Charles University

Faculty of Science

Study programme: Zoology

Mgr. Marina Kipson

Ecology and synathropy of bats in the Mediterranean region in comparison with the Central Europe

Ekologie a synantropie netopýrů v oblasti Středomoří ve srovnání se střední Evropou

Doctoral thesis

Supervisor: prof. RNDr. Ivan Horáček, CSc.

Prague, 2026

Declaration

Hereby I declare that this Ph.D. thesis is exclusively my own work, and that it has not been submitted (or any of its parts) in order to obtain any academic degree earlier or at another institution. All publications and other sources used in the thesis have been properly quoted.

Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

Acknowledgements

I would like to thank my supervisor, Prof. Ivan Horáček, for his patience and guidance throughout my long PhD journey. Prof. Horáček could only be described as a living encyclopedia, covering not just biology but also art, architecture, and just about everything else. Despite his vast knowledge, what sticks with me most are his endless stories from his rich and fascinating life experience, which, in some cases, have the status of legends. These range from someone being arrested in the field (the famous "The doors were slightly opened" sentence from Lebanon) to lost baggage containing sea fish, initially intended to teach students in an anatomy class, but which, in the end, caused a smell havoc and led to an entire container being burned down. And, obviously, witnessing him first-hand take the stage to mumble along the didgeridoo at a wedding was priceless. These stories have also enriched my life, and I will be forever grateful for them.

I would also like to thank Radek Kris Lučan for being a part of this *Hypsugo savii* journey from the very start till the end. From helping with the study design to fieldwork and, later, shaping manuscripts, he was a tremendous driving force in it all. Throughout, we have got to know each other well, sometimes in very challenging and demanding fieldwork situations, and I am just glad we all survived to tell the story 😊. Thank you immensely!

I am endlessly grateful to my husband Martin, who was my biggest cheerleader throughout this entire process, believing I could finish it, even when I stopped believing. He was not only my greatest source of emotional support but also did all the fieldwork alongside me. I know it was sometimes very challenging to track bats while we could hear the entire village screaming as they watched the World Cup football game. Thanks for sticking it out! I also wish to thank my two girls, Dora and Anna, for showing me a whole new level of life and love with kids, making every single moment so much more precious and worthwhile.

Huge thanks are also due to my parents, Dragica and Rudo, who not only provided for everything I needed to get where I am in life, but also enabled the minimum costs of this research, which was basically centred around our seaside house. Also, to my sister Karolina, who has actively participated in fieldwork data collection and has become quite adept at tracking bats, a skill that was certainly not high on her personal list of priorities.

Also, to all the people who participated in the fieldwork, some for a couple of days, some for a few seasons – it would not have been possible without you! Thank you Ana Pušić, Helena Jahelková, Tomaš Bartonička, Marcel Uhrin, Edita Maxinova, Dina Rnjak, Petra Žvorc, Daniela Hamidović, Vida Zrnčić and Jana Vandrovcová. Also, thank you to Ladislav Naďo for the statistics and to Michal Andreas for the diet analysis.

Finally, I wish to thank all my friends I have met throughout my academic journey. The list would be very long, but I am sincerely grateful to all of you for supporting me in various parts of my life. Thank you all!

List of studies included in the doctoral thesis and the contribution of the candidate

Paper 1

Kipson, M., Gazaryan, S. and Horáček, I. (2023) 'Savi's pipistrelle *Hypsugo savii* (Bonaparte, 1837)', in Russo, D. (ed.) *Chiroptera. Handbook of the mammals of Europe*. Cham: Springer Nature Switzerland AG. Available at: https://doi.org/10.1007/978-3-030-44029-9_162

MK was responsible for reviewing the existing literature, collating most of the published information and writing the book chapter. Estimated contribution: 75%.

Paper 2

Uhrin, M., Hüttmeir, U., **Kipson, M.**, Estók, P., Sachanowicz, K., Bücs, S., Karapandža, B., Paunović, M., Presetnik, P., Bashta, A.T., Maxinová, E., Lehotská, B., Lehotský, R., Barti, L., Csösz, I., Szodoray-Paradi, F., Dombi, I., Jére, C., Pocora, I. and Benda, P. (2015) 'Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and southeastern Europe: a review', *Mammal Review*, 46(1), pp. 1–16. Available at: https://doi.org/10.1111/mam.12050.

MK was responsible for data review and update for Croatia and contributed to interpreting results and reviewing the manuscript. Estimated contribution: 15%.

Paper 3

Kipson, M., Šálek, M., Lučan, R., Uhrin, M., Maxinová, E., Bartonička, T., Andreas, M., Kipson, K., Pušić, A., Rnjak, D., Ňado, L. and Horáček, I. (2018) 'Foraging habitat, home-range size and diet of a Mediterranean bat species, Savi's pipistrelle', *Acta Chiropterologica*, 20(2), pp. 351–360. Available at: https://doi.org/10.3161/15081109ACC2018.20.2.007

MK was responsible for data collection and methodology, interpretation of results, and manuscript writing. Estimated contribution: 75%.

Paper 4

Kipson, M., Šálek, M., Naďo, L., Jahelková, H., Horáček, I. and Lučan, R. (*In review*) 'Ground-level rock crevices as reproductive roosts of Savi's pipistrelle (*Hypsugo savii*) in semi-arid landscapes of the Eastern Mediterranean', *submitted manuscript*.

MK was responsible for data collection and methodology, interpretation of results, and manuscript writing. Estimated contribution: 75%.

Paper 5

Maxinová, E., **Kipson, M**., Naďo, L., Hradická, P. and Uhrin, M. (2016) 'Foraging strategy of Kuhl's pipistrelle at the northern edge of the species distribution', *Acta Chiropterologica*, 18, pp. 215–222. Available at: https://doi.org/10.3161/15081109ACC2016.18.1.012

MK was responsible for data collection and contributed to the interpretation of results and the review of the manuscript. Estimated contribution: 20%.

The supervisor of this doctoral thesis and co-author on papers 1, 3 and 4, prof. RNDr. Ivan Horáček, CSc., approves the contribution of the student Marina Kipson as stated above.

prof. RNDr. Ivan Horáček, CSc.

The first and last author and co-author on papers 2 and 5, prof. RNDr. Marcel Uhrin, PhD., approves the contribution of the student Marina Kipson as stated above.

prof. RNDr. Marcel Uhrin, PhD.

Table of contents

1. Introduction

1.1.Climate and land use changes as driving forces of shifting species distribution ranges

Globally, increased human-induced environmental pressures, particularly climate and land-use changes, are affecting biodiversity, and these two drivers are projected to be the primary cause of future biodiversity changes in this century (Sala et al., 2000). Climatic changes have already been documented to affect life-history traits across species from many taxa (Parmesan and Yohe, 2003), in particular by shifting the ranges of species poleward and to higher elevations, as well as affecting their phenology, mainly through spring advancement (Pounds et al., 1999; Root et al., 2003; Thuiller, 2004). Modelling the future distribution of species under different projected climate change scenarios has received increased attention over the last two decades (Beaumont et al., 2007; Jetz et al., 2007; Huntley et al., 2008; Rebelo et al., 2010; Bilgin et al., 2012). Initially, these predictions were based solely on climate envelope models (Pearson and Dawson, 2003; Araújo and Rahbek, 2006; Hijmans and Graham, 2006; Rebelo et al., 2010; Bilgin et al., 2012). However, to assess whether a species is vulnerable to such changing environments and to guide its future conservation action (Araújo et al., 2011; Wang et al., 2022), it is crucial to understand the extrinsic and intrinsic drivers of these dynamics. Intrinsic factors that can influence the adaptive response of species include patterns of genotypic plasticity, life-history traits, foraging strategies, habitat preferences, and related ecophysiological and behavioural adaptations, as well as species-specific variability in these variables. Among the extrinsic factors, a crucial role could be played by those related to changes in the habitat mosaic, which influence the spatial availability of suitable living habitats and foraging grounds for a given species, and/or the effects of climate change that affect it, either indirectly (via climate change-driven environmental variables) or directly by interfering with metabolic capacities, namely thermoregulation and water balance. All these factors may, in species-specific combinations, act as prerequisites for actual range changes (Travis and Dytham, 2004; Bradshaw and Holzapfel, 2006; Anderson et al., 2009).

Over the past decade, increasing attention has been paid to investigating species traits as potential predictors of range shifts (Estrada et al., 2016; Fialas et al., 2025; Warmer et al.,

2025). To occupy new areas during a climate change-induced shift, a species needs traits that enable it to reach those areas and establish a viable population (Estrada et al., 2016). The first step may depend on the species' ability to relocate, which may be influenced by natal dispersal, migration strategies, and home range size (Estrada et al., 2016). In the second phase, to persist and increase its population in a newly occupied area, the species might benefit from traits that determine its reproductive strategy, competitive ability, and dietary and habitat requirements, with generalist species considered more adaptable (Estrada et al., 2016).

Species traits also largely determine their response to another external driver of shifts in species' potential distributions: changes in land use. Here, urbanisation accounts for a large share of current land-use changes. Whereas in the 1950s only 20% of the global population lived in urban areas, today that percentage is 45%, and by 2050, as much as two-thirds of the global population is projected to live in cities (United Nations, 2025). Between 2018 and 2023, the land take for artificial structures in Europe, predominantly used for residential areas (41%), was shown to be twice as large as previous estimates (Venter et al., 2026), indicating that this is indeed a major driver of land-use change. Because of urbanisation, natural habitats become fragmented and ultimately lost to construction sites, thereby affecting the presence and distribution of native species (Pyšek, 1998). Although overall species richness can be increased in urban habitats, McKinney (2006) noted that, on a global scale, cities offer similar ecological conditions and lead to biotic homogenisation, with the same introduced or native species utilising urban areas worldwide. The negative effects of urbanisation on biodiversity could include the loss of natural habitats and their fragmentation (Amburgey et al., 2021; Liu et al., 2016), higher densities of potential predators, including domestic and medium-sized carnivores adaptable to urbanisation (Crooks and Soulé, 1999; Patroneck et al., 1997), road mortality (Šálek et al., 2023), increased chemical pollution (Brogan et al., 2017), light and noise pollution (Kajanka et al., 2024), and direct conflict with humans (Ratnarathorn et al., 2026). On the other hand, some species can profit and thrive in urban areas by taking advantage of heterogeneous habitats (Magle et al., 2012), the absence of large predators (in the case of medium-size forms, Crooks and Soulé, 1999), increased food availability (Baker and Harris, 2007), and increased temperatures due to the urban heat island effect (Arnfield, 2003). According to species' responses to the process of urbanisation,

they can be classified as: (i) urban avoiders or species restricted to natural habitats, sensitive to disturbance and proximity to human-made structures; (ii) urban adapters, which can exploit resources in urban areas but still use their natural sources; (iii) and urban exploiters, which tend to be quite dependent on urban ecosystems and are tightly connected with human presence (McKinney, 2002). Species that manage to occupy urbanised areas are usually equipped with ecological and behavioural traits that enable them to exploit such habitats. The pre-adaptations arising during their evolutionary history are often accompanied by increased phenotypic plasticity and behavioural opportunism, predisposing them to the concurrent exploration of novel resources (Magle et al., 2012). The term synanthropic classifies species tightly connected to humans and places of their habituation, which in turn enable them to expand their ranges and population densities (Francis and Chadwick, 2012).

1.2.Bats as a study group

Bats are a group of terrestrial mammals with a global distribution, with over 1500 species recognised (Simmons and Cirranello, 2026), constituting almost a fifth of all mammalian species. They are an essential part of healthy ecosystems (Jones et al., 2009) and provide diverse ecosystem services (Kunz et al., 2011), such as insectivorous bats in Europe, which contribute to effective pest control (Maslo et al., 2022; Russo et al., 2018). The diversity of bats, accompanied by distinct species-specific habitat requirements, roosting preferences, and foraging strategies, makes them a highly promising model group for studying the effects of environmental changes on community dynamics and, consequently, for tracing these changes, even those of minute amplitude, in detail (Kunz and Fenton, 2005). Likewise, bats tend to be more sensitive than other animal groups to changes in land use (Mickleburgh et al., 2002) and climate (Sherwin et al., 2013), being, at the same time, particularly disposed to respond, at local and regional scales, to respective changes with rapid spatial shifts.

Roost preference is a crucial factor in bat biology (Kunz, 1982), directly shaping the geographic distribution of individual species and the overall structure of bat communities (Findley, 1993; Russo et al., 2004). In temperate latitudes, bats vary their roost preferences across the annual cycle, moving among roost types used for hibernation, migration, maternity colonies, swarming, and mating (Kunz, 1982). Bats are highly social, forming colonies whose sizes are clearly related to preferred roost type. The availability of suitable

roosts and their spatial distribution therefore affect both overall population size and the size of individual groups (Fenton, 1970; Kunz, 1982). Roost selection can influence several factors relevant to bats' survival and population dynamics, e.g. ensuring offspring development (Racey, 1973; Tuttle and Stevenson, 1982; Wilde et al., 1999; Rodrigues et al., 2003; Lausen and Barclay, 2006), minimising parasite load and predation (Lewis, 1996; Lausen and Barclay, 2006; Lima and O'Keefe, 2013), reducing the impact of extreme weather conditions (Briggler and Prather, 2003) and influencing the distance to foraging areas (Lumsden et al., 2002). Temperate-zone bats, characterised by heterothermy, depend on microclimatic conditions within their roosts, which directly influence their energy expenditure and the use of torpor (Kurta, 1986; Law and Chidel, 2007; Lučan and Radil, 2010). European bat species use a wide range of natural day roosts, from caves and trees (cavities and fissures under the bark) to crevices in and under rocks and cliffs (Kunz and Lumsden, 2003). On the other hand, diverse human-made structures can often provide suitable roosting conditions similar to natural roosts (mine tunnels, fissures in building walls, loft spaces corresponding to spatial caves), which can frequently be used by bats (Kunz and Reynolds, 2003; Voigt et al., 2016). This is particularly true in Europe, where, in contrast to North America, the vast majority of local species prefer to roost in human-made structures, presumably as an adaptive response to their long coexistence with humans across the continent (Lučan et al., 2025). Research on bats in buildings suggests that synanthropic roosts can be chosen over natural ones due to more suitable microclimatic conditions, which allow lower energy costs (Lausen and Barclay, 2006; Law and Chidel, 2007), faster weaning and growth of young, and better anti-predator protection (Lausen and Barclay, 2006). The urban heat island effect, with towns often having higher temperatures than surrounding areas (Arnfield, 2003), could also affect the utilisation of artificial structures by heterothermic organisms such as bats.

Another important aspect of bat ecology in the context of anthropogenic changes is prey availability, foraging habitat preferences, and predispositions to respond to these changes. The degree of prey selection and dietary breadth are often used as essential variables for classifying a species as a specialist or a generalist (Davidson-Watts et al., 2006; Salsamendi et al., 2008; Zeale et al., 2011). The presumption here is that generalist species may be more adaptable to environmental change (Estrada et al., 2016), whereas being a dietary specialist

can even increase the risk of extinction (Safi and Kerth, 2004). However, many bat species can exhibit dietary opportunism, enabling them to shift their diet preferences when preferred prey is unavailable, a characteristic that can be underestimated without comprehensive comparative studies. For example, in *Myotis nattereri,* both seasonal and regional responses in diet selection in relation to prey availability have been documented (Razgour et al., 2023). Spatial distribution of feeding grounds (related to the environmental mosaic pattern) is another component of this complex. Throughout the reproductive season, lactating females might prefer to forage closer to the roosts due to intensive offspring feeding, which might lead to smaller home-range sizes (**Paper 3**). Unfortunately, in most instances, relevant data on between-region variation in home range, particularly those comparing areas with differing anthropogenic impact, are still urgently needed.

The highest diversity of bats in Europe occurs in the Mediterranean region (Horáček et al. 2000; Ulrich et al., 2007). It is projected that many Mediterranean bat species will experience range contraction by 2050, especially in the southern part of their range. In contrast, gains are expected in the northern parts of their range (Fialas et al., 2025). These shifts would effectively move the current pattern of bat species richness northwards in Europe, without accounting for the potential spread of North African species (Fialas et al., 2025). However, these models and projections sometimes fail to capture the species dynamics observed in nature (Mori et al., 2026) and remain to be validated against future occurrence records.

Currently, many bat species, whose ranges are centred in the Mediterranean and thus represent the true Mediterranean faunal elements, reach their northern distributional limit in Central Europe (e.g. *Rhinolophus euryale*, *Miniopterus schreibersii*, *Myotis emarginatus*, *Myotis blythii*; see **Paper 2**). In these thermophilous species, similarly to those whose ranges are extended to the northern margins of the central European belt (*Myotis myotis, Rhinolophus hipposideros, Rhinolophus ferrumequinum*), the roost choice shows a clear cline variation: in the Mediterranean, they are nearly strict cave-dwellers inhabiting karstic caves or rock crevices, whereas in Central Europe (where cave microclimate does not provide appropriate conditions for breeding) they are confined to roosts in anthropogenic structures (Horáček, 1984; Schober and Grimmberger, 1997). Consequently, their colonisation of Central Europe in the past was driven by both their ability to use caves for

winter hibernation and a novel behavioural shift to form maternity colonies in larger, warm spaces within human-made structures (e.g., attics in churches, castles, etc.; **Paper 2**). Therefore, synanthropy played a crucial role in the extensive range enlargement of the Mediterranean cave-dwelling species and their expansion into central and northern Europe, which had not been colonised prior to the Holocene. Some of them represent now even the most common mid-European bat species, e.g. *Myotis myotis, Rhinolophus hipposideros, Myotis emarginatus* (Horáček, 1984; Horáček et al. 2000; Horáček, 2026a).

Two bat species, *Hypsugo savii* and *Pipistrellus kuhlii*, historically strictly confined to the region of the inner Mediterranean, have undergone an extraordinary range shift in Europe over the past 30 years, a pattern widely documented (Strelkov et al., 1985; Spitzenberger, 1997; Sachanowicz et al., 2006; Danko, 2007; Reiter et al., 2010; Ancillotto et al., 2016; **Paper 2**). Their northern distribution ranges are now largely within Central Europe (Amichai and Korine, 2023; **Paper 2**), and reports of mixed colonies of both species come from the northern margin in Slovakia (Danko, 2007), and recently also from the core of their distribution in Italy (Ancillotto et al., 2018). Both species share small body size, adaptations for aerial foraging (short auricles, pointed wings) or roosting in fissures, primarily in rocky habitats with sparse or no vegetation cover, and, correspondingly, a considerable capacity to withstand extreme thermal conditions (comp. e.g., Horáček and Benda, 2004). In the Mediterranean, both species were recorded roosting in human structures, albeit more rarely for *Hypsugo savii* (Đulić, 1958), whereas in Italy, *Pipistrellus kuhlii* was the most common bat roosting in human structures throughout the previous century (Lanza, 1959). Therefore, identifying the specific ecological traits that enabled them to expand their distribution could also help us better understand how these changes affect biodiversity patterns in general. Unfortunately, little attention was given to the ecology of both species prior to their range expansion; therefore, detailed studies of their habitat requirements, roosting preferences, and range sizes have been largely lacking from the historical core of their distribution.

1.3.Savi's pipistrelle (*Hypsugo savii*)

Savi's pipistrelle (*Hypsugo savii*) is a small-bodied bat species, recognisable by its contrasting colouration (black muzzle, ears and wing membrane), white belly, and, most typically, brown dorsal pelage with golden tips. Its dorsal fur, however, shows remarkable

variability, as described in detail for Croatia (Dulic, 1975) and for France and Switzerland (Arlettaz et al., 1993), ranging from unicoloured to various types of bicoloured hair (Dulic, 1975). Until 2000, it was mostly referred to as *Pipistrellus savii*, a polytypic species occurring from the Mediterranean to northern India and Japan, as well as Canary and Cape Verde Islands, however, following revisions in its taxonomy since 1985, and relations to some Oriental forms (Horáček and Hanák, 1985), the argumentation for the genus *Hypsugo* was provided (Horáček et al., 2000) and confirmed by subsequent genetic analyses (Hoofer and Van Den Bussche, 2003). Later, a separate species, *alashanicus,* was recognised in the Asian part of the range, with recent studies also proposing a separate status for populations in northern India (*austenianus*, see Gojznikar and Mayer, 2025) and *stubbei* in Mongolia (see Dolch et al., 2021).

The range of Savi's pipistrelle stretches across the W Palearctic from NW Africa, the islands of Cape Verde and the Canary, around the Mediterranean Sea, the Near East, Crimea, Transcaucasia, to Turkmenistan, Kyrgyzstan, Kazakhstan, Tajikistan, and northern Afghanistan (**Paper 1**). Further genetic analyses identified a clade from the Canary and Cape Verde Islands as *darwinii*, with additional findings of this clade in NW Africa, western Mediterranean islands, southern Spain and Italy (as *H. cf. darwinii*). Results of genetic screening, including both mtDNA and nDNA markers, indicate a split in W Palearctic into three allopatric clades: **(i)** Balkans (including eastern Mediterranean islands), Crimea, Transcaucasia, and the Near East (Israel, Lebanon, Syria, Turkey, Iran) corresponding to *H. s. caucasicus* (Satunin, 1901), **(ii)** Spain and Switzerland corresponding to *H.s.ochromixtus* (Cabrera, 1904) (the names *nigrans* Crespond, 1844 and *maurus* Blasius, 1853 might also be used), **(iii)** Canary and Cape Verde Islands, Morocco, southernmost Spain, west Mediterranean islands (Malta, Sardinia, Balearics etc.), Italy, Slovenia, Austria, Hungary, and the Czech Republic corresponding to *H.s. savii* also covering *H.cf darwinii* which would be denoted as a nominotypical subspecies due to its occurrence in Italy (Horáček, 2026b). It would appear that clades (i) and (ii) are almost entirely restricted to lithophilous habitats and roost in rocky fissures, or even vertical-ground level rock crevices (recorded in **Paper 4**), whereas clade (iii) has less strict habitat preferences, appearing from farmlands to shrublands and regularly roosting in human-made objects (Horáček, 2026b).

Altitudinal faunistic records span from sea level to high mountains, with the species holding the current European altitudinal record at 3300 m a.s.l. (Garrido-Garcia, 2000). The core of its distribution lies within the Mediterranean region, and until the 1990s, there was only one record from north of the Alps (Horáček and Benda, 2004). In the last 30 years, however, its distribution has changed dramatically, spreading mainly north of the Alps and now occurring across countries within Central Europe: Slovakia (Danko, 2007), the Czech Republic (Reiter et al., 2010; Jahelková et al., 2014; Bartonička et al., 2017), Hungary (Görföl et al., 2007), southern Poland (Kohyt et al., 2024; **Paper 2**), and Saxony in Germany (Ohlendorf, 2019). The spread has also very likely occurred across all countries within the Balkan region; however, due to the lack of faunistic bat research in the Balkans prior to the 1990s, compared with Central European countries, it might have been overlooked in some Balkan countries in the past (for more details, see **Paper 2**). It was also recently confirmed in Western Ukraine, Uzhgorod (Vlaschenko et al., 2023), indicating eastward spread at this northern margin, although, so far, its range in Crimea, across the Caucasian region, and southern Russia has not shown northward expansion and has remained unchanged (see Lissovsky et al., 2025; **Paper 1**).

Savi's pipistrelle is primarily a lithophilous species, inhabiting the Mediterranean rocky habitats with bushy, dry-tolerant vegetation (**Paper 1**), where it is most abundant. It roosts primarily in hard-to-reach rock fissures within extensive rocky habitats (Đulić, 1958; Horáček and Benda, 2004; Quetglas and Garrido, 2005; Dietz et al., 2009; **Paper 4**). In general, lithophilous bat species have received much less attention in terms of their detailed roosting ecology than species roosting in trees (Kerth et al., 2001; Willis and Brigham, 2007; Otto et al., 2016; Drake et al., 2020) or caves (Law and Chidel, 2007; Uhrin et al., 2010; Rajasegaran et al., 2018), at least for methodological reasons confined to limited accessibility to locate fissure roosts dispersed in rocky exposures. Likewise, most studies on these types of roosts were conducted in North America (Chruszcz and Barclay, 2002; Lausen and Barclay, 2002; Neubaum, 2018; Moosman et al., 2023), and data on similar rock-dwelling European species are largely lacking. Apart from its lithophilous nature, Savi's pipistrelle was already recorded roosting in artificial structures in Croatia and Italy in the mid-20th century (Đulić, 1958), indicating a predisposition of the species toward synanthropic adaptations. Because its natural roosts are quite difficult to locate, much more

data is available on its ability to roost in various fissures across different building types. The specific roosts found included space behind roof gutters and roller shutters (Vernier, 1995), fissures in old buildings and ruins (Benda et al., 2006), an unused shepherd's cabin (Strelkov and Shaimardanov, 1983), a crevice on a balcony (Stoycheva et al., 2009), cracks in tunnels (Stojanovski, 1994), and cracks in walls and crevices behind tiles (Ancillotto et al., 2018). One accidental finding of a roost at ground level beneath a rock was reported in Spain (Alcalde and Gosá, 2009). As with patterns described in other Mediterranean bat species above, recent records from newly occupied areas in Central Europe, at its novel northern margin, come mainly from urbanised areas (**Paper 2**), with identified roosts being exclusively synanthropic (Freitag, 1996; Reiter et al., 2010; Danko, 2007).

Savi's pipistrelle is an aerial hawker, characterised by hunting in open spaces. Despite being described as common within the Mediterranean region, most older records were purely observational or based on echolocation studies. These included descriptions of hunting above tree crowns (Gaisler, 1994), above mountain meadows and freshwater bodies (Russo and Jones, 2002; di Salvo et al., 2009), around cliffs and even over the sea (Dulic, 1970), and around lamps in urbanised areas (Vernier, 1995). Only two detailed radiotracking studies on its foraging habitats have been performed to date, and neither has confirmed a preference for urban habitats, as both cases showed a preference for natural ones (Ancillotto et al., 2018, **Paper 3**). For example, in Italy, both sexes foraged primarily in extensive farmland, which was also the most preferred habitat within individual home ranges (Ancillotto et al., 2018), whereas reproductive females in Croatia showed slightly different preferences during pregnancy and lactation (**Paper 3**). While pregnant females preferred rocky pastures, their preference for riparian habitats increased later in lactation, indicating a greater importance of water bodies (**Paper 3**). As water is a limiting factor within this semi-arid Mediterranean region, it often harbours greater insect abundance (Wenninger and Inouye, 2008), which in turn creates a preferred foraging area for bats (Zahn and Maier, 1997; di Salvo et al., 2009). Due to low humidity during the summer months, evaporative water loss in bats increases (Webb et al., 1995), and they need to seek water bodies to drink and compensate for the water deficit (McLean and Speakman, 1999). Similarly, during lactation, females may have a greater need for water (Adams et al., 2008), and severe droughts even disrupt their reproductive cycles (Amorim et al., 2015). Water bodies largely determine habitat

preferences and roost selection in the Mediterranean region (Salsamendi et al., 2012), and this resource is expected to become scarcer as the climate changes. The species can show considerable mobility, crossing long distances during foraging bouts (maximum recorded distance 14,2 km) and even crossing open sea (**Paper 3**).

Savi's pipistrelle is considered to feed opportunistically, and analyses of faecal pellets show considerable variation across regions and seasons, driven by local food availability. However, a large-scale study investigating seasonal changes in its diet is lacking (**Paper 1**). The species appears to take advantage of swarming insects, particularly Formicoidea, which occur in high concentrations and were recorded in faecal pellets from Syria, Croatia, Turkey, Lebanon and the Greek islands (Benda et al., 2006; Dietz et al., 2009; Whitaker and Karataş, 2009; Žďárská, 2013, **Paper 3**). It can even contribute to pest control in Mediterranean agroecosystems, where a considerable proportion of its diet comprises agricultural pest species (Ancillotto et al., 2023). A more detailed overview of dietary preferences from individual studies on the species is provided in **Paper 1**.

1.4.Kuhl's pipistrelle (*Pipistrellus kuhlii*)

Kuhl's pipistrelle is also a small bat, and one of its most recognisable characteristics is a wide white band along the posterior margin of the wing membrane (Bogdanowicz, 2004; Dietz et al., 2009). Kuhl's pipistrelle species complex appears to be monophyletic (Çoraman et al., 2013), with studies indicating the presence of four mitochondrial lineages: "*maderensis*" at islands in the Atlantic (Pestano et al., 2003), "*lepidus*" in Eastern Europe and the Middle East (Çoraman et al., 2013), with the other two lineages, Western and Eastern, coexisting in sympatry in the Geneva region in Switzerland, with Western covering W Europe and the Eastern lineage appearing in Italy, Eastern Mediterranean and North Africa (Andriollo et al., 2015).

The core area of the species in Europe has been clearly confined to the inner Mediterranean, extending into Northern Africa and the Middle East, covering the Arabian Peninsula, and reaching into SW Asia (Amichai and Korine, 2023). A shift in its distribution range was already recorded in the 1980s, with records of more northern occurrences documented along its northern boundary, from southern France to the eastern part of the European range in Russia (Strelkov et al., 1985). In Eastern Europe, its range expansion

seemed to follow rivers as corridors (Sachanowicz et al., 2006). There is also evidence that the species has recently spread further northward in Russia, reaching the middle Volga region (Lissovsky et al., 2025). Prior to expansion into Eastern Europe, an extensive increase in overall abundance since the late eighties was well documented in Azerbaijan, being associated with urban habitats and clearly synanthropic roost preferences (Rakhmatulina, 2005). In Ukraine, it was initially restricted to Crimea, but it has since spread throughout the country from the east, first occupying the eastern and central parts and then moving into western Ukraine (Sachanowicz et al., 2006). Therefore, the origin of the species in Central Europe could have followed the eastern route via Ukraine, or moved northwards from the Mediterranean, with both routes potentially occurring simultaneously (Sachanowicz et al., 2017). This differs from the Savi's pipistrelle, which has only recently been confirmed, apart from ultrasound calls, in Western Ukraine (Vlaschenko et al., 2023), and the species' range along its eastern border in Europe (in the Caucasian region) seems to remain largely unchanged (**Paper 1**, Lissovsky et al., 2025). In examining the causes of range expansion in Kuhl's pipistrelle, it seems that changes are mainly driven by climate change, with temperatures during the coldest three months of the year being the most significant factor predicting its occurrence (Ancillotto et al., 2016). It seems that expansion to Eastern Europe is associated with wintering in urban habitats (Hukov et al., 2020). Apart from moving north, the species is also expanding at the southern border of its range, in Israel, from the Mediterranean to the desert region (Greenfeld et al., 2018), where this is connected to anthropogenic changes, namely urbanisation, but also increased water accessibility (Korine et al., 2016).

One of the prominent traits of this species is its tolerance of seemingly unsuitable conditions within urban areas, evident in both roosting and foraging strategies, extended through opportunistic behavioural shifts that favour urban habitats, resulting in rapid increases in abundance and further promoting components of a strictly synanthropic way of life and the prosperity of synanthropic populations. It can be illustrated, e.g., by its tolerance of night street illumination, which it frequently exploits as a nearby feeding resource, taking advantage of insect prey that the light attracts (Sachanowicz et al., 2006; Ancillotto et al., 2016; **Paper 5**). All newly expanded records of the species come from urban areas (Strelkov et al., 1985; Reiter et al., 2007; **Paper 5**), suggesting its strict synanthropic adaptations as a

key factor of its range expansion, often being associated with climate change as a key extrinsic background driver (Ancillotto et al., 2016). Regarding its foraging strategy, the species is an aerial hawker, hunting its prey in the open air during flight, and is capable of foraging in diverse clustered habitats under conditions of a sufficiently large grain of habitat mosaic, i.e., that the clusters are not very dense (Kalko and Schnitzler, 1993). The species can forage in open landscapes over natural and agricultural habitats, around water bodies, close to the edge of vegetation, and around illuminated areas within a gradient of urbanised areas, from villages to cities (Kalko and Schnitzler, 1993; Serangeli et al., 2012; Ancillotto et al., 2016; **Paper 5**). The foraging grounds closer to the roost are preferred, with a maximum recorded distance being 4,5 km (**Paper 5**). The species is flexible in its diet, described as a "selective opportunist", meaning it is not tied to a particular habitat or prey for foraging, but rather hunts where insects are abundant (Amichai and Korine, 2023). Particularly, the Kuhl's pipistrelle uses the opportunity to hunt Chironomidae during their night swarming and emergence from water bodies (Goiti et al., 2003; Benda et al., 2006; Amichai et al., 2015), yet it has also been recorded feeding on numerous agricultural pest species, including diverse moths, dipterans, etc. (Cohen et al., 2020). Under conditions of a disturbed habitat mosaic, feeding opportunism might confer a considerable competitive advantage for this species, and it has been hypothesised that it could replace less competitive species in newly occupied areas within its distribution range (Greenfeld et al., 2018; Kohyt et al., 2024).

2. The research projects of the present PhD thesis

The above survey demonstrated that both *Hypsugo savii* and *Pipistrellus kuhlii* share several similarities, indicating which drivers promoted their extensive northward range expansion, quite exceptional among the current bat fauna of Europe. The well-pronounced warming characterising the last five decades and synchronous habitat rearrangements promoting a warm, tree-less landscape rich in diverse urban rearrangements are often cited as the main extrinsic drivers of the respective range expansions. Among the intrinsic factors, the well-pronounced synurbisation and synanthropy, either in roosting, habitat preferences, and foraging strategies, are perhaps the first to be mentioned. Further, both species are small

aerial hawkers, forming small colonies in diverse fissure roosts, confined to rocky and/or open habitats with sparse vegetation cover in the Mediterranean. Nevertheless, they represent quite different, deeply separated clades, showing distinct phylogeographies and presumably the initial life-trait patterns from which the common intrinsic factor underlying the range expansion evolved.

Unfortunately, almost no information on that point is available. We do not know which are the behavioural drivers integrating their colonies, patterns in roost occupancies and spatial dynamics of their populations, and are still unable to answer also explicit questions whether the behavioural traits sparsely reported from expanding populations in newly colonised areas of central Europe refer to the qualities present throughout the whole species range or are just the specificities of expanding populations.

The present PhD research project was intended to address these questions using robust comparative records. I focused particularly on *Hypsugo savii*, which, despite some recent contributions, remains one of the least investigated European bat species. I performed a series of field studies primarily in the original core of the species' range in the Mediterranean region, and in the expanding populations of *Pipistrellus kuhlii* in Central Europe.

Steps of the project (summarised in individual research papers representing Papers 1-5 of the thesis) were as follows:

1. Provide a revised, full, updated account of the current knowledge on Savi's pipistrelle, namely its common name, taxonomy and systematics, palaeontology, current distribution, description, physiology, genetics, life history, habitat and diet, behaviour, and future challenges for research and management (**Paper 1**).

2. Gather and review all faunistic evidence for the newly recorded spread in the distribution range of Savi's pipistrelle to Central Europe and shed light on the potential mechanisms behind this range extension (**Paper 2**).

3. Provide detailed ecological data on habitat and dietary preferences, as well as the size of the home range in reproductive females of Savi's pipistrelle from the core of its distribution area in the Mediterranean region, which would provide a basis for

understanding its specific traits that could contribute to its northward expansion (**Paper 3**).

4. Investigate the roosting ecology of reproductive females of Savi's pipistrelle in the Mediterranean region and potential changes throughout their reproductive cycle, and in identifying their roost selection based on structural and thermal characteristics (**Paper 4**).

5. Contribute to the knowledge on foraging and roosting preferences of Kuhl's pipistrelle at its recently occupied northern distribution margin (in Slovakia) and to compare this with the previous findings from the Mediterranean region (**Paper 5**).

3. References

Adams, R.A. and Hayes, M.A. (2008) 'Water availability and successful lactation by bats as related to climate change in arid regions of western North America', *Journal of Animal Ecology*, 77, pp. 1115–1121.

Alcalde, J.T. and Gosá, A. (2009) 'The discovery of two Savi's pipistrelles under a stone reveals its adaptation to shrub steppe habitats', *Munibe*, 57, pp. 303–305.

Amburgey, S.M., Miller, D.A.W., Rochester, C.J. et al. (2021) 'The influence of species life history and distribution characteristics on species responses to habitat fragmentation in an urban landscape', *Journal of Animal Ecology*, 90, pp. 685–697. Available at: https://doi.org/10.1111/1365-2656.13403

Amichai, E., Blumrosen, G. and Yovel, Y. (2015) 'Calling louder and longer: how bats use biosonar under severe acoustic interference from other bats', *Proceedings of the Royal Society B: Biological Sciences*, 282. Available at: https://doi.org/10.1098/rspb.2015.2064

Amichai, E. and Korine, C. (2023) 'Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817)', in Russo, D. (ed.) *Chiroptera. Handbook of the mammals of Europe*. Cham: Springer. Available at: https://doi.org/10.1007/978-3-030-44029-9_69

Amorim, F., Mata, V.A., Beja, P. and Rebelo, H. (2015) 'Effects of a drought episode on the reproductive success of European free-tailed bats (*Tadarida teniotis*)', *Mammalian Biology*, 80, pp. 228–236.

Ancillotto, L., Santini, L., Ranc, N., Maiorano, L. and Russo, D. (2016) 'Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation', *The Science of Nature*, 103(3), p. 15.

Ancillotto, L. et al. (2018) 'What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection', *Behavioural Processes*, 157, pp. 540–546. Available at: https://doi.org/10.1016/j.beproc.2018.06.002

Ancillotto, L. et al. (2023) 'Predator-prey traits and foraging habitat shape the diet of a common insectivorous bat', *Acta Oecologica*, 118, p. 103890. Available at: https://doi.org/10.1016/j.actao.2023.103890

Anderson, B.J. et al. (2009) 'Dynamics of range margins for metapopulations under climate change', *Proceedings of the Royal Society B: Biological Sciences*, 276, pp. 1415–1420. Available at: https://doi.org/10.1098/rspb.2008.1681

Andriollo, T., Naciri, Y. and Ruedi, M. (2015) 'Two mitochondrial barcodes for one biological species: the case of European Kuhl's pipistrelles (Chiroptera)', *PLoS One*, 10, e0134881. Available at: https://doi.org/10.1371/journal.pone.0134881

Araújo, M.B. and Rahbek, C. (2006) 'How does climate change affect biodiversity?', *Science*, 313, pp. 1396–1397. Available at: https://doi.org/10.1126/science.1131758

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. and Thuiller, W. (2011) 'Climate change threatens European conservation areas', *Ecology Letters*, 14(5), pp. 484–492.

Arlettaz, R., Guibert, E., Lugon, A., Médard, P. and Sierro, A. (1993) 'Variability of fur coloration in Savi's bat (*Hypsugo savii*)', *Bonner Zoologische Beiträge*, 44, pp. 293–297.

Arnfield, A.J. (2003) 'Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island', *International Journal of Climatology*, 23(1), pp. 1–26.

Baker, P.J. and Harris, S. (2007) 'Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain', *Mammal Review*, 37, pp. 297–315. Available at: http://dx.doi.org/10.1111/j.1365-2907.2007.00102

Bartonička, T., Benda, P. and Juda, J. (2017) 'První nálezy a fenologie netopýra Saviova (*Hypsugo savii*) na Děčínsku (Chiroptera: Vesperilionidae)', *Lynx, series nova*, 48.

Beaumont, L.J., Pitman, A.J., Poulsen, M. and Hughes, L. (2007) 'Where will species go? Incorporating new advances in climate modelling into projections of species distributions', *Global Change Biology*, 13, pp. 1368–1385. Available at: https://doi.org/10.1111/j.1365-2486.2007.01357.x

Benda, P. et al. (2006) 'Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology', *Acta Societatis Zoologicae Bohemicae*, 70, pp. 1–329.

Bilgin, R., Keşişoğlu, A. and Rebelo, H. (2012) 'Distribution patterns of bats in Eastern Mediterranean region in a climate change perspective', *Acta Chiropterologica*, 14, pp. 425–437. Available at: https://doi.org/10.3161/150811012X661747

Bogdanowicz, W. (2004) '*Pipistrellus kuhlii* (Kuhl, 1817)—Weißrandfledermaus', in Krapp, F. (ed.) *Handbuch der Säugetiere Europas*. Wiebelsheim: AULA-Verlag, pp. 875–908.

Bradshaw, W.E. and Holzapfel, C.M. (2006) 'Evolutionary response to rapid climate change', *Science*, 312, pp. 1477–1478. Available at: https://doi.org/10.1126/science.1127000

Briggler, J.T. and Prather, J.W. (2003) 'Seasonal use and selection of caves by the eastern pipistrelle bat (*Pipistrellus subflavus*)', *American Midland Naturalist*, 149, pp. 406–412.

Brogan, J.M., Green, D.J., Maisonneuve, F. and Elliott, J.E. (2017) 'An assessment of exposure and effects of persistent organic pollutants in an urban Cooper's hawk (*Accipiter cooperii*) population', *Ecotoxicology*, 26, pp. 32–45. Available at: https://doi.org/10.1007/s10646-016-1738-3

Chruszcz, B.J. and Barclay, R.M.R. (2002) 'Thermoregulatory ecology of a solitary bat roosting in rock crevices', *Functional Ecology*, 16, pp. 18–26.

Cohen, Y., Bar-David, S., Nielsen, M. et al. (2020) 'An appetite for pests: synanthropic insectivorous bats exploit cotton pest irruptions and consume various deleterious arthropods', *Molecular Ecology*. Available at: https://doi.org/10.1111/mec.15393

Çoraman, E., Furman, A., Karataş, A. and Bilgin, R. (2013) 'Phylogeographic analysis of Anatolian bats highlights the importance of the region for preserving the chiropteran mitochondrial genetic diversity in the Western Palaearctic', *Conservation Genetics*, 14, pp. 1205–1216. Available at: https://doi.org/10.1007/s10592-013-0509-4

Crooks, K. and Soulé, M. (1999) 'Mesopredator release and avifaunal extinctions in a fragmented system', *Nature*, 400, pp. 563–566. Available at: https://doi.org/10.1038/23028

Danko, Š. (2007) 'Reprodukcia *Hypsugo savii* a *Pipistrellus kuhlii* na východnom Slovensku: ďalšie dôkazy o ich šírení na sever', *Vespertilio*, 11, pp. 13–24.

Davidson-Watts, I., Walls, S. and Jones, G. (2006) 'Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats', *Biological Conservation*, 133(1), pp. 118–127. Available at: https://doi.org/10.1016/j.biocon.2006.05.027

Di Salvo, I., Russo, D. and Sara, M. (2009) 'Habitat preferences of bats in rural area of Sicily determined by acoustic surveys', *Hystrix, the Italian Journal of Mammalogy*, 20(2), pp. 137–146.

Dietz, C., Nill, D. and von Helversen, O. (2009) *Bats of Britain, Europe and Northwest Africa*. London: A & C Black.

Dolch, D., Stubbe, M., Batsaikhan, N., Stubbe, A. and Steinhauser, D. (2021) '*Hypsugo stubbei* sp. nov., a novel cryptic bat species of the genus *Hypsugo* (Vespertilionidae, Chiroptera, Mammalia) from Mongolia. Results of the Mongolian-German Biological Expeditions Since 1962, No. 347', *bioRxiv* (preprint). Available at: https://doi.org/10.1101/2021.03.30.437544

Drake, E.C., Gignoux-Wolfsohn, S. and Maslo, B. (2020) 'Systematic review of the roost-site characteristics of North American forest bats: implications for conservation', *Diversity*, 12, p. 76.

Đulić, B. (1958) 'Über die Ökologie der Alpenfledermaus *Pipistrellus savii* auf der Insel Mljet', *Säugetierkundliche Mitteilungen*, 6, pp. 10–11.

Dulic, B. (1970) 'Ökologische Beobachtungen der Fledermäuse der Adriatischen Inseln', *Zeitschrift für Säugetierkunde*, 35, pp. 45–51.

Dulic, B. (1975) 'Morphology of the hair of *Pipistrellus savii* Bonaparte, 1837', in Olembo, R.J., Castelino, J.B. and Mutere, F.A. (eds) Proceedings of the Fourth International Bat Research Conference. Kenya: Kenya National Academy for Advancement of Arts and Sciences, pp. 51–61.

Estrada, A., Morales-Castilla, I., Caplat, P. and Early, R. (2016) 'Usefulness of species traits in predicting range shifts', *Trends in Ecology & Evolution*, 31(3), pp. 190–203. Available at: https://doi.org/10.1016/j.tree.2015.12.014

Fenton, M.B. (1970) 'Population studies of *Myotis lucifugus* in Ontario', *Life Sciences Contributions, Royal Ontario Museum*, 77, pp. 1–34.

Fialas, P.C. et al. (2025) 'Changes in community composition and functional diversity of European bats under climate change', *Conservation Biology*, 39, e70025. Available at: https://doi.org/10.1111/cobi.70025

Findley, J.S. (1993) *Bats: A Community Perspective*. Cambridge: Cambridge University Press.

Francis, R.A. and Chadwick, M.A. (2012) 'What makes a species synurbic?', *Applied Geography*, 32(2), pp. 514–521. Available at: https://doi.org/10.1016/j.apgeog.2011.06.013

Freitag, B. (1996) '*Pipistrellus savii* (Bonaparte, 1837) – Erstnachweis für die Steiermark (Mammalia, Chiroptera)', *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark*, 125, pp. 237–238.

Gaisler, J. (1994) 'The bats *Pipistrellus kuhlii* and *Hypsugo savii* on the island of Rab (Croatia)', *Folia Zoologica*, 43(3), pp. 279–280.

Garrido-Garcia, J.A. (2000) 'New altitude record for Chiroptera in Europe', *Myotis*, 37, p. 10.

Goiti, U., Vecin, P., Garin, I. et al. (2003) 'Diet and prey selection in Kuhl's pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in south-western Europe', *Acta Theriologica*, 48, pp. 457–468. Available at: https://doi.org/10.1007/bf03192492

Gojznikar, J. and Mayer, F. (2025) 'Mitochondrial DNA reveals the impact of Pleistocene glaciations on a widespread Palearctic bat species', *Mammalian Biology*, 105, pp. 253–264. Available at: https://doi.org/10.1007/s42991-024-00449-9

Görföl, T., Dombi, I. and Zsebök, S. (2007) 'Az alpesi denevér (*Hypsugo savii* Bonaparte, 1837) Magyarországon – a faj hazai adatainak áttekintése, új eredmények', in Molnár, V. (ed.) Proceedings of the V and VI Hungarian Bat Conservation Conferences. Szeged: Csemete Természet- és Környezetvédelmi Egyesület, pp. 85–97.

Greenfeld, A., Saltz, D., Kapota, D. et al. (2018) 'Managing anthropogenic driven range expansion behaviourally: Mediterranean bats in desert ecosystems', *European Journal of Wildlife Research*, 64, p. 24. Available at: https://doi.org/10.1007/s10344-018-1182-1

Hijmans, R.J. and Graham, C.H. (2006) 'The ability of climate envelope models to predict the effect of climate change on species distributions', *Global Change Biology*, 12, pp. 2272–2281. Available at: https://doi.org/10.1111/j.1365-2486.2006.01256.x

Hoofer, S.T. and Van Den Bussche, R.A. (2003) 'Molecular phylogenetics of the chiropteran family Vespertilionidae', *Acta Chiropterologica*, 5, pp. 1–63.

Horáček, I. (1984) 'Remarks on the causality of population decline in European bats', *Myotis*, 21–22, pp. 138–147.

Horáček, I. and Hanák, V. (1985) 'Generic status of *Pipistrellus savii* and comments on classification of the genus Pipistrellus (Chiroptera, Vespertilionidae)', *Myotis*, 23–24, pp. 9–16.

Horáček, I., Gaisler, J. and Hanák, V. (2000) 'The bats of the Palearctic region: a taxonomic and biogeographic review', in Wołoszyn, B.W. (ed.) Proceedings of the 8th EBRS. Krakow: PAN, pp. 11–157.

Horáček, I. and Benda, P. (2004) '*Hypsugo savii*', in Krapp, F. (ed.) *Handbuch der Säugetiere Europas*. Wiebelsheim: Aula, pp. 911–941.

Horáček, I. (2026a) 'A history of European mammals', in Mitchell-Jones, A.F. (ed.) *Atlas of European mammals*. London: Thompson, pp. 1–15.

Horáček, I. (2026b) '*Hypsugo savii* (Bonaparte, 1837)', in Mitchell-Jones, A.F. (ed.) *Atlas of European mammals*. London: Thompson, pp. 190–191.

