

Social influences on territorial signaling in male greater sac-winged bats

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Abstract Acoustic territorial displays are common among birds but comparatively rare among mammals. An exceptionally vocal mammal well-known for its elaborate territorial displays is the polygynous greater sac-winged bat, *Saccopteryx bilineata*. Male *S. bilineata* are often philopatric and establish small territories in their birth colony in which females can roost during the day. During territorial defense, males produce complex territorial songs that are learned through vocal imitation. Territorial songs are mainly produced at dawn and dusk. We studied social influences on male vocal activity and the occurrence of vocal signatures in territorial songs of 27 male *S. bilineata* from 12 different-sized colonies in Panama. Males produced significantly more territorial songs when they had more territorial neighbors or when they had females roosting in their territories, indicating that male vocal activity rises with increasing male–male competition. Territorial songs are multisyllabic vocalizations with low-frequency buzz syllables being most prominent. We found statistical evidence for a pronounced individual signature encoded in the buzz syllables of territorial songs that could facilitate individual recognition among rival neighbors. Additionally, we found a vocal group signature in territorial songs, suggesting that young males may learn territorial songs from more than one tutor male. Resident male *S. bilineata* appear to cooperatively defend their colony against male intruders, making a group signature in territorial songs potentially advantageous.

Keywords Individual signature · Group signature · Territorial song · *Saccopteryx bilineata*

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Introduction

Territoriality is found in all vertebrate taxa (Maher and Lott 2000) and can be defined as the defense of a fixed space that includes resources to exclude potential competitors (Maher and Lott 1995). Territories may be defended to improve food availability and quality, to protect refuges, to monopolize mates, or to avoid high population densities or predation pressure (Maher and Lott 2000). The defense mechanisms vary in intensity; aggressive physical contact between rivals only occurs when signals that define the territory borders have been ignored by an intruder (Gese 2001).

Acoustic territorial defense is a complex system depending on many factors. The influence of ecological factors (e.g., habitat characteristics) is well-studied (e.g., Wiley 1991; Brumm 2004), whereas the influence of social factors on territorial vocalizations has received less attention (Maher and Lott 2000). The increase of potential rivals and females to be defended can enhance the strength of male territorial defense (male rivals: Berger and Cunningham 1991; McElligott and Hayden 1999; Fernandez-Juricic et al. 2001; Cornick and Markowitz 2002; Liu 2004; number of females: Fernandez-Juricic et al. 2001; Kunc and Wolf 2008). Some species produce acoustic territorial signals with an individual signature (Marler and Hobbett 1975; Reby et al. 1999; Bee and Gerhardt 2001; Frommolt et al. 2003; Tripovich et al. 2005) that could facilitate individual recognition among rivals. For species which defend their territory as group or family, a vocal signature encoding group or family affiliation is advantageous (birds: Brown and Farabough 1997; Baker 2004; Radford 2005). In mammals, studies on group-specific vocal signatures in territorial signals are rare, even though several species have been found to defend their territory acoustically as a group (e.g., lions, wolves, howler monkeys). Group-specific vocal signatures in territorial signals can either be caused by genetic relatedness within a group (Mitani 1985) or by vocal convergence of group members (Boughman 1998;

Crockford et al. 2004). Among mammals, species that defend their territories with vocalizations acquired through vocal production learning are exceedingly rare (Janik and Slater 1997; Boughman and Moss 2003). The greater sac-winged bat, *Saccopteryx bilineata*, is an exception to this general pattern (Knörnschild et al. 2010) and provides a remarkably well-suited opportunity to study learned vocal signatures in mammalian territorial vocalizations.

S. bilineata is a common insectivorous bat in the Neotropical lowlands. It prefers well-lit cave entrances, large tree cavities, or the outside walls of trees and buildings as day roosts (Yancey et al. 1998) and forms stable, long-lasting colonies of up to 60 individuals (Bradbury and Emmons 1974). The basic social unit is a harem male with one to eight females; colonies may contain several harem groups. Harem males defend territories of up to 2 m² of vertical roosting surface and try to attract females to settle there (Bradbury and Emmons 1974). Nonharem males which are queuing for access to a territory with females may also be present (Voigt and Streich 2003). Harem males do not have exclusive reproductive access to the females of their harem; however, harem holders have a higher reproductive success than nonharem males (Heckel et al. 1999). Given that females are larger than males (Bradbury and Emmons 1974) and that males are not able to physically control them, there is a high potential for female choice (Heckel et al. 1999; Heckel and von Helversen 2003; Nagy et al. 2007; Voigt et al. 2008). Both males and females show a high level of fidelity to their colony and even their particular roosting spot within (Bradbury and Emmons 1974; Tannenbaum 1975). Adult bats maintain a minimum distance of 5–8 cm to their conspecifics (Bradbury and Emmons 1974; Tannenbaum 1975). Young females disperse from their natal colonies before they become reproductively active (Nagy et al. 2007). Many young males, however, are philopatric (Nagy et al. 2007) and queue for harem access in their natal colony (Voigt and Streich 2003). Hence, males from the same colony descend from only a few patrines (Nagy et al. 2007). Resident males appear to cooperatively defend their colony against unrelated intruders (Nagy et al. 2012).

