Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae)

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Defense of territories in many animal species involves the advertisement of territory holder quality by acoustic signaling. In the sac-winged bat *Saccopteryx bilineata*, males engage in territorial countersinging when reoccupying their day-roost territories in the morning and in the evening before abandoning the roost for the night. Females roost mainly in male territories, and territory holders are reproductively more successful than nonterritorial males. In territorial songs of male *S. bilineata*, we distinguished 6 syllable types and parameterized their acoustic properties. The analysis of 11 microsatellite loci allowed assignments of juveniles to their parents. Males had a higher reproductive success both when they uttered more territorial songs per day and when their long buzz syllables had a lower end frequency of the fundamental harmonic. Long buzzes had a harsh quality due to a pulsation of the fundamental frequency at the syllable onset and also had the highest sound pressure level of all syllable types in most territorial songs. Territorial songs and especially long buzz syllables are thus likely to advertise territory holder quality and competitive ability. *Key words:* acoustic communication, Chiroptera, microsatellites, parentage analysis, *Saccopteryx bilineata*, sexual selection, territorial song. *[Behav Ecol 17:810–817 (2006)]*

In many animal species, territory defense involves signaling with "long-distance threat signals" (Bradbury and Vehrencamp 1998), and often, the respective signals facilitate territory boundary demarcation and individual recognition of territorial neighbors versus strangers (Temeles 1994; Stoddard 1996). Yet, territorial signals have often evolved beyond what is necessary for owner and territory boundary identification and convey measures of the opponents' quality, condition, or motivation during mutual assessment (Bradbury and Vehrencamp 1998). Such signaling of traits is prone to deceit, and hence, reliability of signals has to be ensured by a direct linkage of form to content (e.g., when signal pitch is directly linked to body mass) or an additional cost imposed on cheats (Zahavi 1975, 1977; Grafen 1990; Maynard Smith 1991; Fitch and Hauser 2003).

Acoustic signals are in common use in territorial conflicts and have the advantage over other modalities to travel far, also in a cluttered environment or in darkness that may, for example, confine the efficiency of visual signaling. Acoustic traits that can impart information about the competitive quality of their senders are, for example, vocalization rate (Clutton-Brock and Albon 1979) and spectral frequency (Davies and Halliday 1978; Leonard and Horn 1995; Galeotti et al. 1997; Collins 2004).

In terrestrial mammals, acoustic display is not as common as in other groups (e.g., anurans and songbirds), and signaling involves mainly olfactory and visual cues (Bradbury and Vehrencamp 1998). Some of the few examples of acoustic

territorial signaling occur in primates, such as baboons, *Papio cynocephalus* (Kitchen et al. 2003; Fischer et al. 2004); howler monkeys, *Alouatta* (Sekulic 1982); orangutans, *Pongo* (Mitani 1985); and gibbons, *Hylobates* (Mitani 1988). Among mammals, bats probably rely the most on acoustic cues for orientation and communication. Acoustic territorial signaling has been shown for several bat species. For example, social calls are uttered by male *Pipistrellus pipistrellus* during territorial defense (Lundberg and Gerell 1986; Barlow and Jones 1997), and territorial males of *Pipistrellus nanus* engage in vocal "duels" with low-frequency multisyllable vocalizations (O'Shea 1980). Male *Nyctalus noctula* emit songs from mating roosts that they defend against other males (Gebhard 1997). *Cardioderma cor* sing to delineate feeding territories (McWilliam 1987), and the calling behavior of *Epomophorus wahlbergi* males has been proposed to serve a dual function in spacing out males and attracting females (Wickler and Seibt 1976). In the sac-winged bat *Saccopteryx bilineata*, males utter territorial songs and engage in territorial countersinging (Behr and von Helversen 2004). Males of this species also produce screech-inverted-V calls, and several acoustic features of this call type have been shown to correlate with the number of females in a male's territory (Davidson and Wilkinson 2002, 2004).

Saccopteryx bilineata is a neotropical and insectivorous bat species with a polygynous mating system that shows evidence of both male territorial competition and female mate choice (Heckel and von Helversen 2003; Behr and von Helversen 2004). Females are larger than males, and sexual selection seems to favor small and symmetric males (Voigt et al. 2005). Males defend stable territories in the colony against other males. These territories are used as day roost by up to 8 females during the entire year. Nonterritorial males roost in the vicinity of territories of other males or by themselves (Bradbury and Emmons 1974; Tannenbaum 1975; Bradbury and Vehrencamp 1976, 1977; Voigt and Streich 2003).

Territorial displays, apart from territorial countersinging (Behr and von Helversen 2004), are composed of optical and olfactory signaling (Voigt and von Helversen 1999; Voigt 2002) and sometimes escalate to vigorous fights (Tannenbaum 1975; Voigt and Streich 2003; Behr and von Helversen 2004). Territory owners have a greater reproductive success than nonterritorial males (Heckel and von Helversen 2002). However, males are unable to monopolize mating of the females in their territories, for up to 70% of the young have been shown to be fathered by males other than the territory holder (Heckel et al. 1999; Heckel and von Helversen 2003). Thus, apart from male competition, female choice is likely to represent an important sexual selection factor in this species and accounts for the elaborate male courtship behavior (Bradbury and Vehrencamp 1977; Voigt and von Helversen 1999) that comprises courtship songs. Courtship songs from different males have been shown to be individually distinguishable by their acoustic characteristics (Behr and von Helversen 2004), paralleling the findings for territorial songs described here.