Hukov, V., Timofieieva, O., Prylutska, A., Rodenko, O., Moiseienko, M., Bohodist, V., Domanska, A. and Vlaschenko, A. (2020) 'Wintering of an urban bat (*Pipistrellus kuhlii lepidus*) in recently occupied areas', *European Journal of Ecology*, 6(1), pp. 102–120. Available at: https://doi.org/10.17161/eurojecol.v6i1.13629

Huntley, B., Collingham, Y.C., Willis, S.G. and Green, R.E. (2008) 'Potential impacts of climatic change on European breeding birds', *PLoS One*, 3, e1439. Available at: https://doi.org/10.1371/journal.pone.0001439

Jahelková, H. et al. (2014) 'First record of *Hypsugo savii* in Prague and summary of winter records of *Pipistrellus nathusii* from Prague and close surroundings (Czech Republic)', *Vespertilio*, 17, pp. 95–101.

Jetz, W., Wilcove, D.S. and Dobson, A.P. (2007) 'Projected impacts of climate and land-use change on the global diversity of birds', *PLoS Biology*, 5, e157. Available at: https://doi.org/10.1371/journal.pbio.0050157

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. and Racey, P.A. (2009) 'Carpe noctem: the importance of bats as bioindicators', *Endangered Species Research*, 8(1–2), pp. 93–115. Available at: https://doi.org/10.3354/esr00182

Mathiaparanam, K.J., Mulder, R.A. and Hale, R. (2024) 'Anthropogenic double jeopardy: urban noise and artificial light at night interact synergistically to influence abundance', *Environmental Pollution*, 363, 125078. Available at: https://doi.org/10.1016/j.envpol.2024.125078

Kalko, E.V. and Schnitzler, H.-U. (1993) 'Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection', *Behavioral Ecology and Sociobiology*, 33, pp. 415–428. Available at: https://doi.org/10.1007/BF00170257

Kerth, G., Weissmann, K. and König, B. (2001) 'Day roost selection in female Bechstein's bats', *Oecologia*, 126, pp. 1–9.

Kohyt, J. et al. (2024) 'Spatiotemporal use of urban rivers by local bat populations in a large city (Cracow, Southern Poland)', *Urban Ecosystems*, 27, pp. 1663–1673. Available at: https://doi.org/10.1007/s11252-024-01545-x

Korine, C., Adams, R. and Russo, D. et al. (2016) 'Bats and water: anthropogenic alterations threaten global bat populations', in Voigt, C.C. and Kingston, T. (eds.) *Bats in the Anthropocene: conservation of bats in a changing world*. Cham: Springer, pp. 215–241.

Kunz, T.H. (1982) 'Roosting ecology of bats', *Ecology of bats*, pp. 1–55.

Kunz, T.H. and Lumsden, L.F. (2003) 'Ecology of cavity and foliage roosting bats', in Kunz, T.H. and Fenton, M.B. (eds.) *Bat ecology*. Chicago: University of Chicago Press, pp. 3–89.

Kunz, T.H. and Reynolds, D.S. (2003) 'Bat colonies in buildings', in O'Shea, T.J. and Bogan, M.A. (eds.) *Monitoring trends in bat populations of the United States and territories: problems and prospects*. U.S. Geological Survey, pp. 91–102.

Kunz, T.H. and Fenton, M.B. (eds.) (2005) *Bat ecology*. Chicago: University of Chicago Press.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. and Fleming, T.H. (2011) 'Ecosystem services provided by bats', *Annals of the New York Academy of Sciences*, 1223, pp. 1–38. Available at: https://doi.org/10.1111/j.1749-6632.2011.06004.x

Kurta, A. (1986) 'Factors affecting resting and postflight body temperature of little brown bats', *Physiological Zoology*, 59, pp. 429–438.

Lanza, B. (1959) 'Chiroptera', in Toschi, A. and Lanza, B. (eds.) *Fauna d'Italia. Vol. IV: Mammalia (Generalità, Insectivora, Chiroptera)*. Bologna: Calderini, pp. 187–473.

Lausen, C.L. and Barclay, R.M.R. (2002) 'Roosting behaviour of female big brown bats in rock crevices', *Canadian Journal of Zoology*, 80, pp. 1069–1076.

Lausen, C.L. and Barclay, R.M.R. (2006) 'Benefits of living in a building', *Journal of Mammalogy*, 87, pp. 362–370.

Law, B.S. and Chidel, M. (2007) 'Bats under a hot tin roof', *Australian Journal of Zoology*, 55, pp. 49–55.

Lewis, S.E. (1996) 'Low roost-site fidelity in pallid bats', *Behavioral Ecology and Sociobiology*, 39, pp. 335–344.

Lima, S.L. and O'Keefe, J.M. (2013) 'Do predators influence the behaviour of bats?', *Biological Reviews*, 88, pp. 626–644.

Lissovsky, A.A. et al. (2025) *Atlas of mammal distribution in the European part of Russia*. Moscow: KMK Scientific Press.

Liu, Z., He, C. and Wu, J. (2016) 'The relationship between habitat loss and fragmentation during urbanization: an empirical evaluation from 16 world cities', *PLoS ONE*, 11(4), e0154613. Available at: https://doi.org/10.1371/journal.pone.0154613

Lučan, R.K. and Radil, J. (2010) 'Population structure of *Myotis daubentonii* responding to microclimate of anthropogenic roosts', *Biologia*, 65, pp. 1072–1080.

Lučan, R.K., Jor, T., Romportl, D. and Morelli, F. (2025) 'Use of synanthropic roosts by bats in Europe and North America', *Mammal Review*, 55(3), e12380.

Lumsden, L.F., Bennett, A.F. and Silins, J.E. (2002) 'Location of roosts in fragmented landscapes', *Biological Conservation*, 106, pp. 237–249.

Maslo, B., Mau, R.L., Kerwin, K., McDonough, R., McHale, E. and Foster, J.T. (2022) 'Bats provide a critical ecosystem service by consuming a large diversity of agricultural pest insects', *Agriculture, Ecosystems & Environment*, 324, 107722. Available at: https://doi.org/10.1016/j.agee.2021.107722

Magle, S.B., Hunt, V.M., Vernon, M. and Crooks, K.R. (2012) 'Urban wildlife research: past, present, and future', *Biological Conservation*, 155, pp. 23–32. Available at: https://doi.org/10.1016/j.biocon.2012.06.018

McKinney, M.L. (2002) 'Urbanization, biodiversity, and conservation', *BioScience*, 52(10), pp. 883–890.

McKinney, M.L. (2006) 'Urbanization as a major cause of biotic homogenization', *Biological Conservation*, 127(3), pp. 247–260. Available at: https://doi.org/10.1016/j.biocon.2005.09.005

McLean, J.A. and Speakman, J.R. (1999) 'Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation', *Functional Ecology*, 13, pp. 360–372.

Mickleburgh, S.P., Hutson, A.M. and Racey, P.A. (2002) 'A review of the global conservation status of bats', *Oryx*, 36(1), pp. 18–34. Available at: https://doi.org/10.1017/S0030605302000054

Moosman, P.R. Jr., Marsh, D.M., Pody, E.K. and Brust, T.J. (2023) 'Differential selection of roosts by *Myotis leibii*', *Journal of Mammalogy*, 104, pp. 723–738.

Mori, E. et al. (2026) 'On the move: southern range expansion of Italian parti-coloured bats', *Mammalian Biology*, pp. 1–14.

Neubaum, D.J. (2018) 'Unsuspected retreats of little brown myotis', *Journal of Mammalogy*, 99, pp. 1294–1306.

Ohlendorf, B. (2019) 'Neue Fledermausarten in Sachsen: Weißrandfledermaus (*Pipistrellus kuhlii*) & Alpenfledermaus (*Hypsugo savii*)'. Available at: http://www.fledermaus-aksa.de/wp-content/uploads/2019/08/19-Neue-Fledermausarten-in-Sachsen-1.pdf

Otto, M.S., Becker, N.I. and Encarnacão, J.A. (2016) 'Roost characteristics and heterothermy', *Ecological Research*, 31, pp. 385–391.

Parmesan, C. and Yohe, G. (2003) 'A globally coherent fingerprint of climate change impacts across natural systems', *Nature*, 421, pp. 37–42. Available at: https://doi.org/10.1038/nature01286

Patroneck, G.J., Beck, A.M. and Glickman, L.T. (1997) 'Dynamics of dog and cat populations in a community', *Journal of the American Veterinary Medical Association*, 201, pp. 637–642.

Pearson, R.G. and Dawson, T.P. (2003) 'Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?', *Global Ecology & Biogeography*, 12, pp. 361–371. Available at: https://doi.org/10.1046/j.1466-822X.2003.00042.x

Pestano, J., Brown, R.P., Suárez, N.M. and Fajardo, S. (2003) 'Phylogeography of pipistrelle-like bats within the Canary Islands, based on mtDNA sequences', *Molecular Phylogenetics and Evolution*, 26(1), pp. 56–63.

Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. (1999) 'Biological response to climate change on a tropical mountain', *Nature*, 398, pp. 611–615. Available at: https://doi.org/10.1038/19297

Pyšek, P. (1998) 'Alien and native species in Central European urban floras: a quantitative comparison', *Journal of Biogeography*, 25(1), pp. 155–163. Available at: https://doi.org/10.1046/j.1365-2699.1998.251177.x

Quetglas, J. and Garrido, J.A. (2005) 'Rastros y señales de murciélagos ibéricos', *Galemys*, 17, pp. 53–62.

Racey, P.A. (1973) 'Environmental factors affecting gestation length', *Journal of Reproduction and Fertility*, 61, pp. 123–129.

Rajasegaran, P., Shazali, N. and Anwarali Khan, F.A. (2018) 'Microclimate and physiological effects in cave roosts of bats', *Zoological Science*, 35, pp. 521–527.

Rakhmatulina, I.K. (2005) *Bats of Azerbaijan (Fauna, ecology, zoogeography)*. Baku: Institute of Zoology, National Academy of Sciences of Azerbaijan (in Russian).

Ratnarathorn, N. et al. (2026) 'Effects of rapid urbanisation on human–snake conflicts in a tropical mega-city: challenges to biodiversity conservation and healthcare systems', *Landscape and Urban Planning*, 269, 105582. Available at: https://doi.org/10.1016/j.landurbplan.2026.105582

Razgour, O., Ibáñez, C., Puechmaille, S.J. and Juste, J. (2023) '*Myotis nattereri* species complex (*M. nattereri*, *M. crypticus* and *M. escalerai*)', in Russo, D. (ed.) *Chiroptera. Handbook of the mammals of Europe*. Cham: Springer. Available at: https://doi.org/10.1007/978-3-030-44029-9_57

Rebelo, H., Tarroso, P. and Jones, G. (2010) 'Predicted impact of climate change on European bats in relation to their biogeographic patterns', *Global Change Biology*, 16(2), pp. 561–576. Available at: https://doi.org/10.1111/j.1365-2486.2009.02021.x

Reiter, A., Benda, P. and Hotovy, J. (2007) 'First record of the Kuhl's pipistrelle, *Pipistrellus kuhlii* (Kuhl, 1817), in the Czech Republic', *Lynx*, 38, pp. 47–54.

Reiter, A., Bartonička, T., Lučan, R.K. and Řehák, Z. (2010) 'New records of *Hypsugo savii* in the Czech Republic', *Vespertilio*, 13–14, pp. 121–125.

Rodrigues, L., Zahn, A., Rainho, A. and Palmeirim, J.M. (2003) 'Roosting behaviour of *Myotis myotis*', *Mammalia*, 67, pp. 321–335.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003) 'Fingerprints of global warming on wild animals and plants', *Nature*, 421, pp. 57–60. Available at: https://doi.org/10.1038/nature01333

Russo, D. and Jones, G. (2002) 'Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls', *Journal of Zoology*, 258(1), pp. 91–103.

Russo, D., Cistrone, L., Jones, G. and Mazzoleni, S. (2004) 'Roost selection by barbastelle bats (*Barbastella barbastellus*) in beech woodlands of central Italy: consequences for conservation', *Biological Conservation*, 117(1), pp. 73–81.

Russo, D., Bosso, L. and Ancillotto, L. (2018) 'Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications', *Agriculture, Ecosystems & Environment*, 266, pp. 31–38. Available at: https://doi.org/10.1016/j.agee.2018.07.024

Sachanowicz, K., Wower, A. and Bashta, A.T. (2006) 'Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe', *Acta Chiropterologica*, 8(2), pp. 543–548.

Sachanowicz, K., Piskorski, M. and Tereba, A. (2017) 'Systematics and taxonomy of *Pipistrellus kuhlii* (Kuhl, 1817) in Central Europe and the Balkans', *Zootaxa*, 4306 (1), pp. 53–66.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. (2000) 'Global biodiversity scenarios for the year 2100', *Science*, 287, pp. 1770–1774. Available at: https://doi.org/10.1126/science.287.5459.1770

Salsamendi, E., Garin, I., Almenar, D., Goiti, U., Napal, M. and Aihartza, J. (2008) 'Diet and prey selection in Mehelyi's horseshoe bat *Rhinolophus mehelyi* (Chiroptera, Rhinolophidae) in the south-western Iberian Peninsula', *Acta Chiropterologica*, 10 (2), pp. 279–286.

Salsamendi, E., Arostegui, I., Aihartza, J., Almenar, D., Goiti, U. and Garin, I. (2012) 'Foraging ecology in Mehelyi's horseshoe bats: influence of habitat structure and water availability', *Acta Chiropterologica*, 14, pp. 121–132.

Safi, K. and Kerth, G. (2004) 'A comparative analysis of specialization and extinction risk in temperate-zone bats', *Conservation Biology*, 18 (5), pp. 1293–1303.

Schober, W. and Grimmberger, E. (1997) *The bats of Europe and North America*.

Serangeli, M.T., Cistrone, L., Ancillotto, L. et al. (2012) 'The post-release fate of hand-reared orphaned bats: survival and habitat selection', *Animal Welfare*, 21, p. 9.

Sherwin, H.A., Montgomery, W.I. and Lundy, M.G. (2012) 'The impact and implications of climate change for bats', *Mammal Review*. Available at: https://doi.org/10.1111/j.1365-2907.2012.00214

Simmons, N.B. and Cirranello, A.L. (2026) *Bat species of the world: a taxonomic and geographic database*. Version 1.10.

Spitzenberger, F. (1997) 'Distribution and range expansion of Savi's bat in Austria', *Zeitschrift für Säugetierkunde*, 62, pp. 179–181.

Stojanovski, L. (1994) 'Contribution to the knowledge on bats (Chiroptera) in Macedonia', *Ekologija i Zaštita Životne Sredine*, 1 (2), pp. 59–62.

Stoycheva, S., Georgiev, D., Pandourski, I. and Tilova, E. (2009) 'Bat diversity in two large towns of the Upper Thrace, Bulgaria (Chiroptera)', *Lynx*, 40, pp. 83–93.

Strelkov, P.P. and Shaimardanov, R.T. (1983) 'The new data on the distribution of bats (Chiroptera) in Kazakhstan', *Fauna, sistematika i biologia mlekopitayushchikh. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR (Leningrad)*, 119, pp. 3–42 (in Russian).

Strelkov, P.P., Unkurova, V.I. and Medvedeva, G.A. (1985) **'**New data on *Pipistrellus kuhlii* and dynamics of its range in the USSR', *Zoologichesky Zhurnal*, 64 (1), pp. 87–97.

Šálek, M., Bažant, M., Klvaňa, P., Vermouzek, Z. and Václav, R. (2023) ‘Historical changes in mortality patterns of diurnal and nocturnal raptors in the Czech Republic, Central Europe: 1913–2017’, *Biological Conservation*, 282, 110073. Available at: https://doi.org/10.1016/j.biocon.2023.110073

Thuiller, W. (2004) ‘Patterns and uncertainties of species’ range shifts under climate change’, *Global Change Biology*, 10, pp. 2020–2027. Available at: https://doi.org/10.1111/j.1365-2486.2004.00859.x

Travis, J.M.J. and Dytham, C. (2004) ‘A method for simulating patterns of habitat availability at static and dynamic range margins’, *Oikos*, 104 (2), pp. 410–416.

Tuttle, M.D. and Stevenson, D. (1982) ‘Growth and survival of bats’, in Kunz, T.H. (ed.) *Ecology of bats*. New York: Plenum Press, pp. 105–150.

Uhrin, M., Kaňuch, P., Krištofík, J. and Paule, L. (2010) ‘Phenotypic plasticity in the greater mouse-eared bat in extremely different roost conditions’, *Acta Theriologica*, 55, pp. 153–164.

Ulrich, W., Sachanowicz, K. and Michalak, M. (2007) ‘Environmental correlates of species richness of European bats (Mammalia: Chiroptera)’, *Acta Chiropterologica*, 9 (2), pp. 347–360.

United Nations (2025) *World urbanization prospects 2025: summary of results*. New York: United Nations.

Venter, Z.S. et al. (2026) ‘Europe’s land take and the loss of nature and cropland to artificial surfaces’, *Nature Communications*, 17, 5122. Available at: https://doi.org/10.1038/s41467-026-71931-w

Vernier, E. (1995) ‘Presence and distribution of bats in Padova’, *Myotis*, 32–33, pp. 193–195.

Vlaschenko, A. et al. (2023) ‘Leaping on urban islands: further summer and winter range expansion of European bat species’, *European Journal of Ecology*, 9 (1). Available at: https://doi.org/10.17161/eurojecol.v9i1.18664

Voigt, C.C., Phelps, K.L., Aguirre, L.F., Schoeman, M.C., Vanitharani, J. and Zubaid, A. (2016) ‘Bats and buildings: the conservation of synanthropic bats’, in Voigt, C. and Kingston, T. (eds.) *Bats in the Anthropocene: conservation of bats in a changing world*. Cham: Springer, pp. 427–462.

Wang, D., de Knegt, H.J. and Hof, A.R. (2022) ‘The effectiveness of a large protected area to conserve a global endemism hotspot may vanish in the face of climate and land-use changes’, *Frontiers in Ecology and Evolution*, 10, 984842.

Warmer, F.E.M., van Vliet, W.A., van Hooft, P. and Hof, A.R. (2025) ‘The role of intrinsic factors in explaining range shifts of European breeding birds: a meta-analysis’, *Ecology and Evolution*, e71308. Available at: https://doi.org/10.1002/ece3.71308

Webb, P.I., Speakman, J.R. and Racey, P.A. (1995) ‘Evaporative water loss in two sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentonii*: relation to foraging mode and implications for roost site selection’, *Journal of Zoology*, 235, pp. 269–278.

Wenninger, E.J. and Inouye, R.S. (2008) ‘Insect community response to plant diversity and productivity in a sagebrush steppe ecosystem’, *Journal of Arid Environments*, 72, pp. 24–33.

Whitaker, J.O. and Karataş, A. (2009) ‘Food and feeding habits of some bats from Turkey’, *Acta Chiropterologica*, 11, pp. 393–403.

Wilde, C.J., Knight, C.H. and Racey, P.A. (1999) ‘Influence of torpor on milk protein secretion’, *Journal of Experimental Zoology*, 284, pp. 35–41.

Willis, C.K. and Brigham, R.M. (2007) ‘Social thermoregulation and roost preferences’, *Behavioral Ecology and Sociobiology*, 62, pp. 97–108.

Zahn, A. and Maier, S. (1997) ‘Jagdaktivität von Fledermäusen an Bächen und Teichen’, *Zeitschrift für Säugetierkunde*, 62, pp. 1–11.

Zeale, M.R.K., Butlin, R.K., Barker, G.L.A., Lees, D.C. and Jones, G. (2011) ‘Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces’, *Molecular Ecology Resources*, 11, pp. 236–244. Available at: https://doi.org/10.1111/j.1755-0998.2010.02920.x

Žďárská, L. (2013) *Potravní ekologie netopýrů východního Středomoří [Feeding ecology of bats in the Eastern Mediterranean]*. MSc thesis. Charles University in Prague, Prague.

Paper 1

Kipson, M., Gazaryan, S. and Horáček, I. (2023) 'Savi's pipistrelle *Hypsugo savii* (Bonaparte, 1837)', pp. 95-112 in Russo, D. (ed.) *Chiroptera. Handbook of the mammals of Europe*. Cham: Springer Nature Switzerland AG. Available at: https://doi.org/10.1007/978-3-030-44029-9_162

Savi's Pipistrelle *Hypsugo savii* (Bonaparte, 1837)

7

Marina Kipson, Suren Gazaryan, and Ivan Horáček

Contents

M. Kipson (*) · I. Horáček
Department of Zoology, Charles University in Prague, Prague, Czech Republic
e-mail: marinakipson@gmail.com; ivan.horacek@natur.cuni.cz

S. Gazaryan
UNEP/EUROBATS Secretariat, Bonn, Germany e-mail: suren.gazaryan@eurobats.org

D. Russo (ed.), *Chiroptera*, Handbook of the Mammals of Europe,
https://doi.org/10.1007/978-3-030-44029-9_162

Common Names

English	Savi's pipistrelle
German	Alpenfledermaus
French	Vespère de Savi
Spanish	Murciélago montañero
Italian	Pipistrello di Savi
Russian	Кожановидный нетопырь

Taxonomy and Systematics

The prior name of the species is *Vespertilio savii* Bonaparte 1837 (type locality: Pisa, Italy); however, in most of the older literature it is reported under the name *Vesperugo maurus* Blasius, 1853 suggesting its relations with species now comprised within the genera *Pipistrellus* and *Nyctalus*. With regards to differences from these bats, Kolenati 1856 placed the species in the separate genus *Hypsugo*. Most subsequent authors classified the species within the genus *Pipistrellus,* often as a separate group within that genus (Miller 1907, 1912; Tate 1942; Ellerman and Morrison-Scott 1966; Hill and Harrison 1987; Koopman 1994), yet the doubts on its generic assignment persisted. Due to its resemblance to *Eptesicus* in dental and external characters, the species was either included in that genus (in subgenus *Amblyotus*, e.g., by Ognev 1928) or considered as an element of support for the identification of a large genus *Vespertilio* covering all clades of *Pipistrellus-Vespertilio-Eptesicus* grade proposed, e.g., by Kuzyakin (1950). Much later, Horáček and Hanák (1985) and Menu (1987), who analyzed the taxonomic distribution of characters used in vespertilionid taxonomy (dentition, baculum, penial morphology, postcranial skele-ton, karyology, etc.) for a large set of taxa belong-ing to *Vespertilio* sensu Kuzyakin (1950), demonstrated a distinct position of *savii* and sev-eral forms closely related to it (*darwini*, *alashanicus, velox, corrensis, ariel, arabicus, austenianus, pulveratus, mordax, affinis*) and suggested to place the species in a separate genus, *Hypsugo* Kolenati, 1856. Distinct differ-ences from *Pipistrellus* were also supported by further morphological comparisons (Hill and Har-rison 1987 who proposed *Hypsugo* as a subgenus of *Pipistrellus*) and by electrophoretic data (Ruedi and Arlettaz 1991).

Volleth (1989), Volleth and Heller (1994) found that *Hypsugo* shared chromosomal apomorphies with Vespertilioninae rather than Pipistrellinae. Arguments for a separate generic status of *Hypsugo* were discussed in details by Horáček et al. (2000). The generic status of *Hypsugo* was finally supported by the study of mtDNA (Hoofer and Van Den Bussche 2003), which generated approximately 2.6 kilobase pairs of mitochondrial DNA (mtDNA) sequence encompassing three adjacent genes (12S rRNA, tRNAVal, 16S rRNA) for 120 vespertilionids representing 110 species, 37 of 44 genera, and all subfamilies. At the same time, the study confirmed that the genus *Hypsugo* is a polytypic clade. Recent assessment (Simmons 2005; Burgin 2019) recognized 18 species within the genus, distributed mostly in the Oriental and Ethiopian

regions. Recently, Hutterer et al. (2019) segregated sub-Saharan taxa into a separate genus *Parahypsugo*.

In the traditional view, within its W-Palearctic range, several forms of this species have been con-sidered as subspecies (Simmons 2005): they were described as *Vespertilio ochromixtus* Cabrera, 1904 (type locality: Sierra de Guadarrama, Spain), *Scotophilus darwini* Tomes, 1959 (Las Palmas, Canary Isl.), *Vesperugo caucasicus* Satunin, 1901 (Tiflis ¼ Tbilisi, the Caucasus), and *Amblyotus tauricus* Ognev 1927 (Karadagh, Crimea). The latter two were downgraded to a subspecies rank (Bobrinskii et al. 1944) and are now considered clear synonyms of *H. savii* without assignment to any distinct subspecies (Pavlinov and Lissovsky 2012). However, the situation with the remaining forms and taxonomic status of the traditional *H. savii* is more complicated, in particular with regards to recent molecular studies.

Pestano et al. (2003) demonstrated a deep divergence between individuals of *H.savii* from mainland Spain and the Canary Islands (6.3–7.2% in uncorrected cytb and 3.8–4.4% in 16S rRNA), contrasting to shallow divergences among individuals from different islands of the Canary archipelago. Mayer et al. (2007) reported considerable difference between a bat caught in Morocco and *H. savii* from European mainland (9.6% in nd1). Regarding similar sequence differences observed by Pestano et al. (2003) between individuals from the Iberian Peninsula and the Canary Islands, Mayer et al. (2007) suggested a separate species status for putative clade colonizing the NW Africa, Spain, and Canary Islands provisionally denoted as *Hypsugo* cf. *darwinii* (Tomes, 1859). Veith et al. (2011) found the haplotypes close to this clade also in Sicily and Sardinia, and Dondini et al. (2016) reported it from a small island of Montecristo near coast of Tuscany, Italy.

Another molecular study by Ibanez et al. (2006) analysed mitochondrial (Cytb and ND1) and nuclear (RAG2) DNA sequences for each of the 28 bat species known for Iberia, and found three different lineages in the European samples of *H. savii*. One lineage was represented by two bats from southern Iberia, whereas another lineage was found as far north as Switzerland. These two lineages are sympatric in Andalusia, southern Spain. The third lineage corresponds to Savi's pipistrelles from the Eastern Mediterranean. Recently, the Iberian lineage was found on Malta (Mifsud and Vella 2019). The third lineage in the sense of Ibanez et al. (2006) was later discovered in Turkey (as Clade 2 in Çoraman et al. 2013). The divergences between the clades were relatively high; Clade 2 (South-eastern Europe and Near East) differed from Clade 1 (South-western Europe) by ca. 7% on ND1 and 8% on Cytb and by ca. 9% on ND1 and 8% on Cytb from Clade 3 of Çoraman et al. 2013 (North Africa and Iberia). Mayer et al. (2007) reported a mitochondrial DNA sequence from one Israeli sample of *H.* cf. *savii* (nd1) that differed by 13.8% from other sequences of the species from the same area.

In short, the respective data suggest appearance of at least four distinct clades of *H. savii* within the W Palearctic: (1) Southern Levant, separated by the deepest divergence from the others, supposedly extending in the southern part of the range, (2) E-Mediterranean clade recorded in Croatia, Turkey and Levant (including Israel), (3) W-Mediterranean lineage (for which the name *H. ochromixtus* Cabrera, 1904 is available) recorded from Spain to Switzerland, (4) SW Mediterranean (including NW Africa and S Spain) clade supposedly close to Canarian *H. darwinii*, recently recorded in Sardinia, Sicily and Tuscany. The emerging view, supported by multiple records of sympatric distribution of particular clades (1 and 2 in Israel, 2 and 3 in Spain, 2 and 4 in Sardinia and Italy), suggests separate species status for all these clades. Unfortunately, until present day such a conclusion would be quite premature for several reasons.

First, the available samples are quite insufficient in both size and geographical coverage. In most instances the published studies have examined just a few individuals relying only on a single mitochondrial marker, often using a different one (cytb, nd1, 16SRNA). A complex investigation providing relevant data on patterns in genetic variation within particular populations and their geographic correlates, cross-controlled by application of multiple markers, both mitochondrial and nuclear, is missing. The relationships between

particular clades and type populations, based on the names available for nomenclature expression of phylogenetic divergences (within West Palearctic in total 12 names – Simmons 2005), were not examined in details, and except for *H. darwinii* (in Canary Islands), they are not obvi-ous. Prior to answering these question by pro-found comparative studies (including elucidation of actual distributional status of particular clades), any taxonomical proposal is to be regarded as a provisional hypothesis only.

Paleontology

Similar to other non-cave-dwelling species, *H. savii* appears only exceptionally in the fossil record. A single mandible assigned to the species was found in cave deposits of the Early Middle Pleistocene age in Hundsheim, Austria (Rabeder 1972). The species was further reported in inter-glacial assemblage of the Mikulino(¼ Eemian) age in Matuska Cave, Russian Caucasus (Rossina et al. 2006), a Late Pleistocene site Aquiilón P7 in Spain (Galán et al. 2016), and in Holocene sites in Italy (Riparo Salasini, Salari and Kotsakis 2011) and southern Hungary (Mélyvölgyi-kõfülke cave, formerly identified as *Eptesicus nilssonii* – Görföl et al. 2010). The Early Preboreal record from Býčí Skála cave (Czech Republic) demonstrates the species' range expansion in the Early Holocene almost at the modern northern range margin in Central Europe and its capacity for considerable range dynamics (Horáček et al. 2014).

Current Distribution

The Savi's pipistrelle is a thermophilous species that occupies a large W Palearctic range from W Mediterranean to Central Asia, Afghanistan, and Middle East, allopatric to E Asian ranges of its sister clades. The center of its European range is the Mediterranean region. *H. savii* is a typical inhabitant of rocky habitats. Most records come from moun-tain regions, yet it occurs at a wide range of altitudes from coastal areas up to 3,300 m above sea level (Garrido-Garcia 2000). The species' current range in Europe spans across the Mediterranean region (including many islands) from Spain, France, and Italy to the Levant region (Israel, Lebanon, W Syria, Hatay province in Turkey) of the Eastern Mediterranean and the Balkans (all countries of the region) and Carpathians to West Ukraine (Juste and Paunović 2016). The temporal shift of the northern range margin of the species was reviewed by Reiter et al. (2010) and Uhrin et al. (2015), indicating a continuing range expansion after 1990. Until 1990 the northernmost range margins passed along the Danube in Bulgaria and Serbia, and only a single historical record was reported from the north of the Alps (Horáček and Benda 2004). Currently, the species regularly occurs in most regions of Slovakia and the Czech Republic including records of breed-ing colonies (Reiter et al. 2010; Jahelková et al. 2014) up to the Děčín district (northern Bohemia, Czech Republic) near the German border (Bartonička et al. 2017). Occasional vagrants or transported animals have been documented in Brit-ain (Fisher 1998) and in Hamburg and Wuppertal in Germany (Ohlendorf et al. 2000; Skiba 2010). Recently, a male was found in Dresden and a breed-ing population was ultimately reported from Leipzig (Ohlendorf 2019) (Fig. 1).

However, earlier findings (Lehmann and Engemann 2007) imply that a resident population might colonized Saxony even before.

It is uncertain whether some Romanian and all Ukrainian records that derive from acoustic data reflect real presence of the species or represent misclassified calls of other bats (e.g., *Pipistrellus kuhlii)*. Yet, any evidence of netted bats or other-wise documented specimens are still lacking for the Ukrainian Carpathians (L. Godlevska, pers. comm.). New records of the species come pre-dominately from urban areas, and the species' spread is often associated with its synanthropic roosting behavior (Uhrin et al. 2015), and conve-nient microclimatic roost conditions (Reiter et al. 2010). At the same time, climate change may also contribute to the range expansion in Europe (Rebelo et al. 2010; Ancillotto et al. 2018). On the other hand, no range expansion has been observed both in Southern Ukraine and in the south of Russia (Gazaryan, unpublished data).

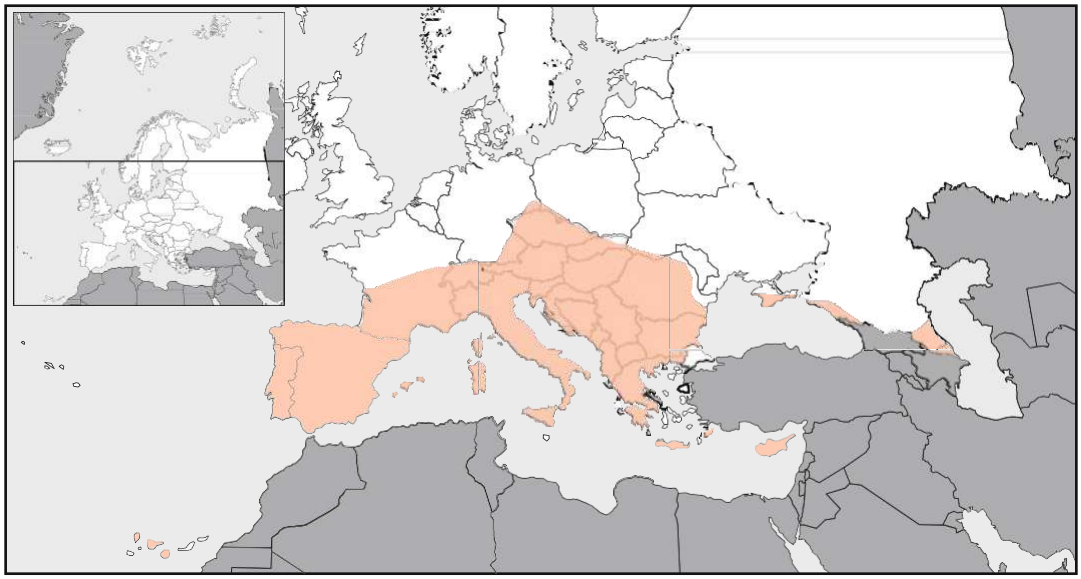


Fig. 1 Distribution is based on the IUCN Red List of Threatened Species. Version 2017-2, Article 1F reports and author's own data. (Map template: © Getty Images/iStockphoto)

Hypsugo savii is one of the most common and widespread bats in the Levant region with numerous records in W Syria and Lebanon (Benda et al. 2006, 2016) reaching the southern range margin in northern Israel (Mendelssohn and Yom-Tov 1999). Although it does not rank among common species in Turkey, and most of its Turkish records come from the coast areas, *H. savii* is most probably distributed throughout the entire Anatolia (Benda and Horáček 1998; Karataş and Sözen 2006).

In the Transcaucasia, *H. savii* was recorded across Georgia (Bukhnikashvili et al. 2004), Armenia, and Azerbaijan (Rakhmatulina 1999, 2005). In the North Caucasus, the species was recorded only from Krasnodar Region and Dagestan (Gazaryan and Dzamirzoyev 2005; Gazaryan 2007). From the Caucasus, the range stretches further eastwards through Iran to Central Asia and northern Afghanistan, with Hindu Kush mountains as a natural border of the species range (Benda and Gaisler 2015). In Iran, *H. savii* is particularly common in the northern regions but its records are scattered also in most other mountain regions of the country including the eastern Baluchistan where the species reaches the southernmost margin of its range (Benda et al. 2012). The bats from Mongolia formerly considered as *H.savii* (comp. Horáček and Hanák 1985) in fact belong to *H. alaschanicus,* a species ranging from Mongolia to Japan (Horáček et al. 2000). This outlook is supported by current molecular studies (Datzmann et al. 2012). The record from the North Africa are restricted to the mountain regions of N Atlas and the Mediterranean coast regions in Morocco, Algeria, and Tunisia, while the species is absent from Libya and Egypt (Juste and Paunović 2016). The molecular data (16S RNA) suggest a close relationship between the North African population and individuals from Sardinia and Sicily, and the populations of the Canary islands (Tenerife, El Hierro, La Gomera and Gran Canaria) tentatively referred to a separate taxon of unconfirmed species status, *H.. darwinii* (Pestano et al. 2003, also see section on "Taxonomy and Systematics").

Description

Size and Morphology

Hypsugo savii (Fig. 2) is a small-sized bat species in comparison to other Palearctic bat species (length of forearm 30–37.3 mm, weight 4.5–9.0 g, hind foot <8.0 mm). The ears are short (length 11.5–16.0 mm) and broadly rounded, the basis of the earlobe ascends from below the eyes (Horáček and Benda 2004). The tragus is blunt and at its broadest width almost as wide as the length of its inside margin (length of tragus 4.7–7.0 mm), the antitragus is not so evident but still marks a delineation in the conch. Its wing membranes, muzzle, and ears are very dark to black. The wings are moderately broad and pointed. The plagiopatagium attaches at the base of the toe. The Post-calcarial lobe (epiblema) of the tail membrane never contains a transversal cartilage slat (as in genus *Pipistrellus*) and can vary from a narrow edge along calcar up to a considerable overlap. The tip of the tail projects outside of the tail membrane by one or two last vertebrae (3.0–5.0 mm). The penis is characteristic in its morphol-ogy and is bent under a right angle between its root and apex, enlarging distally with a baculum that is placed within the distal half of the penis. Baculum is long like in pipistrelloid bats but flat, roof-like on section (not rounded as in pipistrelloid genera), with disc-like terminal enlargements above the urethra muzzle, unique among Palearctic vespertilionid bats. The skull is more robust than in other *Pipistrellus* species, the rostrum is relatively broader, shorter and more compact having its dorsal surface flattened thus making the dorsal profile of the frontal region more straight or convex (condylobasal length 12.0–14.5 mm). The ridges on the edge of orbits are very pronounced (similar to *Vespertilio*) and the zygomatic arch lacks dorsal broadening. The postmaxillary part of the palate is longer than in *Pipistrellus*, and the mandibula is short. The coronoid process is blunter than in *Eptesicus* or *Vespertilio* and not directed forwards unlike in such genera, whereas the processus angularis is thicker and longer than in *Pipistrellus*. The basisphenoid pits are absent (Horáček and Hanák 1985; Horáček and Benda 2004).

The humerus shows characteristics similar to those of *Eptesicus* and *Pipistrellus* species of the same size, yet its proximal epiphysis is somewhat narrower and certain differences are observed in shape of its distal epiphysis: a broad processus spinosus does not extend to the level of the distal margin of trochlea and the epitrochlea basin is less pronounced. The vertebral column consists of 38 vertebrae, the caudal part of sacrum is not shortened, the first tail vertebra is narrower than tail margin of the sacrum, and the tibia is roughly of the same length as the femur (whereas it is clearly longer than the femur in *Pipistrellus*).

Fig. 2 Savi's pipistrelle from Croatia (photo by Marina Kipson)

Dentition

Dentition is myotodont and more robust that in *Pipistrellus* spp. The dental formula is i 2/3, c 1/1, p 1-2/2, m 3/3, total 32 or 34. *Hypsugo savii* has a broad and bicuspid I1, while I2 is unicuspid, well developed and reaches the height of the second cusp of I1. The upper canine is wide with a distinct crest terminating at inflated distal margin of the crown which appear in direct contact with P4. P2 is small, displaced to the inner side of the tooth-row parallel to distal margin of canine or (in ca 20% of individuals) it is missing entirely (comp. Figure 3). The large upper premolar P4 is broad

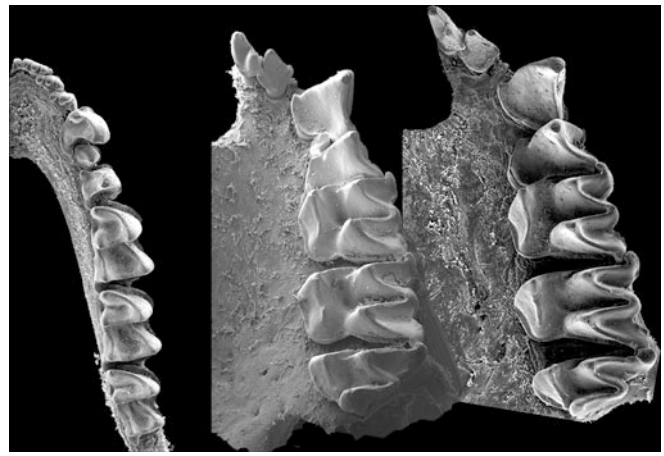


Fig. 3 Occlusal view of the lower and upper dentitions (with and without P2) of *Hypsugo savii* (specimens from Bulgaria)

and short and lacks the cingular cuspules and distinct talon basin. The first and second upper molars are robust with high protocones and post-protocrista terminating with well pronounced hypocones. The protoconal fossa is broad with a spacious distal slope: paralophs, metalophs as well as trans- or distocristas are entirely missing. M3 is moderately reduced with completely retained metacone. The lower incisors are trifid, all of roughly the same size overlapping each other by about half of a tooth width. The c1 is broad with a distinct posterior basin, only slightly higher than the molar protoconid. The lower pre-molar p2 is small, rounded on section of a half-height of p4 that is square on section with slightly enlarged cingular basin at lingo distal crown mar-gin. The lower molars are large, showing m1>m2>m3 scaling. The talonids are much wider that trigonids. In m1 and m2, all molars are distinctly myotodont with a high-staying poscristid and large distally tapered hypoconulids at the lingual base of the crowns. The talonid of m3 is completely retained and relatively long.

Pelage

Compared to the true pipistrelle bats, adult *H. savii* are characterized by a conspicuously contrasting coloration pattern: almost black membranes, muzzle, and auricles; bright white pelage at ventral side; and warm brown coloration on the back with gold hair tips. At the same time, the species exhibits an extraordinary variability in dorsal fur coloration. Dulic (1975) recognized six different types of dorsal hair coloration from specimens found on the Dalmatian islands, with the most frequent one described as having lighter ochraceous hair tips and dark brown base with completely dark head. Similarly, in southern France and Switzerland, the majority of animals has bicolor dorsal fur (81% and 76.1%, respectively) (Arlettaz et al. 1993). Dorsal hairs of bicolored individuals are dark brown to blackish at base with golden, beige, or blond coloration at apical tips; exceptionally, hairs can be even grey with silver tips. However, although this is the most typical phenotype of *H. savii*, some individuals can be unicolor. On Dalmatian islands, this color type was found in 2.8% of the individuals, possibly associated with young animals. In south-ern France and Switzerland, this type occurs in 19 and 24% of bats respectively, being present regardless on the age structure of individuals (Arlettaz et al. 1993). Individuals from the Levant region and Middle East are exclusively bicolored, the pale apical part takes more than one third of dorsal hair length by which their dorsal coloration tends to be of a paler appearance (Benda et al. 2006, 2012). Ventral pelage is bicolor, hairs are relatively long with dark bases and bright white tips.

Age Determination

As a general rule, the coloration of juvenile *H. savii* is less contrasting in comparison to adult individuals – the membranes, face, and muzzle are greyish brown, and the pelage lacks a distinct bicolor pattern. The pelage of juveniles is dark greyish brown on the dorsal side and without bright whitish pattern on the ventral side. However, the reliability of these characters is questioned by the broad variation observed in this species (see above). In juvenile or yearling male bats, the disc-like distal termination of baculum is not completely ossified.

Physiology

Studies on the thermal physiology of *H. savii* showed that the species can undergo longer periods of overheating on a daily basis, making it potentially more resistant to extreme heatwaves (Kuzyakin 1950; Ancillotto et al. 2018). The peak body temperature measured within the study in Italy reached 46.5 °C (Ancillotto et al. 2018). This is the highest body temperature ever measured in a free-ranging bat. Both males and females performed daily overheating bouts and torpor bouts at least once during the study period (aver-age of three consecutive days and nights per indi-vidual), although there were significant differences in temperature oscillations between males and females. In females, oscillations of body temperature were narrower with both torpor and overheating bouts lasting less and being shallower or less intense than in males (Ancillotto et al. 2018).

Genetics

Cytogenetics

The karyotype (in G-banding aspect) retains the ancestral arrangement known for the Vespertilionid bats that also appears in genera such as *Myotis* or *Pipistrellus:* the diploid number of chromosomes (2n) is 44, and the fundamental number (FN) is 55 (Volleth 1989; Zima et al. 1991; Reina et al. 1995). From autosomal chromosomes, three pairs are large and one pair is medium metacentric, the rest of the 17 pairs are acrocentric and vary in size from small to large. The X chromosome is a medium-size metacentric one, whereas the Y chromosome is dot-like acrocentric (Reina et al. 1995). Volleth (1989) and Volleth and Heller (1994) demonstrated that *H. savii* exhibits an apomorhic arrangement of the autosome 11, the character shared with other clades of Vespertilionini. The nucleolus organizer region (NOR) is situated in chromosome 15 which also possesses a secondary constriction below the centromere (Volleth 1989; Reina et al. 1995).

Phylogeography

Based on mitochondrial markers (cytb and nd1), two haplotypes can be found in the Iberian Peninsula, one of which restricted only to the southern tip of the peninsula, whereas a third haplotype is distributed in the eastern Mediterranean (Ibanez et al. 2006). This distinction, however, was not that clear by using a nuclear marker RAG2, leaving the relationships among lineages unresolved probably due to a slower mutation rate of the nuclear marker (Ibanez et al. 2006). On the other hand, the divergence between mainland Spain and the Canary Islands was 6.3–7.2% in uncorrected cytb and 3.8–4.4% in 16S rRNA, suggesting a monophyletic origin of both lineages, whereas the divergence among individuals on the Canary Islands themselves was much lower (Pestano et al. 2003). Another study based on mtDNA (nd1) and 16S rRNA showed that a specimen from Morocco differed from the European lineage by 9.6%, showing at the same time a close relationship with those from the Canary Islands (Mayer et al. 2007). Based on 16S rRNA, Veith et al. (2011) demonstrated that two haplotypes of *H. savii* occur on Sardinia, one belonging to the European *H. savii* lineage and another one forming a group with specimens from Sicily, the Canary Islands, and Morocco (Pestano et al. 2003; Mayer et al. 2007). A particularly deep divergence

(13.8%) is suggested by a single individual from Israel (Mayer et al. 2007).

Life History

No systematic data on the annual life cycle and life history traits are available. The available anecdotic observations concerning reproduction can be summarized as follows. Birth dates span from the beginning of June to the end of July. In Croatia, pregnant females were found from mid-June until the end of July (Dulic 1970) and the appearance of subadults peaked from the end of July until mid-August (Dulic 1958, 1970). In Bulgaria and northern Greece, the majority of births are thought to occur from the beginning until mid-June (Dietz et al. 2009), although a pregnant female was also caught in Greece in the second half of June (Hanák et al. 2001). However, findings of subadult animals in the Eastern Rhodopes in Bulgaria in the middle and at the end of July confirm that births mainly occur in the first half of June (Ivanova and Gueorguieva 2004; Tilova et al. 2005). In the Middle East, lactating females were caught in the beginning of June (n ¼ 6) (Benda et al. 2006). Pregnant females from Syria (n ¼ 2) had two embryos (Benda et al. 2006); two out of three pregnant females from Bulgaria carried two embryos (Horáček and Benda 2004), and bats in captivity (n ¼ 6) had two pups attached to their nipples (Vergari and Dondini 1998), suggesting that twins are common in this species. Spermatogenesis probably occurs in May, and in the first half of June testes are still abdominal whereas in the first half of July they descend to the scrotum and subsequently enlarge to reach their summer maximum (Horáček and Benda 2004).

Habitat and Diet

Spatial Movements

There are only two radio-tracking studies up to date that followed spatial movements of the species, one from Italy and the second one set in Croatia. In Italy, home ranges of males and females measured on average 2.0 ± 1.3 km^2, with the mean straight distance between roosts and foraging areas being 2.9 ± 1.6 km. In the study, home range size in males was almost twice as that of females, and males also and travelled longer distances than females (Ancillotto et al. 2018). In Croatia, a radiotracking study on reproductive females found that the median home range size of pregnant females was 50.8 km^2, whereas the median of lactating females was 24.1 km^2; however, home range sizes (95% kernel) were not significantly different between the two conditions. The maximum straight distance from the roost to the foraging site was 14.2 km in pregnant females and 9.3 km in lactating females (Kipson et al. 2018). In the latter study, pregnant females could regularly cross a sea channel near the roost to reach the mountain slopes on the other shore (the shortest distance for crossing the sea channel was 3.3 km), whereas lactating females did not cross the sea and in general stayed closer to their roosts (Kipson et al. 2018).

Habitat Selection

Hypsugo savii is primarily a lithophilous species that inhabits Mediterranean habitats rich in cliffs with sub-xeric bushy vegetation. It also occurs in a broad spectrum of other habitats from coastal wetlands to sub-mountain grasslands or woodland areas in mountain valleys. The altitudinal range of its records spans from the sea-level to the alpine zone, including the current European altitudinal record for a bat of 3300 m a.s.l. (Garrido-Garcia 2000). Most of the records come from the sub-mountainous and mountainous regions (Ibanez et al. 1992; Juste and Paunović 2016). However, the recently expanding populations also colonized the medium altitude and lowland regions (Paunović et al. 2015).

