Function of pipistrelle social calls: field data and a playback experiment

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Abstract. The study aimed to determine whether the so-called social calls that are produced by foraging bats of two phonic types of *Pipistrellus pipistrellus* serve a social function. First, the relationship between insect availability and the rate of production of social calls was measured at a foraging site of both phonic types. Second, playback experiments of social calls of the two phonic types were conducted in the field to determine the response of foraging bats to these calls, and to determine whether the calls are used in communication within or between phonic types. Two hypotheses are suggested for the function of social calls: that they may be used either to attract other bats to a food patch, or in agonistic interactions between bats in defence of a food patch. At relatively low insect densities, the rate of social call production of both phonic types increased significantly as insect density decreased. When social calls of each phonic type were broadcast, there was a significant reduction in bat activity of the same phonic type. In contrast, playbacks of social calls resulted in no change in activity of the other phonic type. The results supported the food patch defence hypothesis, that social calls are used to warn off other bats of the same phonic type when insects are scarce. The results also supported the hypothesis that the two phonic types are sibling species. Social calls were shown to serve a social function in intraspecific communication, but there was no communication between phonic types.

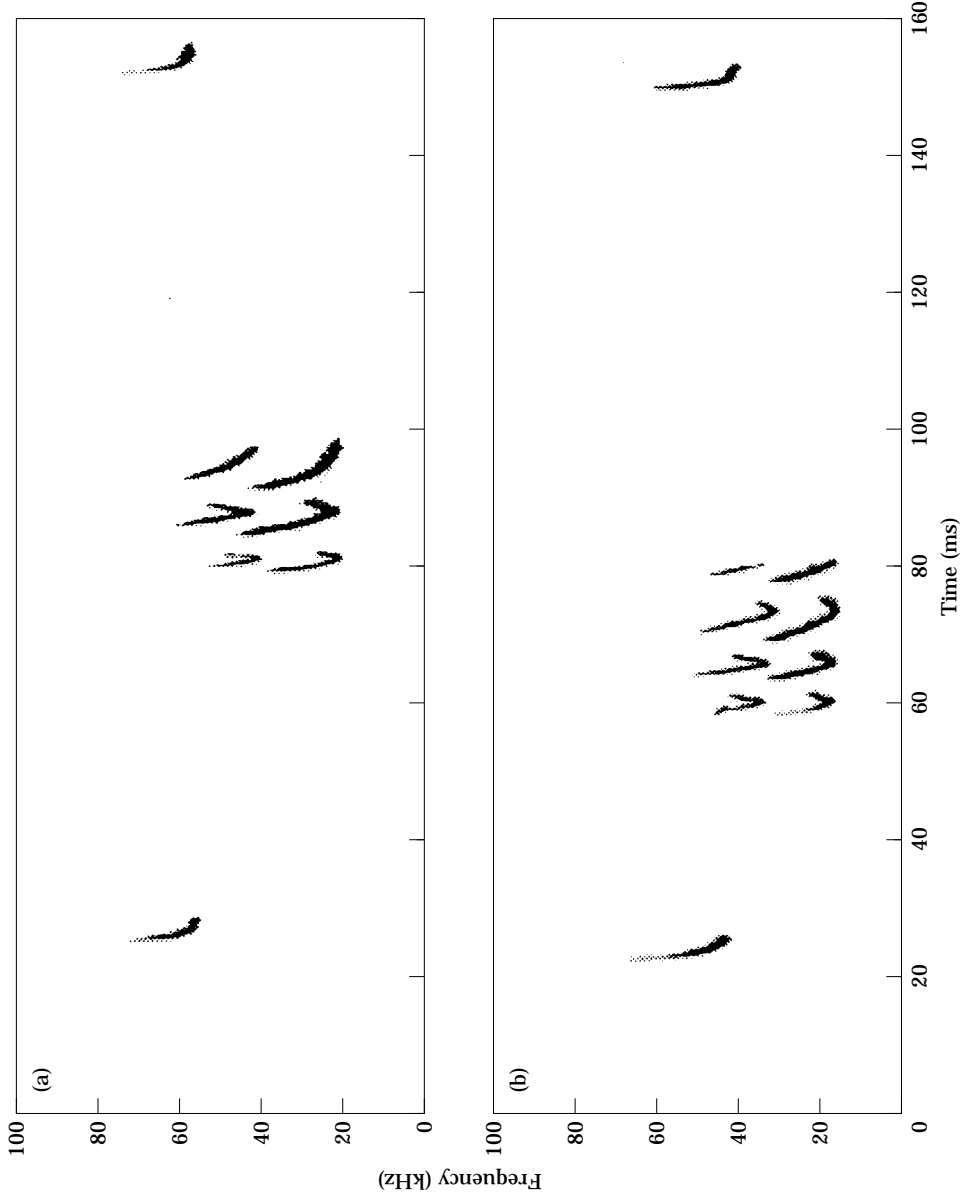© 1997 The Association for the Study of Animal Behaviour

