The social calls of Kuhl’s pipistrelles *Pipistrellus kuhlii* (Kuhl, 1819): structure and variation (Chiroptera: Vespertilionidae)

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Abstract  
The aim of this study was to describe the structure of social calls produced by Kuhl’s pipistrelles *Pipistrellus kuhlii*. Bats foraging around street lamps in the Campania region, Southern Italy, were recorded. Calls were produced by bats during chases and, similarly to those of *Pipistrellus pipistrellus*, were probably used to repel conspecifics from hunting sites. Calls often had three components, lasted on average 34 ms and contained most energy at about 17 kHz. A positive correlation was found between the frequencies of maximum amplitude of echolocation and social calls. Social calls from two adjacent populations differed in their peak frequencies, and possible hypotheses for this variation are given. The structure of *P. kuhlii* social calls was compared with those of the 45 and 55 kHz *P. pipistrellus* phonic types. Kuhl’s pipistrelle calls lasted longer and showed lower values of minimum and peak frequencies. These differences can help to discriminate between field recordings of *P. kuhlii* and *P. pipistrellus* where the two species occur sympatrically.

Key words: Chiroptera, communication, *Pipistrellus kuhlii*, social calls

INTRODUCTION

The Kuhl’s pipistrelle *Pipistrellus kuhlii* (Kuhl, 1819) is a small vesperilionid with a body mass of 5–10 g and a forearm of 31–37 mm (Schober & Grimmberger, 1997). It is distributed through south and south-west Europe, including the Balkans and the Mediterranean islands, extending northwards to Switzerland, France and Austria, eastwards to the Caucasus (Schober & Grimmberger, 1997) and southwards to Africa (Corbet, 1978).

*Pipistrellus kuhlii* echolocation search calls are 8–12 ms long (Schnitzler et al., 1987) and consist of a short frequency-modulated (FM) component followed by a terminal part of almost constant frequency (CF). The terminal part corresponds to the frequency of highest energy, generally 35–40 kHz (Schnitzler et al., 1987; Ahlén, 1990; Barataud, 1996). Call structure varies depending on whether the bat flies in cluttered or uncluttered habitats (Kalko & Schnitzler, 1993). Like many other bat species, bats from the genus *Pipistrellus* also emit vocal signals for communication (Ahlén, 1981, 1990; Miller & Degn, 1981; Fenton, 1985). These calls may serve different functions: *Pipistrellus pipistrellus*, for example, produces social calls in an aggressive context (Barlow & Jones, 1997a), songflight calls by males to attract females to the roost in the mating season (Lundberg & Gerell, 1986; Gerell-Lundberg & Gerell, 1994; Barlow & Jones, 1997b), and distress calls to attract conspecifics and probably to enite other bats to mob predators (Russ, Racey & Jones, 1998).

Social calls can be used to discriminate between different pipistrelle species: significant differences exist between the structures of advertisement calls of *P. pipistrellus* and *Pipistrellus nathusii* (Barlow & Jones, 1996), and even the two cryptic species of *P. pipistrellus*...
can be separated by examining the structure of their songflight and social calls (Barlow & Jones, 1997).

Although *P. kuhlii* is known to emit social calls (Ahlén, 1990; Barataud, 1996), no detailed description of these signals has been reported so far.

In the present study we: (1) provide a detailed analysis of social calls emitted by foraging Kuhl’s pipistrelles, (2) test the hypothesis that bats emitting echolocation calls with higher peak frequencies also produce social calls with higher frequencies of maximum energy, (3) investigate whether there are geographical differences in social call structure between two populations < 100 km apart.

We also discuss the possibility of discriminating *P. kuhlii* in flight from other pipistrelle species producing similar echolocation calls (*P. pipistrellus*, *P. nathusii*) by examining social calls.

**METHODS**

**Field recordings**

From August to October 1998, we recorded social calls emitted by foraging bats in the Campania region, Southern Italy (14°15′E, 40°50′N). *Pipistrellus kuhlii* is the most common bat species in this area. Almost all calls analysed were recorded in the Benevento and Naples provinces, about 70 km apart. Only 1 call was recorded in the Salerno Province.

