Territorial counter-singing in male sac-winged bats (*Saccopteryx bilineata*): low-frequency songs trigger a stronger response

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Abstract In many animal species, individuals compete for resources but avoid escalated conflicts by threat displays, i.e. a mutual signalling behaviour that enables the opponents to predict the outcome of the conflict without the necessity of actual fighting. For example, territory holders may use acoustic signals to communicate not only their own identity and the borders of their territory but also their competitive quality, fighting ability and motivation. Here, we show that male sac-winged bats, *Saccopteryx bilineata*, adjust their vocal territorial displays according to the fundamental frequency of territorial songs of their opponents. In playback experiments with territorial males, low-frequency stimuli elicited a higher territorial song rate and length than high-frequency stimuli. Male *S. bilineata* that sing more often and with lower fundamental frequencies have been shown to sire more offspring than their competitors. Fundamental frequency of territorial songs, hence, may reveal male quality and, consequently, the resulting threat posed to competing males. We argue that this is reflected in the increased response of competitors to low-frequency territorial songs shown here. Such competitive signalling behaviour has been shown in a few mammal species like red deer and baboons but, thus far, not in bats.

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Introduction

Honest signalling and territorial conflicts

Competition for resources and territoriality as an attempt to gain exclusive access to them is a widespread phenomenon amongst individuals of most animal species. This competition may escalate to serious fights with a risk of injury for the animals involved (reviews for mammalian species in Clutton-Brock et al. 1982; Huntingford and Turner 1987). In most species, however, actual fighting occurs far less frequently than one may expect from the omnipresence of conflicts over territories and resources. Usually, a system of increasingly insistent threats has evolved that results in a retreat of one opponent before a conflict reaches its climax (Bradbury and Vehrencamp 1998).

The signals involved have to enable the opponents to predict the outcome of an escalated conflict—this implies the ability to detect cheats that merely bluff but are likely to lose a serious fight. Thus, signals have to be honest in the sense that they provide information on factors influencing the competitive quality of the opponents and the outcome of a potential fight (reviewed in Bradbury and Vehrencamp 1998; Fitch and Hauser 2003). Examples of such factors are physical ability and motivation.

Birds are, of course, well known to use acoustic signals in interactions with territorial competitors. Different song characteristics have been shown to reflect aspects of male competitive ability. Examples are song frequency (Shackelton and Ratcliffe 1994; Leonard and Horn 1995; Galeotti et al. 1997; Christie et al. 2004), song

rate (Otter et al. 1997), the repetition rate of specific song elements (Rehsteiner et al. 1998), song intensity (Dabelsteen and Pedersen 1990) and song repertoire and complexity (Krebs et al. 1978; Yasukawa et al. 1980). Also, birds not actively involved may extract information from vocal interactions of other individuals in communication networks (case studies in, e.g. McGregor and Dabelsteen 1996; Naguib and Todt 1997; Peake et al. 2002; Mennill and Ratcliffe 2004).

In mammals, there are several examples of indicator mechanisms (sensu Andersson 1994) that are assumed to transfer information between territorial opponents, many of which are acoustic signals—as in wolves, *Canis lupus* (Harrington and Mech 1979), lions, *Panthera leo* (McComb et al. 1993; Grinnell et al. 1995), howler monkeys, *Alouatta seniculus* (Sekulic 1982), orangutans, *Pongo pygmaeus* (Mitani 1985), and gibbons, *Hylobates agilis* (Mitani 1988). Evidence for signals conveying information in a territorial context usually stems from the response of the competitors to different gradations of the signal. These reactions can be tested for in behavioural experiments. Such experimental evidence is essential to understand the influence of sexual selection on the evolution of social communication and the signals relevant in its context. Nevertheless, such experiments have rarely been conducted for mammalian species (e.g. Clutton-Brock and Albon 1979; Kitchen et al. 2003; Fischer et al. 2004) and, thus far, never in bats.

Male territoriality in *Saccopteryx bilineata*

S. bilineata is a polygynous insectivorous bat species common in the neotropics. Males vigorously compete for small territories (covering an area of about 1–2 m^2) in the daytime roosts (Tannenbaum 1975; Voigt and Streich 2003; Behr and von Helversen 2004) and for the access to females (on average two to three) that roost in these territories the whole year round. The mating season, however, is restricted to December and January (Bradbury and Emmons 1974, Voigt and Schwarzenberger 2008, own observations). Mating has only very rarely been observed in the day roost.