Most courtship behavior occurs when females return to the roost in the morning. A short while earlier, males reoccupy their day-roost territories, which entails a peak in male territorial conflicts and territorial song activity. A reverse sequence of courtship and territoriality is observed in the evening before the animals abandon the colony for the night (Behr and von Helversen 2004).

Territorial songs in *S. bilineata* are complex in their acoustic structure, and we hence expected them to be individually distinguishable for different males. Additionally, if males compete acoustically for day-roost territories and access to mates, acoustic traits in territorial songs may convey information about the sender's competitive quality. This acoustic information, then, would manifest itself in the senders' reproductive fitness and fitness-related parameters (Collins 2004).

Here, we analyze territorial songs of male *S. bilineata* territory holders for differences among males and test for a correlation of individual song characteristics, physical traits, the number of females in a male's territory, and the number of offspring he sired.

METHODS

Study site and period

We recorded male territorial songs in an *S. bilineata* day roost at La Selva field station of the Organization for Tropical Studies in Costa Rica's Atlantic lowland wet forest area ($10°26'$N, $83°59'$W; Province Heredia). Recording of songs took place from 10 February until 21 May 1999. During a subsequent field season in the same study area from 5 January to 25 March 2004, sound pressure levels (SPLs) of territorial songs from 3 males were measured.

The number of territorial songs uttered per male was determined for 15 males during 1 entire day of simultaneous observation in April 1999. For acoustic analysis, we recorded 10 territorial songs from 12 of these males by scan sampling. Songs were only included in the analysis when they matched our acoustic criteria (see Acoustic Recording and Analysis Technique) and when they were uttered during the main activity periods about 2 h before dusk and 2 h after dawn.

The study colony is located in an abandoned hut surrounded by secondary forest and plantations at an altitude of 30 m above sea level. Starting in 1994, virtually all animals in the roost have been captured, measured, and individually marked with color rings attached to the forearm (Heckel et al. 1999; Voigt and von Helversen 1999). During the study period, about 50 individuals (about half of them females) were

observed in the colony. The animals roosted in or in the vicinity of 16 male territories at the inner walls of the building. Bats were habituated to observers inside the hut, and recordings could be performed without disturbing the animals.

Acoustic recording and analysis technique

Territorial songs were recorded with a microphone setup that had a free field response of ± 10 dB from 0.5 to 32 kHz and of ± 18 dB from 0.5 to 90 kHz. We used an oval parabolic reflector with an attached infrared pointer to be able to focus on single individuals even when many males vocalized simultaneously. Assignment of songs to single males was facilitated by the fact that individuals in *S. bilineata* do not roost in clusters but singly at fixed positions in the day roost. Details on the analogous recording device and subsequent digitization have been given elsewhere (Behr and von Helversen 2004).

Peak equivalent SPL was measured in digital high-quality recordings of 20 songs made with a one-quarter–inch Brüel & Kjær microphone type 4939 (free field frequency response ± 2 dB from 4 Hz to 100 kHz), a GRAS preamplifier type 26 AB, a GRAS power module 12 AA (20-dB amplification), a National Instruments A/D DAQCard 6062E, and a notebook computer. The recording device was calibrated at 124-dB SPL prior to each session with a Brüel & Kjær pistonphone type 4228. SPL was calculated for a distance of 0.1 m from the bat's snout and corrected for atmospheric attenuation for a frequency of 20 kHz (Bazley 1976).

Acoustic analysis of songs was done in Avisoft-SASLab Pro (2003). Spectrograms were generated using a 1024-point fast fourier transform (FFT) and a Hamming window with 75% overlap (frequency resolution 488 Hz, time resolution 0.512 ms). Statistical analyses and tests were conducted in SPSS 12.0 (SPSS 2003).

We performed linear stepwise discriminant function analyses (DFAs) to extract independent acoustic parameters that optimally differentiated males. Prior probabilities were adjusted to the sample size per male. We did not apply cross-validation to our DFA data set because our main goal was to optimally differentiate individuals and not to test for a difference among them. Measurements are reported as mean $\pm$ standard deviation (SD) and additionally as median and interquartile range when the skewness (defined as mean/median) was larger than 1.1 or smaller than 0.9. All tests were 2 tailed.

Terminology

In the spectrum of harmonically structured signals, we distinguished fundamental frequency (the equivalent of first harmonic), second harmonic, third harmonic, etc. Signals showing a defined fundamental frequency and harmonic structure were termed tonal when not containing more than 5 harmonics with less than 60 kHz. Signals with more than 5 frequency bands with less than 60 kHz were called multiharmonic. Signals having no discernible fundamental frequency and harmonic structure were called noise bursts or noisy.