We made recordings near street lamps, where *P. kuhlii* commonly forages (Haffner & Stutz, 1985/6) and seems to take advantage of group hunting (Barak & Yom-Tov, 1989).

The habitats occurring at the recording sites in the Benevento province were arable land, olive groves and vineyards, while in the Naples province we carried out recordings in urban areas and suburbs with a mosaic of buildings, small cultivations and gardens. In order to avoid pseudo-replication (Hurlbert, 1984), we made recordings at lamps located at least 2 km apart, and considered for analysis only 1 call sampled at each site. In this way only 1 signal for each bat was represented in the sample.

Recordings were made via the high-frequency output of an S25 bat detector (Ultra Sound Advice, London) connected to a Portable Ultrasound Processor (Ultra Sound Advice, London) which sampled at a rate of 448 kHz and time-expanded (10) a 2 s sequence of calls. The resulting sequence, lasting 20 s, was then replayed and recorded on Sony Metal XR cassettes by means of a Sony Professional Walkman WM D6C. The S25 microphone has a sensitivity of $-57 \pm 3$ dB (ref. 1 V/μbar) from 20 to 120 kHz. We could compare *P. kuhlii* social calls with those by British *P. pipistrellus* described by Barlow & Jones (1997b) as an identical equipment was used in both studies.

**Sound analysis**

The recordings were analysed with the software BatSound release 1.0 (Pettersson Elektronik AB, Uppsala). We adopted a sampling frequency of 44 100 samples/s, with 16 bits/sample; a 512 pt. FFT with a Hamming window was used for analysis.

For each social call, we measured the following parameters: the number of components to the call (*nocomp*), the total duration of the call (*totdur*), the minimum (*fmin*) and maximum (*fmax*) frequencies of the call, and the mean frequency of highest energy (*freq*) by measuring the peak frequency of each component and calculating the average. Duration was measured from oscillograms, and all other parameters were taken from sonagrams.

**Identification of *P. kuhlii***

*Pipistrellus kuhlii* is the most abundant bat species in all localities where we carried out recordings. Its presence in 10 of them was also confirmed by hand-netting the bats soon after ultrasound recordings had been taken.

In all cases, we attributed the social calls recorded to *P. kuhlii* only when they were produced by bats emitting FM–CF echolocation calls with a frequency of maximum amplitude of 36–41.5 kHz. *Pipistrellus kuhlii* echolocation calls show a wider range of peak frequencies (Zingg, 1990); however, the criterion we adopted eliminated any possible risk of confusion with the 45 kHz phonic type of *P. pipistrellus*, as the lowest values of peak frequencies reported for this species from continental Europe (Zingg, 1990) and Great Britain (Vaughan, Jones & Harris, 1997) is 41.6 kHz, and Zingg (1990) indicates values of peak frequency for *P. kuhlii* and *P. pipistrellus* which overlap within the range 41.6–44.8 kHz.

Usually the bats considered for the present study emitted echolocation calls peaking below 40 kHz. No individuals of the 45 kHz *P. pipistrellus* phonic type were captured in the study areas.

*Pipistrellus nathusii* also emits echolocation calls similar to those produced by *P. kuhlii* (Zingg, 1990); however, this species is uncommon in Southern Italy (Lanza, 1959) and is not known to occur in Campania.

**Statistical analysis**

An Anderson–Darling test applied to the parameters measured on social calls and on peak frequencies of echolocation calls revealed that they did not conform to normal distribution, and normality was not obtained through data transformation. Therefore, we used non-parametric tests for univariate analyses: a 2-tailed Mann–Whitney test was applied to test for differences between medians of each parameter, and a Spearman’s rank coefficient was used to explore correlation between the peak frequencies of echolocation and social calls. As
multivariate techniques are robust to departures from normality (Dillon & Goldstein, 1984), we also employed a quadratic discriminant analysis with cross validation to try to separate call samples from the 2 study areas and a MANOVA to obtain values for Wilk’s $\lambda$. Analyses were performed with Minitab release 11.0. In all tests, values of $P < 0.05$ were considered significant.

