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Different songflight calls of *Pipistrellus kuhlii* and *Pipistrellus lepidus* (Vespertilionidae, Chiroptera) in Europe

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Abstract. We analysed and compared the structure and parameters of the songflight calls of expansive *Pipistrellus kuhlii* and *Pipistrellus lepidus*, that recently colonized Central Europe from the south and east, respectively. Bat calls were recorded mainly in urban areas of Central Europe and the Balkans, including a narrow zone of these species' recent parapatric or sympatric occurrence (around the Carpathians and the eastern part of the Pannonian Basin). The newly described songflight calls of *P. lepidus* consist of more elements (median 6), are longer (mean 56.4 ms) and of a higher frequency of maximum energy (mean 25.7 kHz) than those of *P. kuhlii* (median 3, mean 41.0 ms and mean 14.0 kHz, respectively). This finding provides new evidence that *P. lepidus* represents a different species, in accordance with results from previous genetic and morphological studies. Reported differences in songflight calls permit the acoustic discrimination of *P. kuhlii* and *P. lepidus*, which is not possible based on overlapping parameters of their echolocation calls. Our findings enable distributional and ecological studies of these two species, based on acoustic methods, in the context of their rapid European expansion and the local co-occurrence.

Key words: bats, bioacoustic discrimination, biogeography, interspecific differences

Introduction

Males of pipistrelle bats emit distinct songflight calls (advertisement, mating or agonistic calls, representing one type of social calls, referred as type D) that are also used during chases to repel other foraging individuals. The complexity and variability of songflight calls can be used to distinguish among species of the genus *Pipistrellus* and other European bats (e.g. Pfalzer & Kush 2003, Georgiakakis & Russo 2012, Russ 2012, Middleton et al. 2014). The diagnostic character of

songflight calls can be useful when echolocation call parameters overlap between species, like in *Pipistrellus nathusii* and *Pipistrellus kuhlii* or *Pipistrellus pygmaeus* and *Miniopterus schreibersii* (Russo & Papadatou 2014, Dietz & Kiefer 2016). Differences in songflight calls provided one of the most robust arguments to support the specific status of the two cryptic species *Pipistrellus pipistrellus* and *P. pygmaeus* (Barlow & Jones 1997).

Populations of *P. kuhlii* from the south and west of Europe and north of Africa (hereafter *P. kuhlii*),

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and from the east of Europe and the Middle East (hereafter *Pipistrellus lepidus*) may be treated as distinct phylogeographic and morphological species of allopatric origin (Mayer et al. 2007, Dietz & Kiefer 2016, Sachanowicz et al. 2017). In recent decades, both species have spread northwards, *P. kuhlii* from the Balkans and *P. lepidus* from Russia and Ukraine, and their ranges have become parapatric in parts of Central Europe, where both co-occur locally (Strelkov et al. 1985, Strelkov & Iljin 1990, Sachanowicz et al. 2006, 2017, Danko 2007). Adaptation to urban areas, prevalent in Europe, appears to be one of the main factors enabling their expansion, which has similarly been observed in other synanthropic bat species, such as *Hypsugo savii* (Uhrin et al. 2016), and some bird species, such as *Streptopelia decaocto* (Kasperek 1996).

These two pipistrelle species emit frequency modulated (FM) echolocation search signals with an average start frequency of ca 60 kHz, terminal frequencies between 35–45 kHz, and a frequency of maximum energy of 37–41 kHz (Schnitzler et al. 1987, Benda et al. 2006, Berger-Tal et al. 2008, Barataud 2015). However, previous studies of social calls have been conducted mainly within the European range of *P. kuhlii*. The lack of focus on *P. lepidus* social vocalization is a consequence of the fact that the echolocation call parameters of these two species do not differ (Benda et al. 2006, Amichai & Korine 2020, author's own data) and bats from the Middle East (now *P. lepidus*) have, until recently, been treated as representatives of *P. kuhlii* (Benda et al. 2006).