Like other authors (Catchpole 1980; Kanwal et al. 1994), we defined a syllable as a vocalization bout surrounded by silent gaps (≥ 2 ms). Syllables shorter than 2 ms were excluded from the analysis. Syllables were categorized into different syllable types by their length, harmonic structure, and modulation of the fundamental frequency.

Male acoustic song traits

In a first step of acoustic analysis, syllables in territorial songs were detected automatically in Avisoft-SASLab Pro (Specht

2003). Often, the software placed the beginning or end of syllables in background noise or echoes, and these cases had to be corrected manually. In a second step, parameters were measured for each detected syllable (Table 2).

The measured parameters included the time variables syllable duration, pause duration (until the onset of the next syllable), and syllable period (syllable duration plus pause duration). Before measuring frequency variables, the signals were band-pass filtered with a finite impulse response filter and cutoff frequencies of 5 and 25 kHz. Thus, higher harmonics and low-frequency noise were cut off and measured parameters referred to the fundamental frequency of the signals only.

Three frequency parameters were measured: first, the pitch of the fundamental frequency and second the Wiener entropy that quantifies the randomness (or pureness) of sounds. Wiener entropy is the ratio of the geometric mean to the arithmetic mean of the spectrum and is 0 for pure-tone signals and 1 for random noise (Tchernichovski et al. 2000). Third, the bandwidth, that is, the difference between the maximum and minimum of the fundamental frequency, was extracted. Minimum and maximum frequencies were defined as the lowest and highest frequency with the amplitude exceeding a threshold of 15 dB below the peak frequency.

Fundamental frequency, entropy, and bandwidth were measured at different positions in each syllable. The pitch of the fundamental frequency was measured at the center and end of each syllable (syllable onsets were often too noisy to render accurate measurements). Additionally, the minimum, maximum, and mean frequencies for the entire syllable were extracted. The entropy was measured at the syllable center and at the position of the maximum amplitude. For the entire syllable, the minimum and mean were extracted (other measurement positions gave inaccurate or inconsistent values). For the bandwidth, only the mean per syllable gave consistent results. Parameter extraction, again, was done automatically in Avisoft-SASLab Pro (Specht 2003) and then checked manually.

For 2 syllable types (short and long buzzes; see Results), 2 additional acoustical parameters were extracted. These syllable types were characterized by a partly pulsed fundamental frequency. We counted the number of pulses in each syllable and measured the mean pulse period (the duration of a pulse plus the duration of the subsequent silent interval).

Territorial songs uttered during low-activity periods in the middle of the day often lack pulsed syllables, are shorter (Behr and von Helversen 2004), and are apparently lower in sound pressure. Such songs have been named short songs by Bradbury and Emmons (1974) in contrast to long songs of main activity periods. In our analysis, we only included songs uttered during high-activity periods and that contained at least one syllable with at least 20 pulses.

Male physical and reproductive traits

We calculated male age as the time elapsed since a male was first caught. However, this calculation is prone to a limited error because some males were already present in the colony in 1994 when investigations started and a few males immigrated to the colony as adults. When males were caught, body mass (±0.1 g), forearm length (±0.1 mm), and fluctuating asymmetry of forearm length were measured according to Voigt et al. (2005). The number of females in a male's territory was determined by averaging the results of colony census data that were taken once or twice every week during the study period. No changes in male territory ownership were observed during that time.

The reproductive success of a male was measured as the number of offspring he fathered within the colony in the parturition period from June to July 1999, corresponding to the mating season in December 1998 to January 1999 (S Meister, personal communication; own observations—both observations in 1999/2000) and the subsequent acquisition of acoustic data. Long-term sperm storage and delayed fertilization are unlikely to occur in *S. bilineata* (Tannenbaum 1975). First, juveniles were assigned to their mothers by behavioral observations and by genetic analysis of 11 microsatellite loci. The genotypic data were then used to assign paternity (for technical details, see Heckel and von Helversen 2003). All adult bats observed in the study colony during the winter of 1998/1999 and the summer of 1999 were included in the analysis as putative parents.

A total of 33 juveniles were born in the colony in the summer of 1999. Two of these juveniles had mothers that had not been observed in the colony during the mating season. After the microsatellite analysis, only 2 juveniles still had 2 putative fathers. In both cases, the 2 males were a subadult male from the previous year and his father. We assigned the latter as father of the juvenile. Five juveniles (15%) were fathered by males that were not observed in the colony during the mating season, that is, 85% of the juveniles were sired by males of the colony. High levels of intracolony paternity were also found in previous years for the same colony (Heckel et al. 1999; Heckel and von Helversen 2003) as well as in other colonies with lower numbers of juveniles (M Nagy and F Mayer, unpublished data). Thus, assuming that the reproductive success of males outside their colony is accordingly low, the number of offspring within the colony is a reasonable estimate of their reproductive success. The number of offspring sired by 2 colony males contained 1 juvenile each that was not born in the study colony but that immigrated after the weaning period. The 12 males included in the acoustic analysis fathered a total of 22 juveniles.

RESULTS

Acoustic structure of songs

The mean duration ($\pm$SD) of 120 territorial songs of 12 males (10 songs each) was 1.63 ± 0.60 s (range 0.54–4.23 s). A total of 20 territorial songs from 3 males recorded in a subsequent field season had a mean peak equivalent SPL of 116.0 ± 3.9 dBpeSPL (reference distance 0.1 m).