**RESULTS**

**P. kuhlii social calls**

*Pipistrellus kuhlii* foraged at all recording sites, as confirmed by the numerous feeding buzzes (Griffin, Webster & Michael, 1960) they produced. Two or more bats flew by the street lamps, and in most cases we could observe them chasing while emitting social calls. Because of their low frequencies, these signals were distinctly audible to the unaided ear. A total sample of 50 social calls, each from a different bat, was analysed.

Figure 1 (a) shows a typical social call of *P. kuhlii*. Thirty out of 50 Kuhl’s pipistrelles produced three-component social calls, although calls with two, four and, once, five components were recorded (Fig. 2). Calls lasted approx. 34 ms, peaked at 16.6 kHz and showed a mean frequency bandwidth of 26.7 kHz (Table 1).

We found a significant positive correlation between freq and the peak frequency of the echolocation call preceding the social call ($n = 40$, $r_s = 0.342$, $P < 0.05$). The median values of peak frequency measured on the echolocation calls preceding the social calls did not differ significantly between Naples and Benevento ($n_{Naples} = 27, n_{Benevento} = 13, t = 126.0, P = 0.156$).

Of all variables measured on calls from the study areas, only freq showed a significant difference, i.e. bats from Benevento emitted social calls peaking at frequencies about 2 kHz higher than those from Naples (Table 2). A quadratic discriminant analysis with cross validation carried out on samples from the Benevento ($n = 22$) and Naples ($n = 27$) provinces could correctly classify 61.2 % of calls, but the model was not significant (Wilk’s $\lambda = 0.79, F_{5,43} = 2.2, P = 0.07$).

**Comparison between *P. kuhlii* and the two phonic types of *P. pipistrellus***

Sonagrams of social calls of *P. kuhlii*, and of the 45 kHz and 55 kHz *P. pipistrellus* phonic types all show more than one component (Fig. 1a–c). Like *P. kuhlii*, the 55 kHz *P. pipistrellus* phonic type also produces more frequently calls of three components, while the 45 kHz *P. pipistrellus* phonic type generally emits four-component calls (Barlow & Jones, 1997b). Social calls of *P. kuhlii* are longer than those of both phonic types of *P. pipistrellus*, and show lower values of $f_{min}$ and freq.

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**Fig. 1.** Sonagrams of a social call of (a) *Pipistrellus kuhlii*, (b) the 45 kHz phonic type, and (c) the 55 kHz phonic type of *P. pipistrellus*.

**Fig. 2.** Number of components of social calls emitted by 50 *P. kuhlii*. Only one call from each bat was examined.
Table 1. Social call parameters from the 50 Kuhl’s pipistrelles recorded in the present study, and from 24 bats of the 55 kHz phonic type and 22 bats from the 45 phonic type of *P. pipistrellus* after Barlow & Jones (1997b). Q1 and Q3 are the lower and upper quartiles.

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>Pipistrellus kuhlii</em></th>
<th><em>Pipistrellus pipistrellus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Totdur (ms)</td>
<td>34.4 ± 8.31</td>
<td>24.9 ± 3.48</td>
</tr>
<tr>
<td>fmin (kHz)</td>
<td>11.5 ± 0.81</td>
<td>16.6 ± 1.80</td>
</tr>
<tr>
<td>fmax (kHz)</td>
<td>38.2 ± 4.50</td>
<td>39.5 ± 5.69</td>
</tr>
<tr>
<td>freq (kHz)</td>
<td>16.6 ± 2.70</td>
<td>20.8 ± 1.56</td>
</tr>
<tr>
<td>Nocomp</td>
<td>2.9 ± 0.68</td>
<td>3.0 ± 0.42</td>
</tr>
</tbody>
</table>