Foraging habitats are influenced by a considerable individual variation and a quite versatile pattern of habitat selection. In Croatia, pregnant females preferred rocky pastures, followed by forest, meadows and riparian vegetation, and showed lower affinity to illuminated areas

(villages), shrubland and sea. Lactating females showed a greater tendency to forage in riparian habitats. These habitats were followed in importance by meadows, forest and rocky pastures (Kipson et al. 2018). The difference in habitat preferences between reproductive stages of females may reflect prey availability, e.g., swarming insects, within each time period rather than expressing a tight connection to a certain habitat type. Similarly, the preference for forests was primarily related to hunting above the canopy and above clear cuts in open space (Kipson et al. 2018). In Italy, males and females primarily preferred extensive farmland, followed by mixed-coniferous woodland, broadleaved woodland, urban-discontinuous, scrubland, and rocky areas. Within individual home ranges, extensive farmland was still the most preferred habitat type followed by scrubland (Ancillotto et al. 2018). Although some observations and acoustic studies in urban areas indicated that Savi's pipistrelle actively forages at street lights (Vernier 1995; Paunović et al. 2015), neither radio-tracking study (Ancillotto et al. 2018; Kipson et al. 2018) confirmed the supposed preference for foraging in urbanized areas. In fact, the species is not prone to hunt at artificial lights in the presence of more suitable habitat types with sufficient availability of insects. Older studies on *H. savii* habitat preferences were primarily based on observational or acoustic surveys, on which bases the species appeared to hunt above tree crowns (Gaisler 1994), around cliffs and rocks (Dulic 1970), above mountain meadows, freshwater sources (Di Salvo et al. 2009; Russo and Jones 2003), ant colonies (Dietz et al. 2009), over the sea surface (Dulic 1970), and around and above street lamps in urbanized areas (Vernier 1995). The species was also observed hunting during daylight hours (Dulic 1970).

Diet

Diet records based on fecal pellet analyses show a considerable between-region variation supposedly due to local and seasonal differences in food availability and to the opportunistic feeding habits of the species. Unfortunately, a large-scale study analyzing seasonal changes in diet composition is still missing.

The diet analysis presented by Beck (1995) for Switzerland indicated Lepidoptera and Diptera as the most frequent prey (in 53% and 48% of fecal pellets), followed by Hymenoptera (in 30%), Neuroptera (in 30%) and Hemiptera (in 18%), whereas Coleoptera and Trichoptera were found only in 2% and 3% of fecal pellets, respectively. In pellets from south Kyrgyzstan and Bulgaria predominant prey was given by small Cicadoidea (10–60%), Heteroptera (10–40%), and small Lep-idoptera (10–30%), with other groups represented in smaller quantity (Aphidoidea 10–20%, small Coleoptera 5–10%, Diptera 5–10%, Hymenoptera 5–10%, Neuroptera 5%) (Horáček and Benda 2004). Further records of *H. savii* diet from the Mediterranean and the Middle East confirm the species' strategy of taking advantage of high concentrations of swarming insects: in Syria, the main prey were Formicoidea, Heteroptera, Coleoptera, and Lepidoptera (Benda et al. 2006), Coleoptera and Formicoidea were the main diet components in Turkey (Whitaker and Karataş 2009), and Hymenoptera (mostly Formicoidea), Coleoptera, and Heteroptera prevailed in the diet in Lebanon and the Greek islands (Žďárská 2013). Similarly, in Dalmatia (Croatia) faecal pellets contained almost exclusively Formicidae (Dietz et al. 2009). In a detailed diet comparison between pregnant and lactating females in Croatia, ants were a staple in the species' diet in both study groups, with lactating females consuming larger quantities of this prey, followed by Heteroptera in both groups; Aphioidea, nematoceran Diptera and Coleoptera were consumed more often by pregnant females. Other prey items consumed by both groups of females did not differ between reproductive periods (namely, Heteroptera, Lepidoptera, Culicidae, Auchenorrhyncha, Neuroptera, Hymenoptera, and Brachycera). Prey items that were only marginal and occurred in pregnant females included Dermaptera, Orthoptera, Blattodea, Psyllinea, whereas Trichoptera occurred only during the lactating period (Kipson et al. 2018).

Behavior

Roosting Behavior

In natural habitats, *Hypsugo savii* is a lithophilous species, primarily roosting in rock fissures situated in cliffs and other rocky habitats, usually occupied by solitary individuals or small groups. Therefore, these natural roosts are very difficult to find and describe. In urbanized environments, however, the species exhibits a pronounced tendency to colonize fissure roosts in buildings. In northern parts of the range, a preference for artificial structures represents a prevailing characteris-tic of its roosting strategy (Uhrin et al. 2015). The majority of data on the roosting biology of *H. savii* report the species to use a variety of human-made structures rather than rock crevices, but this may be due to the fact that the latter are more difficult to observe. Specifically, roosts were found in attics (Freitag 1996), behind roof gutter and roller type shutters (Vernier 1995), various cracks and voids in historical buildings and ruins (Benda et al. 2006), in a fissure on a balcony (Stoycheva et al. 2009), in abandoned shepherd cabins (Strelkov and Shaimardanov 1983), and in fis-sures in tunnels (Stojanovski 1994). Similarly, most records from the newly colonized area of Central Europe, i.e., Hungary, Austria, Slovakia and Czech Republic, come from urban environments (Uhrin et al. 2015), however older records from buildings are also known from the Mediterranean (Dulic 1958; Vernier 1995). The species is in fact common in buildings in countries such as Italy (D. Russo, pers. comm.). Roosting in rocky fissures was reported many times throughout the species range, e.g., in Kyrgyzstan (Rybin et al. 1987), Transcaucausia (Rakhmatulina 1995), West Syria and Lebanon (Benda et al. 2006, 2016) or Balkans (Benda et al. 2003), and southern Spain (Garrido-Garcia 2000), yet this was established mostly based on visual records of individuals or small colonies leaving their fissure roosts. Besides roosting in shallow crevices in rocks, a new type of roost for a European bat species was noted for the first time in individuals of *H. savii* that were using ground-level space below a rock as their daily shelter (Alcalde and Gosá 2009). Frequent roosting in ground-level rock vertical crevices was also confirmed in a study from Croatia, where the highest number (n ¼ 43) of *H. savii* roosts in natural habitat were discovered (Kipson et al. 2014).

The number of individuals within a colony is usually <20 (Stojanovski 1994; Dietz et al. 2009; Ancillotto et al. 2018), and the most numerous colonies in Croatia contained between 20–40 bats (Dulic 1958), and 30 bats in Bulgaria (Stoycheva et al. 2009). Mean colony size in Italy was 1.8 ± 1.0 for males and 5.6 ± 1.7 for females, respectively (Ancillotto et al. 2018). In Croatia, pregnant females mainly roosted solitarily in ground-level rock crevices, and formed small groups shortly before parturition (2–5 individuals), whereas lactating females were found in groups of 2–9 individuals (Kipson et al. 2014). In Italy and Slovakia, mixed colonies with *Pipistrellus kuhlii* were reported (Danko 2007; Ancillotto et al. 2018). There are almost no reports of hibernacula of *H. savii*; few records of hibernating bats refer to single individuals found in crevices near cave entrances (Paunović et al. 2015, Benda et al. 2016). It is thought that the species hibernate in small groups inside rock fissures and cracks as well as in buildings (Rakhmatulina 2005; Quetglas and Garrido 2005), whereas single individuals were found to hibernate in fissures in building walls in Austria (Spitzenberger 1997), Italy (GIRC 2004) and Bulgaria (Stoycheva et al. 2009).

Group Behavior and Social Structure

Lactating females switch their roosts, probably following a fission-fusion model in which members of one social group (classified as occupying the same roost at the same time) showed repeated splitting and merging of subunits belonging to the group. This type of behavior was observed in Croatia, where lactating females and their young switched roosts and either split or merged with other females on different nights, indicating that they belonged to the same social group whose cohesion is flexible over different nights (Kipson et al. 2014). However, this type of behavior was so

far noted on a small sample and only in one region so it warrants a more detailed investigation before generalizing to all populations.

Regular associations in a common night roost were observed in several sites in Bulgaria, Leba-non and Crete (Horáček unpublished data). This behavior took place in spacious rocky overhangs, high cave entrances or in large human construc-tions like abandoned factory halls, empty ware-houses or a village assembly hall. Individual bats used to appear there about 1 h after sunset with maximum abundance (up to ca 10–20 individuals) around midnight. Arriving bats used to combine temporal swarming flights with resting at separate roosting places without forming pairs or clusters. In a few sites the behavior was observed over several successive nights and for several years. Regular congregations in common night roosts may allow social integration, whereas daytime roosts used only temporarily by single individuals have as such reduced social significance.

Foraging Behavior

The species is an aerial hawker, and hunts its prey in open space, often utilizing locally abundant aerial swarming insects (see section "Diet"). In general, *H. savii* depends on the abundance of prey at various habitat types rather than on any particular habitat type (Kipson et al. 2018). Recent radio-tracking studies revealed preference for more natural habitats when available. There-fore, it is rather an urban-tolerant species than an urban exploiter (Ancillotto et al. 2018).

Echolocation

The echolocation signals of *H. savii* have a typical FM/QCF structure, characterized by two distinct elements: a sharp frequency modulation (FM) component continued with shallower frequency modulation, reaching an almost constant frequency – quasi-constant frequency or QCF (Russo and Jones 2003). The species can be distinguished from bats in the *Pipistrellus* genus because its signals have lower end frequencies and frequencies of maximum energy, whereas the same values are higher than those in genus *Eptesicus*. In the Swiss Alps, call parameters were measured as followed: start frequency at 32.4 kHz, central frequency 32.8 kHz, end frequency 32.0 kHz, sweep bandwidth 2.2 kHz, interpulse interval comprised between two values, 192 and 294 ms (Zingg 1988). A second study from Switzerland showed that the mean call dura-tion was 7.3 ms, lowest call frequency 28.8 kHz, frequency of peak energy 34.9 kHz and highest frequency 48.3 kHz (Obrist et al. 2004). In Greece, the parameters had slightly higher mean values, starting frequency was at 55.5 kHz, ending frequency at 33.7 kHz, frequency of peak energy at 36.7 kHz, bandwidth 8.7 kHz, duration of the signal 6.8 ms and the inter-pulse interval was 148.5 ms (Papadatou et al. 2008). In Italy, mean values were as followed: start frequency 47.3 kHz, end frequency 32.8 kHz, frequency of maximum energy 34.6 kHz, middle frequency 35.1 kHz, duration 8.1 ms and inter-pulse interval 170.7 ms (Russo and Jones 2002). Although echolocation call parameters of *H. savii* can overlap in range with those of *Pipistrellus kuhlii* (a species with partially sympatric distribution) when the former calls in cluttered space, especially in open space the two species may be told apart with good confidence.

Social Calls

Social calls of the species are known only from a single study (Nardone et al. 2017) and appear to show high flexibility and structure. Calls were either produced as a single unit or they were combined into a variety of associations containing 2–9 syllables. Social calls were assessed visually based on the shape of their spectrogram and were classi-fied into five categories: "A - steep downward frequency sweep (FM) followed by a quasi-constant frequency (QCF) part, B - steep down-ward frequency sweep (FM) followed by a rapidly ascending frequency-modulated final part, C - Steep downward frequency sweep (FM) followed by a frequency modulated, highly variable final part, D - Narrow downward frequency sweep

(FM) followed by a frequency modulated part with a rapidly ascending frequency-modulated final portion, E - Steep downward frequency sweep (FM)" (Nardone et al. 2017). The trill like call (type E) was only used in multiple calls and was recorded only during mating season, indicating that it might be connected to reproduction. Single component social calls (types A to D) seem to be used quite often during flight in *H. savii,* whereas in other pipistrelle species they are emitted only occasion-ally. The calls showed in general complex combi-nation of syllables as well as flexibility and rarely recurring motifs, indicating they might serve a wide range of scopes for the species (Nardone et al. 2017).

Parasites and Diseases

Endoparasites reported by Lanza (1999) included three species of Neobacteria, eight species of flat-worms (Digenea), and one roundworm (Nematoda) species (Lanza 1999). In Serbia, 4 species of gastro-intestinal digeneans were found in *H.savii,* namely, *Plagiorchis* sp., *Lecithodendrium linstowi*, *Pro-sthodendrium chilostomum*, *Mesotretes peregrinus* (Horvat et al. 2017). Ectoparasites in Lanza (1999) also included 21 species of mites and ticks (Acari), 5 species of bat flies (Nycteribiidae) and 9 species of flea (Siphonaptera). *H. savii* is a type host of a parasite belonging to Acari, *Spinturnix nobleti*, which was found and described for the first time for this bat species (Denuff et al. 1990).

A novel poxvirus detected for the first time in a bat in Europe (from an individual of *H. savii* in Northern Italy) was consequently named *Hypsugopoxvirus* (Lelli et al. 2019). The genome analyses of the poxvirus showed that it belonged to the *Chordopoxvirinae* subfamily and had the highest nucleotide identity (85%) to *Eptesipoxvirus* (EPTV) found in *Eptesicus fuscus*, in USA. However, the viral ecology and disease associations of the *Hypsugopoxvirus* are not known and need further research (Lelli et al. 2019). Similarly, two beta coronaviruses, closely related to the Middle East respiratory syndrome coronavirus, were obtained from this bat species (Moreno et al. 2017), as well as a novel astrovirus sequence (Dufkova et al. 2015). However, more detailed information on these viruses are so far lacking. Specific antibodies to the European Bat Lyssavirus Type 1 neutralizing were detected in blood samples from the species in Spain (López-Roig et al. 2014). A prevalence of adenoviruses in *Hypsugo savii* (3 out of 50 samples) was reported for Iberia (Rossetto et al. 2020).

Population Ecology

The knowledge of population dynamics and intra and inter species interactions is currently lacking. The overall population of the species is experiencing a northward range expansion, which might be connected to climate change (Ancillotto et al. 2018) and to the synanthropic nature of the species (Uhrin et al. 2015). Climate change modelling scenarios made for European bats predicted that *H. savii* will experience a significant range expansion of >220% until 2060 (Rebelo et al. 2010). Within the last two decades, the species has expanded to the area north of the Alps and it seems that the expansion farther north is still ongoing (see more in section "Current Distribution"). Due to the fact that the species seems to be able to tolerate extreme heat by performing longer overheating bouts (Ancillotto et al. 2018), this bat might persist within its southern range across the Mediterranean despite climate warming, although it is not known how the increased heatwaves and drought might influence reproductive success.

Conservation Status

At the global level, *H. savii* in protected by the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the Agreement on the Conservation of Populations of European Bats (EUROBATS). In Europe, it is listed in Appendix II of Bern Convention and Appendix IV of the EU Directive on the Conservation of Habitats, Flora and Fauna (92/43/EEC). Therefore, *H. savii* is legally protected in most countries within its European range. The species is classified as of Least Concern in both global and

European IUCN Red Lists because no major threats are identified and the range is expanding.

Nevertheless, in connection to wind turbines it is regarded as a high-risk species, frequently con-tributing to casualty counts, especially in the Med-iterranean part of its European range (Rodrigues et al. 2015). The most probable reasons for *H. savii*'s vulnerability to windfarms are its aerial hawker strategy and the tendency to fly in open space, as well as its occurrence in mountain regions where windfarms are often placed (Alcalde and Sáenz 2004). For example, in northern Spain, as much as 62.5% of fatalities under wind turbines were individuals of *H. savii*, with the greatest mortality being recorded from August to October (Alcalde and Sáenz 2004). Furthermore, the first evidence of bat mortality at windfarms in Italy confirmed mortality of *H. savii* (6 out of 7 carcasses found) (Ferri et al. 2011), also ascertained for Croatia (Zagmajster et al. 2007). In a review of known fatalities at wind turbines in Europe (Rodrigues et al. 2015), *H. savii* was represented by 209 cases (53 from Croatia, 44 from Spain, 43 from Portugal, 30 from France, 28 from Greece, 10 from Italy and 1 from Germany). A remarkable case of mortality at a wind turbine was recorded outside its distribution range known at the time of the record, in the German state of Saxony-Anhalt (Lehmann and Engemann 2007). It seems that wind turbines can have a large impact on local populations of the species. However, the possible impact of windfarms on the structure and density of the European population remains unknown due to the lack of research.

Management

There is currently no known management on the populations of the species. The future impact of climate change and increasing droughts within the Mediterranean range of the species, might require active water retention management that would also benefit local populations for which it represents an important habitat type (Kipson et al. 2018). Similarly, due to roosting in human made objects throughout species range, a potential conflict with humans might arise. Therefore, it will be neccessary to preserve these roosts where possible and increase education and awarrenes among pol-icy makers and general public.

Future Challenges for Research and Management

The Savi's pipistrelle is currently ongoing a northward range expansion, and as such presents an interesting model species to study, especially in the light of the changing climatic conditions and adaptability to roosting in human-made structures. However, until recently the species has gained very little research attention and detailed information on its ecology is largely lacking. The challenge is to gain a better insight into its ecology, from the newly colonized regions as well as from the historic core area of its distribution (e.g., roosting, foraging and diet, home range size, and habitat selection). Although the species seems to be well adapted to high temperatures, it is still questionable how potential future changes in climate will affect its reproduction and survival in the Mediterranean region. In places where wind turbines are being planned, monitoring and subsequently proper management of their effect on the species will need to be carried out. Future studies should also focus on resolving the taxonomic questions and genetic relations among the potential various clades within the species' European range.

References

Alcalde JT, Gosá A (2009) The discovery of two Savi's pipistrelles under a stone, reveals its adaptation to shrub steppe habitats. Munibe 57:303–305

Alcalde JT, Sáenz J (2004) First data on bat mortality in wind farms of Navarre (northern Iberian peninsula). Le Rhinolo 17:1–5

Ancillotto L, Budinski I, Nardone V, Di Salvo I, Della Corte M, Bosso L, Conti P, Russo D (2018) What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection. Behav Process 157:540–546

Arlettaz R, Guibert E, Lugon A, Médard P, Sierro A (1993) Variability of fur coloration in Savi's bat *Hypsugo savii*. Bonn Zool Beitr 44:293–297

Bartonička T, Benda P, Juda J (2017) First findings and phenology of *Hypsugo savii* in the Děčín District, Czech Republic (Chiroptera: Vespertilionidae). Lynx (ns) 48:5–14

Beck A (1995) Fecal analyses of European bat species. Myotis 32–33:109–119

Benda P, Gaisler J (2015) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 12. Bat fauna of Afghanistan: revision of distribution and taxonomy. Acta Soc Zool Bohemicae 79:267–458

Benda P, Horáček I (1998) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 1. Review of distribution and taxonomy of bats in Turkey. Acta Soc Zool Bohemicae 62:255–313

Benda P, Ivanova T, Horacek I, Hanák V, Červený J, Gaisler J, Gueorguieva A, Petrov B, Vohralík V (2003) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria. Acta Soc Zool Bohemicae 67:245–357

Benda P, Andreas M, Kock D, Lučan R, Munclinger P, Nová P, Obuch J, Ochman K, Reiter A, Uhrin M, Weinfurtová D (2006) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology. Acta Soc Zool Bohemicae 70:1–329

Benda P, Faizolâhi K, Andreas M, Obuch J, Reiter A, Ševčík M, Uhrin M, Vallo P, Ashrafi S (2012) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 10. Bat fauna of Iran. Acta Soc Zool Bohemicae 76:163–582

Benda P, Abi-Said M, Bou Jaoudes I, Karanouh R, Lucan R, Sadek R, Sevcik M, Uhrin M, Horacek I (2016) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 13. Review of distribution and ectoparasites of bats in Lebanon. Acta Soc Zool Bohemicae 80:207–316

Bobrinskii NA, Kuznetsov BA, Kuzyakin AP (1944) Opredelitel' mlekopitaiuslzchikh SSSR (A guide to mammals of USSR). Sovetskaya Nauka, Moscow. 439pp

Bukhnikashvili A, Kandaurov A, Natradze I (2004) Records of bats in Georgia for the last 140 years. Plecotus, 7:41–57

Burgin CJ (2019) Genus Hypsugo. In: Wilson DE, Mittermeier RA (eds) Handbook of the mammals of the world, vol 9. Bats. Lynx Edicions, Barcelona, pp 809–816

Çoraman E, Furman A, Karataş A, Bilgin R (2013) Phylogeographic analysis of Anatolian bats highlights the importance of the region for preserving the Chiropteran mitochondrial genetic diversity in the Western Palaearctic. Conserv Genet 14(6):1205–1216

Danko Š (2007) Reprodukcia Hypsugo savii a *Pipistrellus kuhlii* na východnom Slovensku: d'alšie dôkazy o ich šírení na sever. Vespertilio 11:13–24

Datzmann T, Dolch D, Batsaikhan N, Kiefer A, Helbig-Bonitz M, Zöphel U, Stubbe M, Mayer F (2012) Cryptic Diversity in Mongolian Vespertilionid Bats (Vespertilionidae, Chiroptera, Mammalia). Results of the Mongolian-German Biological Expeditions Since 1962, No. 299. Acta Chiropterol 14(2):243–264

Denuff J, Volleth M, Keller A, Aellen V (1990) Description of *Spinturnix nobleti* n. sp. (Acari, Mesostigmata, Spinturnicidae), a specific parasite of *Pipistrellus* (*Hypsugo*) *savii* (Chiroptera, Vespertilionidae). Rev Suisse Zool 97(2):477–488

Di Salvo I, Russo D, Sara M (2009) Habitat preferences of bats in rural area of Sicily determined by acoustic surveys. Hystrix Ital J Mammal 20(2):137–146

Dietz C, Von Helverson O, Nill D (2009) Bats of Britain, Europe and Northwest Africa. A&C Black, London

Dondini G, Vergari S, Fichera G, Kiefer A (2016) First record of *Hypsugo cf darwinii* (Tomes, 1859) in Tuscany, Italy. Barbastella 9. https://doi.org/10.14709/BarbJ.9.1.2016.01

Dufkova L, Strakova P, Sirmarova J, Salat J, Moutelikova R, Chrudimsky T, Bartonicka T, Nowotny N, Ruzek D (2015) Detection of Diverse Novel Bat Astrovirus sequences in the Czech Republic. Vector Borne Zoonotic Dis 15(8):518–521

Dulic B (1958) Über die Ökologie der Alpenfledermaus *Pipistrellus savii* (Bonaparte 1837) auf der Insel Mljet (Meleda) in Süddalmatien. Säugtierk Mitt 6:10–11

Dulic B (1970) Ökologische Beoachtungen der Fledermäuse der Adriatischen Inseln. Ztschr Säugtierrk 35:45–51

Dulic B (1975) Morphology of the hair of *Pipistrellus savii* Bonaparte 1837. In: Olembo RJ, Castelino JB, Mutere FA (eds) Proceedings of the fourth international bat research conference, Kenya National Academy for Advancement of Arts and Sciences, pp 51–61

Ellerman JR, Morrison-Scott TCS (1966) Checklist of palaearctic and Indian mammals. British Museum (Natural History), London

Ferri V, Locasciulli O, Soccini C, Forlizzi E (2011) Post construction monitoring of wind farms: first records of direct impact on bats in Italy. Hystrix Ital J Mammal 22(1):199–203

Fisher C (1998) Savi's pipistrelle *Pipistrellus savii* in Britain. Myotis 36:77–81

Freitag B (1996) *Pipistrellus savii* (Bonaparte, 1837) – Erstnachweis für die Steiermark (Mammalia, Chiroptera). Mitt Naturwiss Ver Steiermark 125:237–238

Gaisler J (1994) The bats *Pipistrellus kuhlii* and *Hypsugo savii* on the island of Rab (Croatia). Folia Zool 43(3):279–280

Galán J, Cuenca-Bescós G, López-García JM, Sauqué V, Núñez-Lahuerta C (2016) Fossil bats from the Late Pleistocene site of the Aguilón P7 Cave (Zaragoza, Spain). Comptes Rendus Palevol 15(5):501–514

Garrido-Garcia JA (2000) New altitude record for Chiroptera in Europe. Myotis 37:10

Gazaryan S (unpublished data) Data collected over the years during faunistic surveys in Southern Ukraine and south of Russia

Gazaryan S (2007) Bats Order Chiroptera. In: Red Data Book of the Krasnodar Territory, Krasnodar, pp 419–434. (in Russian)

Gazaryan S, Dzamirzoyev G (2005) Results and perspectives of studies on bat fauna in Dagestan. In: Mammals of mountainous territories. In: Materials International Conference, 4–9 September 2005. KMK Science Press, Moscow, pp 49–57. (in Russian)

GIRC (2004) The Italian bat roost project: a preliminary inventory of sites and conservation perspectives, Hystrix. Ital J Mammal 15(2):55–68

Görföl T, Dombi I, Csorba G (2010) Revision of significant recent and early Holocene bat data from Hungary (Mammalia: Chiroptera). Annls Hist Nat Mus Natn Hung 102:205–210

Hanák V, Benda P, Ruedi M, Horáček I, Sofianidou TS (2001) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 2. New records and review of distribution of bats in Greece. Acta Soc Zool Bohemicae 65:279–346

Hill JE, Harrison DL (1987) The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. Bull Br Mus Nat Hist (Zool) 52:225–305

Hoofer ST, Van Den Bussche (2003) Molecular phylogenetics of the chiropteran family Vespertilionidae. Acta Chiropterol 5:1–63

Horáček I (unpublished data) Observations made during various expeditions within Eastern Meditteranean during 1990s

Horáček I, Benda P (2004) *Hypsugo savii* (Bonaparte, 1837) – Alpenfledermaus. In: Krapp F (ed) Handbuch der Säugetiere Europas. Band 4/II: Fledertiere. Teil II: Chiroptera II. Vespertilionidae 2, Molossidae, Nycteridae. AULA-Verlag, Wiebelsheim, pp 912–941

Horáček I, Hanák V (1985) Generic status of *Pipistrellus savii* and comments on classification of the Genus *Pipistrellus* (Chiroptera, Vespertilionidae). Myotis 23–24:9–16

Horáček I, Hanák V, Gaisler J (2000) Bats of the Palearctic Region: a taxonomic and biogeographic review. In: Woloszyn BW (ed) Proceedings of the VIIIth EBRS, vol 1. Publication of CIC ISEZ PAN, Krakow, pp 11–157. 146pp

Horáček I, Knitlová M, Kipson M (2014) *Hypsugo savii* and other Mediterranean bats colonized Central Europe already in the Earliest Holocene. In: Lina PHC, Hutson AM (eds) Book of abstracts, 13th Bat research symposium, Zagreb Croatia

Horvat Ž, Čabrilo B, Paunović M, Karapandža B, Jovanović J, Budinski I, Bjelić Čabrilo O (2017) Gastrointestinal digeneans (Platyhelminthes: Trematoda) of horseshoe and vesper bats (Chiroptera: Rhinolophidae and Vespertilionidae) in Serbia. Helminthologia 54(1):17–25

Hutterer R, Decher J, Monadjem A, Astrin J (2019) A new genus and species of vesper bat from West Africa, with notes on *Hypsugo, Neoromicia*, and *Pipistrellus* (Chiroptera: Vespertilionidae). Acta Chiropterol 21(1):1–22

Ibanez C, Guillen A, Fernandez R, Perez JL, Guerrero SI (1992) Iberian distribution of some little known bat species. Mammalia 56:433–444

Ibanez C, Garcia-Mudarra JL, Ruedi M, Stadelmann B, Juste J (2006) The Iberian contribution to cryptic diversity in European bats. Acta Chiropterol 8(2):227–297

Ivanova T, Gueorguieva A (2004) Bats (Mammalia: Chiroptera) of the Eastern Rhodopes (Bulgaria and Greece) – species diversity, zoogeography and faunal patterns. In: Beron P, Popov A (eds) Biodiversity of Bulgaria. 2. Biodiversity of Eastern Rhodopes (Bulgaria and Greece). Pensoft & National Museum of Natural History, Sofia, pp 907–927

Jahelková H, Neckárˇová J, Bláhová A, Sasínková M, Weinfurtová D, Hybnerová Z et al (2014) First record of *Hypsugo savii* in Prague and summary of winter records of *Pipistrellus nathusii* from Prague and close surroundings (Czech Republic). Vespertilio 17:95–101

Juste J, Paunović M (2016) *Hypsugo savii*. The IUCN Red List of threatened species 2016: e.T44856A22072380. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T44856A22072380.en. Downloaded on 05 Feb 2020

Karataş A, Sözen M (2006) Bats of the middle and upper Kızılırmak regions, Central Anatolia, Turkey (Chiroptera). Lynx (Praha) (ns) 37:151–159

Kipson M, Šálek M, Lučan RK, Bartonička T, Miková E, Uhrin M, Jahelková H, Pušić A, Kovač D, Majer M, Horáček I (2014) The curious case of Savi's pipistrelle (*Hypsugo savii*): new insight on roosting ecology and behaviour from the Meditteranean region. In: Lina PHC, Hutson AM (eds) Book of abstracts, 13th Bat research symposium, Zagreb Croatia

Kipson M, Šálek M, Lučan R, Uhrin M, Maxinová E, Bartonička T, Andreas M, Kipson K, Pušić A, Rnjak D, Ňado L, Horáček I (2018) Foraging habitat, home-range size and diet of a Mediterranean bat species, Savi's pipistrelle. Acta Chiropterol 20(2):351–360

Koopman KF (1994) Chiroptera: systematics. Handbook of zoology, vol 8, Part 60: Mammalia. Walter de Gruyter, Berlin

Kuzyakin AP (1950) Letuchiye myschi [Bats]. Sovetskaya Nauka, Moscow. 442 pp (in Russian)

Lanza B (1999) I parassiti dei pipistrelli (Mammalia, Chiroptera) della fauna italiana. Museo Regionale di Scienze Naturali, Torino

Lehmann BV, Engemann C (2007) Nachweis einer Alpenfledermaus (*Hypsugo savii*) als Schlagopfer in einem Windpark in Sachsen-Anhalt. Nyctalus 12(2–3): 128–130

Lelli D, Lavazza A, Prosperi A, Sozzi E, Faccin F, Baioni L, Trogu T, Cavallari GL, Mauri M, Gibellini AM, Chiapponi C, Moreno A (2019) *Hypsugopoxvirus*: a novel poxvirus isolated from *Hypsugo savii* in Italy. Viruses 11(6):568

López-Roig M, Bourhy H, Lavenir R, Serra-Cobo J (2014) Seroprevalence dynamics of European bat lyssavirus type 1 in a multispecies bat colony. Viruses 6(9):3386–3399

Mayer F, Dietz C, Kiefer A (2007) Molecular species identification boots bat diversity. Front Zool 4:4

Mendelssohn H, Yom-Tov Y (1999) Mammalia of Israel. Israel Academy of Sciences, Jerusalem

Menu H (1987) Morphotypes dentaires actuels et fossiles des Chiropteres Vespertilionines. 2. Implications systématiques et phylogénétiques. Palaeoverteb Montpellier 17:77–150

Mifsud CM, Vella A (2019) Mitochondrial genetic diversity of bat species from the Maltese islands and applications for their conservation. NE Sci 4(3):276–292

Miller GS (1907) The families and genera of bats. Smithsonian Institution, United States National Museum, Washington, DC. Govt. Print. off

Miller GS (1912) Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British museum. BMNH, London

Moreno A, Lelli D, De Sabato L, Zaccaria G, Boni A, Sozzi E, Prosperi A, Lavazza A, Cella E, Castrucci MR, Ciccozzi M, Vaccari G (2017) Detection and full genome characterization of two beta CoV viruses related to Middle East respiratory syndrome from bats in Italy. Virol J 14:239

Nardone V, Ancillotto L, Russo D (2017) A flexible communicator: social call repertoire of Savi's pipistrelle, *Hypsugo savii*. Hystrix Ital J Mammal 28(1):68–72

Obrist MK, Boesch R, Flückiger PF (2004) Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. Mammalia 68(4):307–322

Ognev SI (1928) Zveri vostochnoi Evropy i severnoi Azii: Nasekomoyadnye i letychie myshi [mammals of eastern Europe and northern Asia: Insectivora and Chiroptera]. Glavnauka Moscow 1:1–631. (in Russian)

Ohlendorf B (2019) Neue Fledermausarten in Sachsen: Weißrandfledermaus (*Pipistrellus kuhlii*) & Alpenfledermaus (*Hypsugo savii*). http://www.fledermaus-aksa.de/wp-content/uploads/2019/08/19-Neue-Fledermausarten-in-Sachsen-1.pdf

Ohlendorf B, Vierhaus H, Heddergott M, Bodino F (2000) Korrektur: Fund einer Nordfledermaus (*Eptesicus nilssoni*) im Hamburg (ds. Z. Bd. 5, p. 220) betraf eine Alpenfledermaus (*Hypsugo savii*). Nyctalus (NF) 7:454

Papadatou E, Butlin RK, Altringham JD (2008) Identification of bat species in Greece from their echolocation calls. Acta Chiropterolog 10(1):127–143

Paunović M, Karapandža B, Budinski I, Jovanović J (2015) New records of the Savi's Pipistrelle *Hypsugo savii* (Bonaparte, 1837) (Chiroptera, Mammalia) from Serbia: an evidence for the expansion of its geographical range. Acta Zool Bulgarica 67(3):389–397

Pavlinov I, Lissovsky A (2012) The mammals of Russia: a taxonomic and geographic reference. KMK Sci Press, Moscow. 602pp

Pestano J, Brown RP, Suarez NM, Fajardo S (2003) Phylogeography of pipistrelle-like bats within the Canary Islands, based on mtDNA sequences. Mol Phylogenet Evol 26(1):56–63

Quetglas J, Garrido JA (2005) Rastros y seňales de murciélagos Ibéricos (Chiroptera). Galemys 17(1–2): 53–62

Rabeder G (1972) Die Insectivoren und Chiropteren (Mammalia) aus dem Altpleistozän von Hundsheim (Niederösterreich). Ann Naturhist Mus Wien 76:375–474

Rakhmatulina IK (1995) Bats' attachment to different shelters in the eastern transcaucasia. Myotis 32–33:197–202

Rakhmatulina IK (1999) On the spatial and seasonal distribution of rare bats (Chiroptera) in the Caucasus. In: Rare mammal species of Russia and neighboring territories. Theriological Society, Moscow, pp 349–375. (in Russian)

Rakhmatulina IK (2005) A Bats of Azerbaijan (fauna, ecology, zoogeography). Baku, publishing house of the Institute of Zoology of NAS of Azerbaijan. 476pp. (in Russian)

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Glob Chang Biol 16:561–576

Reina JM, Pérez-Suárez G, Navlet J, Depaz O (1995) G-, C- and NOR banding of *Hypsugo savii* and *Miniopterus schreibersii* from Spain. Myotis 32–33:57–68

Reiter G, Wegleitner S, Hüttmeir U, Pollheimer M (2010) Die Alpenfledermaus, *Hypsugo savii* (Bonaparte, 1837), in Mitteleuropa. Nyctalus (NF) 15:158–170

Rodrigues L, Bach L, Dubourg-Savage MJ, Karapandža B, Kovač D, Kervyn T, Dekker J, Kepel A, Bach P, Collins J, Harbusch C, Park K, Micevski B, Minderman J (2015) Guidelines for consideration of bats in wind farm projects – revision 2014. EUROBATS Publication Series no 6 (English version). UNEP/EUROBATS Secretariat, Bonn, 133pp

Rossetto F, Iglesias-Caballero M, Liedtke HC, Gomez-Mestre I, Berciano JM, Pérez-Suárez G, de Paz O, Ibañez C, Echevarría JE, Casas I, Juste J (2020) Mating strategy is determinant of adenovirus prevalence in European bats. PLoS One 15(1):e0226203. https://doi.org/10.1371/journal.pone.0226203

Rossina VV, Baryshnikov GF, Woloszyn BW (2006) Dynamics of the Pleistocene bat fauna from the Matuzka Paleolithic site (Northern Caucasus, Russia) (Chiroptera). Lynx (Praha) (ns) 37:229–240

Ruedi M, Arlettaz R (1991) Biochemical systematics of the Savi' s bat (*Hypsugo savii*) (Chiroptera: Vespertilionidae). Z Zool Syst Evol Forsch 29:115–122

Russo D, Jones G (2002) Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. J Zool 258(1):91–103

Russo D, Jones G (2003) Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography 26(2):197–209

Rybin S, Horacek I, Cerveny J (1987) Bats of southern Kirghizia: distribution and faunal Status. In: Hanák V, Horáček I, Cerveny J (eds) European Bat Research. Charles University Press, Praha, pp 421–441

Salari L, Kotsakis T (2011) Late Pleistocene and Holocene bats of Latium (Central Italy). Il Quaternario 24:121–129

Simmons NB (2005) Mammal species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore, pp 312–529

Skiba R (2010) Alpenfledermaus (*Hypsugo savii*) in Wuppertal–Zunahme der Fledermäuse in Norddeutschland? Nyctalus (NF) 15:154–157

Spitzenberger F (1997) Distribution and range expansion of Savi's bat (*Hypsugo savii*) in Austria. Ztschr Säugetierk 62:179–181

Stojanovski L (1994) Contribution to the knowledge on bats (Chiroptera) in Macedonia. Ekol Zašt Život Sred 1(2):59–62

Stoycheva S, Georgiev D, Pandourski I, Tilova E (2009) Bat diversity in two large towns of the Upper Thrace, Bulgaria (Chiroptera). Lynx 40:83–93

Strelkov PP, Shaimardanov RT (1983) The new data on the distribution of bats (Chiroptera) in Kazakhstan. Fauna, sistematika i biologia mlekopitayushchikh. Tr Zool Inst Ak Nauk SSSR Leningrad 119:3.42. (in Russia)

Tate GHH (1942) Results of the Archbold expeditions. No. 47. Review of the vespertilionine bats, with special attention to genera and species of the Archbold collections. Bull Am Mus Nat Hist 80:221–297

Tilova EK, Stoycheva SB, Georgiev DG (2005) New information on the distribution of some bat species (Mammalia: Chiroptera) from Bulgaria. Animal 41:135–144

Uhrin M, Hüttmeir U, Kipson M, Estók P, Sachanowicz K, Bücs S, Karapandža B, Paunović M, Presetnik P, Bashta AT, Maxinová E, Lehotská B, Lehotský R, Barti L, Csösz I, Szodoray-Paradi F, Dombi I, Jére C, Pocora I, Benda P (2015) Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and southeastern Europe: a review. Mammal Rev 46:1–16

Veith M, Mucedda M, Kiefer A, Pidinchedda E (2011) On the presence of pipistrelle bats (*Pipistrellus* and *Hypsugo*; Chiroptera: Vespertilionidae) in Sardinia. Acta Chiropterolog 13:89–99

Vergari S, Dondini G (1998) Causes of death in two species of bats (*Pipistrellus kuhlii* and *Hypsugo savii*) in urban areas of North-central Italy. Myotis 36:159–166

Vernier E (1995) Presence and distribution of bats in the town of Padova (N.E. Italy). Myotis 32-33:193–195

Volleth M (1989) Karyotypevolution und Phylogenie der Vespertilionidae (Mammalia: Chiroptera). PhD Thesis, University of Erlangen. 262pp

Volleth M, Heller KG (1994) Pylogenetic relationship of vespertilionid genera (Mammalia: Chiroptera) as revealed by karyological analysis. Z Zool Syst Evol Forsch 32:11–34

Whitaker JO, Karataş (2009) Food and feeding habits of some bats from Turkey. Acta Chiropterolog 11:393–403

Zagmajster M, Jancar T, Mlakar (2007) First resords of dead bats from windfarms in Croatia. Nyctalus (NF) 12 (2–3):234–237

Žďárská L (2013) Potravní ekologie netopýrů východního Středomoří [Feeding Ecology of Bats in the Eastern Mediterranean]. MSc thesis. Charles University in Prague, Prague, Czech Republic. [In Czech with English summary]

Zima J, Cervený J, Horácek I, Cervená A, Prücha K, Macholán M, Rybin SN (1991) Standard karyology of eighteen species of bats (Rhinolophidae, Vespertilionidae, Molossidae) from Eurasia. Myotis 29:31–34

Zingg PE (1988) Search calls of echolocating *Nyctalus leisleri* and *Pipistrellus savii* (Mammalia: Chiroptera) recorded in Switzerland. Ztschr Säugetierk 53:281–293

Paper 2

Uhrin, M., Hüttmeir, U., Kipson, M., Estók, P., Sachanowicz, K., Bücs, S., Karapandža, B., Paunović, M., Presetnik, P., Bashta, A.T., Maxinová, E., Lehotská, B., Lehotský, R., Barti, L., Csösz, I., Szodoray-Paradi, F., Dombi, I., Jére, C., Pocora, I. and Benda, P. (2015) 'Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and southeastern Europe: a review', *Mammal Review*, 46(1), pp. 1–16. Available at: https://doi.org/10.1111/mam.12050.

Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: a review

Marcel UHRIN* *Institute of Biology and Ecology, Faculty of Science, P. J. Šafárik University in Košice, Moyzesova 11, 040 01 Košice, Slovakia and Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, 165 21 Praha 6, Czech Republic. E-mail: marcel.uhrin@gmail.com*
Ulrich HÜTTMEIR *Austrian Coordination Centre for Bat Conservation and Research, Fritz-Störk-Straße 13, 4060 Leonding, Austria. E-mail: ulrich.huettmeir@fledermausschutz.at*
Marina KIPSON *Department of Zoology, Faculty of Science, Charles University in Prague, Vinicˇná 7, 128 44 Praha 2, Czech Republic. E-mail: marinakipson@gmail.com*
Péter ESTÓK *Eszterházy Károly College, Eszterházy tér 1., 3300 Eger, Hungary. E-mail: batfauna@gmail.com*
Konrad SACHANOWICZ *Museum and Institute of Zoology, Wilcza 64, 00-679 Warsaw, Poland. E-mail: chassan@poczta.onet.pl*
Szilárd BÜCS *Romanian Bat Protection Association, I. B. Deleanu 2, 440014 Satu Mare, Romania. E-mail: szilard_bux@yahoo.com*
Branko KARAPANDŽA *Wildlife Conservation Society 'Mustela', Njegoševa 51, 11000 Belgrade, Serbia. E-mail: branko.karapandza@gmail.com*
Milan PAUNOVIC´ *Department of Biological Collections, Natural History Museum, Njegoševa 51, 11000 Belgrade, Serbia. E-mail: milan.paunovic@nhmbeo.rs*
Primož PRESETNIK *Centre for Cartography of Fauna and Flora, Ljubljana Office, Klunova 3, 1000 Ljubljana, Slovenia. E-mail: primoz.presetnik@ckff.si*
Andriy-Taras BASHTA *Institute of Ecology of the Carpathians, National Academy of Sciences of Ukraine, Kozelnytska st. 4, 79026 Lviv, Ukraine. E-mail: atbashta@gmail.com*
Edita MAXINOVÁ *Institute of Biology and Ecology, Faculty of Science, P. J. Šafárik University in Košice, Moyzesova 11, 040 01 Košice, Slovakia. E-mail: edita.maxinova@gmail.com*
Blanka LEHOTSKÁ *Department of Landscape Ecology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 842 15 Bratislava, Slovakia. E-mail: lehotska@fns.uniba.sk*
Roman LEHOTSKÝ *Miniopterus, Principal Organization of the Slovak Union for Nature and Landscape Conservators, Hlavácˇiková 14, 841 05 Bratislava 4, Slovakia. E-mail: roman.lehotsky@miniopterus.sk*
Levente BARTI *Romanian Bat Protection Association, I. B. Deleanu 2, 440014 Satu Mare, Romania. E-mail: bartilev@yahoo.com*
István CSÖSZ *Romanian Bat Protection Association, I. B. Deleanu 2, 440014 Satu Mare, Romania. E-mail: styepan@freemail.hu*
Farkas SZODORAY-PARADI *Romanian Bat Protection Association, I. B. Deleanu 2, 440014 Satu Mare, Romania. E-mail: farkas.sz.p@gmail.com*
Imre DOMBI *Duna-Dráva National Park Directorate, Tettye tér 9, 7625 Pécs, Hungary. E-mail: imreka@freemail.hu*
Tamás GÖRFÖL *Department of Zoology, Hungarian Natural History Museum, Baross u. 13, 1088 Budapest, Hungary and Institute for Veterinary Medical Research, Centre for Agricultural Research, Hungarian Academy of Sciences, Hungária krt. 21., 1143 Budapest, Hungary. E-mail: gorfol@nhmus.hu*

Sándor A. BOLDOGH *Aggtelek National Park Directorate, Tengerszem oldal 1, 3758 Jósvafö, Hungary. E-mail: sandorboldogh@yahoo.com*
Csaba JÉRE *Romanian Bat Protection Association, I. B. Deleanu 2, 440014 Satu Mare, Romania. E-mail: jerecsaba@yahoo.com*
Irina POCORA *Department of Zoology, Faculty of Biology, Al. I. Cuza' University of Ias¸i, 20 A 'Carol I' Boulevard, 700505 Ias¸i, Romania. E-mail: irinaif23@yahoo.com*
Petr BENDA *Department of Zoology, National Museum (Natural History), Václavské náme˘stí 68, 115 79 Praha 1, Czech Republic and Department of Zoology, Faculty of Science, Charles University in Prague, Vinic˘ná 7, 128 44 Praha 2, Czech Republic. E-mail: petr_benda@nm.cz*

Keywords
Balkans, Carpathians, distribution changes, Pannonia, range expansion

*Correspondence author.

Submitted: 17 January 2015
Returned for revision: 6 March 2015
Revision accepted: 9 June 2015
Editor: KH

doi:10.1111/mam.12050

ABSTRACT

1. Savi's pipistrelle *Hypsugo savii* is a Mediterranean faunal element among the bats; it occurs in southern Europe, the Canary Islands, north-western Africa, most of the Mediterranean islands, in the northern part of the Middle East, in the Crimea, Caucasus, West Turkestan, and northern Afghanistan. The northern margin of its geographical range in Europe reaches the Pyrenees, Massif Central, southern Alps, Dalmatia, Balkan Mountains and southern Crimea, like that of other similar biogeographical elements.
2. Since the 1990s, *Hypsugo savii* started to be found in inland areas of south-eastern Europe and in Central Europe as far northwards as in central Bohemia and southern Poland. These numerous new occurrences seem to be either 1) connected to environmental changes caused by the current climate change; 2) evidence of an intrinsic expansion process powered by the species' synanthropic tendency, including passive human-mediated transport; or 3) a reflection of the increase in field survey efforts.
3. Distributional data on *Hypsugo savii* from central and south-eastern parts of Europe were gathered and evaluated.
4. We provide a detailed review of all records available by the end of 2013. The assessment of temporal distribution of the data clearly shows an ongoing and relatively fast expansion of *Hypsugo savii* from southern to Central Europe, which represents a shift of almost 800 km northwards in the last 20–25 years.
5. Most of the records (65%) originate from urban habitats. This suggests that the synanthropic habits of the species are the most plausible explanation for the northwards shift of the range limits of *Hypsugo savii*.

INTRODUCTION

Savi's pipistrelle *Hypsugo savii* is a bat species distributed in the south-western Palaearctic, marginally penetrating the Oriental region (Horác˘ek et al. 2000). In the Palaearctic, the species is a typical Mediterranean faunal element occurring in southern Europe, Canary Islands, north-west Africa, most of the Mediterranean islands and the northern part of the Middle East. It is also present in the Crimea, Caucasus and West Turkestan and its range stretches to northern Afghanistan. In the continuous European range, the north-ern margin has been delineated to run from the Pyrenees through the Massif Central and the Alps, to northern Pan-nonia and southern Dobrogea (Mitchell-Jones et al. 1999, Horác˘ek & Benda 2004). *Hypsugo savii* roosts in crevices and fissures mainly in karst landscapes, and in similar roosts in towns (Horác˘ek & Benda 2004).

In most of the south-eastern European countries (Slove-nia, Croatia, Bosnia and Herzegovina, Montenegro, Hungary, Romania, and Ukraine), with the partial exception of Bulgaria, systematic bat research using appropriate methods was lacking, thus the presence of *Hypsugo savii* was rarely documented until the year 2000 or even 2010. Never-theless, since the second half of the 1990s, *Hypsugo savii* seems to have undergone significant range changes in Central Europe, where the general knowledge of bat distri-bution has been considerably better than in south-eastern Europe. Single individuals were recorded in Austria in 1985–1996 (Spitzenberger 1997, 2001), which confirmed the occurrence of the species in the country again after a

century of apparent absence (cf. Blasius 1857, von Dalla Torre 1887). Spitzenberger (1997) believed that populations from the higher altitudes of the Alps became extinct in the late 19th century, and that the newly recorded bats origi-nated from northern Italy, where the species is a common inhabitant (Vernier 1995).