Males produce complex territorial songs when returning from their foraging flights at dawn and before leaving their territories at dusk (Bradbury and Emmons 1974; Tannenbaum 1975; Davidson and Wilkinson 2004; Behr and von Helversen 2004). As females leave the roost site earlier in the evening and return later in the morning than the males, the songs are mainly produced when there are no females around (Behr and von Helversen 2004; Behr et al. 2009), suggesting that territorial songs are primarily signals to potential rivals rather than mates. Territorial defense is crucial for harem males to gain access to potential mates; territorial song activity of harem males is positively correlated with their reproductive success (Behr et al. 2006). Playback experiments revealed that harem males perceive low-frequency territorial songs as more of a

threat than high-frequency territorial songs and respond more aggressively to the former (Behr et al. 2009). It is possible that harem males are able to distinguish their rivals individually based on territorial songs; however, a previous study found only moderate statistical evidence for an individual signature in territorial songs (Behr et al. 2006; see also Davidson and Wilkinson 2002). The potential occurrence of a group signature in territorial songs has not been investigated yet. Moreover, it is unclear to what extent male singing activity is influenced by social factors such as the number of potential rivals and mates, the social status of the singer (i.e., harem male or nonharem male), or the stability of the colony composition. An earlier study found that males produced more territorial songs when more rivals, but not more harem females, were present (Behr et al. 2009), but this conclusion was weakened by the low sample size.

In this study, we first investigated whether male singing activity was influenced by social factors associated with male–male competition, namely, the number of potential rivals, the number of females in the respective territories, the stability of the colony composition, and the social status of the males (harem male or nonharem male). We hypothesized that males would produce more territorial songs when they had more to lose, i.e., when they had more rivals and access to more females. Accordingly, we expected harem males to produce more territorial songs than nonharem males. Moreover, we hypothesized that males from unstable colonies would be more vocally active than males from colonies with a stable composition of individuals. Secondly, we reassessed the strength of the individual signature in territorial songs and investigated in which syllable type the vocal signature was encoded. Thirdly, we studied whether territorial songs carried a group signature. We hypothesized the existence of a vocal group signature because pups learn territorial songs by imitating a tutor male from the same colony (Knörnschild et al. 2010) and because males may cooperate to defend their colony against unrelated intruders (Nagy et al. 2012), making an acoustic group signature both likely and potentially advantageous.

Methods

Study site, period, and animals

All data were collected in April 2010, March to May 2011, and July 2011 on Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute. The 15.6-km² island is located in the artificial Gatun Lake, Panamá (9°9'17" N, 79°51'53" W; 25–165 m above sea level) that was created during the construction of the Panamá Canal and forms part of the Barro Colorado Natural Monument (54 km² in total). BCI is covered by a

semievergreen, moist tropical lowland forest (Leigh 1999) and supports a healthy population of *S. bilineata*. We worked with 27 *S. bilineata* males from 12 different colonies. One colony was roosting in a hollow tree (*Dipteryx oleifera*), the rest were roosting on the outside walls of buildings belonging to the field station. Fifteen males were harem males defending a territory with roosting females, whereas 8 males were roosting without female conspecifics in their territories (i.e., nonharem males). The social status of the remaining four males was unknown. The bats were caught with mist nets (Ultrathin Mist Nets M-14; Ecotone, Gdynia, Poland) and banded with split plastic rings on their forearms (A.C. Hughes, size XCL), which makes them individually discernible from a distance. The banding procedure has been established since 1996 (for details, see Heckel et al. 1999) and, to our knowledge, has no negative effects on the bats' behavior or health.

We conducted a daily diurnal census to obtain data on the social background of the males, i.e., social status (harem male or nonharem male), number of females in the territory, number of male rivals in the colony, and colony stability (stable vs. unstable). To document nocturnal territorial behavior, we conducted six night censuses. We checked 11 colonies that were included in our daily diurnal census for the presence of bats once an hour from sunset to sunrise (7:00 pm to 5:00 am; 10–11 checks per colony and night). When bats were present, we counted them and tried to identify the banded bats with the aid of a camera and a dimmed flashlight. Due to the localization of most day roosts and the daily census visits, the animals were habituated to humans, enabling us to make recordings and observations under undisturbed field conditions.

