

Similar is not the same: Social calls of conspecifics are more effective in attracting wild bats to day roosts than those of other bat species

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Abstract Many bat species regularly need to find new day roosts as they require numerous shelters each breeding season. It has been shown that bats exchange information about roosts among colony members, and use echolocation and social calls of conspecifics in order to find roosts. However, it is unclear if wild bats discriminate between social calls of conspecifics and other bat species while searching for roosts. Furthermore, the extent that bats are attracted to potential roosts by each of these two call types is unknown. We present a field experiment showing that social calls of conspecifics and other bat species both attract bats to roosts. During two summers, we played back social calls of Bechstein's bats (*Myotis bechsteinii*) and Natterer's bats (*Myotis nattereri*) from different bat boxes that can serve as roosts for these species. All experimental bat boxes were monitored with infrared video to identify the approaching bat species. Three species (*M. bechsteinii*, *M. nattereri*, and *Plecotus auritus*) approached the boxes significantly more often during nights when bat calls were played compared to nights without playbacks. Bechstein's bats and Natterer's bats were both more attracted to social

calls of conspecifics than of the other species, whereas *P. auritus* did not discriminate between calls of either *Myotis* species. Only Bechstein's bats entered experimental boxes and only at times when calls from conspecifics were played. Our findings show that wild bats discriminate between social calls of conspecifics and other bat species although they respond to both call types when searching for new roosts.

Keywords Communication · Eavesdropping · Echolocation · Playback · Roost finding · Social calls · Species discrimination

Introduction

Small vertebrates frequently suffer high predation risks and/or high energetic costs and thus often strongly depend on shelters for survival and reproduction (Kappeler 2009). As a result, it is crucial for them to find suitable shelters. Optimal shelters offer protection from predators (Manser and Bell 2004) and adverse climatic conditions (Genoud and Bonaccorso 1986; Schwarzkopf and Alford 1996), are free of parasites (Christe et al. 1994; Reckardt and Kerth 2007), and are close to feeding grounds (Kunz and Fenton 2003). The need for finding shelters is particularly high if many are required as it is typical for bats that roost in tree cavities and frequently switch day roosts (Kerth and König 1999; Willis and Brigham 2004). Roost switching helps bats to reduce parasite infestation in roosts that get increasingly infested the longer the bats use them (Lučan 2006; Reckardt and Kerth 2007). It also enables bats to select ideal roosting temperatures that depend on changing weather conditions and the bats' reproductive status (Kerth et al. 2001a; Pretzlaff et al. 2010). The need of finding new roosts is further enhanced as colonies of many tree cavity-

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roosting bats regularly split into several subgroups that use separate roosts (Kerth and König 1999; O'Donnell 2000; Popa-Lisseanu et al. 2008; Willis and Brigham 2004). Moreover, roost switching of individuals between the colony's subgroups contributes to group cohesion as this maintains the contact between the colony members during temporary fission events (Willis and Brigham 2004).

It has been shown that in some bat species such as Bechstein's bats, colony members exchange information about the location of suitable roosts, but what cues bats use for this information transfer is largely unknown (Kerth and Reckardt 2003). Ruczyński et al. (2007) showed that under lab conditions, noctule bats (*Nyctalus noctula*) used echolocation calls of conspecifics played back from an artificial tree cavity to find the roost. The echolocation system of bats is an adaptation to orientation in the dark (Schnitzler and Kalko 2001) but may also be used for inadvertent communication (Dechmann et al. 2009; Gillam 2007; Siemers and Kerth 2006). Echolocation calls can indicate the presence and location of the emitting bats, as well as their age and sex (Kazial et al. 2008; Masters et al. 1995). They thus are suited for passively transferring information to eavesdropping individuals (Fenton 2003; Gillam 2007). By using playbacks, Barclay (1982) showed that echolocation calls attract free-ranging little brown bats (*Myotis lucifugus*) to roosting sites. Nevertheless, echolocation calls are of limited use for information transfer due to their high frequencies, which limit detection ranges, and the constraints on their structure for use in orientation (Siemers and Kerth 2006).

Social calls, which are intentionally emitted signals in contrast to echolocation calls, are probably much more important for communication in bats. Their lower frequencies and higher structural variability allow for longer detection ranges and coding of more information (Pfalzer and Kusch 2003). Social calls are used in various social interactions (Pfalzer and Kusch 2003) and have been shown to attract (Russ et al. 2004; Wilkinson and Boughman 1998) or repel (Barlow and Jones 1997) other bats from feeding sites, depending on the species and situation. In pallid bats (*Antrozous pallidus*), social calls lead individuals to crevices where conspecifics roost (Vaughan and O'Shea 1976). Moreover, a recent study by Chaverri et al. (2010) showed that neotropical Spix's disk-winged bats (*Thyroptera tricolor*), which have been captured and then released close to an unfamiliar roost where a conspecific was located, were attracted by social calls of this conspecific to the roost. However, the extent that free-ranging bats use social calls of conspecifics and other bat species for roost finding is largely unknown.