Between 1991 and 2005, *Hypsugo savii* was recorded for the first time in several European countries outside the limits of the continuous range delineated in 2000 (Horáčˇek & Benda 2004), i.e. in Hungary, Czech Republic, and Slova-kia (Dobrosi 1994, Gaisler 2001, Lehotská & Lehotský 2006, Görföl et al. 2007). In this period, several findings were also reported from northern Germany and Great Britain (Fisher 1998, Ohlendorf et al. 2000). Nevertheless, these records were evaluated as single strays and/or individuals trans-ported by humans.

In the last published account of the species' geographical range, based on the data available by 2000, Horáčˇek & Benda (2004) showed the northern range margin of *Hypsugo savii* in Central Europe to be at the main Alpine range in central Austria and western Slovenia, continuing along the Adriatic Sea coast, Kosovo, southern Serbia to the northern slopes of the Balkan Mountains in Bulgaria. Later, the northern limits of the species' range were redefined by inclusion of new records; the range included small areas in Hungary, isolated spots at the Slovakian-Hungarian border and in south-eastern Austria, and covered the whole of Romania (Dietz et al. 2007, Dietz & Kiefer 2014). In the Balkans, the occurrence of *Hypsugo savii* in Belgrade (Serbia) was considered to be an outlier from its continuous range (Hutson et al. 2008). The last analysis of the species' range, made from the Central European perspective (Reiter et al. 2010a), showed a continuation of its expansion to the north: the species appeared as a new faunal element in northern Austria and in the south-eastern Czech Republic. Reiter et al. (2010a) suggested that the individuals appear-ing in the latter areas were most probably of Alpine origin, whereas the individuals recorded in Hungary originated from the Adriatic populations.

Here, we present a review of the current state of the species' geographical range in Central and south-eastern Europe, as comprehensive as possible, and discuss the level and causality of changes in the species' range in these regions as recorded in the last 20 years.

METHODS

Geographical coverage

We focused on the central and south-eastern parts of Europe, including the territories of Austria, Bavaria (Germany), Czech Republic, Slovakia, Hungary, Poland, Ukraine, Romania, Bulgaria, Slovenia, Croatia, Serbia, Macedonia, Bosnia and Herzegovina, and Montenegro. Geographically, the targeted area covers the eastern Alps, the whole Carpathians, Bohemian Massif, Dinaric Mountains, the Pannonian lowland and the Crimea.

Data collection

Original findings, collection data and published records of *Hypsugo savii* from the target countries were gathered (see Appendix S1). In the field, original data were collected by inspections of roosts, mist-netting and recording of echolo-cation calls. Accidental findings of bats were also included. The echolocation calls were detected using portable bat detectors (Pettersson D220, D240x, D980, Pettersson Elektronik, Sweden; Tranquility Transect, Courtpan Design, UK; Batlogger, Elekon, Switzerland); some of them were recorded in time-expansion mode and subsequently analysed (using BatSound, Pettersson Elektronik, Sweden; BatExplorer, Elekon, Switzerland). The echolocation calls were identified based on the species' characteristics available from its European range (Russo & Jones 2002, Papadatou et al. 2008).

Beside the standard faunistic information (site, date, number of bats, method of data collection, for details see Appendix S1), all records were also defined by a general description of the habitat, as natural (sites with more or less natural conditions without any urbanized areas), park (sites in an urbanized area, usually with a significant proportion of vegetation cover and without higher buildings, e.g. city parks or gardens), urban (sites situated in almost com-pletely urbanized areas of large towns and usually with higher buildings), or unknown (no habitat data available). For sites in natural, urban and park habitats, the average latitude of the records for each year was calculated. Using a generalized linear model with quasi-Poisson distribution, interaction effects of the year, latitude and habitat category were calculated in R (Anonymous 2014). Effects for habitat–latitude–year interactions were visualised using the package 'effects' (Fox 2003).

RESULTS AND DISCUSSION

Altogether, we gathered 1187 records of *Hypsugo savii* (Table 1, Appendix S1) from the geographical area under consideration. The development of the known range in six subsequent periods is shown in cumulative maps (Fig. 1); the country accounts of the *Hypsugo savii* records are given below in a south to north arrangement.

Bulgaria

Although the first record of *Hypsugo savii* in Bulgaria was from the Black Sea shore in 1926 (Beron 1961), the species was not considered a regular member of the Bulgarian

Table 1. Review of *Hypsugo savii* records in central and southern parts of Europe. Records are expressed as a number of database items, countries are arranged in geographical order from south to north

		Habitat type				Type of records					
Country	First reported appearance	Natural	Park	Urban	Unknown	Detected/ Radiotracked bats	Found/ observed bats	Netted/ captured bats	Unknown	Σ	%
Bulgaria	1926	87		25	2	13	10	70	21	114	9.6
Macedonia	1938	8	8	1		9		7	1	17	1.4
Serbia	1981	57	4	17		42	13	22	1	78	6.6
Montenegro	1923	12	3	3	2	8	3	9		20	1.7
Croatia	1894	42	4	5	7	15	8	28	7	58	4.9
Bosnia and Herzegovina	1925	4				2		1	1	4	0.3
Romania	1899	20	6	5	1	23	5	4		32	2.7
Hungary	1991	7	21	76	2	67	16	23		106	8.9
Slovenia	1939	74	26	88	1	140	24	13	12	189	15.9
Austria	c. 1860	52	93	251	8	341	55	4	4	404	34.0
Germany: Bavaria	before WWII	2	2	3	1	3	4		1	8	0.7
Slovakia	2005	10	19	92		85	29	7		121	10.2
Ukraine: Crimea	1926	7	1	1	2	5		4	2	11	0.9
Ukraine: Carpathian region	2009	2	2	5		9				9	0.8
Czech Republic	2001		3	11	1	4	10	1		15	1.3
Poland	2013		1				1			1	0.1
Σ		384	193	583	27	766	178	193	50	1187	
%		32.4	16.3	49.1	2.3	64.5	15.0	16.3	4.2		

fauna for rather a long time (Benda et al. 2003). The first finding of the species from Bulgaria was followed by several records made in the 1970s and 1980s (Benda et al. 2003), confirming its occurrence in the southern and central parts of the country. These records revealed *Hypsugo savii* as rather a common species in rocky areas of the country (76% of the records came from natural habitats). After 1991, new records came from the Danubian lowland (Pandurska & Beshkov 1998); the northernmost known site was near Nišovo in 1999 (Benda et al. 2003). Only a few recent records are available from Bulgaria (e.g. Tilova et al. 2005, Stoycheva et al. 2009). These data do not suggest any con-siderable range modification; however, some of them indi-cate the regular occurrence of the species in larger towns (Plovdiv, Stara Zagora).

Macedonia

Although only a few dispersed records are available from Macedonia, for a long time the whole country has been considered a part of *Hypsugo savii's* range (Kryštufek et al. 1992, 1998, Stojanovski 1994). The northernmost and first known record from the country was from Skopje in 1985 (Kryštufek et al. 1992) and a stable population of *Hypsugo savii* was documented via recordings of its echolocation calls in this town in 2013 (Micevski et al. 2014).

Serbia

The first findings of *Hypsugo savii* were from two sites (Petrlaška Pec´ina Cave, Žagubica) in the eastern part of Serbia in 1981 (Petrovic´ 1983, Miric´ & Paunovic´ 1995), situated near the sites known from neighbouring Bulgaria (Benda et al. 2003). The first record in Belgrade is from 1994. Since then, numerous new sites have been gradually recorded throughout Serbia, particularly in 2010–2013 (Paunovic´ et al. 2015), when more systematic acoustic surveys were carried out. A significant number of records come from Vojvodina (southern Pannonia). Of the total of 84 records, most were from water bodies and in farmland (35%), while 21% of the records were from urban areas (Paunovic´ et al. 2015). Reproduction of the species was proved by findings of pregnant or lactating females. Single hibernating specimens were found in crevices of buildings. In general, the occurrence of *Hypsugo savii* was documented from the whole country with the exception of the southern-most parts, where bat surveys were carried out only occasionally.

Montenegro

The oldest record of *Hypsugo savii* from this country was from Cetinje in 1923 (Horác˘ek & Benda 2004). Based on further records from 1997 to 2013, the species seems to be widespread in the western part of the country (Presetnik et al. 2014a). There is no evidence of changes in local populations of the species, but knowledge is very limited; only 20 records are known. *Hypsugo savii* was found in Montenegro at altitudes of up to 1750 m above sea level.

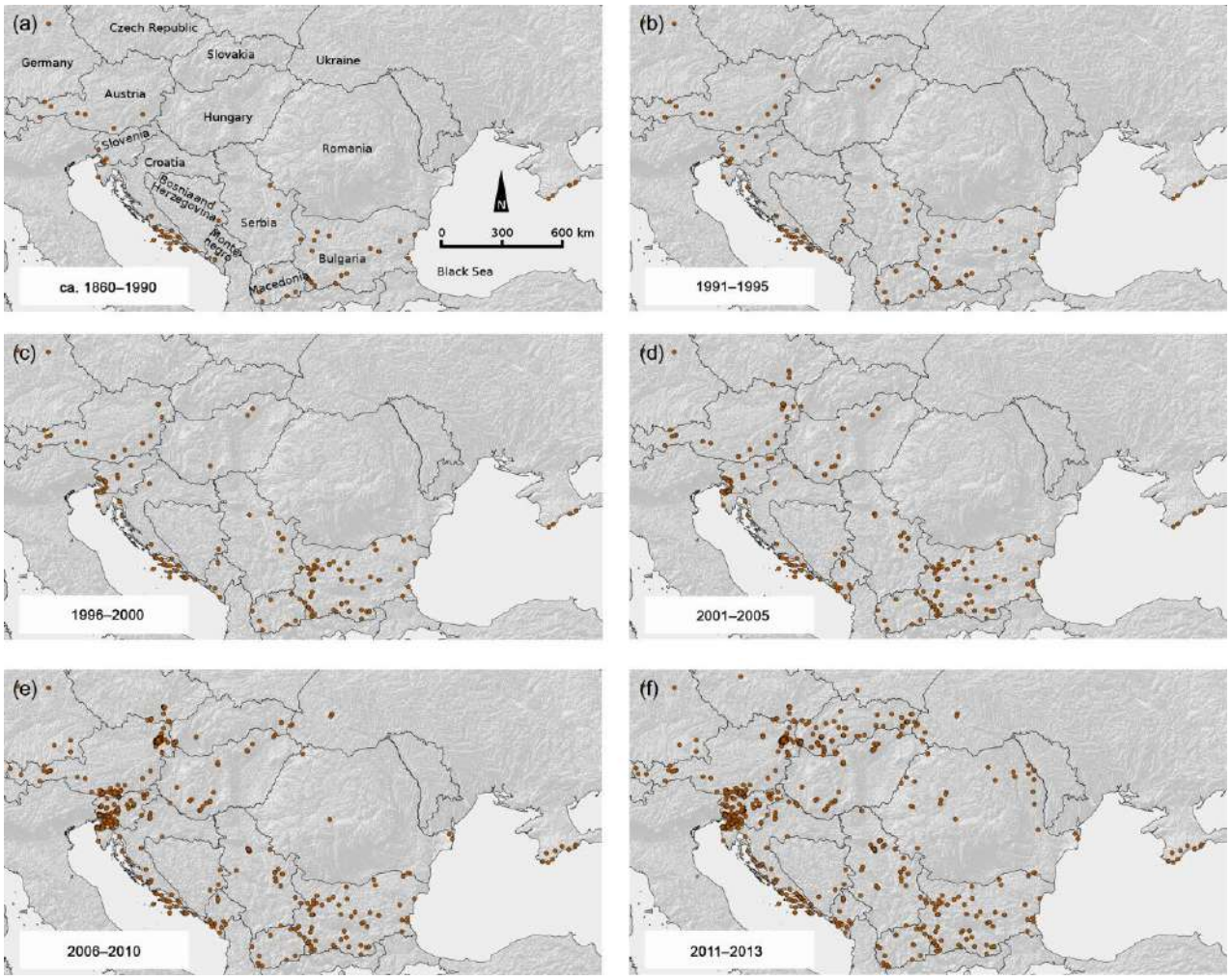


Fig. 1. Maps of cumulative records of *Hypsugo savii* (dots) in southern and central parts of Europe in six periods from c. 1860 until the end of 2013.

Croatia

Until 2000, *Hypsugo savii* was known from Croatia exclusively from the Dalmatian shore including several islands (Wettstein 1919, Djulic´ 1959, Dulic´ 1970, Cˇ ervený & Kryštufek 1988, Horácˇek & Benda 2004). Rovinj was then the northernmost known Croatian locality (Dulic´ & Mrakovcˇic´ 1984). This picture of occurrence was later supplemented with further records (Zagmajster et al. 2007). In the region of the Adriatic coast, regular reproduction of the species was confirmed (Kipson et al. 2014). *Hypsugo savii* was the most commonly caught bat in the Paklenica National Park in 2008–2013 (Kovacˇ et al. 2010, original records) This National Park is characterized by rocky habi-tats rising from the sea level up to an altitude of 1757 m. In 2010–2012, the species was recorded for the first time in the continental part of Croatia, in Zagreb and its surroundings (120 km from the sea coast). By the end of 2012, the northernmost record of *Hypsugo savii* from the country was from the Drava River at the border with Hungary (220 km from the coast). The Zagreb localities geographically correspond with the Slovenian records from Brežice (found by the first bat detector inventory in 2008), and the records docu-mented along the Drava River are situated just between the localities of *Hypsugo savii* in eastern Slovenia (Spodnji Cvetkovci, 2011) and southern Hungary (Pécs, 2001). The majority of the Croatian records come from natural habitats (72%).

Bosnia and Herzegovina

One of the oldest records of *Hypsugo savii* from southern parts of Europe is from eastern Bosnia from 1925 (Bolkay 1926). However, information on bat distribution in Bosnia and Herzegovina is very limited (Kotrošan et al. 2005), and almost no current data on this bat species are available.

Recently, only three other records have been reported from the southern part of the country (Miljevina, Podvelež; Ciechanowski et al. 2005, Presetnik et al. 2014b). All known sites of *Hypsugo savii* occurrence in Bosnia and Herzegovina are situated in the southern sub-Mediterranean part of the country, but almost no research was carried out in the other parts.

Romania

The first record of *Hypsugo savii* in Romania was from Bazias¸ (Banat) in 1899 (Méhely 1900), although it was originally reported as *Eptesicus nilssonii* (Topál 1959). The subsequent Romanian record was obtained almost a century later, when Ra˘dulet (1996) reported a finding in southern Dobrogea (Ba˘neasa) in 1993. Based on records of echolocation calls, the species was registered for the first time in the Danube Delta in 2007 (Pocora & Pocora 2008). Since 2009, mostly via the use of bat detectors, more than 20 sites of the species' occurrence have been recorded in various regions within the Carpathian mountain range (original data) and also in Moldavia (Prut River catchment, Pocora & Pocora 2011). The most recent and the northern-most locality for *Hypsugo savii* in Romania (Satu Mare) is situated in an urban environment. The majority of the Romanian records (63%) represent findings from natural habitats. The record of *Hypsugo savii* from Ros¸ia Montana˘ (Murariu & Pop 2011) seems to be erroneous; judging from published photographs of the bat, the specimen is a juvenile *Myotis myotis* or *Myotis blythii*.

Hungary

In Hungary, *Hypsugo savii* was recorded for the first time in 1991; this record could be considered either as evidence of possible expansion of the range of *Hypsugo savii* or as a consequence of previously low bat research effort in the country. The species was at that time recorded in the north of the country, only 30 km south of the Slovakian border (Miskolc; Dobrosi 1994). Another record appeared close to the urban area of Eger in 1994 (Estók 1995). Several other records originating mostly from larger towns were docu-mented subsequently (Budapest, Kaposvár, Pécs, Szekszárd). *Hypsugo savii* seems to be a widespread, but rare bat species in Hungary (Estók et al. 2007). It has been found all over the country, but most of the available records come from settlements and their surroundings. In total, 72% of the Hungarian records were reported from urban habitats (Dombi & Somogyvári 2003, Szatyor et al. 2003, Görföl et al. 2007). Reproduction of the species was confirmed by findings of maternity roosts in two towns in southern Hungary (Bonyhád, Szekszárd).

Slovenia

Several older records of *Hypsugo savii* were reported from Slovenia before World War II and later in 1977 and 1984 (Gulino & Dal Piaz 1939, Kryštufek 1984, Spitzenberger & Mayer 1988); all of them originate from the south-western part of the country (Gorica, C˘ rni Kal, Škocjanske jame Cave). Since 1990, the number of records has increased con-tinuously; the first finding in the east-central part of Slove-nia was made in 1992 (Velenje), later records came from Ljubljana in 1995 (Kryštufek & Donev 2005, Presetnik et al. 2009). Geographically, these sites lie between the known *Hypsugo savii* localities on the Adriatic Sea coast and those in Carinthia and Styria (Austria). After 2006, methodologi-cally adequate bat studies started in central, eastern and northern Slovenia; however, no convincing evidence of changes in the geographical range of *Hypsugo savii* is avail-able from these regions. Currently, the species is rather common in Ljubljana (Presetnik et al. 2009). Sites with *Hypsugo savii* made up approximately 6% of all bat sites recorded in the city, based mainly on incidentally obtained data and on a few unsystematic ultrasound surveys (Presetnik 2010). A systematic ultrasound survey in the northern part of Ljubljana in 2011 revealed that 21% of all bats detected were *Hypsugo savii* (original records). Gener-ally, the species is present almost all over the country; the most abundant occurrence is known from the sub-Mediterranean region close to the sea shore. Several sites with maternity roosts and/or pregnant or lactating females are known from the country. Near the sea coast, *Hypsugo savii* was discovered to roost in natural cliff crevices.

Austria

Several historical records of *Hypsugo savii* from Austria are available from the Alpine habitats of Tyrol and Salzburg, which were obtained in the period of c. 1840–1880 (Blasius 1857, von Dalla Torre 1887). During most of the 20th century, the range of *Hypsugo savii* in Austria was limited to Carinthia, where the first recent record was from Klagenfurt in 1985 (Spitzenberger & Mayer 1988). Several additional records also derive from this region (Spitzenberger 1995, 2001). After 1995, new records appeared in Styria and in Vienna, lying in the south-eastern and north-eastern parts of the country (Freitag 1996, Spitzenberger 1997). These findings were the first records interpreted as a new expan-sion of the species' range and not as documentation of its regular occurrence (Spitzenberger 1997). The most impor-tant data supporting this opinion came from Vienna, where no records were documented before 1988, despite a rather intensive and long-term bat survey (Spitzenberger 1990). In the period 1990–2010, the species' occurrence was recorded regularly in this large city (Hüttmeir et al. 2010, Reiter et al.

2010a, original records). Carinthia and Tyrol are areas included in the continuous range of *Hypsugo savii* delin-eated in 2000 (Horácˇek & Benda 2004), while the findings in Lower Austria and Vienna were new discoveries. At present, the species regularly occurs in three parts of Austria, in Carinthia in the south, in Styria, Lower Austria and Vienna in the east, and in Tyrol and Vorarlberg in the west (Walder & Vorauer 2011, Dobner et al. 2013).

Germany (Bavaria)

Although a possible record of *Hypsugo savii* from Bavaria was mentioned in literature dating from before World War II (Issel et al. 1978), a small maternity colony was reported from the Alps (Kahmann 1958) and some other sites were recorded (Meschede & von Helversen 2004), the latter authors considered the species to be locally extinct. However, just a few years later, a finding of one bat and several bat detector observations indicated possible re-colonisation of southern Bavaria (Meschede & Rudolph 2010).

Slovakia

Although the whole territory of Slovakia is situated com-pletely outside the previously acknowledged range of *Hypsugo savii* in Europe (Horácˇek & Benda 2004), an old published record of this species from Slovakia is available (Babor 1943). However, this record is considered doubtful, and is not clear evidence of the species' occurrence (Lehotská et al. 2012). The first appropriately documented record from Slovakia was from Bratislava in 2005 (Lehotská & Lehotský 2006); however, this city lies only 50 km east of Vienna (Austria) where an abundant population was estab-lished in the 1990s at the latest. Further records of *Hypsugo savii* were from towns situated in the western and eastern parts of the country (Bratislava, Nitra, Michalovce), adja-cent to Austrian and Hungarian occurrence localities. Evi-dence of reproduction was recorded in eastern Slovakia (Danko 2007). In 2013, an acoustic survey was performed in Slovakia, covering the whole territory of the country includ-ing urban, forest and agricultural landscape types. Results of this survey indicated presence of the species in most of the larger towns (Cel'uch et al. 2015); thus, the majority of Slovakian records (76%) come from urban habitats. In con-clusion, *Hypsugo savii* currently inhabits almost the entire territory of Slovakia with the exception of its northern part.

Ukraine (Crimea)

Hypsugo savii is known to occur only in the southern part of the peninsula, on the southern slopes of the Krimskye gory Mountains (Crimean Mountains; Dulickij & Kovalenko 2003, Bashta 2009); however, a special survey focused on the species' occurrence in towns along the sea coast has not been made. A rather common occurrence of the species in these mountains was documented in 2009 (Uhrin et al. 2009), but no data on possible range changes or even shifts northwards to the lowland steppe habitats are available.

Ukraine (Carpathian region)

Until the end of the 1990s, *Hypsugo savii* was reported to be a rare species in Ukraine (Bashta 2009), having been recorded in the Crimea only. Through the use of bat detec-tors, *Hypsugo savii* calls were first recorded in this region at eight sites in 2009–2013. This suggests the presence of *Hypsugo savii* in and around settlements of various sizes (Mukacˇeve, Užgorod; Bashta 2012). Since all the available data on the occurrence of *Hypsugo savii* in western Ukraine consist of records of echolocation calls, the actual occu-pancy of this region should be confirmed by a finding of an individual, by mist-netting for example.

Czech Republic

The first record of *Hypsugo savii* in the Czech Republic was from Žabcˇice in southern Moravia, in 2001 (Gaisler 2001). The site lies at the westernmost edge of Pannonia, near the Austrian border (80 km north of Vienna). In 2003–2013, 12 other findings originating mostly from urban habitats were reported (Brˇeclav, Brno, Znojmo). The presence of breeding females was recorded several times (Gaisler & Vlašín 2003, Bartonicˇka & Kaňuch 2006, Reiter et al. 2010b). These records indicate the successful establishment of resident populations of *Hypsugo savii* in the south-eastern Czech Republic, which originate from and are probably connected with the populations of Lower Austria. The latest record from Prague (an adult male found in December 2013; Jahelková et al. 2014) represents surprising new evidence of a possible further shift of the known range of *Hypsugo savii* to central Bohemia. Previous occurrence of the species in Prague is very unlikely considering the rather extensive bat research carried out there between 1955 and 2009 (Hanák et al. 2009). The record from Prague represents the north-ernmost known occurrence of this species within the Central European range.

Poland

Despite the geographical proximity of the known breeding sites in the Czech Republic and Slovakia (Danko 2007, Reiter et al. 2010b), *Hypsugo savii* had not been recorded in Poland until 2013 (Pucek & Raczyn´ ski 1983, Sachanowicz et al. 2006a). There are two older reports of individuals sup-posedly representing this species found in Wrocław (south

west Poland; Schlott 1932, 1942). The first specimen, collected in 1931, was later identified as *Vespertilio murinus* (Kock & Bogdanowicz 1998). For the second record made in 1939, no details were provided (Schlott 1942); however, its identification remains doubtful, particularly in the light of the previous misidentification. The first confirmed record of *Hypsugo savii* in Poland is of an adult individual found during daytime at a building in the western Carpathians in 2013. Circumstances of the finding (the condition of the bat and the fact that the site was located near a truck base) suggest passive transport of the bat, e.g. in a truck load (see Fisher 1998); however, natural appearance of this bat cannot be excluded, as the locality lies only 90 km north of the nearest site of this species in Slovakia. The natural pres-ence of *Hypsugo savii* in southern Poland, particularly in the Carpathians, seems to be very likely and may be confirmed in the near future.

GENERAL SYNOPSIS

A considerable shift of the northern margin of the geographical range has been documented in Europe for many animal species, mostly those able to fly or make long-distance movements, such as insects, birds and mammals (Krištín et al. 2007, Balbontín et al. 2008, Drees et al. 2011, Arnold et al. 2012, Caravaggi et al. 2014). Based on several studies, it is believed that such shifts are connected with climate changes, and that such patterns in species' ranges follow poleward range shifts (Parmesan et al. 1999, Battisti et al. 2005, Hellmann et al. 2008, Moreno-Rueda et al. 2012).

Similar range changes were also reported in bats. Lundy et al. (2010) suggested that *Pipistrellus nathusii*, known as a mobile and migratory species, adapted its range size in response to recent climate change. The margin of its range in Great Britain shifted considerably northwards between 1940 and 2006, and the pattern of this shift coincides well with the pattern of the climatic changes observed on the island. Two Mediterranean bat species, *Pipistrellus kuhlii* and *Hypsugo savii*, expanded from their original core area of distribution in the thermo-Mediterranean zone of southern Europe towards the north. In the case of *Pipistrellus kuhlii*, scarce data were published from various parts of its Euro-pean range (Strelkov et al. 1985, Bauer 1996, Paunovic´ & Marinkovic´ 1998, Cel'uch & Ševc˘ík 2006, Sachanowicz et al. 2006b, Popczyk et al. 2008, Chis¸amera & Murariu 2009, Wawrocka et al. 2012). A range expansion of *Hypsugo savii* was suggested to have occurred already in the early 1990s, based on records from north-eastern Austria (Spitzenberger 1997). This suggestion was supported by results of an analy-sis from the Central European perspective (Reiter et al. 2010a). Here we provide a detailed review of geographical patterns in the range changes of *Hypsugo savii*, based on all records available by the end of 2013. The temporal distribu-tion of the records clearly shows a relatively fast expansion of the species to Central Europe. Originally, this species was distributed in a limited range along the Dalmatian coast, Macedonia, and Greece, and reaching the Black Sea coast in Bulgaria. However, in the less studied regions (Balkans and Pannonia), adequate surveys were not carried out until after 2000. Therefore, we cannot compare the currently known range with the range before 1990.

A gradual data accumulation in 5-year periods (Fig. 1) shows a considerable enlargement of the original range of *Hypsugo savii* and a shift of its northern margin by almost 800 km northwards (from the Dalmatian coast to southern Poland). Until 1990 (Fig. 1a), the northernmost sites of the species were known from Carinthia and Styria (Austria; Spitzenberger 2001) and its presence was already recorded in central-eastern Serbia at the western edge of the Southern Carpathians (Miric´ & Paunovic´ 1995), where also a single record was known from Romania (Topál 1959). However, due to the lack of data, we cannot show that the populations from Serbia and Austria were already in contact along the Sava and Danube rivers and their tributaries.

We can suppose that the expansion wave of *Hypsugo savii* to Central Europe started just before 1990. Already in 1991, *Hypsugo savii* was found in north-eastern Hungary close to the Slovakian border (Dobrosi 1994), and these sites (Miskolc and Eger) lie approximately 300 km from the closest records made in the same period (Fig. 1b), in Bel-grade (Serbia) and Vienna (Austria). Therefore, we can assume that the Serbian, Hungarian, and Lower Austrian populations were at that time in contact across the Pannonian plains and the surrounding Dinaric, Carpathian, and Alpine mountains. However, considering the well-documented bat research tradition in Vienna (Spitzenberger 1990), *Hypsugo savii* may indeed have represented a new species for the area in the early 1990s.

In the period 1995–2000 (Fig. 1c), new records were reported from the central Alps, where *Hypsugo savii* appeared at sites north of its historical range in Tyrol (Blasius 1857). New findings were made also in north-eastern Hungary (Görföl et al. 2010), central Serbia and eastern Austria (Reiter et al. 2010a). In the subsequent 5-year period (2001–2005, Fig. 1d), more records were made in these countries, supplemented by records from Slo-venia. Undeniable new evidence of *Hypsugo savii*'s range expansion appeared, when this species was found for the first time in the Czech Republic and in Slovakia (Gaisler 2001, Lehotská & Lehotský 2006); its known occurrence in these countries is restricted to large towns (Gaisler & Vlašín 2003, Lehotská 2006a, Reiter et al. 2010a).

With increasing effort in field surveys in 2005–2010 (Fig. 1e), the species was for the first time documented in the Romanian section of the Carpathians. The species'

echolocation calls were also detected for the first time north and east of the Carpathian range, and *Hypsugo savii* first appeared in the Carpathian part of Ukraine and in the Romanian part of the Danube Delta (Pocora & Pocora 2008, 2011, Bashta 2012); further records were reported also from Bavaria (Meschede & Rudolph 2010). In this period, *Hypsugo savii* was found to be widespread throughout Slo-venia, northern Croatia, Serbia, Slovakia, and Romania. During the last period (2011–2013), when research intensi-fied, the species' spread to the north continued and the first records in Poland and Bohemia were documented (Fig. 1f). The data further indicate that *Hypsugo savii* is widespread along all sea shores in the region under consideration, and that the Balkan populations could be connected with those of the Crimea (Ukraine).

During the last 20 years, the northern margin of the geographical range of *Hypsugo savii* in Central and Eastern Europe has shifted approximately to the latitude of 50° N, where the northernmost known record sites are currently situated (central Bohemia, southern Poland). However, there are some regions within the range (north-eastern Romania, western Ukraine, parts of Slovakia) where only echolocation data are available, so the species' occurrence still remains to be confirmed by collection of a specimen or a roost finding. Such evidence is needed because the ranges of call parameters of *Hypsugo savii* may overlap partially with those of *Pipistrellus kuhlii* (Dietz & Kiefer 2014), and therefore, some of the acoustic identifications could actually represent *Pipistrellus kuhlii*.

In Western Europe, including Germany, no extensive range change has been observed similar to that in south-eastern Europe. Nevertheless, *Hypsugo savii* has been newly recorded in various parts of Germany (Lehmann & Engemann 2007, Adorf & Starrach 2010, Skiba 2010). Some of these records were based on acoustic recordings only and thus, as stated earlier, should be interpreted with caution. The species was even recorded in Great Britain and the Channel Islands (Hudson 1993, Fisher 1998), although the records are considered to represent human-mediated move-ments and not evidence of natural range expansion. Only a few records were reported from sites situated in the western and northern parts of Europe, viz. Wallasey and Wick (Great Britain; Fisher 1998) or Neustadt and Hamburg (Germany; Ohlendorf et al. 2000, Katzenstein 2000). These records were from sites associated with sea coasts or even large harbours, and thus, transport by ship from southern European towns is likely. Further field survey is necessary to confirm whether *Hypsugo savii* has been able to establish stable populations in any of these areas. Human-mediated dispersal is, perhaps surprisingly, a considerable agent of change in species' ranges (e.g. Kaňuch et al. 2012).

Three hypotheses could be applied to explain the range expansion by *Hypsugo savii* documented here. The northward shift in range limits could be 1) connected to general environmental changes caused by the current climate change; 2) evidence of an intrinsic expansion process powered by the species' synanthropisation and ongoing urbanisation, including passive transport by humans; or 3) a reflection of the increase in field survey effort made in the relevant countries. The documented course of the range development rather conforms to the models calculated for several bat species in Europe. Rebelo et al. (2010) predicted future changes in the geographical ranges of several bat species in response to climate change in the next tens of years; however, their projections varied considerably under different climate change scenarios. The greatest increase in the geographical range area in all the scenarios used was predicted for *Hypsugo savii*. Although it was not modelled here, our data correspond well with the models proposed. There is currently no evidence of any decrease or contrac-tion in the geographical range of *Hypsugo savii* in the Medi-terranean, as was modelled for metapopulations under climate change (Anderson et al. 2009, Drees et al. 2011). Such metapopulations are expected to shift faster on the northern range margin (leading edge) and in contrast, they are expected to respond to climate change more slowly on the southern range margin (trailing edge).

We stress that the enlargement of the range of *Hypsugo savii* could be undoubtedly confirmed only for the Central European countries (Austria, Bavaria, Hungary, Slovakia, Czech Republic). In the southern and eastern European countries, there was an enormous increase in the numbers of researchers involved in bat surveys in the late 1990s, and acoustic mapping methods started to be used commonly after 2005. These aspects led to an increase in the number of *Hypsugo savii* findings in these countries. Older local reports focused mainly on cave-dwelling bat species, and consideration of changes in *Hypsugo savii* distribution over a longer time scale is almost impossible.

Two-thirds (65%) of the records evaluated from the whole area of Central and south-eastern Europe originate from urban habitats, from both park (16%) and completely urbanised (49%) habitats (Table 1, Fig. 2). This suggests that hypothesis 2, concerning synanthropisation as a driver for the northwards shift of the species' range limit, is the most plausible. This view is supported by the model of interactions year–latitude–habitat based on the data gath-ered here (Table 2); this model explained 91% of data vari-ability. While no pattern of changes in natural habitat could be observed in terms of time course and latitude, in both urbanised habitats (park and urban), the number of records seems to be increasing within the time course and with increasing latitude (Fig. 3). It seems that the spreading process followed the occupation of towns and, despite its original preference for rocky habitats, *Hypsugo savii* is cur-rently fully adapted to urban conditions and expands to the

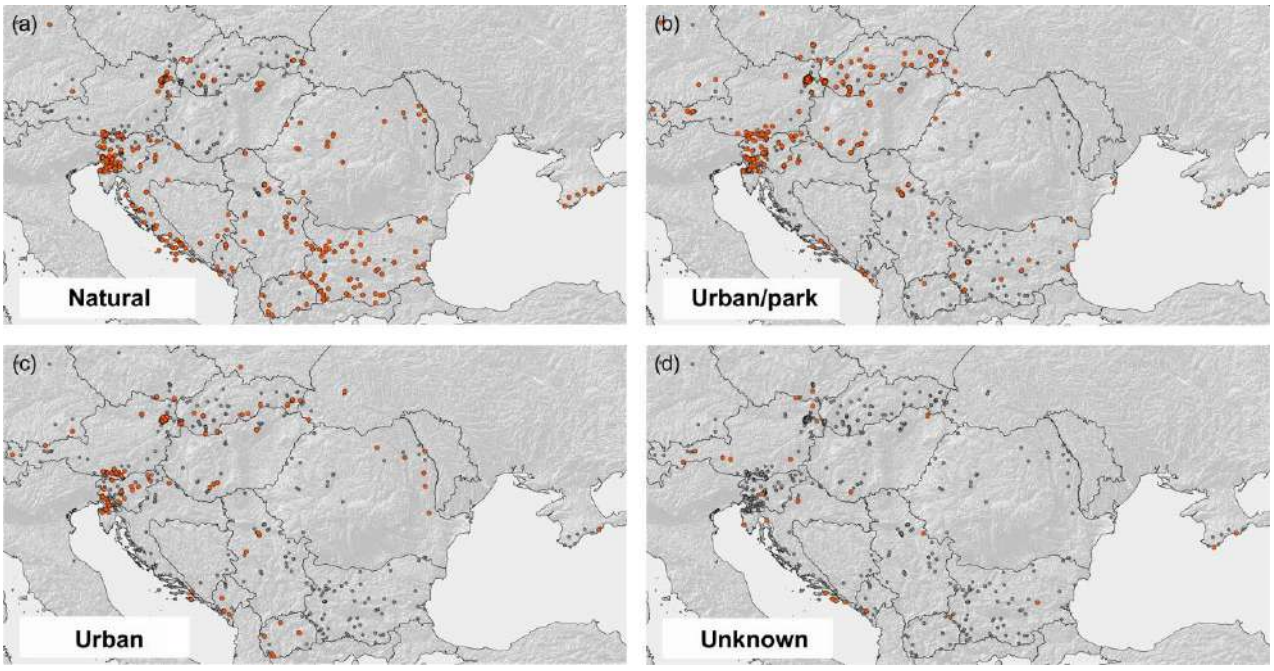


Fig. 2. Map of records of *Hypsugo savii* in southern and central parts of Europe in different habitats (larger red dots). Smaller grey dots denote all other records.

north via roosting in built-up areas. Good evidence of such roost occupation by *Hypsugo savii* comes from large towns (Bratislava, Brno, Prague, Vienna), where the former absence of the species is undoubtedly well documented by previous surveys (Gaisler 1979, Spitzenberger 1990, Gaisler et al. 1998, Lehotská 2006b, Hanák et al. 2009). On the other hand, the chance of finding small bats is considerably higher in settlements than in open fields.

The affinity to synanthropy in *Hypsugo savii*, originally a strictly Mediterranean species, seems to be a natural phenomenon. This bat is a frequently documented forager in urban habitats, performing its flights in edge areas of large towns (Russo & Ancillotto 2014). This could be an essential ground for the successive expansion northwards to the cli-matically less suitable parts of Europe. However, the use of urban environments is not a new habit in this species, which was frequently documented to roost in towns also in Mediterranean and sub-Mediterranean zones (Dulic´ 1970, Vernier 1995). The species occupies fissures and crevices in buildings, as do other petrophilous species with affinities to synanthropy, such as *Pipistrellus kuhlii*, *Nyctalus noctula*, *Vespertilio murinus*, and *Plecotus* spp. In all these taxa, which include not only typically Mediterranean species, range expansion northwards has also been suggested (Bogdanowicz 2004, Horác˘ek & Benda 2004, Sachanowicz et al. 2006b).

The pattern of the current distribution of *Hypsugo savii* in Central Europe (Fig. 4) is now similar to the ranges of several true Mediterranean faunal elements among bats, which reached Central Europe in the past, particularly *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Myotis blythii*, and *Myotis emarginatus*. While these taxa colonised the northern parts of Pannonia thanks to their ability to roost in caves in winter, in combination with their tendency to create maternity colonies in large attics, *Hypsugo savii* (and perhaps also *Pipistrellus kuhlii*) spread probably due to its ability to use the high concrete blocks of flats that were built in Central Europe in the last few decades. These build-ings were inhabited during the expansion wave some 20–50 years after their construction. Towns with such roost types should be treated as 'inland islands' because their environ-ments differ considerably from the surroundings (Marzluff et al. 2008), and these species can use such 'islands' to occupy new areas. This mechanism is probably the main prerequisite for the range expansion of *Hypsugo savii*.

Based on the data we collected, we can conclude that various reasons for range changes in *Hypsugo savii* should be considered. At least for some areas in southern Europe (the Balkans and Pannonia), the increase in the number of *Hypsugo savii* records may reflect an increase in systematic survey effort, rather than a real range expansion. In con-trast, in Central European countries, the range expansion of *Hypsugo savii* seems to be a real and natural process. This conclusion is supported by the fact that traditional bat research carried out in almost all of these countries in the past resulted in repeatedly confirmed absence of *Hypsugo*

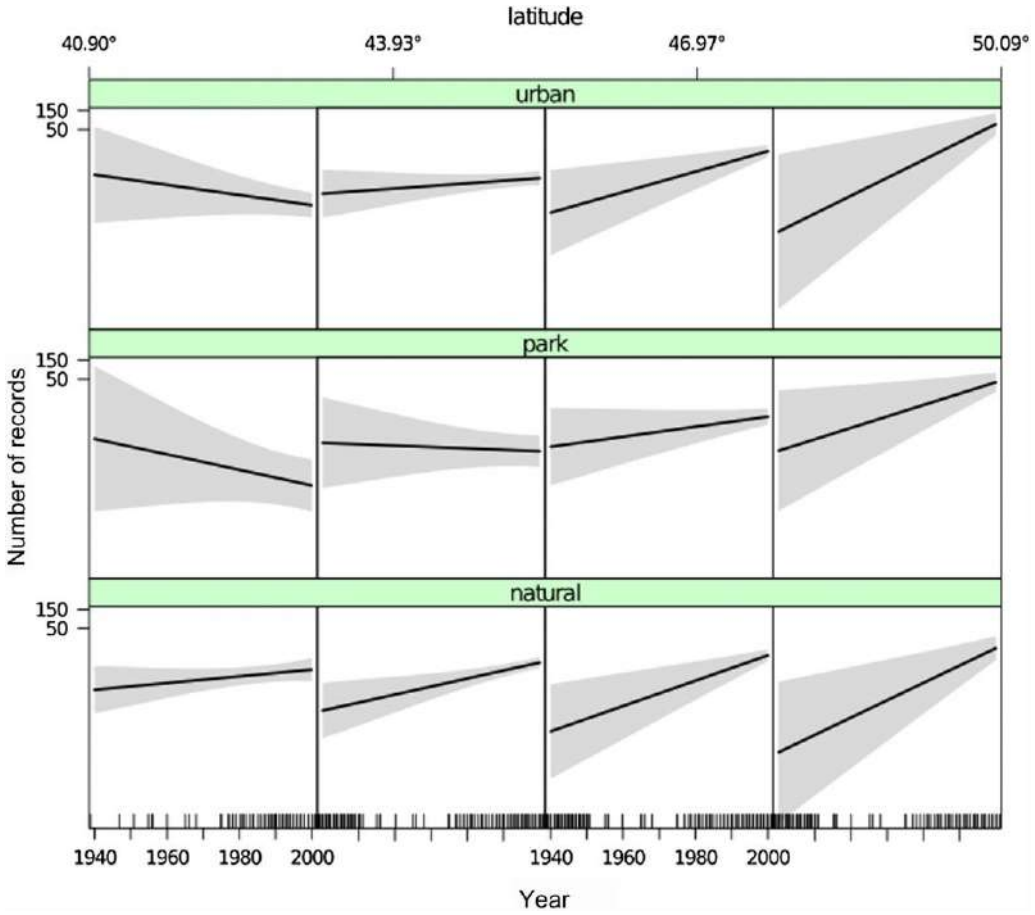


Fig. 3. Effects of interactions between year, habitat category and latitude on the number of records of *Hypsugo savii* in Central and south-eastern Europe. The *y* axis is on a log scale; models are visualised using four representative latitudes.

savii, before the current expansion wave appeared. Based on the data we present, it is difficult to determine whether climate change or synanthropisation tendencies enabled the range expansion of *Hypsugo savii*. Therefore, we suggest that further monitoring and specifically focused research activi-ties should be intensified.

ACKNOWLEDGEMENTS

The research was supported by grants from the Cultural and Educational Grant Agency (KEGA # 012UPJŠ-4/2014) of the Ministry of Education, Science Research and Sport of the Slovak Republic, and from the Ministry of Culture, Czech Republic (DKRVO 2015/14, 00023272). Data from eastern Romania were gathered within the CNCSIS-UEFISCSU (PN II-RU PD – 326/2010) project, funded by the Romanian Education and Research Office, investigations in western Ukraine were partly supported by the Darwin Initiative within the project 'Monitoring biodiversity indica-tors through volunteer networks across Eurasia' (# EIDP036). We thank Beata Kaczmarczyk and Maciej Fik for providing photos of the bat from Juszczyn and details of its

Table 2. Results of the generalized linear model analysis of interaction effects of year, latitude and habitat (natural, park, urban) category within the set of data on *Hypsugo savii's* range expansion in Central and south-eastern Europe

Category	d.f.	Deviance residuals	d.f. residuals	Deviation	*P*
Null			91	2111.85	
Year	1	1169.69	90	942.16	<0.001***
Latitude	1	354.78	89	587.38	<0.001***
Habitat	2	152.07	87	435.32	<0.001***
Year : latitude	1	105.18	86	330.14	<0.001***
Year : habitat	2	24.44	84	305.69	0.017*
Latitude : habitat	2	102.58	82	203.11	<0.001***
Year : latitude : habitat	2	2.60	80	200.52	0.649

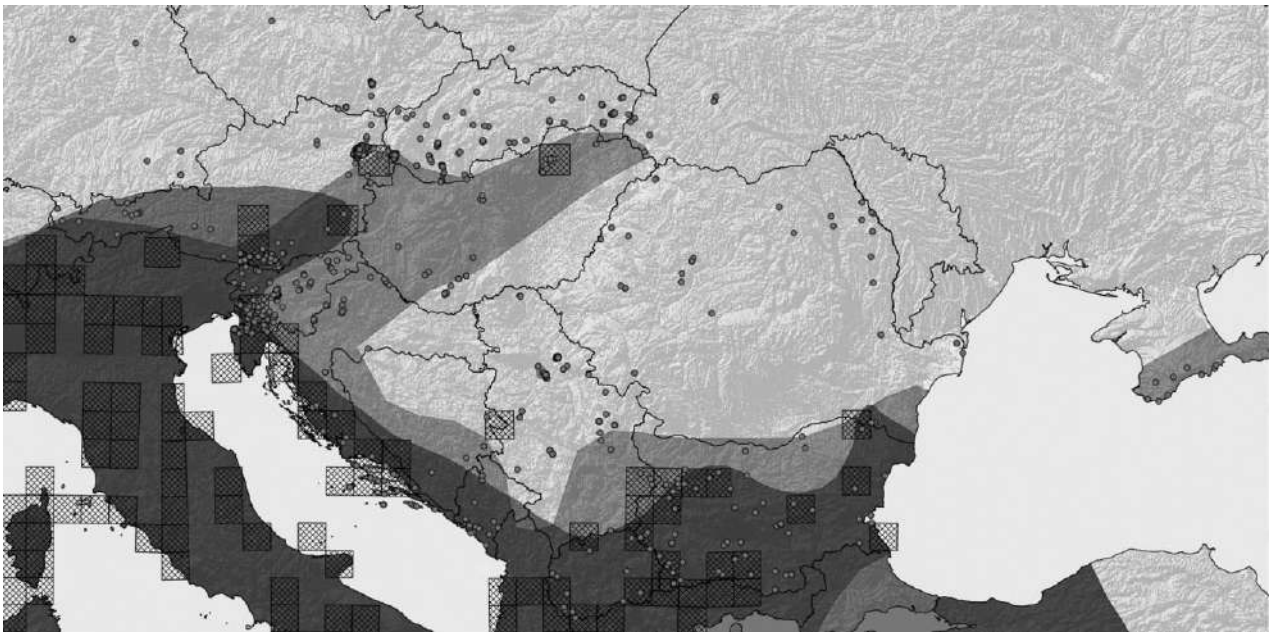


Fig. 4. Map of the development of assumptions about the delimitation of *Hypsugo savii*'s range in southern and central parts of Europe. Legend: diagonal hatched squares – *The Atlas of European Mammals* (Mitchell-Jones et al. 1999), dark grey area – *Handbuch der Säugetiere Europas* (Horáčˇek & Benda 2004), pale grey area – *The IUCN Red List of Threatened Species* (Hutson et al. 2008); grey dots – all records available by the end of 2013 (this study).

finding, and Štefan Danko, Martin Cel'uch, Michal Rendoš, Martin Ševcˇík, Marina Đurovic´, Ilhan Dervovic´, Tarik Dervovic´, Jasminko Mulaomerovic´, Maja Cipot, Valentina Inkret, Andrej Kapla, Brina Knez, Lea Likozar, Roman Maurer, Jana Mlakar, Alenka Petrinjak, Monika Podgorelec, Veronika Ramovš, Marjetka Šemr, David Stankovic´, Aja Zamolo, and Simon Zidar for their help in the field or for providing their original unpublished data.

REFERENCES

Adorf F, Starrach M (2010) Neue bioakustische Nachweise der Alpenfledermaus, *Hypsugo savii* (Bonaparte, 1837), und des Riesenabendseglers, *Nyctalus lasiopterus* (Schreber, 1780), aus der Bundesrepublik – eine kritische Betrachtung mit Anmerkungen zur artspezifischen Dispersionsdynamik. *Nyctalus (N. F.)* 15: 171–179.

Anderson BJ, Akçakaya HR, Araújo MB, Fordham DA, Martinez-Meyer E, Thuiller W et al. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B* 276: 1415–1420.

Anonymous (2014) *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

Arnold J, Humer A, Heltai M, Murariu D, Spassov N, Hackländer K (2012) Current status and distribution of golden jackals *Canis aureus* in Europe. *Mammal Review* 42: 1–11.

Babor JF (1943) *Slovenská fauna*, Vydanie Slovenskej akadémie vied a umení, Bratislava, Slovakia.

Balbontín J, Negro JJ, Sarasola JH, Ferrero JJ, Rivera D (2008) Land-use changes may explain the recent range expansion of the black-shouldered kite *Elanus caeruleus* in southern Europe. *Ibis* 150: 707–716.

Bartonicˇka T, Kanˇuch P (2006) Savi's pipistrelle (*Hypsugo savii*): bat species breeding in the Czech Republic (Chiroptera: Vespertilionidae). *Lynx, n. s.* 37: 19–21.

Bashta A-T (2009) Survey of current state and distribution of bats (Chiroptera) in Ukraine. *Studia chiropterologica* 6: 43–79.

Bashta A-T (2012) *Hypsugo savii* Bonaparte, 1856 (Chiroptera: Vespertilionidae) – novij vid fauni rukokrilich Karpatskogo regionu (Ukraina). *Naukovij visnik Užgorodskogo universitetu, Seria Biologija* 33: 195–197.

