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REVIEW

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

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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 (Horáček 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 northern margin has been delineated to run from the Pyrenees through the Massif Central and the Alps, to northern Pannonia and southern Dobrogea (Mitchell-Jones et al. 1999, Horáček & Benda 2004). *Hypsugo savii* roosts in crevices and fissures mainly in karst landscapes, and in similar roosts in towns (Horáček & Benda 2004).

In most of the south-eastern European countries (Slovenia, 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. Nevertheless, 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 distribution 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 originated 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 (Horáček & Benda 2004), i.e. in Hungary, Czech Republic, and Slovakia (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 transported by humans.

In the last published account of the species' geographical range, based on the data available by 2000, Horáček & 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 appearing 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 echolocation 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 completely 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 considerable range modification; however, some of them indicate 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 Pećina Cave, Žagubica) in the eastern part of Serbia in 1981 (Petrović 1983, Mirić & Paunović 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 (Paunović 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 (Paunović 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 southernmost parts, where bat surveys were carried out only occasionally.

Montenegro

The oldest record of *Hypsugo savii* from this country was from Cetinje in 1923 (Horáček & 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.

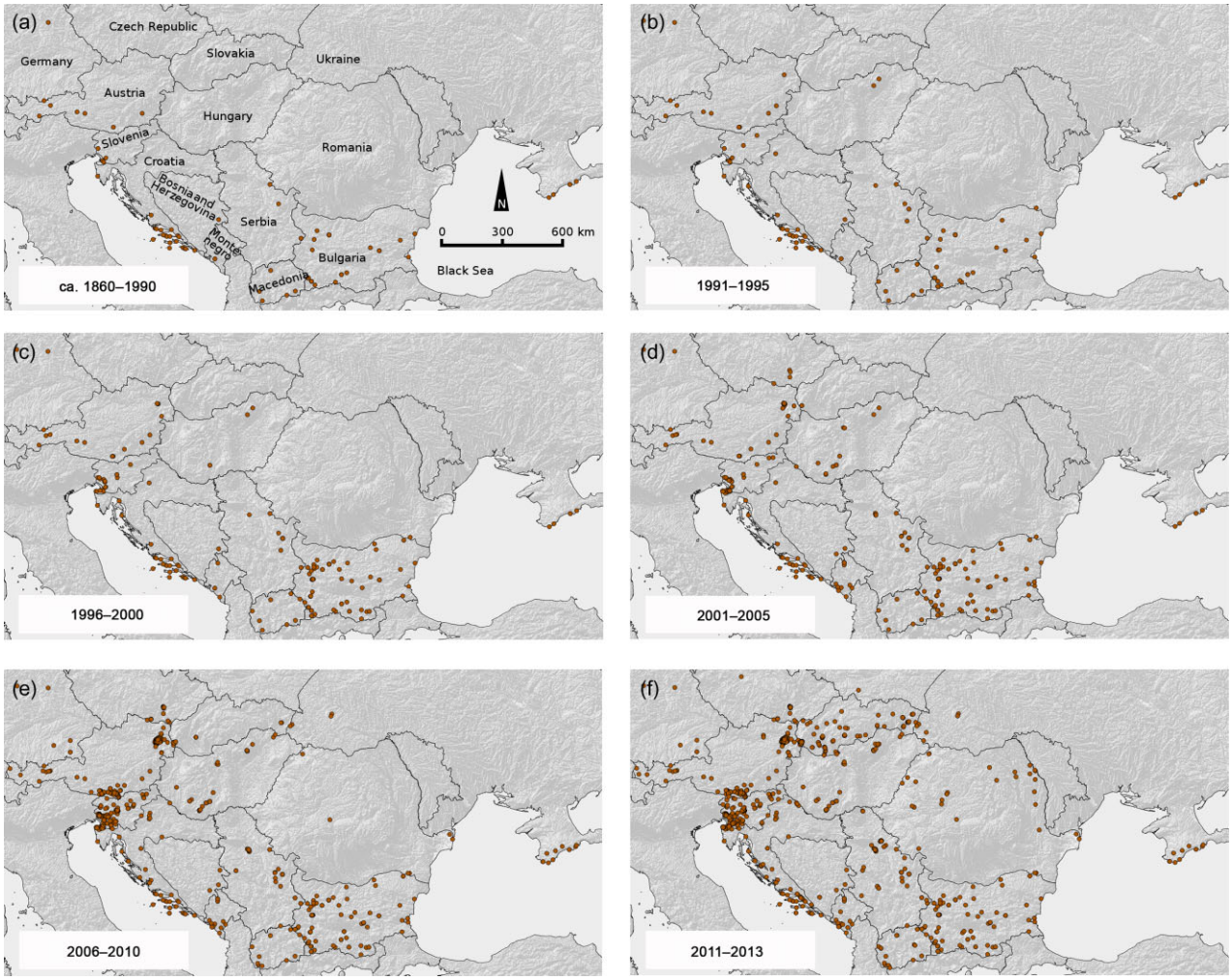

Fig. 1. Maps of cumulative records of *Hypsugo savii* (dots) in southern and central parts of Europe in six periods from c. 1860 until the end of 2013.

Croatia

Until 2000, *Hypsugo savii* was known from Croatia exclusively from the Dalmatian shore including several islands (Wettstein 1919, Djulić 1959, Dulić 1970, Červený & Kryštufek 1988, Horáček & Benda 2004). Rovinj was then the northernmost known Croatian locality (Dulić & Mrakovčić 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 (Kovač et al. 2010, original records) This National Park is characterized by rocky habitats 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 documented 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 Baziaş (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 Rădulet (1996) reported a finding in southern Dobrogea (Băneasa) 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 northernmost 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 Roşia Montană (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 