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TYPES OF THE BAT ASSEMBLAGES (CHIROPTERA) RECORDED IN SLOVAKIA

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Abstract

Quantitative data on bats derived from the winter census (35 records), analysis of thanatocoenoses either in caves (16 records) or in rock crevices (18 records), and the owl pellets analysis (24 records) were applied to characterise the types of bat assemblages in Slovakia, which are demonstrated as clusters of diagnostic species showing positive deviations from the mean in modified contingency tables. The results of analyses of the four quantitative data sets are compared.

Introduction

Long-term research on bats in Slovakia began in the fifties (V a c h o l d 1955, 1961). The important wintering sites were monitored by G a i s l e r & H a n á k (1972), and the summer sightings of bats were reviewed by H o r á č e k et al. (1979). The results of the winter census carried out during the eighties have not yet been published. At present, the winter census of bats in Slovakia is coordinated by M. U h r i n, and information on the current results have been included in the Newsletter of the Czech Bat Conservation Trust (CBCT).

The first summary of the subfossil osteological record of bats in erstwhile Czechoslovakia was published by H o r á č e k (1976). Important findings of bats in the food of owls were presented by S c h a e f f e r (1972), and O b u c h (1985) reported on records (ascertained before 1980) of skeletal remnants including also rich bat fauna.

The results of bat studies performed in Slovakia have been evaluated from a faunal point of view, bat protection in important hibernacula, and faunal development in the Holocene. This paper aims to apply the bulk of quantitative data in characterisation of individual bat assemblages defined according to common features of the species composition. Similarity patterns have been derived from calculations of significant deviations in the composition of a particular sample from average values (O b u c h 1991).

Material and Methods

The collection sites are numbered from 1 to 67, and arranged according to geographical regions of Slovakia. Several types of data were collected at each site (Fig. 1).

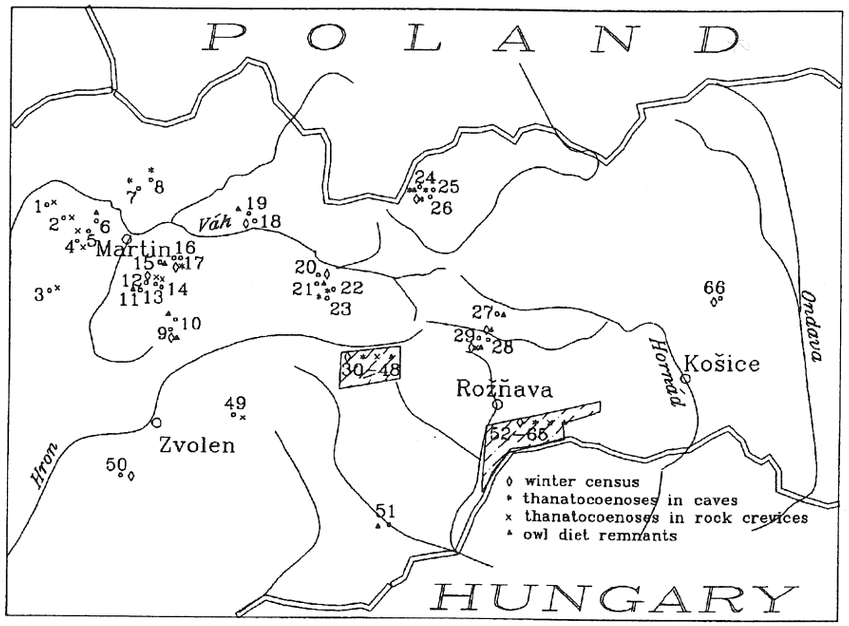


Fig. 1. Location of the sites studied.

Unpublished results of winter censuses conducted in various regions of Slovakia in 1979 to 1990, summarized by I. Horáček, with participation of P. Bürger, J. Červený, Š. Danko, J. Gaisler, L. Gordon, V. Hanák, J. Obuch and J. Zima, are indicated as Horáček et al., unpublished. Unpublished results of winter censuses undertaken in the Slovakian karst in 1992 and 1993, summarized by M. Uhrin, with participation of Fulín, Levendovský, Matis, Obuch, Pačenovský and Sitášová, are indicated as Uhrin et al., unpublished. Unpublished results of winter censuses performed by M. Uhrin in the Muránska planina plateau in 1992 and 1993 are indicated as Uhrin, unpublished. Data by Uhrin were presented in the supplement of the CBCT Newsletter, No. 2.