Sound recording and analysis

Recordings and observations were made in the main vocal activity period of the day, about 1 h after dawn and before dusk. To assess male vocal activity, we observed each of 22 males (14 harem males and 8 nonharem males) at least two times in the morning and two times in the evening and counted every territorial song they emitted during a 30-min observation period (the first 30 min after entering the roost in the morning and the last 30 min before flying out in the evening). For the song structure analysis, we recorded territorial songs of 18 males (16 harem males and 2 nonharem males) during the main activity periods at dawn and dusk. All songs included in the analysis could be attributed to one certain male by simultaneous behavioral observations. In total, 136 territorial songs were recorded (4–10 songs per male). Songs were recorded on two to five different days for each male to minimize the potential effect of song similarity within the same day.

The recording equipment permitted high-quality ultrasonic recordings (500 kHz sample rate and 16 bit depth

resolution). We used an ultrasonic microphone (Avisoft USG 116Hme with condenser microphone CM16; frequency range, 1–200 kHz) connected to a laptop computer (JVC, MP-XP741DE) running the software Avisoft-Recorder v4.2 (R. Specht, Avisoft Bioacoustics, Berlin, Germany). The software allowed us to monitor the spectrograms of our sound recordings in the field. Acoustic analyses of the songs were performed with the software Avisoft-SASLab Pro v5.1 (R. Specht, Avisoft Bioacoustics, Berlin, Germany). Spectrograms were generated using a 1,024-point FFT and a Hamming window with 87.5 % overlap, which resulted in a frequency resolution of 488 Hz and a time resolution of 0.256 ms.

Territorial songs are social vocalizations with a complex structure; they consist of different syllables that gradually merge from one syllable type into the other (Fig. 1; see also Behr and von Helversen 2004; Behr et al. 2006, 2009). We defined the smallest unit (“syllable”) as a vocalization bout surrounded by silence, following Behr and von Helversen (2004). Although syllables were the smallest unit, we divided some syllables into syllable parts for analysis if the syllable was composed of two different acoustical structures that were not separated by silence (e.g., a noisy and a tonal part; for details on syllable terminology, see Knörnschild and von Helversen 2008). We visually classified the territorial song syllables into five different syllable types that were combined into three different syllable categories: variable start syllables (VS; consisting only of one syllable type with the same name), variable tonal syllables (VT; consisting of the syllable types “tonal” and “trill”), and buzz syllables (B; consisting of the syllable types “short buzzes” and “long buzzes”). Both short and long buzzes were composed of a noisy (BN) and a tonal part (BT) and, optionally, of a prefix (BP) (Fig. 2). Our classification was based on the acoustical structure of a syllable as well as its time of appearance in the song. To a large extent, our classification follows the classification established by Behr and colleagues (minor differences to Behr et al. 2006: “noise bursts” were never recorded in this study, BP was added as a new syllable part, VS in our study correspond to “short tonal,” and VT in our study corresponds partly to “inverted V” and “trill” in the study of Behr et al. 2006).

For each syllable (or, in the case of buzz syllables, syllable part), we measured three temporal parameters (duration, interval between successive syllables, and time span from start to maximum amplitude), one waveform parameter (energy as $1 \text{ V}^2\text{s}$) and five spectrum-based parameters (peak frequency, minimum and maximum frequencies [–15 dB relative to the peak frequency of the signal], bandwidth, and entropy). The five spectrum-based parameters were averaged over the entire syllable and measured at six points distributed equally over each syllable (start, end, and four intermediate locations). Thus, we measured 39 acoustic parameters per syllable. We

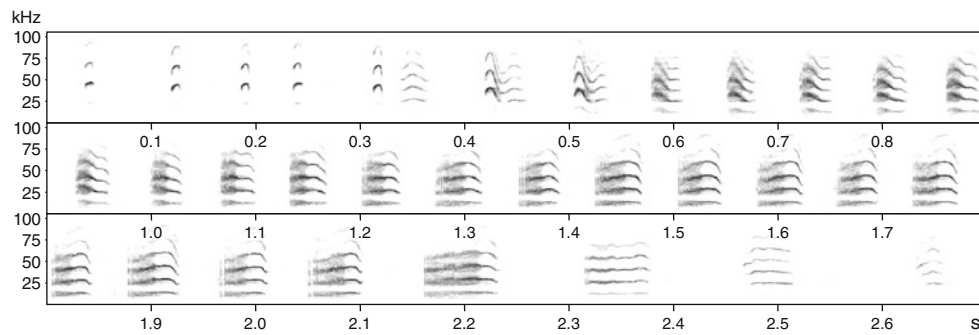


Fig. 1 Territorial song of a male *S. bilineata*. Spectrograms plot frequency as a function of time and were generated using a 1,024-point FFT and a Hamming window with 87.5 % overlap. A territorial song starts with variable syllables (VS; 0–0.55 s), followed by buzz syllables

without prefix (BN and BT; short buzz syllables, 0.55–1.25 s; long buzz syllables, 1.25–2.25 s), and finally some variable tonal syllables (VT; 2.3–2.65 s)

