Biologia **65**/2: 349—361, 2010
Section Zoology
DOI: 10.2478/s11756-010-0020-z

Changes in abundance of hibernating bats in central Slovakia (1992–2009)

Marcel Uhrin[1,3], Petr Benda[2,3], Ján Obuch[4] & Peter Urban[5]

[1] *Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, SK–96001 Zvolen, Slovakia; e-mail: marcel.uhrin@gmail.com*
[2] *Department of Zoology, National Museum (Natural History), Václavské nám. 68, CZ–11579 Praha 1, Czech Republic; e-mail: petr.benda@nm.cz*
[3] *Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ–12844 Praha 2, Czech Republic*
[4] *Comenius University, Botanical Garden, SK–03815 Blatnica, Slovakia; e-mail: obuch@rec.uniba.sk*
[5] *Department of Biology and Ecology, Faculty of Natural Sciences, Matej Bel University in Banská Bystrica, Tajovského 40, SK–97401 Banská Bystrica, Slovakia; e-mail: urban@fpv.umb.sk*

Abstract: An analysis of long-term changes in abundance of hibernating bats as revealed from the annual monitoring programme conducted in four mountain regions of the Western Carpathians (Muránska planina Mts, Revúcka vrchovina Mts, Slovenský kras Mts, Štiavnické vrchy Mts) during the period 1992–2009 is providing in the paper. Data from 52 hibernacula were analysed. Among 18 bat species recorded, an apparent population increase of three most abundant thermophilous and originally cave dwelling species of bats, *Rhinolophus hipposideros*, *R. ferrumequinum*, *Myotis myotis*, was observed. In other bat species (e.g., *R. euryale*, *M. emarginatus*, *M. mystacinus*, *M. dasycneme*, *Barbastella barbastellus*), population trends could not be detected and because of data scarcity, they should be evaluated from more extensive datasets obtained from a wide range of hibernacula or from a completely different type of evidence.

Key words: Chiroptera; long-term monitoring; winter census; Carpathians; TRends and Indices for Monitoring data (TRIM)

Introduction

In many plant and animal species, considerable changes in abundance and distribution patterns can be observed in the last decades. These changes have several causes, originating both from intensive human impact and from natural processes. These causes may include e.g. agricultural intensification, urbanisation, hunting, trade and pollution on the side of human impacts, and endogenous population changes, changes in genetic structure or even global environmental changes on the side of natural processes (Primack 2004). All these impacts negatively affect also bat populations and thereby this vertebrate group is considered to be globally threatened (Hutson et al. 2001). Several temperate bat species (e.g., *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis myotis*) have undergone rapid population decline in western and central Europe since the middle of the 20th century (e.g., Roer 1972; Bárta et al. 1981; Ransome 1989; Kokurewicz 1990; Weinreich & Oude Voshaar 1992; Řehák 1997; Bontadina et al. 2000). However, a subsequent reversing trend and population rebound have been observed in the above mentioned species and also in several others (*Myotis emarginatus*, *Barbastella barbastellus*) in some regions of Europe since the 1980s (e.g., Kowalski & Lesiński 1991; Zima et al. 1994; Řehák & Gaisler 1999; Bontadina et al. 2000; Gaisler & Chytil 2002; Horáček et al. 2005; Lesiński et al. 2005). Only in several species, notably in *Myotis daubentonii*, stable or increasing population numbers have been reported from the whole period of the second half of the 20th century until now (Daan et al. 1980; Gaisler et al. 1981; Řehák 1997; Horáček et al. 2005).

While the latter positive trend in bat populations in Europe has been recently mirrored also in higher frequency of bats in owl diet (Lesiński et al. 2008), so far little is known about reasons triggering such considerable changes in numbers of various bat species. Usually, direct human impacts, such as various disturbances in roosts (including mass bat ringing, e.g., Bárta et al. 1981) and accumulation of pesticides were considered to be the main threats affecting bat communities. However, the changes were sometimes explained also by global climatic or environmental oscillations seeing that the development of bat numbers in hibernacula conspicuously correlated with annual variation of global temperature (Gaisler et al. 1981; Horáček 1984; Kulzer 1995; Horáček et al. 2005). The assumed correlation of a long-term increase of *M. daubentonii* populations with the growth of its main prey, i.e. water surface swarming insects, caused probably by widespread eutrophisation

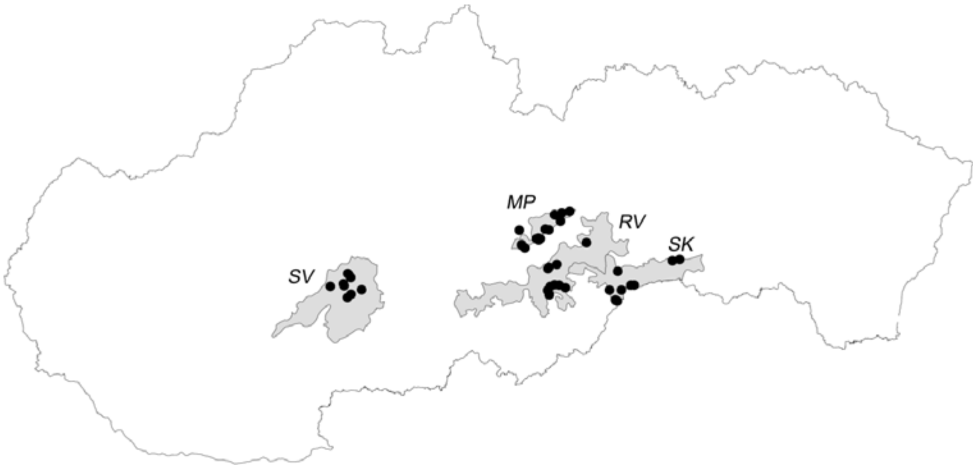

Fig. 1. Map of study regions and sites in Slovakia. MP – Muránska planina Mts, RV – Revúcka vrchovina Mts, SK – Slovenský kras Mts, SV – Štiavnické vrchy Mts.

of water bodies, was not supported by the analysis of more extensive samples (Kokurewicz 1995). Similarly, changes in prey abundance and possible competition for food between expanding and declining bat species were found unlikely to explain population changes in *R. hipposideros* (Arlettaz et al. 2000; Bontadina et al. 2008).

Considering the above mentioned facts, accurate monitoring and population data collecting with the aim of tracking population changes are necessary for understanding ecology of the species. Finally, assessment of these data is essential for effective conservation and management planning (e.g., Spellerberg 1991; Battersby & Greenwood 2004; Pereira & Cooper 2006). Although it is rather difficult to find precise data on the abundance of bats and their changes in particular regions (Thomas & LaVal 1988), in the temperate zone long-term population variations can be well estimated by counting hibernating bats in their underground roosts. Several programmes based on such winter censuses have been performed in Europe, in some cases for tens of years already (e.g., Gaisler 1975; Daan et al. 1980; Baar et al. 1986; Bauerová et al. 1989; Wołoszyn 1994; The Bat Conservation Trust 2001; Horáček et al. 2005; Boldogh & Estók 2007). Several Slovak sites were included in the programme of census of hibernating bats carried out in Czechoslovakia since 1969 (Gaisler 1975), however, later on these roosts were checked rather occasionally. The winter census programme in Slovakia was resumed in the last decade of the 20^{th} century, covering a considerably larger number of winter roosts. Whereas only fragmented and regionally limited data have been published so far (e.g., Uhrin 1993, 1998a; Danko 1997; Lehotská 2002; Mihál 2004), the aim of this study is to provide an analysis of long-term population changes of hibernating bats as revealed from the annual monitoring programme conducted in four mountain regions of the Western Carpathians during the period 1992–2009 and its comparison with the trends already demonstrated in other regions of Europe.

Material and methods

Study sites

The data analysed in this study were gathered during winter bat censuses in four distinct geomorphological units of the Western Carpathians (Fig. 1).

(1) Muránska planina Mts [MP] – karstic region situated in central Slovakia (approximately 20°01′ E, 48°46′ N). With the exception of one site (abandoned railway tunnel Dielik), all monitored sites are limestone caves. Altogether, data from 18 hibernacula coming from the period of 17 years (1993–2009) were analysed. The mountain area is protected as a national park.

(2) Revúcka vrchovina Mts [RV] – region with varied geological conditions in central Slovakia. Several underground spaces in its central part (approximately 20°04′ E, 48°32′ N) were checked (7 limestone caves, 2 abandoned mines and 1 abandoned railway tunnel). These sites were censused for the period of 13 years (1997–2009) only.

(3) Slovenský kras Mts [SK] – situated in the southern part of central Slovakia (approximately 20°35′ E, 48°35′ N) and represented by several karstic plateaus. Bats were monitored in 12 limestone caves for the period of 18 years (1992–2009). The region is protected as a national park.

(4) Štiavnické vrchy Mts [SV] – volcanic mountain range in central Slovakia (approximately 18°53′ E, 48°26′ N). Altogether 12 man-made underground sites (mines) were monitored for the period of 16 years (1994–2009). The region has a status of a protected landscape area.

Bat records from winter censuses from the above described regions until 2001 were compiled and published in the Catalogue of Bat Hibernacula of Slovakia (Hapl et al. 2002; Matis et al. 2002a; Uhrin et al. 2002b, c, d, e), together with characteristics of the particular sites. For the purpose of this study, data from 52 hibernacula were analysed (Table 1). Since the two abandoned railway tunnels included in the monitoring programme (Dielik – MP, Slavošovce – RV) had different physical characteristics than the other roosts and also the composition of their bat communities was specific, they were excluded from the log-linear analysis of population trends (see below).