Over the last decade we recorded specific social calls at a variety of sites in Central and south-eastern Europe, which were different from those of other *Pipistrellus* species and have not been yet described from Europe. This type of a call was initially recorded in South-East Poland, during summer and autumn, at known *P. lepidus* roosts in crevices of building walls and their vicinity that are used by sexually active displaying males (songflights and false landing behaviour observed in some cases), capture sites of adult sexually active males, and near a female colony roost. These recorded calls thus represented songflight calls, that are used for the purpose, among others, of mate attraction. No *P. kuhlii* were captured at these localities. Such a call was recently described as a male courtship song of *P. kuhlii* from Israel (Amichai & Korine 2020), but this type of a call is specific to *P. lepidus* and has not been reported for

European *P. kuhlii* (e.g. Russ 2012, Middleton et al. 2014).

In a previous study we showed that European *P. lepidus* and *P. kuhlii* differ not only in genetics, but also in their morphology and morphometry (Sachanowicz et al. 2017). The aim of the present study was to test whether *P. lepidus* and *P. kuhlii* also differ in their songflight call structure and parameters, which would support the species status of *P. lepidus*. We provide measurements and a sonogram of the songflight calls of this species, enabling its acoustic separation from *P. kuhlii* and other *Pipistrellus* species in further ecological (e.g. habitat use, behaviour), distributional and monitoring studies.

Material and Methods

We analysed 67 songflight call samples of *P. lepidus* and 47 of *P. kuhlii*, recorded from July to October 2011–2017 in Central Europe and the Balkans, mainly in allopatric parts of the geographic ranges of both species, but also in areas where they recently co-occurred, either in parapatry or sympatry (Fig. 1), recorded previously based on morphological and genetic studies (Sachanowicz et al. 2017). To avoid pseudo-replication, we have considered only recordings made at localities that were at least 500 m apart, using a single call sequence from each site (see Hurlbert 1984, Russo & Jones 1999). The calls of *P. lepidus* were sampled in Poland (n = 49 samples), Slovakia (n = 6), Ukraine (n = 4), Romania (n = 4) and Moldova (n = 4), and those of *P. kuhlii* in Poland (n = 8), Slovakia (n = 9), Ukraine (n = 2), Romania (n = 8), Slovenia (n = 2), Croatia (n = 2) and Albania (n = 16), (Fig. 1).

Bat calls were recorded in urban areas, near roosts in crevices of buildings, used by displaying males at night (confirmed by mist-netting in some cases), or inhabited by bat colonies, and at foraging/commuting sites in city parks and along street transects. We used full-spectrum Batlogger automatic recorders (Elekon AG, Switzerland) in real time with a sampling rate of 312.5 kHz and a frequency range of 10–150 kHz. The recordings were analysed using BatSound 3.3 (Pettersson Elektronik AB, Sweden). Signals were displayed as sonograms with an FFT size 512 Hanning window. Call measurements were taken from the first harmonics. Temporal parameters were measured from the oscillograms and frequency parameters – from the sonograms and power spectra. The term