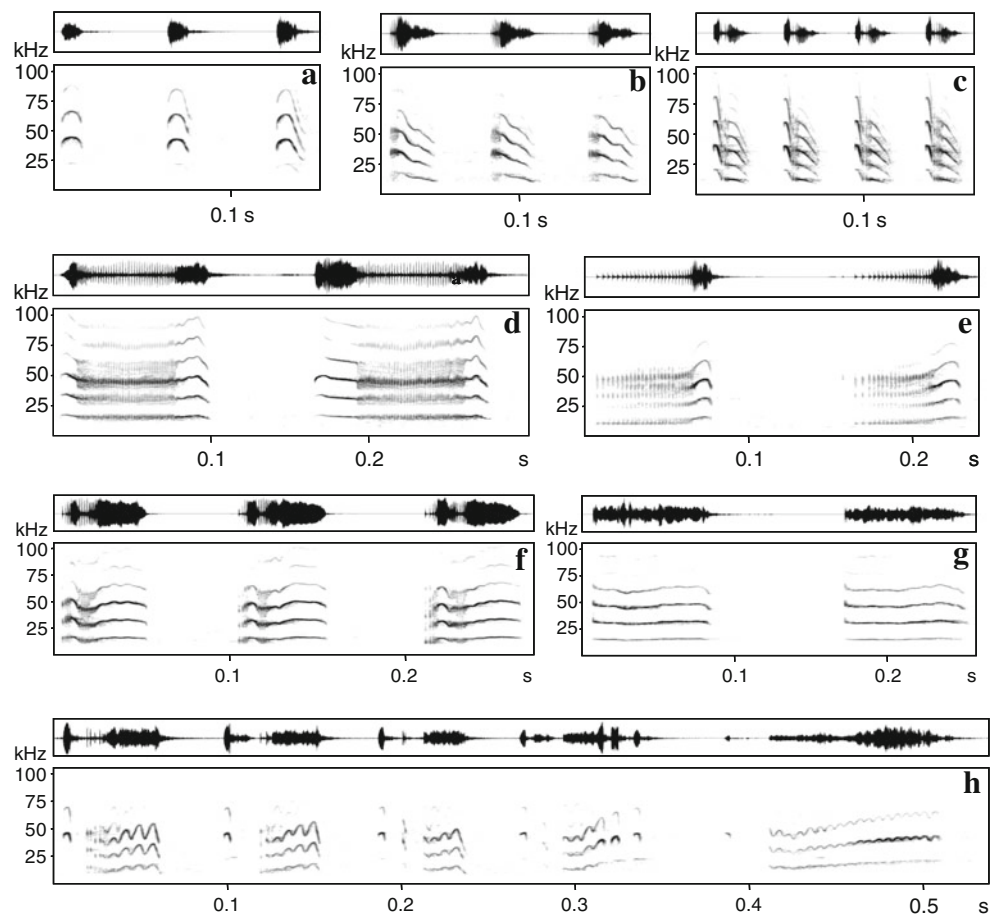
measured all spectrum-based parameters in the harmonic with the highest recording quality and subsequently recalculated all measurements for the first harmonic; this harmonic normally had the highest sound pressure level. Furthermore, we gathered some general data from each song: mean peak frequency of all buzz syllables, loudest harmonic in the entire song, total song length, total number of syllables, and song complexity (based on a rating system from 1 to 7 points; 1 point each for the presence of different syllable types or parts, 1 point for

exceptionally long and pulsed buzz syllables, and finally, 1 point for songs with an abnormal composition of syllable types).

Statistical methods

For the statistical analysis, we calculated the mean values for each measured parameter per syllable type per song. Values for syllable types belonging to the same syllable category

Fig. 2 All different syllable types uttered by male *S. bilineata* in territorial songs. Oscillograms plot changes in voltage over time. Spectrograms plot frequency as a function of time and were generated using a 1,024-point FFT and a Hamming window with 87.5 % overlap. **a** Variable start syllable, **b** short buzz, **c** short buzz with prefix, **d** long buzz with prefix, **e** long buzz, **f** connected syllable: buzz–tonal–buzz–tonal, **g** variable tonal, **h** trill



were pooled. The mean acoustical parameters were combined into principal components (PCs) to obtain fewer and uncorrelated variables using principal component analyses (PCA) with varimax rotation. We performed separate PCA for general song data and different syllable categories (and, in the case of buzz syllables, syllable parts) to fulfill the Kaiser–Meyer–Olkin (KMO) and Bartlett’s test criteria. KMO measures sampling adequacy and is an index that we used together with Bartlett’s test to examine the appropriateness of our factor analysis. Only PCs with eigenvalues >1 were selected (general song data: three PCs explaining 78 % of data variance; VS syllables: six PCs explaining 88 % of data variance; BP syllables: five PCs explaining 91 % of data variance; BN syllables: six PCs explaining 89 % of data variance; BT syllables: five PCs explaining 90 % of data variance; VT syllables: seven PCs explaining 87 % of data variance).