We present an experimental field study investigating whether wild free-ranging bats react to social calls of conspecifics and other bat species when searching for roosts at night. In the summers of 2008 and 2009, we

conducted a playback experiment to examine if social calls of Bechstein's bats (*Myotis bechsteinii*) and Natterer's bats (*Myotis nattereri*) attract conspecifics and other tree cavity-roosting bats to bat boxes that can serve as communal day roosts for each of them (the different species do not roost together). For the playbacks, we used bat calls available from a Sussex AutoBat (Hill and Greenaway 2005). We analyzed the effects of different bat calls played at night from bat boxes on Bechstein's bats and, to a lesser extent, on Natterer's bats and brown long-eared bats (*Plecotus auritus*). The behavior of the approaching bats was filmed with infrared video. Playbacks of social calls of Bechstein's bats from the AutoBat have been successfully used to lure Bechstein's bats into mist nets (Goiti et al. 2007; Hill and Greenaway 2005, 2008). We therefore assumed that if Bechstein's bats, Natterer's bats, and brown long-eared bats use social calls of conspecifics and/or other bat species to find roosts, then bats would approach more often to bat boxes where social calls are played back during our experiment. Moreover, if bats can distinguish between calls of conspecifics and that of other bat species, they should be more attracted to calls of conspecifics because Bechstein's bats, Natterer's bats, and brown long-eared bats roost separately from each other during summer.

Methods

Study population and site

The study was carried out from July to September 2008 and from August to September 2009 in a deciduous forest near Würzburg, Germany. Over the last 20 years, a large number of bat boxes (2FN, Schwegler, Germany) have been placed and monitored in an area of about 0.5 km². Maternity colonies from three bat species have been found: One Bechstein's bat colony, one Natterer's bat colony, and three colonies of brown long-eared bats. All five colonies used tree cavities and bat boxes as day roosts within our study area. During 2008 and 2009, there were 169 and 124 bat boxes available for the bats, respectively. All boxes were checked every morning for roosting bats, which can be seen with a flashlight through the entrances of the boxes without opening them (Kerth and König 1999).

All adult Bechstein's bats and all adult brown long-eared bats had been marked with individual passive integrated transponder (PIT) tags (Trovan, Germany; Kerth and König 1999) for previous research. Colony sizes are available for both species as we monitored occupied boxes daily with automatic PIT-tag readers that allow for determining the number and identity of bats emerging from the roosts in the evening (Kerth and Reckardt 2003). These data were also used to confirm that the bats had left their roosts and thus were

active during the experimental nights. Moreover, we captured colonies at least once per year. The Bechstein's bat colony comprised 14 PIT-tagged adult females and 11 unmarked juveniles in 2008, as well as 18 PIT-tagged adults and 11 unmarked juveniles in 2009. Taken together, the three long-eared bat colonies comprised 42 PIT-tagged adult females and at least 11 unmarked juveniles in 2008, and 48 PIT-tagged adults and at least six unmarked juveniles in 2009 (not all juveniles could be captured in 2008 and 2009). The Natterer's bats had not been marked but we estimated their colony size at least once a year by visual inspection after opening the boxes in which they roosted. This colony contained 20–30 bats (adults and juveniles) in both years.

Playbacks

We used the Sussex AutoBat (University of Sussex, UK; Hill and Greenaway 2005) for playing back bat calls. The

AutoBat is a synthesizer consisting of a microprocessor, a frequency generator, and an amplifier, supplied by a 12-V battery (Hill and Greenaway 2005). From eight different call types that had been uploaded to the AutoBat by the manufacturer, we used three: BPSC, BESC, and NPSC (for sonograms, see Fig. 1). BPSC is based on a single social call that is repeated in a sequence of five calls. Each sequence lasts about 0.5 s and is continuously emitted from the AutoBat with gaps of ca. 1.5 s between sequences (Fig. 1). BESC contains a 1.6-s-long sequence of 52 echolocation calls and a social call that is repeated three times. This sequence is also emitted continuously from the AutoBat with gaps of ca. 3 s between sequences (Fig. 1). All Bechstein's bat social calls in BPSC and BESC had been recorded in England with an automated recorder that ran all night from outside a tree cavity that served as maternity roost for a colony of at least 30 adult females (Hill and Greenaway 2005; D. Hill, personal communication). As