Census method

The annual census was usually carried out in the last ten-day period of January or the first ten-day period of February

Table 1. Dominance (d) and frequency (F) of hibernating bats recorded in four regions of central Slovakia. Data from particular regions are arranged according to species' frequency.

MP (1993–2009)			RV (1997–2009)			SK (1992–2009)			SV (1994–2009)		
Species	d (%)	F (%)	Species	d (%)	F (%)	Species	d (%)	F (%)	Species	d (%)	F (%)
Rhip	22.1	82.0	*Rhip*	34.2	85.0	*Rhip*	37.5	92.9	*Rhip*	54.2	95.5
Mmyo	11.4	74.9	*Bbar*	60.5	42.9	*Rfer*	10.4	82.5	*Mmyo*	10.0	77.3
Bbar	43.0	40.4	*Mmyo*	1.2	25.2	*Mmyo*	10.1	58.5	*Rfer*	24.4	29.5
Rfer	0.4	36.9	*Rfer*	0.5	19.3	*Mema*	2.5	34.4	*Mema*	1.3	28.0
Paur	0.1	20.4	*Eser*	0.4	14.3	*Mdau*	0.9	27.9	*Bbar*	8.0	26.5
Mmys	0.2	19.2	*Paus*	0.4	11.2	*Reur*	29.4	23.0	*Mdau*	0.9	24.2
Mema	0.4	16.9	*Mdau*	0.2	8.4	*Bbar*	4.6	21.3	*Paur*	0.3	12.9
Mdau	0.1	14.9	*Paur*	0.1	5.9	*Mdas*	1.0	18.6	*Mbech*	0.1	7.6
Enil	0.1	11.4	*Reur*	0.2	5.6	*Paus*	0.2	12.6	*Mmys*	0.1	6.1
Eser	0.0	7.8	*Mema*	0.1	5.6	*Paur*	0.2	9.3	*Mnat*	0.2	5.3
Ppip	17.7	7.5	*Mnat*	0.1	5.6	*Mmys*	0.1	7.7	*Paus*	0.1	3.1
Mnat	0.0	5.9	*Mbech*	0.1	2.8	*Eser*	1.5	6.6	*Eser*	<0.01	1.5
Mdas	0.0	5.5	*Mschr*	2.0	1.7	*Ppip*	0.8	6.6	*Mschr*	<0.01	1.5
Mschr	4.2	3.1	*Mmys*	<0.01	0.9	*Enil*	0.1	5.5	*Enil*	<0.01	0.8
Mbech	<0.01	2.7	*Ppip*	<0.01	0.8	*Nnoc*	0.4	4.9	*Ppip*	–	–
Paus	<0.01	1.6	*Mdas*	–	–	*Mnat*	0.1	4.4	*Mdas*	–	–
Reur	<0.01	1.2	*Enil*	–	–	*Mbech*	0.1	3.8	*Reur*	–	–
Nnoc	<0.01	0.4	*Nnoc*	–	–	*Mschr*	<0.01	1.1	*Nnoc*	–	–
indet.	<0.01	–	indet.	<0.01	–	indet.	0.2	–	indet.	0.3	–
No. of species		18	No. of species		15	No. of species		18	No. of species		14
No. of sites		18	No. of sites		10	No. of sites		12	No. of sites		12
No. of records		55958	No. of records		6213	No. of records		13921	No. of records		7141
Mean no. of records/year		3291.6	Mean no. of records/year		477.9	Mean no. of records/year		773.4	Mean no. of records/year		446.3
SD		2931.5	SD		100.7	SD		437.6	SD		219.2

Species abbreviations: *Bbar* – *Barbastella barbastellus*, *Enil* – *Eptesicus nilssonii*, *Eser* – *E. serotinus*, *Mbech* – *Myotis bechsteinii*, *Mdas* – *M. dasycneme*, *Mdau* – *M. daubentonii*, *Mema* – *M. emarginatus*, *Mmyo* – *M. myotis*, *Mmys* – *M. mystacinus*, *Mnat* – *M. nattereri*, *Mschr* – *Miniopterus schreibersii*, *Nnoc* – *Nyctalus noctula*, *Paur* – *Plecotus auritus*, *Paus* – *P. austriacus*, *Ppip* – *Pipistrellus pipistrellus*, *Reur* – *Rhinolophus euryale*, *Rfer* – *R. ferrumequinum*, *Rhip* – *R. hipposideros*. For region abbreviations see Fig. 1.

on the same census track within the particular hibernaculum and mostly by the same people. Hence, the data series coming from the particular sites are well representative and objective within the respective hibernaculum. Only very few counts made in November or December were included in the analysis. Non-tactile visual species determination and counting of bats without disturbing them (e.g., by ringing) were applied in the course of the census. For further assessment we used the following method of bat species group classification, slightly modified after Bauerová et al. (1989): the species pairs of *Myotis myotis* / *M. blythii* and *M. mystacinus* / *M. brandtii* were assessed together as one species (as *M. myotis* and *M. mystacinus*, respectively). According to the previous studies (e.g., Gaisler & Hanák 1973; Uhrin 1998b), the numbers of these sibling species (*M. blythii, M. brandtii*) make up approximately one third (*M. blythii*) and almost half (*M. brandtii*) of counted bats, respectively. Total numbers of bat records and values of species dominance and frequency are given in Table 1. The high variation is caused by the considerable fluctuations in some species (e.g., forming large aggregations), therefore the trends were calculated only for separate species and not for the whole bat community. Within the data sets from the four regions, there are some missing counts in particular years and sites because of different reasons. They represent 3.6% of the whole data set in RV, 15.3% in SK, 17.3% in MP and 31.3% in SV. It is recommended that the proportion of missing counts should not exceed 50% of all analysed data (Pannekoek & van Strien 2009), therefore our data are proper for further analysis using the log-linear Poisson regressions.

Data analyses

We used the log-linear Poisson regression to estimate missing data and to model population trends (ter Braak et al. 1994). All procedures were run using the free TRends and Indices for Monitoring data software (TRIM; Pannekoek & van Strien 2009). To calculate population trends, a linear model with serial correlation between annual counts as well as overdispersion from Poisson observations was used in TRIM. To test the significance of slope parameters, the Wald statistic was used. In Table 2 only data where enough observations were available for the species / region pairs are shown. Simple linear regression and correlation analysis were also used for demonstrating changes in particular species / site pairs. The variables were compared by a non-parametric statistic (r_s, Spearman rank correlation test, 2–tailed). Linear regression, correlation analysis and non-parametric statistic analyses were performed using the Statistica software (StatSoft 2001).

Results

Altogether 18 bat species were recorded during winter censuses in the four regions under study (Table 1). Only in one species (*Rhinolophus hipposideros*), population indices could be compiled using the log-linear regression and patterns of its population trend could be shown for all studied regions. In other six bat species (*Rhinolophus ferrumequinum*, *Myotis myotis*, *M. emarginatus*, *M. mystacinus*, *M. dasycneme*, and *Barbastella bar-*