To find the syllable category that encodes the most information about individuality, we reduced our original data set and included only the PCs for BN and BT syllables and for the general song data, thereby reducing the number of independent variables from 32 to 14 PCs (reduced data set I). In a second step (reduced data set II), we did not use the mean acoustic parameters of all buzz syllables, but a reduced data set consisting of the acoustic parameters of the first (buzz 1), middle (buzz 2), and last (buzz 3) buzz syllable of a song. To make both reduced data sets comparable, we extracted the same total amount of PCs as for the reduced data set I (buzz 1 syllables: three PCs explaining 57 % of data variance; buzz 2 syllables: five PCs explaining 65 % of data variance; buzz 3 syllables: three PCs explaining 54 % of data variance). We also included the 3 PCs for the general song data, adding up to 14 PCs as independent variables for the reduced data set II.

Statistical analyses were conducted in STATISTICA v10.0 (StatSoft Europe GmbH), SPSS v17.0 (SPSS Statistics), and R v2.10.0 (R Development Core Team 2008). Normal distribution of these data was assessed using Kolmogorov–Smirnov tests. We used paired-sample *t* tests to compare morning and evening song activities between males. To analyze the pattern of song production during high-activity periods, we divided the activity period into six sections at 5 min and calculated the song rate per minute for each section and bat. With this data, we calculated a repeated-measures analysis of variance (ANOVA) to compare morning and evening activity patterns.

Furthermore, we investigated the influence of social factors (number of females in the territory, number of male rivals in the colony, mean colony size, and colony stability) on the production rate and acoustic structure of territorial songs. The individual male song rate equaled the number of territorial songs each male produced per minute and was termed “male vocal activity.” We used multiple regressions to test for a relation between male vocal activity and the two

metric social factors (number of females in the territory and number of male rivals in the colony). We used an independent-sample *t* test to test for differences in vocal activity between males from stable and unstable colonies and between harem males and nonharem males. Sequential Bonferroni corrections were applied following Holm (1979). Additionally, we conducted a multivariate analysis of variance (MANOVA) with seven dependent variables (mean peak frequency of buzz syllables, loudest harmonic, total song length, total number of syllables, song complexity, and the first PC derived from the acoustic parameters of BN and BT) and two covariates (number of harem females and number of male rivals) to test for an effect of social factors on the acoustic song parameters.

To test for an individual signature in territorial songs, we performed a discriminant function analysis (DFA with cross-validation). We performed a separate DFA on all three data sets (original data set, reduced data set I, and reduced data set II) to narrow down the location of the individual signature. We conducted one-tailed binomial tests (following Mundry and Sommer 2007) to investigate whether the classifications obtained by the respective DFAs were better than random classifications. To ascertain whether there was a reduced classification success due to information loss for the reduced data sets, we calculated a one-factorial ANOVA to compare correct classifications between all three data sets.

To test for a group signature in territorial songs, we calculated mean PCs for each male (thus avoiding the use of multiple data points from the same male) and used them in a DFA (with cross-validation) that assigned males to their respective social groups. We included data from 16 males belonging to 5 different social groups; 2 males that were the sole representatives of their respective social group were excluded from the analysis (male #1 and #6). Mean PCs were calculated separately for all three data sets. We used a one-tailed binomial test (following Mundry and Sommer 2007) to test whether the classification success obtained by the DFAs was better than expected for a random classification.

Cumulative data on the nocturnal presence of individual males in their territories was obtained over each census night and subsequently averaged per male. We used an independent-samples *t* test to compare the nocturnal presence of harem and nonharem males in their respective territories.

Results

Diurnal male vocal activity pattern

The temporal distribution of diurnal territorial songs was not random but clumped in a main activity period at dawn and

dusk. However, there was no significant difference between dawn and dusk song activity for the 22 males we monitored (t test for paired samples, $t_{21}=0.184$, $P=0.855$). Therefore, we used the pooled activity data of dawn and dusk observations for further analyses.

When males arrived at the roost in the morning, they immediately started to sing. Therefore, the peak of male singing activity occurred during the first time section of our observation period. Contrary to this, song activity in the evening was peaking in the last time section of our observation period because males had their highest singing activity right before they flew out. Song activity varied significantly across the 30-min observation period (repeated-measures ANOVA; time: $F_{5,210}=6.957$, $P<0.001$, $\lambda^2=0.142$; dawn/dusk: $F_{1,42}=0.197$, $P=0.659$, $\lambda^2=0.005$; time \times dawn/dusk: $F_{5,210}=27.184$, $P<0.001$, $\lambda^2=0.393$; Fig. 3), indicating that the males had the highest singing activity when the females had not yet arrived in the colony or when they had already left.

