

# Behavioral evidence for eavesdropping on prey song in two Palearctic sibling bat species

Patricia L. Jones · Rachel A. Page ·  
Manfred Hartbauer · Björn M. Siemers

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**Abstract** Eavesdropping on prey communication signals has never before been reported for a Palearctic bat species. In this study, we investigated whether lesser and greater mouse-eared bats, *Myotis blythii oxygnathus* and *Myotis myotis*, find tettigoniid bushcrickets (Tettigoniidae) by eavesdropping on their mate-attraction song. Tettigoniids are known to be the most important prey item for *M. blythii oxygnathus*, while carabid beetles and other epigaeic arthropods are the most important prey for its sibling species, *M. myotis*, in many places in Europe. *M. myotis* locates walking beetles by listening for their rustling sounds. We compared these two species' response to four acoustic prey cues: calling song of two tettigoniid species,

the rustling sound made by walking carabid beetles, and a control tone. Individuals of both bat species attacked the speaker playing tettigoniid song, which clearly indicates that both species eavesdrop on prey-generated advertisement signals. There were, however, species differences in response. *M. blythii oxygnathus* exhibited stronger predatory responses to the calling song of two species of tettigoniid than to the beetle rustling sound or the control. *M. myotis*, in contrast, exhibited stronger predatory responses to the beetle rustling and to one tettigoniid species but not the other tettigoniid or the control. Our study (1) for the first time demonstrates eavesdropping on prey communication signals for Palearctic bats and (2) gives preliminary evidence for sensory niche partitioning between these two sympatric sibling bat species.

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P. L. Jones · R. A. Page · B. M. Siemers (✉)  
Sensory Ecology Group, Max Planck Institute for Ornithology,  
Eberhard-Gwinner-Strasse 11,  
82319 Seewiesen, Germany  
e-mail: siemers@orn.mpg.de

P. L. Jones  
Section of Integrative Biology, University of Texas at Austin,  
1 University Station C0930,  
Austin, TX, USA

R. A. Page  
Smithsonian Tropical Research Institute,  
MRC 0580-06,  
Apartado 0843-03092, Panama City, Republic of Panama

M. Hartbauer  
Department of Zoology, Karl-Franzens Universität,  
Universitätsplatz 2,  
8010 Graz, Austria

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## Introduction

Eavesdropping on advertisement signals by predators and parasitoids is a behavior that can have important ecological and evolutionary effects. Peake (2005) defines eavesdropping as “the use of information in signals by individuals other than the primary target.” Using heterospecific signals to locate prey has been found across sensory modalities, including auditory (Ryan et al. 1982), chemical (Stowe et al. 1995; Roberts et al. 2001), and visual signals (Lloyd and Wing 1983). Eavesdropping can be an important selective force on the mate-attraction signals of prey (reviewed in Zuk and Kolluru 1998) and may also influence the

evolution of auditory capabilities (Bruns et al. 1989; Robert et al. 1992), ecology (Tuttle et al. 1985), and foraging behavior (Page and Ryan 2005) of predators. Eavesdropping on prey cues has been described for multiple species of bats in the Southern Hemisphere (Tuttle and Ryan 1981; Tuttle et al. 1985; Belwood and Morris 1987; Ryan and Tuttle 1987; Bailey and Haythornthwaite 1998) and North America (Buchler and Childs 1981; Spangler 1984; ter Hofstede et al. 2008), but never before in the Palearctic region.

Studies of eavesdropping by bats have often examined predation on tettigoniid bushcrickets (Orthoptera: Tettigoniidae) (Spangler 1984; Belwood and Morris 1987; Tuttle et al. 1985; Bailey and Haythornthwaite 1998; ter Hofstede et al. 2008), likely due to the fact that the song of tettigoniids extends well into the ultrasonic range (Heller 1988), exceeding 100 kHz in at least one tropical species (Morris et al. 1994). Therefore, frequency components of many bushcricket songs overlap with the hearing range of echolocating bat species, which is typically 20 to 80 kHz (Pollak et al. 1972). In Europe, tettigoniids make up a large proportion of the diet of the lesser mouse-eared bat, *Myotis blythii oxygnathus* (Arlettaz et al. 1997), but it is unknown how *M. blythii oxygnathus* locate their prey in the dense grass habitats where they forage (Arlettaz 1999). In this study, we investigated whether *M. blythii oxygnathus* find tettigoniids by eavesdropping on their calling song.

