Linking Activity of Common Pipistrelles, *Pipistrellus Pipistrellus*, in an Urbanised Area With a Nearby Mass Swarming Site

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Abstract

The Erňa cave, a mass winter hibernaculum and important swarming site of the common pipistrelle, *Pipistrellus pipistrellus*, is located in the Slovak Karst, near the Košice urban agglomeration in eastern Slovakia. Over the past two decades, the unusual behaviour of late summer or autumn accidental but abundant occurrences of this species have been observed in buildings (so-called invasions) in Košice. It has been hypothesised that these events are related to bats swarming and hibernating in the Erňa cave; however, causality has not been confirmed. We measured the relative activity of bats from the end of the breeding season through the invasions and autumn swarming prior to the onset of hibernation by recording their echolocation calls on car-based transects in order to find any spatial and temporal linkage between activity in the urban area and the swarming site. Over two years we recorded 6,253 sequences with echolocation calls of *P. pipistrellus* and 5,239 records of other bats along four transects totalling 7,121 km in length. Spatial pattern analysis found that the city agglomeration presented a local hotspot of the species' activity, especially during the invasion season. Multivariate generalised additive modelling confirmed an increased density of records of *P. pipistrellus* between the urban area and the hibernaculum in the pre-hibernation season, whereas this pattern was not found to be consistent on the control transects near the city. Contrary to that, other bat species showed little variation in their activity between transects and seasons. The obtained results suggest that the relatively short geographical distance between the urban agglomeration and the large swarming site is likely a clue to the frequent city invasions of the species, although the role of the city as a hibernation area cannot be completely omitted.

Introduction

The common pipistrelle bat, *Pipistrellus pipistrellus* (Schreber, 1774), is one of the most widespread and abundant of Western Palearctic vespertilionid bat species, occurring over almost all of Europe, with a northern limit at 56°N in southern Scandinavia. It also ranges into North Africa, Asia Minor and through the Middle East up to Afghanistan (Horáček et al. 2000; Benda et al. 2004; Hulva et al. 2004). The species was recognized as being a sibling of a very similar cryptic species, *Pipistrellus pygmaeus* (Leach, 1825), only two decades ago (Barratt et al. 1997; Mayer and von Helversen 2001) and there are still gaps in the knowledge about its specific ecology and behaviour. In general, *P. pipistrellus* is a very flexible species occurring in habitats within a gradient from highly urbanised city centres to settlements in rural landscapes, where they often prefer woodlands and waters (Barlow 1997; Dietz et al. 2009; Todd and Williamson 2019). The species can even use habitats associated with human-made linear infrastructures, like railways, mostly in an intensively managed agricultural landscape (Vandeveldt et al. 2014). During seasons of activity these bats occupy variable shelters but with tendency to prefer synanthropic spaces. For example, crevices in buildings can be maternity roosts, which can be switched very frequently, although bats can sometimes be found in rock or tree fissures or in bat boxes (Feyerabend and Simon 2000; Dietz et al. 2009). Similarly, individuals and clusters of bats hibernate mainly in above-ground roosts, such as tree holes, the attics of churches and houses, behind cladding boards and under roof coverings, but also in cellars, tunnels and natural caves (Kretzschmar and Heinz 1995; Uhrin 1995; Park et

al. 1996; Kaňuch et al. 2010). This species also forages over a wide range of habitat types, e.g., calm rivers or woodland edges and short isolated tree lines along roads (Vaughan et al. 1997; Warren et al. 2000; Davidson-Watts et al. 2006; Nicholls and Racey 2006; Sattler et al. 2007; Abbott et al. 2009; Todd and Waters 2017). Foraging sites of the species are often very close to the colony roost (Davidson-Watts et al. 2006).