A territorial song (Figure 1) consisted on average ($\pm$SD) of 20.1 ± 7.6 syllables (range 6–46 syllables). We classified a total of 2478 syllables into 6 different syllable types (Table 1) according to spectral and temporal properties. All except the least common syllable type (noise burst) were produced by each male. Relative numbers of syllables per syllable type were similar in different males' repertoires. Syllables of different types were usually arranged in a specific temporal pattern in songs and gradually merged into one another. Definitions of syllable types were therefore arbitrary to a certain degree.

Most songs started with short tonal syllables (shorter than 12 ms and either constant in frequency or upward frequency modulated; Figures 1 and 2e) that were similar to constant frequency echolocation calls. Short tonal syllables usually gave way to inverted V syllables (up- and downward frequency modulated) toward the middle of songs (Figures 1 and 2c). In most cases, the first inverted V syllables of a song were more upward and less downward modulated than later syllables.

Inverted V syllables were followed by short buzz syllables (a tonal fraction headed by a series of less than 20 noise bursts or pulses; Figures 1 and 2a), usually in the second half of a song. Typically, short buzz syllables showed an inverted V–shaped
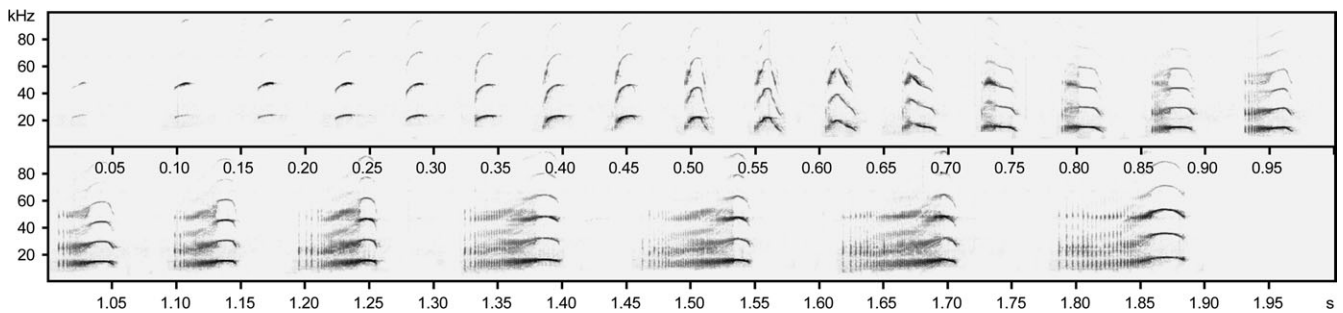
Figure 1
Sonogram of a male *Saccopteryx bilineata* territorial song. Frequency is plotted as a function of time (parameters of the FFT are given in Methods). Short tonal syllables (0–0.46 s) are followed by inverted V (0.48–0.63 s), short buzz (0.66–1.05 s), and long buzz (1.10–1.89 s) syllables.

fundamental frequency of the tonal fraction. Long buzz syllables (headed by more than 20 pulses; Figures 1 and 2b) at the end of songs often had a nearly constant fundamental frequency and a longer duration than short buzz syllables. The number of pulses in buzz syllables significantly increased with the consecutive position number of syllables in a song ($r_s = 0.38$, $P = 0.001$, $n = 72$; syllable position number averaged per male and for 6 classes of pulse number per syllable).

A few songs began with trills (more than one up-and-down frequency modulation; Figure 2d) instead of short tonal syllables. Noise burst or multiharmonic syllables (no distinct harmonic structure or multiharmonic with more than 5 frequency bands less than 60 kHz; Figure 2f) occurred interspersed with other syllable types, mainly in the first half of songs.

The fundamental frequency of syllables decreased during the course of songs, and long buzz syllables, which usually ended songs, had the lowest values in most frequency parameters (Table 2). Long buzz syllables also had the highest SPL of all syllable types in 70% of the high-quality recordings of territorial songs we analyzed ($n = 20$ songs from 3 males) whereas they accounted for only 23% of all syllables (test for a difference in the distribution of percentages: $\chi^2 = 24.6$, degrees of freedom = 1, $P < 0.001$; see Table 1 for relative frequency of occurrence of syllable types). Short and long buzz and inverted V syllables were the most common syllable types and together accounted for 79% of all syllables (Table 1). Therefore, these syllable types were included in the further analyses.

Acoustic differences among males

To quantify male territorial song characteristics, we parameterized song syllables using 15 time and frequency parameters (Table 2). Syllable parameters were not independent. We thus performed linear stepwise DFAs for the 3 syllable types analyzed (inverted V, short buzz, and long buzz). DFAs yielded between 6 and 11 independent discriminant axes (Table 3) that optimally differentiated syllables from different males.