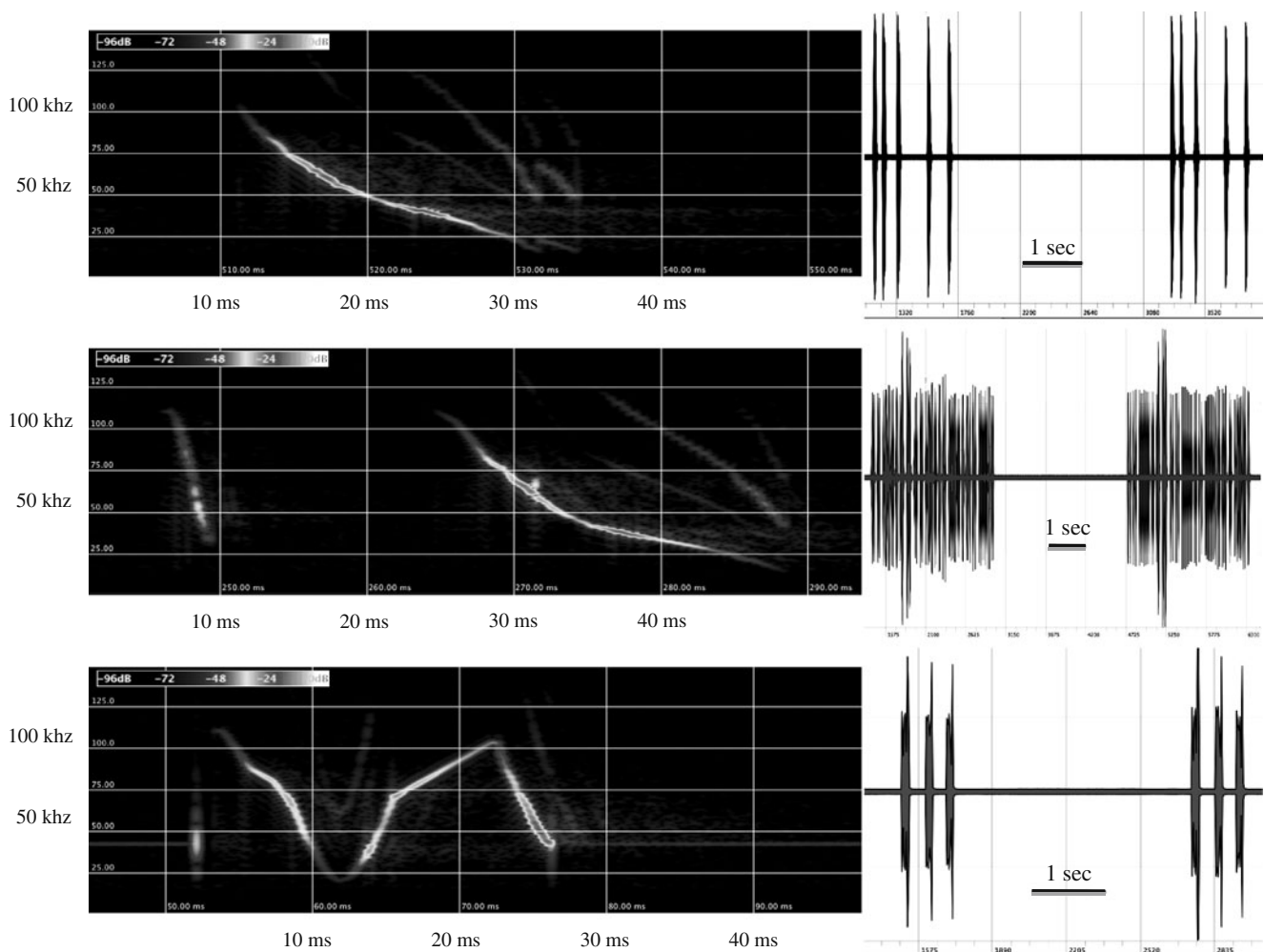


Fig. 1 Sonograms (*left*) and time sequences (*right*) of the three call types emitted from the AutoBat. From *above to below*: BPSC, BESC, and NPSC. The call frequency (in kilohertz) of the sonograms is given on the *y*-axes and the time (in millisecond) is given on the *x*-axes. The

recordings were done with a batcorder (eco Obs, Runkel, Marckmann and Schuster GbR, Germany) and visualized with the program bcAnalyze (eco Obs, Runkel, Marckmann and Schuster GbR, Germany)

there were no volant juveniles at the time of recording, adult females had emitted the recorded calls. The manufacturer selected the clearest calls and synthesized them. BPS and BESC contain a different social call, repeated five and three times, respectively. The sequence of 52 Bechstein's bats echolocation calls in BESC originate on three calls from one released adult female (D. Hill, personal communication). All calls used for the playbacks are similar in structure and shape to social and echolocation calls recorded from members of our studied Bechstein's bat colony inspecting potential day roosts in the study site (Fig. 2). Finally, NPSC is based on a recording of a male Natterer's bat in front of a mist net in England (D. Hill, personal communication). It contains a highly modulated social call. This call is emitted in sequences of three calls of ca. 0.25 s each. Again, sequences are emitted continuously from the AutoBat with gaps of about 1 s between sequences (Fig. 1). The AutoBat's output exceeds the natural rate of a single bat's social calling (D. Hill pers. communication), and thus we expect it to be representative of a situation where many bats are calling simultaneously. We played back one call type per night, from dusk to dawn, each.

During our experiments, the AutoBat's loudspeaker was placed inside bat boxes, without blocking the box entrances. For identification of marked Bechstein's bats and brown long-eared bats that may enter the box during the experiment, all experimental boxes were equipped with automatic transponder readers (Kerth and Reckardt 2003).