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A et al. (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* 15: 2084–2096.

Bauer K (1996) Ausbreitung der Weißrandfledermaus *Pipistrellus kuhlii* (Kuhl, 1819) in Österreich (Chiroptera, Vespertilionidae). *Mitteilungen der Abteilung für Zoologie am Landesmuseum Joanneum in Graz* 50: 17–24.

Benda P, Ivanova T, Horáčˇek I, Cˇervený J, Gaisler J, Gueorguieva A et al. (2003) Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 3. Review of bat distribution in Bulgaria. *Acta Societatis Zoologicae Bohemicae* 67: 245–357.

Beron P (1961) Contribution a la connaissance des chauves-souris Bulgares. *Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium* 3: 189–195.

Blasius JH (1857) *Naturgeschichte der Säugethiere Deutschlands und der angrenzenden Ländern von Mitteleuropa*, Druck und Verlag von Friedrich Vieweg und Sohn, Braunschweig, Germany.

Bogdanowicz W (2004) *Pipistrellus kuhlii* (Kuhl, 1817) – Weißrandfledermaus. In: Krapp F (ed) *Handbuch der Säugetiere Europas. Band 4/II: Fledertiere. Teil II: Chiroptera II. Vespertilionidae 2, Molossidae, Nycteridae*, 876–908. AULA-Verlag, Wiebelsheim, Germany.

Bolkay SJ (1926) Additions to the mammalian fauna of the Balkan peninsula. *Glasnik zemaljskog muzeja u Bosni i Hercegovini* 38: 159–180.

Caravaggi A, Montgomery WI, Reid N (2014) Range expansion and comparative habitat use of insular, congeneric lagomorphs: invasive European hares *Lepus europaeus* and endemic Irish hares *Lepus timidus hibernicus*. *Biological Invasions* 17: 687–698.

Cel'uch M, Ševc˘ík M (2006) First record of *Pipistrellus kuhlii* (Chiroptera) from Slovakia. *Biologia* 61: 637–638.

Cel'uch M, Uhrin M, Bac˘kor P, Ševc˘ík M (2015) Prvé výsledky monitoringu netopierov pomocou autotransektov na Slovensku. *Vespertilio* 18: in press.

Chis¸amera G, Murariu D (2009) New records of Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817) (Chiroptera: Vespertilionidae) and its present range in Romania. *Studia Chiropterologica* 6: 81–87.

Ciechanowski M, Sachanowicz K, Rachwald A, Benda P (2005) First records of *Tadarida teniotis* (Rafinesque, 1814) (Chiroptera, Molossidae) from Serbia and Montenegro and from Bosnia and Herzegovina. *Mammalia* 69: 257–260.

C˘ervený J, Kryštufek B (1988) A contribution to the knowledge of the bats of Central and Southern Dalmatia, Yugoslavia (Chiroptera, Mammalia). *Biološki vestnik* 36: 17–30.

Danko Š (2007) Reprodukcia *Hypsugo savii* a *Pipistrellus kuhlii* na východnom Slovensku: d'alšie dôkazy o ich šírení na sever. *Vespertilio* 11: 13–24.

Dietz C, Kiefer A (2014) *Die Fledermäuse Europas. Kennen, bestimmen, schützen*, Franckh-Kosmos Verlags GmbH, Stuttgart, Germany.

Dietz C, von Helversen O, Nill D (2007) *Handbuch der Fledermäuse Europas und Nordwestafrikas. Biologie, Kenzeichen, Gefährdung*, Franckh-Kosmos Verlags GmbH & Co. KG, Stuttgart, Germany.

Djulic´ B (1959) Beitrag zur Kenntnis der geographischen Verbreitung der Chiropteren Kroatiens. *Glasnik prirodna˘ckog muzeja/Bulletin du Muséum d'Histoire Naturelle* 14B: 67–112.

Dobner M, Vorauer A, Walder C (2013) Fledermäuse in ausgewählten Wäldern Vorarlbergs/Österreich: Habitatpräferenzen und Charakterisierung der Fledermausfauna. *inatura – Forschung online* 4: 19.

Dobrosi D (1994) Adatok a Bükk denevérfaunájához. *Folia historico naturalia musei Matraensis* 18: 191–197.

Dombi I, Somogyvári O (2003) Szekszárd, a ritka denevérek hazája. *Paeonia* 2003: 103–106.

Drees C, Brandmayr P, Buse J, Dieker P, Gurlich S, Habel J et al. (2011) Poleward range expansion without a southern contraction in the ground beetle *Agonum viridicupreum* (Coleoptera, Carabidae). *Zookeys* 100: 333–352.

Dulickij AI, Kovalenko IS (2003) Materialy po rukokrylym Kryma v zoologic˘eskich sobranijach Ukrainy i Rossii. *Voprosy razvitija Kryma* 15: 197–210.

Dulic´ B (1970) Ökologische Beobachtungen der Fledermäuse der Adriatischen Inseln. *Zeitschrift für Säugetierkunde* 35: 45–51.

Dulic´ B, Mrakovc˘ic´ M (1984) Morphological characteristics of a population of *Pipistrellus savii* from some Adriatic Islands. *Myotis* 22: 83–85.

Estók P (1995) Az alpesi denevér (*Pipistrellus savii*) újabb magyarországi megkerülése. *Denevérkutatás* 1: 18.

Estók P, Görföl T, Szatyor M (2007) Alpesi denevér *Hypsugo savii* (Bonaparte, 1837). In: Bihari Z, Csorba G, Heltai M (eds) *Magyarország emlöseinek atlasza*, 103–104. Kossuth Kiadó, Budapest, Hungary.

Fisher C (1998) Savi's pipistrelle *Pipistrellus savii* in Britain. *Myotis* 36: 77–81.

Fox J (2003) Effect displays in R for generalised linear models. *Journal of Statistical Software* 8: 1–27.

Freitag B (1996) *Pipistrellus savii* (Bonaparte, 1837) – Erstnachweis fur die Steiermark (Mammalia, Chiroptera). *Mitteilungen des Naturwissenschaftlicher Vereins für Steiermark* 125: 237–238.

Gaisler J (1979) Results of bat census in a town (Mammalia: Chiroptera). *V˘estník Československé spole˘cnosti zoologické* 43: 7–21.

Gaisler J (2001) A mammal species new to the Czech Republic – Savi's pipistrelle *Hypsugo savii*. *Folia zoologica* 50: 231–233.

Gaisler J, Vlašín M (2003) Second record of Savi's pipistrelle (*Hypsugo savii*) in the Czech Republic. *Vespertilio* 7: 181–182.

Gaisler J, Zukal J, R˘ehák Z, Homolka M (1998) Habitat preference and flight activity of bats in a city. *Journal of Zoology* 244: 439–445.

Görföl T, Dombi I, Zsebök S (2007) Az alpesi denevér (*Hypsugo savii* Bonaparte, 1837) Magyarországon – a faj hazai adatainak áttekintése, új eredmények. In: Molnár V (ed) *Az V. Magyar denevérvédelmi konferencia (Pécs, 2005. december 3–4.) és a VI. Magyar denevérvédelmi konferencia (Mártély, 2007. október 12–14.) kiadványa*, 85–97. Csemete Természet- és Környezetvédelmi Egyesület, Szeged, Hungary.

Gulino G, Dal Piaz G (1939) I Chirotteri Italiani. *Bollettino dei Musei di Zoologia e Anatomia comparata* 47: 61–103.

Hanák V, Neckár˘ová J, Benda P, Hanzal V, Ande˘ra M, Horác˘ek I et al. (2009) Fauna netopýru˚ Prahy: pr˘ehled nálezu˚ a poznámky k urbánním populacím netopýru˚. *Natura Pragensis* 19: 3–89.

Hellmann JJ, Pelini SL, Prior KM, Dzurisin JDK (2008) The response of two butterfly species to climatic variation at the edge of their range and the implications for poleward range shifts. *Oecologia* 157: 583–592.

Horáčˇek I, Benda P (2004) *Hypsugo savii* (Bonaparte, 1837) – Alpenfledermaus. In: Krapp F (ed) *Handbuch der Säugetiere Europas. Band 4/II: Fledertiere. Teil II: Chiroptera II. Vespertilionidae 2, Molossidae, Nycteridae*, 912–941. AULA-Verlag, Wiebelsheim, Germany.

Horáčˇek I, Hanák V, Gaisler J (2000) Bats of the Palearctic region: a taxonomic and biogeographic review. In: Wołoszyn BW (ed) *Proceedings of the VIIIth EBRS Vol. 1, Approaches to biogeography and ecology of bats*, 11–157. Chiropterological Information Center & Institute of Systematics and Evolution of Animals PAS, Kraków, Poland.

Hudson AM (1993) The British record of Savi's pipistrelle *Pipistrellus savii*. *Bat News* 30: 6.

Hutson AM, Spitzenberger F, Juste J, Aulagnier S, Palmeirim JM, Paunovic´ M et al. (2008) *Pipistrellus savii*. In: IUCN (ed) The IUCN Red List of Threatened Species. Version 2014.3. http://www.iucnredlist.org.

Hüttmeir U, Bürger K, Wegleitner S, Reiter G (2010) *Ergänzende Erhebungen und Einschätzung des Erhaltungszustandes der Fledermäuse in Wien. Endbericht*, Umweltschutzabteilung der Stadt Wien, Wien, Austria.

Issel B, Issel W, Mastaller M (1978) Zur Verbreitung und Lebenweise der Fledermäuse in Bayern. *Myotis* 15: 19–97.

Jahelková H, Neckářˇová J, Bláhová A, Sasínková M, Weinfurtová D, Hybnerová Z et al. (2014) First record of *Hypsugo savii* in Prague and summary of winter records of *Pipistrellus nathusii* from Prague and close surroundings (Czech Republic). *Vespertilio* 17: 95–101.

Kahmann H (1958) Die Alpenfledermaus, *Pipistrellus savii* Bonaparte, 1837 in den Bayrischen Alpen, und biometrische Mitteilungen über die Art. *Zoologischer Anzeiger* 160: 87–94.

Kanˇuch P, Berggren Å, Cassel-Lundhagen A (2012) Colonization history of *Metrioptera roeselii* in northern Europe indicates human-mediated dispersal. *Journal of Biogeography* 40: 977–987.

Katzenstein H (2000) Nachweis einer Alpenfledermaus (*Hypsugo savii*) in Ostholstein. *Nyctalus (N. F.)* 7: 453–454.

Kipson M, Šálek M, Lucˇan RK, Bartonicˇka T, Miková E, Uhrin M et al. (2014) The curious case of Savi's pipistrelle, *Hypsugo savii*: new insight on roosting ecology and behaviour from the Mediterranean region. In: Hutson AM, Lina PHC (eds) *XIIIth European Bat Research Symposium. 1–5 September 2014 Šibenik, Croatia. Book of abstracts*, 91. Croatian Biospeleological Society & HINUS Ltd., Zagreb, Croatia.

Kock D, Bogdanowicz W (1998) Eine historische Fledermaus-Sammlung aus dem südlichen Polen (Mammalia: Chiroptera). *Senckenbergiana biologica* 77: 123–126.

Kotrošan D, Bjedov V, Kryštufek B (2005) Stanje istraženosti faune sisara Bosne i Hercegovine. *Radovi šumarskog fakulteta Univerziteta u Sarajevu* 1: 29–55.

Kovacˇ D, Drdar Ž, Randi D, Josic´ D, Hamidovic´ D (2010) Bat fauna research of Paklenica National Park with special emphasis on altitude distribution. In: Horáčˇek I, Benda P (eds) *15th International Bat Research Conference – the conference manual. Programme, abstracts, list of participants. Prague, 23–27 august 2010,* 197. Praha, Poland.

Krištín A, Kanˇuch P, Sárossy M (2007) Did the northern range of distribution of two tropical orthopterans (Insecta) change recently? *Polish Journal of Ecology* 55: 297–304.

Kryštufek B (1984) Novi in redki netopirji (Chiroptera, Mammalia) v favni Slovenije. *Biološki vestnik* 32: 45–54.

Kryštufek B, Donev NR (2005) The atlas of Slovenian bats (Chiroptera). Atlas netopirjev Slovenije (Chiroptera). *Scopolia* 55: 1–92.

Kryštufek B, Vohralík V, Flousek J, Petkovski S (1992) Bats (Mammalia: Chiroptera) of Macedonia, Yugoslavia. In: Horáčˇek I, Vohralík V (eds) *Prague Studies in Mammalogy*, 93–111. Charles University Press, Prague, Poland.

Kryštufek B, Petkovski S, Košelj K (1998) Additions to bat fauna of Macedonia (Chiroptera, Mammalia). *Folia zoologica* 47: 237–239.

Lehmann B, Engemann C (2007) Nachweis einer Alpenfledermus (*Hypsugo savii*) als Schlagopfer in einem Windpark in Sachsen-Anhalt. *Nyctalus (N. F.)* 12: 128–130.

Lehotská B (2006a) Druhý nález vecˇernice Saviho (*Hypsugo savii*) na Slovensku. *Vespertilio* 9–10: 225–226.

Lehotská B (2006b) Netopiere (Chiroptera) urbanizovaného prostredia Bratislavy. *Acta Environmentalica Universitatis Comenianae* 14: 55–63.

Lehotská B, Lehotský R (2006) First record of *Hypsugo savii* (Chiroptera) in Slovakia. *Biologia* 61: 192.

Lehotská B, Lehotský R, Cel'uch M, Ševcˇík M (2012) Vecˇernica Saviho – *Hypsugo savii*. In: Krištofík J, Danko Š (eds) *Cicavce Slovenska. Rozšírenie, bionómia a ochrana*, 403–405. Veda, Bratislava, Slovakia.

Lundy M, Montgomery I, Russ J (2010) Climate change-linked range expansion of Nathusius' pipistrelle bat, *Pipistrellus nathusii* (Keyserling & Blasius, 1839). *Journal of Biogeography* 37: 2232–2242.

Marzluff JM, Shulenberger E, Endlicher W, Alberti M, Bradley G, Ryan C et al. (2008) *Urban Ecology. An International Perspective on the Interaction between Humans and Nature*, Springer Science & Business Media, New York, USA.

Méhely L (1900) *Magyarország denevéreinek monographiája*,A Magyar Tudományos Akadémia támogatásával kiadja a Magyar Nemzeti Múzeum, Budapest, Hungary.

Meschede A, Rudolph B-U (2010) *1985–2009: Fledermausmonitoring in Bayern, 94*, Byerisches Landesamt für Umwelt, Augsburg, Germany.

Meschede A, von Helversen O (2004) Alpenfledermaus *Hypsugo savii* (Bonaparte, 1837). In: Meschede A, Rudolph B-U (eds) *Fledermäuse in Bayern*, 294–295. Ulmer Verlag, Stuttgart, Germany.

Micevski N, Presetnik P, Micevski B, Cel'uch M (2014) Contribution to knowledge about Macedonian bat fauna. *Vespertilio* 17: 103–114.

Miric´ D, Paunovic´ M (1995) Novi nalaz planinskog slepog miša *Pipistrellus savii* (Bonaparte, 1837) (Chiroptera, Mammalia) u Srbiji. *Zbornik radova, Naša ekološka istina '95', II-17, Borsko jezero*, 367–370.

Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F et al. (1999) *The Atlas of European Mammals*, 496. Academic Press, London, UK.

Moreno-Rueda G, Pleguezuelos JM, Pizarro M, Montori A (2012) Northward shifts of the distributions of Spanish reptiles in association with climate change. *Conservation Biology* 26: 278–283.

Murariu D, Pop DA (2011) Observations on the bat fauna (Mammalia: Chiroptera) of Ros¸iu Montanaˇ (Romania). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* 54: 529–540.

Ohlendorf B, Vierhaus H, Heddergott M, Bodino F (2000) Korrektur: Fund einer Nordfledermaus (*Eptesicus nilssoni*) im Hamburg (ds. Z. Bd. 5, p. 220) betraf eine Alpenfledermaus (*Hypsugo savii*). *Nyctalus (N. F.)* 7: 454.

Pandurska RS, Beshkov VA (1998) Species diversity of bats in underground roosts of the Western Stara Planina Mts. (Bulgaria). *Vespertilio* 3: 81–91.

Papadatou E, Butlin R, Altringham JD (2008) Identification of bat species in Greece from their echolocation calls. *Acta Chiropterologica* 10: 127–143.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579–583.

Paunovic´ M, Marinkovic´ S (1998) Kuhl's pipistrelle *Pipistrellus kuhlii* Kuhl, 1817 (Chiroptera, Vespertilionidae) – a new species in the mammal fauna of Serbia, with data on its Balkan distribution range, status and ecology. *Proceedings of the fauna of Serbia, Natural and mathematical sciences* 5: 167–180.

Paunovic´ M, Karapandža B, Budinski I, Jovanovic´ J (2015) New records of the Savi's pipistrelle *Hypsugo savii* (Bonaparte, 1837) (Chiroptera, Mammalia) from Serbia: an evidence for the expansion of its geographical range. *Acta Zoologica Bulgarica* 67: 389–397.

Petrovic´ P (1983) Nova vrsta sisara za faunu SR Srbije – Savijev netopir *Pipistrellus savii* Bonaparte, 1837 (Chiroptera, Mammalia). In: Anonymous (ed) *Zbornik radova o fauni SR Srbije, knjiga 2*, 263–266. SANU, Belgrade, Serbia.

Pocora I, Pocora V (2008) Abundance and habitat use of bat (Chiroptera) species in the Letea Forest area (Danube Delta). *Scientific Annals of the Danube Delta Institute* 14: 57–64.

Pocora I, Pocora V (2011) The use by bats (Chiroptera: Vespertilionida) of various habitat types in Moldova and the Danube delta (Romania). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* 54: 223–242.

Popczyk B, Lesin´ ski G, Baumann A, Wojtowicz BW (2008) Kuhl's pipistrelle, *Pipistrellus kuhlii* (Kuhl, 1817) or *Pipistrellus lepidus* Blyth, 1845, in Central Poland – accidental records or a result of expansion? *Nyctalus (N. F.)* 13: 279–281.

Presetnik P (2010) Netopirji v Ljubljani – kratko godrnjanje o raziskanosti znotraj kroga Ljubljanskih obvoznic. *Glej, netopir!* 7: 21–26.

Presetnik P, Koselj K, Zagmajster M (2009) Atlas netopirjev (Chiroptera) Slovenije. Atlas of bats (Chiroptera) of Slovenia, 152. Center za kartografijo favne in flore, Miklavž na Dravskem polju.

Presetnik P, Paunovic´ M, Karapandža B, Đurovic´ M, Ivanovic´ Cˇ, Ždralevic´ M et al. (2014a) Bats (Mammalia: Chiroptera) of Montenegro. *Vespertilio* 17: 129–156.

Presetnik P, Mulaomerovic´ J, Dervovic´ T (2014b) First confirmation of Rhinolophus blasii in Bosnia and Herzegovina and its possible maternity roost. In: Hutson AM, Lina PHC (eds) *XIIIth European Bat Research Symposium. 1–5 September 2014 Šibenik, Croatia*. Book of abstracts, 136. Croatian Biospeleological Society & HINUS Ltd., Zagreb, Croatia.

Pucek Z, Raczyn´ ski J (1983) *Atlas rozmieszczenia ssaków w Polsce. Atlas of Polish mammals, 188&183*, Pan´ stwowe Wydawnictwo Naukowe, Warszawa, Poland.

Raˇdulet N (1996) *Pipistrellus savii* (Bonaparte, 1837) (Chiroptera: Vespertilionidae) signalé pour la premiére fois en Roumanie. *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* 36: 385–389.

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology* 16: 561–576.

Reiter A, Bartonicˇka T, Lucˇan RK, Rˇ ehák Z (2010a) New records of *Hypsugo savii* in the Czech Republic. *Vespertilio* 13–14: 121–125.

Reiter G, Wegleitner S, Hüttmeir U, Pollheimer M (2010b) Die Alpenfledermaus, *Hypsugo savii* (Bonaparte, 1837), in Mitteleuropa. *Nyctalus (N. F.)* 15: 158–170.

Russo D, Ancillotto L (2014) Sensitivity of bats to urbanization: a review. *Mammalian Biology* 80: 205–212.

Russo D, Jones G (2002) Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology* 258: 91–103.

Sachanowicz K, Ciechanowski M, Piksa K (2006a) Distribution patterns, species richness and status of bats in Poland. *Vespertilio* 9–10: 151–173.

Sachanowicz K, Wower A, Bashta A-T (2006b) Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe. *Acta Chiropterologica* 8: 543–548.

Schlott M (1932) *Pipistrellus savii* Bonaparte aus Deutschland. *Zeitschrift für Säugetierkunde* 7: 263.

Schlott M (1942) Zur Kenntnis heimischer Fledermäuse. *Der Zoologische Garten (N.F.)* 14: 35–48.

Skiba R (2010) Alpenfledermaus (*Hypsugo savii*) in Wuppertal – Zunahme der Fledermäuse in Norddeutschland? *Nyctalus (N. F.)* 15: 154–157.

Spitzenberger F (1990) *Die Fledermäuse Wiens*, J&V Edition Wien Verlags GmbH., Wien, Austria.

Spitzenberger F (1995) Die Säugetiere Kärntens. Teil I. *Carinthia II* 185(105): 247–352.

Spitzenberger F (1997) Distribution and range expansion of Savi's bat (*Hypsugo savii*) in Austria. *Zeitschrift für Säugetierkunde* 62: 179–181.

Spitzenberger F (2001) Alpenfledermaus *Hypsugo savii* (Bonaparte, 1837). In: Spitzenberger F (ed) *Die Säugetierfauna Österreichs*, 249–252. Bundesministerium für Land- und Fortswirthschaft Umwelt und Wasserwirtschaft, Graz, Austria.

Spitzenberger F, Mayer A (1988) Aktueller Stand der Kenntnis der Fledermausfauna Osttirols und Kärntens, zugleich Mammalia austriaca 14 (*Myotis capaccinii* Bonaparte, 1837, *Pipistrellus kuhli* Kuhl, 1819 und *Pipistrellus savii* Bonaparte, 1837). *Annalen des Naturhistorischen Museums in Wien* 90B: 69–91.

Stojanovski L (1994) Prilog kon poznavaneto na liljacite (Chiroptera, Mammalia) na Makedonija. *Ekologija i zaštita na životnata sredina* 2: 59–62.

Stoycheva S, Georgiev D, Pandourski I, Tilova E (2009) Bat diversity in two large towns of the Upper Thrace, Bulgaria (Chiroptera). *Lynx, n. s.* 40: 83–93.

Strelkov PP, Unkurova VI, Medvedeva GA (1985) Novye dannye o netopyre Kulâ (*Pipistrellus kuhlii*) i dinamika ego areala v SSSR. *Zoologiˇceskij Žurnal* 64: 87–97.

Szatyor M, Estók P, Dombi I, Somogyvári O (2003) Ritka denevérfajok (Chiroptera) újabb elöfordulásai Magyarországon. *Állattani Közlemények* 88: 69–72.

Tilova EK, Stoycheva SB, Georgiev DG (2005) New information on the distribution of some bat species (Mammalia: Chiroptera) from Bulgaria. *Animalia* 41: 135–144.

Topál G (1959) Két ritka denevérfaj a Kárpátmedence faunájában. *Vertebrata Hungarica* 1: 89–103.

Uhrin M, Gazaryan S, Benda P (2009) Does *Tadarida teniotis* really occur in Crimea? (Chiroptera: Molossidae). *Lynx, n. s.* 40: 115–126.

von Dalla Torre KW (1887) Die Säugethierfauna von Tirol und Vorarlberg. *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck* 17: 103–164.

Vernier E (1995) Presence and distribution of bats in the town of Padova (N. E. Italy). *Myotis* 32–33: 193–195.

Walder C, Vorauer A (2011) *Die Fledermäuse Tirols*, Amt der Tiroler Landesregierung, Abteilung Umweltschutz, Innsbruck, Austria.

Wawrocka K, Bartonicˇka T, Reiter A (2012) *Pipistrellus kuhlii*,a bat species breeding and hibernating in the Czech Republic. *Vespertilio* 16: 351–356.

Wettstein O (1919) Beiträge zur Kenntnis der Fauna Dalmatiens. II Säugetiere. *Zoologische Jahrbücher: Abteilung für Systematik, Geographie und Biologie der Tiere* 42: 192–194.

Zagmajster M, Jancar T, Mlakar J (2007) First records of dead bats (Chiroptera) from wind farms in Croatia. *Nyctalus (N. F.)* 12: 234–237.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Appendix S1. List of records of *Hypsugo savii* in central and southern parts of Europe.

Paper 3

Kipson, M., Šálek, M., Lučan, R., Uhrin, M., Maxinová, E., Bartoničkа, T., Andreas, M., Kipson, K., Pušić, A., Rnjak, D., Ňado, L. and Horáček, I. (2018) 'Foraging habitat, home-range size and diet of a Mediterranean bat species, Savi's pipistrelle', *Acta Chiropterologica*, 20(2), pp. 351–360. Available at:

https://doi.org/10.3161/15081109ACC2018.20.2.007

Acta Chiropterologica, 20(2): 351–360, 2018
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2018.20.2.007

Foraging habitat, home-range size and diet of a Mediterranean bat species, Savi's pipistrelle

MARINA KIPSON[1, 11], MARTIN ŠÁLEK[2, 3], RADEK LUČAN[1], MARCEL UHRIN[4], EDITA MAXINOVÁ[4], TOMÁŠ BARTONIČKA[5], MICHAL ANDREAS[6], KAROLINA KIPSON[7], ANA PUŠIĆ[8], DINA RNJAK[9], LADISLAV NAĎO[10], and IVAN HORÁČEK[1]

[1]*Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Prague, Czech Republic*
[2]*The Czech Academy of Sciences, Institute of Vertebrate Biology, Květná 8, 603 65 Brno, Czech Republic*
[3]*Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, Suchdol, 16521 Prague, Czech Republic*
[4]*Department of Zoology, Faculty of Science, P. J. Šafárik University in Košice, Moyzesova 11, 04001 Košice, Slovakia*
[5]*Department of Botany and Zoology, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic*
[6]*Department of Biology, Faculty of Science, University of Hradec Králové, Rokitanského 62, 50003 Hradec Králové, Czech Republic*
[7]*Brace Oruzec 20, 10360 Sesvete, Zagreb, Croatia*
[8]*Primorska 12, 10000 Zagreb, Croatia*
[9]*Geonatura Ltd. Consultancy in Nature Protection, Fallerovo šetalište 22, Zagreb, Croatia*
[10]*Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, 960 53 Zvolen, Slovakia*
[11]*Corresponding author: E-mail: marinakipson@gmail.com*

The Mediterranean is considered one of the richest biodiversity regions in Europe, and bats contribute to this species richness. Within the last two decades, certain bat species traditionally considered as representatives of the Mediterranean have spread northwards and colonized areas outside this region. In our study, we focused on ecological requirements of one of these bat species, the Savi's pipistrelle (*Hypsugo savii*). We used radio-telemetry and diet analysis to describe habitat use, home-range size and diet composition of reproductive females of Savi's pipistrelle in the traditional core of its distribution range in the Mediterranean region. Our results indicate that Savi's pipistrelle is able to fly long distances and utilize a wide range of habitats within its home-range, with affinities for particular habitats depending on its reproductive status. In particular, pregnant females favoured rocky pastures and forest areas, followed by meadows and riparian habitat, whereas the affinity for riparian habitat increased in lactating females, followed closely by meadows, forest and rocky pastures. The larger affinity for riparian habitats during lactation might indicate its importance for successful rearing of young, which could be influenced in the future by increasing droughts and water shortage in the Mediterranean region. Nevertheless, based on our radio-telemetry and diet analysis the species shows a high degree of flexibility, as an opportunistic forager that flies across large areas on a nightly basis, which may be a good predisposition for colonizing new areas.

Key words: Chiroptera, Mediterranean region, habitat affinity, *Hypsugo savii*, reproductive status, riparian vegetation, radio-telemetry

INTRODUCTION

Anthropogenic habitat modifications in synergy with global climate change are predicted to be the main forces that will cause dramatic biodiversity changes within this century (Sala *et al*., 2000) and specific adaptive rearrangements in the species will persist (Klausmeyer and Shaw, 2009). The Mediterranean, in particular, is predicted to be one of the most affected ecosystems in terms of biodiversity loss (Sala *et al*., 2000). At the same time, Mediterranean countries harbor the peak diversity of bats in Europe (Ulrich *et al*., 2007), an animal group essential to healthy ecosystems (Jones *et al*., 2009), and providing beneficial ecosystem services (Kunz *et al*., 2011). Diversity of bats and inter-species differences in foraging strategy, habitat requirements and roosting biology make them a suitable model group for detailed analyses of the effects of environmental changes (Kunz and Fenton, 2003). Similarly, empirical studies demonstrate that bats react more sensitively than other groups to both land-use (Mickleburgh *et al*., 2002) and climatic change (Sherwin *et al*., 2013). Furthermore, there is clear evidence that certain Mediterranean bat species have undergone a rapid northward expansion

during recent decades (Spitzenberger, 1997; Danko, 2007; Reiter *et al*., 2010; Uhrin *et al*., 2016). Identification of intrinsic factors promoting range expansion in these species can thus contribute to a better comprehension of changes to the ecosystem. However, more detailed information on the biology of bats in the Mediterranean region is urgently needed.

An important aspect of bat biology is habitat preference (Kunz and Fenton, 2003), which can change during the different stages of the reproductive cycle. In the semi-arid Mediterranean region, water resources and riparian habitats with an abundance of insects (Wenninger and Inouye, 2008) present attractive foraging grounds for bats (Zahn and Maier, 1997; di Salvo *et al*., 2009). Moreover, the affinity of bats in the Mediterranean to water resources is further increased due to a dramatic drop in atmospheric humidity during hot summer months. This causes higher evaporative loss in bats (Webb *et al*., 1995), which forces them to rebalance water loss by direct intake through drinking (McLean and Speakman, 1999).Water consumption can increase during gravidity-lactation with lactating females having higher daily rates of water exchange than non-reproductive females (Adams *et al*., 2008). In extreme cases, severe droughts can even cause a disruption in the reproductive cycle of female bats (Amorim *et al*., 2015). Therefore, water and riparian habitats in the Mediterranean can be crucial factors in determining habitat preferences, roost selection and movements of individual bat species (Salsamendi *et al*., 2012).

From 2012 to 2014 we conducted a systematic field study of one of the least studied European bat species, Savi's pipistrelle (*Hypsugo savii*) to investigate its ecology. The species has been long considered as typical representative of the Mediterranean fauna with its original European range almost strictly delimited by the northern margin of the Mediterranean region (Horáček and Benda, 2004). During the last 20 years the distributional range of this species expanded northwards to the area north of the Alps (Spitzenberger, 1997; Danko, 2007; Reiter *et al*., 2010). This shift is usually attributed to the combination of temperature increase and the species' flexibility to colonize urban habitats (Uhrin *et al*., 2016). Although the species originally roosted in rock crevices, its capacity to roost alternatively in human-made structures was recorded for the first time in the middle of the last century (Đulić, 1958) and more recently most of the roosting data comes from urban environments (Vernier, 1995; Freitag, 1996; Benda *et al*., 2006, 2007; Stoycheva *et al*., 2009). Based on acoustic survey studies conducted within the Mediterranean region Savi's pipistrelle is often regarded as a common species, with most of its activity records coming from a close proximity to water bodies (Russo and Jones, 2002; di Salvo *et al*., 2009; Hintze *et al*., 2016), and/or from urbanized areas (Russo and Ancillotto, 2014). Nevertheless, detailed information on habitat use in Savi's pipistrelle are not common.

In this study we provide the first data on habitat affinity, home-range size and diet composition of reproductive females of Savi's pipistrelle in the traditional core of its distributional range in the Mediterranean region. In particular, we focus on patterns of variation in these variables during different stages of the reproductive cycle of females. The results give insights into the adaptability of the species and contribute to the overall knowledge of its ecology that might be informative in regards to its recent distributional changes and northward expansion.

Materials and Methods

Study Area

Our study area is located in North Dalmatia (Zadar County), Croatia. It encompasses the southeastern (SE) tip of the island of Pag and adjacent peninsula (44°16'N, 15°19'E; 20 m a.s.l.). The area is characterized by typical sub-Mediterranean climate with hot and dry summers (from June to August mean temperature is 23.2°C and mean precipitation is 46.8 mm). The majority of rain falls in late autumn (mean precipitation in November is 118.4 mm) and winter temperatures are mild (mean temperature from December to February is 7.7°C — Meteorological and Hydrological Service, data from 2017: see www.meteo.hr). The study area is partially included in the NATURA 2000 network. The coastal area is made of limestone, articulated and formed by gulfs and smaller bays divided on the northeastern (NE) side from the mainland by the sea channel (Fig. 1). The NE part of the study site is under the strong influence of Bora winds that enhances soil erosion and limits the growth of vegetation. This leaves the NE coastal belt almost completely bare and with increasing distance from the sea the area is used as rocky pastures (14%) by local inhabitants. The extensive inland valleys are predominately used as meadows and pastures (5%), intersected with small arable fields (1%), with larger parts of former agricultural land now overgrown with shrublands (14%). Freshwater streams with a narrow strip of riparian vegetation (1%) around them are present in the valleys. The planted forests (4%) of Aleppo pine (*Pinus halepensis*) and black pine (*Pinus nigra*) are located on two ridges, above villages consisting of buildings, roads and gardens (4%). The remainder of the study area consists of the Mediterranean Sea (57%). All percentages listed above are calculated from the total area of 'available habitat' — area within a 2.5 km buffer constructed around all obtained telemetry fixes.

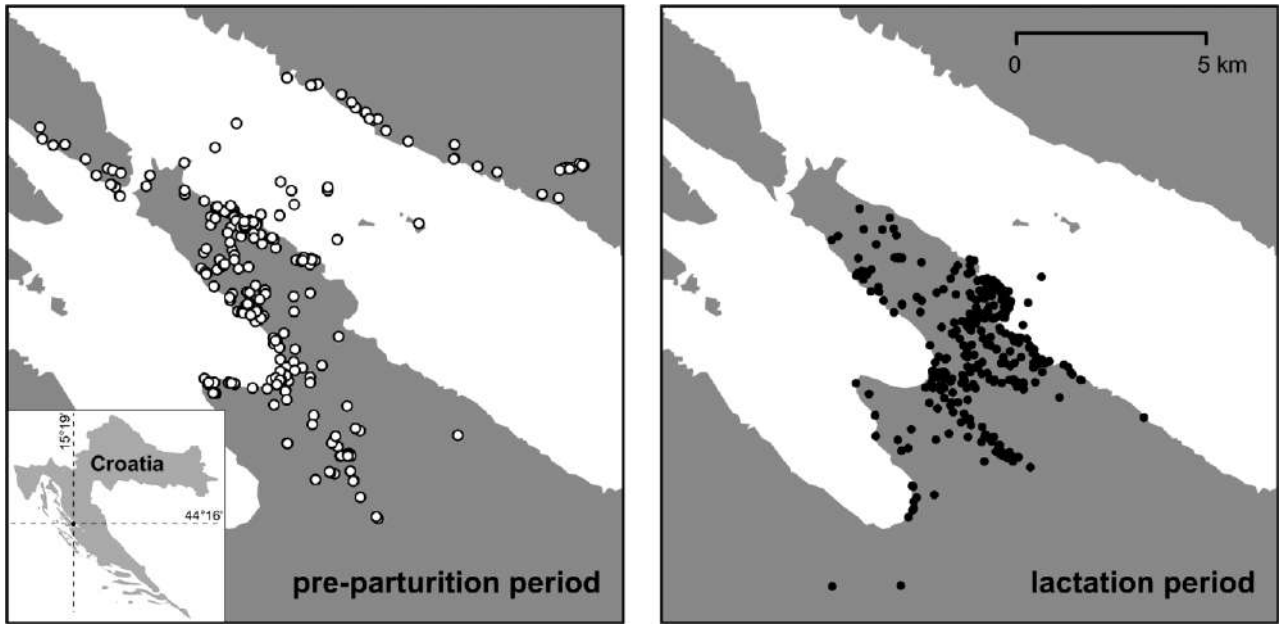


FIG. 1. The map shows radio tracking 'fixes' for *H. savii* in pre-parturition and lactation period. Sea — in white, land — in grey

Bat Capturing and Processing

In June and July from 2012–2014 we captured bats in mist-nets placed over streams (Szewczak *et al*., 1998), and later in the vicinity of roosts. During the study period we captured 54 individuals of *H. savii* (marked 34), out of which only a small proportion were males (n = 5). Captured bats were sexed, aged, measured for forearm length and weight and assessed for reproductive status (Racey, 1988). After processing, all bats were released at the place of capture. After trimming a small patch of dorsal fur, adult females were equipped with radio-transmitters (LB-2X 0.31 Holohil Systems Ltd., Woodlawn, Ontario, Canada). Transmitters were mid-dorsally attached with surgical glue (Perma Type) to the skin and did not exceed 5% of bat body mass. Before release, bats were kept in cloth bags for several minutes to check for satisfactory placement and attachment of the transmitter. Protocols used to handle bats met guidelines proposed for the study of wild animals (Society for the Study of Animal Behaviour, 2006), were approved by the Croatian Ministry for the protection of environment and nature (license numbers: 517-07-1-1-1-12-2, 517-07-1-1-1-13-2, 517-07-1-1-1-14-5), and met legal requirements.

To determine the position of tagged bats during the night we used ICOM R-20 wideband receivers fitted with three-element Yaggi antennas. Locational fixes of bats were taken every 5–10 minutes and were specified by triangulation and homing in. While performing triangulation two or three mobile workers co-ordinated their movements by hand-held FM radios or cell phones. Each observer noted their own GPS position and measured the bearing of each bat location. Locations were assigned into four distance classes (< 80 m, 80–150 m, > 150–350 m, and > 350 m). Classes of confidence in the accuracy of location were tested experimentally before attaching a transmitter onto the bat (see also Bartonička *et al*., 2008). After the data were collected, we visualised researchers´ positions and bearings on the digitalized map, and dismissed the fixes that did not provide reliable triangulation. Locations from this 'homing' method were based on highest accuracy class < 80 m. They were assigned when in close proximity, e.g., close to roosts or feeding sites when signal reception still was attained after disconnecting the Yagi antenna (or using maximum attenuation). Telemetry fieldwork was carried out during favorable meteorological conditions (i.e., no rain or strong wind, ambient temperature above 10ºC) from evening roost emergence to one hour after midnight, which coincides with the period of highest foraging activity of bats (Maier, 1992). Usually we tracked two bats simultaneously over consecutive nights (3.4 ± 2 SD nights per individual).

Diet Analysis

We collected 138 faecal pellets (88 from 18 pregnant and 50 from eight lactating females). When sampling for pellets, females were kept individually in clean cloth sacks for aproximately two hours. Faecal samples were later placed in labelled micro-tubes which were refilled with 70% ethanol. In the laboratory, pellets were softened in water in a Petri dish and then teased apart with a dissecting needle and a pair of tweezers under a binocular microscope (10–50 magnification). Prey categories were identified using comparative slides, methodological works (e.g., Shiel *et al*., 1997), entomological keys, and a reference collection of insects. Percentage volume was assessed according to Obrtel and Holišová (1974) and expressed as the sum of all relative volumes of a particular prey category in individual faecal pellets, divided by the number of faecal pellets in the analyzed set of pellets.

Statistical Analyses

We estimated the size of the foraging areas of each individual by applying 95% kernel estimates to telemetry fixes with an ad hoc smoothing parameter (according to Worton, 1989) using the 'adehabitatHR' package (Calenge, 2006). Accumulation curves of home-range sizes versus number of telemetry fixes were constructed and their asymptotes calculated by the

self-starting Nls Gompertz growth model. This procedure substantially improved the estimation of home-range sizes. Subsequently, the exact Wilcoxon-Mann-Whitney (WMW) test, from the package 'coin' (Zeileis *et al*., 2008) was used to explore seasonal differences in home-range sizes and to compare percentage volume of each prey type in pellets of pre-parturition versus lactating females.

To examine habitat affinities of Savi's pipistrelle, we used an Ecological Niche Factor Analysis (ENFA), which builds on the concept of ecological niche. Purpose of this analysis is to compare the distribution of eco-geographical predictors for a presence data set consisting of locations where the species has been detected with the distribution of predictors of the whole study area. Like the Principal Component Analysis, ENFA summarizes all predictors into a few uncorrelated factors retaining most of the information (Hirzel *et al*., 2001). Output of ENFA reflects the direction in which the species niche mostly differs from the available conditions in the entire study area, or in other words, describes the difference between the means of cells where a bat was recorded in relation to cells of the entire study area (Hirzel *et al*., 2002). Higher absolute values indicate greater departure from the mean available habitat for the corresponding variable. Negative coefficients indicate that the species prefers values that are lower than the mean with respect to the study area, whereas positive coefficients indicate preference for higher-than-mean values.

To perform ENFA, we first constructed a buffer of 2.5 km around all telemetry fixes. The area falling in this circle (hereafter, the available habitat) was transformed into discrete resource units (200 m × 200 m). Subsequently, we used seven raster layers containing the environmental characteristics of this available habitat. In the first six layers each resource unit contained a value reflecting the negative Euclidean (minimal) distance to a particular habitat category. For example, if the resource unit of, the forest environmental layer has a value of -100, the nearest distance from such a unit to the forest is 100 m (if the value is 0 it means that this resource unit lies within the forest habitat). These six layers contained information about the distances to: (i) rocky pastures; (ii) forest, (iii) meadows, (iv) riparian vegetation, (v) shrubland, and (vi) sea. The last raster layer —— light — was derived from 'Earth's city lights' image (Mayhew and Simmon, 2000), by rescaling to 200 m × 200 m resolution. This raster layer contains the information about light pollution (for further details see Doll, 2008).

Telemetry fixes, together with the seven environmental raster layers, were used in the modelling of the bats' foraging habitat by using the 'adehabitatHS' package (Calenge, 2006). Based on our assumption that habitat is equally available in both periods, we treated our data as with a design II study according to Thomas and Taylor (1990). The habitat preferences were analyzed separately for the pre-parturition and lactation period.

Statistical comparisons, as well as the niche modelling, were conducted in R ver. 3.3.0 (R Core Team, 2016). We used QGIS 2.0.1-Dufour (Quantum GIS Development Team, 2013) to perform all operations associated with creation and modification of raster layers.

RESULTS

In total, we used the data from 19 unique radiotracked adult females and obtained 661 valid telemetry fixes (35 ± 13 SD fixes per female, 155 fixes belonged to first distance class, 70 to second, 85 to third and 351 to fourth distance class, 150 additional fixes were not included in the analysis). Estimated home-range size (95% kernel) did not differ significantly between pre-parturition and lactating females (median pre-parturition = 50.8 km^2; median lactation = 24.1 km^2; exact WMW test: Z = -1.55, P = 0.13), however it varied greatly in its maximal size in pre-parturition (range: 10.7–78.6 km^2) and lactation period (range: 21–77.1 km^2, extreme ~170 km^2). Maximum distance from roost during foraging, recorded in a pregnant female, was 14.2 km, whereas maximum distance in a lactating female was 9.3 km. No difference appeared during the beginning of activity, however, prior to the start of their foraging bout females would, upon emergence, often spend shorter time (ca 5–10 min.) by foraging above rocky pastures in the roost vicinity. Roosts (exclusively placed in rocky fissures except for two houses) were predominantly located within the rocky pastures at the northeastern-most edge of the peninsula directly bordering the sea channel. Both pregnant and lactating females used all habitats available within their home-range, however, the frequency of radiotracking records in particular habitat types was far from equal to its contribution to the actual landscape mosaic.

ENFA revealed that Savi's pipistrelle females foraged in various types of habitat in both reproductive periods (Fig. 2). During pregnancy females foraged above rocky pastures, forest, meadows and riparian vegetation. They exhibited lower affinity towards area illuminated by artificial light, shrubland and sea. During lactation the affinity for foraging in riparian habitats increased considerably, followed by meadows, forest and rocky pastures. In both periods a freshwater stream surrounded by riparian vegetation was frequently revisited by females, with higher regularity for lactating individuals (Table 1). Both pre-parturition and lactating females flew in the vicinity of the sea, positioned close to their

TABLE 1. Affinity towards foraging habitat of Savi's pipistrelle. The first three largest values are highlighted in bold

Habitat type	Period	
	Pre-parturition	Lactation
Rocky pastures	**0.78**	0.73
Forest	**0.78**	**0.89**
Meadows	**0.65**	**0.88**
Riparian	0.55	**0.89**
Shrubland	0.31	0.48
Lights	0.18	0.48
Sea	0.14	0.11

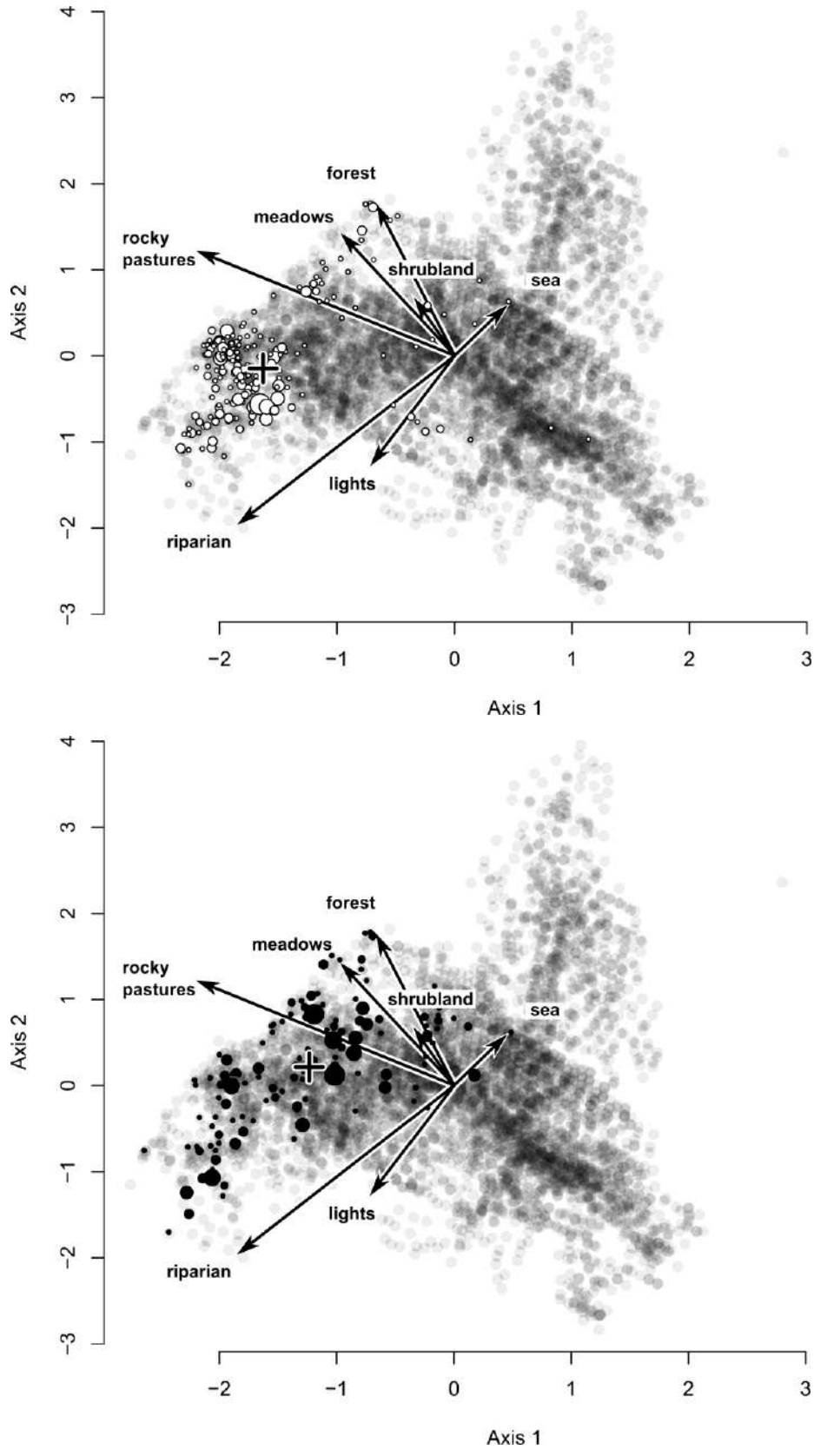


FIG. 2. Habitat affinity of *H. savii* in pre-parturition and lactation period. Black crosses represent marginality vectors for females in both reproductive periods. Grey points present available resource units, whereas white and black circles represent used resources units of pre-parturition and lactating females respectively. Direction of black arrows indicates the level of correlation between habitat types (same direction = positive, opposite direction = negative)

roosts. However we recorded only pregnant females flying across the sea directly from their roosts to reach the mountain slopes positioned across the peninsula (shortest possible distance is 3.3 km).