Feeding bats may communicate by eavesdropping on the echolocation calls of other bats (see review in Fenton 1995) or by means of specific social calls (Fenton 1985). The precise functions of social calls are rarely known. They are often ascribed an agonistic function, implying territoriality, but this is suggested from casual observations and there is little supporting evidence (Fenton 1985).

Pipistrellus pipistrellus produces intense so-called social calls during flight near the roost or at foraging sites (Ahlén 1981; Miller & Degn 1981). Social calls are often produced during chases (Miller & Degn 1981; Racey & Swift 1985; Lundberg & Gerell 1986) and most chases are observed at low insect densities (Racey & Swift 1985). It is not known, however, whether the so-called social calls do have a social function. There are two phonic types of *P. pipistrellus* in Britain, its echolocation calls falling into two distinct frequency bands (Jones & van Parijs 1993). Echolocation calls have a predominant

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energy around 55 kHz in one phonic type, and around 45 kHz in the other. The two phonic types occur in sympatry over much of Britain and are probably sibling species (Jones & van Parijs 1993; Barratt et al. 1995). The social calls of the two phonic types of *P. pipistrellus* differ (Fig. 1); calls of the 45 kHz phonic type consist of more components and are of longer duration and lower frequency than those of the 55 kHz phonic type (Barlow & Jones 1997).

We suggest two possible functions of social calls. First, social calls may be produced to advertise food patches to other bats, if there are benefits of foraging in groups. Some bats eavesdrop on the echolocation calls of other individuals to locate feeding areas or potential prey items (Barclay 1982; Balcombe & Fenton 1988; Fenton 1995). Similarly, social calls may be produced specifically to communicate information about food patches to other bats. The costs of advertising a food patch may be small if bats feed on swarms of insects and cannot monopolize the whole swarm (Barclay 1982). The energetic cost of producing social calls, and the cost of attracting

Figure 1. Typical sonagrams of a sequence of echolocation calls and a social call for the 55 kHz phonic type (a) and the 45 kHz phonic type (b).

other bats to a food patch could be outweighed by the benefits of listening to the social calls of other individuals, for example to track a moving food patch to prolong time spent feeding on it (Brown et al. 1991), or to locate new food patches. Atmospheric attenuation is low at the frequencies of social calls (Lawrence & Simmons 1982), so bats could locate feeding areas at distances further from them than could be detected with echo-location calls, and reduce searching time for food. There is some evidence, however, that an increase in bat density reduces foraging efficiency which may increase the cost of advertising a food patch (Barclay & Brigham 1994). As insect density decreases, the benefits of listening to food patch advertisement calls are likely to increase, by increasing foraging efficiency (Brown et al. 1991). The food patch advertisement hypothesis therefore predicts that social call rate would increase as insect density decreases. The costs of interference competition are also likely to increase as insect density decreases, however, therefore increasing the cost of advertising a food patch. The food patch advertisement hypothesis predicts bats would be attracted to social calls, so we would expect an increase in bat activity during playback.

Our second hypothesis is that social calls may be produced in agonistic interactions to warn off other bats from the feeding area of an individual. Agonistic interactions increase in several bat species when food is scarce (Rydell 1986; Kronwitter 1988) although in only a few cases has this increase been directly related to insect density (Bradbury & Emmons 1974; Belwood & Fullard 1984). For defence of food to occur, the cost of defence, which in the case of *P. pipistrellus* amounts to the time and energy costs of producing social calls, should be outweighed by the benefits of defending the feeding area (Brown 1964). *Pipistrellus pipistrellus* feeds mainly on Diptera, particularly nematoceran Diptera (Vaughan 1997) which often swarm (Peng et al. 1992) and it is unlikely that it would be energetically beneficial to defend a swarm when insect densities are high (Barclay 1982). At lower insect densities, however, an individual may benefit in terms of increased access to food if it warned off other bats from a feeding area. The food patch defence hypothesis therefore predicts that social call rate would be high at low insect densities and that bats would be repelled from an

area by social calls, so we would expect a decrease in bat activity during playback.