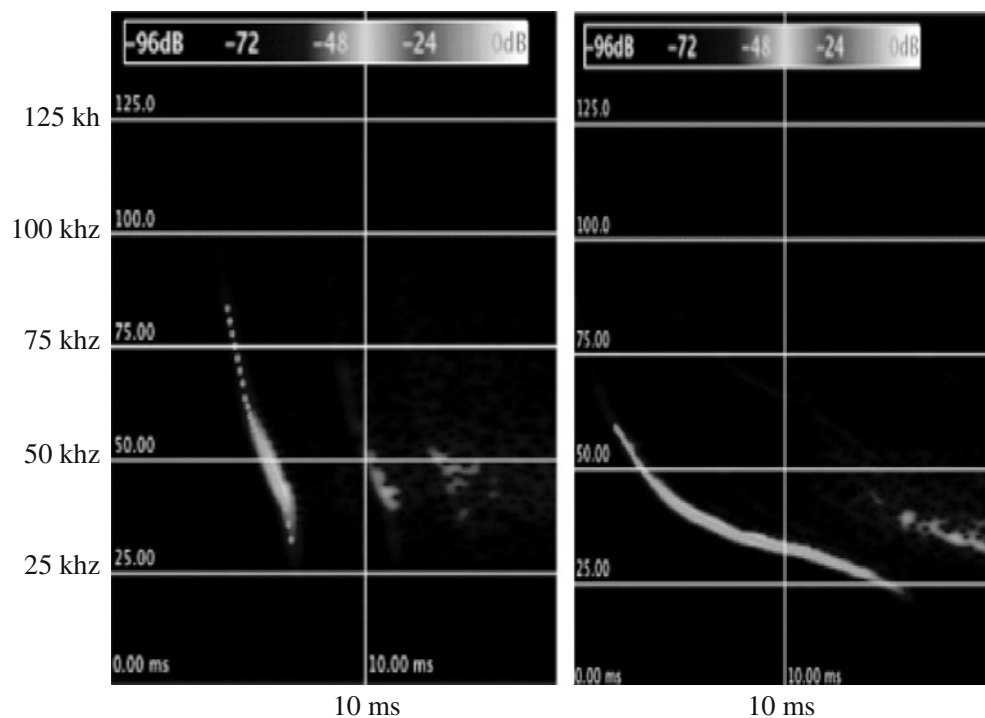
We organized the playback experiment into 10 replicates (six in 2008 and four in 2009), each consisting of four

successive treatment nights (one call type per night and a control night without playbacks). The order of the treatments was chosen randomly per replicate. As the Bechstein's bat was our main target species, we used for the playbacks unoccupied boxes located 30 to 100 m from the nearest occupied Bechstein's bats' day roost. When a replicate was completed after the fourth treatment night, we moved the AutoBat to another unoccupied bat box in the study area that fulfilled the aforementioned criteria and started a new replicate of four playback nights. If the weather allowed for it, we used four successive nights per replicate. However, in cases of rain (2008, nine events; 2009, three events), we had to wait for up to eight nights between treatment nights to finish a given replicate.

Video recordings

To monitor the behavior of bats approaching an experimental bat box, we filmed the boxes during each treatment. The video equipment consisted of a 12-V CCD infrared camera (ICD-47E, Ikegami Tsushinki, Japan) and a 12-V video recorder (in 2008, analog recorder AG-1070 DC, Panasonic, Japan; in 2009, digital recorder PV-500, Law-Mate Technology Co., Ltd., Taiwan). Furthermore, we used a 12-V infrared floodlight (Videor Technical, Germany) for illumination. Recordings started about 1 hour before nightfall and ended soon after sunrise. The camera was mounted on a 1.2-m-high tripod, which was placed in front of the box, about 5 m away. The camera was oriented

Fig. 2 Sonograms of a Bechstein's bat echolocation call (*left*) and a Bechstein's bat social call (*right*). The call frequency (in kilohertz) of the sonograms is given on the *y-axis* and the time (in millisecond) is given on the *x-axis*. Both calls have been recorded from bats flying in front of an unoccupied bat box in the study site using batcorders (eco Obs, Runkel, Marckmann and Schuster GbR, Germany). They were visualized with the program bcAnalyze (eco Obs, Runkel, Marckmann and Schuster GbR, Germany)



towards the bat box and had a viewing radius of approximately 2 m around it.

Analysis of the videos

On each recording, every appearance of bats was registered and the species were determined, mainly by the lengths of their ears and the shape of their faces. Some bats could not be identified because they were only partly visible; these bats were excluded from the subsequent analyses. All video analyses were done by the same person.

We classified the types of bat approaches into: (1) passing bats, (2) circling bats (flying circles in a distance of more than 0.5 m around the bat box), (3) direct approach to the bat box (direct flights towards the bat box with a distance of less than 0.5 m), and (4) bats entering the bat box. In the latter case, we attempted to identify the individuals with the automatic transponder reader attached to the experimental box. Individuals that entered a bat box more than once per night may have recognized that the calls played back did not derive from bats. Thus, we made an additional analysis in which we excluded revisits of bats in the same night. To avoid that a bat was counted twice when it briefly left the visible area while still circling around the box, we defined a new bat's approach when at least 30 s had passed after a bat had been recorded on the videos. Previous video observations with larger viewing radius (about 5 m) suggested that wide-ranging circling behavior of bats around the bat box did not take place for more than 30 s (C. R. Schöner, unpublished data). In cases when several bats were simultaneously present, we defined a new bat approach when the last bat had left the visible area for at least 30 s.

Statistical analysis

We used Fisher's exact tests to compare for each bat species the total number of approaches per treatment over all boxes. In addition, we used non-parametric Friedman tests, matched per box, for comparisons between the different treatments. This way, we controlled for a possible influence of the location of the 10 experimental boxes on the number of approaching bats. First, we performed two Friedman tests to assess the influence of two potentially confounding variables (temperature and treatment order). We tested if the minimal nightly temperatures differed between the four treatment nights of the 10 replicates to exclude that the bats' activity depended on different temperatures in the treatment nights (temperature data were provided by the Bavarian State Institute of Forestry, Department Forest Ecology, Climate and Water Protection). To measure if treatment order per replicate had an effect on the number of approaching bats, we compared the number of arriving Bechstein's bats, which