documented 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, Črni Kal, Škocjanske jame Cave). Since 1990, the number of records has increased continuously; the first finding in the east-central part of Slovenia 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, methodologically adequate bat studies started in central, eastern and northern Slovenia; however, no convincing evidence of changes in the geographical range of *Hypsugo savii* is available 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). Generally, 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 expansion of the species' range and not as documentation of its regular occurrence (Spitzenberger 1997). The most important 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* delineated in 2000 (Horáček & 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 completely outside the previously acknowledged range of *Hypsugo savii* in Europe (Horáček & 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 established 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), adjacent to Austrian and Hungarian occurrence localities. Evidence 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 including 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 conclusion, *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 detectors, *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 (Mukačeve, 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 occupancy 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 Žabčice 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 (Břeclav, Brno, Znojmo). The presence of breeding females was recorded several times (Gaisler & Vlašín 2003, Bartonička & 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 northernmost 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 & Raczyński 1983, Sachanowicz et al. 2006a). There are two older reports of individuals supposedly 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 presence 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 European range (Strelkov et al. 1985, Bauer 1996, Paunović & Marinković 1998, Cel'uch & Ševčík 2006, Sachanowicz et al. 2006b, Popczyk et al. 2008, Chişamera & 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 analysis 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 distribution 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 (Mirić & Paunović 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 Belgrade (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 Slovenia. 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 Slovenia, northern Croatia, Serbia, Slovakia, and Romania. During the last period (2011–2013), when research intensified, 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 movements 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 contraction in the geographical range of *Hypsugo savii* in the Mediterranean, 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 gathered here (Table 2); this model explained 91% of data variability. 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 currently fully adapted to urban conditions and expands to the