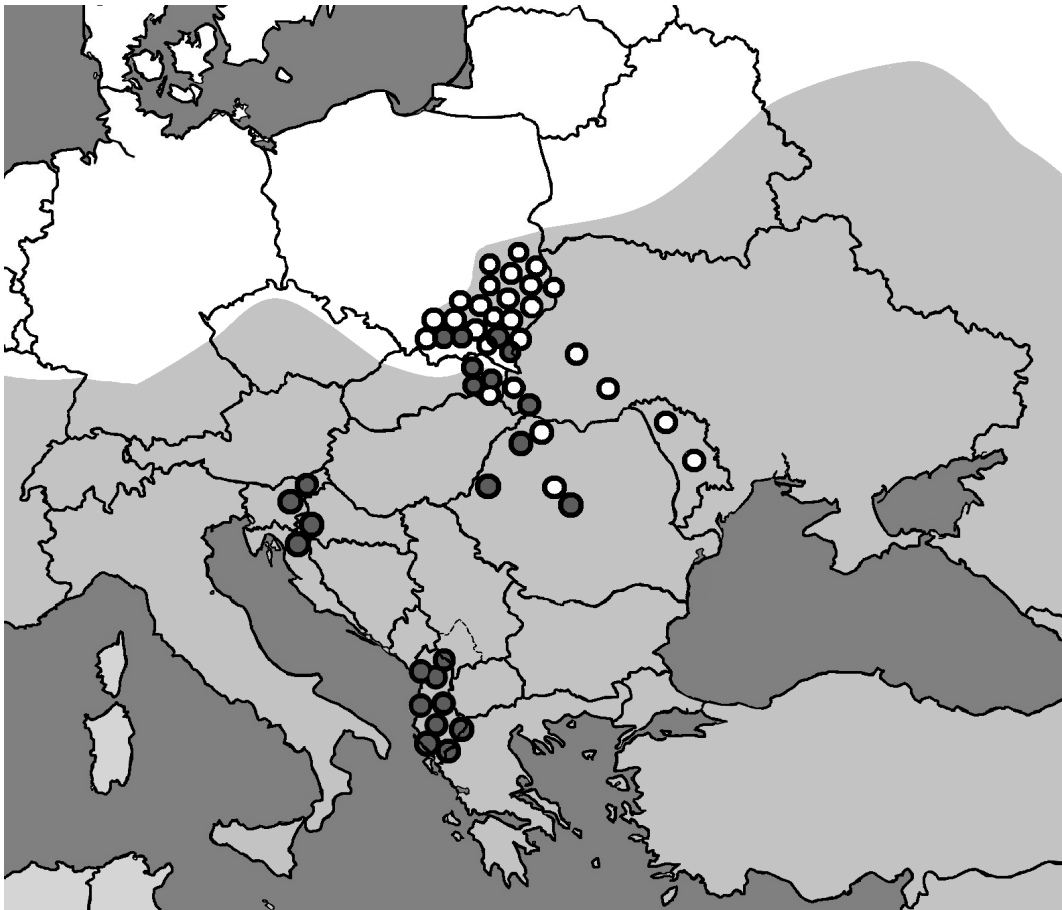


Fig. 1. Distribution of locations where songflight calls of *P. kuhlii* (dark circles) and *P. lepidus* (white circles) were recorded for this study. The northern boundary of *P. kuhlii* sensu lato range (gray) in Central and Eastern Europe based on Shpak & Larchenko (2016), Sachanowicz et al. (2017) and Lučan et al. (2020).

“component” refers to a single pulse in a social call (see Russo et al. 2009, Middleton et al. 2014) and is synonymous with “syllable” (Kanwal et al. 1994).

The following parameters were measured for each songflight call sequence: 1) Beginning (starting) frequency of the individual component of a call

Table 1. Comparison of songflight call parameters of *P. kuhlii* and *P. lepidus* and two-tailed Mann-Whitney U test results for differences between medians of all parameters. Abbreviations are explained in the Material and Methods chapter. *Parameters for which mean/median values were calculated from individual components of a call.