was the species with the most approaches, over the four treatment nights per box. Afterwards, we tested for the effect of our treatments (different call types) by comparing the numbers of approaching bats for each of the three study species. We tested for all bat approaches together and, in the case of Bechstein's bat approaches, also separately for each type of approach (passing, circling, direct approach to the bat box, and entering). As both Bechstein's bat call types (BESC and BPSC) contained social calls, we additionally combined the two call types into a single treatment "Bechstein's bat calls". To compare this treatment with the two other treatments (NPSC and control), we calculated the average number of Bechstein's bat approaches during the two types of Bechstein's bat calls per replicate (total number/2). If the Friedman tests detected significant ($P \leq 0.05$) differences between the treatments, we used Wilcoxon matched pairs tests to explore pairwise differences post-hoc. We corrected the obtained P values for multiple testing using a sequential Bonferroni correction. All tests were done with the software XLSTATPro 2009 (Addinsoft S.A.R.L., USA).

Results

During the 40 observation nights, we recorded 1,004 bat approaches to the 10 experimental boxes in total. Of these approaches, 630 could be assigned to Bechstein's bats, 78 to Natterer's bats, and 61 to brown long-eared bats. Bats that were only partly visible and thus could not be assigned to a particular species made the remaining 235 approaches.

We used Fisher's exact tests to compare the total number approaches of each of the three study species among the four treatments (BPSC, BESC, NPSC, and control) combining the results of all 10 experimental boxes (Fig. 3). We found that all three bat species approached the experimental boxes significantly more often during nights with bat calls than during control nights. The brown long-eared bats did not discriminate between Bechstein's bat and Natterer's bat calls. However, Bechstein's bats and Natterer's bats both approached significantly more often when calls of conspecifics had been played back compared to nights with calls of the respective other species (Table 1).

In the second step of analysis, in which we controlled the box location matched for each of the 10 experimental boxes, we found no significant differences in the minimal temperatures between the 10 nights per each treatment (Friedman test: $Q=5.64$, degrees of freedom (df)=3.00, $P=0.13$, $N=10$). Moreover, the comparison of the number of approaches in the first, second, third, and last nights of each experimental replicate showed that treatment order had no significant influence (Friedman test: $Q=2.17$, df=3.00, $P=0.54$, $N=10$). Thus, the bats did not become

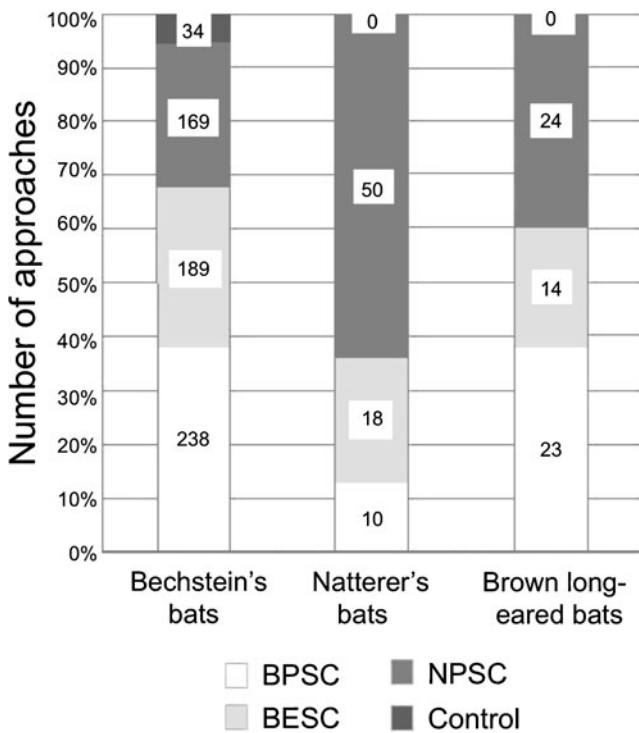


Fig. 3 Numbers and proportions of approaches of three bat species to experimental bat boxes during the four different treatments

familiar with a certain box over the four treatment nights, and the temperature was unlikely to have influenced our results. In 8.4% of all recorded approaches, the Bechstein's bats only passed the box, in 47.3% they circled around the box, in 41.9% they directly approached the box, and in 2.4% they entered the box (Fig. 4). The overwhelming majority of

Bechstein's bat approaches (94.6%) took place during the playback of bat calls: 67.8% during calls of conspecifics (BPSC, 37.8%; BESC, 30.0%) and 26.8% during calls of Natterer's bats. Only 5.4% of the approaches happened in control nights without calls (Fig. 3).

In nights with Bechstein's bat calls (BPSC and BESC), significantly more Bechstein's bat approaches (total number of bat approaches/2) were recorded in front of an experimental box than in nights without calls. The same applied to nights in which Natterer's bat calls had been played back (Friedman test: $Q=9.69$, $df=2.00$, $P=0.008$, $N=10$; for subsequent post-hoc tests see Table 2). In this analysis, with all approaches combined, the total number of Bechstein's bat approaches did not differ significantly between nights with playback calls of conspecifics and nights with playbacks of Natterer's bat social calls. However, when we analyzed the different types of approaches separately, the corresponding Friedman tests were all significant (P values ranged from 0.02 to 0.0001), and post-hoc tests showed that Bechstein's bats passed the experimental bat boxes significantly more often during nights with playbacks of conspecific calls than during nights with playbacks of Natterer's bats. Moreover, Bechstein's bats exclusively entered bat boxes during playbacks of calls of conspecifics (Table 2).