Influence of social factors on male vocal activity

Harem males showed a significantly higher singing activity than nonharem males (independent-samples t test: $t_{21}=3.009$, $P=0.007$, adjusted $\alpha=0.025$; 14 harem males and 8 nonharem males included). Males from colonies which were unstable in their composition over time had a tendency to sing more than males in colonies with a stable composition (independent-samples t test: $t_{21}=1.860$, $P=0.078$, adjusted $\alpha=0.05$; 17 stable and 5 unstable colonies included). Male vocal activity increased significantly with increasing numbers of male rivals and harem females (multiple regression: $F_{2,19}=17.395$, $P<0.0001$, $r^2=0.647$; males: $t=4.467$, $P<0.0001$, $\beta=0.615$; females: $t=3.170$, $P=0.005$, $\beta=0.437$). The augmenting effect of harem female numbers on male vocal activity was mainly caused by the fact that the less vocal nonharem males had no females. When analyzing harem males alone, vocal activity increased significantly with the number of male rivals but not harem females

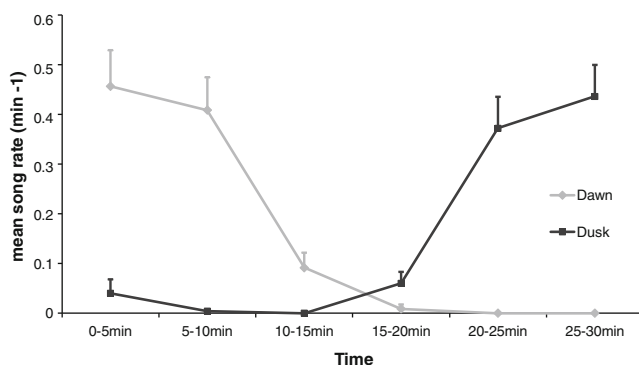


Fig. 3 Song activity patterns of male *S. bilineata* at dawn and dusk. Means \pm SE are shown

(multiple regression: $F_{2,11}=3.453$, $P=0.069$, $r^2=0.386$; males: $t=2.597$, $P=0.025$, $\beta=0.653$; females: $t=1.258$, $P=0.234$, $\beta=0.316$), suggesting that not the actual number of females has an augmenting effect on male vocal activity but whether there are females present or not. Taken together, male vocal activity was influenced by their respective social circumstances. When there was intense male–male competition (indicated by many male rivals and own females to guard and maybe as well by an instable colony composition), males showed higher singing activity than during low male–male competition.

The number of male rivals or own harem females did not have a significant effect on territorial song structure (MANOVA; male rivals: $F_{7,5}=0.732$, $P=0.659$; females: $F_{7,5}=0.373$, $P=0.884$).

Territorial song structure

We classified three syllable categories in territorial songs for our analysis (Fig. 2): variable start syllables (VS), buzz syllables (B), and variable tonal syllables (VT). A song normally began with variable start syllables (VS). However, a territorial song could also begin directly with buzz syllables (B), the most prominent and characteristic syllable category in territorial songs. Buzz syllables appeared in every territorial song and accounted for 62 % of all measured syllables, making them the most prominent syllable type (Table 1). Variable tonal syllables (VT), the third syllable category, consisted of the syllable types “trills” and “variable tonal,” both of which could be found in the middle or at the end of a song (Fig. 2).

Individual and group signature

Territorial songs encoded an individual signature. A DFA performed on the original data set classified 98.59 % (no validation) or 57.35 % (cross-validation) of territorial songs to the correct male that produced them. The correct classification obtained by DFAs was better than random for all three data sets (one-tailed binomial tests: $P<0.0001$ for all three data sets; see Table 2). Regarding the amount of correctly classified territorial songs, there was no significant difference between the three data sets (ANOVA; $F_{2,16}=0.88$, $P=0.42$), indicating that the individual signature was located in the series of buzz syllables at the end of territorial songs (reduced data set I) and that sufficient information for individual identification was present even in only three buzz syllables selected from the whole series (reduced data set II).