All adult individuals present in the day roost maintain a minimum distance of 5 to 8 cm from each other. Colonies can comprise of up to 60 adult individuals distributed in one to 12 harems. In most colonies, harem territories are adjacent to each other. Mostly, adult non-harem males ('peripheral males') roost in the vicinity of the harem territories. Experimental removal of males from their territories usually results in a new male (often a peripheral male from the same colony) claiming ownership within less than 2 h in territories occupied by females (Voigt and Streich 2003). Territory tenure, once established, may last up to 7 years and is mostly ended by the death or disappearance of the territorial male, often preceded by agonistic interactions with a challenger (own observations).

Though male territorial competition is intense, up to 70% of the offspring in a territory are not fathered by the corresponding territorial male. Thus, female choice is supposed to be another important aspect of sexual selection in *S. bilineata* (Heckel et al. 1999; Heckel and von Helversen 2003). Males holding a territory have been shown to be reproductively more successful than their competitors without territory tenure (Heckel and von Helversen 2002). Due to the low territory tenure turnover rate and the year-round territorial defence, the evolution of a reliable signal for competitive ability of males may have been especially advantageous in *S. bilineata* to avoid constant fighting over territory ownership.
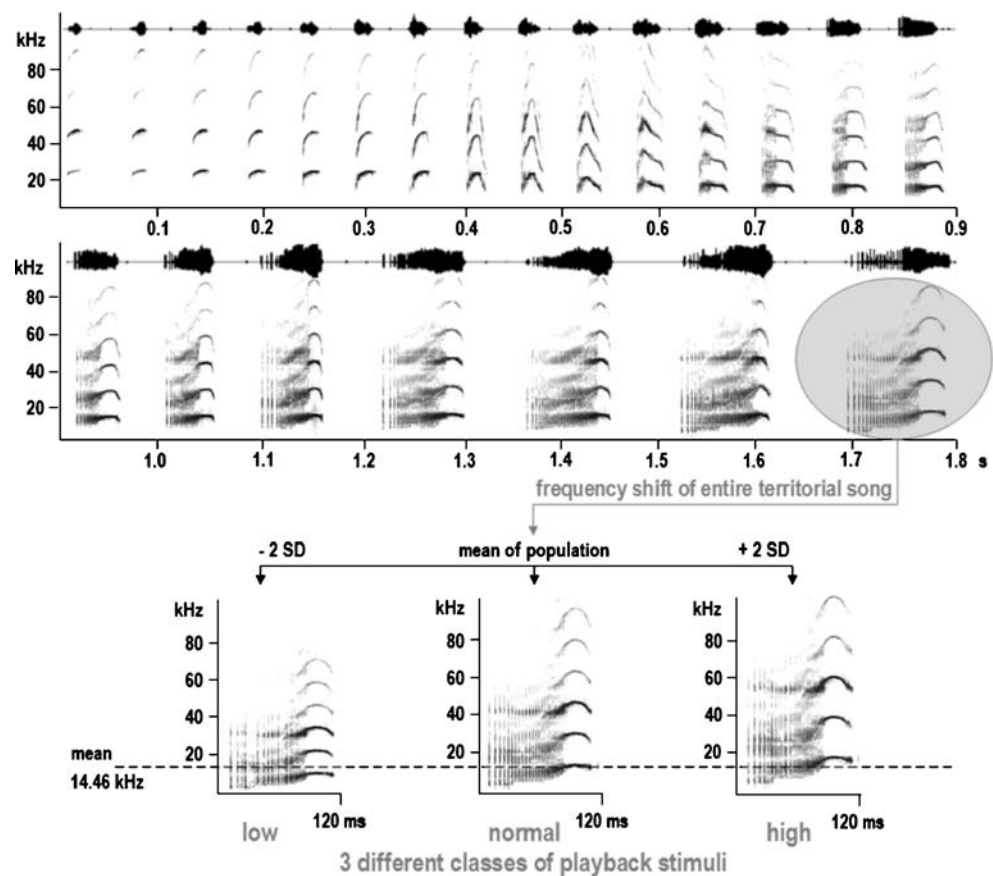
Territorial signalling

The defence of day-roost territories by *S. bilineata* males entails visual and olfactory signalling (Voigt and von Helversen 1999; Voigt et al. 2001) and the production of territorial songs (Bradbury and Emmons 1974; Davidson and Wilkinson 2004; Behr et al. 2006—also see supplementary video). Agonistic territorial interactions between males, for example, an attempt to usurp an occupied territory, are accompanied by an increased territorial song rate of the opponents, followed by aerial chases, mutual wing striking or even biting and clutching each other (own observations). A low fundamental frequency and high repetition rate of songs are correlated with a high reproductive success (Behr et al. 2006).