Prey diversity in faecal pellets was higher in pre-parturition than in lactation females. The diet of Savi's pipistrelle was dominated by ants (Formicoidea) and true bugs (Heteroptera) in both reproductive periods (Fig. 3). In comparison to pre-parturition period, lactating females consumed larger volumes of ants which made ants the staple of their diet (WMW test, Z = -5.50, $P < 0.001$). The opposite trend, larger volumes of prey in pre-parturition than in lactation, were recorded for aphids (Aphidoidea; WMW test, $Z = 3.05$, $P < 0.01$), nematoceran Diptera (Nematocera; WMW test, $Z = 2.85$, $P < 0.01$) — especially in Tipulidae, Chironomidae and Simuliidae — and also in beetles (Coleoptera; WMW test, $Z = 4.40$, $P < 0.001$).

Percentage volume of other prey items (Heteroptera, Lepidoptera, Culicidae, Auchenorrhyncha, Neuroptera, Hymenoptera and Brachycera) did not significantly differ between reproductive periods ($P > 0.05$). Prey items that occurred in small volumes and only in pre-parturition females included Dermaptera, Orthoptera, Blattodea, Psyllinea, whereas Trichoptera occurred only during the lactating period.

DISCUSSION

This study provides the first detailed insight into home-range size, foraging habitat use and diet of Savi's pipistrelle within the Mediterranean region. Our results demonstrate a flexibility in habitat use and diet within the core of its distributional range. This knowledge might be critical in the context of the increasing environmental pressures on Savi's pipistrelles and their survival in this region (Sala *et al*., 2000). Savi's pipistrelle belongs to the group of aerial hawkers (Kunz and Fenton, 2003) — bats that fly and forage within open space, usually above vegetation. Therefore, its flexibility in habitat use may not be surprising since it might not show a clear affinity to a particular habitat if it is able to fly high above it. The species also exhibited remarkably large home-ranges compared to its body size (e.g. detailed study on Kuhl's pipistrelle, similar in its ecology and size to Savi's pipistrelle, showed five times smaller home-ranges, Maxinová *et al*., 2016). Due to the fact that Savi's pipistrelle is present on a majority of Mediterranean islands (Horáček and Benda 2004; Veith *et al*., 2011), the species appears able to cross even larger areas of open space.

Home-range size can strongly depend on various factors such as prey distribution and density (Napal *et al*., 2010), habitat diversity (Dietz *et al*., 2013),

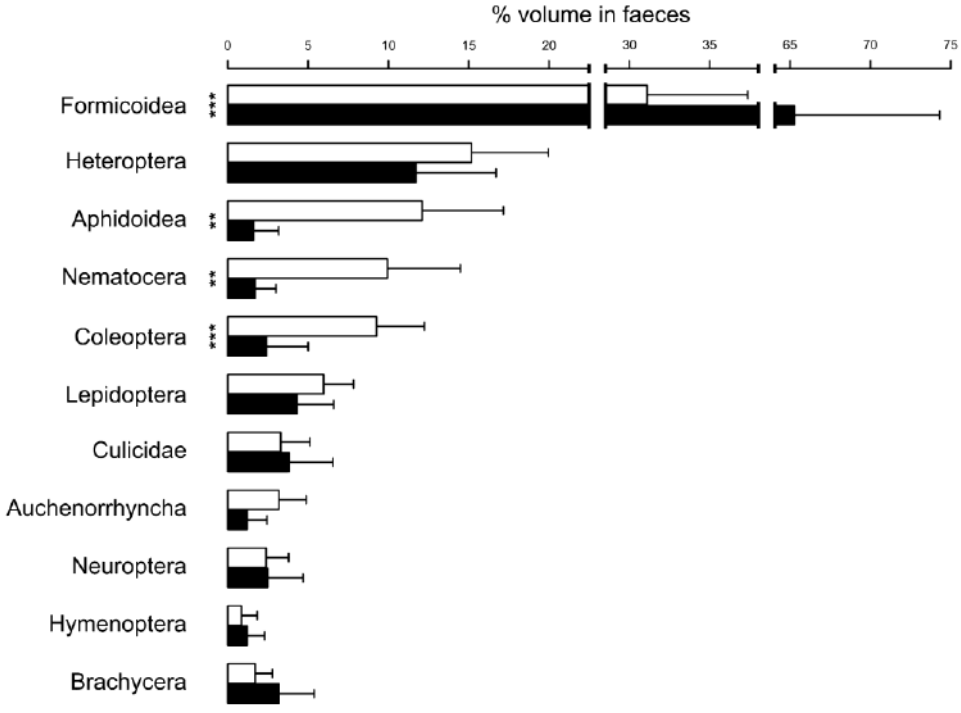


FIG. 3. Diet analysis of *H. savii* in the pre-parturition (white) and lactation (black) period. The comparison is shown only for prey groups that were presented in the pellets during both reproductive periods. The asterix marks significant differences ($P < 0.05$)

as well as distances between preferred roosting and foraging habitats (Hayes and Loeb, 2007). We found that pregnant females occasionally crossed the sea to reach the mountain slopes, whereas lactating bats never exhibited such long flights and their activity was concentrated closer to the roosts. This pattern of behavior between different reproductive stages was observed in other bat species (see e.g., Womack *et al*., 2013; Ciechanowski *et al*., 2017) and can be explained as a consequence of higher energy demands when rearing young (Adams *et al*., 2008), as well as a need for returning during the night due to nursing and therefore staying closer to roosts and offspring (Chiechanowski *et al*., 2017; Henry *et al*., 2002; but see Goiti *et al*., 2006).

Within our study region, Savi's pipistrelle was able to cross all of the habitat types found in the study area, with only lower affinity for shrubland and sea. These findings can be informative to its habitat flexibility and reflect the fact that as aerial hawkers, Savi's pipistrelle may not rely exclusively on a certain type of habitat. Similarly, differences in habitat use between pregnant and lactating females were most likely influenced by prey abundance during the course of their reproductive cycle. During the progression of the reproductive season, the importance of riparian vegetation was more pronounced, probably due to increased dependence of lactating females to replace water loss in comparison to non-reproductive females (Adams *et al*., 2008). Furthermore, during dry summer months, the riparian vegetation can harbor higher insect abundance (Holloway and Barclay, 2000) which can then provide better foraging resources (Salsamendi *et al*., 2012). Similarly, insect richness and abundance can be enhanced by diverse vegetation types (Wenninger and Inouye, 2008), and the landscape composition within the study region, where meadows and forests are in close proximity to the riparian vegetation that might contribute to the overall effect of higher prey availability. Pregnant females showed slightly lower affinities to individual habitat types than lactating individuals, with rocky pastures being the most preferred habitat. At the beginning of the reproductive season, vegetation on karst rocky pastures is flowering (Pipenbaher *et al*., 2011), which can be accompanied by higher abundance of insect species. Furthermore, the preference for rocky pastures could at least partly be attributed to landscape scanning and searching for new roosts due to the fact that pregnant and lactating females had their roosts predominantly in this habitat type (M. Kipson, personal observation). Although there was a preference for forest habitats by pregant females, the bats were observed flying and foraging above the tree canopy or around forest clear-cuts corresponding to the hunting strategy of aerial hawkers in open space.

Studies mainly from urban areas indicate that Savi's pipistrelle is actively foraging around street lights (Vernier, 1995; Paunović *et al*., 2015). Therefore we also tested its affinity to urban habitats by using a proxy of light pollution areas (Maxinová *et al*., 2016). Both pregnant and lactating bats were observed flying over villages and artificially lit areas, and we found Savi's pipistrelles using houses as day roosts (twice). We did not observe Savi's pipistrelle actively foraging around street lamps, which may indicate that the importance of street lights is less prominent in more rural areas with the presence of natural habitats containing more suitable prey than in urbanized areas. Higher affinity of lactating females for lighted areas could also be a consequence of staying closer to the roost and within the peninsula area which is more affected by light pollution, they were never observed crossing the sea channel. On the other hand pregnant females reached mountain slopes across the sea channel, which presents a larger non-illuminated area. Although the affinity for sea was quite low in both reproductive periods, there are earlier observations describing the hunting of Savi's pipistrelle in Croatia above the sea, near cliffs where it roosted (Đulić, 1970; Gaisler, 1994). In our study, we can not confirm this pattern of behaviour, since we were not able to follow closely the bats crossing the sea. However, if such behaviour did occur, we assume that it would not be a very common behaviour, as females had a low affinity towards it, and only a couple of pregnant individuals actively flew across the sea.

The diet analysis confirmed that Savi's pipistrelle can take advantage of high concentrations of swarming insects, in particular ants. The general pattern of the diet composition in our study corresponds with other studies on the species' diet from the Mediterranean and Middle East. For example, the Formicoidea, Heteroptera, Coleoptera and Lepidoptera were dominate prey in Syria (Benda *et al*., 2006), Coleoptera and Formicoidea were identified as major diet components in Turkey (Whitaker and Karataş, 2009), and Hymenoptera (mostly Formicoidea), Coleoptera and Heteroptera were shown to be the prevailing food items in Lebanon and the Greek islands (Žďárská, 2013). The differences in the diet composition between the two reproductive periods could probably be better explained by the changes in the prey availability due to expected higher

abundances of nematoceran Diptera and winged aphids during the more humid spring season, whereas swarming of ants is more typical for summer (Noordijk, 2008).

In conclusion, our results have shown that Savi's pipistrelle is a highly adaptive species that is able to cross large distances on a nightly basis. Having the ability to fly long distances offers a good predisposition for colonizing new areas and changing its distributional range. The species is also able to potentially forage on locally abundant aerial prey sources and various prey items are present in its diet, which might contribute to its flexibility in use of space across different habitats. The habitat preferences probably correspond to the aerial hawker strategy of the species where it does not depend strictly on a particular habitat, as much as on the prey that it finds and hunts in the open space above individual habitats. The recent northward expansion of Savi's pipistrelle's geographic distribution is most likely related to colonization of urban habitats (Uhrin *et al*., 2016). Increased use of urban space in newly colonized areas also has been reported in a congeneric bat that has been spreading northwards, Kuhl's pipistrelle (Ancillotto *et al*., 2016). It seems that despite their high spatial flexibility, the availability of water and riparian resources, which is a scarce habitat within the Mediterranean, may be of crucial importance for successful reproduction in this species.

ACKNOWLEDGEMENTS

We would like to thank to everyone who contributed in the field, namely Helena Jahelková, Jana Křemenová, Petra Žvorc, Daniela Hamidović, Vida Zrnčić and Frank Bonaccorso for language corrections. This project was supported by the Charles University grant (SVV 260 434/2018), Slovak Scientific Grant Agency VEGA (#2/0077/17) and research aim of the Academy of Sciences of the Czech Republic (RVO 68081766), Charles University Research Centre program No. 204069, and Specific Research Project Nr. 2105/2017 from the University of Hradec Králové.

LITERATURE CITED

ADAMS, R. A., and M. A. HAYES. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. Journal of Animal Ecology, 77: 1115–1121.

AMORIM, F., V. A. MATA, P. BEJA, and H. REBELO. 2015. Effects of a drought episode on the reproductive success of European free-tailed bats (*Tadarida teniotis*). Mammalian Biology, 80: 228–236.

ANCILLOTTO, L., L. SANTINI, N. RANC, L. MAIORANO, and D. RUSSO. 2016. Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation. Naturwissenschaften, 103: 1–8.

BARTONIČKA, T., A. BIELIK, and Z. ŘEHÁK. 2008. Roost switching and activity patterns n the soprano pipistrelle, *Pipistrellus pygmaeus*, during lactation. Annales Zoologici Fennici, 45: 503–512.

BENDA, P., M. ANDREAS, D. KOCK, R. K. LUČAN, P. MUCLINGER, P. NOVÁ, J. OBUCH, K. OCHMAN, A. REITER, M. UHRIN, and D. WEINFURTOVÁ. 2006. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology. Acta Societatis Zoologicae Bohemicae, 70: 1–329.

BENDA, P., V. HANÁK, I. HORÁČEK, P. HULVA, R. LUČAN, and M. RUEDI. 2007. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 5. Bat fauna of Cyprus: review of records with confirmation of six species new for the island and description of a new subspecies. Acta Societatis Zoologicae Bohemicae, 71: 71–130.

CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197: 516–519.

CIECHANOWSKI, M., A. ZAPART, T. KOKUREWICZ, M. RUSIŃSKI, and M. LAZARUS. 2017. Habitat selection of the pond bat (*Myotis dasycneme*) during pregnancy and lactation in northern Poland. Journal of Mammalogy, 98, 232–245.

DANKO, Š. 2007. Reprodukcia *Hypsugo savii* a *Pipistrellus kuhlii* na východnom Slovensku: dalšie dôkazy o ich šírení na sever [Reproduction of *Hypsugo savii* and *Pipistrellus kuhlii* in eastern Slovakia: further evidence of their spreading northwards]. Vespertilio, 11: 13–24. [In Slovak with English abstract].

DIETZ, M., J. B. PIR, and J. HILLEN. 2013. Does the survival of greater horseshoe bats and Geoffroy's bats in Western Europe depend on traditional cultural landscapes? Biodiversity and Conservation, 22: 3007–3025.

DI SALVO, I., D. RUSSO, and M. SARÀ. 2009. Habitat preferences of bats in a rural area of Sicily determined by acoustic surveys. Hystrix, the Italian Journal of Mammalogy, 20: 137–146.

DOLL, C. N. 2008. CIESIN thematic guide to night-time light remote sensing and its applications. Center for International Earth Science Information Network of Columbia University, Palisades, NY. Available at http://sedac.ciesin.columbia.edu/tg/.

ĐULIĆ, B. 1958. Über die Ökologie der Alpenfledermaus, *Pipistrellus savii*, auf der Insel Mljet (Meleda) in Süddalmatien. Säugetierkundliche Mitteilungen, 6: 10–11.

ĐULIĆ, B. 1970. Ökologische Beobachtungen der Fledermäuse der Adriatischen Inseln. Zeitschrift für Säugetierkunde, 35: 45–51.

FREITAG, B. 1996. *Pipistrellus savii* (Bonaparte, 1837) — Erstnachweis fur die Steiermark (Mammalia, Chiroptera). Mitteilungen des Naturwissenschaftlicher Vereins für Steiermark, 125: 237–238.

GAISLER, J. 1994. The bats *Pipistrellus kuhli* and *Hypsugo savii* on the island of Rab (Croatia). Folia Zoologica, 43: 279–280.

GOITI, U., J. R. AIHARTZA, D. ALMENAR, E. SALSAMENDI, and I. GARIN. 2006. Seasonal foraging by *Rhinolophus euryale* (Rhinolophidae) in an Atlantic rural landscape in northern Iberian Peninsula. Acta Chiropterologica, 8: 141–156.

HAYES, J. P., and S. C. LOEB. 2007. The influences of forest management on bats in North America. Pp. 207–234, *in* Bats in forests: conservation and management (M. J. LACKI, J. P. HAYES, and A. KURTA, eds.). Johns Hopkins University Press, Baltimore, MD, 329 pp.

Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy, 83: 767–774.

Hintze, F., V. Duro, J. C. Carvalho, C. Eira, P. Correia Rodrigues, and J. Vingada. 2016. Influence of reservoirs created by small dams on the activity of bats. Acta Chiropterologica, 18: 395–408.

Hirzel, A. H., V. Helfer, and F. Metral. 2001. Assessing habitat-suitability models with a virtual species. Ecological modelling, 145: 111–121.

Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological niche factor analysis: how to compute habitat suitability maps without absence data? Ecology, 83: 2027–2036.

Holloway, G. L., and R. M. R. Barclay. 2000. Importance of prairie riparian zones to bats in southeastern Alberta. Ecoscience, 7: 115–122.

Horáček, I., and P. Benda. 2004. *Hypsugo savii* (Bonaparte, 1837) — Alpenfledermaus. Pp. 911–941, *in* Handbuch der Säugetiere Europas Band 4: Fledertiere. Teil II: Chiroptera II. Vespertilionidae 2, Molossidae, Nycteridae (F. Krapp, ed.). Aula-Verlag, Wiebelsheim, 1186 pp.

Jones, G., D. Jacobs, T. Kunz, M. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research, 8: 93–115.

Klausmeyer, K. R., and M. R. Shaw. 2009. Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. PLoS ONE, 4: e6392.

Kunz, T. H., and M. B. Fenton (eds.). 2003. Bat ecology. University of Chicago Press, Chicago, IL, xix + 779 pp.

Kunz, T. H., E. B. de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences, 1223: 1–38.

Maier, C. 1992. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. Journal of Zoology (London), 228: 69–80.

Maxinová, E., M. Kipson, L. Naďo, P. Hradická, and M. Uhrin. 2016. Foraging strategy of Kuhl's pipistrelle at the Northern edge of the species distribution. Acta Chiropterologica, 18: 215–222.

Mayhew, C., and R. Simmon. 2000. NASA GSFC. Earth's city lights. Data courtesy Marc Imhoff of NASA GSFC and Christopher Elvidge of NOAA NGDC.

McLean, J. A., and J. R. Speakman. 1999. Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. Functional Ecology, 13: 360–372.

Mickleburgh, S. P., Hutson, A. M., and P. A. Racey. 2002. A review of the global conservation status of bats. Oryx, 36: 18–34.

Napal, M., I. Garin, U. Goiti, E. Salsamendi, and J. Aihartza. 2010. Habitat selection by *Myotis bechsteinii* in the southwestern Iberian Peninsula. Annales Zoologici Fennici, 47: 239–250.

Noordijk, J., R. Morssinkhof, P. Boer, A. P. Schaffers, Th. Heijerman, and K. V. Sýkora. 2008. How ants find each other; temporal and spatial patterns in nuptial flights. Insectes Sociaux, 55: 266–273.

Obrtel, R., and V. Holišová. 1974. Trophic niches of *Apodemus flavicollis* and *Clethrionomys glareolus* in a lowland forest. Přírodovědné Práce Ústavů ČSAV v Brně (N.S.), 8(7): 1–37.

Paunović, M., B. Karapandža, I. Budinski, and J. Jovanović. 2015. New records of the Savi's pipistrelle *Hypsugo savii* (Bonaparte, 1837) (Chiroptera, Mammalia) from Serbia: an evidence for the expansion of its geographical range. Acta Zoologica Bulgarica, 67: 389–397.

Pipenbaher, N., M. Kaligaric, and S. Skornik. 2011. Floristic and functional comparison of karst pastures and karst meadows from the north Adriatic karst. Acta Carsologica, 40: 515–525.

Quantum GIS Development Team. 2013. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Available at https://www.osgeo.org/projects/qgis/.

Racey, P. A. 1988. Reproductive assessment in bats. Pp. 31–46, *in* Ecological and behavioural methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., xxii + 353 pp.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/.

Reiter, G., S. Wegleitner, U. Hüttmeir, and M. Pollheimer. 2010. Die Alpenfledermaus, *Hypsugo savii* (Bonaparte 1837), in Mitteleuropa. Nyctalus (N.F.), 15: 158–170

Russo, D., and L. Ancillotto. 2014. Sensitivity of bats to urbanization: a review. Mammalian Biology, 80: 205–212.

Russo, D., and G. Jones. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. Journal of Zoology (London), 258: 91–103.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, *et al*. 2000. Biodiversity — global biodiversity scenarios for the year 2010. Science, 287: 1770–1774.

Salsamendi, E., I. Arostegui, J. Aihartza, D. Almenar, U. Goiti, and I. Garin. 2012. Foraging ecology in Mehely's horseshoe bats: influence of habitat structure and water availability. Acta Chiropterologica, 14: 121–132.

Sherwin, H. A., W. I. Montgomery, and M. G. Lundy. 2013. The impact and implications of climate change for bats. Mammal Review, 43: 171–182.

Shiel, C., C. McAney, C. Sullivan, and J. Fairley. 1997. Identification of arthropod fragments in bat droppings. Occasional Publication of Mammal Society (London), 17: 1–48.

Society for the Study of Animal Behaviour. 2006. Guidelines for the treatment of animals in behavioural research and teaching. Animal Behaviour, 71: 245–253.

Spitzenberger, F. 1997. Distribution and range expansion of Savi's bat (*Hypsugo savii*) in Austria. Zeitschrift für Säugetierkunde, 62: 179–181.

Stoycheva, S., D. Georgiev, I. Pandourski, and E. Tilova. 2009. Bat diversity in two large towns of the Upper Thrace, Bulgaria (Chiroptera). Lynx (N.S.), 40: 83–93.

Szewczak, J. M., S. M. Szewczak, M. L. Morrison, and L. S. Hall. 1998. Bats of the White and Inyo mountains of California-Nevada. Great Basin Naturalist, 58: 66–75.

Thomas, D., and E. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management, 54: 322–330.

Ulrich, W., K. Sachanowicz, and M. Michalak. 2007. Environmental correlates of species richness of European bats (Mammalia: Chiroptera). Acta Chiropterologica, 9: 347–360.

Uhrin, M., U. Hüttmeir, M. Kipson, P. Estók, K. Sachanowicz, S. Bücs, B. Karapandža, M. Paunović, P. Presetnik, A.-T. Bashta, *et al*. 2016. Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: a review. Mammal Review, 46: 1–16.

Veith, M., M. Mucedda, A. Kiefer, and E. Pidinchedda. 2011. On the presence of pipistrelle bats (*Pipistrellus* and *Hypsugo*; Chiroptera: Vespertilionidae) in Sardinia. Acta Chiropterologica, 13: 897–899.

Vernier, E. 1995. Presence and distribution of bats in the town of Padova (N. E. Italy). Myotis, 32–33: 193–195.

Webb, P. I., J. R. Spekman, and P. A. Racey. 1995. Evaporative water loss in two sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentonii*: relation to foraging mode and implications for roost site selection. Journal of Zoology (London), 235: 269–278.

Wenninger, E. J., and R. S. Inouye. 2008. Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. Journal of Arid Environments, 72: 24–33.

Whitaker, J. O., Jr., and A. Karataş. 2009. Food and feeding habitats of some bats from Turkey Acta Chiropterologica, 11: 393–403.

Womack, K. M., S. K. Amelon, and F. R. Thompson. 2013. Summer home range size of female Indiana bats (*Myotis sodalis*) in Missouri, USA. Acta Chiropterologica, 15: 423–429.

Worton, B. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology, 70, 164–168.

Zahn, A., and S. Maier. 1997. Jagdaktivität von Fledermäusen an Bächen und Teichen. Zeitschrift für Säugetierkunde, 62: 1–11.

Žďárská, L. 2013. Potravní ekologie netopýrů východního Středomoří [Feeding ecology of bats in the Eastern Mediterranean]. M.Sci. Thesis, Charles University, Prague, Czech Republic, 175 pp. [In Czech with English summary].

Zeileis, A., M. A. Wiel, K. Hornik, and T. Hothorn. 2008. Implementing a class of permutation tests: the coin package. Journal of Statistical Software, 28(8): 1–23.

Received 09 March 2018, accepted 04 October 2018

Associate Editor: Burton Lim

Paper 4

Kipson, M., Šálek, M., Naďo, L., Jahelková, H., Horáček, I. and Lučan, R. (*In review*) ‘Ground-level rock crevices as reproductive roosts of Savi’s pipistrelle (*Hypsugo savii*) in semi-arid landscapes of the Eastern Mediterranean’, *submitted manuscript*

Journal of Arid Environments

Ground-level rock crevices as reproductive roosts of Savi's pipistrelle (Hypsugo savii) in semi-arid landscapes of the Eastern Mediterranean

--Manuscript Draft--

Manuscript Number:	
Article Type:	Research paper
Keywords:	roost preferences; roost microclimate; ground roost; climate change; range expansion
Corresponding Author:	Marina Kipson Charles University Prague, CZECHIA
First Author:	Marina Kipson
Order of Authors:	Marina Kipson
	Martin Šálek
	Ladislav Naďo
	Helena Jahelková
	Ivan Horáček
	Radek Lučan
Abstract:	Roost microclimate and availability are key to bat ecology, especially in arid environments with high thermal stress and limited roosting opportunities. We investigated the roosting ecology of reproductive females of Savi's pipistrelle in a semi-arid Mediterranean landscape. Using radiotelemetry, we located 58 roosts used by 29 females and quantified roosting behaviour, roost structure, and microclimate. Females used vertical, ground-level rock crevices within flat limestone pavement, and only exceptionally used synanthropic roosts. During pregnancy, roosts were mainly occupied by solitary individuals, while smaller, dynamic groups formed near parturition and during lactation, with near-daily roost switching. A conditional logistic regression model showed that roost occupancy was associated with greater crevice depth and narrower entrance width, while entrance length had no effect. Microclimatic measurements revealed that occupied crevices provided cooler daytime conditions and greater thermal stability than nearby controls, whereas nighttime temperatures were similar across all crevices and approached ambient temperatures. Selecting deeper crevices with narrow entrances likely mitigates extreme daytime heat. The combination of solitary or small-group roosting, frequent switching, and structurally protective crevices reflects adaptation to thermal stress and predation risk. These findings provide a baseline for understanding roost selection in semi-arid regions and potential shifts to synanthropic roosting.

Cover letter

Dear Editor,

We are pleased to submit the manuscript entitled
"Ground-level rock crevices as reproductive roosts of Savi's pipistrelle (*Hypsugo savii*) in semi-arid landscapes of the Eastern Mediterranean"
for consideration for publication in the *Journal of Arid Environments*.

In this study, we investigate the roosting ecology of reproductive females of Savi's pipistrelles in a semi-arid Mediterranean limestone landscape in coastal Croatia. Using radiotelemetry alongside detailed structural and microclimatic measurements, we document a previously
undescribed roosting strategy: the predominant use of vertical, ground-level rock crevices within limestone pavements. We show that females select deep crevices with narrow entrances that provide cooler, more thermally stable daytime conditions under extreme ambient temperatures. Roosting occurs solitarily or in small, highly dynamic groups with frequent roost switching.

Our findings address key ecological processes central to the scope of the *Journal of Arid Environments*, including behavioural and physiological responses to thermal stress, habitat use under resource limitation, and adaptations to arid and semi-arid conditions. By focusing on natural, non-synanthropic habitats within the species' core Mediterranean range, this study also provides important baseline data for understanding recent shifts toward synanthropic roosting during climate-driven range expansion in Europe.

We believe that the novelty of documenting ground-level limestone roost use, together with the integration of behavioural, structural, and microclimatic analyses, will be of broad interest
to readers of the journal working on arid-zone ecology, vertebrate behaviour, and conservation biology.

This manuscript has not been published elsewhere and is not under consideration by any other journal. All authors have approved the submitted version and agree to its submission to the
Journal of Arid Environments. All applicable ethical and legal requirements for animal research have been met.

Thank you very much for considering our manuscript. We would be grateful for the opportunity to have it reviewed and would be happy to respond to any questions or suggestions.

Sincerely,

Marina Kipson
(on behalf of all authors)
Department of Zoology, Faculty of Science
Charles University in Prague
Viničná 7, 128 44 Prague, Czech Republic
Email: marinakipson@gmail.com

Highlights

- Savi’s pipistrelles roost mainly in ground-level crevices in arid limestone pavements
- Roosts are occupied solitarily or in small, dynamic groups
- Roost selection favours deep crevices with narrow entrances
- Occupied crevices provide cooler and more stable daytime microclimates
- Frequent roost switching likely reduces predation and thermal stress

Ground-level rock crevices as reproductive roosts of Savi's pipistrelle (*Hypsugo savii*) in semi-arid landscapes of the Eastern Mediterranean

Abstract

Roost microclimate and availability are key to bat ecology, especially in arid environments with high thermal stress and limited roosting opportunities. We investigated the roosting ecology of reproductive females of Savi's pipistrelle in a semi-arid Mediterranean landscape. Using radiotelemetry, we located 58 roosts used by 29 females and quantified roosting behaviour, roost structure, and microclimate. Females used vertical, ground-level rock crevices within flat limestone pavement, and only exceptionally used synanthropic roosts. During pregnancy, roosts were mainly occupied by solitary individuals, while smaller, dynamic groups formed near parturition and during lactation, with near-daily roost switching. A conditional logistic regression model showed that roost occupancy was associated with greater crevice depth and narrower entrance width, while entrance length had no effect. Microclimatic measurements revealed that occupied crevices provided cooler daytime conditions and greater thermal stability than nearby controls, whereas nighttime temperatures were similar across all crevices and approached ambient temperatures. Selecting deeper crevices with narrow entrances likely mitigates extreme daytime heat. The combination of solitary or small-group roosting, frequent switching, and structurally protective crevices reflects adaptation to thermal stress and predation risk. These findings provide a baseline for understanding roost selection in semi-arid regions and potential shifts to synanthropic roosting.

Short running title: Roosting strategy of Savi's Pipistrelle

1. Introduction

Roosting environment is one of the most prominent factors shaping bat biology (Kunz, 1982), affecting both the geographic distribution of individual species and the structure of bat communities (Findley, 1993; Russo et al., 2004). Bats inhabiting temperate regions typically exploit a variety of roost types throughout their annual cycle, switching among them according to season-specific requirements, such as hibernation, migration, maternity colony formation, swarming, and mating (Kunz, 1982). The availability and spatial distribution of suitable roosts within a landscape can determine population and group size (Fenton, 1970; Kunz, 1982), thereby influencing levels of sociality among bat species and populations (Kunz and Lumsden, 2003; Kerth, 2008).

Appropriate roost selection can reduce predation pressure and parasite load (Lewis, 1996; Lausen and Barclay, 2006; Lima and O'Keefe, 2013), buffer adverse weather conditions (Briggler and Prather, 2003), facilitate successful development of offspring (Racey, 1973; Tuttle and Stevenson, 1982; Wilde et al., 1999; Rodrigues et al., 2003; Lausen and Barclay, 2006), and affect commuting distances to foraging grounds (Lumsden et al., 2002). Moreover, the roost microclimate is particularly critical for heterothermic organisms (Vaughan and O'Shea, 1976; Frick et al., 2010), such as bats, in which temperature and thermal stability directly influence torpor use and daily energy expenditure (Kurta, 1986; Law and Chidel, 2007; Lučan and Radil, 2010). These factors are especially relevant in arid and semi-arid environments, where high ambient temperatures and pronounced thermal variability can impose strong physiological constraints.

Despite the importance of roosts, the roosting ecology of lithophilous bat species has received considerably less attention than that of forest-dwelling bats (Kerth et al., 2001; Willis and Brigham, 2007; Otto et al., 2016; Drake et al., 2020) or cave-dwelling species (Law and Chidel, 2007; Uhrin et al., 2010; Rajasegaran et al., 2018). Furthermore, most detailed studies

on rock-crevice roosting bats originate from North America (Chruszcz and Barclay, 2002; Lausen and Barclay, 2002; Neubaum, 2018; Moosman et al., 2023), whereas comparable data from Europe remain scarce. Yet, rock crevices constitute a potentially valuable roosting resource in European arid and semi-arid landscapes, where other roosting opportunities may be limited or absent. Studying the roosting ecology of lithophilous bats in these environments is therefore essential for understanding how bats persist under climatically stressful conditions.

Savi's pipistrelle (*Hypsugo savii*) is a small insectivorous bat species traditionally associated with rocky habitats, where it roosts primarily in inaccessible rock fissures and reaches its peak abundance in extensive rocky landscapes (Đulić, 1958; Horáček and Benda, 2004; Quetglas and Garrido, 2005; Dietz et al., 2009; Kipson et al., 2020). Although it can also use synanthropic roosts (Đulić, 1958), the species is considered a typical lithophilous bat within its native Mediterranean range. Over the past two decades, *H. savii* has expanded northwards into Central Europe (Spitzenberger, 1997; Kaňuch and Bartonička, 2006; Danko, 2007; Reiter et al., 2010; Uhrin et al., 2016), where newly established populations occur almost exclusively in urban environments and rely on synanthropic roosts. This shift in roosting strategy is thought to have facilitated range expansion originally driven by climate change, with urban areas providing a warmer and more thermally stable microclimate due to the heat island effect, as well as a high diversity of potential roosting sites (Ancillotto et al., 2018).

Despite its widespread distribution in the Mediterranean, most published information on *H. savii* from this region is limited to faunistic records and anecdotal observations (Flaquer et al., 2004; Tilova et al., 2005; Dondini and Vergari, 2008; Pandurski and Popov, 2008; Petrov and von Helversen, 2011). Detailed studies addressing its ecology and behaviour, particularly roosting strategy and roost selection, are largely lacking. As a result, *H. savii*

remains one of the least studied bat species in Europe in terms of roosting ecology. At the same time, it represents a valuable model for investigating the transition from natural to synanthropic roost use, a process that many bat species may have undergone in the past (Horáček, 1984; Lučan et al., 2025). Understanding roost selection and roosting behaviour in populations inhabiting natural, non-synanthropic environments is therefore crucial for elucidating the mechanisms underlying this transition.

In this study, we investigated the roosting ecology of reproductive females of Savi's pipistrelle within semi-arid open landscapes within the core of its historical distribution range. Specifically, we aimed to (i) describe roosting strategy, (ii) quantify roost selection based on structural characteristics, and (iii) assess the thermal characteristics of occupied roosts. By focusing on natural rocky habitats prior to recent range expansion and synanthropisation, this study provides new insights into the ecological drivers of roost use in arid and semi-arid environments.

2. Materials and methods

2.1 Study area

The study area (Fig. 1) is located in North Dalmatia, Zadar County, Croatia (see also Kipson et al., 2018), and encompasses the southeastern tip of the island of Pag and the adjacent Bočetina Peninsula, including the villages of Rtina, Ražanac, and Ljubač (geographical centroid: 44.29° N, 15.31° E). Parts of the area are included in the NATURA 2000 network (NW Dalmatia and the island of Pag) due to their high conservation value, with habitats such as eastern Mediterranean screes, sea cliffs, salt meadows, tall humid grasslands, and intertidal mudflats.

The coastline is predominantly limestone, highly articulated with gulfs and small bays (Fig. 1), and separated from the mainland and Mount Velebit by a sea channel approximately

3.5 km wide at its narrowest point. The regional climate is Mediterranean, characterised by hot, dry summers (mean June–August temperature: 23.4 °C; mean precipitation: 45.5 mm) and wetter late autumns (mean November precipitation: 124.4 mm). Winter temperatures rarely drop below 0 °C (mean December–February temperature: 7.8 °C). Climatic data were obtained from the Croatian Meteorological and Hydrological Service for the period 1961–2023 (www.meteo.hr).

The northeastern and eastern parts of the study area, exposed to the Velebit range, are strongly affected by the Bora wind, which enhances soil erosion and results in largely unvegetated limestone pavement with numerous vertical ground-level rock crevices. Further inland, the peninsula is primarily used as rocky sheep pasture, classified as eastern sub-Mediterranean dry grasslands. Human settlements are concentrated on the southern side of the peninsula, while inland valleys are dominated by extensive meadows and pastures interspersed with small-scale agriculture, including vineyards, olive groves, and vegetable gardens. Two freshwater streams flow through the study site, each forming a salt wetland at its estuary. Planted narrow forest belts of Aleppo pine (*Pinus halepensis*) and black pine (*Pinus nigra*) occur above the settlements of Rtina and Ljubač.

2.2 Bat capture and processing

Bats were captured during June and July over three consecutive years (2012–2014) using mist nets placed over one of the study area's streams and, later on, around roosts previously identified by radiotracking (Kipson et al., 2018). For each captured individual, body mass and forearm length were measured, and sex, age, and reproductive status were determined following Racey (1988). Reproductive females were fitted with radio transmitters (LB-2X 0.31; Holohil Systems Ltd., Woodlawn, Ontario, Canada) weighing less than 5% of the bat’s body mass. After trimming a small patch of dorsal fur, transmitters were attached

caudally to the interscapular region using surgical adhesive (Perma-Type). Bats were released immediately at the capture site after ensuring the transmitter was securely attached.

Day roosts were located using ICOM R-20 broadband receivers connected to three-element Yagi antennas, applying the homing-in method. Each individual was tracked daily until transmitter loss (mean tracking duration: 3.4 ± 2.1 days; range: 1–9 days). The relatively short tracking period reflected the extreme roosting environment within sharp limestone crevices, which facilitated rapid transmitter removal. Roosts were visually inspected for the presence of bats or traces (e.g. guano), assigned a unique identifier, temporarily marked with colour, and georeferenced using a GPS unit. All subsequent measurements of roosts were conducted only after bats had vacated the roost.

All bat handling procedures complied with national legislation and were approved by the Croatian Ministry of Environmental Protection and Nature (permit numbers: 517-07-1-1-1-12-2, 517-07-1-1-1-13-2, 517-07-1-1-1-14-5).

2.3 Microhabitat measurements

To characterise roost microhabitat structure, a 1 m² quadrat was centred on each identified roost crevice within the limestone pavement (hereafter “roost quadrat”). Within each quadrat, we measured the depth, width, and length of the roost crevice, as well as all other rock crevices present. Crevices shallower than 5 cm were excluded, as they were considered unsuitable for roosting. Analyses were restricted to structural characteristics of rock crevices because other commonly used microhabitat variables (e.g. aspect, slope, vegetation cover) showed no variation across the limestone pavement and were therefore uninformative. In total, structural data were collected from 45 roost quadrats located within the core roosting area.

2.4 Microclimatic measurements

For each roost crevice, a control crevice was selected by walking 20 m in a random compass direction (Snider et al., 2013). This distance ensured that control crevices were located within the same habitat type while minimising spatial overlap with the roost environment. All control crevices were visually inspected and confirmed to be unused by bats.

Temperature conditions were recorded using iButton data loggers (DS1922 and DS1923), programmed to log temperature hourly for at least 3 consecutive days. Within each crevice, two loggers were installed to capture vertical temperature gradients: one placed 5 cm below the surface ("shallow") and a second placed at ≥15 cm depth ("deep"). Ambient air temperature was recorded simultaneously at the same temporal resolution. Occasional datalogger errors during the monitoring period led to uneven temporal coverage, with some intervals being less comprehensively sampled than others.

Temperature data were categorised into daytime and nighttime periods based on local sunrise and sunset times for each sampling date, using the centre of the roosting area as the reference point. This allowed calculation of temperature stability and deviations from ambient conditions. In total, microclimatic data were obtained from 29 paired roost and control crevices, comprising 18 roosts used by pregnant females and 11 used by lactating females, yielding 31,665 hourly temperature records.

2.5 Statistical analysis

Analyses were conducted in two main stages to evaluate the role of structural characteristics in roost selection by Savi's pipistrelle (*Hypsugo savii*). First, we tested whether structural characteristics of roost crevices differed between gravid and lactating females. As the data were non-normally distributed, comparisons were performed using Wilcoxon signed-

rank tests. As no significant differences were detected, all roosts were pooled into a single category (hereafter “roost crevices”).

Roost selection was then assessed by comparing the structural characteristics of roost crevices with those of adjacent, available crevices within the same 1 m² quadrat using conditional logistic regression (Gail et al., 1980). Each roost quadrat was treated as a stratum to account for paired availability. Model significance was evaluated using analysis of deviance, and fitted relationships were visualised using sigmoid response curves.

Microclimatic data were analysed to address two questions: (1) whether temperature characteristics (stability and deviation from ambient temperature) differed between roost and control crevices, and (2) how these patterns were influenced by time of day (day/night) and measurement depth. Two linear mixed-effects models were performed utilising the restricted maximum likelihood (REML; Beale et al., 2010; Gałecki et al., 2013). Location type (roost or control crevice), depth, and time of day were included as fixed effects, while individual roost identity was treated as a random effect. Approximate p-values were derived using a normal distribution, and effect sizes were quantified using Cohen’s *d* (Rice & Harris, 2005), classified as small (d≈0.2), medium (d≈0.5), or large (d≈0.8). Predicted values with 95% confidence intervals were subsequently calculated and presented. All analyses were performed in R version 4.3.2 (R Core Team, 2023), using the packages *survival* version 3.4-0 (Therneau, 2022), *stringr* version 1.5.0 (Wickham, 2022), *tidyverse* (Wickham et al., 2019), *data.table* version 1.14.8 (Dowle & Srinivasan, 2023), and *lme4* (Bates et al., 2015).

3. Results

3.1 Roost use and social structure

We identified 58 day roosts used by 29 radio-tracked female Savi’s pipistrelles. Of these, 13 pregnant females used 31 unique roosts, 15 lactating females used 19 unique roosts,

and one female used 6 roosts during pregnancy and 2 additional roosts during lactation (Table A1).

During the first half of June, pregnant females predominantly roosted solitarily. Towards the end of June, close to parturition, small maternity groups of 2–5 adult individuals (mean = 3.5) were observed in six roosts. In early July, during the lactation period, solitary roosting was rare (observed in three individuals using five roosts), and most females roosted in small groups comprising 2–9 adult females (mean = 3.2), accompanied by an unknown number of offspring. In three cases, where we caught all lactating females from the same roost, we did not observe females carrying their offspring, indicating that separation of offspring and females might occur during night activity; however, we lack more detailed data on this topic.

Roost switching was frequent, occurring almost daily. The mean number of roosts used per individual was 2.46 ± 1.49 over a mean tracking duration of 3.4 ± 2.12 days. The mean distance between consecutive roosts was 80.0 ± 61.3 m (range: 8–273 m) for pregnant females and 167.8 ± 104.6 m (range: 23–383 m) for lactating females.

Throughout the study period, evening emergence of other bats was frequently observed in proximity (from a few metres up to several tens of metres) to our solitary focal individuals. During lactation, when groups of adult females were captured from a single roost, subsequent tracking revealed fission–fusion dynamics: individuals temporarily roosted in smaller subgroups or, more rarely, solitarily before re-forming groups, often with different group members, including unmarked individuals not present at the initial capture roost.

3.2 Roost types and spatial placement

Although the study area included both vertical and flat rocky habitats, most roosts were located at ground level. The majority of roosts were classified as vertical rock crevices

within limestone pavement (n = 54). Other roost types were rare and included a vertical crevice in a rock boulder (n = 1), synanthropic roosts in an uninhabited house (n = 2; used by the same individual), and horizontal crevice in a small rock cliffs (n = 1; Fig. 1). In one case, a radiotracked bat was found roosting in a ground-level crevice directly below a high rocky cliff containing numerous potential roosting crevices, indicating use of ground-level roosts despite the availability of elevated alternatives (Fig. 2).

3.3 Structural characteristics of ground-level roosts

Model diagnostics indicated that rock-crevice depth and entrance width were significantly associated with the probability of roost occupancy, whereas crevice length was not ($\chi^2 = 0.31$, $p = 0.578$; Table 1). The probability of occupancy increased with increasing crevice depth across all entrance widths. Model predictions further showed that crevices with narrower entrances (1.5 cm) reached higher occupancy probabilities at shallower depths compared to those with wider entrances (4.5 cm; Fig. 3). No differences in structural characteristics were detected between roosts used during pregnancy and those used during lactation (Table 2).

3.4 Microclimatic characteristics of roosts and control crevices

The best-supported model indicated that temperature differences relative to ambient conditions were primarily influenced by crevice type (roost vs. control) during the daytime, with measurement depth also playing a significant role (Table 3; Fig. 4). During daytime, roost crevices exhibited significantly lower temperatures than control crevices at shallow depths (mean difference from ambient: +3.4 °C vs. +4.2 °C), but higher temperatures at deeper positions (+3.1 °C vs. +2.7 °C). At night, temperatures converged between roost and control crevices at both depths, approaching ambient temperatures (deep: +0.81 °C vs.

+0.70 °C; shallow: +0.92 °C vs. +0.56 °C). During microclimatic measurements, ambient temperatures were consistently high (daytime mean = 27.95 °C, range 21.9°C - 28.8°C; nighttime mean = 26.34 °C, range 21.8 °C - 27.5 °C), and temperatures in roost crevices during daytime at a deep position (where most individuals were observed) had a mean of 31.18 °C (range 22.5 °C - 35.9 °C), whereas during nighttime the mean roost temperature was 27.3 °C (range 21.8 °C - 28.9 °C).

3.5 Temperature stability

At night, temperatures within rock crevices were highly stable, typically fluctuating within ±0.7 °C with no detectable differences between roost and control crevices or between shallow and deep measurement positions.

In contrast, daytime temperatures exhibited greater variability, generally fluctuating within ±2.0 °C (Table 4; Fig. 5). Overall diurnal temperature variability did not differ significantly between roosts and control crevices (LMM: $t = -1.136$, $p = 0.256$). However, shallow positions in control crevices tended to exhibit slightly greater temperature fluctuations (±2.3 °C) compared to shallow positions in roost crevices (±1.7 °C).

4. Discussion

Reproductive females of Savi's pipistrelle predominantly selected vertical, ground-level rock crevices situated within flat limestone pavements during the summer reproductive period. This represents a previously undocumented reproductive roosting strategy among European bats, particularly because roosts are placed at ground level. Comparable use of rock crevices has b een reported in several North American bat species, where roosts are typically located higher above ground in talus slopes, boulder fields or cliff faces (Blood and Clark, 1998; Lausen and Barclay, 2003; Neubaum et al., 2006; Rancourt et al., 2005; Moosman et

al., 2017, 2023; Neubaum, 2018), as well as in the alpine bat *Plecotus macrobularis* inhabiting screes and talus fields in mountainous regions of Europe (Alberdi et al., 2015). Underground spaces in screes have also been documented as pre-hibernation sites of *Eptesicus nilssonii* (Michaelsen and Grimstad, 2008) and *Myotis lucifugus* (Blejwas et al., 2021) in high latitudes of Europe and North America, respectively.

For Savi's pipistrelle, previous information on roost use has been limited and largely anecdotal, describing roosting mainly in buildings or cliffs (Đulić, 1958, 1970; Rakhmatulina, 1995; Vernier, 1995; Benda et al., 2006, 2007; Stoycheva et al., 2009; Ancillotto et al., 2018). Although both houses and cliffs were abundant within our study area, they were used only rarely, accounting for just a small fraction of all recorded roosts (3 out of 58 roosts). The pronounced preference for ground-level rock crevices observed in this study, together with incidental observation from Spain (Alcalde and Gosá, 2009), suggests that this roosting strategy may be more widespread within the species' native Mediterranean range than previously recognised, particularly in arid and semi-arid limestone landscapes.

Roosting at ground level is expected to increase exposure to terrestrial and fossorial predators, including small mammals, carnivores and snakes, the latter being particularly diverse in the study area (Zadravec and Gambiroža, 2019). We propose that this elevated predation risk strongly shapes the spatio-temporal organisation of Savi's pipistrelle populations in our study, influencing group size, roost fidelity and roost-switching behaviour. Radiotracked females roosted solitarily or in very small groups even during lactation, a period when most European bat species form large maternity colonies (Dietz et al., 2009). Larger groups likely increase detectability by predators through elevated flight activity, vocalisations and olfactory cues at the roost (Lima and O'Keefe, 2013).

In addition, females switched roosts almost daily, a behaviour that may further reduce the likelihood of being discovered by predators. The energetic costs associated with frequent

roost switching are likely mitigated by the high density of suitable rock crevices typical of karstic landscapes, which dominate much of the species' Mediterranean distribution. Narrow roost entrances may further limit predator access. Collectively, small group size, frequent roost switching and selection of narrow crevices appear to constitute an effective behavioural strategy for minimising predation risk in exposed natural roosts.

Our findings also provide insights into the processes underlying the shift from natural to synanthropic roosts observed, especially during the species' recent northward range expansion. In Central Europe, Savi's pipistrelle occupies urban environments and roosts almost exclusively in buildings (Uhrin et al., 2016). This transition is likely accompanied by changes in roosting behaviour, particularly increased roost fidelity. Indeed, bats roosting in buildings exhibit much higher fidelity than individuals using natural roosts (Ancillotto et al., 2018). Buildings generally provide enhanced protection from predators (Voigt et al., 2016), reducing the need for frequent roost switching. Thus, relaxation of predation pressure may facilitate larger, more stable roosting groups in synanthropic populations.

Microclimatic conditions emerged as another key factor shaping roost selection. Deeper crevices were used more frequently and maintained significantly cooler temperatures than control crevices at shallower depths during the daytime, when ambient temperatures were extremely high. Deeper, tube-like crevices may promote a chimney (stack) effect, in which cooler air from lower sections rises, buffering thermal extremes near the roosting area. Given the high temperatures during the reproductive period, selecting roosts with strong cooling capacity appears crucial for reproductive females.