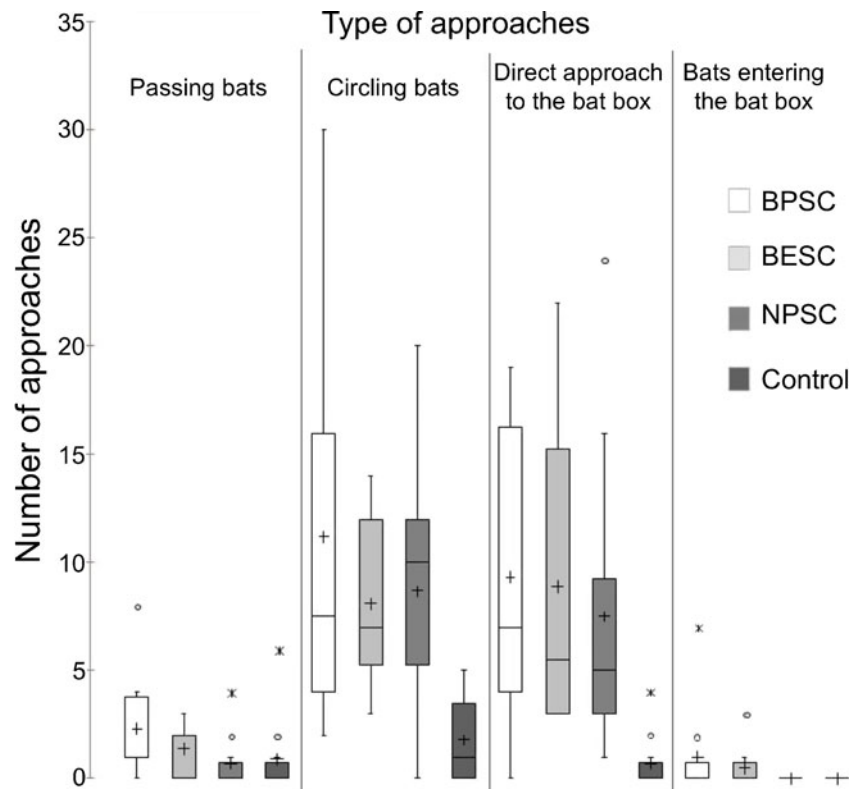
In nine of the 15 cases when Bechstein's bats had entered an experimental box, the entering individual could be identified by its transponder. The remaining six cases probably involved unmarked juveniles. One of the nine identified individuals entered a bat box four times in one night, whereas each of the eight other identified bats entered a box only once. However, even when we only

Table 1 P values obtained from Fisher's exact tests comparing the total numbers of approaches of the three bat species among the four treatments over all 10 experimental bat boxes

Bat species/treatment		Bechstein's bats	Natterer's bats	Brown long-eared bats
BPSC vs. BESC	df	1	1	1
	N	427	28	37
	P	0.10	0.42	0.36
BPSC vs. NPSC	df	1	1	1
	N	407	60	47
	P	0.0001	0.0002	1.00
BESC vs. NPSC	df	1	1	1
	N	358	68	38
	P	0.44	0.01	0.36
BPSC vs. control	df	1	1	1
	N	272	10	23
	P	0.0001	0.03	0.0001
BESC vs. control	df	1	1	1
	N	223	18	14
	P	0.0001	0.001	0.006
NPSC vs. control	df	1	1	1
	N	203	50	24
	P	0.0001	0.0001	0.0001

The underlying data are presented in Fig. 3. All significant P values remained significant after a sequential Bonferroni correction

Fig. 4 Number of Bechstein’s bat approaches summed up over all 10 replicates and given separately for each type of call. The approaches were grouped into four types of approaches. *Boxplots* show the median, the 25% and the 75% quartiles, and outliers (*White circle*, 1.5–3.5^x interquartile range; *asterisk*, >3.5^x interquartile range; and *plus sign* represents the mean of the data)



accepted one entering per bat in the same night and only one unidentified individual entering per night, at least 11 Bechstein’s bats entered the bat boxes when Bechstein’s bat calls (BPSC and BESC) were played back. In contrast, there was no entering during control nights and nights with the Natterer’s bat calls (NPSC; Wilcoxon matched pairs test: $W=34.00$, $P=0.05$, $N=10$).

Finally, like Bechstein’s bats, Natterer’s bats and brown long-eared bats approached the experimental boxes significantly more often during the treatments with bat calls than during the control nights when we pooled all types of approaches (passing, circling, direct approaches to the box, and entering the box; Friedman test, Natterer’s bats: $Q=12.06$, $P=0.002$, $df=2$, $N=10$; brown long-eared bats: $Q=$

Table 2 Wilcoxon matched pairs test for pairwise comparisons of the numbers of Bechstein’s bat approaches combined and separately for each type of approach between three treatments. All significant P values remained significant after a sequential Bonferroni correction

		Bechstein's bat calls vs. NPSC	Bechstein's bat calls vs. control	NPSC vs. control
All approaches	W	44.00	55.00	53.00
	P	0.10	0.006	0.01
	N	10	10	10
Passing bat	W	52.00	39.50	24.00
	P	0.009	0.18	0.70
	N	10	10	10
Circling bat	W	35.50	54.00	2.00
	P	0.41	0.008	0.01
	N	10	10	10
Direct approach to the bat box	W	37.00	55.00	0.00
	P	0.33	0.006	0.006
	N	10	10	10
Entering bat box	W	34.00	34.00	0.00
	P	0.05	0.05	1.00
	N	10	10	10

11.47, $P=0.003$, $df=2$, $N=10$; Fig. 4). In this analysis, neither Natterer's bats nor brown long-eared bats significantly discriminated between calls from Bechstein's bats and Natterer's bats (Table 3). However, when we analyzed the two Bechstein's bat call types separately, Natterer's bats approached significantly more often to social calls of their own species than to pure social calls of Bechstein's bats (NPSC vs. BPSC, Wilcoxon matched pairs test: $W=0.00$, $P=0.01$, $N=10$; Fig. 5).