Table 1
Number of syllables per syllable type in 120 territorial songs of 12 *Saccopteryx bilineata* males

Syllable type	n	%
Short buzz	823	33
Long buzz	568	23
Inverted V	576	23
Trill	235	9
Short tonal	192	8
Noise burst	84	3

These axes were used as variables in the further correlation analysis. We chose axis 1 of inverted V and axes 1 and 2 of short and long buzz syllables, respectively, for further analysis because they comprised distinctly more information than subsequent axes (Table 3). Males differed significantly in the acoustic traits for all 3 syllable types ($P < 0.001$; Table 3), indicating different acoustic repertoires.

DFA axes are linear combinations of the original parameters and are determined by these parameters to a varying degree (Table 4). End frequency and other frequency parameters had the strongest influence on the first 2 discriminant axes of short and long buzz syllables (Table 4), whereas syllable duration and minimum entropy contributed most to the first axis of inverted V syllables.

Song parameters and reproductive success

Reproductive success of males was measured as the number of offspring sired within the colony in the natal period that followed the mating season when acoustic recordings were made. A single male fathered between 0 and 5 juveniles.

For 12 males, we correlated their reproductive success with 5 acoustic territorial song parameters and with the number of songs emitted during one all-day observation (Bonferroni correction for 6 analyses: $\alpha = 0.0083$). Acoustic song parameters were medians per male of the 5 discriminant axes described above (1 for inverted V and 2 for both short and long buzz syllables).

Discriminant axis 1 of long buzz syllables was negatively correlated ($r_s = -0.80$, $P = 0.0017$, $n = 12$) with male reproductive success (Figure 3a). Because this axis was most influenced by syllable end frequency and minimum frequency (Table 4), a negative correlation of the fundamental frequency of long buzzes and reproductive success can be derived. This is confirmed by Figure 3b, which shows the end frequency of long buzz syllables plotted against male reproductive success ($r_s = -0.61$, $P = 0.034$, $n = 12$). Also, male reproductive success showed a tendency to increase with the total number of long buzz syllables produced by a male ($r_s = 0.52$, $P = 0.084$, $n = 12$). The other 4 discriminant functions of long and short buzz and inverted V syllables showed no significant correlation with reproductive success (Spearman rank correlation, $P > 0.2$). The correlation of the number of females in a male's territory and the acoustic territorial song traits mentioned was not significant either (Spearman rank correlation, $P > 0.2$).

Song activity for 15 males was between 0 and 48 songs uttered during 1 entire day. Song activity was positively correlated with reproductive success ($r_s = 0.76$, $P = 0.0011$, $n = 15$; Figure 3c) and also with the number of females in male territories ($r_s = 0.54$, $P = 0.040$, $n = 15$).
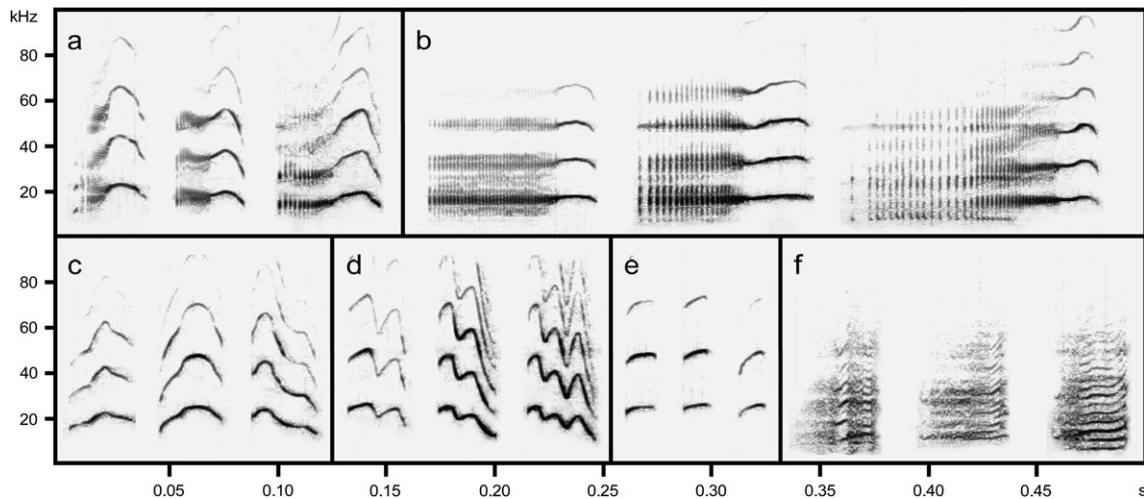
Figure 2
Sample sonograms for the 6 syllable types in territorial songs of 12 *Saccopteryx bilineata* males. Syllables are not presented in their original order and spacing but after their relative frequency of occurrence in songs. (a) Short buzz, (b) long buzz, (c) inverted V, (d) trill, (e) short tonal, and (f) noise burst.

Thus, song traits seem, at least in part, to reflect the quality of the territory a male is able to defend or the number of females it is able to attract to its territory. This could possibly be due to a signaling of physical abilities and quality by song traits. Direct measures of physical abilities are age, body mass, forearm length, or fluctuating asymmetry of forearm length. However, none of these variables were significantly correlated with reproductive success, song frequency, or DFA axes for the data set analyzed here (Spearman rank correlation, all $P > 0.2$).