The territorial songs (Fig. 1) uttered by *S. bilineata* males have a duration of about 1.6 s and consist of a series of approximately 20 syllables from different syllable types that gradually merge into one another (Bradbury and Emmons 1974; Behr and von Helversen 2004; Behr et al. 2006). Commonly, territorial songs start with syllables similar to echolocation calls that are followed by inverted-V-shaped syllables. Songs are usually ended by several buzz syllables of increasing duration. Buzz syllables are tonal and headed by a series of short pulses. They have been shown to have the lowest fundamental frequency and the highest sound pressure level of all syllable types in territorial songs (Behr et al. 2006). Due to these extreme acoustic characteristics, buzz syllables are easily perceivable also for human listeners.

Territorial songs are short, rather stereotyped, frequently repeated and allow the singer to listen for territorial songs (i.e. counter-songs) of other males (Behr and von Helversen 2004). Also, songs are individually distinguishable (Bradbury and Emmons 1974; Behr et al. 2006) and hence comply with design features that facilitate mutual recognition and assessment of opponents during counter-singing (Catchpole 1987; Bradbury and Vehrencamp 1998). Males engage in territorial counter-singing mainly when reoccupying their day-roost

territories in the morning and also in the evening before abandoning them for the night. Main song activity coincides with a peak in male agonistic interactions (Bradbury and Emmons 1974; Behr et al. 2006). Since females return to the roost later than the males and leave earlier in the evening (Bradbury and Emmons 1974; Tannenbaum 1975; Voigt and von Helversen 1999), the majority of territorial songs are vocalised in the absence of females (Behr and von Helversen 2004).

Song traits and reproductive success

Several vocalisation types of *S. bilineata* males are individually distinguishable (Bradbury and Emmons 1974; Davidson and Wilkinson 2002, 2004; Behr and von Helversen 2004) and some of their acoustic characteristics have been shown to be correlated to the number of females roosting in a male's territory (Davidson and Wilkinson 2004; Behr et al. 2006). Territorial songs from different males are individually discernible and a low fundamental frequency of songs and a high song rate are correlated with a high reproductive success (Behr et al. 2006). Individuals of both sexes may use information from territorial songs in their decision making. To repel rivals and to attract females are two functions that are not mutually exclusive and that are often combined in one signal, for example, in many bird songs

(Vehrencamp 2000; Collins 2004). Females may use the information exchanged in male territorial singing to choose a mate (McGregor 1993). However, design features and song activity patterns suggest that territorial songs are mainly used in a context of information transfer between competing males (see previous section—"Territorial signalling").

With the playback experiments presented here, we addressed the potential function of territorial song in male–male contests. If territorial songs convey information in the context of male competition, then males ought to increase their territorial response to playback stimuli simulating intruders with high quality (in terms of repro-ductive success) because such intruders constitute a higher imminent threat to the territory owner. Red deer, for example, have been shown to adapt their own roaring rate to the roaring rate of a challenger and, hence, to his competitive ability and the imminent threat he represents for the harem holder (Clutton-Brock and Albon 1979).

The fundamental frequency of *S. bilineata* territorial songs had previously been shown to be correlated with male reproductive success and, hence, was likely to play a role in the mutual assessment of males (Behr et al. 2006). We experimentally varied the fundamental frequency of territorial songs (high, normal and low) in playbacks and tested for differences in the acoustic response behaviour of free-living males in their natural habitat.

Methods

Study site and animals

Recordings and playback experiments were performed from December 2003 to March 2004 at La Selva Biological Station of the Organisation for Tropical Studies (OTS) in Costa Rica, Province Heredia (10° 25′ N, 84° 0′ W). The six study colonies of S. bilineata contained a total of 68 individuals, 19 males and 49 females, roosting in 15 territories (one to five per colony) on the wooden walls of buildings. Playback experiments were performed in four of these colonies that contained one, two or five (in two colonies) territorial males. Monitoring of S. bilineata colonies in La Selva has started in 1994. Each year, individuals were caught with mist nets and individually marked with coloured and numbered plastic rings (A.C. Hughes, size XCL), rendering them individually discernable from a distance. Due to the long-term project at the study site, animals were accustomed to the presence of observers at the roosts and playbacks could be performed causing only a minimum of disturbance. During the study period, census data were obtained in all colonies in 1- or 2-day intervals. The census revealed the affiliation of females to male territories (2.8±2.7 females per territory, median 2.0, range 0–7).

Recording and playback setup

Baseline data on vocal activity were gathered for 11 S. bilineata males (eight of which were also used in playback sessions). The number of territorial songs uttered per male was counted on separate days (1 day per male) during the main period of song activity (30 min in the morning and evening). No playbacks were performed in the colony of the respective male on that day.