Discussion

The aim of our study was to investigate whether free-ranging Bechstein's bats and two other forest living bat species that all have maternity colonies in our study site are attracted to potential day roosts by social calls of conspecifics and other bat species. We also investigated whether Bechstein's bats and Natterer's bats are able to distinguish between social calls of conspecifics and the respective other bat species.

Bechstein's bats, brown long-eared bats, and Natterer's bats approached experimental bat boxes significantly more often when bat social calls were played back compared to control nights without calls. This indicates that all three species are attracted by social calls to potential roosts. Bechstein's bats and Natterer's bats approached bat boxes during playbacks of conspecifics and those of the other species. Even brown long-eared bats approached boxes significantly more often when calls of the two *Myotis* species had been played back compared to control nights. Ruczyński et al. (2009) described that playbacks of echolocation calls of conspecifics did not improve roost finding of brown long-eared bats in the lab. Our results suggest that brown long-eared bats respond to social calls of other bat species and could use them for finding potential roosts. To fully examine the importance of acoustic cues for roost finding in brown long-eared bats, playback studies with social and echolocation calls of this species have to be conducted in the wild.

Because bats emit a great variety of social calls (Pfalzer and Kusch 2003), it is not feasible to cover the full

repertoire of a species' social calls in a single playback experiment. In our experiment, we used only one type of Bechstein's bat social calls—but a different call in each of the two treatments (BPSC and BESC). These social calls have been recorded in a foreign colony in a situation when female Bechstein's bats were flying around their day roost. The call structure of these social calls was very similar to the social calls, which we had recorded in our study colony during exploration behavior of unoccupied roosts (Figs. 1, 2; C. R. Schöner, unpublished data). Therefore, our played Bechstein's bat social calls should be representative for the type of social calls that is emitted near potential day roosts. In case of NPSC, we had only one call available that was obtained from a single bat flying in another situation (in front of a mist net). Thus, potentially, the approaching bats in our study could have discriminated between Bechstein's bat calls and the Natterer's bat call because the calls may have differed as a result of the different situation at which they were emitted. However, such a situational variation would not explain why Natterer's bats and Bechstein's bats both preferred calls of conspecifics to calls of the respective other species, in a situation where they both approached potential day roosts. In addition, all played call sequences had an artificial call composition, thus their temporal structure (call rate, inter-call interval, etc.) was no longer context specific. An artificial call composition was also used in another study (Schuchmann and Siemers 2010) that showed that two species of horseshoe bats are able to discriminate between the echolocation calls of several other Rhinolophid bat species. This suggests that bats can discriminate on the basis of the calls themselves independently of the temporal structure and composition of call sequences.

Previous field studies have shown that playbacks of social calls of one bat species can attract several bat species at foraging sites (Russ et al. 2004) or into mist nets (Hill and Greenaway 2005). Russ et al. (2004) explained that this inter-specific attraction is a result of selection towards a convergent structure of social calls, for example to attract other bat species as defense against predators. However, in our experiment, the played back social calls were effective in attracting other bat species even though the social calls

Table 3 Wilcoxon matched pairs tests comparing the numbers of all approaches of Natterer's bats and brown long-eared bats between three treatments. All significances remained after a sequential Bonferroni correction

Bat species		Bechstein's bat calls vs. NPSC	Bechstein's bat calls vs. control	NPSC vs. control
Natterer's bats	<i>W</i>	12.50	49.00	0.00
	<i>P</i>	0.15	0.01	0.009
	<i>N</i>	10	10	10
Brown long-eared bats	<i>W</i>	12.00	45.00	52.00
	<i>P</i>	0.21	0.002	0.004
	<i>N</i>	10	10	10

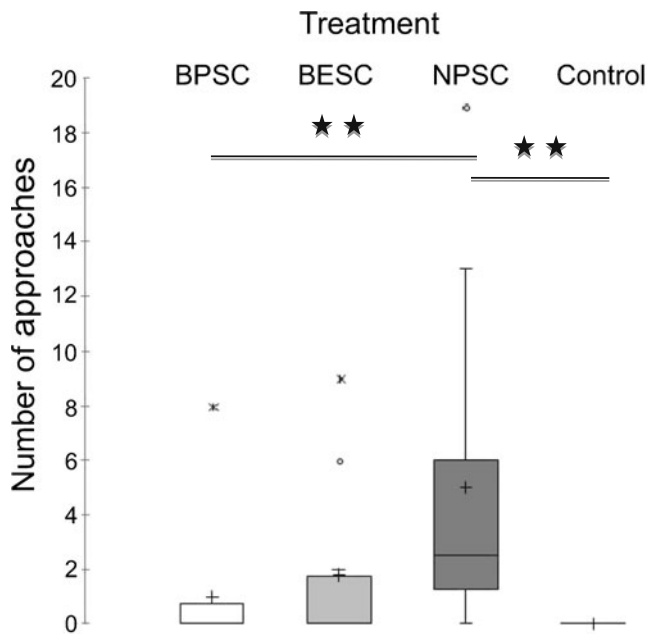


Fig. 5 Boxplots showing the total number of Natterer's bat approaches during the 10 replicates, separately for each type of call. Boxplots show the median, the 25% and the 75% quartiles, and outliers (White circle, 1.5–3.5^x interquartile range; asterisk, >3.5^x interquartile range; and plus sign represents the mean of the data). Significant differences ($P < 0.01$) are indicated by two stars