A. Census in Hibernacula

Veľká Fatra Mts.: Izbica cave, No. 9, total numbers (12. 2. 1961, 28. 2. 1963, 26. 2. 1964, Gaisler & Hanák 1972); Gader valley, No. 12, total numbers (1960 to 1993, original data); Belianska valley, No. 16, total numbers (1. 1. 1980, 28. 12. 1989, 7. 1. 1990, 9. 3. 1991, original data).

Chočské vrchy Mts.: Liskovská cave, No. 18, total numbers (14. 2. 1968, 11. 2. 1969, 6. 2. 1970, Gaisler & Hanák 1972; 6. 2. 1988, Horáček et al. unpublished).
Nízke Tatry Mts.: Demänovské caves, No. 20, total numbers (Vachold 1961; 29. 2. 1964, Gaisler & Hanák 1972).
Belianske Tatry Mts.: Belianska cave, No. 26, total numbers (1. 3. 1963, 1. 3. 1964, Gaisler & Hanák 1972; 16. 2. 1990, Horáček et al.. unpublished).
Slovenský raj Mts.: Stratenská cave, No. 28 (15. 2. 1990, Horáček et al. unpublished); Dobšinská ľadová cave, No. 29, total numbers (3. 3. 1963, 2. 3. 1964, 15. 2. 1968, Gaisler & Hanák 1972; 1969 to 1973, Gaisler 1975; 21. 2. 1979, 8. 1. 1982, 19. 3. 1987, 4. 2. 1988, Horáček et al. unpublished).
Muránska planina plateau: Michňová chasm, No. 33, total numbers (Vachold 1955; 16. 2. 1961, Gaisler & Hanák 1972; 5. 2. 1988, Horáček et al. unpublished; 19. 2. 1993, Uhrin, unpublished); Netopierov cave, No. 34 (Vachold 1955; 16. 2. 1961, Gaisler & Hanák 1972; 5. 2. 1988, Horáček et al. unpublished; 14. 1. 1993, Uhrin, unpublished); Kostolík cave, No. 35a (Vachold 1955); No. 35b, total numbers (15. 2. 1961, Gaisler & Hanák 1972; 5. 2. 1988, Horáček et al. unpublished; 19. 1. 1993, Uhrin, unpublished); Martincová cave, No. 36, total numbers (10. 4. 1979, 30. 10. 1981, 25. 10. 1983, original data; 5. 2. 1988, Horáček et al. unpublished; 20. 11. 1992, Uhrin, unpublished); tunnel at Dielik, No. 38 (20. 2. 1993, Uhrin, unpublished); Husleho cave, No. 39 (20. 2. 1993, Uhrin, unpublished); Bobačka cave, No. 46, total numbers (20. 2. 1979, 7. 1. 1982, 5. 2. 1988, Horáček et al. unpublished; 7. 3. 1993, Uhrin, unpublished); Čertova cave, No. 47 (9. 12. 1992, Uhrin, unpublished); Ladzianského cave, No. 48, total numbers (15. 2. 1961, Gaisler & Hanák 1972; 20. 2. 1979, 7. 1. 1982, 5. 2. 1988, Horáček et al. unpublished; 20. 2. 1993, Uhrin, unpublished).
Štiavnické vrchy Mts.: gallery at Antol, No. 50 (14. 11. 1970, Palášthy 1971a).
Slovenský kras Mts.: Domica cave, No. 52a, total numbers (23. 2. 1979, 20. 2. 1980, 2. 2. 1988, Horáček et al. unpublished; 13. 2. 1993, Uhrin et al. unpublished); Domica cave, No. 52b, total numbers (9. 12. 1988, Horáček et al. unpublished; 3. 12. 1992, Uhrin et al. unpublished); Čertova diera cave, No. 53a, total numbers (10. 12. 1956, 5. 2. 1958, Gaisler & Hanák 1972; 2. 2. 1988, 12. 2. 1989, Horáček et al. unpublished); Čertova diera cave, No. 53b, total numbers (1969 to 1973, Gaisler 1975; 13. 2. 1993, Uhrin et al. unpublished); Ardovská cave, No. 54, total numbers (1969 to 1973, Gaisler 1975; 22. 2. 1979, 2. 2. 1988, Horáček et al. unpublished; 20. 1. 1993, Uhrin et al. unpublished); Milada cave, No. 55, total numbers (2. 2. 1988, 16. 12. 1988, Horáček et al. unpublished; 13. 2. 1993, Uhrin et al. unpublished); Májkova cave, No. 56, total numbers (14. 12. 1988, Horáček et al. unpublished; 14. 2. 1993, Uhrin et al. unpublished).; Erňa cave, No. 60, total numbers (27. 1. 1989, Horáček et al. unpublished; 14. 2. 1993, Uhrin et al. unpublished); Hačavská cave, No. 62, total numbers (7. 2. 1958, Gaisler & Hanák 1972; 13. 1. 1989, Horáček et al. unpublished; 14. 2. 1993, Uhrin et al. unpublished); Drienovecká vyvieračka cave, No. 63a, total