In this study we aimed to investigate the relationship between insect density and the rate at which social calls are produced at a feeding site by the two phonic types of *P. pipistrellus* and to use playback experiments, first to determine whether these calls do have a truly social function by determining how bats respond to them, and second to determine whether they are used in communication either within or between the two phonic types.

METHODS

Insect Density and Social Call Rate

On three nights in July 1995, we used a 12 inch Johnson–Taylor insect suction trap (Johnson & Taylor 1955) to estimate the availability of aerial insects at a site at the edge of a small lake near Bristol in southwest England (Ordnance Survey Grid Reference: ST536734) where both phonic types of *P. pipistrellus* were found foraging. The catch was separated into 20-min periods. On each night we started the trap 20 min after sunset and finished when only single bats remained foraging (approximately 3 h later). We converted the number of insects caught in each 20-min period to aerial insect density per 1000 m^3 of air. We monitored bat activity of the two phonic types for the same 20-min periods each night at the lake with a bat detector set to time expansion. We used time expansion as it is a broadband method allowing echolocation calls and social calls of both phonic types to be recorded simultaneously. Time-expanded recordings were made via a Pettersson D-980 detector to a cassette tape recorder (Sony Walkman WM-D6C). Recordings consisted of 3 s in real time expanded 10 times and downloaded to the cassette tape recorder. Therefore, 3 s in every 33 s of bat activity was recorded by time expansion. In each 20-min period, we recorded activity at three points separated by 25 m along the edge of the lake. We sampled at each of these points for 5 min during each 20-min period.

We used a Digital Signal Processing Sona-Graph (Kay 5500; transform size 512 pts, 400 Hz resolution) to analyse the recordings. We used the number of bat passes as a measure of bat activity, as it is not possible to count directly numbers of

individuals in the field (Fenton 1970). Bat passes were assigned to phonic type by the frequency measured from echolocation calls. Bats producing echolocation calls of frequencies less than 49 kHz were assigned to the 45 kHz phonic type, and those producing calls of more than 52 kHz to the 55 kHz phonic type (Jones & van Parijs 1993). We counted the number of bat passes of each phonic type recorded during the 5 min at each of the three points per 20-min period, and then summed the total number of passes over these points. We also counted the total number of social calls of each phonic type recorded during each 20-min period. Social calls were assigned to phonic type by the bat pass within which they were recorded and from the number of components in the calls (Barlow & Jones 1997). Social calls of two or three components were assigned to the 55 kHz phonic type and those of four or five components were assigned to the 45 kHz phonic type. Based on this simple method, around 90% of calls would be correctly classified (Barlow & Jones 1997). In the analysis, we investigated the relationship between the rate of production of social calls, calculated as the ratio of social calls to bat passes, and aerial insect density using log-linear regression. The rate of production of social calls was transformed using the logarithmic transformation, as this gave the best fit for the regression equations (Sokal & Rohlf 1995). Insect density decreases with time after dusk (Lewis & Taylor 1964; Peng et al. 1992) and we therefore also investigated the relationship between social call rate and time with log-linear regression. We carried out the regression for each phonic type on each night.

Field Recordings

In April and May 1995, we recorded social calls and echolocation calls produced by the two phonic types at 13 foraging sites within a 40-km radius of Bristol in southwest England. This is outside the usual mating period of *P. pipistrellus*, when males produce advertisement calls during a songflight display (Lundberg & Gerell 1986; Gerell-Lundberg & Gerell 1994). Songflight calls are very similar to social calls in both phonic types (Barlow & Jones 1997). We therefore carried out the study at the end of the period in which mating may still occur, to minimize the possibility that our field recordings were of songflight calls. Songflight calls are produced at regular intervals

(Lundberg & Gerell 1986) whereas social calls are produced irregularly. No bats producing regularly repeated calls were encountered during field recording. We made time-expanded recordings via the high frequency output of an S-25 bat detector (Ultra Sound Advice) to a Portable Ultrasound Signal Processor (PUSP, Ultra Sound Advice) linked to a cassette tape recorder. The S-25 microphone has a frequency response of ± 3 dB from 20 to 120 kHz. Using the Sonagraph, we assigned social calls to phonic type from the frequency of echolocation calls produced by the bat in the same recording sequence, as described in the previous section. We used one social call recording per phonic type from each field recording site visited.