We recorded territorial songs at 500-kHz sampling rate and 12-bit resolution with a one-fourth inch Brüel and Kjær microphone type 4939 (free field response ±2 dB from 4 Hz to 100 kHz), a G.R.A.S. preamplifier type 26 AB, a G.R.A.S. power module 12 AA (20-dB amplification), a National Instruments A/D DAQCard 6062E and a notebook computer running Avisoft-Recorder software (version 2.9, R. Specht, Berlin, Germany). The directional characteristic of the microphone was focussed by a 0.33-m-diameter parabolic reflector. An infrared pointer was attached to the setup that could be located in a night-vision device (Litton Monocular M911). This setup permitted recordings of individual bats even if conspecifics were vocalising in the vicinity. For sound pressure measurements, no parabolic reflector was used and the recording device was calibrated at 124 dB SPL prior to each session with a Brüel and Kjær pistonphone type 4228. Sound pressure levels were calcu-

lated for a distance of 0.1 m from the bat's snout and corrected for spherical and atmospheric attenuation at a frequency of 20 kHz (Bazley 1976). For playback experiments, we used the same notebook computer, software and A/D Card as described above. The signal was fed into an ultrasonic amplifier (Avisoft Ultrasonic Power Amplifier; frequency response of ±1 dB from 0.1 to 100 kHz) and an ultrasonic speaker (Avisoft Ultrasonic ScanSpeak R2904-700000) with a frequency response of ±8 dB from 4 to 115 kHz positioned in the periphery of the focal male's territory. Amplitudes of playback stimuli were adjusted to 116 dB peSPL at a distance of 0.1 m as measured in recorded territorial songs. Vocal responses to playbacks were recorded with a lower sample rate (76 kHz) and a simplified microphone setup (free field response ±10 dB from 0.5 to 32 kHz and ±18 dB from 0.5 to 90 kHz—details are given in Behr and von Helversen 2004) that did not allow for a measurement of fundamental frequency in the songs recorded. Acoustic analysis of songs was performed in Avisoft-SASLab Pro (version 4.1, R. Specht, Berlin, Germany) and has been described before in detail (Behr et al. 2006). Spectrograms were generated using a 1,024-point FFT and a Hamming window with 75% overlap.

Playback stimuli

To reduce pseudo-replication (McGregor 1992), we used territorial songs from three different males (i.e. donor males) as stimuli in our playbacks. The difficult recording situation in most colonies which resulted in poor-quality recordings unsuitable for presentation in playback experiments prevented us from including more bats as donor males. Sound pressure measurements of 20 songs from donor males rendered a mean peak equivalent sound pressure level of 116.0±3.9 dB peSPL at a distance of 0.1 m, to which we adjusted the amplitude of playbacks. In 23 songs from donor males, we measured the fundamental frequency at the end of buzz syllables that in an earlier field study had been shown to be negatively correlated with reproductive success (Behr et al. 2006). Frequency medians per song did not differ significantly (t test, $t_{141}=-0.009$, $P>0.9$) between that earlier study (14.45±2.07 kHz) and the data presented here (14.46±2.73 kHz). As playback stimuli, we chose territorial songs with a median end frequency of buzz syllables near to the population mean in order to avoid using unnaturally extreme frequency values. Three different territorial songs were chosen as stimuli from each donor male. Songs were filtered for background noise and then shifted up or down in frequency (shift of 4 kHz of the fundamental frequency in buzz elements) using time domain harmonic scaling (Rabiner and Schafer 1978) in CoolEdit 2000 (Syntrillium, Phoenix, USA). This rendered three different stimulus types with high, normal and low

fundamental frequencies (Fig. 1). Playback stimuli lay within two standard deviations of the mean and within the natural range measured in the study colony. Most sensory perception follows a logarithmic scale (e.g. frequency perception in humans—Stevens and Volkmann 1940). Hence, the equal shift of 4 kHz up and down in our stimulus types is likely to lead to a larger shift down in frequency than up, as perceived by the bats. We do not know, however, how the response of *S. bilineata* males is correlated to the frequency perceived.

Playback trials

In playback sessions, we positioned the speaker at the edge of the focal male's territory at least 10 min before the playback session started. Focal males were perched in a maximum distance of 6 m from the speaker. All playbacks were performed during the main song activity periods half an hour after males entered the roost in the morning and before they left it in the evening (Behr et al. 2006). Nine territorial males were tested in three separate playback sessions on three different days for their vocal response (counter-songs) to low-, normal- and high-frequency playback stimuli. Three additional males had to be excluded from the analysis due to an incomplete playback dataset. In order to simulate the intrusion of a foreign male, we always chose stimuli from donor males from a different colony. Each focal male was tested with stimuli from only one donor male since a mixture of territorial songs from different donor males may have evoked a different reaction than the one to a single intruder that we wanted to test for. Playback sessions had a total duration of 9 min and consisted of three consecutive phases: a pre-observation phase, a playback phase and a post-observation phase (each 3 min long). In every playback phase, three stimuli were repeated four times each with silent intervals of 10, 13 or 16 s (males usually insert variable silent intervals between their songs). We randomised the order of silent intervals, stimuli in playback sessions and playback sessions presented to a focal male. During the pre-observation phase, we recorded the spontaneous vocal behaviour of the focal male before the playback, during the playback phase its vocal response to the stimuli and during the post-observation phase its vocal behaviour after the playback. The recordings were used to measure the length and rate of territorial songs uttered by the focal males. The counter-song length and rate of the playback phase was corrected for the focal male's motivational status prior and after the playback: values of the playback phase were divided by the mean values of pre- and post-observation phases. In pre-observations, the spontaneous song length and rate of each focal male did not differ significantly for playback sessions with stimuli of low, normal and high fundamental