of Bechstein's bats and Natterer's bats showed substantial structural and temporal differences (Fig. 1). In contrast, echolocation calls of these two bat species are very similar to each other in structure (Siemers and Kerth 2006; Schnitzler and Siemers 2000; Skiba 2003). This similarity may explain why Natterer's bats discriminated only between NPSC and BPSC, both containing only social calls (Fig. 3). Another reason can be seen in the communicational function of echolocation calls. Gillam (2007) showed that bats eavesdropping on echolocation calls are capable to locate promising food patches quickly. Similar inter-specific reactions could probably facilitate the finding of new roosts as well.

It is noteworthy that unspecific ultrasound noise is unlikely to attract bats to roosts. Willis et al. (2009), for example, showed that bats avoid potential roosts where ultrasound noise was artificially emitted, and Schaub et al. (2008) showed that foraging bats avoid ultrasound noise under controlled lab conditions. Even though this does not exclude that any kind of modulated ultrasound attracts bats, universal attraction to modulated ultrasound could not explain why Bechstein's bats and Natterer's bats both responded stronger to the pure social calls of their own species, whereas brown long-eared bats showed no discrimination between the two *Myotis* species.

An alternative explanation on why all three of our study species approached bat boxes from which calls of other bat

species were emitted could be inter-specific competition for roosts. In our study area, the Bechstein's bat colony, the Natterer's bat colony, and the three long-eared bat colonies all used the same type of bat boxes as day roosts. Even though they do not roost together in the same box at the same time, they sometimes occupy a given box after each other (G. Kerth, unpublished data). Similarly, Simmons and Voss (1998) observed that different bat species sequentially use the same roosts. Moreover, PIT-tagged Bechstein's bats and brown long-eared bats sometimes entered a box at night within minutes after each other during another experiment (G. Kerth, unpublished data), suggesting that they respond to each other's nightly activity at roosts. When inspecting boxes, Bechstein's bats regularly emit social and echolocation calls (Fig. 2; C.R. Schöner, unpublished data), which might attract not only colony members but also other bat species.

Humphrey (1975) showed that the availability of roosts is one of the most important factors explaining the occurrence of different bat species. Inter-specific competition might emerge when species have to defend limited space (Schoener 1983), e.g., access to day roosts in bats. Therefore, it could be important for the members of a bat colony to know which roosts in their roosting area are occupied by other bat species. This could allow them to learn about new roosts and at the same time avoid the occupation of these roosts while they are still used by other bat species. Bechstein's bats often occupy day roosts several weeks after they had first inspected them at night (Kerth and Reckardt 2003). For comparison, different bird species sometimes do share roosts (Chapman et al. 1989; Lyon and Caccamise 1981). Caccamise and Fischl (1985) suggest that the occupation of other bird species signals the birds that at least minimal roosting requirements are guaranteed. We assume that bat species with similar roost requirements such as our three study species respond to each other's social calls when searching for new roosts in order to gain information about the location of suitable roosts.

Even though Bechstein's bats and Natterer's bats reacted to social calls of the respective other species, we found multiple pieces of evidence that both species were able to distinguish them from social calls of conspecifics (Tables 1, 2; Fig. 5). Most strikingly, Bechstein's bats only entered experimental boxes when Bechstein's bat calls had been played back. Our results indicate that eavesdropping bats are attracted by conspecifics' social calls. As social calls, unlike echolocation calls, are not required for orientation and thus are intentionally emitted signals, bats may use social calls to actively guide colony members to potential roosts. This has also been suggested by Chaverri et al. (2010) for a neotropical bat species (*T. tricolor*). In Bechstein's bats and probably in many other bats that

frequently switch roosts, the selection of new roosts involves group decisions (Kerth et al. 2006; Kerth 2008). Moreover, the bats profit energetically from the presence of additional colony members (Pretzlaff et al. 2010). Therefore, it should be important for them to attract as many colony members as possible to their roost. Social calls are better suited for this task since they can be heard over longer distances than echolocation calls due to their lower frequencies (Siemers and Kerth 2006; Chaverri et al. 2010). Social calls could facilitate the reunion of the colony members in a roost after they had hunted separately or had split into different roosting groups, as it is both the case in Bechstein's bats (Kerth and König 1999; Kerth et al. 2001b) and probably in many other forest living bat species. At the same time, our results indicate that other bat species can eavesdrop on social calls making them potentially costly for the emitting bats as they may increase inter-specific roost competition. It will be highly rewarding for future studies to examine to what degree social calls contain information about the identity of the calling bats and whether the bats can use these calls to recognize individual colony members.

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