| Parameters | Start-freq* (kHz) | Freq-max-En* (kHz) | End-freq* (kHz) | Min-freq* (kHz) | Tot-freq (kHz) | Comp-dur* (ms) | Int-puls-dur* (ms) | Tot-dur (ms) | No-of-comp |
|-------------------|-------------------|--------------------|-----------------|-----------------|----------------|----------------|--------------------|--------------|------------|
| <i>P. kuhlii</i> | n = 149 | n = 149 | n = 149 | n = 149 | n = 47 | n = 149 | n = 102 | n = 47 | n = 47 |
| Mean | 28.7 | 14.0 | 11.3 | 11.3 | 14.0 | 9.4 | 14.5 | 41.0 | 3.1 |
| SD | 5.70 | 1.27 | 1.15 | 1.15 | 1.01 | 2.76 | 3.08 | 10.32 | 0.86 |
| Median | 27.8 | 13.7 | 11.3 | 11.3 | 13.7 | 9.3 | 14.5 | 41.1 | 3 |
| Range | 18.4-45.5 | 11.9-19.9 | 8.1-17.6 | 8.1-17.6 | 12.1-17.3 | 3.8-16.6 | 8.3-25.9 | 11.4-91.1 | 1-5 |
| <i>P. lepidus</i> | n = 409 | n = 409 | n = 279 | n = 391 | n = 67 | n = 409 | n = 336 | n = 67 | n = 67 |
| Mean | 39.9 | 26.2 | 20.5 | 15.0 | 25.7 | 5.3 | 10.3 | 56.4 | 6.1 |
| SD | 6.09 | 2.34 | 3.86 | 2.49 | 3.42 | 1.89 | 1.45 | 16.46 | 1.72 |
| Median | 39.5 | 26.5 | 20.2 | 14.8 | 26.1 | 5.4 | 10.4 | 55.1 | 6 |
| Range | 21.6-57.0 | 17.5-34.2 | 12.5-36.6 | 9.1-24.9 | 22.4-30.7 | 1.2-11.0 | 6.4-15.5 | 26.3-115.6 | 3-12 |
| U-test | Z = -14.2 | Z = -17.7 | Z = 16.6 | Z = 12.9 | Z = 8.9 | Z = -14.2 | Z = -11.5 | Z = 5.1 | Z = 8.0 |
| | P < 0.05 | P < 0.001 | P < 0.05 | P < 0.05 | P < 0.001 | P < 0.05 | P < 0.05 | P < 0.05 | P < 0.001 |

