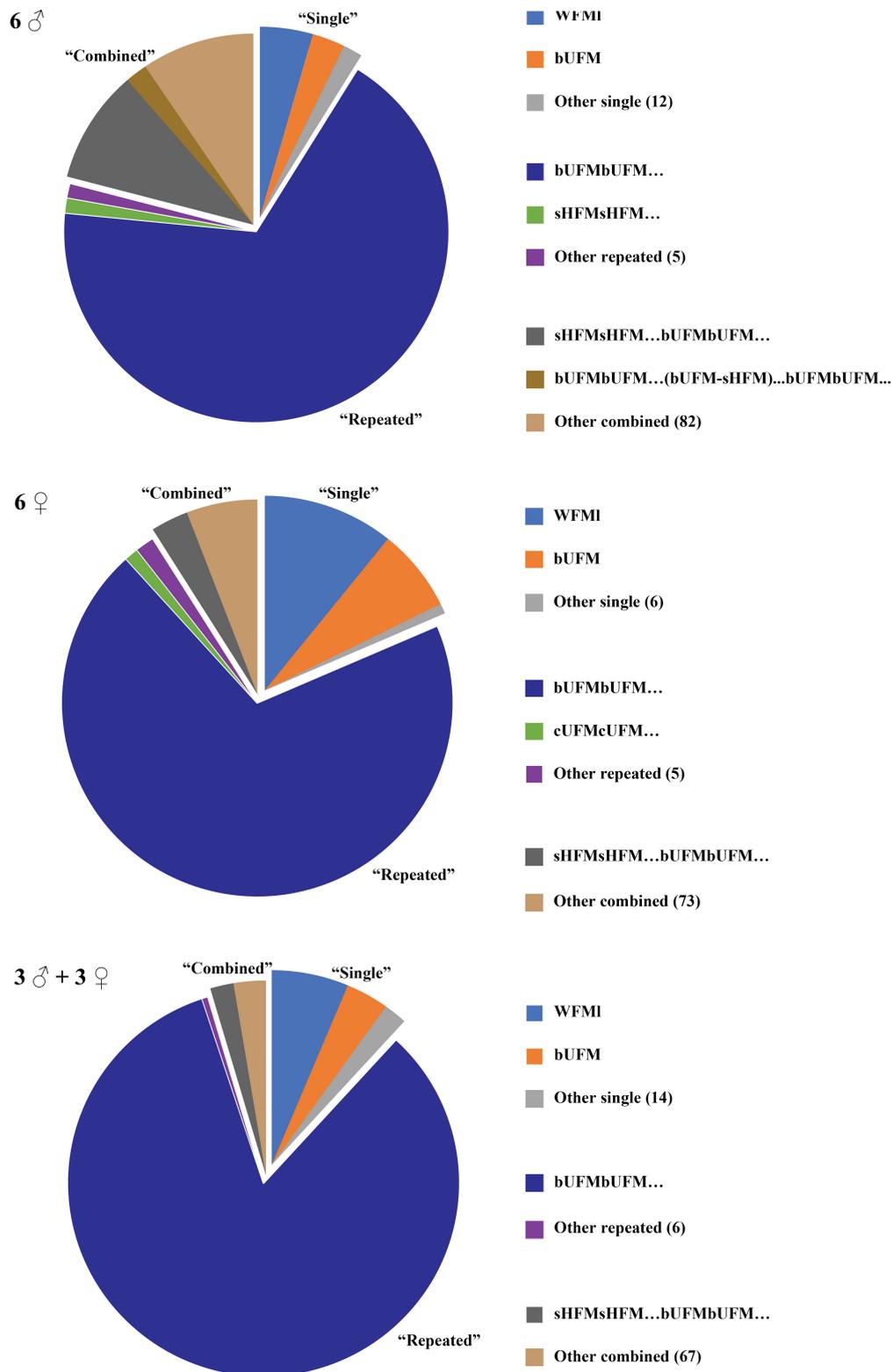
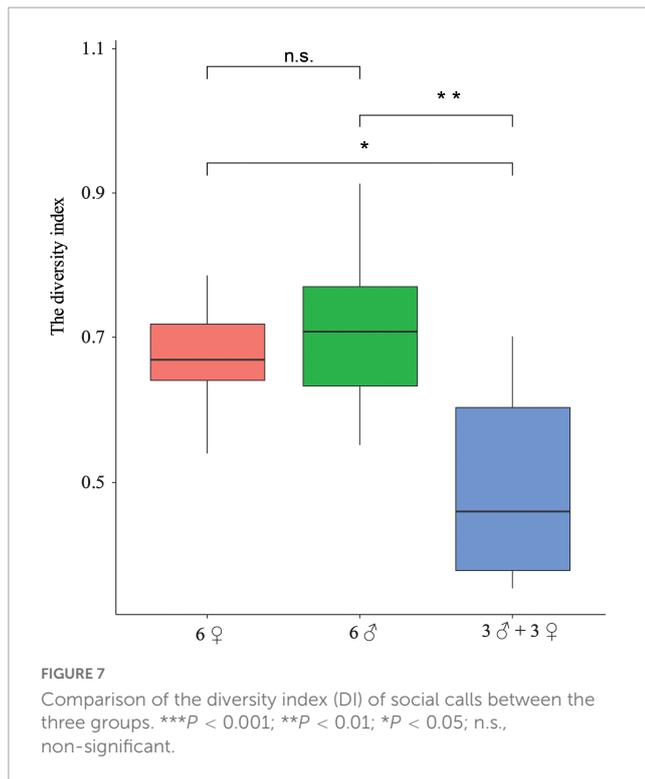