Roost crevices also exhibited greater thermal stability, as indicated by lower temperature differences between shallow and deep sections compared to control crevices. Such stability is consistent with previous studies showing that rock-crevice roosts enable bats to employ torpor effectively even during reproduction (Chruszcz and Barclay, 2002; Lausen

and Barclay, 2003; Moosman et al., 2023). These findings corroborate early observations suggesting high thermal tolerance in Savi's pipistrelle (Kuzyakin, 1950) and align with recent work demonstrating the species' ability to withstand extreme roost microclimates (Ancillotto et al., 2018). More broadly, our results support the hypothesis that thermal physiology and roost preference have co-evolved in bats (Czenze et al., 2021), particularly in species inhabiting hot and arid environments.

Finally, we observed that lactating females shared roosts with other radiotracked or unmarked individuals, with groups forming, dissolving and reassembling over a short time period and on rare occasions even exhibiting a day of solitary roosting. This pattern is characteristic of fission–fusion social organisation, widely documented in bats (Patriquin and Ratcliffe, 2016). Consequently, the functional social unit (colony) is likely substantially larger than the number of individuals occupying a single roost at any given time. We hypothesise that the reduction of predation pressure associated with synanthropic roosting during northward expansion may facilitate a shift from many small, ephemeral roosting groups to fewer, larger and more stable colonies. Further comparative studies across the species' range are required to test this hypothesis.

In conclusion, the frequent use of vertical ground-level rock crevices within limestone pavements represents a novel, previously underappreciated roosting strategy for Savi's pipistrelle. Together with similar incidental observations from the western Mediterranean, our findings suggest that this strategy may be widespread within the species' native range, although largely overlooked. This contrasts sharply with the predominantly synanthropic roosting observed in newly colonised northern areas, highlighting the species' remarkable behavioural flexibility. However, reliance on open rocky habitats may also increase vulnerability to anthropogenic threats, such as wind farms, which are often located on exposed rocky ridges in the Mediterranean region (Ferri et al., 2016) that coincide with both

preferred roosting (this study) and foraging habitats (Kipson et al., 2018). Our study therefore underscores the conservation importance of ground-level rocky habitats in arid and semi-arid landscapes, which are frequently neglected as potential bat roosting sites.

References

Alberdi, A., Aihartza, J., Aizpurua, O., Salsamendi, E., Brigham, R.M., Garin, I., 2015. Living above the treeline: roosting ecology of the alpine bat *Plecotus macrobullaris*. *Eur. J. Wildl. Res.* 61, 17–25.

Alcalde, J.T., Gosá, A., 2009. The discovery of two Savi's pipistrelles under a stone reveals its adaptation to shrub steppe habitats. *Munibe* 57, 303–305.

Ancillotto, L., Budinski, I., Nardone, V., Di Salvo, I., Della Corte, M., Bosso, L., Conti, P., Russo, D., 2018. What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection. *Behav. Process.* 157, 540–546.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J., Elston, D.A., 2010. Regression analysis of spatial data. *Ecol. Lett.* 13, 246–264.

Benda, P., Andreas, M., Kock, D., Lučan, R.K., Munclinger, P., Nová, P., Obuch, J., Ochman, K., Reiter, A., Uhrin, M., Weinfurtová, D., 2006. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology. *Acta Soc. Zool. Bohem.* 70, 1–329.

Benda, P., Hanák, V., Horáček, I., Hulva, P., Lučan, R., Ruedi, M., 2007. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 5. Bat fauna of Cyprus. *Acta Soc. Zool. Bohem.* 71, 71–130.

Blejwas, K.M., Pendleton, G.W., Kohan, M.L., Beard, L.O., 2021. The Milieu Souterrain Superficiel as hibernation habitat for bats: implications for white-nose syndrome. *J. Mammal.* 102, 1110–1127.

Blood, R.B., Clark, M.K., 1998. *Myotis vivesi*. *Mamm. Species* 588, 1–3.

Briggler, J.T., Prather, J.W., 2003. Seasonal use and selection of caves by the eastern pipistrelle bat (*Pipistrellus subflavus*). *Am. Midl. Nat.* 149, 406–412.

Chruszcz, B.J., Barclay, R.M.R., 2002. Thermoregulatory ecology of a solitary bat roosting in rock crevices. *Funct. Ecol.* 16, 18–26.

Czenze, Z.J., Smit, B., van Jaarsveld, B., Freeman, M.T., McKechnie, A.E., 2022. Caves, crevices and cooling capacity: roost microclimate predicts heat tolerance in bats. *Funct. Ecol.* 36, 38–50.

Danko, Š., 2007. Reproduction of *Hypsugo savii* and *Pipistrellus kuhlii* in eastern Slovakia: further evidence of northward expansion. *Vespertilio* 11, 13–24.

Dietz, C., Nill, D., von Helversen, O., 2009. *Bats of Britain, Europe and Northwest Africa*. A & C Black, London.

Dondini, G., Vergari, S., 2008. Teriofauna dell'Appennino Pistoiese (Toscana). *Natura Modenese* 8, 35–48.

Dowle, M., Srinivasan, A., 2023. data.table: extension of data.frame. R package version 1.14.8.

Drake, E.C., Gignoux-Wolfsohn, S., Maslo, B., 2020. Systematic review of the roost-site characteristics of North American forest bats: implications for conservation. *Diversity* 12, 76.

Đulić, B., 1958. Über die Ökologie der Alpenfledermaus *Pipistrellus savii* auf der Insel Mljet. *Säugetierkd. Mitt.* 6, 10–11.

Đulić, B., 1970. Ökologische Beobachtungen der Fledermäuse der Adriatischen Inseln. *Z. Säugetierkd.* 35, 45–51.

Fenton, M.B., 1970. Population studies of *Myotis lucifugus* in Ontario. *Life Sci. Contrib. R. Ont. Mus.* 77, 1–34.

Ferri, V., Battisti, C., Soccini, C., 2016. Bats in a Mediterranean mountainous landscape. *Environ. Manage.* 57, 1240–1246.

Findley, J.S., 1993. *Bats: A Community Perspective*. Cambridge Univ. Press, Cambridge.

Flaquer, C., Ruíz-Jarillo, R., Arrizabalaga, A., 2004. Contribution to the knowledge of chiropteran fauna of Catalonia. *Galemys* 16, 39–55.

Frick, W.F., Reynolds, D.S., Kunz, T.H., 2010. Influence of climate and reproductive timing on demography of little brown myotis. *J. Anim. Ecol.* 79, 128–136.

Gail, M.H., Lubin, J.H., Rubinstein, L.V., 1980. Likelihood calculations for matched case-control studies. *Biometrika* 68, 703–707.

Gałecki, A., Burzykowski, T., 2013. *Linear Mixed-Effects Models*. Springer, New York.

Horáček, I., 1984. Remarks on the causality of population decline in European bats. *Myotis* 21, 138–147.

Horáček, I., Benda, P., 2004. *Hypsugo savii*. In: Krapp, F. (Ed.), *Handbuch der Säugetiere Europas*, Vol. 4/II. Aula-Verlag, Wiesbaden, pp. 912–941.

Kaňuch, P., Bartonička, T., 2006. Savi's pipistrelle (*Hypsugo savii*) breeding in the Czech Republic. *Lynx* 37, 19–21.

Kerth, G., 2008. Causes and consequences of sociality in bats. *BioScience* 58, 737–755.

Kerth, G., Weissmann, K., König, B., 2001. Day roost selection in female Bechstein's bats. *Oecologia* 126, 1–9.

Kipson, M., Šálek, M., Lučan, R.K., Uhrin, M., Maxinová, E., Bartonička, T., Andreas, M., Kipson, K., Pušić, A., Rnjak, D., Naďo, L., Horáček, I., 2018. Foraging habitat, home range and diet of Savi's pipistrelle. *Acta Chiropterol.* 20, 351–360.

Kipson, M., Gazaryan, S., Horáček, I., 2020. *Hypsugo savii*. In: Hackländer, K., Zachos, F.E. (Eds.), *Handbook of the Mammals of Europe*. Springer, Cham.

Kunz, T.H., 1982. Roosting ecology of bats. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Plenum Press, New York, pp. 1–55.

Kunz, T.H., Lumsden, L.F., 2003. Ecology of cavity and foliage roosting bats. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. Univ. Chicago Press, Chicago, pp. 3–89.

Kurta, A., 1986. Factors affecting resting and postflight body temperature of little brown bats. *Physiol. Zool.* 59, 429–438.

Kuzyakin, A.P., 1950. *Bats (Letuchie myshi)*. Sovietskaya Nauka, Moscow.

Lausen, C.L., Barclay, R.M.R., 2002. Roosting behaviour of female big brown bats in rock crevices. *Can. J. Zool.* 80, 1069–1076.

Lausen, C.L., Barclay, R.M.R., 2003. Thermoregulation and roost selection by reproductive female big brown bats. **J. Zool.** 260, 235–244.

Lausen, C.L., Barclay, R.M.R., 2006. Benefits of living in a building. *J. Mammal.* 87, 362–370.

Law, B.S., Chidel, M., 2007. Bats under a hot tin roof. *Aust. J. Zool.* 55, 49–55.

Lewis, S.E., 1996. Low roost-site fidelity in pallid bats. *Behav. Ecol. Sociobiol.* 39, 335–344.

Lima, S.L., O'Keefe, J.M., 2013. Do predators influence the behaviour of bats? *Biol. Rev.* 88, 626–644.

Lučan, R.K., Radil, J., 2010. Population structure of *Myotis daubentonii* responding to microclimate of anthropogenic roosts. *Biologia* 65, 1072–1080.

Lučan, R.K., Jor, T., Romportl, D., Morelli, F., 2025. Use of synanthropic roosts by bats in Europe and North America. *Mammal Rev.* 55, e12380.

Lumsden, L.F., Bennett, A.F., Silins, J.E., 2002. Location of roosts in fragmented landscapes. *Biol. Conserv.* 106, 237–249.

Michaelsen, T.C., Grimstad, K.J., 2008. Rock scree as a new habitat for bats. *Nyctalus* 13, 122–126.

Moosman, P.R., Andersen, P.R., Frasier, M.G., 2017. Use of rock crevices in winter. *Banisteria* 48, 9–13.

Moosman, P.R. Jr., Marsh, D.M., Pody, E.K., Brust, T.J., 2023. Differential selection of roosts by *Myotis leibii*. *J. Mammal.* 104, 723–738.

Neubaum, D.J., 2018. Unsuspected retreats of little brown myotis. *J. Mammal.* 99, 1294–1306.

Neubaum, D.J., O'Shea, T.J., Wilson, K.R., 2006. Autumn migration and rock crevice hibernacula. *J. Mammal.* 87, 470–479.

Otto, M.S., Becker, N.I., Encarnacão, J.A., 2016. Roost characteristics and heterothermy. *Ecol. Res.* 31, 385–391.

Pandurski, I., Popov, V., 2008. Monitoring study on bats (Mammalia, Chiroptera) in Eastern Rhodopes, Bulgaria. *Conference "Exploration and protection of karst and caves" 50th years Student Speleological Club "Akademic" – Sofia*.

Patriquin, K.J., Ratcliffe, J.M., 2016. Fission–fusion dynamics in bats. In: Ortega, J. (Ed.), *Sociality in Bats*. Springer, Cham, pp. 65–103.

Petrov, B.P., von Helversen, O., 2011. Bats of the Western Rhodopes. *Biodivers. West. Rhodopes II*, 525–581.

Quetglas, J., Garrido, J.A., 2005. Rastros y señales de murciélagos ibéricos. *Galemys* 17, 53–62.

R Core Team, 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Racey, P.A., 1973. Environmental factors affecting gestation length. *J. Reprod. Fertil.* 61, 123–129.

Racey, P.A., 1988. Reproductive assessment in bats. In: Kunz, T.H. (Ed.), *Ecological and Behavioural Methods for the Study of Bats*. Smithsonian Inst. Press, Washington, DC, pp. 31–46.

Rajasegaran, P., Shazali, N., Anwarali Khan, F.A., 2018. Microclimate and physiological effects in cave roosts of bats. *Zool. Sci.* 35, 521–527.

Rakhmatulina, I.K., 1995. Bats' attachment to shelters in Transcaucasia. *Myotis* 32–33, 197–202.

Rancourt, S.J., Rule, M.I., O'Connell, M.A., 2005. Maternity roost selection of *Myotis evotis*. *J. Mammal.* 86, 77–84.

Reiter, A., Bartonička, T., Lučan, R.K., Řehák, Z., 2010. New records of *Hypsugo savii* in the Czech Republic. *Vespertilio* 13–14, 121–125.

Rice, M.E., Harris, G.T., 2005. Comparing effect sizes in follow-up studies. *Law Hum. Behav.* 29, 615–620.

Rodrigues, L., Zahn, A., Rainho, A., Palmeirim, J.M., 2003. Roosting behaviour of *Myotis myotis*. *Mammalia* 67, 321–335.

Russo, D., Cistrone, L., Jones, G., Mazzoleni, S., 2004. Roost selection by barbastelle bats. *Biol. Conserv.* 117, 73–81.

Snider, E.A., Cryan, P.M., Wilson, K.R., 2013. Roost selection by western long-eared myotis. *J. Mammal.* 94, 640–649.

Spitzenberger, F., 1997. Distribution and range expansion of Savi's bat in Austria. *Z. Säugetierkd.* 62, 179–181.

Stoycheva, S., Georgiev, D., Pandourski, I., Tilova, E., 2009. Bat diversity in urban areas of Bulgaria. *Lynx* 40, 83–93.

Therneau, T., 2022. A package for survival analysis in R. R package version 3.4-0.

Tilova, E.K., Stoycheva, S.B., Georgiev, D.G., 2005. New information on bat distribution in Bulgaria. *Animalia* 41, 135–144.

Tuttle, M.D., Stevenson, D., 1982. Growth and survival of bats. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Plenum Press, New York, pp. 105–150.

Uhrin, M., Kaňuch, P., Krištofík, J., Paule, L., 2010. Phenotypic plasticity in the greater mouse-eared bat in extremely different roost conditions. *Acta Theriol.* 55, 153–164.

Uhrin, M., Hüttmeir, U., Kipson, M., Estók, P., Sachanowicz, K., Bücs, S., Karapandža, B., Paunović, M., Presetnik, P., Bashta, A.-T., Maxinová, E., Lehotská, B., Lehotský, R., Barti, L., Csösz, I., Szodoray-Paradi, F., Dombi, I., Görföl, T., Boldogh, S.A., Jére, C., Pocora, I., Benda, P., 2016. Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: A review. *Mammal Rev.* 46, 1–16.

Vaughan, T.A., O'Shea, T.J., 1976. Roosting ecology of the pallid bat. *J. Mammal.* 57, 19–42.

Vernier, E., 1995. Presence and distribution of bats in Padova. *Myotis* 32–33, 193–195.

Voigt, C.C., Phelps, K.L., Aguirre, L.F., Schoeman, M.C., Vanitharani, J., Zubaid, A., 2016. Bats and buildings. In: Voigt, C., Kingston, T. (Eds.), *Bats in the Anthropocene*. Springer, Cham, pp. 427–462.

Wickham, H., 2022. stringr: simple, consistent wrappers for string operations. R package version 1.5.0.

Wickham, H., Averick, M., Bryan, J., et al., 2019. Welcome to the tidyverse. *J. Open Source Softw.* 4, 1686.

Wilde, C.J., Knight, C.H., Racey, P.A., 1999. Influence of torpor on milk protein secretion. *J. Exp. Zool.* 284, 35–41.

Willis, C.K., Brigham, R.M., 2007. Social thermoregulation and roost preferences. *Behav. Ecol. Sociobiol.* 62, 97–108.

Zadravec, M., Gambiroža, P., 2019. First report on the conservation status of amphibians and reptiles in Croatia. Zagreb.

Tables

Table 1. Analysis of Deviance for Cox Model focused on crevice occupancy. Table includes log-likelihood values, Chi-squared statistics ($\chi 2$), degrees of freedom (Df), and p-values for predictor variables.

Analysis of Deviance Table (Cox model)

	loglik	χ^2	Df	p-value
NULL	-116.356			
crevice depth	-92.4	47.91	1	<0.001
width of entrance	-82.338	20.13	1	<0.001
length of entrance	-82.183	0.31	1	0.578

Table 2. Testing the difference of physical measurements between roosts used by pregnant and lactating females.

	median (min-max)		Wilcoxon test	
parameter	pregnant	lactating	z	p
depth (cm)	38.5 (13-67)	40 (25-67)	-0.620	0.535
width of opening (cm)	2.25 (1.5-4.5)	2 (1.5-5)	-0.194	0.846
length of opening (cm)	6.75 (2.5-22)	7 (2.5-29)	-0.887	0.376

Table 3. Estimates and effect sizes from a linear mixed-effects modelling of the temperature profile of roosting and random rock crevices.

	Estimate	Std. Error	t-value	approx. p-value	Cohen's d
Intercept	2.905	0.148	19.54	<0.001	
group$_{roost}$	0.19	0.026	7.3	<0.001	-0.062
depth$_{shallow}$	0.549	0.041	13.19	<0.001	-0.206
period$_{night}$	-2.281	0.026	-86.77	<0.001	1.006

Table 4. Estimates and effect sizes from linear mixed-effects modelling of temperature stability of roosting versus random rock crevices.

	Estimate	Std. Error	t-value	approx. p-value	Cohen's d
Intercept	1.165	0.067	23.86	<0.001	
group$_{roost}$	-0.028	0.025	-1.14	0.256	0.041
depth$_{shallow}$	0.271	0.039	6.96	<0.001	-0.198
period$_{night}$	-1.041	0.025	-41.27	<0.001	1.403

Figures

Figure 1. The position of all roosts of reproductive females of Savi's pipistrelle, showing that the majority of them are aggregated in a narrow limestone pavement strip along the sea coast in the NE part of the study area.

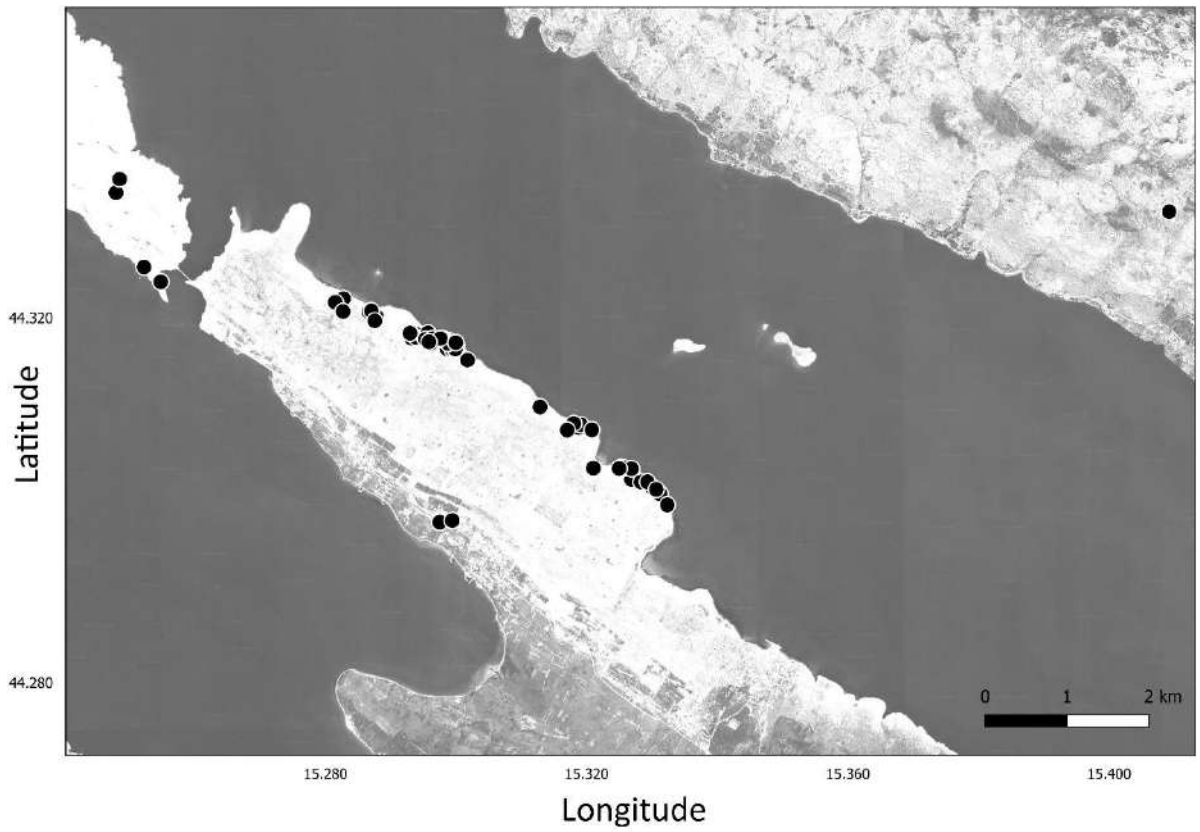


Figure 2. The type of habitat and rock-crevices used for roosting by female Savi's pipistrelle. Upper row showing the appearance of limestone pavement where majority (54) of roosts were found, middle row shows a typical roost and vertical ground-level rock-crevice used by bats, lower left showing one case where the female chose a ground-level vertical roost despite the abundance of potential cliff crevices, lower right showing Savi's pipistrelles roosting in the vertical ground-level rock-crevice.

Figure 3. Probability of occupancy in relation to crevice depth for various widths of roost rock-crevice entrance (based on conditional regression model).

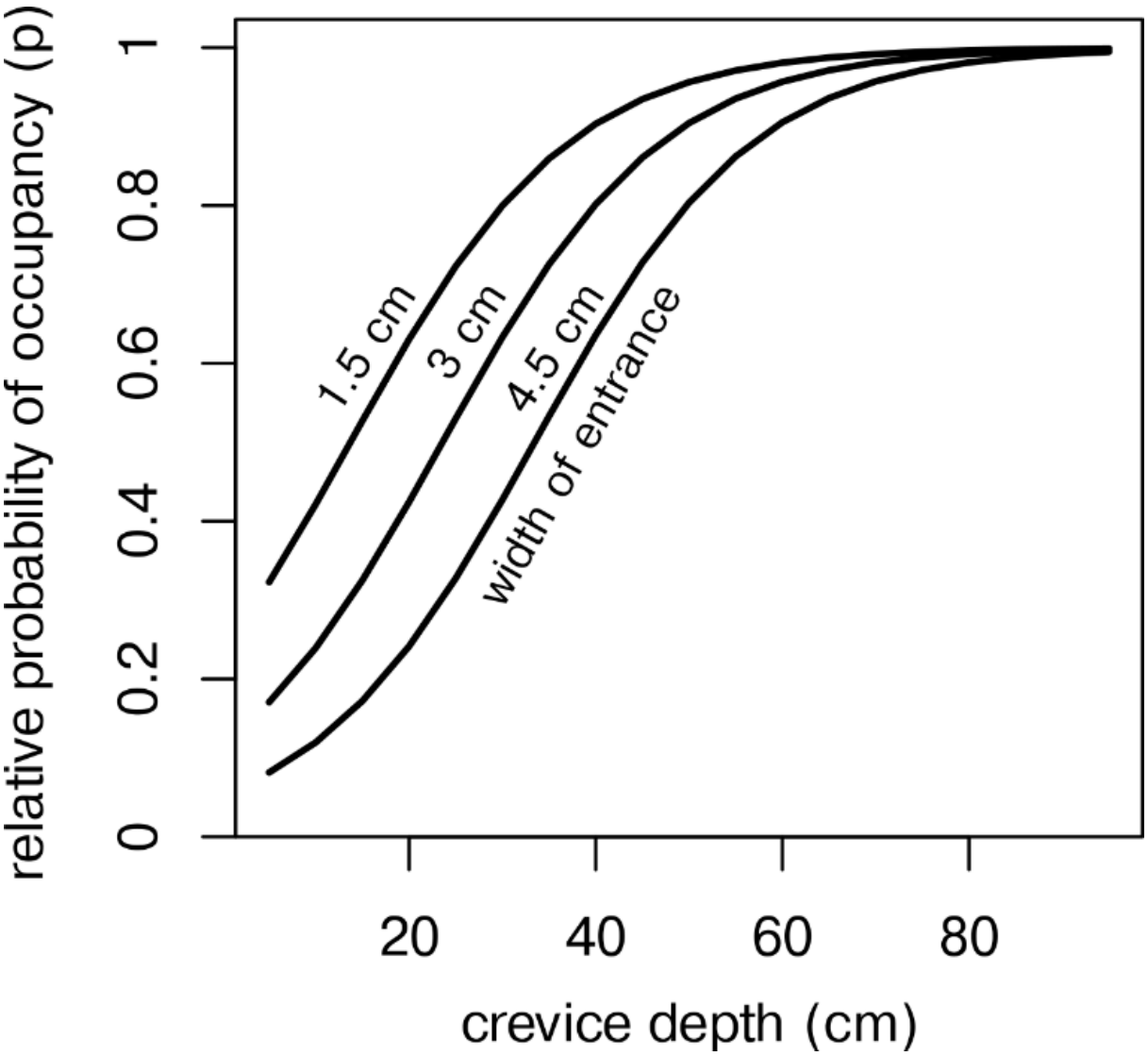


Figure 4. Predicted difference values between the ambient and rock-crevice temperatures. These predictions are based on combinations of factors, including whether the rock-crevice is occupied by a bat, the depth of measurement within the crevice (shallow vs deep position), and the time period of the day. When the intervals do not overlap, it indicates a statistically significant difference.

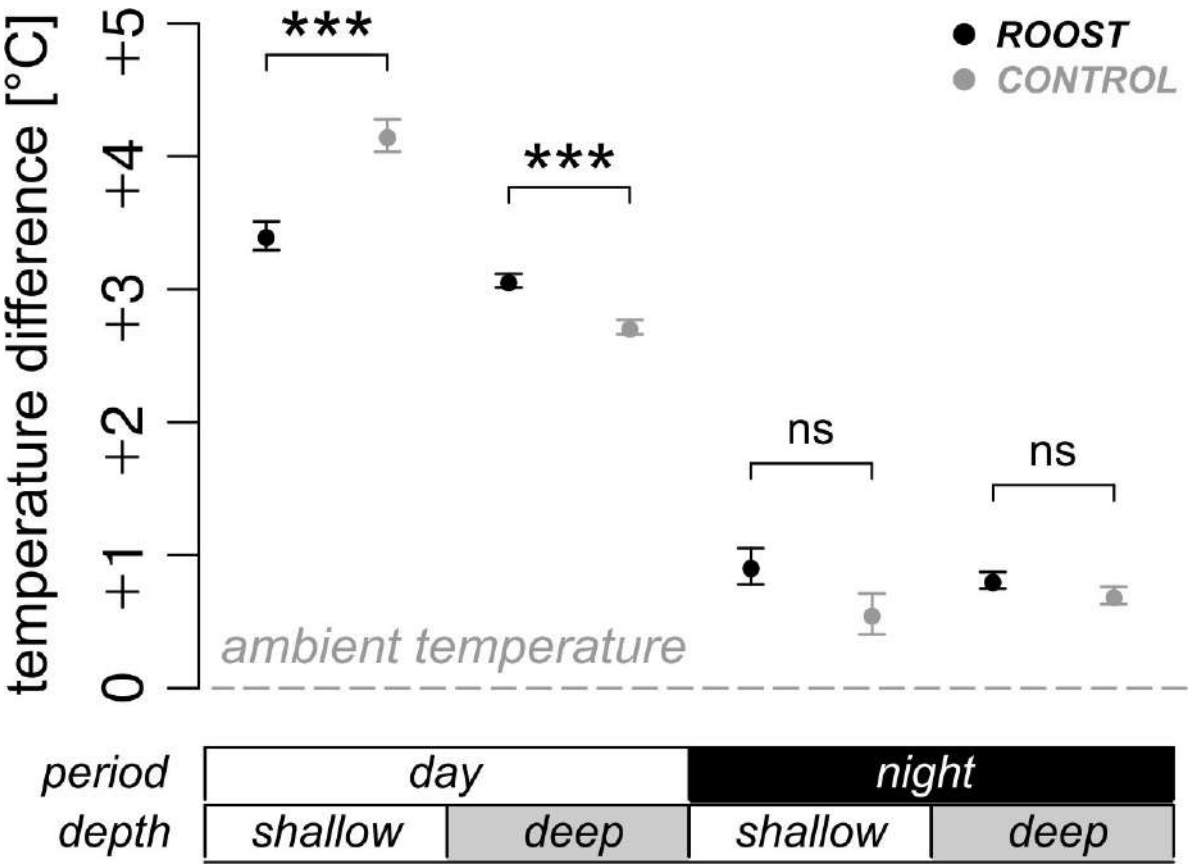
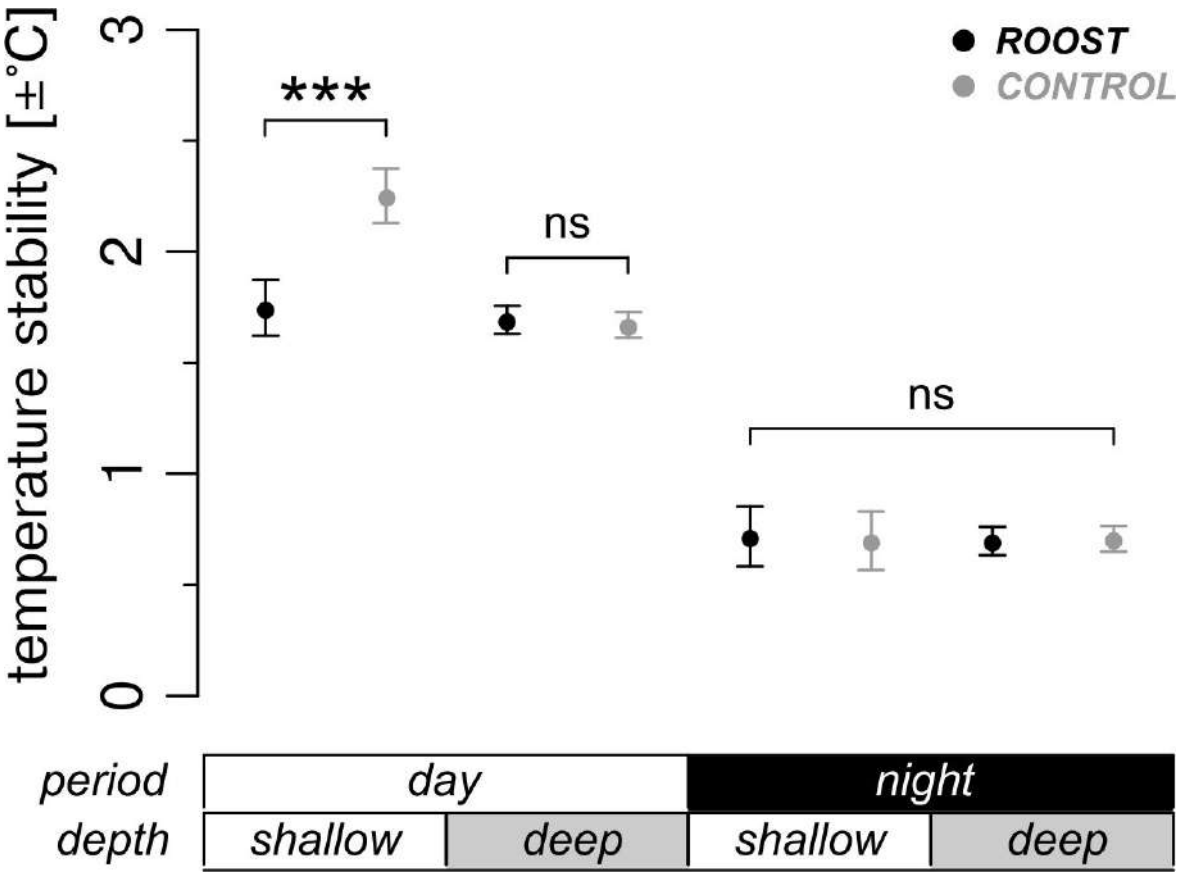


Figure 5. Predicted difference values for the temperature stability of crevices. These predictions are based on combinations of factors, including whether crevice is occupied by bat, the depth of measurement within the crevice (shallow vs deep), and the time period of the day. When the intervals do not overlap, it indicates a statistically significant difference.



Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Title page

Ground-level rock crevices as reproductive roosts of Savi's pipistrelle (*Hypsugo savii*) in semi-arid landscapes of the Eastern Mediterranean

Marina Kipson[1*], Martin Šálek[2,3], Ladislav Naďo[4], Helena Jahelková[1], Ivan Horáček[1], Radek K. Lučan[1]

[1] Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 12844 Prague, Czech Republic

[2] Institute of Vertebrate Biology, Academy of Sciences, Czech Republic, Květná 8, 60365 Brno, Czech Republic

[3] Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Suchdol, 16500 Prague, Czech Republic

[4] Slovak Bat Conservation Society, 08501 Bardejov, Slovakia

*** Corresponding author:** Marina Kipson, Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Prague, Czech Republic. Email: marinakipson@gmail.com

Appendix I

Table A1. Overview of individual bat measurements, number of tracking days and utilised roosts.

Bat ID	**Reproduction status**	**Forearm lenght/ mm**	**Mass/g**	**No. of tracking days**	**No. of roosts**
HS1	Pregnant	33,6	8	1	1
HS2	Pregnant	34,8	9,5	3	2
HS3	Pregnant	33,7	7,5	2	2
HS4	Pregnant	32,6	6,5	1	1
HS6	Pregnant	34,1	8,1	3	3
HS7	Pregnant	34,1	7	3	3
HS8	Pregnant	33	9	3	3
HS9	Pregnant	35,8	10	2	2
HS11	Pregnant	34,1	9,75	4	4
HS19	Pregnant	34,9	10,5	1	1
HS20	Pregnant	36	11,5	3	2
HS21	Pregnant	34,1	11,5	9	6
HS21	Lactating			4	2
HS22	Pregnant	31,4	11	3	2
HS23	Pregnant	34,9	9,5	6	5
HS25	Lactating	36,6	9	3	1
HS27	Lactating	34,6	10	1	1
HS28	Lactating	34,5	9,5	1	1

HS29	Lactating	35,3	8,5	1	1
HS31	Lactating	34,1	8,5	1	1
HS35	Lactating	36,1	9	3	1
HS114	Lactating	34,3	10	4	4
HS115	Lactating	35,6	7	7	5
HS116	Lactating	33,1	7	6	4
HS117	Lactating	34,6	7	5	3
HS118	Lactating	33,4	7	7	5
HS119	Lactating	33,9	8	2	2
HS120	Lactating	33,4	8	7	4
HS121	Lactating	33,5	7	3	1
HS122	Lactating	34,2	7	3	1

Acknowledgements

We want to thank everyone who contributed to the fieldwork, namely Ana Pušić, Tomaš Bartonička, Karolina Kipson, Marcel Uhrin, Edita Maxinova, Rudo Kipson, Dragica Kipson, Dina Rnjak, Petra Žvorc, Daniela Hamidović, Vida Zrnčić and Jana Vandrovcová.

CRediT authorship contribution statement

Marina Kipson: Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualisation. **Martin Šálek**: Writing – review & editing, Methodology, Investigation, Conceptualisation. **Ladislav Naďo**: Writing – review & editing, Formal analysis, Data curation, Visualisation. **Helena Jahelková**: Writing – review & editing, Methodology, Investigation. **Ivan Horáček**: Writing – review & editing, Supervision, Resources, Methodology, Conceptualisation. **Radek Lučan**: Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualisation.

Funding

This project was supported by the Charles University grant (SVV 260 792/2025) and the Charles University Research Centre program No. 204069. MŠ was partly supported by the project of the Czech Academy of Sciences (Strategie AV21 Krize biodiverzity) and the research aim of the Czech Academy of Sciences (RVO 68081766).

Data availability

Data will be made available on request.

Paper 5

Maxinová, E., Kipson, M., Naďo, L., Hradická, P. and Uhrin, M. (2016) ‘Foraging strategy of Kuhl’s pipistrelle at the northern edge of the species distribution’, *Acta Chiropterologica*, 18, pp. 215–222. Available at: https://doi.org/10.3161/15081109ACC2016.18.1.012

Acta Chiropterologica, 18(1): 215–222, 2016
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2016.18.1.012

Foraging strategy of Kuhl's pipistrelle at the northern edge of the species distribution

EDITA MAXINOVÁ[1, 6], MARINA KIPSON[2], LADISLAV NAĎO[3], PETRA HRADICKÁ[4], and MARCEL UHRIN[1, 5]

[1]*Department of Zoology, Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Moyzesova 11, 040 01 Košice, Slovakia*
[2]*Vertebrate Zoology Research Group, Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Praha, Czech Republic*
[3]*Department of Animal Ecology, Institute of Forest Ecology, Slovak Academy of Sciences, Štúrova 2, 960 53 Zvolen, Slovakia*
[4]*Department of Animal Physiology, Institute of Biology and Ecology, Faculty of Science, Pavol Jozef Šafárik University in Košice, Moyzesova 11, 040 01 Košice, Slovakia*
[5]*Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, 165 21 Praha 6, Czech Republic*
[6]*Corresponding author: E-mail: edita.maxinova@gmail.com*

Rapid range expansion of Kuhl's pipistrelle (*Pipistrellus kuhlii*) has been observed throughout Europe, and in addition to its natural habitats of temperate grasslands and agricultural areas, the species is common in city centres, where it roosts in human-made structures. It has been suggested that the flexibility of this species in regard to different human-induced changes, such as climate change and urbanization, is responsible for the apparent range shift. Although *P. kuhlii* exhibits one of the highest degrees of synanthropy among bat species in Europe, its ecology has thus far not been thoroughly studied. This study aims to describe its foraging and roosting selection in Central Europe (eastern Slovakia), where the northernmost maternity colony of *P. kuhlii* roosts in human settlements. Radio-tracking was conducted during the pre-parturition and post-lactation periods. We identified six artificial roosts within the study area that were interlinked, with bats switching between them. Ten individuals were used for modelling foraging-habitat utilization, which revealed that bats were highly selective. The only habitat type that bats clearly preferred, regardless of season, was an urban illuminated area close to a river. Only slight avoidance — of open areas — was observed during the pre-parturition period.

Key words: Chiroptera, urban, telemetry, prefabricated houses, foraging habitat

INTRODUCTION

Urbanization is currently one of the most prominent and increasing human-induced habitat alterations worldwide, acting as a homogenizing force on the environment (McKinney, 2006). The loss of structural variability has a huge impact on species persistence in such newly created landscapes (Sala *et al*., 2000). However, the impact of urbanization on biodiversity can be mixed, ranging from complete avoidance to exploitation (McKinney, 2008), and is usually connected to life-history traits of individual species (Kark *et al*., 2007).

It has been noted that certain bat species benefit from using artificial buildings as roosting sites and adapt well to life in towns (Bihari, 2004; Neubaum *et al.*, 2007; Scales and Wilkins, 2007). The generally higher temperatures in cities in contrast to the surrounding landscape (Arnfield, 2003) could influence thermoregulation within roosts and consequently enhance energy savings and reproductive phenology (e.g. birth dates) while also providing better anti-predator protection and/or enabling faster juvenile development (Neuweiler, 2000; Lausen and Barclay, 2006). On the other hand, the higher level of traffic in towns may increase bat mortality in urban areas through collisions with vehicles (Lodé, 2000).

Among urban dwelling bat species, Kuhl's pipistrelle (*Pipistrellus kuhlii*) exhibits one of the highest degrees of synanthropy among Western Palearctic bat species (Yom-Tov and Kadmon, 1998; Mendelssohn and Yom-Tov, 1999; Bogdanowicz, 2004). It is a small vespertilionid that usually forms colonies of 20–100 females with their pups (Bogdanowicz, 2004). Probably the main reason behind the strong exploitation of urban habitats is that this opportunistic aerial hawker largely benefits from

foraging in areas where lights attract insects (Haffner and Stutz, 1985).

In the last three decades, based on newly gathered records (Sachanowicz *et al.*, 2006; Popczyk *et al*., 2008; Dietz *et al.*, 2009; Dietz and Kiefer, 2014), a rapid range expansion of *P. kuhlii* in a northward direction has been observed throughout most of Europe (Fig. 1 A). This fact is particularly interesting because this species is considered to be sedentary, at least according to banding data (Hutterer *et al*., 2005). It has been proposed that both flexibility towards climate change and urbanization could explain this significant northward expansion of the species' range (Uhrin *et al*., 2016).

Although different hypotheses have been proposed for the range expansion of *P. kuhlii*, more detailed data about its ecology, more specifically its habitat utilization, are thus far lacking. Therefore, we aimed to describe foraging and roosting preferences of the species at the northernmost border of its distribution and compare our findings with preference observed in its core area. This should provide

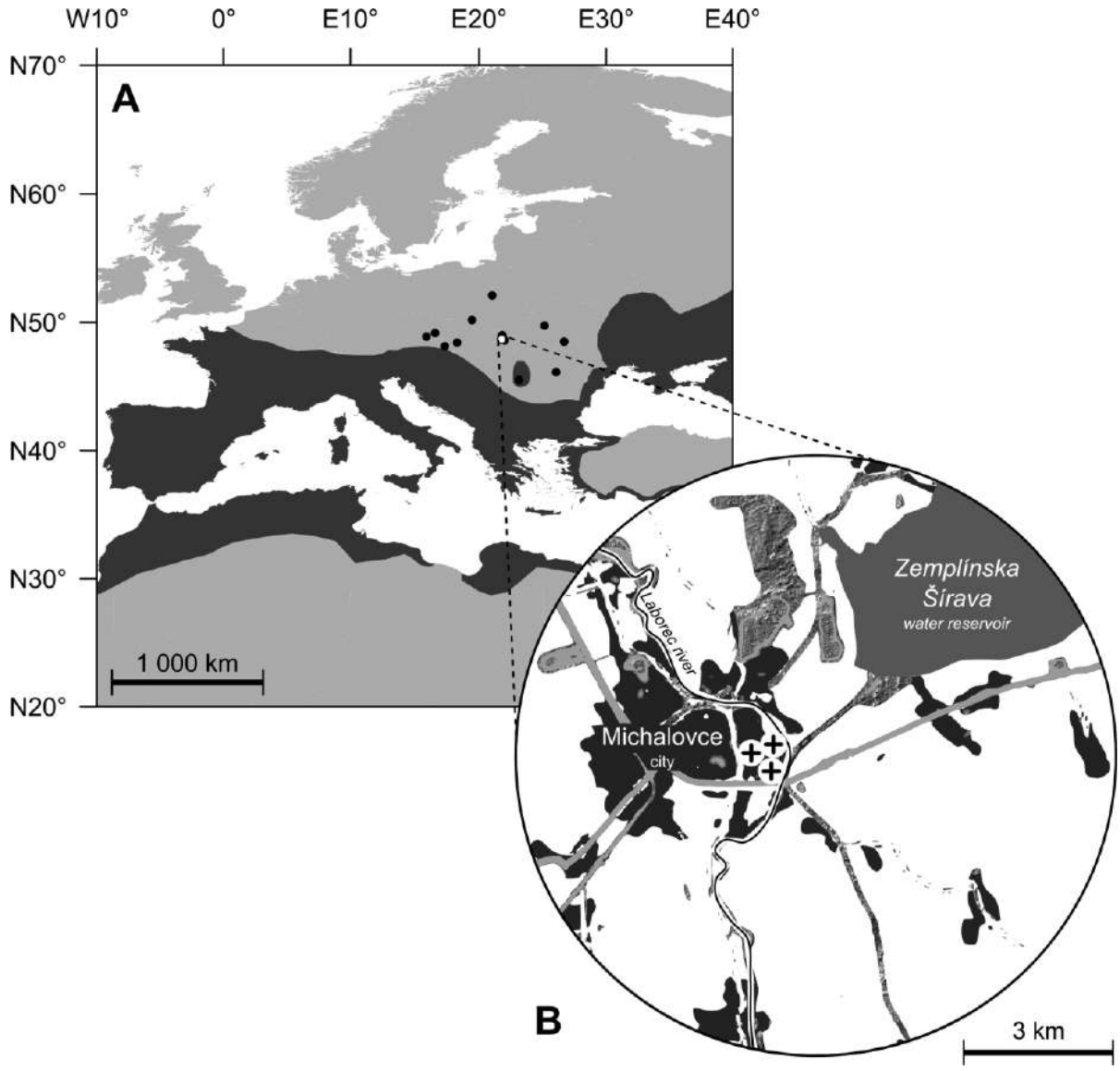


FIG. 1. Distribution map of Kuhl's pipistrelle in Europe (A) and the study area (B). The dark grey area represents the current range of Kuhl's pipistrelle distribution (Dietz *et al*., 2009; Dietz and Kiefer, 2014); black circles represent recently reported records outside the known core range (Ceľuch and Ševčík, 2006; Sachanowicz *et al*., 2006; Danko, 2007; Reiter *et al*., 2007; Popczyk *et al*., 2008; Barti, 2010; Wawrocka *et al*., 2012; authors' unpublished data), which indicate the directions of recent expansion of the species towards the north. The white circle marks the location of our study site. (B) The dark grey area represents the urban habitat of the city of Michalovce neighbouring the Zemplínska Šírava reservoir to the north-east and small patches of deciduous forest to the north. The three black crosses in white circles represent the six roosting locations of *P. kuhlii*

a plausible explanation for its rapid expansion as well as contribute to the growing body of literature about the Kuhl's bat ecology.

Materials and Methods

Study Area

The study was conducted in the city of Michalovce (eastern Slovakia; 48°45'N, 21°55'E, 114 m a.s.l.), where during data collection for this study the northernmost known maternity colony of *P. kuhlii* roosted (Fig. 1 B). Within the city area roosting of the species *Hypsugo savii* was confirmed between concrete panels in prefab houses, and the presence of *Vespertilio murinus* and *Nyctalus noctula* was also recorded (Danko, 2007). The surrounding landscape is covered mainly by agricultural lowlands, broadleaved forests and the Zemplínska Šírava reservoir, with an area of 33 km^2. The city covers ca. 52 km^2 and has almost 39,000 inhabitants. The average annual temperature is 9.1°C, with the maximum in July (20.4°C) and the minimum in January (-3.6°C). Average annual precipitation is 593 mm. Fluorescent and sodium lamps are used in the city throughout the night, although their intensity is reduced from 11:00 to 04:00. The city centre is mostly illuminated, in contrast to the city edges.

Radio-tracking

Radio-tracking of Kuhl's pipistrelles was conducted in June (pre-parturition period) and August (post-lactation period) in 2013. Altogether, 10 individuals (three males and two females in June and two males and three females in August) were mist-netted next to a prefabricated house during the evening emergence from the roost and at the foraging site. After partial clipping of the fur on the back, a radio transmitter (LB-2N, 0.41 g — Holohil Systems Ltd., Ontario, Canada) was attached with adhesive glue (Osto-Bond — Montreal Ostromy, Quebec, Canada). Individuals were monitored simultaneously using ICOM Receivers IR-20 and AVM LA12-Q and a hand-held three-element Yagi antenna. We used two methods to locate a bat: (1) the 'homing in' method (e.g., White and Garrot, 1990), when the observer established the bat's position by approaching the subject tracked as close as possible by car or on foot, and (2) the biangulation (or triangulation) method. Foraging locations were taken every five minutes in both periods, and a total of 19 nights of monitoring were conducted.

Seasonal Differences in Foraging Behaviour and Foraging Niche Modelling

We estimated the size of the foraging areas of each individual by applying a 95% kernel to its telemetry fixes (i.e. 95% kernel estimates). Subsequently, the Student's *t*-test was used to explore seasonal differences in (i) feeding-area sizes and (ii) the maximal distance travelled by a bat from the roost to the feeding area. These two variables are presented as the mean ± standard deviation. We used a niche modelling approach to characterize the preferred foraging habitat of Kuhl's pipistrelle. A circle six km in radius was constructed around the centroid of all the bat relocation coordinates ($n_{relocations}$ = 339; range = 9–85 per bat). The area falling in this circle (hereafter, the available habitat) was transformed into discrete resource units (squares 200 × 200 m). Subsequently, we used six layers containing the environmental characteristics of this available habitat (Fig. 2). In the first five layers each resource unit contained a value reflecting the Euclidean (minimal) distance to a particular habitat category. In other words, if the resource unit of, for example, the urban environmental layer has a value of 100, the nearest distance from such a unit to the urban habitat is 100 m (if the value is 0 it means that this resource unit lies within the urban habitat). These five layers contained information about the distances to the: (i) urban habitat; (ii) open habitat, (iii) forest, (iv) water reservoir, (v) river. The last layer, 'Earth's city lights' image (Mayhew and Simmon, 2000), was rescaled to 200 × 200 m resolution and contains the information about light pollution (for details about its original resolution and units see Doll, 2008).