frequency (Friedman test, $P>0.15$, $N=9$), suggesting that the motivational status of focal males was comparable on the different days the playback sessions were conducted.

Additionally, we investigated if the motivational status of focal males depended on the weather by testing for an influence of the amount of nightly rainfall (prior to a playback session) on spontaneous vocal behaviour during the pre-observation of playback sessions using 11 males (nine males with complete and two males with incomplete playback datasets). Data on rainfall for the La Selva property were provided by the OTS.

Statistical analyses

Statistical analyses and tests were conducted in SPSS (version 12.0, SPSS Inc., Chicago, IL, USA). All tests were two-tailed (critical $\alpha=0.05$). Friedman and Wilcoxon tests were conducted calculating exact instead of asymptotic P values (after Mundry and Fischer 1998). Means and one standard deviation are given if not stated differently.
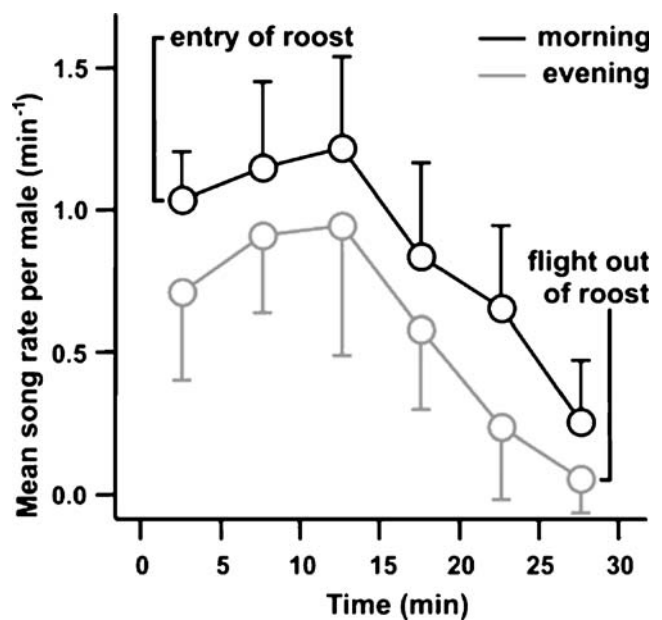
Fig. 2 Spontaneous song rate per male and 5-min interval for 11 *S. bilineata* males including eight of the nine males from playback experiments and three additional males from colonies not used in the playback analysis. Males were recorded on separate days, 1 day each. Song rate is given for the main periods of song activity half an hour after males entered the roost in the morning and before they left in the evening. For more clarity, *error bars* show only one tail of the symmetric 95% confidence range of means. Song rate was lower in the evening than in the morning (Wilcoxon test, $Z=-2.76$, $P=0.003$, $N=11$)

Results

Spontaneous song activity

Spontaneous territorial song activity of *S. bilineata* males was restricted to about half an hour during the main song periods in the morning and in the evening (Fig. 2). The song rate was higher during the 30 min after bats entered the roost in the morning (median 0.93 songs per male and minute) than during the 30 min before they left it in the evening (median 0.50 songs per male and minute). In the evaluation of playback experiments, we corrected for differences in spontaneous song rate (see "Methods" section). Not only did spontaneous song activity depend on the time of day, but it also decreased significantly with higher amounts of rainfall in the previous night (Spearman rank correlation of the amount of nightly rainfall and the number of spontaneous songs uttered per male during the 3-min phase before presentation of playback of stimuli, $r_s=$ −0.67, $P=0.025$, $N=11$ including all nine males from playback experiments and two additional males). Also, spontaneous song rate was greater in males with more territorial neighbours ($r_S=0.670$, $P=0.017$, $N=12$ including all nine males from playback experiments and three additional males), but also males without territorial neighbours responded to playbacks.