*M. blythii oxygnathus* has a morphologically very similar, but ecologically distinct sibling species, the greater mouse-eared bat, *Myotis myotis* (taxonomy and phylogeography discussed in Ruedi and Mayer 2001 and Bogdanowicz et al. 2009). Studies from central Europe have indicated that *M. myotis* and *M. blythii oxygnathus* avoid competition by foraging in different habitats and on the different prey associated with those habitats. *M. myotis* predominantly forages in forests and other areas with open, accessible soil (Arlettaz 1999), and mainly preys on large, epigaeic arthropods such as carabid beetles (Arlettaz 1996; Arlettaz et al. 1997), which it finds by listening for their rustling sounds (Kolb 1961; Arlettaz et al. 2001; Siemers and Güttinger 2006). *M. blythii oxygnathus*, in contrast, tends to forage in dense grass (Arlettaz 1999) and largely consumes tettigoniids (Arlettaz 1996; Arlettaz et al. 1997). The difference in diet between these two species in central Europe is disparate enough that fecal sample analysis has been suggested as a method for species identification (Arlettaz et al. 1997).

Simulated echolocation calls of *M. myotis* induce *Tettigonia viridissima* to exhibit escape responses (Schulze and Schul 2001), and repetitive ultrasonic 30 kHz pulses (10 ms pulse duration) frequently induce song cessation in this tettigoniid species (Hartbauer et al. 2010). The echolocation calls of *M. blythii oxygnathus* and *M. myotis*

are very similar (Russo et al. 2007), and the tettigoniids' behavior is most likely a generalized response to ultrasonic stimuli. *T. viridissima*'s song cessation in response to ultrasound could indicate that European bats are eavesdropping on tettigoniid song. We investigated whether the two bat species utilize the same prey cues (tettigoniid songs and beetle rustling) or instead if differences in sensory ecology play a role in partitioning their diet spectra.

The means by which sympatric species partition resources to enable stable coexistence have long been a topic of discussion and debate (e.g., Pianka 1981; Hubbell 2001; Tilman 2004). Many studies have examined coexistence maintained by morphological differences between species (reviewed in Schluter 2000). More recently, researchers have begun to examine the role of sensory ecology in partitioning resources between sympatric species (Tuttle et al. 1985; Bernays and Wcislo 1994; Swift and Racey 2002; Siemers and Schnitzler 2004; Siemers and Swift 2006; Safi and Siemers 2010). Differences in sensory ecology could allow one species to take advantage of a resource less accessible to the competing species. For example, a number of bat species detect prey by listening for the sound of prey movement (Fiedler 1979; Anderson and Racey 1991; Faure and Barclay 1992; Swift and Racey 2002; Siemers and Swift 2006). Relying on listening for prey sound versus using high-resolution echolocation allows two morphologically alike bat species to access different types of prey, resulting in dietary niche separation (Siemers and Swift 2006). Bat foraging behavior that utilizes eavesdropping could also have implications for resource partitioning between closely related species (Tuttle et al. 1985).

In this study we tested the following two hypotheses: First, we hypothesized that *M. blythii oxygnathus* eavesdrop on the mate-attraction signals of tettigoniids to locate individual prey ("eavesdropping hypothesis"). We thus predicted that they would attack or inspect a speaker playing tettigoniid song. Secondly, we hypothesized that the different food niches of the sibling bat species are mirrored in their different responses to acoustic prey cues ("sensory niche partitioning hypothesis"). We predicted that *M. blythii oxygnathus* would respond more strongly to playback of tettigoniid song than to playback of the rustling sounds of carabid beetles, and conversely that *M. myotis* would be more attracted to carabid rustling sound than to the song of tettigoniids.