Relocation coordinates, together with the six environmental layers, were used in the modelling of the bats' foraging habitat by using the 'adehabitatHS' package (Calenge, 2006). Based on our assumption that habitat is equally available in both seasons, we treated our data as with a design II study according to Thomas and Taylor (1990). The foraging habitat preferences were analysed separately for the pre-parturition (June) and post-lactation (August) periods; we thus performed two independent inferences about habitat selection. Marginality vectors were calculated for both periods and visualized in niche space. These vectors measure the distance between what is available on average in an environment and what is used on average by animals; i.e. they describe the strength and direction of selection. All statistical comparisons, as well as the niche modelling, were conducted in R ver. 3.2.2 (R Core Team, 2015).

Results

Roosts Localization and Foraging Trips

We identified six artificial roosts between which the tracked bats regularly switched. Three roosts were localized in crevices within prefabricated houses, two under the wood trim on family houses and one in a school building. The distances between the roosts were 0.04–0.88 km. The size of the bat groups varied from 30 to 100 individuals. The maximum number of roosts used varied among the tracked individuals (up to three roosts per bat).

The flying patterns of *P. kuhlii* were distinctive: bats began to emerge fast from the roost entrance in quick succession shortly after sunset (ca. 40 minutes after sunset in June and 28 minutes in August). Female emerged from the roosts earlier after sunset than males (XX: 17.8 ± 8.2 min; YY: 36 ± 12.9 min; *t*-test: t = -3.70, $d.f.$ = 16, $P < 0.01$). For the commuting flights bats used the Laborec River bed, which provides a linear landscape feature. The maximum distance between the roost and a feeding area did not significantly differ between the two tracking periods (pre-parturition: 3179 ± 3123 m; post-lactation: 4221 ± 2584 m; *t*-test: t = -0.57, $d.f.$ = 8, P = 0.59) or between the sexes (XX: 3217 ± 2367 m;

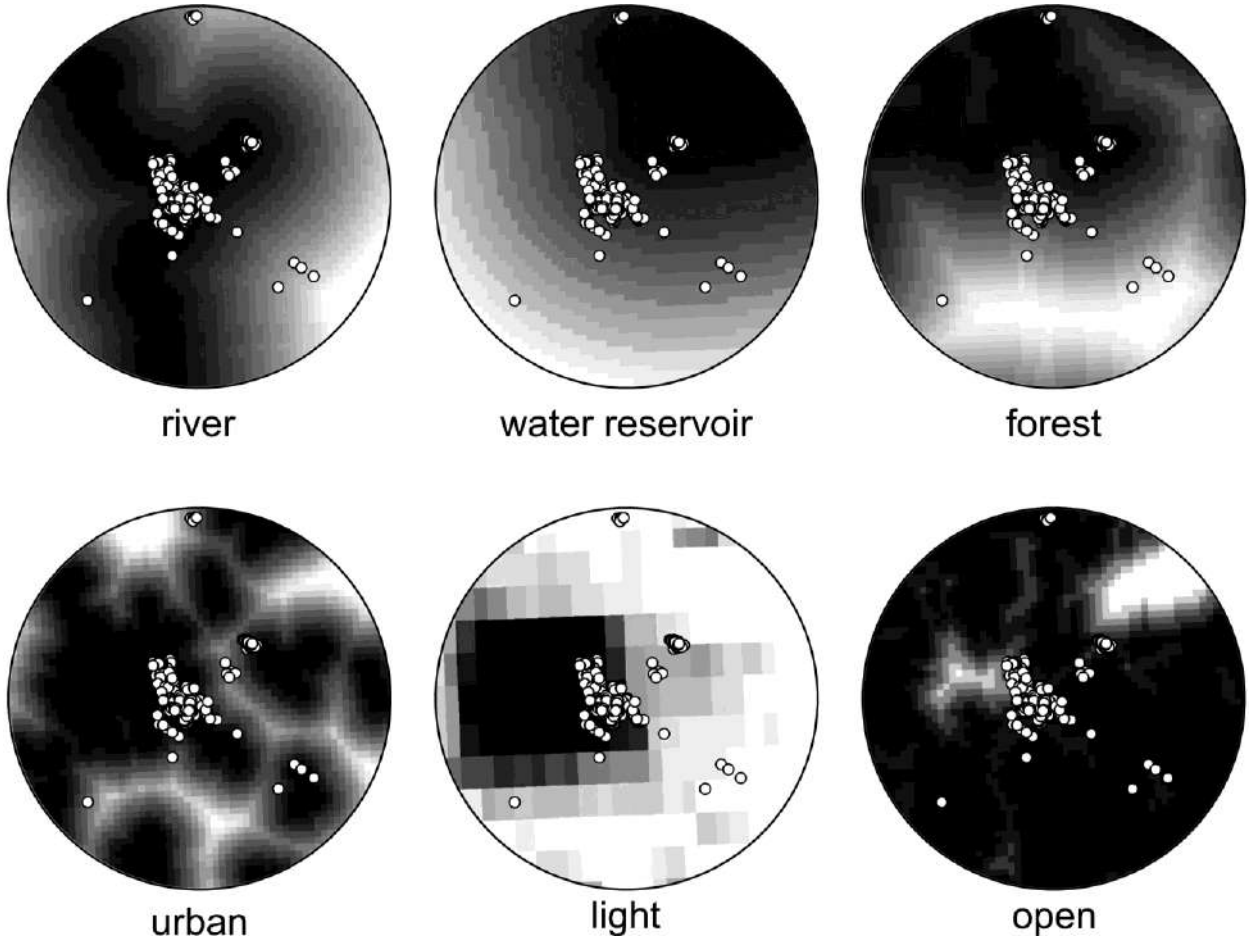


FIG. 2. The six environmental layers (rasters) used for niche modeling. Each layer consists of pixels coding the Euclidean (minimum) distance towards a particular habitat category, i.e. from close distance (black) to long distance (white), except for the 'light' layer, which codes the intensity of artificial light pollution (for more details on the layers, see the Materials and Methods section). White points represent spatial distribution of all the fixes (n = 339) obtained by telemetry of 10 *P. kuhlii* individuals over the whole data collection period (points are given without differentiation of the sex of the tracked bat and/or the season)

YY: 4173 ± 3305 m; *t*-test: t = -0.52, *d.f.* = 8, P = 0.61). Similarly, no significant difference was found in the size of the feeding areas (95% kernel estimates) between the periods (pre-parturition: 8.6 ± 8.5 km^2; post-lactation: 13 ± 20.5 km^2; *t*-test: t = -0.45, *d.f.* = 8, P = 0.67) or between the sexes (XX: 5.2 ± 4.12 km^2; YY: 16.4 ± 20.2 km^2; *t*-test: t = -1.20, *d.f.* = 8, P = 0.26).

Selection of Foraging Habitat

Ecological niche modelling revealed that bats were highly selective towards their foraging habitat. The only habitat type which the bats clearly preferred in the pre-parturition and post-lactation periods was an illuminated urban area close to a river (Table 1 and Fig. 3). Only slight avoidance was observed towards open areas in the pre-parturition period.

DISCUSSION

The reason behind this rapid expansion of Kuhl's bat seems to be a combination of multiple factors,

TABLE 1. Preferred foraging habitat of Kuhl's pipistrelle. Values are scores from discriminant analysis reflecting the relative selection of bats towards a particular habitat type. The first three largest values are highlighted in bold; negative values may indicate avoidance

Habitat type	Period	
	Pre-parturition	Post-lactation
River	**1.17**	**1.58**
Light	**0.99**	**1.21**
Urban	**0.81**	**0.94**
Water reservoir	0.77	0.44
Forest	0.66	0.23
Open	-0.10	0.09

most likely driven by warmer climates further north facilitated by the pre-existing preference for roosting in buildings (Ancillotto *et al.*, 2016). Our results do not support the alternative explanation that the expansion towards the north is caused by a change in a habitat-utilization strategy. Habitat selection patterns of Kuhl's pipistrelle from the northern edge of distribution described in this study match well the foraging behaviour of bats from core areas of distribution (cf. Serangeli *et al*., 2012; Ancillotto *et al*., 2016). Bats consistently in both cases strongly preferred built-up areas illuminated by artificial

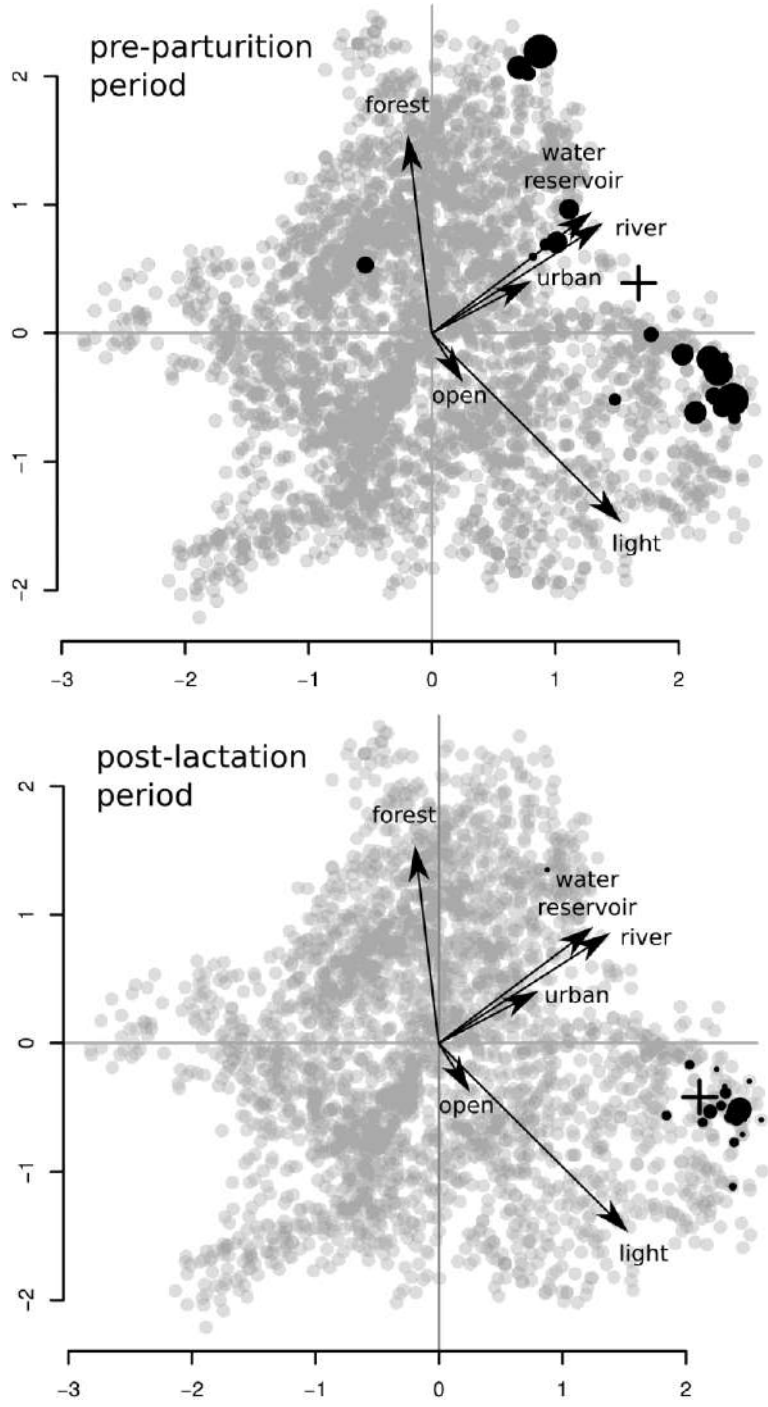


FIG. 3. Selection toward the foraging habitat of Kuhl's pipistrelle. Grey circles represent available resource units, whereas black circles represent used resource units. The size of the circles indicates the relative weight of usage. Marginality vectors (black crosses) are visualized in the niche space in both periods. These vectors measure the distance between what is available on average in the environment and what is used on average by the animals, i.e. they describe the strength and direction of selection

lights as well as to forage in riparian habitats along a river and occasionally near a reservoir or in a woodland habitat. All of these habitat types were already recorded as important foraging ground for Kuhl's pipistrelle (Russo and Jones, 2003; Korine and Pinshow, 2004).

The increasing level of urbanization and the associated artificial light pollution in combination with changes in the climate in recent decades might have increased the size of local populations of *P. kuhlii* as well as of other bat species and thus speed-up the rate of colonization. Although some studies confirm that insect abundance can be negatively affected by urbanization (McIntyre, 2000; Kalcounis-Rueppell *et al*., 2007), the urban environment probably offers better prey availability for opportunistic hunters.

Species-specific responses to light may be a function of flight morphology and echolocation. For example, *Myotis* spp., which use broad bandwidth echolocation signals and have a fluttering flight and often forage around vegetation, were only recorded away from street lights (Furlonger *et al.*, 1987; Rydell, 1992). Similarly, despite the presence of street lit areas within the home range of *Rhinolophus ferrumequinum*, they were never used by this species, which is classified as photophobic (Jones and Morton, 1992; Day *et al*., 2015). On the other hand, relatively fast flying bats that typically forage in open spaces and use long range echolocation pulses, such as *Eptesicus*, *Nyctalus* and *Pipistrellus* species, could take advantage of street lights (Rydell, 1991, 1992, 2006; Blake *et al*., 1994). For such light-tolerant bat species, artificial lights create an illuminated night niche that acts as a very effective artificial feeding resource (Stone *et al.*, 2015) because of the higher insect density (moths in particular) attracted to such lights (Eisenbeis *et al.*, 2006; van Langevelde *et al.*, 2011). Densities of *Pipistrellus* sp. were found to be ten-times higher in lit versus dark areas in England (Rydell and Racey, 1995). Furthermore, these species were observed hunting in smaller groups around street lamps, either in circles or patrols along long stretches of flight corridors (Barak and Yom-Tov, 1989; Russo and Jones, 1999).

Strongly illuminated urban foraging habitats, parks, as well as areas around a reservoir could provide a high abundance of Chironomidae and other nematoceran insects and thus serve as an easy and abundant food source. Additionally, illuminated rivers can be used as a landmark for commuting both to and from feeding areas and also as a reference landscape element for searching for new roost.

It seems that Kuhl's pipistrelle did not show any signs of avoidance towards illuminated commuting routes, although we cannot assess at which degree artificial lighting can impact their flight paths (Stone *et al.*, 2009), forcing them to fly lower and faster (Polak *et al.*, 2011). Similarly, the colony that we tracked was located close to the edge of the town and in the near vicinity of the riparian vegetation that the bats usually followed. Furthermore, Tomassini *et al*. (2013) even explained the increased size of the brain of *P. kuhlii* with respect to the increase of illumination, which may have confronted bats with new cognitive challenges, such as exploiting patchily distributed food at street lamps, thus requiring increased spatial memory and the development of novel foraging strategies to feed on new prey types.

In conclusion, our study, as with previous ecological studies (Russo and Jones, 2003; Ancillotto *et al.*, 2012, 2016; Serangeli *et al*., 2012), has shown that *P. kuhlii* is ecologically and behaviourally a highly flexible and adaptable species which can benefit from urbanization; it can use artificial roosts and select hunting places in illuminated urban areas and can thus be classified as a true urban exploiter (Kark *et al*., 2007).

ACKNOWLEDGEMENTS

We wish to offer thanks for a Small membership grant of the Slovak Bat Conservation Society for financial support as well as to the Cultural and Educational Grant Agency (KEGA # 012UPJŠ-4/2014) and the Scientific Grant Agency (VEGA # 2/0035/13) of the Ministry of Education, Science Research and Sport of the Slovak Republic. We express many thanks to Monika Balogová, Stanislav Danko, Martin Dobrý, Renáta Chromá and Peter Ľuptáčik for their help in the field. Two anonymous referees are gratefully acknowledged for valuable and insightful comments and insightful suggestions to an earlier version of the manuscript. This study was conducted under licence from the Ministry of Environment of the Slovak Republic (6497/2012-2.2).

LITERATURE CITED

ANCILLOTTO, L., M. T. SERANGELI, and D. RUSSO. 2012. Spatial proximity between newborns influences the development of social relationships in bats. Ethology, 118: 331–340.

ANCILLOTTO, L., A. TOMASSINI, and D. RUSSO. 2015. The fancy city life: Kuhl's pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. Wildlife Research, 42: 598–606.

ANCILLOTTO, L., L. SANTINI, N. RANC, L. MAIORANO, and D. RUSSO. 2016. Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation. The Science of Nature, 103: 1–8.

ARNFIELD, A. J. 2003. Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and

the urban heat island. International Journal of Climatology, 23: 1–26.

Barak, Y., and Y. Yom-Tov. 1989. The advantage of group hunting in Kuhl's bat *Pipistrellus kuhlii* (Microchiroptera). Journal of Zoology (London), 219: 670–375.

Barti, L. 2010. First record of *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) from Transylvania and a morphological approach to the *lepidus* taxon. Acta Siculica, 2010: 155–168.

Bihari, Z. 2004. The roost preference of *Nyctalus noctula* (Chiroptera, Vespertilionidae) in summer and the ecological background of their urbanization. Mammalia, 68: 329–336.

Blake, D., A. M. Hutson, P. A. Racey, J. Rydell, and J. R. Speakman. 1994. Use of lamplit roads by foraging bats in southern England. Journal of Zoology (London), 234: 453–462.

Bogdanowicz, W. 2004. *Pipistrellus kuhlii* (Kuhl, 1817) — Weißrandfledermaus. Pp. 876–908, *in* Handbuch der Säugetiere Europas. Band 4/II: Fledertiere. Teil II: Chiroptera II. Vespertilionidae 2, Molossidae, Nycteridae (F. Krapp, ed.). AULA-Verlag, Wiebelsheim, 1186 pp.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197: 516–519.

Ceľuch, M., and M. Ševčík. 2006. First record of *Pipistrellus kuhlii* (Chiroptera) from Slovakia. Biologia, 61: 637–638.

Danko, Š. 2007. Reprodukcia *Hypsugo savii* a *Pipistrellus kuhlii* na východnom Slovensku: ďalšie dôkazy o ich šírení na sever. Vespertilio, 11: 13–24.

Day, J., J. Baker, H. Schofield, F. Mathews, and K. J. Gaston. 2015. Part-night lighting: implications for bat conservation. Animal Conservation, 18: 512–516.

Dietz, C., and A. Kiefer. 2014. Die Fledermäuse Europas. Kennen, Bestimmen, Schützen. Franckh-Kosmos Verlags GmbH, Stuttgart, 400 pp.

Dietz, C., O. von Helversen, and D. Nill. 2009. Bats of Britain, Europe and Northwest Africa. A&C Black, London, 400 pp.

Doll, C. N. 2008. CIESIN thematic guide to night-time light remote sensing and its applications. Center for International Earth Science Information Network of Columbia University, Palisades, NY. Available online at http://sedac.ciesin.columbia.edu/tg/.

Eisenbeis, G., C. Rich, and T. Longcore. 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. Pp. 191–198, *in* Ecological consequences of artificial night lighting, 2 (C. Rich and T. Longcore, eds.). Island Press, Washington, D.C., 458 pp.

Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology, 65: 284–288.

Haffner, M., and H. P. Stutz. 1985. Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at street-lamps. Myotis, 23–24: 167–172.

Hutterer, R., T. Ivanova, C. Meyer-Cords, and L. Rodrigues. 2005. Bat migrations in Europe. A review of banding data and literature. Naturschutz und Biologische Vielfalt, Bonn, 28: 1–176.

Jones, G., and M. Morton. 1992. Radio-tracking studies on habitat use by greater horseshoe bats (*Rhinolophus ferrumequinum*). Pp. 521–537, *in* Wildlife telemetry. Remote monitoring and tracking of animals (I. G. Priede and S. M. Swift, eds.). Ellis Horwood, Chichester, 708 pp.

Kalcounis-Rueppell, M. C., V. H. Payne, S. R. Huff, and A. L. Boyko. 2007. Effects of waste water treatment plant effluent on bat foraging ecology in an urban stream system. Biological Conservation, 138: 120–130.

Kark, S., A. Iwaniuk, A. Schalimtzek, and E. Banker. 2007. Living in the city: can anyone become an 'urban exploiter'? Journal of Biogeography, 34: 638–651.

Korine, C., and B. Pinshow. 2004. Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev Desert. Journal of Zoology (London), 262: 187–196.

Lausen, C. L., and R. M. R. Barclay. 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. Journal of Mammalogy, 87: 362–370.

Lodé, T. 2000. Effect of a motorway on mortality and isolation of wildlife populations. AMBIO, 29: 163–166.

Mayhew, C., and R. Simmon. 2000. NASA GSFC. Earth's City Lights. Data courtesy Marc Imhoff of NASA GSFC and Christopher Elvidge of NOAA NGDC.

McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America, 93: 825–835.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation, 127: 247–260.

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosystems, 11: 161–176.

Mendelssohn, H., and Y. Yom-Tov. 1999. A report of birds and mammals which have increased their distribution and abundance in Israel due to human activity. Israel Journal of Zoology, 45: 35–47.

Neubaum, D. J., K. R. Wilson, and T. J. O'Shea. 2007. Urban maternity-roost selection by big brown bats in Colorado. Journal of Wildlife Management, 71: 728–736.

Neuweiler, G. 2000. The biology of bats. Oxford University Press, Oxford, UK, 310 pp.

Polak, T., C. Korine, S. Yair, and M. W. Holderied. 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. Journal of Zoology (London), 285: 21–27.

Popczyk, B., G. Lesiński, A. Baumann, and B. W. Wojtowicz. 2008. Kuhl's pipistrelle, *Pipistrellus kuhlii* (Kuhl, 1817) or *Pipistrellus lepidus* (Blyth, 1845), in Central Poland — accidental records or a result of expansion? Nyctalus (N.F.), 13: 279–281.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at http://www.R-project.org/.

Reiter, A., P. Benda, and J. Hotový. 2007. First record of the Kuhl's pipistrelle, *Pipistrellus kuhlii* (Kuhl, 1817), in the Czech Republic. Lynx (N.S.), 38: 47–54.

Russo, D., and G. Jones. 1999. The social calls of Kuhl's pipistrelles *Pipistrellus kuhlii* (Kuhl, 1819): structure and variation (Chiroptera: Vespertilionidae). Journal of Zoology (London), 249: 476–481.

Russo, D., and G. Jones. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography, 26: 197–209.

Rydell, J. 1991. Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. Ecography, 14: 203–207.

Rydell, J. 1992. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology, 6: 744–750.

RYDELL, J. 2006. Bats and their insect prey at streetlights. Pp. 43–60, *in* Ecological consequences of artificial night lighting, 2 (C. RICH and T. LONGCORE, eds.). Island Press, Washington, D.C., 458 pp.

RYDELL, J., and P. A. RACEY. 1995. Street lamps and the feeding ecology of insectivorous bats. Symposia of the Zoological Society of London, 67: 291–307.

SACHANOWICZ, K., A. WOWER, and A.-T. BASHTA. 2006. Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe. Acta Chiropterologica, 8: 543–548.

SALA, O. E., F. S. CHAPIN, J. J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, L. F. HUENNEKE, R. B. JACKSON, A. KINZIG, *et al*. 2000. Global biodiversity scenarios for the year 2100. Science, 287: 1770–1774.

SCALES, J. A., and K. T. WILKINS. 2007. Seasonality and fidelity in roost use of the Mexican free-tailed bat, *Tadarida brasiliensis*, in an urban setting. Western North American Naturalist, 67: 402–408.

SERANGELI, M. T., L. CISTRONE, L. ANCILLOTTO, A. TOMASSINI, and D. RUSSO. 2012. The post- release fate of hand-reared orphaned bats: survival and habitat selection. Animal Welfare, 21: 9–18.

STONE, E. L., G. JONES, and S. HARRIS. 2009. Street lighting disturbs commuting bats. Current Biology, 19: 1123–1127.

STONE, E. L., S. HARRIS, and G. JONES. 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. Mammalian Biology, 80: 213–219.

THOMAS, D., and E. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management, 54: 322–330.

TOMASSINI, A., P. COLANGELO, P. AGNELLI, G. JONES, and D. RUSSO. 2013. Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or urbanization? Journal of Biogeography, 41: 944–953.

UHRIN, M., U. HÜTTMEIR, M. KIPSON, P. ESTÓK, K. SACHANOWICZ, S. BÜCS, B. KARAPANDŽA, M. PAUNOVIĆ, P. PRESETNIK, A.-T. BASHTA, *et al*. 2016. Status of Savi's pipistrelle *Hypsugo savii* (Chiroptera) and range expansion in Central and south-eastern Europe: a review. Mammal Review, 46: 1–16.

VAN LANGEVELDE, F., J. A. ETTEMA, M. DONNERS, M. F. WALLIS DE VRIES, and D. GROENENDIJK. 2011. Effect of spectral composition of artificial light on the attraction of moths. Biological Conservation, 144: 2274–2281.

WAWROCKA, K., T. BARTONIČKA, and A. REITER. 2012. *Pipistrellus kuhlii*, a bat species breeding and hibernating in the Czech Republic. Vespertilio, 16: 351–356.

WHITE, G. C., and R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, 383 pp.

YOM-TOV, Y., and R. KADMON. 1998. Analysis of the distribution of insectivorous bats in Israel. Diversity and Distributions, 4: 63–70.

Received 21 October 2015, accepted 22 February 2016

Summary of results and Conclusions

The studies undertaken in the framework of my PhD project have contributed to the growing body of knowledge on the ecological requirements and behavioural specificities of two bat species, *Hypsugo savii* and *Pipistrellus kuhlii*, which are currently expanding their ranges northwards in Europe.

Paper 1 provides a comprehensive overview of the current knowledge on *Hypsugo savii,* including a survey of major published literature. The respective book chapter serves as a reference work vital to zoological studies, summarising the current state of knowledge on all aspects of its biology. In this work, we have provided a synopsis of all available literature on the species' common name, taxonomy and systematics, palaeontology, current distribution, description, physiology, genetics, life history, habitat and diet, behaviour, and future challenges for research and management. The species chapter in the Handbook of European Mammals provides a reliable platform for future updates as further literature becomes available. Similarly, this reference work provides a solid baseline for identifying gaps vital for further research on the described species.

Following this, **Paper 2** provides a detailed faunistic overview and maps the northward spread of *Hypsugo savii* into Central Europe from the Mediterranean region. We present a detailed temporal and spatial account of this change from the 1990s onwards, providing evidence of a shift of almost 800 km north (from the Adriatic coast to southern Poland). Regarding the mechanisms behind these expansions, it appears that the species' ability to roost in urban areas is a key factor in its successful spread, as it uses built-up areas to move northward. However, the role of recent climatic change cannot be excluded and would need to be assessed further.

As there was very little data on the ecological requirements of Savi's pipistrelle, we have provided the first detailed study of diet, habitat preferences and home range size in reproductive females from Croatia in **Paper 3**. Our results showed that the species can fly longer distances (even crossing the sea) and utilise a wide range of habitats within its home range. Habitat preferences shifted slightly over the reproductive period: pregnant females utilised rocky pastures and forest areas, followed by meadows and riparian habitats, whereas lactating females showed a greater affinity for riparian habitats, followed by meadows, forest and rocky pastures. Our dietary analysis showed the species' ability to feed on swarming insects that occur locally in higher abundance, namely Formicoidea. Overall, its habitat preferences and diet indicate that Savi's pipistrelle is a highly flexible species, probably more tied to locally abundant airborne prey than to any specific habitat type. Its home range was also remarkably large; compared with the study on *Pipistrellus kuhlii* in Slovakia, it was five times larger. Despite descriptions in the literature of hunting in urbanised areas, we have not recorded the species actively hunting there, as it preferred more natural habitats within its foraging radius. This was in line with the second radiotracking study from Italy, in which the species roosted in artificial structures but foraged outside urban areas. Therefore,

it seems that, in addition to its ability to use synanthropic roosts, its traits as a highly mobile species, capable of crossing longer distances and showing flexibility in foraging and diet, could also have played a role in the species' shift northwards. On the other hand, because lactating females showed a greater affinity for riparian habitats, it remains unclear whether predicted increases in drought and water scarcity will negatively affect the species in the future within the Mediterranean region, leading to a retraction on the southern edge of its distribution.

In **Paper 4**, we examined roost selection and the structural and microclimatic conditions within the roosts of reproductive females of Savi's pipistrelle. The literature contains very few descriptive records of roosts for this species, and these predominantly come from human-made objects or from observations of emergence from cliffs. Despite the availability of synanthropic roosts and cliffs in our study in Croatia, females predominantly chose ground-level vertical rock crevices within flat limestone pavement. These types of roosts have been described here for the first time in reproductive females among European bats, specifically because of their placement at ground level. Females showed very little fidelity to their roosts, switching almost daily, choosing roosts with narrower openings, and forming only smaller groups during lactation, whereas solitary roosting was dominant in pregnant females, which we hypothesise is a response to potential predation risk, as the roosts are at ground level. Likewise, females chose slightly deeper and more thermally stable crevices, but given the generally high ambient and roost temperatures, the species appears to be very heat-tolerant. These findings can provide insight into how the process of synanthropisation influences individual species' behaviour. Most likely, the shift to synanthropic roosts across different parts of the range can lead to behavioural flexibility, due to reduced predator pressure, resulting in larger groups and higher roost fidelity. We observed that the socially connected group size of lactating females within rock crevices exceeded the number of females roosting together on a given day, as they followed a fission-fusion model, in which group members merged and dissolved with different individuals on different days. Our findings show that the species is adaptable in its roosting strategy across its range and can tolerate extreme temperatures. On the other hand, ground-level vertical crevices in open habitats might be an overlooked roosting habitat across semi-arid regions and might be under increased pressure from other anthropogenic changes, such as wind farms.

Paper 5 focuses on the second species studied, *Pipistrellus kuhlii*, providing insight into its foraging habitat preferences, home range size, and roosting in Slovakia, at the northern margin of its distribution. We found that the species clearly demonstrated the ability to use synanthropic roosts, which were the only roosts used in the study, and to forage in urbanised, illuminated areas next to a water source. Based on our results, the species appears to fully exploit urbanised areas and is highly adaptable in this regard, which is comparable to the results of other studies from its southern range

in Europe. Most probably, these characteristics, combined with the effect of climate change, have largely contributed to its northward expansion.

In conclusion, the research undertaken within the framework of the present PhD project provides valuable new details that considerably refine current knowledge on the ecological requirements and behaviour of two bat species, *Hypsugo savii* and *Pipistrellus kuhlii*. Their extraordinary northward range expansion in Europe over the last few decades, most likely driven by climatic changes, was undoubtedly preformed in considerable degree also by the intrinsic drivers related both to original setting of their ecological requirements (including roosting and habitat preferences, foraging, and dietary flexibility and opportunistic behavioural components) and to current adaptive rearrangements of them, which finally promoted their abundance increase and range expansions. Despite some general commonalities between the species (mostly related to strong synanthropic and synurbanisation trends in expanding populations), we also found species-specific preferences: among others, Kuhl's pipistrelle foraged in urbanised areas with artificial light, a behaviour typically observed in this species, whereas Savi's pipistrelle preferred natural areas for foraging. Correspondingly, Savi's pipistrelle flew over greater distances during its nightly bouts (having thus significantly larger home ranges), and it even preferred, at least in the Mediterranean region, natural roosts where available. At the same time, it appears that the fission-fusion drivers are considerably more pronounced in *Hypsugo savii,* for which the fission-fusion behaviour (accompanied by an opportunistic pattern of roost selection) seems to be an axial element of social organisation and group dynamics. A common feature shared by both studied species is their ability to utilise synanthropic roosts, which, along with their flexibility in foraging and diet and opportunistic choice of diverse overground fissure roosts (almost everywhere available), obviously acted as the most essential predispositions for the rapid northward spread observed in recent decades.

Curriculum vitae

MARINA KIPSON

marinakipson@gmail.com

EDUCATION

PhD in Zoology **Sep 2011 - present**

Charles University in Prague

- Thesis title: Ecology and synanthropy of bats in the Mediterranean region in comparison with the Central Europe
- Supervisor: Prof. RNDr. Ivan Horáček, CSc.

Master (MSc.) in Biodiversity, Conservation and Management **Sep 2009 - Sep 2010**

University of Oxford, School of Geography, Centre for the Environment (OUCE)

- MSc thesis title: Parrots, pigeons and hornbills: can we identify a pattern in their traits that brings them closer to extinction?
- Supervisor: Prof. Robert J. Whittaker

Master (MSc.) in Biology- ecology **Sep 2003 - Apr 2009**

University of Zagreb, Faculty of Science, Department of Biology

- MSc thesis title: Toxicodynamics of prometryne in mice blood
- Supervisor: Prof. Petar-Oskar Springer

WORK EXPERIENCE

Czech Society for Ornithology, Prague **Oct 2015 - Present**

EuroBird Portal Assistant

- Coordinating activities of developing bird monitoring and capacity building in SE Europe

European Breeding Bird Atlas 2 Communication Officer

- Member of the coordination team of EBBA2
- Capacity building in SE and E Europe
- Communication activities

Institute for Vertebrate Biology, Brno Project Assistant **Feb 201**

- Preparing the documentation for decision on developing Species Action Plan for Little Owl and Ortolan Bunting in Czechia

PROFESSIONAL TRAINING

The Vincent wildlife trust and Croatian Biospeleological Society **Sep 2014**

Participant at the workshop on capacity building, bat monitoring and trend analysis in the Dinaric Arc

LIST OF PUBLICATIONS

1. Fialas, P.C. et al. (2025) 'Changes in community composition and functional diversity of European bats under climate change', Conservation Biology, 39, e70025. Available at: https://doi.org/10.1111/cobi.70025
2. Kipson, M., Gazaryan, S., Horáček, I. (2020) 'Savi's pipistrelle Hypsugo savii (Bonaparte, 1837)'. In: Hackländer, F. E. Zachos (eds.), Handbook of the Mammals of Europe, Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-319-65038-8_162-11
3. Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvanova, A., Kalyakin, M., Bauer, H., Foppen, R. (2020) 'European Breeding Bird Atlas 2: Distribution, Abundance and Change'. European Bird Census Council & Lynx Editions, 967 pp.
4. Kipson M., M. Šálek, R. Lučan, M. Uhrin, E. Maxinová, T. Bartonička, M. Andreas, K. Kipson, A. Pušić, D. Rnjak, L. Naďo, I. Horáček (2018) 'Foraging habitat, home-range size and diet of a Mediterranean bat species, Savi's pipistrelle', Acta Chiropterologica, 20(2): 351–360.
5. Šálek, M., Hula, V., Kipson, M., Daňková, R., Niedobová, J., Gamero, A. (2018) 'Bringing diversity back to agriculture: Smaller fields and non-crop elements enhance biodiversity in intensively managed arable farmlands', Ecological Indicators, 90(8). DOI:10.1016/j.ecolind.2018.03.001
6. Maxinová, E., M. Kipson, L. Naďo, P. Hradická, M. Uhrin (2016) 'Foraging Strategy of Kuhl's Pipistrelle at the Northern Edge of the Species Distribution', Acta Chiropterologica 18(1): 215–222
7. Uhrin, M., U. Hüttmeir, M. Kipson,..., I. Pocora, P. Benda (2016) 'Status of Savi's pipistrelle Hypsugo savii (Chiroptera) and range expansion in Central and south-eastern Europe: A review', Mammal Review, 46 (1): 1-16.
8. Šálek, M., Chrenkova, M., Dobrý, M., Kipson, M., Grill, S., Václav, R. (2016) 'Scale-dependent habitat associations of a rapidly declining farmland predator, the Little Owl Athene noctua, in contrasting agricultural landscapes', Agriculture Ecosystems & Environment. 224. 56-66. 10.1016/j.agee.2016.03.031.
9. Šálek, M., Havliček, J., Riegert, J., Nešpor, M., Fuchs, R., Kipson, M. (2015) 'Winter density and habitat preference of three declining granivorous farmland birds: The importance of the keeping of poultry and dairy farms', Journal for Nature Conservation, 24, 10-16.
10. Šálek, M., Chrenková, M., Kipson, M. (2013) 'High population density of Little Owl (Athene noctua) in Hortobagy National Park, Hungary, Central Europe', Polish Journal of Ecology, 61, 165-169.

OTHER PUBLICATIONS

1. Hamidović, D., D. Josić, M. Kipson, A. Komerički, V. Pintar, D. Rnjak, G. Rnjak, V. Zrnčić, M. Zadravec, P. Žvorc, N. Tvrtković (2019) 'Prva procjena stanja očuvanosti šišmiša - Chiroptera u Republici Hrvatskoj', Zagreb.
2. Herrando, S., Franch, M., Voříšek, P., Kipson, M., Milanesi, P., Keller, V. (2017) 'EBBA2: Latest pilot maps, modelling work and planning ahead', Bird Census News. 30. 12-18.
3. Herrando, S., Keller, V., Voříšek, P. , Kipson, M., Franch, M., Anton, M., Pla, M., Villero Pi, D., Sierdsema, H., Kampichler, C., Telenský, T., Gillings, S., Johnston, A., Gottschalk, T., Guélat, J., Sattler, T., Brotons, L., Titeux, N., Jiguet, F., Milanesi, P. (2017) 'High resolution maps for the second European Breeding Bird Atlas: a first provision of standardised data and pilot modelled maps', Vogelwelt. 137. 33-41.
4. Keller, V., Bauer, H., Franch, M., Herrando, S., Kipson, M., Milanesi, P., Voříšek, P. (2016) 'EBBA2: Der zweite europäische Brutvogelatlas macht Fortschritte', Die Vogelwarte. 54.
5. Šálek, M., Beran, V., Hanzlíková, M., Kipson, M., Molitor, P., Praus, L., Procházka, V., Šimeček, K., Vít, P., Zeman, V. (2016) 'Strnad zahradní (Emberiza hortulana) v České republice: změny početnosti a současné rozšíření v jádrových oblastech /Ortolan Bunting Emberiza hortulana in the Czech Republic: population changes and current distribution in core areas/', Sylvia. 52. 34-52.
6. Kipson, M. 2012 - Fauna šišmiša (Chiroptera) na odabranim područjima regionalnog parka Mura-Drava – Završni izvještaj, 63 pp., Državni zavod za zaštitu prirode.
7. Kipson, M. (2008) 'Inventarizacija faune šišmiša u Parku prirode Lastovsko otočje'. U: (M. Prvan, V. V. Čavrak, ur.) Zbornik radova Interdisciplinarnog istraživačkog projekta Lastovsko otočje, Udruga studenata biologije - "BIUS", Dupinov san, Zagreb.

CONFERENCE PAPERS

1. Hamidovic, D., Josić, D., Kipson, M., Komerički, A., Pintar, V., Rnjak, D., Rnjak, G., Zrnčić, V., Zadravec, M., Žvorc, P., Tvrtković, N. 2021. Conservation status of Croatian Bats compared to other EU member states call for unified approach. 15th European Bat Research Symposium
2. Keller, V., Franch, M., Herrando, S., Kipson, M., Milanesi, P., Voříšek, P. 2019. European breeding bird atlas 2: the final results emerged. Bird Numbers 2019.
3. Voříšek, P., Herrando, S., Keller, V., Franch, M., Kipson, M., Milanesi, P. 2019. Using standardised EBBA2 data on farmland birds to inform EU policies. Bird Numbers 2019.
4. Hamidović D., M. Kipson, N. Fressel, P. Presetnik, C. Corben, S. Puechmaille, A. Glover, K. Barlow, H. Schofield, D. Rnjak 2015. An overview of bat fauna research status for wider area of Krka National Park. Oral presentation. Znanstveno-stručni skup „Vizija i izazovi upravljanja zaštićenim područjima prirode u Republici Hrvatskoj: aktivna zaštita i održivo upravljanje u Nacionalnom parku „Krka".
5. Linhart,P., Ptáček, L., Machlica, L., Müller, L., Jaška, P., Průchová, A., Chrenková, M., Kipson, M., Šálek, M. 2014. Acoustic monitoring of individuals in birds: lessons from owls and songbirds. Lecture. Ecology and acoustics: emergent properties from community to landscape, Paris, France.
6. Kipson M., M. Šalek, R.K. Lučan, T. Bartonička, E. Miková, M. Uhrin, H. Jahelková, A. Puńić, D. Kovač, M. Majer, I. Horáček. 2014. The curious case of Savi's pipistrelle (Hypsugo savii): New insight on roosting ecology and behaviour from the Mediterranean region. Oral presentation. 13th European Bat Research Symposium. Book of Abstracts.
7. Miková, E., Uhrin, M., Balogová, M., Danko, S., Hradická, P., Chromá, R., Kipson, M., Luptačik, P. 2014. Habitat selection in Pipistrellus kuhlii. Poster presentation. 13th European Bat Research Symposium, Šibenik. Book of Abstracts
8. Horáček, I., Knitlová, M., Kipson, M. 2014. Hypsugo savii and other Mediterranean bats colonizes Central Europe already in the earliest Holocene. Poster presentation. 13th European Bat Research Symposium, Šibenik. Book of Abstracts
9. Kipson M. , Šálek M. , Lučan R.K., Jahelková H., Horáček I. 2013. Bats living beneath our feet: roosting strategy of Savi's pipistrelle (Hypsugo savii). Poster presentation, Zoologicke dny, Brno, Czech Republic.
10. Kipson, M., Josić, D., Medvedović, J., Žvorc, P., Šálek, M. 2012. Results of conducted bat survey in the area of Mura-Drava Regional park with directions for future. Poster presentation, 11th Croatian Biological Congress, Šibenik, Croatia. Book of Abstracts.
11. Kipson M., D. Hamidović, P. Žvorc, N. Fressel, D. Kovač, D. Josić, V. Zrnčić. 2010. Bats in caves – conservation and monitoring. Oral presentation. Meeting of Croatian speleologists, Book of Abstracts.
12. Hamidović D., P. Žvorc, M. Kipson, N. Fressel, D. Kovač, D. Josić, V. Zrnčić. 2010. White Nose Syndrome in bats, how can speleologist help. Oral presentation.Meeting of Croatian speleologists, Book of Abstracts.
13. Fressel, N., Žvorc, P., Kipson, M., Zrnčić, V., Hamidović, D. 2010. Activity and roosting ecology of mixed colony of Miniopterus schreibersii and Rhinolophus euryale in a cave near Zagreb: improving current bat monitoring and cave management. Poster presentation. 15th International Bat Research Conference, Prague, Czech Republic. Book of Abstracts.
14. Kovač, D., S. Drakulić, N. Fressel, D. Josić, M. Kipson, V. Zrnčić. 2009. Bat fauna of Paklenica National Park: Searching for new swarming sites and migration roosts. Poster presentation. 1st International Symposium on Bat Migration, Berlin, Germany. Book of Abstracts.
15. Hamidović, D., Zupan, I., Jokić, M., Žvorc, P., Kipson, M., Fressel, N., Cvitanović, H. 2009. Conservation of the longfingered bat, Myotis capaccinii – necessity for transboundary cooperation in SE Europe. Poster presentation. 1st International Symposium on Bat Migration, Berlin, Germany. Book of Abstracts.
16. Žvorc, P., Hamidović, D., Kipson, M. 2009. Cave dwelling bats in the Vrana Lake Nature Park. Poster presentation. 1st International Symposium on Bat Migration, Berlin, Germany. Book of Abstracts.
17. Kipson, M., J. Medvedović, D. Kovač, S. Drakulić, N. Fressel, V. Zrnčić, D. Josić, A. Jagarinec, A. Prohaska, Ž. Jaković. 2008. Bat fauna at two Croatian islands distant from the coast: the island of Vis and the island of Lastovo. Poster presentation. XI EBRS, Cluj-Napoca, Romania. Book of Abstracts.
18. Žvorc P., Hamidović D., Kipson M. 2008. Bats of the Vrana Lake Nature Park. Poster presentation. XI EBRS, Cluj-Napoca, Romania. Book of Abstracts.

19. Žvorc P.,Hamidović D., Kipson M. 2008. Monitoring of bats in the Veternica cave. Poster presentation. XI EBRS, Cluj-Napoca, Romania. Book of Abstracts.
20. Jagarinec A.,Hamidović D., Žvorc P., Medvedović J., Kipson M., Budinski I. 2005. Microclimate preferences of bat species hibernating in the Veternica cave. Poster presentation. 10th European Bat Research Symposium, Galway, Ireland. Book of Abstracts

PROJECTS

Project leader

1. 2023-2026 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
2. 2020 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
3. 2019 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
4. 2018 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
5. 2017 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
6. 2016 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
7. 2015 - Monitoring (praćenje stanja) šišmiša u Nacionalnom parku Plitvička jezera, Financed by: JU Nacionalni park Plitvička jezera, Croatian Biospeleological Society
8. 08/2011 – 09/2012 - Strenghtening the support and scientific evidence for conservation of Europe's Amazon through monitoring of bats as bioindicators and support of the community, Financed by: Rufford Small Conservation Grants
9. 08/2011 – 12/2011 - Blind for bats, Financed by: Zamah and National agency for the development of civil society (Nacionalna agencija za razvoj civilnog drustva)

Team member

1. 05/2014 - 12/2016 - Projekt integracije u EU Natura 2000 / Field research and laboratory processing for collecting new inventory data for taxonomic groups: Actinopterigii and Cephalaspidomorphi, Amphibia and Reptilia, Aves, Chiroptera, Decapoda, Lepidoptera, Odonata, Plecoptera, Trichoptera No. MENP/QBS/13/0, Naručitelj: Oikon d.o.o., Krajnji naručitelj: Ministry of Environmental and Nature Protection (World Bank loan), Bat expert
2. 04/2007 - 04/2008 - Interdisciplinarni istraživački kamp „Lastovsko otočje" / Leader of bat research group/ Interdisciplinary Biology Research Camp "Lastovo Archipelago 2007" developed by BIUS in cooperation with the Dolphin Dream Society and Association for nature, environment, and sustainable development – SUNCE
3. 11/2006 - 11/2007 - Istraživački projekt „Inventarizacija faune sliva rijeke Like" pod sponzorstvom Zelene Akcije i u sklopu projekta "Bioraznolikost-Zeleni pojas Velebit" / Leader of bat research group / Research project „Inventarisation of flora and fauna of Lika river", Financed by: Green ActionAssociation
4. 2006 - Biološki istraživački kamp „Park prirode Učka 2006" / Leader of bat research group / Biological research camp "Učka Nature Park 2006"
5. 2016 - Istraživanje faune šišmiša špilji Vrlovka i prijedlog njihovog trajnog monitoringa, Financed by: Javna ustanova NATURA VIVA za upravljanje zaštićenim dijelovima prirode na području Karlovačke županije
6. 04/2008 - 04/2009 - Istraživanje biološke raznolikosti područja NP Paklenica, Biodiversity research of Paklenica National Park 2008
7. 11/2007 - 11/2008 -Biological inventarisation of rivers Glina, Ričica and upper Una (in Ličko-senjska County), Financed by: Green Action Association, as a part of the project „Promoting the protection of

border rivers and the sustainable use of natural resources in the border area of Croatia and B and H"

8. 2008 – Monitoring šišmiša u Parku prirode Vransko jezero, Financed by: JU PP Vransko jezero
9. 2008 – Vrednovanje i zaštita podzemne faune i špiljskih vrsta šišmiša šireg područja kanjona rijeke Dobre, Financed by: Hrvatska elektroprivreda d.d.
10. 2005 - Biološki istraživački kamp „Vis 2005“ , Biological research campus “Vis 2005”
11. 2007 – 2008 – Zaštita dugonogog šišmiša (Myotis capaccinii) za zaštitu krškog staništa / Conservation of the longfingered bat Myotis capaccinii for the conservation of the karstic habitat in Croatia, Financed by: Whitley Fund for Nature, Dr avnog zavoda za zaštitu prirode, Fonda za zaštitu okoliša i energetsku učinkovitost i Ministarstva kulture
12. 2007 - Trajni monitoring šišmiša u špilji Veternici, Financed by: JU “Park prirode Medvednica”
13. 2007 - Inventarizacija faune šišmiša Parka prirode Vransko jezero. Financed by: JU Park prirode Vransko jezero
14. 2006 - Istraživanje ekologije šišmiša u spilji Veternici i prijedlog njihovog trajnog monitoringa, Financed by: JU “Park prirode Medvednica”
15. 2005 - Istraživanje ekologije šišmiša u spilji Veternici i prijedlog njihovog trajnog monitoringa, Financed by: JU “Park prirode Medvednica”
16. 2005 - Biološki istraživački kamp „Vis 2005“ , Biological research campus “Vis 2005