The so-called invasion behaviour of common pipistrelle bats during the swarming time in late summer and in autumn (note that the original term 'autumn invasion' is not used here as in the context of biological invasions, possibly one may rename it as 'incursion') has been described as a remarkable species-specific ecological trait (Sachteleben 1991). These invasions represent the flight of numerous groups of individuals into unoccupied or inhabited buildings and similar human-made spaces, which are often unsuitable as roosts in general and can act negatively as ecological traps (e.g., Palášthy and Gaisler 1965; Sachteleben and von Helversen 2006). As revealed from a recent review, such an unusual behaviour of this species is limited within its range to several cities of Central Europe (mainly Germany, Czechia, Slovakia; Nusová et al. 2019a). It has been hypothesised that autumn invasions are related ecologically to the close proximity of a mass swarming site, which also act as a mass underground hibernaculum. For instance, invasions in the Košice urban agglomeration (eastern Slovakia) were positively correlated with the number of bats hibernating in the largest known hibernaculum of the species, the Erňa cave (Nusová et al. 2019a); however, the causality of this relationship is not yet understood.

It seems to be a rule that most swarming bats originate from the related hibernacula (Fenton 1969; Glover and Altringham 2008; van Schaik et al. 2015), and mass hibernacula also play a role as important swarming sites (Sendor and Simon 2003; Nusová et al. 2020); however, in the case of mass winter aggregations of common pipistrelles in the caves of the Carpathian Mountains (e.g. Dumitrescu and Orghidan 1963; Nagy and Szántó 2003; Horáček and Jahelková 2005; Nagy and Postawa 2011; Nusová et al. 2017), the question of the geographic origin of these bats arises. Ringing observations have suggested mostly short-distance seasonal movements for this species (Palášthy 1988; Avery 1991; Gaisler et al. 2003). In contrast, molecular data has revealed a substantial level of gene flow among summer colonies, which indicates some migratory status, that is, either mate-conditioned long-distance movements or sex-biased long-distance dispersal (Bryja et al. 2009; Nusová et al. 2017). Nevertheless, an analysis of stable hydrogen isotope ratios in the fur of bats swarming during the autumn at the Erňa cave revealed that members of this mass hibernacula aggregation are both local bats and occasional facultative migrants, which may undertake long-distance seasonal movements (Nusová et al. 2020).

Thus, a study of the activity of common pipistrelle bats in the commuting area between their natural hibernaculum and nearby large urban agglomeration could bring new insight into understanding the causality behind the specific late summer or autumn invasion behaviour. Therefore, we compared the activity of *P. pipistrellus* and other bat species in the city of Košice and surrounding zones (different directions, mostly in the Košická kotlina Basin, monitored by car-based transects), including the direction towards the Erňa cave, from the end of the breeding season through the late summer invasions and autumn swarming, prior to the onset of hibernation. We used additive modelling to test the hypothesis

that the relative activity (number of echolocation records) of common pipistrelles, unlike other bats, will be higher in the city and in the area between the city and the mass hibernaculum. Similarly, we hypothesised that the activity in such a commuting area will increase during the course of autumn season.

Material And Methods

Study area

The Košická kotlina Basin (eastern Slovakia) is characterised by a fragmented landscape with different habitats, mostly agricultural land and less deciduous or mixed forests, but also some fishponds and water reservoirs. It is a densely urbanised environment with many villages of various sizes, while the city of Košice (208 m a.s.l.), extending over an area of ca. 244 km² and with a population of 239,000 inhabitants, is located in the centre of the basin (Fig. 1a). The rural parts of the study area and the city provide plenty of roosting opportunities for common pipistrelles and many other bat species (e.g., *Rhinolophus hipposideros*, *Myotis myotis*, *M. emarginatus*, *M. daubentonii*, *Nyctalus noctula*, *Eptesicus serotinus*, *Pipistrellus pygmaeus*, *Pipistrellus kuhlii* and *Hypsugo savii*; Matis 1998; Matis et al. 2002; Cel'uch et al. 2016; Kucková 2018; Nusová et al. 2019b, c). A mass hibernaculum of pipistrelles is located 33 km southwest of Košice in the Erňa cave in the Slovak Karst (380 m a.s.l.), near the border with the Košická kotlina Basin. Since the late 1980s thousands of hibernating pipistrelles have been recorded annually there with increasing abundance up to 50,000–70,000 individuals during the last winters; this cave is also known as massive swarming site of the species (Nusová et al. 2020).