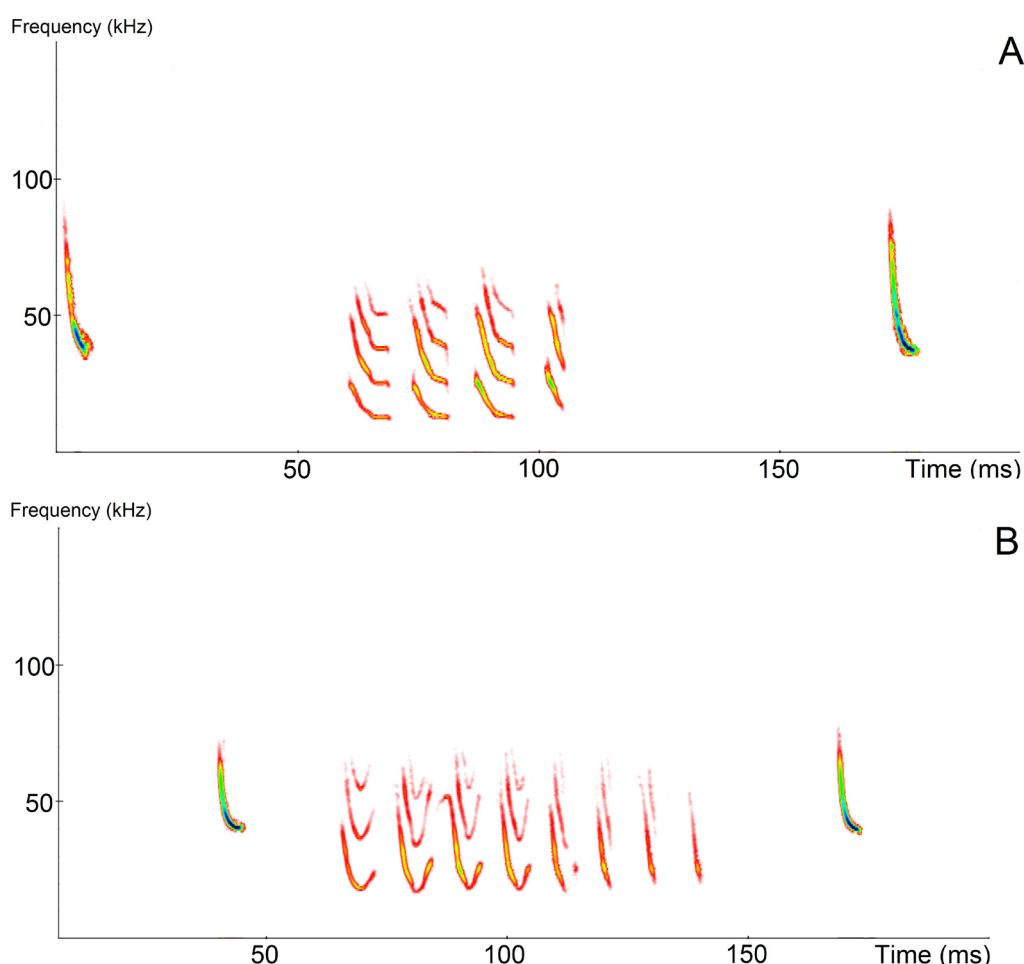


Fig. 2. Sonograms of the songflight call of A) *P. kuhlii*, 5.07.2013, Humenné, Slovakia, and B) *P. lepidus*, 27.07.2013, Przemyśl, Poland.

(Start-Freq); 2) The lowest (minimum) frequency of the individual component of a call (Min-Freq); 3) Terminal (ending) frequency of the individual component of a call (End-Freq); 4) Frequency of the highest energy of the individual component of a call (Freq-max-En); 5) Frequency of the highest energy of a whole sequence (Tot-freq); 6) Total duration of a sequence (Tot-dur); 7) Duration of individual components within a sequence (Comp-dur); 8) Inter-pulse interval duration within a sequence (Int-pulse-dur); 9) The number of components within a sequence (No-comp).

In all cases we attributed the recorded songflight calls to *P. kuhlii* or *P. lepidus* when they were accompanied by echolocation calls typical for these species frequency of maximum energy of 36-40 kHz to avoid confusion of the possibility of simultaneous records of the songflight calls of *P. pipistrellus* or *P. pygmaeus* (Russ 2012, Barataud 2015). STATISTICA ver. 12.5 was used to generate summary statistics for songflight call parameters and to perform a two-tailed Mann-Whitney U test for differences between medians.

Results

The songflight calls of both species were simple in structure, containing several uniform components of the same frequency: 1-5 (median 3) FM notes in *P. kuhlii*, and 3-12 (median 6) in *P. lepidus* (Table 1, Fig. 2A, B). All frequency parameters were significantly higher in *P. lepidus*, with the most obvious difference in the mean frequency of maximum energy of a sequence: *P. lepidus* 25.7 ± 3.42 kHz, *P. kuhlii* 14.0 ± 1.01 kHz (Table 1, Fig. 3A-C). The higher number of components in the calls of *P. lepidus* resulted in a longer call duration (mean 56.4 ms), which in some cases was twice as long as that of *P. kuhlii* (Table 1, Fig. 3D). Other temporal parameters also differed in both species, with a longer duration of individual components and inter-pulse intervals in *P. kuhlii*. All temporal parameters also differed significantly between these species (Table 1).

In terms of call structure, frequency and duration largely differed between *P. kuhlii* (Fig. 4) and *P. lepidus* (Fig. 5), with almost no overlapping ranges