## Materials and methods

### Animals and flight room

Our study was conducted in August 2009 at the Tabachka Bat Research Station (Ruse district, northern Bulgaria); the

field station of the MPIO Sensory Ecology Group, run in cooperation with the directorate of the Rusenski Lom Nature Park. Capture, husbandry, and behavioral studies were carried out under license of the responsible Bulgarian authorities (MOEW-Sofia and RIOSV-Ruse, 57/18.04.2006, 100/04.07.2007, 193/01.04.2009, and 205/29.05.2009). We adhered to the ABS/ASAB guidelines for ethical treatment of animals. Adult male *M. blythii oxygnathus* and *M. myotis* were caught at their roost caves in harp traps before dawn. At the field station, bats were kept under relatively constant, naturalistic temperature and light regime (14 h light: 10 h dark) with ad lib access to water and mealworms. If necessary, there were also hand-fed mealworms to maintain capture weight.

Bats were released together into a large flight room (8 m by 4 m; 2 m height) at least 3 h before dusk to become habituated to the room. At dusk, when experiments were initiated, all of the bats in the flight room were caught, and then only one bat was released into the flight room and tested at a time. Upon release, the bat was allowed to acclimate for 5 min before the tests began.

#### Experimental procedure

Each bat was exposed to a total of four different stimuli: calling song of two different European tettigoniid species (prey mate-attraction sounds), the rustling sounds of walking carabid beetles (prey locomotion sounds), and a tone (control). Each of the stimuli was broadcast using Avisoft Bioacoustics Recorder USGH through an Avisoft ScanSpeak Ultrasound speaker (frequency response  $\pm 4.5$  dB between 5 and 90 kHz) and Avisoft Ultra-SoundGate Player 116 USB box for D/A conversion. The speaker was placed in the center of the room and surrounded by branches with leaves for partial concealment. Four video cameras were positioned so that the speaker was clearly visible, and the video screen was marked so that we could determine when the bat flew within 1 m of the speaker.

Each playback lasted for a total of 6 min; stimuli were broadcast for 30 s, and then 30 s of silence followed. We expected bats to approach stimuli quickly, i.e., within the 30-s playback phases. Such a swift approach is important for efficient foraging and the prevention of prey escape (Nyberg 1971). Approaches during the 30-s silence phases were regarded to be less likely driven by foraging motivation. We thus compared the number of approaches during playback and silent phases as a measure of the bats' interest in the acoustic stimulus.

Each bat received the four 6-min stimuli in random order with 1 min in between each trial, a total of 27 min of testing for each bat. In the interval between trials, we entered the room and if the bat was hanging on the wall gently nudged

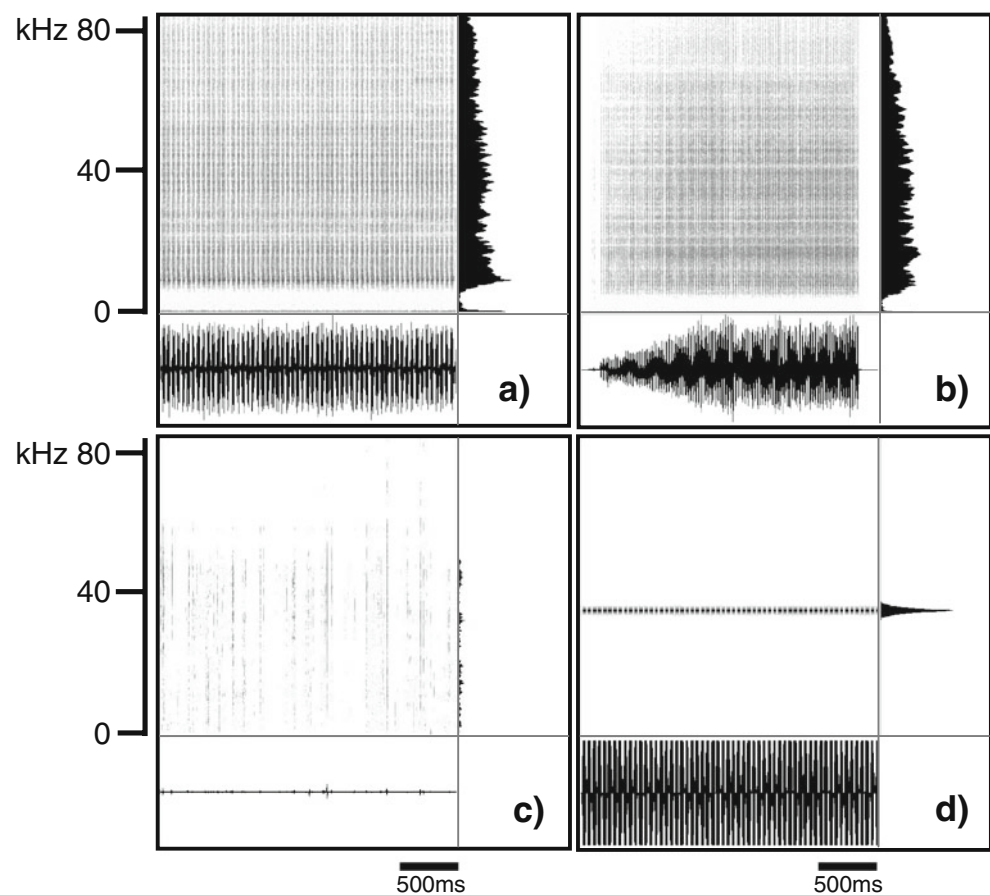
it into flight to ensure that the bat was equally alert for all tests. During the tests, we quantified the number of times the bat approached within 1 m of the speaker broadcasting the stimulus, and recorded whether the approach was in 30 s when the stimulus was playing or during the 30 s of silence. We also recorded landings on the speaker.