Data collection

Echolocation calls of bats were recorded along four car-based transects (Roche et al. 2011; Cel'uch et al. 2016) designed to cover different areas of the Košická kotlina Basin. In addition, an *urban* transect in the city of Košice and a *link* transect which was assumed to catch the higher activity of bats in an expected commuting area between the natural swarming site/hibernaculum and nearby city, were monitored. We also monitored two different *control* transects (*A* and *B*) having a similar landscape structure to the *link* (a rural area with predominant agricultural habitats) but located outside the supposed commuting area (Fig. 1a). These transects were directed north and southeast of the city, i.e., in the opposite directions as the *link* transect. The *link* ended 1 km before the Erňa cave to avoid overestimation of the relative activity on this transect due to the mass swarming site. For sampling the bat activity, we used the automatic Batlogger M bat detector system (Elekon, Switzerland) for real-time, full spectrum recording of echolocation calls. The ultrasonic external microphone of the detector was fixed with a tripod on the roof of a car that passed along different roadways at a constant speed of ca. 30 km.h⁻¹. In two years (from 7 June to 6 November 2017 and from 12 June to 8 November 2018), each transect was sampled repeatedly at about 10-day intervals with a tolerable deviation of 1–2 days considering optimal weather conditions for recording the activity of the bats. This period covered three different seasons in regard to the particular life cycle of the species in the area. The first season of *post-breeding* represented the time when

most of the bats had still formed maternity colonies but offspring were almost fully weaned, thus until the season of *invasions* begin. Most of the invasions of common pipistrelles in Košice were found to last about one month in the late summer (Nusová et al. 2019a); therefore, this season was set according to the highest number of records with a ± 14 -day window around this date, which fell on 2 August 2017 or 4 August 2018, respectively. The last season was called *pre-hibernation*; this was the remaining time of bat activity prior to winter torpor in a hibernaculum.

The mean length of the transect was 66 km, but due to some construction works or the traffic situation, the length sometimes varied. Recording started on average about 85 minutes after sunset (full dark) and lasted for about 135 minutes (Table 1). A bat record was a time sequence (mean $\pm$ SD; 4.25 ± 4.00 s) with echolocation calls (11.51 ± 12.10 calls per record) determined as some bat species in a default manner by the BatExplorer 2.0 ultrasound analysis software (Elekon, Switzerland). However, automatic species determination by the software was manually controlled to remove possible errors from the final data set (Rydell et al. 2017). In order to find out whether the flight corridor between an invaded urban area and a swarming site is associated with higher relative activity we compared *P. pipistrellus* (peak frequency 44.74 ± 8.90 kHz) activity on the transects with all other bats in general. Each record was automatically referenced by geographical coordinates and the actual outdoor temperature. Automatic species determination by the software was manually controlled to remove possible errors from the final data set (Rydell et al. 2017); species determination was conducted among parameters provided by analysis software using the criteria of searching and social call characteristics known for European species (e.g., Russo and Jones 2002; Middleton et al. 2014; Barataud 2015 and own data).

Table 1

Summary table for car-based data sampling on road transects (mean and range). Records are the total number of time sequences (4.25 ± 4.00 s) determined as echolocation calls of *Pipistrellus pipistrellus* (*P. pip*) and other bat species in total

transect	samplings (n)	start after sunset (min)	length (km)	duration (min)	<i>P. pip.</i> (n)	other bats (n)
2017						
Urban	13	74 (27–104)	61 (58–67)	157 (140–174)	955	646
Link	13	90 (46–156)	55	114 (97–141)	599	408
control A	14	93 (40–234)	48 (38–49)	97 (78–122)	318	439
control B	13	92 (34–181)	92 (60–95)	167 (93–191)	583	637
2018						
urban	14	90 (61–202)	62	148 (133–182)	1635	1099
link	14	81 (60–159)	57	118 (110–127)	738	557
control A	14	84 (61–120)	52 (51–56)	99 (91–104)	743	702
control B	14	79 (60–99)	97	172 (156–184)	682	751