Male responses to playbacks

Apart from uttering territorial songs themselves, some males responded to the playbacks by immediately leaving their roost, flying or landing close to the speaker or even hovering in front of it for a short while. Such responses were usually observed at the beginning of playbacks. Usually, males that responded in the described way also replied with a high territorial song rate to the playbacks.

The song rate during the first 0–5 s after the presentation of stimuli (Fig. 3—median for all males 3.7 min^{-1}) was higher than or equal to the song rate during the ensuing 5–10-s interval (median 2.3 min^{-1}) in the playback trials of all except one male (this result was, however, not significant: Wilcoxon test, $Z=-2.0$, $P=0.055$, $N=9$). Thus, the majority of songs seem to have been immediate responses to the stimuli. The short time interval between playback stimuli and the response suggested that counter-songs were actually triggered by the playback stimuli and not by territorial songs of neighbouring males, which could have been the case in multi-male colonies.

Song response behaviour

The fact that territorial males actually responded to intruders simulated by playback stimuli enabled us to test
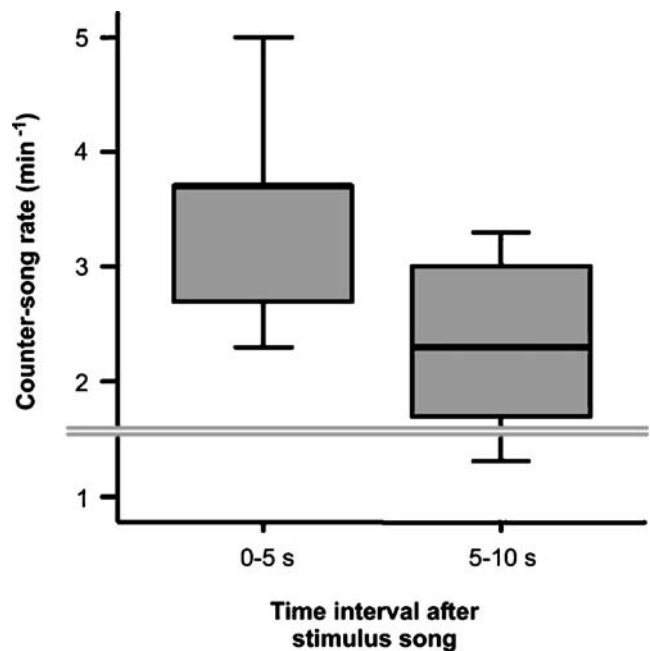
Fig. 3 Latency of response to single playback stimuli: song activity of nine *S. bilineata* males during 0–5 and 5–10 s after playback of single stimuli (rates are based on the number of songs initiated in that time period and extrapolated as songs per minute). Ten seconds was the minimum interval between two playback stimuli. The *double grey bar* indicates the median of the baseline song activity 3 min prior to and after playbacks (1.6 songs per minute). *Boxes* show median and interquartile range with minimum and maximum values as *whiskers*. Outliers and extreme values (with a distance from the box larger than 1.5 times the interquartile range) are not shown. Values for each male are means from three playbacks with high-, normal- and low-frequency stimuli. For all except one male, song activity was higher during the first 0–5 s than during the second 5–10-s interval after stimulus presentation. This result was, however, not significant (Wilcoxon test, $Z=-2.0$, $P=0.055$, $N=9$)