numbers (6. 2. 1958, 17. 2. 1961, Gaisler & Hanák 1972); Drienovecká vyvieračka cave, No. 63b (16. 2. 1968, Gaisler & Hanák 1972); Drienovecká vyvieračka cave, No. 63c (3. 2. 1988, Horáček et al. unpublished); Drienovecká vyvieračka cave, No. 63d (25. 2. 1993, Uhrin et al. unpublished); Jasovská cave, No. 65, total numbers (8. 12. 1956, 16. 2. 1968, Gaisler & Hanák 1972; 1969 to 1973, Gaisler 1975; 22. 2. 1979, 21. 2. 1980, 9. 1. 1982, 19. 3. 1987, 3. 2. 1988, Horáček et al. unpublished; 12. 2. 1993, Uhrin et al. unpublished).
Slanské vrchy Mts.: Dubník mines, No. 66a, total numbers (Palášthy & Olejár 1963, Palášthy 1969); Dubník mines, No. 66b (Palášthy 1971b).

B. Thanatocoenoses in Caves

Malá Fatra Mts.: Stratenec chasm, No. 7, subfossil remnants (18. 6. 1977, 28. 7. 1977, 15. 11. 1978, Obuch 1985a); Malý Fatranský Kriváň chasm, No. 8, subrecent remnants (7. 10. 1977, Obuch 1985a).
Veľká Fatra Mts.: Ziarna cave, No. 2, recent remnants (26. 11. 1978, Obuch 1985a; 28. 12. 1989, original data).
Nízke Tatry Mts.: Záskočie cave, No. 22, subfossil remnants (Rybář 1979); Mŕtvych netopierov cave, No. 23, subfossil remnants (30. 1. 1988, original data).
Belianske Tatry Mts.: Muránska cave, No. 24, subfossil remnants (16. 10. 1977, Obuch 1985a); Alabastrová cave, No. 25, subrecent remnants (Horáček 1976); Belianska cave, No. 26, recent and subrecent remnants (Horáček 1976).
Slovenský raj Mts.: Dobšinská ľadová cave, No. 29, recent and subrecent remnants (Horáček 1976).
Muránska planina plateau.: Malá Stožka chasm, No. 31, subrecent and subfossil remnants (18.–19. 7. 1974, 4. 4. 1976, 16. 5. 1979, Obuch 1985a, b); Hradová chasm, No. 32, subrecent remnants (2. 4. 1980, Obuch 1985a, b); Netopierov cave, No. 34, recent remnants (11. 7. 1981, Obuch 1985a, b); Slaniniarka cave, No. 42, recent remnants (21. 9. 1993, leg. M. Uhrin, unpublished).
Slovenský kras Mts.: Zbojnícka cave, No. 58, subfossil remnants (19. 9. 1991, original data); Ohniště cave, No. 59, subfossil remnants (20. 9. 1991, original data); Erňa cave, No. 60, subrecent and subfossil remnants (14. 2. 1993, original data).

C. Thanatocoenoses in Rock Crevices

Strážovské vrchy Mts.: Brada, Čierna cave, No. 1a (16. 10. 1977, Obuch 1985a); Brada, probe, No. 1b (11. 10. 1971, leg. V. Ložek, Obuch 1985a); Slnečné skaly, Bujačka, No. 2a (25. 5. 1980, Obuch 1985a); Slnečné skaly, Martinský komín, No. 2b (25. 5. 1980, Obuch 1985a).
Malá Fatra Mts.: Kľačno, Mokrá valley, No. 3 (30. 9. 1979, Obuch 1985); Turie, Dolná Roveň, No. 4 (23. 4. 1978, Obuch 1985a); Višňovská valley, Valentínov diel, No. 5 (25. 3. 1978, Obuch 1985a).
Veľká Fatra Mts.: Sokolovo, ledge, No. 13 (14. 8. 1990, original data); Dedošová, ledge, No. 14 (30. 10. 1977, Obuch 1985a).