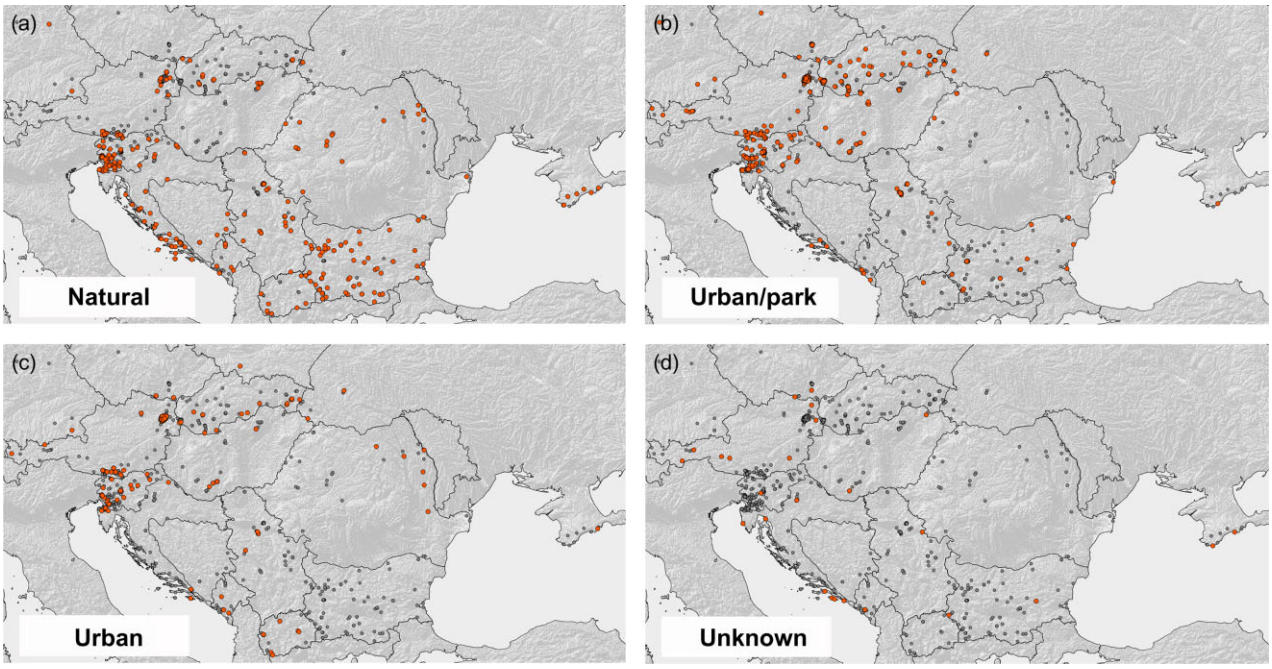

Fig. 2. Map of records of *Hypsugo savii* in southern and central parts of Europe in different habitats (larger red dots). Smaller grey dots denote all other records.

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 climatically 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 (Dulić 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, Horáček & 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 buildings 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 environments 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 contrast, 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*