We tested a total of 13 *M. myotis* individuals and 22 *M. blythii oxygnathus* individuals. Of the 33 bats tested, 10 (77%) of the *M. myotis* and 13 (60%) of the *M. blythii oxygnathus* flew within 1 m of the speaker in response to at least one of the four stimuli. We classified the bats that approached at least one stimulus as “responsive” and excluded the non-responsive bats from our analysis. All bats were released at the site of capture upon completion of the experiments.

#### Playback stimuli

Examples of the playback stimuli are depicted in Fig. 1 in spectrogram and waveform representation. We used calling songs from two large European species of tettigoniid: *T. viridissima* and *Tettigonia cantans*. Tettigoniid calling songs were recorded using a 1/4-in. microphone (Type 40BE, G.R.A.S. Inc.; frequency range, 10 Hz–100 kHz) at a distance of 30 cm from a singing male (sampling rate, 166 kHz). Song recordings were made at the University of Graz by one of us (MH) with captive tettigoniids. Tettigoniid song is relatively stereotypical within species (3–10% variation of time parameters between individuals), but at the same time song parameters in these poikilothermic animals strongly depend on ambient temperature and thus on body temperature (>50% difference for 6° temperature difference). To capture some of this temperature-dependent song variation that potentially might affect the salience or attractiveness of tettigoniid song to bats, we chose to use recordings from two different temperatures for each *Tettigonia* species, which were randomly assigned to the tested bats. Unfortunately, we were limited in the number of available tettigoniids and could not present each bat with the song of a different individual insect. One *T. viridissima* individual was recorded at 28°C (62.5 Hz syllable rate) and another one at 22°C (40 Hz). Similarly, one *T. cantans* was recorded at 28°C (45.5 Hz) and another one at 21°C (26.3 Hz). The temperature difference did not affect the bats' behavior, and thus for each species, the data from the two temperatures were pooled [*T. cantans*: Fisher's exact test ( $N=16$  at 28°C, 7 at 21°C)  $p=0.405$ ; *T. viridissima*: Fisher's exact test ( $N=17$  at 28°C, 6 at 22°C)  $p=0.640$ ]. As even the large temperature-driven differences in song structure did not affect the bats' propensity to approach the playback speaker, we argue that the much smaller variation between *Tettigonia* individuals does very likely not play a role either. Despite our limited sample of individual tettigoniids, we are thus