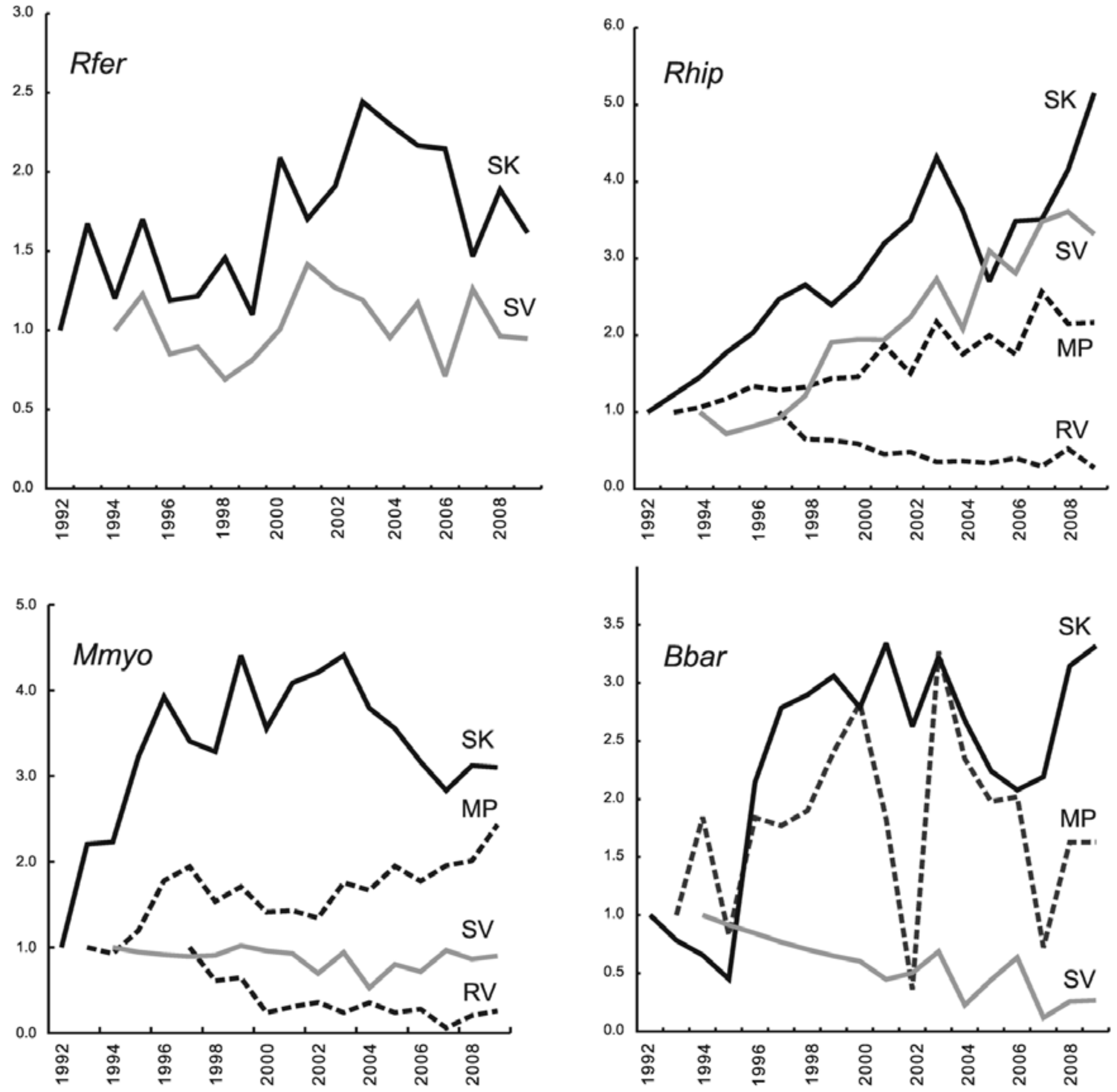

Fig. 2. Population indices for selected hibernating bat species in central Slovakia. Indices are abundances relative to the abundance in the base year (index = 1). For region abbreviations see Fig. 1, for species abbreviations see Table 1.

bastellus) these indices were calculated only for some of the regions. In the remaining species these indices were uncertain because of the scarcity of data. Only the results of linear regression and correlation analyses per particular species-site pairs are given in Table 3.

Horseshoe bats, Rhinolophus spp.

In the greater horseshoe bat (*R. ferrumequinum*), dominance and species frequency varied within the ranges of d = 0.4–24.4% and F = 19.3–82.5%, respectively (Table 1). Only in the SK region where the frequency of this species was the highest, a significant population trend classified as a moderate increase (3% per year within the period evaluated) could be recognised (Table 3, Fig. 2). The values recorded in other regions did not fit the model well, so any trends seem to be uncertain. In the SV region (Table 3, Fig. 2), the slope parameter (1.0048) suggests a stable population (Wald test 0.11, $P = 0.737$, n.s.).

In the particular hibernacula of all the regions, *R. ferrumequinum* showed stable (or not significantly declining) or increasing numbers (Table 3). The only exception was the Stará Domica cave (SK), but the species' abundance was low at this site.

The lesser horseshoe bat (*R. hipposideros*) was the most frequent bat species in all four regions (F = 82.0–95.5%). Values of its dominance varied within the range of 22.1–54.2% and with the exception of the RV region, the dominance of this species was always the highest (Table 1). A general population trend found in this species is given in Fig. 2 jointly for all four regions monitored. While in three regions its hibernating populations increased in numbers at the rate of 5–11% per year (Table 2), they moderately declined in the RV region (8% decrease per year within the whole study period). This trend was mainly affected by a significant decline in the Burda cave ($rs = -0.84$, $P < 0.01$) and in the Zráz mine ($rs = -0.62$, $P < 0.05$; Table 3, Figs 3A, B). Wintering population of *R. hipposideros* in the Burda cave declined from the initial number of 243 bats in 1997 down to 38 in 2009. In other sites

Table 2. Parameters of overdispersion (od), serial correlation (sc) and goodness of fit (Chi-square) taken into account by TRIM software and slope (sl) parameters calculated by the linear model [with values of Wald-test (Wt) for its significance] and interpretation (overall multiplicative trend model) of the trends for species / region data sets.

Region	od	sc	Chi-sq	df	*P*	Wt (df = 1)	*P*	sl	SE	Trend
Rhinolophus ferrumequinum (Schreber, 1774)										
MP	1.038	0.365	142.25	137	0.362	0.19	0.659	0.990	0.030	uncertain
RV	1.355	–0.061	90.79	67	0.028	1.17	0.279	1.023	0.089	uncertain
SK	2.369	0.143	402.69	170	0.000	9.37	0.002	1.030	0.010	moderate increase**
SV	2.266	0.161	174.48	77	0.000	0.11	0.737	1.005	0.010	stable
Rhinolophus hipposideros (Borkhausen, 1797)										
MP	10.393	0.619	2203.35	212	0.000	28.33	0.000	1.052	0.011	moderate increase**
RV	5.802	0.238	562.80	97	0.000	28.38	0.000	0.926	0.015	moderate decline**
SK	8.113	0.290	1379.19	170	0.000	48.92	0.000	1.079	0.014	strong increase*
SV	4.181	0.234	497.50	119	0.000	97.96	0.000	1.114	0.013	strong increase*
Rhinolophus euryale Blasius, 1853										
SK	120.848	0.144	12930.70	107	0.000	3.81	0.051	1.044	0.578	uncertain
Myotis myotis (Borkhausen, 1797)										
MP	3.364	0.340	743.45	221	0.000	37.14	0.000	1.039	0.007	moderate increase**
RV	1.307	0.125	98.03	75	0.038	11.76	0.001	0.880	0.052	moderate decline*
SK	2.290	0.251	389.28	170	0.000	4.60	0.032	1.030	0.015	moderate increase*
SV	1.610	0.222	191.63	119	0.000	0.58	0.447	0.987	0.014	stable
Myotis emarginatus (E. Geoffroy, 1806)										
MP	1.567	–0.027	177.03	113	0.000	26.79	0.000	1.120	0.063	uncertain
RV	0.924	–0.152	20.34	22	0.562	0.05	0.823	0.962	0.037	uncertain
SK	2.295	0.082	305.18	133	0.000	17.68	0.000	1.108	0.050	moderate increase*
SV	2.081	–0.008	206.03	99	0.000	5.58	0.018	1.138	0.093	uncertain
Myotis mystacinus (Kuhl, 1817)										
MP	1.981	–0.055	269.39	136	0.000	19.44	0.000	1.135	0.058	moderate increase*
SK	1.109	–0.037	102.00	92	0.223	3.11	0.078	1.114	0.973	uncertain
Myotis daubentonii (Kuhl, 1817)										
MP	1.153	–0.048	177.50	154	0.094	0.02	0.902	1.003	0.052	uncertain
RV	1.026	0.016	58.46	57	0.422	2.89	0.089	0.996	0.110	uncertain
SK	1.396	–0.025	205.19	147	0.001	13.54	0.000	1.148	0.247	uncertain
SV	1.472	–0.116	153.10	104	0.001	12.11	0.001	1.182	0.097	uncertain
Myotis dasycneme (Boie, 1825)										
MP	1.392	–0.004	112.76	81	0.011	1.37	0.242	1.173	0.762	uncertain
SK	1.444	0.324	89.50	62	0.013	22.26	0.000	1.176	0.070	moderate increase*
Myotis bechsteinii (Kuhl, 1817)										
MP	0.922	–0.033	60.82	66	0.657	2.76	0.097	0.809	0.482	uncertain
RV	scarce data									
SK	1.110	0.062	65.49	59	0.262	0.19	0.663	1.073	0.386	uncertain
SV	0.920	–0.033	64.41	70	0.666	0.20	0.652	0.985	0.087	uncertain
Myotis nattereri (Kuhl, 1817)										
MP	1.308	–0.028	82.40	63	0.051	0.23	0.632	0.975	0.102	uncertain
RV	0.899	–0.065	26.96	30	0.626	0.47	0.491	0.834	0.148	uncertain
SK	1.366	–0.055	105.20	77	0.018	0.24	0.623	0.947	0.438	uncertain
SV	0.990	–0.148	43.58	44	0.490	9.25	0.002	1.489	0.427	uncertain
Plecotus auritus (L., 1758)										
MP	1.011	–0.074	212.28	210	0.443	0.50	0.480	0.981	0.036	uncertain
RV	0.939	–0.143	28.16	30	0.562	0.45	0.504	0.904	0.114	uncertain
SK	1.210	0.112	89.55	74	0.105	4.29	0.038	1.288	1.154	uncertain
SV	1.172	0.046	70.31	60	0.171	0.30	0.584	1.010	0.180	uncertain

Table 2. (continued)