Harem males that roosted within earshot of one another (i.e., belonged to the same social group) exhibited a group signature in their territorial songs (Fig. 4). A DFA performed on the original data set (mean values for each of 16 males) classified 100 % (no validation) or 75 % of males (cross-validation) to the correct social group they were

Table 1 Number of measured syllables per syllable category and syllable type/part in 136 territorial songs of 18 *S. bilineata* males

| Syllable category | Syllable type/part | Number | Percent |
|-------------------------------|---|--------|---------|
| Variable start syllables (VS) | Variable start syllable | 496 | 17 |
| Buzz syllables (B) | Prefix part (BP) of short or long buzz | 432 | 14 |
| Buzz syllables (B) | Short buzz with noisy part (BN) and tonal part (BT) | 1,077 | 36 |
| Buzz syllables (B) | Long buzz with noisy part (BN) and tonal part (BT) | 779 | 26 |
| Variable tonal syllables (VT) | Variable tonal | 174 | 6 |
| Variable tonal syllables (VT) | Trill | 23 | 1 |

associated with. A lower classification success was obtained when performing a DFA with the reduced data sets I and II (see Table 2). The classification success obtained by the DFAs was better than random for the original data set and the reduced data set I but not for the reduced data set II (one-tailed binomial test; original data set: $P < 0.0001$; reduced data set I: $P = 0.0267$; reduced data set II: $P = 0.0817$; random correct classification was 20 % for each of the five social groups; see Table 2). Therefore, we cannot definitely pinpoint the location of the group signature in territorial songs.

Nocturnal territorial behavior

During all night censuses, we found some bats in their day roosts. Right after sunrise, there were only very few bats present (2.2 % of mean colony size), but during the night the number of roosting bats increased (up to 19.2 % of mean colony size at 12 pm). Between 2:00 and 3:00 am, the number started to decrease again until 5:00 am (right before sunrise) when almost no bats were present in the roosts anymore (1.8 % of mean colony size).

Altogether, we could identify 40 bats; 16 harem males that were sitting exclusively in their territories, 13 nonharem males, and 11 others (females and pups), all of which were found in the same territories as during the day. Some harem males appeared to remain in their territory almost all night long. For example, one banded and identified harem male was on average present at 7.75 of 11 census points during the night. In contrast, the nonharem male from the same

roost was on average only present at 3.25 census points throughout the night. In general, harem males spent significantly more time in their respective territories during the night than nonharem males (independent-samples t test: $t_{26} = 5.274$, $P < 0.0001$). We could never directly observe any obvious territorial disputes, even though the continued presence of harem males in their territories during the night suggests a form of territorial defense. However, we heard territorial songs at irregular intervals throughout the night and especially during the hours of high bat presence in the roosts.

Discussion

The vocal activity of *S. bilineata* males was distinctly influenced by social factors. The production rate of territorial songs increased significantly with increasing numbers of male rivals and the presence of females in a male's territory, indicating that male vocal activity rises with increasing male–male competition. This finding is in concordance with studies on other taxa (birds: Woodward 1997; Liu 2004; Kunc et al. 2007; sea lions: Fernandez-Juricic et al. 2001; deer: McElligott and Hayden 1999; bison: Berger and Cunningham 1991) and with the prediction of McGregor and Peake (2000) that the social environment has a major influence on communication behavior. Our results are partly consistent with an earlier study on *S. bilineata* (Behr et al. 2009) which found that the number of male rivals but not

Table 2 DFA classification success illustrating individual and group signatures (with three data sets differing in the degree of data reduction) in territorial songs of male *S. bilineata*

| Discriminant function analyses | Mean classification success [%] | | | Random classification success [%] |
|---|---------------------------------|--------------------|---------------------|-----------------------------------|
| | Original data set | Reduced data set I | Reduced data set II | |
| Individual signature [no validation] | 98.59 | 80.28 | 78.87 | 5.56 |
| Individual signature [cross-validation] | 57.35 | 51.47 | 50.74 | 5.56 |
| Group signature [no validation] | 100.00 | 100.00 | 100.00 | 20.00 |
| Group signature [cross-validation] | 75.00 | 43.80 | 37.50 | 20.00 |

For the individual signature, 18 males were included in the DFA. For the group signature, 16 males from 5 social groups were included in the DFA. Validation was obtained by “leave-one-out cross-validation”

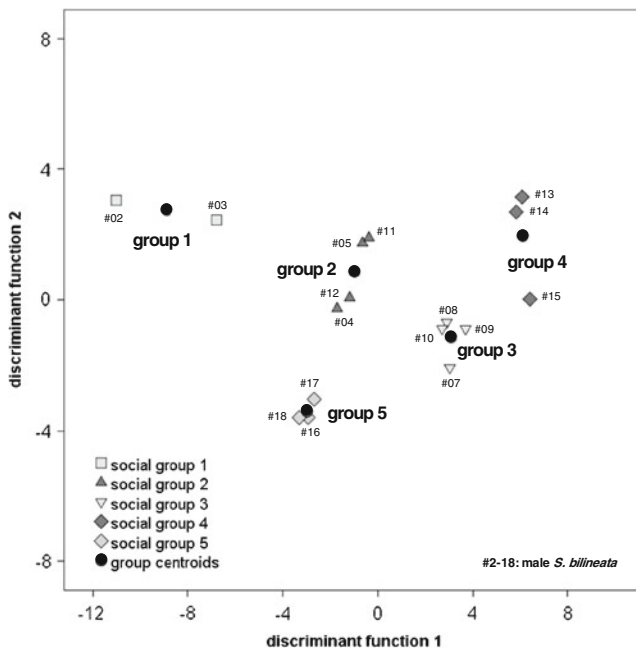


Fig. 4 Group signature in territorial songs of 16 male *S. bilineata* from 5 different social groups. The first two discriminant functions define a signal space in which the relative location of each male is depicted. Males with similar territorial songs cluster together