Playback Experiment

We used a SIGNAL/RTS sound analysis system (Engineering Design, Belmont, Massachusetts) to sample sequences from field recordings. We selected single social calls, or sections of tape noise and recorded them onto experimental and control tapes. We used each social call at only one playback site, to avoid pseudoreplication (Hurlbert 1984; McGregor 1992). Each social call used was recorded twice onto the playback tape. We visited 13 playback sites, and we therefore recorded 13 experimental tapes and 13 control tapes of each phonic type. At each playback site we used field recordings from a different site.

In the field, we used the PUSP to digitize a social call from an experimental tape, or tape noise from a control tape. The signal was recompressed and the output was played from the PUSP in real time via an ultrasound amplifier and capacitance speaker (Ultra Sound Advice), every 10 s for 3 min per trial. The signal was broadcast every 10 s for 3 min in each control trial. The rate of production of social calls used in playback was similar to that found in the field recordings. The signal output from the speaker was registered by the bat detector at approximately the same distance at which social calls produced by bats were detected during field recording, suggesting that the intensity of playbacks was similar to the intensity of social calls produced by bats. We visited one playback site, where both phonic types were found foraging, on each of 13 nights during

May 1995. We carried out playback beginning 45 min after sunset. At each playback site, we carried out a control and experimental trial of one phonic type, and we alternated the order of trials between nights. After a 15-min pause, we carried out a control and experimental trial of the other phonic type. We also alternated the order of playback experiments of the two phonic types between nights.

Bat Activity

We measured the response of bats of each phonic type to playback by recording bat activity continuously during each trial, via an S-25 bat detector set to frequency division linked to a cassette tape recorder. We used frequency division because it is a broadband method and also allows continuous recording (Zingg 1990). We kept the direction and height of the capacitance speaker and bat detector constant at 70 cm throughout the experiment.

We used the Sonagraph to count the number of bat passes of each phonic type for each trial, and we carried out this analysis blind. We assigned each bat pass to phonic type by the frequency measured from echolocation calls as before. We also counted the number of social calls produced by bats of each phonic type during each trial. We assigned social calls to phonic type only by the bat pass within which they were recorded, as individual components of social calls cannot be resolved from frequency-divided recordings.

In the analysis we considered separately the responses of bats to the two experiments, playback of social calls of the 45 kHz phonic type and playback of social calls of the 55 kHz phonic type. We tested the distribution of the responses of the two phonic types to playback for normality with the Ryan–Joiner test (Ryan et al. 1985). In all cases, the data were neither normally nor symmetrically distributed. We therefore used sign tests (Siegel & Castellan 1988) to investigate the difference in bat activity and in numbers of social calls produced between experimental and control trials. As the response of both phonic types to playback of each phonic type were measured simultaneously, we adjusted P-values according to the Bonferroni method (Altman 1991) within each phonic type playback experiment. All statistical analysis was carried out on MINITAB (Ryan et al. 1985).
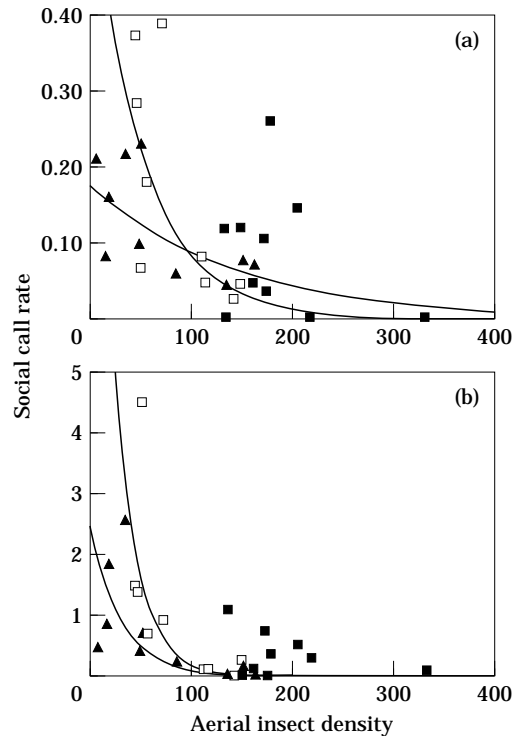
Figure 2. The rate of production of social calls, measured as the ratio of numbers of social calls to number of bat passes, relative to aerial insect density per 1000 m^3 over 3 nights for the 45 kHz phonic type (a) and the 55 kHz phonic type (b). For both phonic types the lines show the relationships found between these two parameters on 2 of the 3 nights. On the third night (■), no significant relationship was found for either phonic type. Each point represents one 20-min sampling period for insects, with bat activity recorded at three points for 5 min during that period. (a) Night 1 (▲): log $Y=0.33–0.0021X$; night 2 (□): log $Y=0.17–0.00072X$. (b) Night 1 (▲): log $Y=1.44–0.010X$; night 2 (□): log $Y=0.84–0.0053X$.