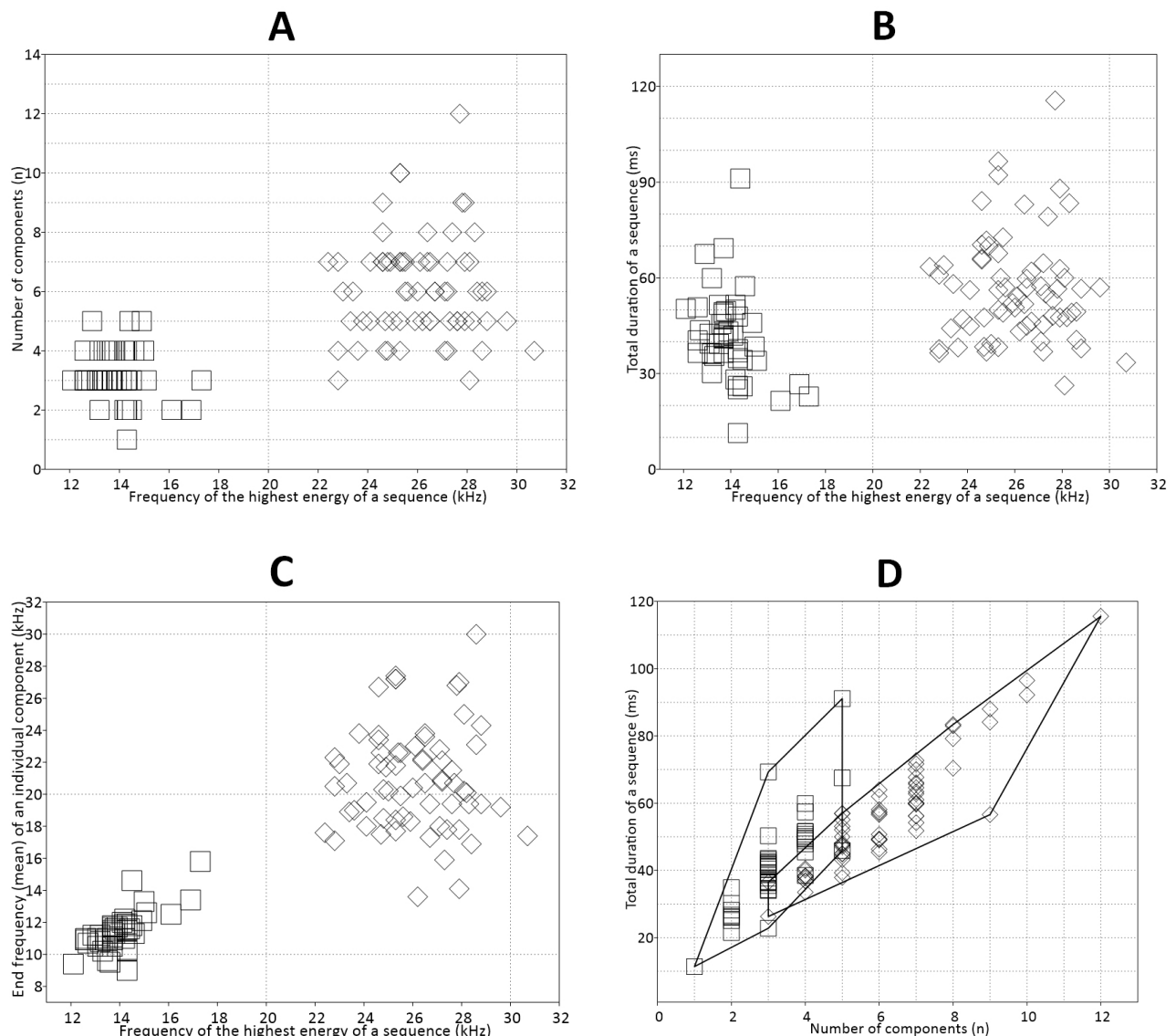


Fig. 3. A-D) Scatter plots of frequency and duration parameters of songflight calls of *P. kuhlii* (squares) and *P. lepidus* (diamonds).

(Table 1, Fig. 3A-D), their songflight calls can be used for acoustic separation of these species. The species-specific calls of *P. lepidus* were recorded only in the eastern part of Central Europe, while those of *P. kuhlii* in the Balkans and over a large part of Central Europe (from Albania and Slovenia in the south and west to Slovakia, Ukraine and Poland in the north-east). In some regions, specific calls of both species were recorded in the same area and even localities, indicating local co-occurrence with parapatric or slightly overlapping ranges around the Carpathian Mountains (Fig. 1).

Discussion

Despite a wide geographic range, studies on the variability of songflight calls in different populations of *P. kuhlii* sensu lato are lacking, and the social calls

of eastern populations, here designated as *P. lepidus*, have not been analysed previously. In contrast to completely overlapping echolocation call parameters between *P. kuhlii* and *P. lepidus*, differences in their songflight calls might be expected, based on well-known calls of *P. kuhlii* from southern and western Europe (e.g. Russo & Jones 1999, Middleton et al. 2014, Barataud 2015, Lučan et al. 2020) and anecdotal data on male *P. lepidus* songflight calls from the Middle East, with sonograms recorded in Syria and Israel published as calls of *P. kuhlii* without any parameters and/or comments on their specific characteristics (Benda et al. 2006, Amichai & Korine 2020). Species-specific songflight calls of these species have been confirmed in the present work.