DISCUSSION

Several parameters extracted from *S. bilineata* territorial songs correlated with male reproductive success. Social context and acoustic structure of territorial songs suggest that this correlation is most likely due to honest signaling of stamina and aggressive motivation in the mutual assessment of territorial males. Such signaling has, thus far, rarely been shown in mammals and, to our knowledge, in no bat species.

DFAs of territorial songs from 12 males extracted independent acoustic parameters that allowed for a discrimination of songs from different individuals. One of these parameters (discriminant function 1 of long buzz syllables) correlated with the reproductive success of males inside their colony and was influenced most by the end frequency of the fundamental harmonic of long buzz syllables. The median of the fundamental end frequency, itself, was negatively correlated with the male's reproductive success. Also, reproductive success showed both a tendency of positive correlation with the number of long buzz syllables contained in territorial songs and a positive correlation with the number of territorial songs uttered by a male per day.

The correlation of male territorial song traits with reproductive success could at least in part be accounted for by the significant correlation of song traits with the number of females roosting in a male's territory because this number has been shown to be positively correlated with the male's reproductive success (Heckel and von Helversen 2003; M Nagy,

Table 2
Acoustic parameter values for 6 types of syllables in 120 territorial songs from 12 male *Saccopteryx bilineata*

Parameter	Short buzz[a]	Long buzz[a]	Inverted V[a]	Trill	Short tonal	Noise burst
Pause after syllable (ms)	44 ± 21	55 ± 22	39 ± 24	32 ± 22	29 ± 24	38 ± 18
Syllable duration (ms)	35 ± 10	55 ± 16	25 ± 10	32 ± 11	9 ± 3	20 ± 15
Syllable period (ms)	74 ± 32	103 ± 36	60 ± 32	55 ± 35	34 ± 31	62 ± 29
Center frequency (kHz)	16.3 ± 2.3	13.7 ± 2.1	18.7 ± 3.1	18.1 ± 2.2	22.0 ± 1.8	
End frequency (kHz)	14.1 ± 2.6	14.3 ± 2.3	15.9 ± 4.1	13.5 ± 3.1	21.2 ± 3.1	
Mean frequency (kHz)	16.3 ± 2.2	14.8 ± 2.0	18.4 ± 3.2	18.0 ± 2.6	21.6 ± 1.7	
Minimum frequency (kHz)	11.5 ± 2.0	10.1 ± 2.0	12.7 ± 3.1	12.6 ± 2.4	19.2 ± 2.9	
Maximum frequency (kHz)	17.8 ± 2.4	16.8 ± 1.8	20.7 ± 2.8	22.0 ± 1.3	22.6 ± 1.6	
Center entropy	0.15 ± 0.05	0.20 ± 0.04	0.17 ± 0.07	0.18 ± 0.06	0.21 ± 0.10	0.23 ± 0.06
Mean entropy	0.17 ± 0.03	0.18 ± 0.02	0.19 ± 0.03	0.20 ± 0.03	0.17 ± 0.05	0.22 ± 0.03
Minimum entropy	0.11 ± 0.02	0.11 ± 0.02	0.12 ± 0.03	0.12 ± 0.02	0.14 ± 0.05	0.16 ± 0.04
Entropy at maximum amplitude	0.12 ± 0.02	0.12 ± 0.02	0.12 ± 0.03	0.13 ± 0.03	0.15 ± 0.06	0.18 ± 0.05
Mean bandwidth (kHz)	4.9 ± 2.5	6.7 ± 2.2	5.6 ± 3.1	7.7 ± 3.1	3.3 ± 1.5	7.2 ± 3.8
Pulse number	11 ± 4	30 ± 10				
Pulse period (ms)	0.76 ± 0.38	0.81 ± 0.30				

Frequency measurements refer to the fundamental frequency and are not given for noise burst syllables. Only short and long buzz syllables contained pulses that are quantified by 2 additional parameters. Values for pulse periods are medians per syllable. For a more detailed parameter definition, see Methods.

[a] Syllable types that were included in the correlation analysis of songs and male reproductive success.

Table 3

Results of linear stepwise DFAs for 3 territorial song syllable types from 12 male *Saccopteryx bilineata*

Syllable type	Number of discriminant axes	Number of parameters included	Wilks lambda	*P*	% of correctly assigned syllables	% of explained interindividual variance		
						Axis 1	Axis 2	Axis 3
Inverted V	6	7	0.52	<0.001	34.7	41.9[a]	23.6	15.6
Short buzz	9	9	0.33	<0.001	37.8	34.8[a]	30.8[a]	17.1
Long buzz	11	12	0.18	<0.001	43.7	26.4[a]	24.2[a]	15.2

The percentages of variance explained by the first 3 DFA axes are given for each syllable type. The a priori probability for classification was calculated from group sizes.

[a] Marks axes that explained distinctly more variance than subsequent axes and that were included as variables in the subsequent correlation analysis.

unpublished data; but see Voigt et al. 2005). Either successful males may be able to defend better territories with more roosting females or females may choose to roost in territories of attractive males.