Geospatial analysis

Information about habitat structure in the study area was obtained from Corine Land Cover data (100 m GeoTiff raster, CLC 2018 version 20 downloaded from <https://land.copernicus.eu/>) and processed in the package 'raster' 3.0–12 (Hijmans 2020) of the R 3.6.3 software (R Core Team 2020). We used the main habitat level of the Corine Land Cover (i.e., artificial surfaces, agricultural areas, forest and seminatural areas, water bodies; Fig. 1) as the relevant habitat resolution for our echolocation data. Spatial data layers were first manipulated in the R-packages 'rgdal' 1.4-8 (Bivand et al. 2019) and 'maptools' 0.9-9 (Bivand and Lewin-Koh 2019) into a format supported by the package 'spatstat' 1.63-3 (Baddeley et al. 2015). Using this R-package we modelled the relationship between the point pattern intensity of the *P. pipistrellus* records and the distribution of Corine Land Cover habitats as a covariate using a non-homogeneous Poisson point process model. Thus, we fit the model that assumes that point process intensity is a function of habitat quality. Because numerous records during the invasions time in the city of Košice would likely overestimate the effect of artificial surfaces in this area (Fig. 1a), the model was

based only on records from the three rural transects collected during both years. Bat records were transformed into a ppm object to fit the point process model to an observed point pattern.

Statistical modelling

Because we expected nonlinear patterns in bat activity, we employed a multivariate generalised additive model (GAM) with Gamma error distribution, log link and smoothing parameters selected by the Restricted Maximum Likelihood method (Wood 2011). The number of records per kilometre of transect was the response variable explained by the date and the outdoor temperature. The temperature was calculated as the mean value recorded during the transect. The effects of these continuous predictors were fitted with penalized cubic regression splines. Using a factor-smooth interaction, we calculated a different smooth for each transect (fixed factor) in the R-package 'mgcv' 1.8–28 (Wood 2019). To test whether the relative frequency of social calls in the records differs among transects or seasons we fitted a model of independence for two-way tables and visualised them in mosaic plots using the R-package 'vcd' 1.4-6 (Meyer et al. 2020).

Results

During the two monitored periods we recorded 6,253 sequences with echolocation calls of *P. pipistrellus* (2,455 in 2017, 3,798 in 2018; Fig. 1b) along four selected car-based transects totalling 7,121 km in length (Table 1). In addition, we collected 2,130 and 3,109 records of other bats in 2017 and 2018, respectively. The non-homogeneous Poisson point process model revealed that mainly artificial surfaces predict the frequency of common pipistrelles records in the area ($Z = -50.56$, $p < 0.001$), with the city of Košice as the likely hotspot of the species activity there (Fig. 1c).

In total, we recorded significantly more *P. pipistrellus* than other bats only on the *link* transect (Mann-Whitney U -test, $p < 0.05$; Fig. 2). The GAM models, using date and outdoor temperature as explanatory variables, showed different approximate significances of the factor-smooth interactions in nonlinear patterns in the relative activity of common pipistrelles along the monitored transects (Table 2). Spline fits for *P. pipistrellus* in different periods were found to be congruent only in the *urban* and *link* transects. While the *urban* transect had a double apical increase with the first peak in the *invasion* season and next towards the onset of hibernation (Fig. 3a), the *link* located between the city and the mass hibernaculum showed smoothly increasing activity during the study period in both years (Fig. 3b). The activity patterns observed on the control transects differed between years, suggesting a lower tendency in the *pre-hibernation* season with some sudden increase (Fig. 3c, d). The effect of temperature fitted with the spline was, as expected, highly significant for both years ($p < 0.001$; Table 2), with decreased activity of bats under 15°C. The deviance explained (the goodness-of-fit statistics) in the GAM models for *P. pipistrellus* was 74.8% for 2017 and 75.6% for 2018, respectively. In contrast to the common pipistrelle, no differences between transects and seasons were found when the activity of other bat species altogether were modelled (the GAM deviance explained was 43.7% and 48.2%, respectively; Fig. 4, Table 3). A significantly higher relative frequency of social calls in the echolocation records of *P.*

pipistrellus was found during the pre-hibernation season only, and this display was no more frequent in the urban area than in the other transects (Fig. 5).