Region	od	sc	Chi-sq	df	P	Wt (df = 1)	P	sl	SE	Trend
Plecotus austriacus (Fisher, 1829)										
MP	scarce data									
RV	2.830	–0.045	158.50	56	0.000	3.94	0.047	0.923	0.144	uncertain
SK	1.165	0.085	133.97	115	0.109	3.20	0.074	0.835	0.604	uncertain
Pipistrellus pipistrellus (Schreber, 1774)										
MP	37.083	–0.018	964.16	26	0.000	1.49	0.223	1.549	2986.497	uncertain
SK	7.581	0.017	204.68	27	0.000	5.15	0.023	1.163	1.623	uncertain
Barbastella barbastellus (Schreber, 1774)										
MP	2.718	0.120	415.82	153	0.000	0.27	0.605	1.006	0.022	stable
RV	2.158	–0.031	185.61	86	0.000	6.74	0.009	0.859	0.088	uncertain
SK	1.866	0.377	225.76	121	0.000	10.15	0.001	1.080	0.029	moderate increase**
SV	3.736	–0.203	306.33	82	0.000	5.61	0.018	0.905	0.036	moderate decline**
Eptesicus serotinus (Schreber, 1774)										
MP	1.355	–0.091	105.72	78	0.020	0.99	0.321	0.951	0.065	uncertain
RV	0.893	–0.110	29.46	33	0.644	0.00	0.980	1.001	0.048	uncertain
SK	56.055	–0.133	1569.53	28	0.000	2.13	0.145	0.779	1.732	uncertain
Eptesicus nilssonii (Keyserling et Blasius, 1839)										
MP	1.120	–0.028	84.02	75	0.223	1.07	0.300	1.041	0.043	uncertain
SK	0.831	–0.049	23.27	28	0.719	5.09	0.024	1.244	0.838	uncertain
Nyctalus noctula (Schreber, 1774)										
SK	6.107	–0.017	79.40	13	0.000	5.84	0.016	1.185	0.334	uncertain

Statistical significance: * $P < 0.05$, ** $P < 0.01$. For region abbreviations see Fig. 1.

within the RV region, both slow increases and slow decreases (not significant) or a stable state without any remarkable changes could be observed (Table 3). In all sites analysed in the SV region (Table 3) we observed increasing numbers of this species (in some of the sites the trend was not significant). In the large Schöpfer mine, a strong increase was detected ($rs = 0.89$, $P < 0.01$). In the remaining two regions, MP and SK, *R. hipposideros* showed population decrease in some cave hibernacula, in several cases a significant one (Table 3). Despite this, based on the changes in the numbers counted at other sites, *R. hipposideros* showed a generally increasing trend of the numbers of wintering individuals, supporting the model calculated using the log-linear regression with imputed data. Even at the sites inhabited by higher numbers of the lesser horseshoe bat, a slight population increase (Figs 3C–F) was observed.

Occurrence of the Mediterranean horseshoe bat (*R. euryale*) is restricted to karstic areas in the southern part of central Slovakia (see also Uhrin et al. 1996), it is absent from the SV region. Among the regions under study, only in SK this species showed higher dominance and frequency values (29.4% and 23.0%, respectively). Neither log-linear nor linear regression and correlation analyses showed any detectable population trends (Tables 2, 3).

Mouse-eared bats, Myotis myotis s.l.

Regarding species frequencies ($F = 25.2$–77.3%; Table 1), mouse-eared bats represented the second to third most frequent species unit within the regions under study. A moderate increase (MP: $P < 0.01$; SK: $P < 0.05$) or stable population (SV) were observed (Fig. 2). The rates of increase in the former two regions (MP, SK) reached 3% per year and per site. At the most populated site, the Martincová cave (MP), a slight increase was observed ($rs = 0.77$, $P < 0.01$; Table 3). In the RV region, an approximately 13 per cent decline of the *M. myotis* populations was detected ($P < 0.05$) within the study period. A significant decline of 9% per year was observed (0.913, SE 0.027; Wald test 6.67, $P < 0.01$) in the SK region in 2003–2009 (Fig. 2).

Small Myotis bats

Recorded abundances and frequencies of the small *Myotis* bats were found low in the period under study and their population trends were not detected and remain uncertain (Table 1). Only in the SK region a moderate increase of *M. emarginatus* and *M. dasycneme* populations was observed, estimated at 10% and 17% per year, respectively. In *M. dasycneme* this general trend corroborates with the picture from two hibernacula (the Hačavská and Marciho caves in the northern part of SK), where this bat was the most frequent and

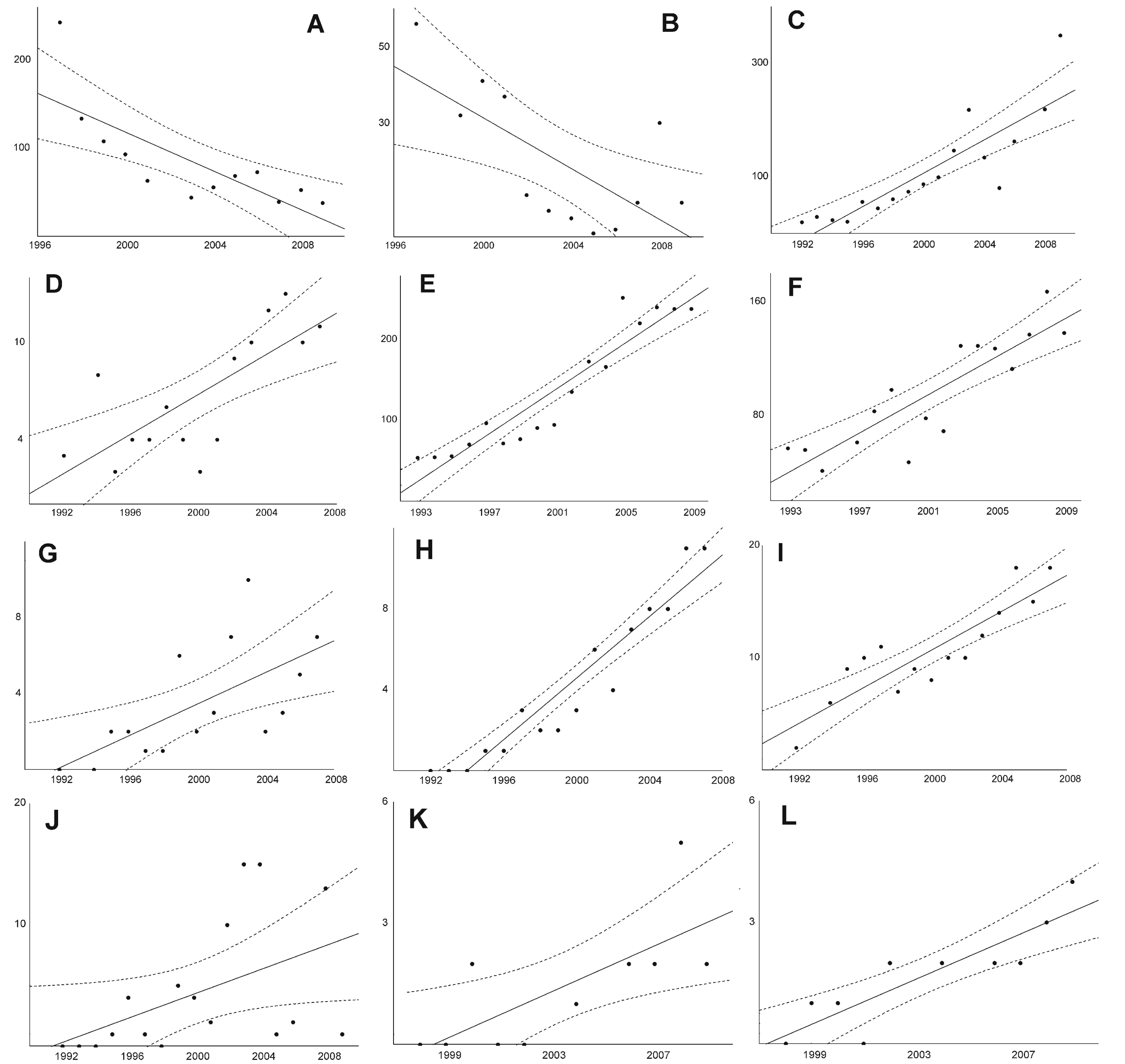

Fig. 3. Changes in abundance of hibernating bats demonstrated by the linear regression (solid line) and its confidence limits at $P = 0.95$ (dashed lines) in selected species-site pairs (A – *Rhip*, RV, Burda cave; B – *Rhip*, RV, Zráz gallery; C – *Rhip*, SK, Čertova diera cave; D – *Rhip*, SK, Marciho cave; E – *Rhip*, MP, Bobačka nová cave; F – *Rhip*, MP, Čertova cave; G – *Mdas*, SK, Marciho cave; H – *Mdas*, SK, Hačavská cave; I – *Mema*, SK, Marciho cave; J – *Mema*, SK, Čertova diera cave; K – *Mmys*, MP, Havrania cave; L – *Mmys*, MP, Oči cave). For region abbreviations see Fig. 1, for species abbreviations see Table 1, for statistics see Table 3.

its numbers showed a significant increase (Table 4, Figs 3G, H). A similar trend was recorded also in the Marciho cave for hibernating populations of *M. daubentonii* ($rs = 0.57$, $P < 0.05$; Table 3). In *M. emarginatus* we observed an increasing abundance in four hibernacula (Table 3), being significant in two of them (Figs 3I, J). A moderate increase was detected in *M. mystacinus* wintering in the MP region. Such a pattern was visible mainly in the data from two hibernacula, where this species was frequent and showed a significant increase (Table 4, Figs 3K, L).

Barbastelle, Barbastella barbastellus

Very diverse trends were detected in numbers of wintering individuals of *B. barbastellus* (Fig. 2). While in MP (with the exception of the Dielik tunnel) the populations showed a stable nature, in the other three regions we detected different pictures. Barbastelles in SK showed a moderate increase (7% per year) but in SV they experienced a moderate decline (ca. 10%). The abandoned railway tunnels Dielik [MP] and Slavošovce [RV] were not included in these models. In the Dielik tunnel, mass winter aggregations of ca. 6,000 individuals were found in 1993 (Uhrin 1995). The winter checks of the Slavošovce tunnel started in 1998. In these two separately evaluated sites, *B. barbastellus* showed clearly distinct patterns in wintering and numbers. While in the Dielik tunnel we detected a rapid

Table 3. Correlation of the actual abundances of particular species in the localities where their frequency was ≥50% to the respective values predicted by linear regression models.