Although social context and acoustic structure of territorial songs indicate a role in male competition (Behr and von Helversen 2004), it is likely that females use the information conveyed in male countersinging for mate choice decisions. Also, due to their high SPL and low spectral frequency, territorial songs travel far, and females may use these male vocalizations both to locate roost sites unknown to them and as a signal for roost safety from predation and sexual harassment because there is already a male perched in it. Because design features for territorial and mate attraction signals are similar, no serious trade-off is imposed when combining both functions in one signal (Bradbury and Vehrencamp 1998; Collins 2004). Thus, male *S. bilineata* territorial songs may play a role as well in male competition as in mate attraction as has also been suggested for many bird songs (Kodric-Brown and Brown 1984; Searcy and Andersson 1986; Vehrencamp 2000).

In both cases, male territorial songs may communicate male quality. However, we found no correlation between acoustic parameters extracted from territorial songs and male age, body mass, forearm length, or fluctuating asymmetry of forearm length. Neither age nor physical traits predicted the number of offspring sired by males. This contrasts with a recent analysis of male traits and reproductive success for the same colony that revealed small and symmetric males to have a higher than mean reproductive success (Voigt et al. 2005). The differing outcomes are due to different underlying data sets and possibly to the fact that the analyses presented here are restricted to 12 males and 1 reproductive season, whereas the analysis performed by Voigt et al. (2005) included 21 males and parentage data from 6 years. It thus remains necessary to test for a correlation of physical and acoustic traits in a more ample data set.

We used correlation analysis of acoustic, physical, and reproductive traits of male *S. bilineata* to determine the role of acoustic signaling in territoriality and in the mutual assessment of rival males. A correlation approach is often used to test the role of acoustics in male competition (Collins 2004). However, additional playback experiments would be desirable to show a direct influence of male acoustic traits on rival response.

Support for a relationship between acoustic and reproductive traits comes from the analysis of the vocal repertoire of male *S. bilineata* from Trinidad by Davidson and Wilkinson (2002, 2004). They found a negative correlation of the number and spectral frequency of inverted V components in screech-inverted-V calls (whistles) and the number of females in male territories. Also, males with a longer duration of the

Table 4

Within group correlation coefficients of measured syllable parameters and computed discriminant function axes

Syllable type	Long buzz		Short buzz		Inverted V
DFA axis number	1	2	1	2	1
Pause after syllable[b,c]	0.105	0.481	−0.115	0.041	0.022
Syllable duration[b,c,d]	−0.244	−0.148	0.372	0.148	0.580
Syllable period[b,c]	−0.010	0.358	0.006	0.110	0.143
Center frequency[b,d]	0.084	0.657	−0.313	0.371	0.137
End frequency[b,c,d]	0.464	0.425	−0.456	0.591	−0.218
Mean frequency[c]	0.077	0.334	−0.392	0.548	0.040
Minimum frequency[b,c,d]	0.313	0.222	−0.035	0.433	0.229
Maximum frequency	0.187	0.349	−0.338	0.219	0.077
Center entropy[b]	−0.282	0.038	0.145	−0.319	−0.129
Mean entropy[b,c,d]	−0.282	0.038	0.145	−0.319	−0.129
Minimum entropy[b,c,d]	0.072	0.053	−0.237	−0.473	−0.278
Entropy at maximum amplitude	0.192	0.387	0.318	−0.334	−0.270
Mean bandwidth[b]	0.170	0.372	0.298	−0.343	−0.247
Pulse number[b]	−0.291	0.116	−0.110	−0.146	
Pulse period[b,c]	0.109	−0.450	0.259	−0.057	

Only DFA axes included in subsequent correlation analyses are shown. The 2 highest correlation coefficients of each axis are underlined. Parameters that were included in stepwise DFAs are indicated by "b" for long buzz syllables, "c" for short buzz syllables, and "d" for inverted V syllables.
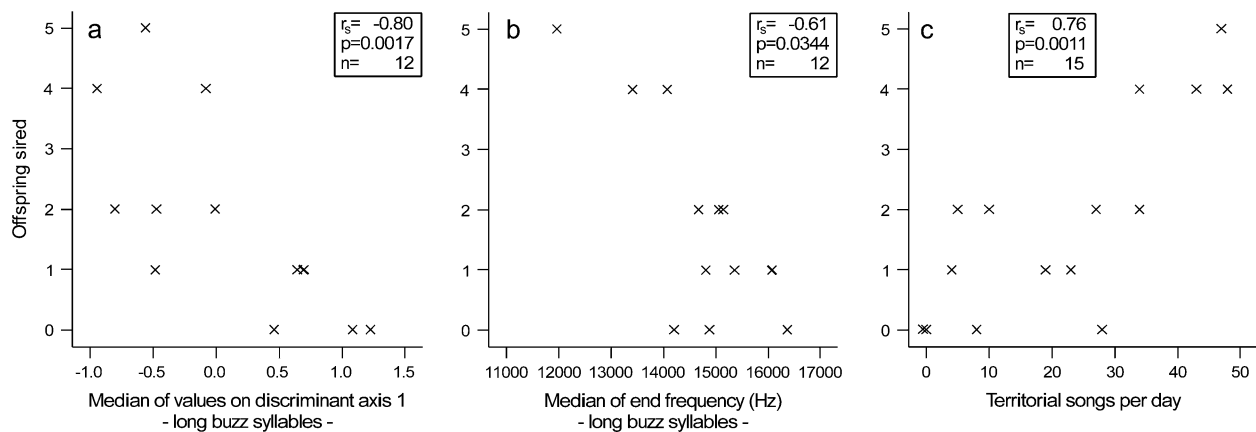
Figure 3
Correlation of territorial song traits and reproductive success in *Saccopteryx bilineata* males. Nonparametric correlations were significant for the medians of the first discriminant axis of long buzz syllables (a) and the number of songs uttered by males during one all-day observation (c). The values of the first discriminant axis in (a) were influenced most by the end frequency of the fundamental harmonic of long buzz syllables whose correlation with reproductive success is shown in (b).