Table 2
Summary of generalised additive models explaining the number of *P. pipistrellus* records per kilometre of transect by date and outdoor temperature, with a factor-smooth interaction for each transect (urban, link, control A, control B)

<i>year 2017</i>	estimate (SE)	<i>t</i>	<i>p</i>
fixed effect			
intercept	-0.56 (0.06)	-8.62	< 0.001
smooth terms	effective df	<i>F</i>	<i>p</i>
date × urban	3.93	3.21	0.002
date × link	1.00	11.53	< 0.001
date × control A	1.00	24.40	< 0.001
date × control B	1.18	0.92	0.41
temperature	3.71	20.59	< 0.001
<i>year 2018</i>	estimate (SE)	<i>t</i>	<i>p</i>
fixed effect			
intercept	-0.16 (0.07)	-2.36	0.024
smooth terms	effective df	<i>F</i>	<i>p</i>
date × urban	4.79	3.50	0.007
date × link	1.00	4.05	0.05
date × control A	2.34	2.35	0.09
date × control B	4.70	4.49	0.002
temperature	3.49	11.11	< 0.001

Table 3

Summary of generalised additive models explaining the number of all bat species but *P. pipistrellus* records per kilometre of transect by date and outdoor temperature, with a factor-smooth interaction for each transect (urban, link, control A, control B)

<i>year 2017</i>	estimate (SE)	<i>t</i>	<i>p</i>
fixed effect			
intercept	-0.43 (0.07)	-6.09	< 0.001
smooth terms	effective df	<i>F</i>	<i>p</i>
date × urban	2.22	1.22	0.25
date × link	1.00	1.72	0.20
date × control A	1.00	2.38	0.13
date × control B	1.00	0.65	0.42
temperature	1.55	3.01	0.06
<i>year 2018</i>	estimate (SE)	<i>t</i>	<i>p</i>
fixed effect			
intercept	-0.17 (0.07)	-2.57	0.014
smooth terms	effective df	<i>F</i>	<i>p</i>
date × urban	1.35	0.16	0.72
date × link	1.00	0.03	0.86
date × control A	1.00	0.35	0.56
date × control B	1.00	1.00	0.32
temperature	2.82	7.16	< 0.001

Discussion

The presented observational study aimed to uncover the possible reasons behind the very frequent and abundant so-called autumn invasions (more information about this behaviour see Nusová et al. 2019a) of common pipistrelles in the city of Košice in eastern Slovakia. Since the first observation, reported in September 1996 (Matis 1997), this specific behaviour has occurred regularly and caused recurrent seasonal conflicts with humans that has resulted in the injury and death of many bats there (Nusová et al. 2019a). Apparently, at the same time the bat invasions began in Košice, a significant increase in the abundance of hibernating individuals in the Erňa was also observed (Matis et al. 2002), indicating a possible causal relationship between these sites (Nusová et al. 2019a). A better understanding of such a

relationship is therefore important not only from the viewpoint of the species' natural history but also for its local conservation. We found consistent patterns of flight activity of pipistrelles in the city and in the potential commuting area between the city and the cave. Although the activity was temporarily elevated during invasions in the city, the generally increasing tendency along both of these transects towards the onset of hibernation time suggested a common mechanism driving this local pattern. In contrast to seasonal variation on the control transects located in the adjacent area (Fig. 3) or to other bat species (Fig. 4), the pattern for *P. pipistrellus* on the *urban a link* transects was consistent in both study years.