FIGURE 6 Proportion of call sequence types among the three groups. Sequences with occurrence frequencies >1% are represented in the figure. “Other” indicates sequences with frequencies <1%. Numbers in parentheses indicate the number of sequence types.

different conspecific social groups possibly being encoded in the acoustic structure of vocalizations in primates (Toshiaki et al., 2006; Crockford et al., 2010).

Social competition is one of the driving forces of the evolution of vocal complexity. It has been found in animal groups such as mammals (Fernández-Vargas, 2018), birds



(Dalziell and Welbergen, 2016), and lissamphibians (Zhu et al., 2017). In natural groups, competition between males and competition between females can lead to aggressive behavior and may promote complex calls. In this study, the all-female group showed many territorial and aggressive behaviors along with abundant vocalizations as well. In highly clustered bat colonies, females encounter many competitive pressures, including limited habitats and food resources. For example, female Asian particolored bats (*Vespertilio sinensis*) frequently compete for central roost spots in nursery colonies and emit aggressive vocalizations (Zhao et al., 2019). Our results suggested that intense social interactions with complex vocalizations also exist in female Himalayan leaf-nosed bats. The correlation between higher vocal complexity and aggressive levels in the all-male and all-female groups suggest that aggression may facilitate complex social vocalizations, which is consistent with previous studies.

The proportion and number of “Combined” sequences in the all-male group in this study were significantly higher than those in the other groups (Figure 4), suggesting that male bats may have a stronger ability to switch between different syllables and combine more complex social call sequences. This result corresponds with the findings in other taxa, including primates (Arnold and Zuberbühler, 2006; Ouattara et al., 2009; Cäsar et al., 2013), birds (Engesser et al., 2016; Suzuki et al., 2016), and dwarf mongooses (*Helogale parvula*) (Collier et al., 2020), as well as with a previous study that observed “Combined” sequences in greater horseshoe bats (*Rhinolophus ferrumequinum*) that encountered aggressive or distressing circumstances (Zhang et al., 2019). In *H. armiger*, a previous study also found that vocalizations of “Combined” sequences were frequently emitted during antagonistic interactions, such as when a bat was bit or attacked suddenly by another bat (Sun et al., 2018). The

functions of “Combined” vocalizations have been documented in other animal taxa. For example, serrate-legged small treefrogs (*Kurixalus odontotarsus*) produce more compound calls to attract females and suppress rivals (Zhu et al., 2017). Bocon toadfish (*Amphichthys cryptocentrus*) emit compound calls with broadband and tonal components to transmit individual selection-linked information to females (Staaterman et al., 2018). Mountain (*Gorilla beringei beringei*) and western gorillas (*Gorilla gorilla gorilla*) combine acoustic units into compound vocalizations to constitute a form of phonological syntax to transmit more messages (Hedwig et al., 2015). Our study provides an extra potential function of the combinatoriality in animal communication (i.e., “Combined” sequences play important roles in intense social interactions among *H. armiger* males). From the results, we speculate that the syntax may exist in *H. armiger* social vocalizations, but this requires further investigation.

Nevertheless, “Repeated” sequences occurred more frequently in the vocal repertoires of *H. armiger*, where the occurrence frequencies of “Repeated” sequences were 66.58, 70.19, and 82.05% in the all-male, all-female, and mixed groups, respectively. Similar findings have been observed in a broad range of animal taxa, but the function of repeated calls varies across species and contexts, such as the interactive calling of male American green tree frogs (*Hyla cinerea*) and family-specific calls of stripe-backed wrens (*Campylorhynchus nuchalis*) (Klump and Gerhardt, 1992; Price, 1999). Additionally, repeated call sequences of long-finned pilot whales (*Globicephala melas*) were suggested to maintain contact and cohesion, as well as possibly play a role in individual or group identification (Zwamborn and Whitehead, 2017). Single syllable repetitive calls are the most probable sequence form of greater horseshoe bats (*R. ferrumequinum*) under aggressive background (Zhang et al., 2019). Call repetition may increase the possibility of being detected or suggest higher behavioral intensity (Ficken et al., 1994; Moors and Terhune, 2004). In our study, *H. armiger* tended to use “Repeated” sequences in antagonistic interactions. In a previous study, it was discovered that *bUFM* sequences encoded different information potentials in aggressive circumstances (Sun et al., 2018). In aggressive context, repeated calls can increase the intensity of a signal display and may convey stronger emotional states (Payne and Pagel, 1997). Call repetition is a type of redundancy used to reduce the masking of signals from background noise or calls of other individuals (Brumm and Slater, 2006). Therefore, the “Repeated” sequences observed in this study may indicate better co-ordination in radical conflicts to obtain more roosting space during competition, as well as possibly serve as a social signature.