Taxonomic revisions in the genus *Pipistrellus* in Europe started with the separation of *P. pygmaeus*



Fig. 4. General appearance and colouration of *P. kuhlii*, 29.09.2005 Karkavec, Albania (photo Konrad Sachanowicz).



Fig. 5. General appearance and colouration of *P. lepidus*, 30.07.2013 Przemyśl, Poland (photo Michał Piskorski).

from *P. pipistrellus* (Jones & van Parijs 1993, Barratt et al. 1997), which was initially based on differences in their echolocation (“phonic types” 55 kHz and 45 kHz, respectively), but subsequently morphological and genetic traits were apparent, as well as their different songflight calls. Later, *Pipistrellus hanaki* was split off from the *P. pipistrellus* species complex and its distinctive social calls were highlighted (Benda et al. 2004, Georgiakakis & Russo 2012). The morphological

and morphometric differences between *P. kuhlii* and *P. lepidus* are much more evident (Sachanowicz et al. 2017) (Fig. 4, 5) than those between *P. pipistrellus* and *P. pygmaeus* (Dietz & Kiefer 2016), and correspond with their deep genetic divergence (Mayer et al. 2007, Veith et al. 2011, Kruskop et al. 2012, Sachanowicz et al. 2017). The different songflight calls reported in the present study, and their formerly allopatric geographic ranges in Europe that offered no possibility for

hybridization with *P. kuhlii*, provide further support for the specific status of *P. lepidus*. The potential for hybridization between *P. lepidus* and *P. kuhlii* within their recently established contact zone, and even their local syntopic occurrence in Central Europe (eastern Slovakia and Hungary, south-western Ukraine and south-eastern Poland – Danko 2007, Sachanowicz et al. 2017, this work), seems unlikely. Considering different songflight calls, the presence of behavioural reproductive barriers may be assumed, driven by the inter- and intraspecific acoustic recognition of mating males by conspecific females through sexual selection. Such a mechanism could prevent potential hybridization, but its presence remains to be further tested using playback experiments. In two such ecologically similar species, different songflight calls confirm their allopatric evolutionary history and may also suggest the possibility of some differences in mating behaviour, even if the mating system of these bats seems to be the same (resource defence polygyny, Amichai & Korine 2020).

The extent of overlap in the geographic and ecological distribution between *P. kuhlii* and *P. lepidus* remains to be studied, particularly in their new contact zone across Central Europe. Based on acoustic methods and differences in the songflight calls of these bats, we confirmed their presence in some areas and recorded both species in countries where they had not been reported previously (Sachanowicz et al. 2017). This method should be tested to identify populations of *P. kuhlii* and *P. lepidus* in different parts of Asia Minor and the Middle East, where representatives of these species

(or one of them) are highly variable in morphology (Benda et al. 2006).

The songflight calls of *P. lepidus* and *P. kuhlii* are simple in structure, consisting of a few uniform components, similar to songflight calls of *P. pipistrellus* and *P. pygmaeus* (Middleton et al. 2014). The calls of *P. lepidus* differ from those of other *Pipistrellus* species by their highest frequency (higher even in comparison with those of *P. pygmaeus*) and the total duration, consisting of the highest number of components – up to 12, which was not recorded in the other species. The calls of *P. kuhlii* are similar in structure and number of components to those of *P. pipistrellus*, but are longer and the highest energy frequency is lower (Middleton et al. 2014). The calls of all these species are different from the more complex and longer songflight calls of *P. nathusii*, including unusual calls, comprising three to five separate motifs (Russ & Racey 2006, Jahelková et al. 2008, Jahelková 2011, Middleton et al. 2014).

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