Table 2. Social call parameters of Kuhl’s pipistrelles from the provinces of Naples (n = 27) and Benevento (n = 22), values of Mann–Whitney *t* statistic and corresponding levels of significance *P*. For each parameter the value from the Benevento sample is given below that from the Naples sample.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Naples</th>
<th>Benevento</th>
<th>Mann–Whitney <em>t</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Totdur (ms)</td>
<td>33.5 ± 7.04</td>
<td>34.4 ± 8.72</td>
<td>0.952</td>
<td></td>
</tr>
<tr>
<td>fmin (kHz)</td>
<td>11.4 ± 0.79</td>
<td>11.5 ± 0.86</td>
<td>0.543</td>
<td></td>
</tr>
<tr>
<td>fmax (kHz)</td>
<td>37.4 ± 4.91</td>
<td>39.2 ± 3.93</td>
<td>0.117</td>
<td></td>
</tr>
<tr>
<td>freq (kHz)</td>
<td>15.7 ± 2.20</td>
<td>17.8 ± 2.84</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Nocomp</td>
<td>2.8 ± 0.56</td>
<td>3.0 ± 0.79</td>
<td>0.387</td>
<td></td>
</tr>
</tbody>
</table>

(Discussion).

**Discussion**

**Pipistrellus kuhlii social calls**

The social calls of *P. kuhlii* we describe were all emitted during chases in foraging grounds, and are therefore probably equivalent in function to those observed in *P. pipistrellus*, i.e. they are used for food patch defence (Barlow & Jones, 1997a).

We also noticed that social calls were more frequent on cold nights, probably because insect density is reduced by low air temperatures (Williams, 1961). At low insect densities, *P. pipistrellus* performs most chases (Racey & Swift, 1985) and produces higher social call rates (Barlow & Jones, 1997a).

Our study shows that bats emitting echolocation calls at higher peak frequencies also produce social calls with a higher frequency of maximum amplitude. This relationship does not occur in *P. pipistrellus* (Barlow & Jones, 1997b).

As our data show no difference between echolocation call frequencies from the Naples and Benevento areas, the microgeographical variation observed in *freq* cannot be explained by the above discussed relationship between peak frequencies of echolocation and social calls. This difference could be the result of random effects of natural variation. A further hypothesis, however, is that the Kuhl’s pipistrelles from Naples emit social calls at lower frequencies as a result of an acoustic adaptation process aimed to reduce attenuation and degradation of propagating calls in a complex habitat such as the urban area, while bats from Benevento produce social calls with higher frequency as they forage in simpler, uncluttered habitats. The acoustic adaptation to habitat structure (Morton, 1975; Wiley & Richards, 1978) is known to occur at a microgeographical scale in several bird and mammal species (e.g. Galeotti, Appleby & Redpath, 1996; Slobodchikoff, Ackers & Van Ert, 1998).

**Comparison between *P. kuhlii* and the two phonic types of *P. pipistrellus***

Social calls of *P. kuhlii* show lower values of *freq* and *fmin* than those by both British *P. pipistrellus* phonic types (Barlow & Jones, 1997b). These differences are also likely to exist where these species occur sympatrically, as social calls of *P. pipistrellus* from France, Portugal, Sweden, are very similar to those described for Britain (G. Jones, pers. obs.). Values of *freq* are inversely related to body size between species, as *P. kuhlii*, which calls at the lowest frequencies, is larger than *P. pipistrellus*, and the 55 kHz *P. pipistrellus*, which calls at the highest frequencies, is smaller than the...
45 kHz phonic type (Jones & Parjis, 1993; Barlow & Jones, 1997b). Larger bat species bear larger vocal tracts, and tend to produce echolocation calls at lower frequencies than smaller species (Barclay & Brigham, 1991; Jones, 1995; Vaughan et al., 1997). The negative relation to body size observed in pipistrelle social calls might be interpreted accordingly.