**Fig. 1** Representative examples of the playback stimuli in spectrogram representation with waveform below and averaged power spectrum on the right. **a** Continuous pulsed calling song of *T. viridissima* at 28°C ambient temperature. **b** One verse of *T. cantans* song (28°C); verses were repeated with 2-s intervals. **c** Rustling sound produced by a carabid beetle (*C. monilis*) walking on dry grass. Note that the amplitude of the rustling sounds is much fainter than the tettigoniid song. **d** A pulsed tone as negative control stimulus (35 kHz; pulse duration 30 ms)



confident that our results are generally applicable for both investigated *Tettigonia* species and across a range of natural ambient temperatures. Natural amplitudes for both tettigoniid calling songs are quite loud with peak levels at 1 m of 94 dB SPL for *T. viridissima* (Keuper et al. 1988), and 84–87 dB SPL for *T. cantans* (M Hartbauer, unpublished). Tettigoniid songs of both species were average RMS-adjusted and broadcast at an average RMS amplitude of 75 dB SPL and a peak amplitude of 95 dB SPL, 1 m from the speaker. Playback amplitudes were determined with a broadband Avisoft condenser microphone (Type CM16/CPMA) and ultrasound recording interface (UltraSoundGate 416H, Avisoft-Bioacoustics, Berlin, Germany), which we had calibrated against a 1/8-in. measurement microphone (Type 40 DP, G.R.A.S., Holte, Denmark). *T. viridissima* generally sings nonstop for hours, so for this species, the 30 s of playback was constant (double syllable rate 13.9 Hz at 22°C and 19.6 Hz at 28°C). *T. cantans*, on the other hand, generally sings for 1–4 s (mean  $\pm$  SD, 4.3 $\pm$ 1.4 s (21°C); 2.68 $\pm$ 0.62 s (28°C)) interrupted by pauses of 3–6 s (mean $\pm$ SD, 5.7 $\pm$ 7.4 s (21°C); 3.78 $\pm$ 3.39 s (28°C)) (Grossauer 2010). We approximately replicated this natural call timing by playing a 2.4-s call followed by 2 s of silence repeatedly for 30 s.

The third stimulus was a recording of the rustling noises produced when different individual carabid beetles (*Carabus monilis*) walk on dry grass (mown meadow), broadcast at an average RMS amplitude of 46 dB SPL 1 m from the speaker. The rustling sounds were recorded with a 1/2-in. high-sensitivity condenser microphone (Type 40HH, G.R.A.S., Holte, Denmark), sampled at 192 kHz and high-pass-filtered at 500 Hz. These beetle rustling sounds are series of faint, broadband, click-like signals with the main energy content between 3 and 30 kHz; some energy goes up to 50 kHz and for single, loud transients to 100 kHz (for details see Goerlitz et al. 2008).

The final stimulus was a negative control to which we did not expect the bats to respond. Here, we used Cool Edit 2000 (Syntrillium Inc.) to create a pulsed tone at the same dominant frequency as the *T. cantans* song (35 kHz). Each pulse of sound was 30 ms long and tapered for 5 ms on either side with 15 ms of silence in between. This is approximately the same timing as the sound pulses within the natural tettigoniid song and was played at a peak amplitude of 96.5 dB SPL 1 m from the speaker. This peak amplitude is within range of the tettigoniid peak amplitude levels (our tettigoniid peak playback amplitude was 95 dB SPL; see above).

## Statistics

Statistics were computed using SPSS 15.0 for Windows. To account for multiple tests per species, we followed Neuhauser (2004) and, in addition to the individual  $p$  values, computed summary  $p$  values from the truncated product method (TPM). TPM  $p$  values were calculated using a program (tpm.exe) provided at <http://statgen.ncsu.edu/zaykin/tpm/> (see Zaykin et al. 2002) to test whether any of the tests with  $p < 0.05$  are indeed significant (Neuhauser 2004).

## Results

### Attacks on the speaker

Seven out of the 23 responsive bats briefly landed on the loudspeaker during playback trials (see [Supplementary videos](#) for examples). Brief landings of this type are typically seen in prey capture bouts in both *M. myotis* and *M. blythii oxygnathus* (Arlettaz et al. 2001; Russo et al. 2007; Schaub et al. 2008). A total of 28 landing events occurred, 27 during the 30-s playback phases and a single one during an interspersed 30-s silent phase (Table 1). Each bat showed landing behavior for just one of the four playback stimuli it received. In all seven bats, this was always an acoustic prey cue and never the control tone. Out of the 28 landings, 27 occurred during playback trials with tettigoniid calling song (six out of seven bats). The single landing attack of the seventh bat was during playback of carabid rustling sound. Individuals of both bat species attacked the speaker during tettigoniid song playback.