the presence of females in a territory had a positive effect on male vocal activity. The observed differences between the two studies are probably caused by the different sample sizes (7 harem males and 5 nonharem males in Behr et al. 2009, 14 harem males and 8 nonharem males in our study). Our study provides the first unambiguous evidence that increasing male–male competition augments male vocal activity in bats.

Territorial songs of *S. bilineata* were individually distinct and most signature information was encoded in the conspicuous buzz syllables at the end of territorial songs. Buzz syllables were the most frequent syllable type in territorial songs. The individual signature in territorial songs may enable *S. bilineata* males to individually recognize their rivals or to distinguish between neighbors and strangers. Individual signatures in territorial songs could also facilitate mate recognition in *S. bilineata*. Females that eavesdrop on aggressive male–male interactions must distinguish between the rivals if they want to base their mate choice decisions on the outcome of vocal combats (Fernandez-Juricic et al. 1999, 2001).

We found compelling evidence for a group signature in territorial songs. Vocal similarities between philopatric and, therefore, often related *S. bilineata* males (Nagy et al. 2007) are to be expected; however, our results may also indicate that young males imitate territorial songs not only from the harem male they grow up with (Knörnschild et al. 2010) but also from other males belonging to their colony. It is possible that young bats are attracted by aggressive male–male interactions between adult *S. bilineata* during their vocal

learning phase. This “social eavesdropping hypothesis” (sensu Beecher et al. 2007) has been proposed for vocal production learning in other taxa (song sparrows: Beecher et al. 2007; Templeton et al. 2010; humans: Oshimatakane 1988; Akhtar et al. 2001). Our nocturnal observations revealed that harem males spent considerable time in their territory at night and produced territorial songs. Thus, young males probably have ample opportunities during the day and at night to eavesdrop on male territorial songs and gain experience by observing aggressive male–male interactions. An acoustic group signature is potentially advantageous in *S. bilineata* because males appear to cooperatively defend their colony against unrelated intruders (Nagy et al. 2012).

Our study confirms earlier observations on nocturnal male territorial behavior in *S. bilineata* (Tannenbaum 1975, which was the only study conducted in Panama up to now). Numerous other previous studies on *S. bilineata*, conducted in Costa Rica or in Trinidad (Voigt et al. 2008; Davidson and Wilkinson 2002, 2004), have never reported regular nocturnal presence of harem males in their territories (for an overview, see Voigt et al. 2008). The nocturnal presence of Panamanian *S. bilineata* at the day roost could be a local adaptation caused by the high population density at our study site. It is possible that high population densities result in increased male–male competition which, in turn, might make nightly territorial defense mandatory. This hypothesis could be tested with further studies on Panamanian colonies that are located in areas with lower population densities. Alternatively, *S. bilineata* could afford to return to their day roosts at night during times of high food availability.

Our study found differences in syllable usage between *S. bilineata* colonies from Panama and Costa Rica (Behr et al. 2006). Novel Panamanian syllables were the prefix of buzz syllables and connected syllables which consisted of several buzz and tonal parts. Given that *S. bilineata* is capable of vocal production learning through imitation (Knörnschild et al. 2010), it is not surprising to find different syllable types in different geographical regions, as has been shown for song birds (Borror 1961). Studies on regional dialects in territorial songs on both small and large geographical scales are the next logical step to deepen our understanding of the complex territorial defense behavior of *S. bilineata*.

To conclude, our study indicates that territorial songs of male *S. bilineata* have the potential to encode much more information about the singer than previously thought (Behr et al. 2006, 2009), such as individual identity and social group affiliation. Moreover, our study demonstrates that male vocal activity rises with increasing male–male competition in *S. bilineata*. Thus, our results contribute to the growing body of evidence that bats’ ability to convey social information through vocalizations represents one of the most elaborate vocal communication systems found in non-human mammals.

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Ethical standards All field work were approved by the Smithsonian Tropical Research Institute's Institutional Animal Care and Use Committee, adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, and were in compliance with the current laws of Panama and Germany.

Conflict of interest The authors declare that they have no conflict of interest.

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