Pipistrellus kuhlii calls also last longer than those by P. pipistrellus, and an experienced listener might in many cases individuate this further difference by hearing the different ‘rhythm’ of the consecutive call components in time-expanded calls, which appears slower in P. kuhlii (Barataud, 1996). Duration, however, is one of the most variable parameters in Kuhl’s pipistrelle social calls because it is related to the number of components, and may overlap between social calls of P. kuhlii and P. pipistrellus.

The parameter \( f_{\text{max}} \) differs clearly only between the Kuhl’s pipistrelle and the 45 kHz \( P. \ pipistrellus \) phonic type. However, its measurement may not be reliable, as higher frequencies are more deeply affected by atmospheric attenuation (Griffin, 1971; Pye, 1980; Lawrence & Simmons, 1982).

A combined use of \( f_{\text{min}}, f_{\text{eq}}, \) and \( \tau_{\text{dur}} \) measured on time-expanded social calls should help to discriminate between field recordings of unknown Pipistrellus whenever the identification based on echolocation calls is uncertain. The differences in frequency values observed are not sufficiently large to permit the usage of heterodyne detectors for a social call-based species identification.

In areas where \( P. \ nathusii \) and \( P. \ kuhlii \) occur sympatrically, a discrimination based on social calls should be easy to carry out as the former species emits typical advertisement and social calls constituted by a main part with a larger (five to seven) number of components, and a final, higher-pitched trill (Barlow & Jones, 1996).

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REFERENCES


Paracrobeles psammophilus sp. nov. (Nematoda: Cephalobidae) from El Saler, Valencia (Spain)

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Abstract

Paracrobeles psammophilus sp. nov. (Nematoda: Cephalobidae) is described from soil of the Dehesa de El Saler (province of Valencia, Spain). This is the second record of a species of the genus Paracrobeles Heyns, 1968. The new species is characterized by rounded cheilorhabdions and the large spicules and gubernaculum of males.

INTRODUCTION

The genus Paracrobeles, proposed by Heyns (1968) to include only Paracrobeles laterellus Heyns, 1968, a species recorded in South Africa, is characterized by the presence of a well developed median bulb with thick-walled lumen in the oesophageal metacorpus and by the absence of fringes in the labial probolae.

We have obtained nematodes from soil of the Dehesa de El Saler whose morphological features agree with those considered characteristic for the genus Paracrobeles Heyns, 1968. However, characters such as rounded cheilorhabdions and the large size of spicules and gubernaculum in males permit a clear separation of the species.

MATERIALS AND METHODS

Sampling was conducted on a monthly basis for 12 consecutive months (April 1992–March 1993) in order to study the variations in nematode numbers throughout an annual cycle. The sample site was a small clearing in a pine Pinus halepensis forest located in the fixed and stabilized dunes of the Dehesa de El Saler (37°40′N; 0°30′E; UTM 30SYJ35). The vegetation in the clearing was typical Mediterranean underbrush (Phillyrea angustifoliae–Rhamnetum angustifoliae) (Costa & Mansanet, 1981).

Edaphic samples were collected with an 8 × 25 cm (inner diameter × height) metallic corer. Subsequently, the organic stratum (upper 7–8 cm) was separated from the mineral stratum consisting of the soil remaining within the corer. Using this methodology, 3 samples were collected every month throughout the study period from 3 different sampling sites in the study area. The samples were processed immediately. Samples of plant material were also taken at each sampling site to observe the presence of Paracrobeles psammophilus in the edaphic fraction associated with the roots. For each sample, we processed 100 cm³ from each of the 2 edaphic strata by the Baermann funnel technique and 100 cm³ by centrifugal flotation (Nombela & Bello, 1983), as well as 15 g of roots. Once isolated, the nematodes were fixed in a solution of 4% formaldehyde with calcium carbonate and mounted according to Seinhorst (1959, 1962).

Monthly variation in nematode numbers was calculated by taking into account only individuals obtained by the centrifugal flotation technique. This technique seemed more appropriate for quantitative analyses than...