for the nature and encoding of the information transferred by territorial songs: we tested for differences in the acoustic response behaviour of males to playback songs with experimentally manipulated fundamental frequencies (high, normal and low frequency). The length (Friedman test, $\chi^2=$ 6.9, $P=0.031$, $N=9$) and rate (Friedman test, $\chi^2=18$, $P<0.001$, $N=9$) of counter-songs were significantly higher in response to the lower-frequency stimulus type (Fig. 4). Pairwise post hoc comparisons between different stimulus types showed a significant difference between all three stimulus types for counter-song rate (Friedman post hoc tests, $Q\geq3$, $P<0.01$, $N=9$) but only between low- and high-frequency stimulus types for counter-song length (Friedman post hoc tests, $Q=3.7$, $P<0.001$, $N=9$). Both parameters, song rate and length, could have been influenced by the number of females perched in a male's territory—a number likely to indicate the value of a territory and, hence, the potential loss from a male's point of view. However, there was no significant correlation for
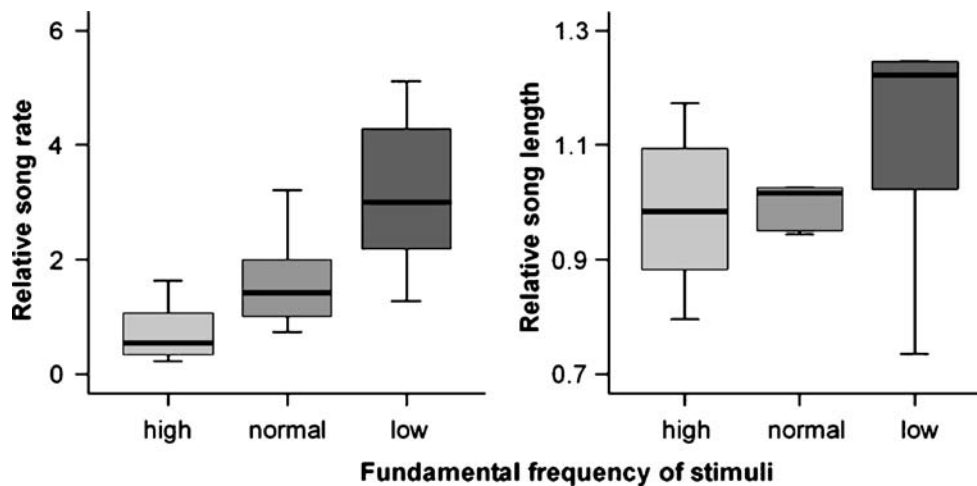
Fig. 4 Song rate (**a**) and length (**b**) of nine territorial *S. bilineata* males in playbacks with high-, normal- and low-frequency stimulus types (stimulus frequency is indicated by different shades of grey). Song rate and length are given for the entire 3-min period of playback presentation and relative to spontaneous song behaviour 3 min prior to and after playbacks (playback-phase values were divided by the mean values of pre- and post-phases—for details, see "Methods" section).

Details on *boxes* are given in the legend of Fig. 3. Differences in song rate were significant (Friedman test, χ^2=18, $P<0.001$, N=9), also in pairwise post hoc comparisons (Friedman post hoc tests, $Q\geq3$, $P<$ 0.01, N=9). Differences in mean song length were significant (Friedman test, χ^2=6.9, P=0.031; N=9) but only between high- and low-frequency stimulus types in pairwise post hoc comparisons (Friedman post hoc test, Q=3.7, $P<0.001$, N=9)

any of the three stimulus types (Spearman rank correlation of the number of females in a male's territory and counter-song rate and length relative to the spontaneous song behaviour prior to and after playbacks, $P>0.2$, N=9 for the nine males also included in the analysis of playback experiments).

Discussion

Territorial song behaviour and reproductive success of *S. bilineata* males

In *S. bilineata* males, a lower fundamental frequency of territorial songs is correlated with a higher reproductive success (Behr et al. 2006) and also with longer and more frequent counter-songs of competing males, as we could show in the playback experiments described here. Song fundamental frequency, hence, is an acoustic trait that conveys information on male reproductive fitness and that, consequently, indicates the imminent threat to territorial competitors, which adjust their response behaviour accordingly.

However, male song behaviour was not significantly dependent on the number of females present in the territory, a number that could indicate its value for the male. Possibly, the fact that territory tenure of *S. bilineata* males can last for many years may result in a certain independence of territory value from the momentary number of females roosting in it.

Signal design features and song activity patterns suggest that territorial songs are used in a context of information transfer between competing males. However, it seems likely that these songs play an additional role in female attraction and female choice as it has been shown for bird species (Otter et al. 1999; Poesel et al. 2001; Mennill et al. 2002). One reason is that females should benefit from choosing males that dominate in territorial interactions (Poesel et al. 2004).

Validity of playback experiments

A general problem of the experimental design we used is that it measures the response of a territory holder to a simulated intruder with the actual interest being the deterrence of an intruder by a territory holder (Searcy and Nowicki 2000). However, it is often assumed that when a certain acoustic trait indicates high competitive ability or aggressiveness, it will do so in all male rivalry situations and hence also cause a stronger response from male territory owners (e.g. Peake et al. 2002).

S. bilineata males respond with counter-songs to territorial songs of other males (Behr and von Helversen 2004) and intra-sexual counter-singing is generally assumed to serve the mutual assessment of rivals (Bradbury and Vehrencamp 1998). The costly singing behaviour of a high-quality opponent, therefore, is likely to elicit costly answers from a male trying to outplay its virtual adversary. This is especially true for territory holders facing the danger of losing a long-term territory as in *S. bilineata*. On the other hand, in order to reduce the cost of holding a territory, males should choose to answer with low-cost signals to songs indicating low-quality opponents that represent only a smaller threat of losing the territory.

There are many examples of territorial males in vertebrate species that increase the intensity of their territorial display in response to signals indicating an opponent of high quality, motivation or aggressiveness (e.g. Clutton-Brock and Albon 1979; Järvi et al. 1980; Catchpole 1983; Slabbekoorn and Cate 1997; see also review in Collins 2004).