Site, region	n	r^2	rs	P
R. ferrumequinum				
Bobačka nová, MP	17	0.170	−0.361	0.155
Dielik, MP	16	0.745	0.844	0.000
Husleho, MP	13	0.004	−0.049	0.874
Kostolík, MP	17	0.099	0.377	0.136
Michňová, MP	17	0.283	0.532	0.028
Osiská, MP	15	0.019	−0.108	0.700
Burda, RV	12	0.081	0.250	0.434
Ardovská, SK	16	0.095	−0.443	0.086
Čertova diera, SK	17	0.063	0.276	0.283
Domica, SK	16	0.080	0.241	0.368
Hačavská, SK	16	0.545	0.661	0.005
Líščia, SK	15	0.237	−0.566	0.028
Majkova, SK	18	0.077	0.282	0.257
Marciho, SK	15	0.009	0.143	0.612
Milada, SK	18	0.135	0.352	0.151
Stará Brzotínska, SK	15	0.420	0.574	0.025
Stará Domica, SK	12	0.349	−0.630	0.028
Vápencová, SK	10	0.037	−0.274	0.443
Ignác, SV	16	0.033	0.182	0.500
Schöpfer, SV	15	0.190	0.143	0.611
R. hipposideros				
Bobačka nová, MP	17	0.887	0.941	0.000
Bobačka stará, MP	15	0.311	−0.642	0.010
Brestová, MP	17	0.348	0.633	0.006
Čertova jaskyňa, MP	16	0.758	0.870	0.000
Dielik, MP	16	0.802	0.921	0.000
Husleho, MP	13	0.005	−0.011	0.972
Kostolík, MP	17	0.415	−0.623	0.008
Ladzianskeho, MP	17	0.405	0.695	0.002
Martincová, MP	17	0.515	0.796	0.000
Michňová, MP	17	0.205	0.434	0.082
Netopierov, MP	12	0.714	0.951	0.000
Osiská, MP	15	0.207	−0.476	0.073
Paseky, MP	9	0.192	−0.392	0.297
Prandlovo, MP	12	0.045	−0.289	0.362
Burda, RV	12	0.595	−0.839	0.001
Drienocká, RV	13	0.046	−0.250	0.409
Chvalovská, RV	13	0.097	−0.316	0.293
Malá Drienčanská, RV	12	0.059	0.384	0.217
Maruškin, RV	12	0.001	−0.180	0.577
Sušiansky vrch, RV	8	0.306	−0.639	0.088
Špaňopoľská, RV	12	0.305	0.537	0.072
Veľká Drienčanská, RV	13	0.158	−0.321	0.284
Zráz, RV	12	0.474	−0.623	0.030
Ardovská, SK	16	0.144	0.371	0.157
Čertova diera, SK	17	0.745	0.936	0.000
Domica, SK	16	0.004	0.196	0.468
Hačavská, SK	16	0.385	0.547	0.028
Líščia, SK	15	0.044	0.241	0.387
Majkova, SK	18	0.014	−0.091	0.718
Marciho, SK	15	0.560	0.753	0.001
Milada, SK	18	0.128	0.325	0.188
Stará Brzotínska, SK	15	0.145	0.264	0.342
Stará Domica, SK	12	0.431	0.579	0.049
Vápencová, SK	10	0.290	−0.457	0.184
Ignác, SV	16	0.164	0.430	0.096
Laura, SV	16	0.452	0.681	0.004
Kamenný, SV	16	0.247	0.429	0.097
Kysihýbel, SV	10	0.785	0.894	0.000
Kunia, SV	9	0.524	0.683	0.042
Nad Rabensteinom, SV	6	0.838	0.943	0.005
Olovená, SV	9	0.800	0.845	0.004
Pod Rabensteinom, SV	5	0.015	0.053	0.933
Schöpfer, SV	15	0.795	0.882	0.000
Rabenstein, SV	7	0.001	0.127	0.786
Repište, SV	12	0.494	0.742	0.006
Zlatý Stôl, SV	11	0.447	0.513	0.107
R. euryale				
Ardovská, SK	16	0.234	0.330	0.212
Domica, SK	16	0.076	−0.127	0.640
M. myotis				
Bobačka nová, MP	17	0.021	0.158	0.545
Bobačka stará, MP	15	0.580	−0.755	0.001
Brestová, MP	17	0.276	0.491	0.045
Čertova jaskyňa, MP	16	0.316	0.646	0.007
Dielik, MP	16	0.810	0.918	0.000
Havrania, MP	10	0.114	0.441	0.202
Husleho, MP	13	0.076	−0.296	0.325
Ladzianskeho, MP	17	0.381	−0.566	0.018
Martincová, MP	17	0.638	0.772	0.000
Michňová, MP	17	0.027	0.124	0.634
Netopierov, MP	12	0.525	−0.728	0.007
Oči, MP	10	0.106	0.362	0.304
Osiská, MP	15	0.126	0.373	0.171
Zlatnica, MP	13	0.331	−0.632	0.021
Burda, RV	12	0.027	−0.142	0.660
Sušiansky vrch, RV	8	0.013	−0.287	0.491
Čertova diera, SK	17	0.240	0.425	0.089
Hačavská, SK	16	0.221	0.363	0.167
Majkova, SK	18	0.000	−0.032	0.901
Marciho, SK	15	0.033	−0.177	0.527
Milada, SK	18	0.049	−0.193	0.444
Stará Brzotínska, SK	15	0.215	0.434	0.106
Ignác, SV	16	0.085	0.356	0.176
Laura, SV	16	0.538	−0.739	0.001
Kamenný, SV	16	0.633	−0.806	0.000
Kunia, SV	9	0.169	−0.549	0.126
Kysihýbel, SV	10	0.357	0.494	0.147
Nad Rabensteinom, SV	6	0.870	0.928	0.008
Olovená, SV	9	0.192	0.411	0.272
Rabenstein, SV	7	0.093	−0.464	0.294
Schöpfer, SV	15	0.000	0.135	0.631
M. emarginatus				
Bobačka nová, MP	17	0.177	0.426	0.088
Michňová, MP	17	0.421	0.660	0.004
Čertova diera, SK	17	0.235	0.574	0.016
Majkova, SK	18	0.044	0.486	0.041
Marciho, SK	15	0.776	0.851	0.000
Milada, SK	18	0.032	0.115	0.648
Olovená, SV	9	0.739	0.849	0.004
Schöpfer, SV	15	0.077	0.658	0.008
M. mystacinus				
Havrania, MP	10	0.519	0.743	0.014
Oči, MP	10	0.776	0.913	0.000
M. daubentonii				
Čertova jaskyňa, MP	16	0.067	0.277	0.298
Hačavská, SK	16	0.128	0.446	0.083
Marciho, SK	15	0.346	0.569	0.027
Milada, SK	18	0.082	0.119	0.639
Ignác, SV	16	0.113	0.453	0.078
Kysihýbel, SV	10	0.255	0.409	0.241
M. dasycneme				
Hačavská, SK	16	0.907	0.979	0.000
Marciho, SK	15	0.425	0.752	0.001
P. auritus				
Hačavská, SK	16	0.654	0.836	0.000
P. austriacus				
Stará Domica, SK	12	0.267	−0.529	0.077
P. pipistrellus				
Dielik, MP	16	0.677	−0.749	0.001
Zbojnícka, SK	15	0.321	0.599	0.018
B. barbastellus				
Bobačka stará, MP	15	0.016	−0.122	0.665
Brestová, MP	17	0.046	0.345	0.175
Čertova jaskyňa, MP	16	0.030	0.131	0.627

Table 3. (continued)

Site, region	n	r^2	rs	P
B. barbastellus (continued)				
Dielik, MP	16	0.573	−0.753	0.001
Havrania, MP	10	0.067	−0.289	0.419
Martincová, MP	17	0.000	0.185	0.478
Netopierov, MP	12	0.246	−0.502	0.096
Oči, MP	10	0.471	0.724	0.018
Chvalovská, RV	13	0.189	−0.407	0.167
Slavošovský, RV	12	0.226	0.664	0.018
Sušiansky vrch, RV	8	0.009	−0.258	0.538
Zráz, RV	12	0.059	0.193	0.547
Hačavská, SK	16	0.346	0.418	0.107
Kysihýbel, SV	10	0.453	−0.652	0.041
Nad Rabensteinom, SV	6	0.241	−0.486	0.329
Pod Rabensteinom, SV	5	0.381	0.667	0.219
Rabenstein, SV	7	0.000	−0.143	0.760
E. serotinus				
Oči, MP	10	0.066	−0.235	0.514
Slavošovský, RV	12	0.105	−0.304	0.338
Hačavská, SK	16	0.085	0.300	0.259
E. nilssonii				
Havrania, MP	10	0.133	0.350	0.321
Oči, MP	10	0.046	−0.244	0.497
Zlatnica, MP	13	0.026	0.134	0.662
Hačavská, SK	16	0.185	0.475	0.063
N. noctula				
Zbojnícka, SK	15	0.253	0.537	0.039
M. schreibersii				
Dielik, MP	16	0.177	−0.781	0.000

Explanations: n – number of bat species; r^2 – coefficient of determination of the regression (squared Pearson's r); rs – the respective values of non-parametric Spearman correlation and their statistical significances (P). For region abbreviations see Fig. 1.