Firstly, we have to consider the spatial structure of the habitats that determine the activity of the common pipistrelles. The habitats along the rural transects we investigated in the area of the Košická kotlina Basin had a characteristic mosaic and patchy structure that is used by this very flexible species during the active seasons of the year, i.e., open habitats, woodlands, waters and settlements with human-made linear infrastructures (e.g., Barlow 1997; Boughey et al. 2011a, b; Kusch and Schmitz 2013; Vandeveld et al. 2014; Todd and Williamson 2019). On the other hand, the common pipistrelle, together, for example, with the ecologically similar species *P. kuhlii* and *Hypsugo savii* (but still significantly less abundant in the Košice city; own unpublished data), has recently been often considered to be a synurbic species using cities as both roosting and foraging areas (Simon et al. 2004; Russo and Ancillotto 2015; Maxinová et al. 2016; Uhrin et al. 2016). As found from our transect data, pipistrelles foraged in a wide spectrum of habitat type, while the higher level of flight activity above artificial surfaces may be associated with suitable living space for this species. Whereas in rural areas, the appropriate level of prey could be expected until the onset of frosty nights and the common pipistrelle can forage effectively there (Davidson-Watts et al. 2006; Lundy and Montgomery 2010; Verboom and Huitema 2010; Kusch and Schmitz 2013; Todd and Waters 2017), in the inner parts of cities, sufficient insect density could be attracted by artificial lighting and bat foraging could be enlarged in time by the heating effect of the city (Rydell and Racey 1995; but see Stone et al. 2015; Russo and Ancillotto 2015) or the presence of artificial water sources (e.g. Nystrom and Bennett 2019). Because artificial surfaces significantly enhanced the activity of common pipistrelles during the invasion season (Fig. 3), it is unlikely that some variation in habitat structure would shape differences in the flight activity of bats along the monitored rural transects.

The main swarming activity in common pipistrelles at hibernacula is observed in early August (van Schaik et al. 2015, Bartoničková et al. 2016), and this behaviour is associated with frequent emission of social calls (e.g., Barlow and Jones 1997; Budenz et al. 2009; Middleton et al. 2014; Chaverri et al. 2018; Schmidbauer and Denzinger 2019). Whereas the timing of the swarming season overlaps with the peak of invasions in the Košice urban agglomeration (Nusová et al. 2019a), interestingly, in the city and its surroundings, more social calls were recorded until before hibernation (Fig. 5). This may suggest that the Košice area is not the primary place of mating. On the other hand, an extraordinary and persistent swarming of thousands of bats occurs at the Erňa cave until the onset of hibernation (Nusová et al. 2020). Such temporal distribution of swarming activity during the pre-hibernation season is known to be highly variable and in fact it is usually suppressed by unfavourable weather conditions, not excluding lower temperatures (Nusová et al. 2020). Cold weather causes decreased activity of prey abundance (Speakman 1991; Parsons et al. 2003; Ignaczak et al. 2019) and bats are forced to intensively feed upon

prey which is signified by increased flight activity (Šuba et al. 2011). If, for example, bats swarming at the cave commute to the city to feed during the late season, when food availability is limited (Fenton 1982; Ransome 1990), this could explain the increased activity in the pre-hibernation season in Košice. Such a pattern contrasts with the control transects, where food availability may have more stochastic characteristics at that time. Increased flight activity of the species in August and September was also observed in the urban agglomeration of the city of Brno (southern Moravia; Gaisler et al. 1998), where a large pipistrelle hibernaculum exists (Gaisler and Bauerová 1986) and invasions have been repeatedly reported (Palášthy and Gaisler 1965; Gaisler and Bartonička 2010). The increased level of commuting at a swarming site also suggests flight activity on an important autumn migration corridor along the Vltava River valley close to the biggest hibernaculum of the species in Bohemia (Hanzal and Kříž 2017; Bartonička et al. 2019). Local preference for a particular swarming site makes these observations different to species habitat preferences in other urbanised areas, where invasion behaviour and mass swarming sites have not been observed. For example, despite the fact that *P. pipistrellus* is also considered to be well-adapted to the urban landscape in the UK, it has shown a negative response to urbanization at the local scale (e.g., Hale et al. 2012; Lintott et al. 2016).