### Approaches to the speaker

*M. blythii oxygnathus* approached the speaker more often during the 30 s playback phases than during the 30-s silent phases for song playback of both tettigoniid species, but not for the rustling of carabid beetles or the control tone (Fig. 2a).

**Table 1** Number of landing events on speaker for all seven bats that showed landing behavior

Species	Individual	<i>T. viridissima</i>	<i>T. cantans</i>	Rustle	Tone
<i>M. myotis</i>	39	0	1	0	0
<i>M. myotis</i>	65	0	4	0	0
<i>M. blythii oxygnathus</i>	22	0	0	1	0
<i>M. blythii oxygnathus</i>	24	1	0	0	0
<i>M. blythii oxygnathus</i>	14	3 <sup>a</sup>	0	0	0
<i>M. blythii oxygnathus</i>	25	0	12	0	0
<i>M. blythii oxygnathus</i>	31	0	6	0	0
# of individual bats that landed		2	4	1	0

<sup>a</sup> One landing event of this bat was during an interspersed 30-s silent phase. All others were during the 30-s playback phases

Generally, *M. myotis* was more responsive than *M. blythii oxygnathus*, (repeated measures ANOVA, between subjects effect,  $F_{1,21}=7.6$ ,  $p=0.012$ ; compare Fig. 1a, b). Specifically, *M. myotis* approached the speaker more often during the 30-s playback phases than during the 30-s silent phases for the carabid rustling sounds and the *T. cantans* song. There was no difference for *T. viridissima* song or the control tone (Fig. 2b).

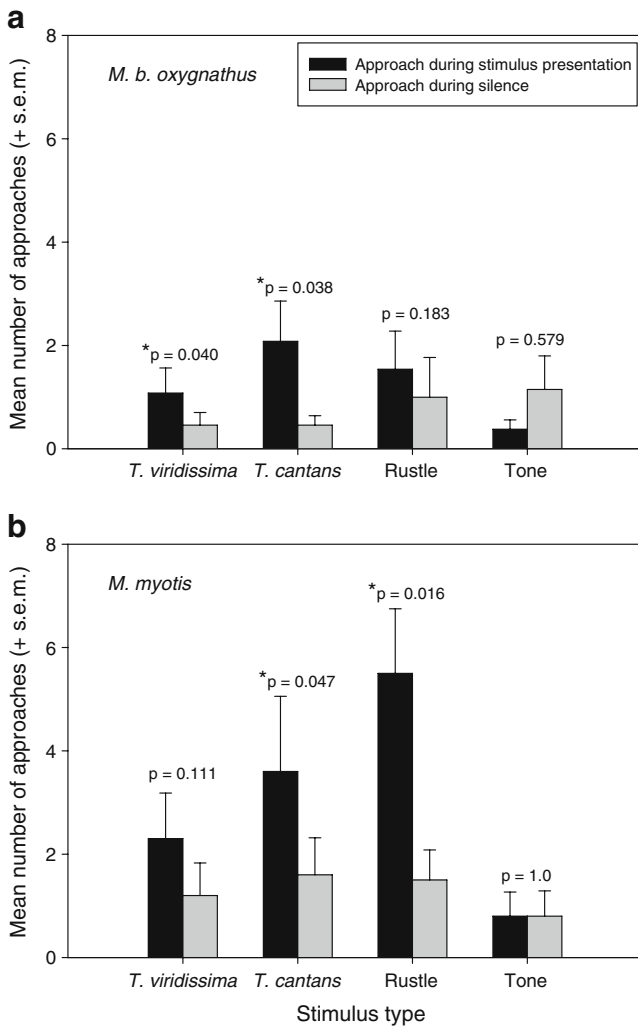
This pattern is also demonstrated in the proportions of individual bats that approached the speaker in response to different stimuli (Fig. 3). A considerably larger proportion of *M. myotis* reacted to the carabid rustling sounds than did *M. blythii oxygnathus* (eight out of 10 *M. myotis* versus five out of 13 *M. blythii oxygnathus*;  $\text{Chi}^2=4.0$ ,  $p=0.046$ ).