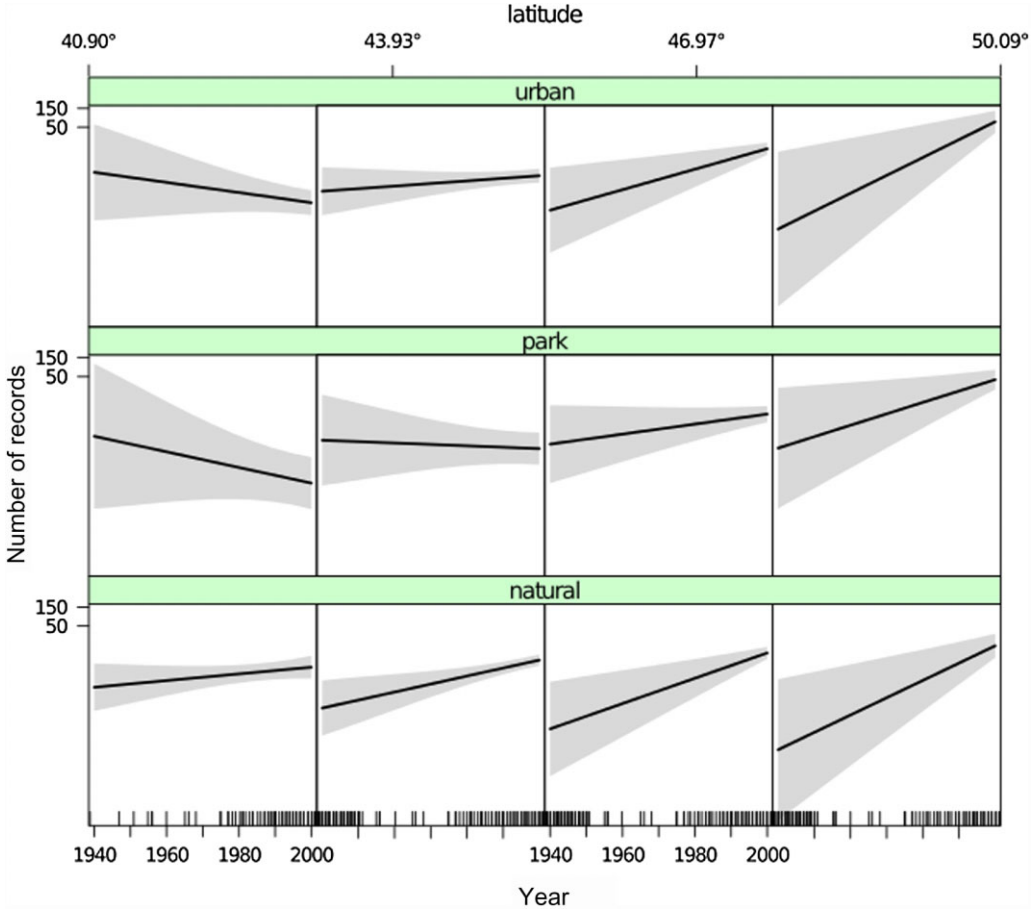

Fig. 3. Effects of interactions between year, habitat category and latitude on the number of records of *Hypsugo savii* in Central and south-eastern Europe. The *y* axis is on a log scale; models are visualised using four representative latitudes.

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 activities should be intensified.

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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

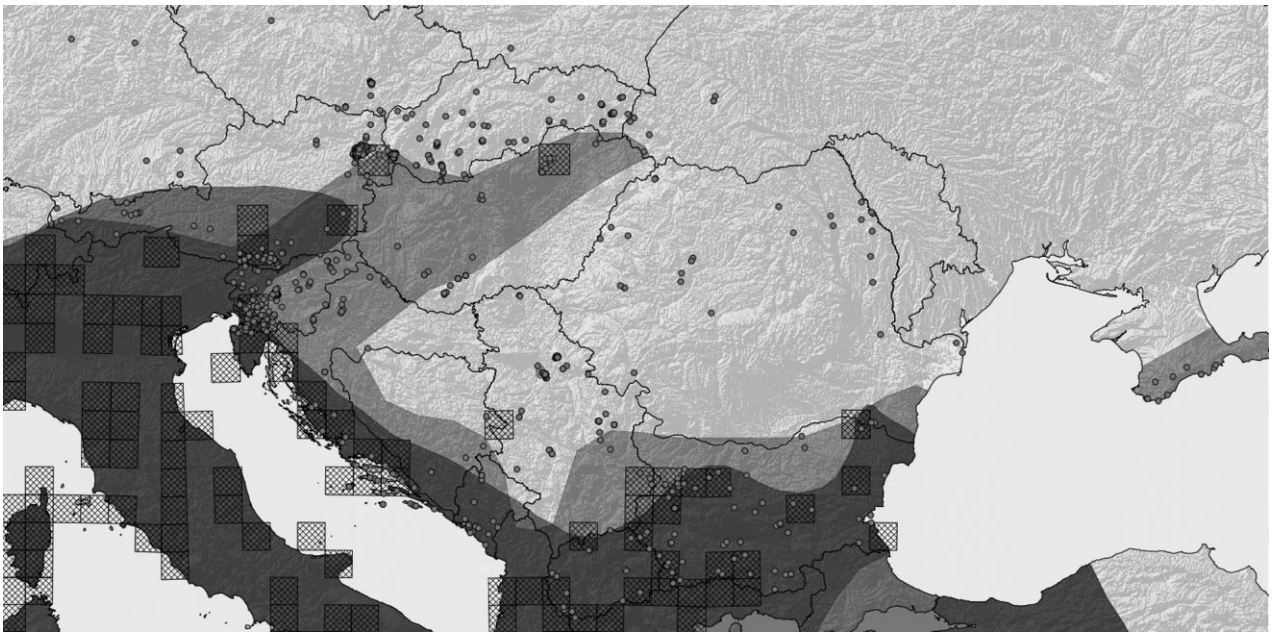

Fig. 4. Map of the development of assumptions about the delimitation of *Hypsugo savii*'s range in southern and central parts of Europe. Legend: diagonal hatched squares – *The Atlas of European Mammals* (Mitchell-Jones et al. 1999), dark grey area – *Handbuch der Säugetiere Europas* (Horáček & Benda 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).

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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.