Yet another problem may arise when playback stimuli simulate a very intimidating opponent and the focal animal chooses to retreat or decrease rather than increase its response (Collins 2004). There are some examples, especially in bird species, of high-intensity signals causing a retreat or lower response than low-intensity signals (Dabelsteen and Pedersen 1990; Otter et al. 1999; Langemann et al. 2000; Cramer and Price 2007; Hardouin et al. 2007; reviewed by Vehrencamp 2001).

Explanations for this behaviour often imply that animals have the opportunity to avoid opponents when retreating to a different part of their territory, which is usually the case in bird species but not in the small daytime roost territories of *S. bilineata*. Also, we used playback stimuli with frequencies well within the natural range that may not be perceived as an extremely intimidating challenger. Moreover, in *S. bilineata*, territory tenure is lifelong and displacement of a territorial male usually entails serious agonistic interactions and fighting (Tannenbaum 1975; Voigt and Streich 2003). Displaced territory owners were found dead a short while after losing their territory or otherwise disappeared from the roost and were never observed again. It thus seems unlikely that a territory holder would not respond to an intruder, however potent its territorial song.

Signal reliability

A pattern commonly observed in different animal species is that aggressive senders produce low-frequency and broad-band noisy signals in contrast to vocalisations of submissive individuals that tend to be higher in frequency and cover a narrower frequency band hence perceived as a purer tone (Morton 1977; Bradbury and Vehrencamp 1998).

However, the signalling of individual intentions or quality as well to competitors as to potential mates is prone to deceit and there has to exist a mechanism that prevents signallers from being dishonest. Several mechanisms have been put forward that may impede such cheating (reviewed in Vehrencamp 2000; Collins 2004). In index signals, message form and content are directly linked due to the physical design of the signal (Maynard Smith and Harper 1995). This has been shown for example for call pitch, body size and fighting ability in anurans (e.g. Davies and Halliday 1978) but seems to be uncommon in mammals, where the fundamental frequency of vocalisations depends on larynx size that, itself, is not necessarily linked to body

mass (Fitch and Hauser 2003). For example, studies in red deer (McComb 1991) and humans (van Dommelen 1993) have failed to show a dependency of fundamental frequency and body mass (but see Pfefferle and Fischer 2006). The same is true for two previous studies in *S. bilineata* (Davidson and Wilkinson 2004; Behr et al. 2006).

Handicap signalling (Zahavi 1975, 1977; Grafen 1990; Maynard Smith 1991) seems more likely to ensure the reliability of information on male quality in *S. bilineata* territorial songs (Behr et al. 2006). In handicap signals, "high-quality" signals are too costly to produce for low-quality males. In our example, the cost to pay would most probably be an energetic one and increase with longer, lower-frequency and more frequently repeated songs as it has similarly been assumed for red deer (Clutton-Brock and Albon 1979) and baboons (Fischer et al. 2004) in mammals or black-capped chickadees (Otter et al. 1997) and water pipits (Rehsteiner et al. 1998) in birds.

Territorial songs contain harsh buzz syllables and are the loudest of all *S. bilineata* social vocalisations (Behr et al. 2006), two characteristics that are assumed to increase energetic expenditure (Obwerger and Goller 2001) and that have been shown to correlate with male competitive abilities in birds (Galeotti et al. 1997; Otter et al. 1997; Rehsteiner et al. 1998). Correspondingly, spontaneous territorial song activity was lower after rainy nights that are generally assumed to limit the foraging time and prey density available to insectivorous bats and hence their energetic budget. Consequently, an energetic cost imposed on singers is the most likely explanation for our finding that *S. bilineata* males that utter more and lower-frequency territorial songs have a higher reproductive success and that males increase their acoustic territorial activity in response to low-frequency playback stimuli.

Territorial signalling by competing males

Counter-signalling by competing males has been analysed in behavioural experiments in several bird and anuran species (reviewed in Andersson 1994; Bradbury and Vehrencamp 1998; Collins 2004) but rarely in mammals (e.g. Clutton-Brock and Albon 1979; Kitchen et al. 2003; Fischer et al. 2004). This is possibly due to the fact that in many mammalian species social communication is based mainly on olfactory cues that are more difficult to investigate than the acoustic and optic signals prevalent for example in most bird species. Bats are exceptional mammals with respect to their dependence on the acoustic sense for orientation and also social communication. However, the mainly nocturnal activity and the inaccessibility of roosts impede a thorough analysis of social interactions in many bat species. This is not true for *S. bilineata* and therefore this species constitutes an

exceptional opportunity to study the social interactions and communication structure of a mammalian species. This may explain why *S. bilineata* is one of the few mammalian and the first bat species for which territorial signalling with songs that reflect male quality has now been shown.

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