## Discussion

### Eavesdropping on prey mate-attraction signals

Both *M. myotis* and *M. blythii oxygnathus* exhibited predatory behavior (landed on the speaker) in response to the song of *T. cantans* and *T. viridissima*, two tettigoniid species that are abundant in Bulgaria (Fauna Europaea 2010). No bats landed on the speaker in response to the control tone, indicating that the response is not generalized to any sound at this frequency but rather particularly to these insects' mate-attraction signals. Our experiments thus supported the eavesdropping hypothesis not only for *M. blythii oxygnathus* but also, unexpectedly, for *M. myotis*. This is the first time eavesdropping behavior has been demonstrated in a Palearctic bat species.

Foraging behavior in which bats predate on tettigoniids by eavesdropping on their mate-attraction signals could be an important selective force influencing the acoustic communication of tettigoniids. Changes in calling behavior that reduce predation have been demonstrated in temperate (Spangler 1984; Faure and Hoy 2000) and Neotropical tettigoniids (Belwood and Morris 1987). Belwood and Morris (1987) showed that tettigoniid species calling in forested areas with an abundance of foliage gleaning bats



**Fig. 2** Mean number of approaches within 1 m of the speaker for each stimulus during stimulus presentation versus during the interspersed silent phases for *M. blythii oxygnathus* (**a**,  $n=13$  individuals) and for *M. myotis* (**b**,  $n=10$  individuals).  $p$  values from paired  $t$  tests are given above each stimulus type. To account for multiple tests per species, we computed summary  $p$  values from the truncated product method (see “Materials and methods”). These were  $p=0.0111$  for *M. blythii oxygnathus* and  $p=0.0045$  for *M. myotis*

(FGB) have lower call duty cycles than species in open areas with fewer FGBs, and species in forested areas used more vibratory communication signals, a behavior which is safe from acoustic eavesdropping and absent in tettigoniid species from open areas. They also found that FGBs are more successful at locating tettigoniid individuals with higher duty cycle calls, indicating that eavesdropping by bats has likely selected for reduced song duty cycle and increased substrate-born signaling in the forest tettigoniid species with which FGBs most frequently co-occur.

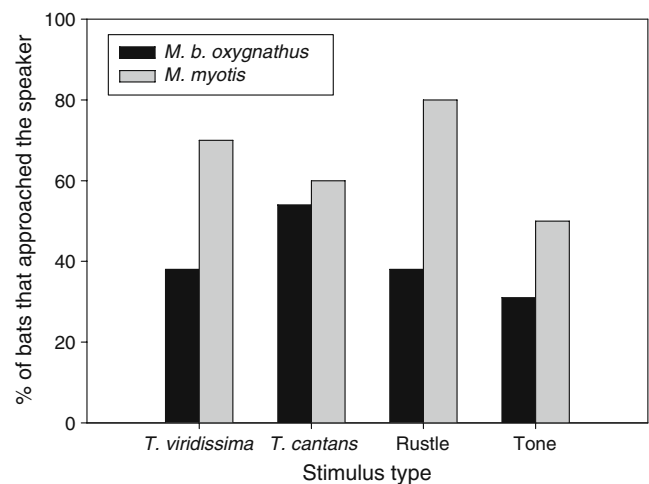
Eavesdropping responses of *M. myotis* and *M. blythii oxygnathus* to the song of *T. cantans* and *T. viridissima* could therefore be affecting the calling and mate choice

behavior of these and other Palearctic tettigoniid species. Male *T. viridissima* experience less call attenuation when they call from higher sites on vegetation, but they are not typically found on the highest vegetation points available (Arak and Eiriksson 1992). This may reflect a trade-off between maximizing the range over which their signals can be detected, and minimizing predation risk, possibly from eavesdropping bats as well as visually hunting birds. For instance, male field crickets, *Teleogryllus oceanicus*, are less likely to be consumed by bats when calling from their preferred refuges than when calling in the open, and they produce longer calls, which are more attractive to bats, from refuges than when in the open (Bailey and Haythornthwaite 1998).

The singing location preferences of the two tettigoniid species, however, are different. *T. cantans* generally sings from relatively conspicuous places on vegetation 0.5–2 m off the ground (Hartbauer, personal observations), while *T. viridissima* males usually sing from more elevated and hidden locations in tall bushes and trees (Arak and Eiriksson 1992; Hartbauer, unpublished data). This difference in conspicuousness of singing sites could render *T. cantans* generally more accessible to bats than *T. viridissima*.