Table 4. Overview of bat population trends in central Slovakia (1992–2009).

Species	Overall trend
Rhinolophus ferrumequinum	stable → (moderate) increase
Rhinolophus hipposideros	(local) decline → moderate → strong increase
Rhinolophus euryale	stable
Myotis myotis	(local) decline → moderate increase
Myotis emarginatus, M. mystacinus, M. daubentonii, M. dasycneme	stable ↔ (local) moderate increase
Barbastella barbastellus	(local) moderate decline ↔ stable ↔ (local) moderate increase + fluctuations

decline (Table 4) of the numbers of bats in aggregations, in the Slavošovce tunnel we observed a continuous increase of abundance since the beginning of the monitoring (Table 4). After the apparent decline of barbastelles (and also of common pipistrelles, see below) in the Dielik tunnel, a significant increase of other species, not present or registered only in low abundance in the hibernaculum prior to 1999, was observed (Table 4): *R. ferrumequinum* ($rs = 0.84$, $P < 0.01$), *R. hipposideros* ($rs = 0.92$, $P < 0.01$), *M. myotis* ($rs = 0.92$, $P < 0.01$) (Table 3).

Other species
Several other species known to occur in the regions under study were found occasionally during the monitoring and their abundance and frequency was low (Table 1). Thus, no dynamics in their numbers were detected and their trends remain uncertain. In some species, e.g., *Plecotus auritus* and/or *Nyctalus noctula* (Schreber, 1774), certain development could be observed in the particular sites (see the correlation analysis, Table 3). Especially the rapid decline of the common pipistrelles (*Pipistrellus pipistrellus*) and long-winged bats *Miniopterus schreibersii* (Kuhl, 1817) in the Dielik tunnel (Table 3) is noteworthy. In 1993–1998, aggregations of hundreds (min. 940, max. 2074, mean 1557) of *P. pipistrellus* were observed at the site. After 1999 a rapid breakdown was detected and in 2001–2009 only individuals (min. 0, max. 72, mean 22) hibernated in the roost. Aggregations of *M. schreibersii* (min. 214, max. 1100, mean 589) accompanied the above mentioned species in the period 1995–1998. Since 2001 only one individual of the long-winged bat has been observed.

Discussion

In three most frequent species of hibernating bats (*Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis myotis*) we recorded stable population numbers or even their obvious increase in more than one of the four studied regions. Such a pattern is very similar to the trends documented in these species in several regions of central Europe over the last 20 years (Řehák 1997; Řehák & Gaisler 1999; Fuszara & Jurczyszyn 2002; Horáček et al. 2005), where a continuous population growth can be observed. During our monitoring period, the numbers of the most common species, *R. hipposideros*, increased markedly in three regions of central Slovakia similarly as it was already documented in man-made (mines) or natural (caves) hibernacula in eastern or western Slovakia. While in the Dubník mines in eastern Slovakia numbers of this species doubled in 1987–1995 (Danko 1997), in two caves in the Lesser Carpathians in western Slovakia a rapid increase was observed in 1995–2002 (Lehotská 2002). For instance, the increase in the Plavecká cave can be demonstrated by the recorded number of ca. 40 bats in 1995 and ca. 190 bats in 2002

(Lehotská 2002). In our study, numbers of *R. ferrumequinum* were found to increase only in the karstic region of the Slovenský kras Mts (SK), which is a region where almost a complete Slovakian population of the species is concentrated during the vegetation period (Uhrin et al. 1996). In other regions under study, the populations of *R. ferrumequinum* seem to be stable (SV) or the changes in numbers remain uncertain. The Slovakian population is believed to be a part of a metapopulation inhabiting the northern margin of the Pannonian lowland of southern Slovakia and northern Hungary (Bihari 2001). In several sites of northern Hungary, *R. ferrumequinum* (and also *R. euryale*) showed stable population numbers although with remarkable fluctuations (Bihari 2001; Boldogh & Estók 2007), but in some roosts decline in numbers was recorded (Paulovics & Márton 2008). In Switzerland an increase of a small isolated population of the greater horseshoe bat was documented within the period 1986–2006 in one summer colony, whose roost was restored (Bontadina et al. 2008).

In *R. euryale* we did not detect any clear population trends. One of the possible reasons is that the census method used could not cover changes in numbers between subsequent years because of high fluctuation of "wintering colonies" of this species within particular parts of cave systems. Such fluctuations were documented in the Domica-Baradla cave system, where the population of approximately 1000 individuals of the Mediterranean horseshoe bat was evidenced to occur (Bobáková 2002). During winter the population used several particular sites within the whole cave system for roosting and the bats were usually active throughout the hibernation period. However, considering this behaviour pattern and the observed presence of aggregations throughout the respective winter periods, we can estimate the population of this species as stable, even slowly growing. This opinion is also supported by the observations in summer, when a slight shift in roost preferences was observed in this species and its synanthropic roosting was documented (Horáček & Zima 1979). At present, a remarkable portion of the *R. euryale* population in Slovakia uses loft spaces as summer roosts (Matis et al. 2002b).

Irrespective of the region and/or particular site, the population of the greater mouse-eared bat, *Myotis myotis*, was increasing or stable. In *M. blythii*, the species whose numbers were included in the numbers of the former species in this study, no clear increase of abundance was observed in Slovakia and thus the detected growth in numbers is most probably due to the *M. myotis* population increase (Uhrin et al. 2008).

In the barbastelle, *Barbastella barbastellus*, a generally slow increase in counted numbers can be stated. Polish populations seem to be stable or even increasing in their numbers (Lesiński et al. 2005) and the barbastelle numbers are evaluated as increasing in several hibernacula of the Czech Republic (Řehák & Gaisler 1999; Horáček et al. 2005). Indications of an increase in numbers of hibernating barbastelles were reported also from the northern margin of its distribution range in Lithuania (Baranauskas 2001). On the other hand, especially in the hibernacula where mass winter aggregations were found, complete destruction of such aggregations with cascade patterns in consecutive years was usually observed as a consequence of research activities, changes in microclimate in the roost or predation (e.g., by the stone marten) (Obuch 1995; Danko 1997; Horáček et al. 2005). This situation occurred most obviously in the Dielik tunnel (MP). However, the general trend in populations of this species indicates that barbastelles are able to find relatively quickly an alternative winter roost with similar conditions and form similar mass aggregations there. In our case it was the Slavošovce tunnel (RV), situated at the distance of 20 km from the original aggregation site, the Dielik tunnel (MP).

Several other species such as *Myotis daubentonii*, *M. bechsteinii*, *M. nattereri*, *Plecotus auritus*, *P. austriacus*, *Eptesicus serotinus*, *E. nilssonii*, occurred in winter roosts in very low abundance and were found occasionally. They were usually hidden in various crevices and small holes in cave walls or ceiling and could be easily omitted. Hence, their numbers could be underestimated. The potential of winter census as a method of monitoring of these species seems to be rather low (The Bat Conservation Trust 2001). On the other hand, in some specific hibernacula with a limited amount of crevices and fissures, such as mines or cellars, the numbers of bats can be counted more precisely. In these types of winter roosts, increase of the numbers was documented in several regions of central Europe (Řehák & Gaisler 1999; Horáček et al. 2005; Kaňuch et al. 2008).

Considering causality of the changes in bat populations (mainly of their growth) during the last 20 or 30 years, one basic question can be raised: is this increase only a manifestation of population recovery after the rapid decline in the preceding periods or does it reflect a real population increase? Since the same population trend can be found also on the basis of data coming from region, where no research activities (e.g., bat ringing) occurred in the period of the deepest population decline, we can presume that the increasing trends in numbers of several hibernating species do reflect actual population growth (Horáček et al. 2005). Most of our monitored sites are roosts where no ringing was carried out during winter. Only the pattern found in the Revúcka vrchovina Mts, where we documented a moderate decline of two most abundant species, *R. hipposideros* and *M. myotis*, is questionable. No methods causing disturbance of bats (ringing) were used there during our study. Presumably this pattern can be explained by intensive human disturbance in the region, including illegal visiting of caves, fire making etc. (cf. Uhrin et al. 2002a). This is certainly true for the Burda cave, where a rapid decline in numbers of *R. hipposideros* was recorded. On the contrary, sites in the other studied regions are mostly inaccessible, either are grilled/gated or have a generally difficult access. All these sites are also situated in large protected areas (national parks or protected landscape areas) with a specific regime of human activities.