In conclusion, invasions into the city could perhaps be considered as a twin swarming site of the same common pipistrelle population(s) related to a particular mass hibernaculum. In addition, such cities can serve as hibernation sites, too, where on warmer days bats can even find a suitable amount of prey. This was confirmed in another well-adapted urban bat species *Nyctalus noctula* in Central Europe (Kaňuch et al. 2005). In Košice, the hibernation and winter activity of common pipistrelles were also recently confirmed (M. Cel'uch and own unpublished data) and they are also relatively common in rural areas (Barros et al. 2017; Zahn and Kriner 2016). Furthermore, data on the dynamics of flight activity in Košice is consistent with patterns observed around other European mass swarming sites and/or hibernacula (e.g., Korsten et al. 2016; Bartonička et al. 2019; Giavi et al. 2020). This can support an alternative hypothesis that the city itself could play the part of a mass or dispersal hibernaculum too. We may further conclude that the relatively short geographical distance between an urban agglomeration and a large swarming site is likely a clue to the frequent invasions of the species. Our case study raises the question of whether such unusual behaviour of the common pipistrelle has evolved only recently as a consequence of increased urbanisation in a region with mass hibernacula (for review see Nusová et al. 2019a) or is an altered pre-hibernation behaviour associated with local mass concentration of bats. Thus, to fill this knowledge gap it would be advantageous to study the pre-hibernation activity of common pipistrelles associated with mass hibernacula known in a further region of the Carpathian Mountains (e.g., Dumitrescu and Orghidan 1963; Nagy and Szántó 2003; Nagy and Postawa 2011; Nusová et al. 2017), where no related invasion site has yet to be discovered.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication All authors agreed with the content and all gave explicit consent to submit.

Data availability All bat recordings are available upon request to the corresponding author.

Conflict of interest The authors declare that they have no competing interests.

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Authors' contribution GN, MU, and PK made conception and study design. GN collected data in the field and determined bat calls. PK performed data analysis. MU, PK and GN drafted the manuscript. All authors commented on previous versions and approved the final manuscript.

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Figures

Figure 1

(a) Map of the study area depicting an urban transect (full line) in the city of Košice and three transects located in an adjacent rural area (dashed lines) in the Košická kotlina Basin (eastern Slovakia) with the main level of habitats by Corine Land Cover (100 m raster). The proportion of habitats (doughnut charts) is calculated from a buffer zone of 250 m on each side along the linear transects. Crosses show the centre of the city at St. Elisabeth's Cathedral and the Erňa cave in the Slovak karst. The coordinates reference system is WGS 84/UTM zone 34N (metres). (b) All records of *Pipistrellus pipistrellus* collected. (c) Predicted fit of a non-homogeneous Poisson process model based on records from three transects in a rural area with Corine Land Cover habitats as the covariate.

Figure 2

Relative number of records (a) and calls (b) of *P. pipistrellus* and other bats at four transects during two study years. Box-plots show medians, 25–75% quartiles and non-outlier ranges.

Figure 3

Predicted probability of the number of *P. pipistrellus* records at four transects (a, urban; b, link; c, control A; d, control B; locations see in Fig. 1) as a response to date, holding the outdoor temperature constant, derived from a generalised additive model. Spline fits (solid lines) are shown with 95% confidence limits. The approximate significance of smooth terms, see in Table 2.

Figure 4

Predicted probability of the number of records of all bat species but *P. pipistrellus* at four transects (a, urban; b, link; c, control A; d, control B; locations see in Fig. 1) as a response to date, holding the outdoor temperature constant, derived from a generalised additive model. Spline fits (solid lines) are shown with 95% confidence limits. The approximate significance of smooth terms, see in Table 3.

Figure 5

Presence of social calls fitted by a model of independence for two-way tables in records and visualised in mosaic plots according to transects (a, b) or seasons (c, d) in two years. Each tile is coloured to show the deviation from the expected frequency (residuals) from a Person χ^2 test (red – significantly less, blue – significantly more than expected; intensity shows the magnitude of the residuals).