#### Sensory niche partitioning

Documentation from Switzerland and Portugal (Arlettaz et al. 1997) demonstrates that tettigoniids are the main prey for *M. blythii oxygnathus* in summer and autumn (average May–September percentage volume in fecal samples from Switzerland 60%, with up to 92% in September; from Portugal, 99% in June), and are much less used by *M.*



**Fig. 3** Percentage of the responsive bats (individuals that responded to at least one of the stimuli) that approached within 1 m of the speaker in the 6 min they were exposed to each stimulus.  $N$ , i.e. 100%, was 13 for *M. blythii oxygnathus* and 10 for *M. myotis*

*myotis* (May–September average below 1% in Switzerland; 13.5% in Portugal in June). It is not entirely unproblematic to quantitatively compare *Myotis* diets from these locations due to differences in climate and potential availability of prey over time, but the differences between species remain striking. Yet, in our study in Bulgaria, both *M. blythii oxygnathus* and *M. myotis* exhibited clear predatory responses to tettigoniid song. It is possible that there are regional differences in diet between Bulgarian populations and well-studied populations in central Europe and the Iberian Peninsula (Arlettaz 1996; Arlettaz et al. 1997; Pereira et al. 2002, Zahn et al. 2007), such that Bulgarian *M. myotis* are consuming larger proportions of tettigoniids than elsewhere.

Stable isotope analyses of wing tissue indeed indicated that Bulgarian *M. myotis*, in addition to carabid beetles and other secondary consumer arthropods (Bayesian mixing model estimate, 38%), eat up to 62% tettigoniids or other primary consumers, though *M. blythii oxygnathus* still consumes 30% more of those (up to 93%; BM Siemers, S Greif, I Borissov, SL Heucke-Voigt, CC Voigt, unpublished data). Since these data come from wing tissue, collected in August, rather than fecal samples, the isotope balance is an average over the preceding few months (CC Voigt, personal communication). Regardless, Bulgarian *M. myotis* apparently consume a much larger percentage of primary consumers than their central European counterparts. It is remarkable that trophic resource partitioning between these two sibling species is much more clear-cut in Switzerland than in Bulgaria. It would thus be interesting for future research to investigate whether the clearer trophic segregation in the Swiss populations is also mirrored in sensory ecology, i.e., in stronger differences in responsiveness to prey stimuli (tettigoniid song versus rustling sounds). Pereira et al. (2002) found that crickets were the preferred prey of *M. myotis* in Southern Portugal, and postulated that this could be due to the crickets' conspicuous calling behavior. If *M. myotis* in Portugal indeed eavesdrop on the calls of crickets when foraging, it is not so surprising that Bulgarian *M. myotis* respond to the calling song of tettigoniids.

Our results support the sensory niche partitioning hypothesis by demonstrating differences in sensory ecology between *M. myotis* and *M. blythii oxygnathus* in the predicted direction (*M. myotis* responded more strongly to the rustling sounds of walking arthropods and *M. blythii oxygnathus* more to tettigoniid song); however, these differences were slight. Thus, they are likely not the main factor determining diet partitioning between these two sibling species in the Balkanic area of sympatry. We assume that habitat selection—as documented for Swiss sympatric populations (Arlettaz 1999)—is an additional important mechanism driving resource partitioning.

## Conclusions

The documentation of eavesdropping in a Palearctic bat species, and particularly in two species whose ecology has been relatively well studied, opens up new areas in both chiropteran and tettigoniid behavioral ecology. From the bat perspective, further investigation is needed to understand the use of eavesdropping as a foraging strategy, e.g., quantifying detection distances for singing tettigoniids and the potential for assessing prey taxon (and thereby profitability or accessibility) from tettigoniid song. In turn, the singing and courtship behavior of Palearctic tettigoniids will need reassessment in view of the predation pressure from eavesdropping bats, and the evolution of appropriate defensive measures. For example, do Palearctic tettigoniids in areas with high numbers of eavesdropping bats show reduced duty cycles but increased tremulation in their sexual displays? Are there singing locations safe from predatory bats, and do the tettigoniids retreat to them as a function of bat predation pressure?

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