RESULTS

Insect Density and Social Call Rate

Log-linear regression of social call rate against insect density showed that there was a significant increase in the rate of production of social calls by bats of the 45 kHz phonic type as insect density decreased, on 2 of the 3 nights (night 1: $r^2=0.516$, $N=9$, $P<0.05$; night 2: $r^2=0.428$, $N=10$, $P<0.05$; Fig. 2a). Log-linear regression of social call rate against time showed that the relationships

between social call rate and insect density were stronger, shown by higher r^2 values, than the relationships between social call rate and time (night 1: $r^2=0.410$, $N=9$, NS; night 2: $r^2=0.408$, $N=10$, $P<0.05$) The same relationship was found on the same 2 nights for the 55 kHz phonic type, and the rate of social call production was higher overall (night 1: $r^2=0.614$, $N=9$, $P<0.05$; night 2: $r^2=0.533$, $N=10$, $P<0.05$; Fig. 2b). Log-linear regression of social call rate against time showed that on the first night, this relationship was as strong as that between social call rate and insect density (night 1: $r^2=0.705$, $N=9$, $P<0.01$); on the second night the relationship between social call rate and time was less strong (night 2: $r^2=0.429$, $N=10$, $P<0.05$). On the third night, insect densities did not fall below 140 per 1000 m³, and the rate of production of social calls by both phonic types remained relatively low with no apparent relationship between social call rate and insect density (45 kHz phonic type: $r^2=0.094$, $N=10$, NS; 55 kHz phonic type: $r^2=0.099$, $N=9$, NS; Fig. 2), or between social call rate and time (45 kHz phonic type: $r^2=0.334$, $N=10$, NS; 55 kHz phonic type: $r^2=0.081$, $N=10$, NS).
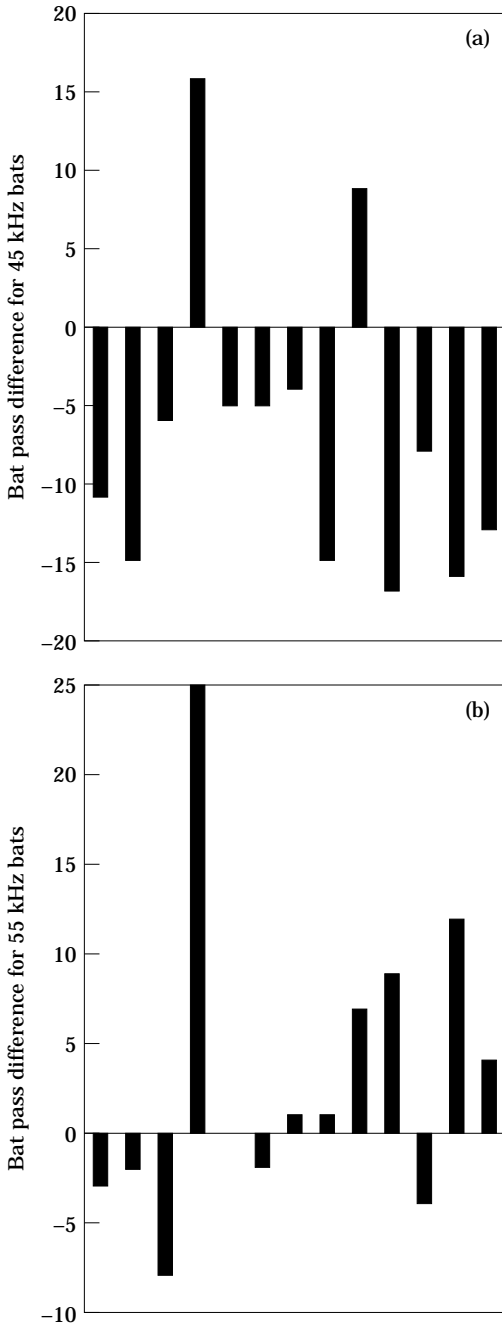
55 kHz Playback Experiment