One of the causes of such population growth could be climate changes to which the increase of some species is conspicuously correlated (Horáček et al. 2005). In our data we do not have exact evidence for this, but most of the species with growing populations are thermophilous species which may follow increasing temperature. The impact of global temperature growth was tested on the model of a North American temperate bat, *Myotis lucifugus* (Le Conte, 1831). As predicted, expansion of its wintering range northward was assumed (Humphries et al. 2002). In our study, population growth can be observed also in species which reach margin of their distribution range in Slovakia or even form isolated populations and are thus considered to be more vulnerable and more sensitive to changes of environmental factors (Gaston 1994; Brown 1995). To support the pattern revealed from winter census, it would be necessary to collect data on abundance changes also in summer roosts (Warren & Witter 2002). Winter censuses can be used as a suitable monitoring method only for a part of the European bat fauna. On the other hand, potential influence of global climate changes could be documented by apparent range changes of several lithophilous or dendrophilous bat species, e.g., *Pipistrellus nathusii* (Keyserling et Blasius, 1839), *P. kuhlii* (Kuhl, 1817), *Hypsugo savii* (Bonaparte, 1837) (Sachanowicz & Ciechanowski 2006; Sachanowicz et al. 2006). Besides temperature increase in consequence of global climate changes, several other mechanisms causing population changes in bats have been discussed. Regarding a continuous growth of *M. daubentonii* populations in Poland, Kokurewicz (1995) concluded that it could be caused by eutrophisation of water bodies and consequently by the increase of the most important prey of this species, non-biting midges (Chironomidae). Arlettaz et al. (2000) studied potential food competition between the recently increasing *P. pipistrellus* and declining *R. hipposideros* and concluded that it could be an ecologically plausible scenario. The increase of *P. pipistrellus* was attributed to the use of a profitable food source represented by insects attracted around street lamps (Rydell 1989).

In conclusion, our data suggest an apparent population increase of thermophilous and originally cave dwelling species of bats, *R. hipposideros*, *R. ferrumequinum*, *M. myotis* in Slovakia (Table 4), a trend observed also in other regions of central Europe in the last two decades. In other bat species, population trends could not be detected and because of data scarcity, they should be evaluated from more extensive datasets obtained from a wide range of hibernacula or from a completely different type of evidence. To identify causes of the population trends recorded by our simple monitoring, a specially designed study is needed.

Acknowledgements

We express thanks to many colleagues who helped us during the census field trips: M. Andreas, J. Babic, P. Bačkor, V. Balaška, D. Baláž, L. Bobáková, I. Bryndza, P. Bryndza, E. Hapl, J. Hotový, V. Hrúz, Ľ. Hoffreiter, M. Kassa, K. Králiková, T. Mihál, A. Reiter, V. Solár, J. Šteffek, I. Valach, S. Zlacká and others. The winter census was carried out mainly as a part of activities of the State Nature Conservancy of the Slovak Republic (Banská Bystrica) and the Administration of Slovak Public Caves (Liptovský Mikuláš). The monitoring programme and data analyses were financially supported by grants from the Ministry of Environment of the Slovak Republic within the *Green Projects* scheme, Czech Science Foundation (206/09/0888), Ministry of Culture of the Czech Republic (MK00002327201) and Czech Bat Conservation Trust. We are grateful to P. Kaňuch for providing valuable comments on the manuscript and for his help with statistical evaluation of the data. We are obliged to E. Cepáková for linguistic revision of the manuscript. This study was conducted under licences from the Ministry of Environment of the Slovak Republic (2598/715/03-5.1pil).

References

Arlettaz R., Godat S. & Meyer H. 2000. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). Biol. Conserv. **93:** 55–60. DOI 10.1016/S0006–3207(99)00112–3

Baar A., Mayer A. & Wirth J. 1986. 150 Jahre Fledermausforschung in der Hermannshöhle. Ann. Naturhist. Mus. Wien **88–89B:** 223–243.

Baranauskas K. 2001. Hibernation of barbastelle (*Barbastella barbastellus*) in Šeškine bunkers in Vilnius (Lithuania). A possible bat population response to climate change. Acta Zool. Lituanica **11:** 15–19.

Bárta Z., Červený J., Gaisler J., Hanák P., Hanák V., Horáček I., Hůrka L., Miles P., Nevrlý M., Rumler Z., Sklenář J. & Žalman J. 1981. Výsledky zimního sčítání netopýrů v Československu: 1969–1979 [Results of the winter census of bats in Czechoslovakia: 1969–1979]. Sbor. Okr. Muz. Most, Řada Přírodov. **3:** 71–116.

Battersby J.E. & Greenwood J.J.D. 2004. Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. Mammal Rev. **34:** 3–29. DOI 10.1046/j.0305–1838.2003.00023.x

Bauerová Z., Gaisler J., Kovařík M. & Zima J. 1989. Variation in numbers of hibernating bats in the Moravian karst: results of visual censuses in 1983–1987, pp. 499–505. In: Hanák V., Horáček I. & Gaisler J. (eds), European Bat Research 1987, Charles Univ. Press, Praha, 720 pp.

Bihari Z. 2001. Characteristics of the northernmost population of *Rhinolophus ferrumequinum* in the Carpathian Basin. Acta Theriol. **46:** 13–21.

Bobáková L. 2002. Kvantitatívne a kvalitatívne zloženie chiropterofauny Domického jaskynného systému [Quantitative and qualitative characteristics of chiropterofauna of Domica cave system], pp. 89–102. In: Urban P. (ed.), Výskum a ochrana cicavcov na Slovensku V. Zborník referátov z konferencie (Zvolen, 12.–13.10. 2001). Štátna ochrana prírody, Centrum ochrany prírody a krajiny, Banská Bystrica, 174 pp.

Boldogh S. & Estók P. (eds) 2007. Földalatti denevérszállások katasztere I. [Catalogue of underground bat roosts in Hungary I]. ANP füzetek III. Aggteleki Nemzeti Park Igazgatóság, Jósvafő, 340 pp.

Bontadina F., Arlettaz R., Fankhauser T., Lutz M., Mühlethaler E., Theiler A. & Zingg P. 2000. The lesser horseshoe bat *Rhinolophus hipposideros* in Switzerland: present status and research recommendation. Le Rhinolophe **14:** 69–83.

Bontadina F., Schmied S.F., Beck A. & Arlettaz R. 2008. Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat. J. Appl. Ecol. **45:** 641–648. DOI 10.1111/j.1365–2664.2007.01417.x

Brown J.H. 1995. Macroecology. University of Chicago Press, Chicago, 269 pp.

Daan S., Glas G.H. & Voute A.M. 1980. Long term changes in bat populations in the Netherlands. Lutra **22:** 1–118.

Danko Š. 1997. Kvalitatívne a kvantitatívne zmeny spoločenstva zimujúcich netopierov v opustených banských dielach v okolí Dubníka (Slanské vrchy) [Qualitative and quantitative changes in the assemblages of wintering bats in abandoned mines near Dubník (Slanské vrchy Hills, E-Slovakia)]. Vespertilio **2:** 5–38.

Fuszara E. & Jurczyszyn M. (eds) 2002. Zimowy monitoring liczebności nietoperzy w Polsce w latach 1993–1999 [Winter monitoring of bat abundance in Poland in 1993–1999]. Nietoperze 3 (1), 178 pp.

Gaisler J. 1975. A quantitative study of some populations of bats in Czechoslovakia (Mammalia: Chiroptera). Acta Sci. Nat. Brno **9:** 1–44.

Gaisler J. & Chytil J. 2002. Mark-recapture results and changes in bat abundance at the cave of Na Turoldu, Czech Republic. Folia Zool. **51:** 1–10.

Gaisler J. & Hanák V. 1973. Apercu de chauves-souris des grottes Slovaques. Slov. Kras **11:** 73–84.

Gaisler J., Hanák V. & Horáček I. 1981. Remarks on the current status of bat populations in Czechoslovakia. Myotis **18–19:** 68–75.

Gaston K.J. 1994. Rarity. Population and community biology series 13. Chapman & Hall, London, 205 pp.

Hapl E., Uhrin M., Bobáková L., Benda P., Andreas M., Reiter A., Hotový J., Obuch J., Stankovič J. & Cselényi K. 2002. Prehľad zimovísk netopierov Silickej a Plešivskej planiny [A synopsis of bat hibernacula of the Silická planina and Plešivská planina plateaues]. Vespertilio **6:** 193–211.

Horáček I. 1984. Remarks on the causality of population decline in European bats. Myotis **21–22:** 138–147.

Horáček I., Hanák V. & Gaisler J. 2005. Dlouhodobé změny biodiversity netopýrů: zpráva o nejrozsáhlejším monitorovacím programu v ČR 1969–2004 [Long-term changes of bat diversity: report on the most extensive monitoring programme in the Czech Republic in 1969–2004], pp. 105–115. In: Vačkář D. (ed.), Ukazatele změn biodiverzity, Academia, Praha.

Horáček I. & Zima J. 1979. Zur Frage der Synanthropie bei Hufeisennasen in der Tschechoslowakei. Nyctalus (N. F.) **1:** 139–141.

Humphries M.M., Thomas D.W. & Speakman J.R. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature **418:** 313–316. DOI 10.1038/nature00828

Hutson A.M., Mickleburgh S. & Racey P.A. (eds) 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group, Gland, Switzerland & Cambridge, UK, 258 pp.

Kaňuch P., Ceľuch M., Danko Š., Fulín M., Matis Š. & Pjenčák P. 2008. K populačným trendom netopierov na zimoviskách *Myotis emarginatus* (východné Slovensko) [On population trends of bats in hibernacula of *Myotis emarginatus* (eastern Slovakia)]. Vespertilio **12:** 132–133.

Kokurewicz T. 1990. The decrease in abundance of the lesser horseshoe bat *Rhinolophus hipposideros* Bechstein, 1800 (Chiroptera, Rhinolophidae) in winter quarters in Poland. Myotis **28:** 109–118.

Kokurewicz T. 1995. Increased population of Daubenton's bat (*Myotis daubentoni* (Kuhl, 1819)) (Chiroptera: Vespertilionidae) in Poland. Myotis **32–33:** 155–161.

Kowalski M. & Lesiński G. 1991. Changes in numbers of bats in Szachownica cave (central Poland) during 10 years. Myotis **29:** 35–38.