We did not classify specific behavioral context, but we do have some interesting behavioral observations (unpublished observations). For example, under a mild behavioral context, such as sleep awakening and grooming behaviors, pure-tone *WFML* occurred most in the three groups, while *bUFMbUFM*... sequences occurred most in the low-level aggressive behaviors, and multi-syllable combination sequences occurred most in the high-level aggressive behaviors. We assume that the phenomena may follow the motivation-structure hypothesis, although behavioral studies are needed to confirm the social significance of syllables. *WFML* is a pure tone with small amplitude and usually does not elicit activity from other bats, presumably being a soft appeasement call. *bUFM* is the most frequently emitted call, and a previous study suggested

that *bUFM* calls may serve the function of territorial defense (Zhang et al., 2021). Additionally, multiple syllable calls are emitted by bats that have been bitten by another bat in aggressive contexts in *H. armiger* (Lin et al., 2016; Sun et al., 2018), and we speculate that they may indicate intense conflict between individuals.

However, some limitations still exist in the present study. First, there are individual differences in vocal output. Especially in all-male group and mixture group, two male individuals produced more vocalizations than others (Table 1). Some studies have shown that vocal output in animals depends on (1) population density (more individuals not only calling at higher densities but also more frequently) (Martínez and Zuberogoitia, 2003; Nijman, 2007; Laiolo and Tella, 2008); (2) annual cycle stage (with animals calling more frequently during the mating and/or the breeding season) (Zuberogoitia, 2011; Mori et al., 2014); and (3) environmental conditions (e.g., rain and wind (Francis et al., 2011a,b)). In addition, individual biological attributes, such as sex and age, also have important effects on vocalizations, which have been found in birds (Zuberogoitia et al., 2019), bats (Habersetzer and Marimuthu, 1986) and primates (De Gregorio et al., 2021). Furthermore, social attributes could influence the vocal output. The males produce more courtship sounds than losers and show significantly shorter courtship latencies and longer courtship durations in the cichlid fish *Oreochromis mossambicus* (Amorim and Almada, 2005). Male *Saccopteryx bilineata* with a higher reproductive success trend to utter more territorial songs per day (Behr et al., 2006). In this study, the two male individuals with more vocalizations might be the dominant individuals in the groups, but it needs further study. Future research could be conducted to investigate the interactions between males of different social status during the mating season, and more samples are needed to improve the generalizability of the results in future studies.

In addition, the experiments were conducted with artificial experimental design because it is difficult to classify individual calls in a natural population with hundreds of individuals. Social vocalizations were recorded from Himalayan leaf-nosed bats maintained in captive research colonies. Furthermore, we observed two types of aggressive behavior, consistent with previous research (Sun et al., 2018). One is the non-physical contact behavior background, or ritualized radical behavior, which emits many *bUFM* repeated sequences. The second is the aggressive context of physical contact, which produces a lot of multi-syllable combination sequences. With the development of technological equipment, especially some small portable sound recorders, future research could record more natural social calls in the field habitat, which could help us understand the evolution of animal acoustic communication.

Overall, we assessed the vocal complexity of different social organizations of *H. armiger* at the intraspecific level and found that bat groups composed of the same sex produced more complex vocalizations than the mixed sex group. The results suggested that sex ratio as a potential driver of the vocal complexity of bats. Therefore, we suggest that the effects of multiple social factors should be comprehensively considered in social complexity research. Bats are a highly social taxa with many complex and unique social behaviors, the present study provides cues for vocalization research to consider social organization, social structure, and mating and breeding systems to explore and interpret the evolutionary processes of vocal complexity.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding authors.

Ethics statement

This animal study was reviewed and approved by Northeast Animal Research Authority of Northeast Normal University.

Author contributions

HG, TJ, JF, BL, and YL participated in the study design and data analysis. HG, CS, XZ, and LG collected the data in the field and laboratory. HG drafted the manuscript. YL revised the manuscript. All authors read and approved the final version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.955540/full#supplementary-material>

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