Bats of the 55 kHz phonic type were significantly less active during experimental playback of social calls of the 55 kHz phonic type than during control trials (Fig. 3a; sign test: $N=13$, $P<0.01$; median difference between experimental and control trials$= -10$). A median of zero would indicate no difference between experimental and control trials. There was no significant difference in the number of social calls produced by bats of the 55 kHz phonic type between experimental and control trials (sign test: $N=9$, NS; median difference$=0$). There was also no significant difference in bat activity (Fig. 3b; sign test: $N=12$, NS; median difference$= -3$), or numbers of social calls (sign test: $N=6$, NS; median difference$=0$) of the 45 kHz phonic type between experimental and control trials.

45 kHz Playback Experiment

Bats of the 45 kHz phonic type were significantly less active during experimental playback of social calls of the 45 kHz phonic type than during control trials (Fig. 4a; sign test: $N=13$, $P<0.05$;
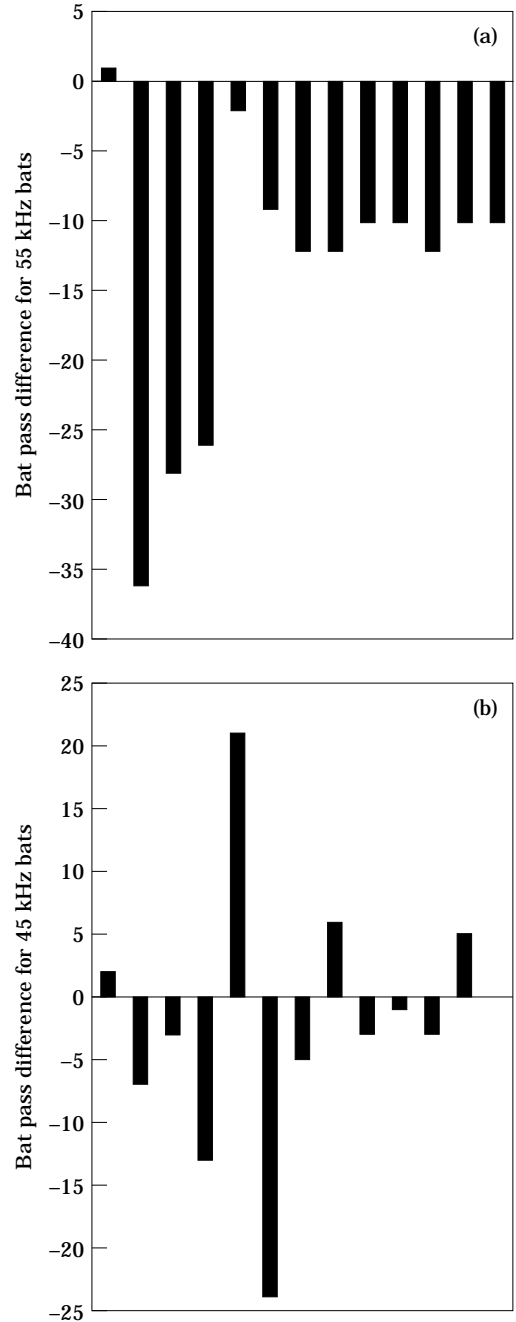
Figure 3. The response of bats of the 55 kHz phonic type (a) and the 45 kHz phonic type (b) to playback of social calls of the 55 kHz phonic type. Each bar represents the difference in bat activity, measured as the number of bat passes, between experimental trials and control trials for one site.