Kulzer E. 1995. Über den Rückzug der Kleinen Hufeisennase *Rhinolophus hipposideros* (Bechstein 1800) aus Baden-Württemberg. Leichinger Höhlenfreund **30:** 3–24.

Lehotská B. 2002. Netopiere Malých Karpát [Bats of the Malé Karpaty Mts (SW Slovakia)]. Lynx, n. s. **33:** 141–184.

Lesiński G., Fuszara E., Fuszara M., Jurczyszyn M. & Urbańczyk Z. 2005. Long-term changes in the numbers of the barbastelle *Barbastella barbastellus* in Poland. Folia Zool. **54:** 351–358.

Lesiński G., Gryz J. & Kowalski M. 2008. Does the diet of an opportunistic raptor, the tawny owl *Strix aluco*, reflect long-term changes in bat abundance? A test in central Poland. Folia Zool. **57:** 258–263.

Matis Š., Pjenčák P. & Uhrin M. 2002a. Zimovanie netopierov v Hačavskej a Marciho jaskyni [Bat hibernation in Hačavská jaskyňa cave and in Marciho jaskyňa cave]. Vespertilio **6:** 231–233.

Matis Š., Pjenčák P., Kürthy A. & Hapl E. 2002b. Prehľad letných nálezov netopierov (Chiroptera) v Národnom parku Slovenský kras [Overwiev of summertime findings of bats in the National Park Slovak Karst]. Natura Carpatica **43:** 195–234.

Mihál T. 2004. Netopiere (Chiroptera) podzemných priestorov Štiavnických vrchov [Bats (Chiroptera) of underground caverns in the Štiavnické vrchy Mts]. Naturae Tutela **8:** 55–82.

Obuch J. 1995. Nové poznatky o výskyte netopierov v jaskynných tanatocenózach [New data on the occurrence of bats in cave thanatocoenoses]. Netopiere **1:** 29–38.

Pannekoek J. & van Strien A. 2009. TRIM 3 Manual (Trends & Indices for Monitoring Data). Project no. 100384. Statistics Netherlands, Voorburg, 58 pp.

Paulovics P. & Márton J. 2008. Egy lehetséges módszer a kereknyergü patkósdenevér (*Rhinolophus euryale* Blasius, 1853) dunántúli maradványállományának megmentésére: megerősítés áttelepítéssel (protokoll tervezet) [One possible way to save the remaining Transdanubian population of the Mediterranean horseshoe bat (*Rhinolophus euryale*) from extinction: strengthening with resettlement (action plan)]. Denevérkutatás **4:** 18–37.

Pereira H.M. & Cooper H.D. 2006. Towards the global monitoring of biodiversity change. Trends Ecol. Evol. **21:** 123–129. DOI 10.1016/j.tree.2005.10.015

Primack R.B. 2004. A primer of conservation biology. 3rd edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, USA, 320 pp.

Ransome R.D. 1989. Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. Biol. J. Linn. Soc. **38:** 71–82.

Roer H. 1972. Zur Bestandsentwicklung der Kleinen Hufeisennase (Chiroptera, Mam.) in westlichen Mitteleuropa. Bonn. Zool. Beitr. **23:** 325–337.

Rydell, J., 1989. Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. Oecologia **80:** 562–565. DOI 10.1007/BF00380082

Řehák Z. 1997. Trendy ve vývoji početnosti netopýrů ve střední Evropě [Long-term changes in the size of bat populations in Central Europe]. Vespertilio **2:** 81–96.

Řehák Z. & Gaisler J. 1999. Long-term changes in the number of bats in the largest man-made hibernaculum of the Czech Republic. Acta Chiropterol. **1:** 113–123.

Sachanowicz K. & Ciechanowski M. 2006. First winter record of the migratory bat *Pipistrellus nathusii* (Keyserling and Blasius 1839) (Chiroptera: Vespertilionidae) in Poland: yet more evidence of global warming? Mammalia **70 (1–2):** 168–169. DOI 10.1515/MAMM.2006.033

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

Spellerberg I. F. 1991. Monitoring Ecological change. Cambridge Univ. Press, Cambridge, 391 pp.

StatSoft Inc. 2001. Statistica (Data Analysis Software System), Version 6. www.statsoft.com.

ter Braak C.J.F., Van Strien A.J., Meijer R. & Verstrael T.J. 1994. Analysis of monitoring data with many missing values: which method?, pp. 663–673. In: Hagemeijer E.J.M. & Verstrael T.J. (eds), Bird Number 1992. Distribution, Monitoring and Ecological Aspects. Proceedings of the 12th International Conference of IBCC and EOAC. Statistics Netherlands, Voorburg/Heerlen & SOVON, Beek-Ubbergen, Noordwijkerhout, The Netherlands.

The Bat Conservation Trust 2001. The UK's National Bat Monitoring Programme. Final Report 2001. DETR Contract Reference No. CR015. The Bat Conservation Trust, London, 155 pp.

Thomas D.W. & LaVal R.K. 1988. Survey and census methods, pp. 77–89. In: Kunz T.H. (ed.), Ecological and Behavioral Methods for the Study of Bats, Smithsonian Institution Press, Washington D. C.

Uhrin M. 1993. Poznámky k spoločenstvu netopierov (Chiroptera) zimovísk Slovenského krasu [Notes to population of bats (Chiroptera) in hibernating places of the Slovak Karst]. Zbor. Východoslov. Múz. Košice, Prír. Vedy **34:** 151–162.

Uhrin M. 1995. The finding of a mass winter colony of *Barbastella barbastellus* and *Pipistrellus pipistrellus* (Chiroptera, Vespertilionidae) in Slovakia. Myotis **32–33:** 131–133.

Uhrin M. 1998a. Poznámky k trendom početností niektorých druhov netopierov na Slovensku [Notes to trends of abundance of several bat species in Slovakia], pp. 49–59. In: Urban P. (ed.), Výskum a ochrana cicavcov na Slovensku III. Zborník referátov z konferencie. SAŽP – COPK & MŽP SR, Banská Bystrica & Bratislava, 156 pp.

Uhrin M. 1998b. Prehľad poznatkov o netopieroch (Mammalia: Chiroptera) systému Dobšinská ľadová jaskyňa – Stratenská jaskyňa [A synopsis of data on bats (Mammalia: Chiroptera) of the Dobšinská ľadová jaskyňa cave – Stratenská jaskyňa cave system]. Aragonit **3:** 15–18.

Uhrin M., Benda P., Obuch J. & Danko Š. 2008. Lesser Mouse-eared Bat (*Myotis blythii*) in Slovakia: distributional status with notes on its biology and ecology (Chiroptera: Vespertilionidae). Lynx n. s. **39:** 153–190.

Uhrin M., Benda P., Obuch J. & Urban P. 2002a. K poznaniu fauny cicavcov Drienčanského krasu a okolia (stredné Slovensko) [Mammal fauna of the Drienčanský kras Karst Region and surrounding areas (central Slovakia)]. Lynx n. s. **33:** 193–247.

Uhrin M., Bobáková L., Hapl E., Andreas M., Benda P., Obuch J. & Reiter A. 2002b. Zimovanie netopierov v slovenskej časti jaskynného systému Domica-Baradla [Bat hibernation in the slovakian part of the Domica-Baradla cave system]. Vespertilio **6:** 237–243.

Uhrin M., Danko Š., Obuch J., Horáček I., Pačenovský S., Pjenčák P. & Fulín M. 1996. Distributional patterns of bats (Mammalia: Chiroptera) in Slovakia. Part 1, Horseshoe bats (Rhinolophidae). Acta Soc. Zool. Bohem. **60:** 247–279.

Uhrin M., Hapl E., Andreas M., Benda P., Bobáková L., Hotový J., Matis Š., Obuch J., Pjenčák P. & Reiter A. 2002c. Prehľad zimovísk netopierov Muránskej planiny [A synopsis of bat hibernacula of the Muránska planina plateau]. Vespertilio **6:** 103–130.

Uhrin M., Hapl E., Andreas M., Benda P., Bobáková L., Hotový J., Matis Š., Obuch J., Pjenčák P. & Reiter A. 2002d. Zimoviská netopierov Revúckej vrchoviny [Bat hibernacula of the Revúcka vrchovina Mts]. Vespertilio **6:** 159–171.

Uhrin M., Hapl E., Urban P., Valach I., Mihál T. & Zlacká S. 2002e. Zimoviská netopierov v Štiavnických vrchoch [Bat hibernacula in the Štiavnické vrchy Mts]. Vespertilio **6:** 287–297.

Warren R.D. & Witter M.S. 2002. Monitoring trends in bat populations through roost surveys: methods and data from *Rhinolophus hipposideros*. Biol. Conserv. **105:** 255–261.DOI 10.1016/S0006–3207(01)00209–9

Weinreich J.A. & Oude Voshaar J.H. 1992. Population trends of bats hibernating in marl caves in the Netherlands (1943–1987). Myotis **30:** 75–84.

Wołoszyn B.W. (ed.) 1994. Zimowe spisy nietoperzy 1988–1992. Publikacje CIC ISEZ PAN, Kraków, 230 pp.

Zima J., Kovařík M., Gaisler J., Řehák Z. & Zukal J. 1994. Dynamics of the number of bats hibernating in the Moravian Karst in 1983 to 1992. Folia Zool. **43:** 109–119.

Received July 2, 2009
Accepted November 15, 2009