inverted V and screech components had more females on their territories. Whistles are vocalized by hover flying males that perform specialized wing strokes to fan odor toward the females (Voigt and von Helversen 1999; Behr and von Helversen 2004) and presumably form part of the complex multimodal courtship behavior of males.

The fundamental frequency of vocalizations has been shown to correlate with body size across different taxa (e.g., Ryan and Brenowitz 1985; see overview in Fitch and Hauser 2003). Also, in some anuran species, the dominant frequency of calls is a static trait (Gerhardt 1991; Gerhardt and Huber 2002) and a reliable predictor of body size (Davies and Halliday 1978; Arak 1988). However, in birds and mammals, fundamental frequency is dependent on syrinx or larynx size that, itself, is not necessarily tied to body mass. This may be the reason why for these taxa data are somewhat ambiguous (Fitch and Hauser 2003) and for some species there is evidence of a correlation of body mass and vocalization frequency (e.g., Galeotti et al. 1997), whereas other studies have failed to show such a dependency, for example, in red deer (McComb 1991) and humans (van Dommelen 1993).

For *S. bilineata* males, we found no correlation of the fundamental frequency of territorial songs and body mass or forearm length. Also, Davidson and Wilkinson (2004) report that the mean maximum frequency of inverted V components of male whistles did not significantly depend on forearm length. Males of *S. bilineata* are smaller than females, and smaller males have been shown to be reproductively more successful than their competitors, possibly due to better maneuverability in aerial confrontations (Voigt et al. 2005). It is thus not surprising that a lower fundamental frequency of long buzzes in reproductively successful males did not correlate with a higher body mass or forearm length in our analysis.

Alternatively, the fundamental frequency of song syllables could be a dynamic trait (Gerhardt 1991; Gerhardt and Huber 2002), and energetic costs rather than body size dependency could prevent low-quality males from producing songs with lower fundamental frequencies (Zahavi 1975, 1977; Grafen 1990; Maynard Smith 1991). Also, song fundamental frequency could function as a conventional signal with a more or less arbitrary design. In this case, its reliability could be ensured by a regular probing of rivals that imposes costs from agonistic interactions on cheats (Guilford and Dawkins 1995).

In our analysis, apart from long buzz fundamental frequency, the median number of long buzzes per territorial song also showed a tendency of positive correlation with male reproductive success. Territorial song rate itself was significantly positively correlated with the number of offspring a male sired. An increased song rate results in higher energy expenditure in several animal species (see overview in Vehrencamp 2000). Song rate, therefore, qualifies as a costly signal and has been shown to be preferred by females. Often, a higher song rate is associated with escalated countersinging interactions among males where it could serve as conventional or, more likely, also as costly signal indicating male competitive ability (Vehrencamp 2000).

Territorial songs of *S. bilineata*, in addition to their high repetition rate and low fundamental frequency, are also characterized by a high SPL (116.0 ± 3.9 dBpeSPL). Low-frequency signals are less attenuated in air and may have evolved so as to reach the receiver with a higher SPL. Low spectral frequency and high SPL rendered *S. bilineata* territorial songs easily audible for the human ear. This is even more striking when taking into account that *S. bilineata* is a rather small bat species—males in this study had a mean body mass of 7.4 ± 0.3 g. In starlings, *Sturnus vulgaris*, loudness of vocalizations is positively correlated with energetic costs (Obwerger and Goller 2001). Generally, harsh and loud signals are likely to be energetically costly and thus may serve as an honest indicator of male physical and fighting abilities (Collins 2004) as has been shown for "rattles" in barn swallows, *Hirundo rustica* (Galeotti et al. 1997), and "snarr" notes in water pipits, *Anthus spinoletta* (Rehsteiner et al. 1998).

Buzzes in *S. bilineata* territorial songs had the highest SPL and also differed from other syllable types in being headed by a series of short pulses that add a harsh or noise burst quality to the otherwise tonal syllables (Behr and von Helversen 2004). The countersinging behavior of males (Behr and von Helversen 2004) with frequently repeated, harsh, loud, low-frequency territorial songs may thus provide a mechanism for mutual assessment of stamina and aggressive motivation level that may also be used as mate choice criterion by females. This possibly accounts for the fact that males that produced more and lower frequency territorial songs also had a higher reproductive success and, to our knowledge, constitutes the first example of honest territorial signaling in a bat species.

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