Figure 4. The response of bats of the 45 kHz phonic type (a) and the 55 kHz phonic type (b) to playback of social calls of the 45 kHz phonic type. Each bar represents the difference in bat activity, measured as the number of bat passes, between experimental trials and control trials for one site.

median difference= − 6). There was no significant difference in the number of social calls produced by bats of the 45 kHz phonic type between experimental and control trials (sign test: $N=8$, NS; median difference=0). There was also no significant difference in bat activity (Fig. 4b; sign test: $N=12$, NS; median difference=1), or numbers of social calls (sign test: $N=10$, NS; median difference= − 1) of the 55 kHz phonic type between experimental and control trials.

DISCUSSION

First we consider the response of bats of each phonic type to playback of social calls of the same phonic type. The reduction in activity of bats of each phonic type that we found during playback suggests that these bats were repelled by social calls, not attracted to them. This supports the food patch defence hypothesis that social calls of *P. pipistrellus* are produced to warn off other bats from a feeding area. The hypothesis is also supported by observations that social calls are often produced during chases and that the number of chases increases with decreasing insect density (Racey & Swift 1985; Lundberg & Gerell 1986). If social calls were used to advertise feeding areas to other bats, we should not expect to observe chases in conjunction with the production of social calls. It is not clear whether social calls are used in direct interactions between a signaller and an individual receiver in all cases, for example during a chase between two bats, or whether the signaller calls to several bats, but it is likely that more than one bat may gather information from a signaller by listening to these long-range calls (McGregor 1993).

Agonistic interactions at low levels of food availability have been suggested as evidence of territoriality in bats (Bradbury & Emmons 1974; Belwood & Fullard 1984; Rydell 1986, 1989; Kronwitter 1988). Definitions of territoriality almost always include some fixed spatial area or site-specific dominance (Kaufmann 1983; Maher & Lott 1995). It is not known if individual *P. pipistrellus* use a fixed foraging range, although there is some evidence that individuals return to the same foraging areas repeatedly (Racey & Swift 1985). It seems unlikely that individuals would defend a fixed area as a feeding territory, as the distribution of the insect prey of *P. pipistrellus* is

patchy and transient in time and space (Peng et al. 1992) and therefore probably not economically defensible. In the playback experiment, we found a reduction in bat activity in response to social calls that had been recorded at a different site to the playback site. If there was site-specific dominance in *P. pipistrellus*, it is unlikely that bats would respond to the social calls of an unknown bat. Also, individuals at a foraging site would have to be able to recognize each other for site-specific dominance to occur. The variation in some calls used in social situations suggests that there may be potential for individual recognition (Fenton 1994), and it is probable that this is the case for social calls of *P. pipistrellus* (Barlow & Jones 1997). Our study suggests, however, that the two phonic types of *P. pipistrellus* are not territorial, but that interference competition probably occurs within each phonic type at low insect densities through defence of food patches and agonistic interactions between bats.

Second, we consider the lack of response of bats of each phonic type to playback of social calls of the other phonic type. The bats were neither repelled from nor attracted to playback of social calls of the other phonic type. There was no evidence therefore of communication between phonic types which suggests that there is resource partitioning between them. If the diets of the two phonic types were very similar, a stronger response of one phonic type to playback of social calls of the other phonic type would be expected. As no significant response was observed, we suggest that the diets of the two phonic types may differ significantly. The frequency ranges and structure of the social calls of the two phonic types overlap and are similar (Barlow & Jones 1997), however, and it is possible that bats of one phonic type may gather information from the social calls of the other phonic type. These results support the hypothesis that the two phonic types are sibling species (Jones & van Parijs 1993; Barratt et al. 1995).

Social calls of the two phonic types of *P. pipistrellus* are very similar to songflight calls (Barlow & Jones 1997), thought to be advertisement calls produced by males in songflight in the mating season to attract females to mating roosts (Lundberg & Gerell 1986; Gerell-Lundberg & Gerell 1994). Calls with similar structure therefore seem to be used in one social situation to attract other bats and in another to warn off other bats.

This does not follow Morton's (1977) motivation-structural rules of mammal communication calls which suggest that calls used to attract other individuals should differ in structure from aggressive calls. However, the rules mainly refer to close contact calls and include only some long-range calls. The songs of many bird species similarly have two main functions, both to attract and to repel other individuals, depending on who receives the signal (Catchpole & Slater 1995). The calls produced by the two phonic types could also have two functions: first in agonistic interactions to repel other bats from a food patch, and second during songflight to attract females for mating.

ACKNOWLEDGMENTS

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