Muránska planina plateau: Malá Stožka, southern face, No. 31 (16. 5. 1979, Obuch 1985a, b); Hrdzavá valley, Brestová, No. 40 (7. 4. 1979, Obuch 1985a, b); Odštiepená skala, ledge, No. 41a (8. 4. 1979, Obuch 1985a, b); Odštiepená skala, under crevice, No. 41b (8. 4. 1979, Obuch 1985a, b); Kášter, No. 44 (30. 7. 1980, Obuch 1985a, b); Cigánka, southern face, No. 45 (31. 7. 1980, Obuch 1985a, b).
Poľana Mts.: Jánošíkova skala, narrow crevice, No. 49a (8.–10. 7. 1978, Obuch 1985a); Jánošíkova skala rock, long crevice, No. 49b (8.–10. 7. 1978, Obuch 1985a).
Slovenský kras Mts.: Zadielská valley, under chimney, No. 61 (9. 5. 1978, Obuch 1985a).

D. Owl Pellets

Malá Fatra Mts.: Stráňavy, Hýrov, No. 6, *Strix aluco,* subrecent remnants (18.–19. 3. 1978, Obuch 1985a, 1992a).
Veľká Fatra Mts.: Izbica cave, entrance hall, No. 9, *S. aluco,* recent remnants (16. 4. 1980, Obuch 1985a); Bystrická valley, cave at a tunnel, No. 10a, *S. aluco,* subfossil remnants (12. 7. 1978, 19. 11. 1978, Obuch 1985a, 1992a); Bystrická valley, chimney, No. 10b, *S. aluco,* recent pellets (1978 to 1993, original data); Havranovo, No. 11, *S. aluco,* subrecent and subfossil remnants (7. 5. 1976, 10. 6. 1976, Obuch 1985a); Necpaly, evangelic church, No. 15, *Tyto alba,* recent pellets (14. 7. 1982, Obuch 1991).
Chočské vrchy Mts.: Predný Choč, Válovy, No. 19, *S. aluco,* recent pellets (20. 5. 1978, Obuch 1985a).
Nízke Tatry Mts.: Demänovská valley, Okno cave, No. 21, *S. aluco,* recent pellets (4. 5. 1990, original data).
Belianske Tatry Mts.: Muránska cave, No. 24, *S. aluco,* subrecent and subfossil remnants (Schaeffer 1973, Obuch 1992a).
Slovenský raj Mts.: Peklisko, No. 27, *S. aluco,* recent pellets (11. 7. 1990, original data); Stratenská cave, entrance, No. 28, *S. aluco,* recent pellets (15. 2. 1990, 9. 7. 1990, Obuch 1992a); Duča cave, entrance, No. 29, *S. aluco,* recent pellets (9. 7. 1990, Obuch 1992a).
Muránska planina plateau.: Mašianske skalky, No. 30, *S. aluco,* subrecent remnants (1979, leg. Darola, Obuch 1985a, b); Martincová cave, No. 36, *S. aluco,* subfossil remnants (10. 4. 1979, Obuch 1985b); Šarkanica cave, No. 37, *S. aluco,* recent pellets (1979 to 1992, original data); Hrdzavá valley, Brestová, No. 40, *S. aluco,* recent pellets (1979 to 1983, original data); Odštiepená skala, No. 41, *S. aluco,* recent pellets (1979 to 1992, original data); Pod Maretkinou, No. 43, *S. aluco,* recent pellets (16. 5. 1978, Obuch 1985a, b).
Rimavská kotlina basin: Rimavské Janovce, church, No. 51, *T. alba,* recent pellets (25. 10. 1981, original data).
Slovenský kras Mts.: Silická ľadnica cave, No. 57, *S. aluco,* recent pellets (1976 to 1985, original data); Zbojnícka cave, No. 58, *S. aluco,* recent pellets (26. 10. 1981, 19. 9. 1991, 14. 2. 1993, original data); Ohnište cave, No. 59, *S. aluco,* recent and subrecent remnants (29. 9. 1991, original data); Pri Hatinách cave, No. 64, *T. alba,* subfossil remnants (25. 9. 1977, original data).
Slovakia: No. 67, *Bubo bubo,* recent samples (1975 to 1992, original data).

Methods

The bat records were arranged quantitatively in contingency tables. The actual numbers of the individuals found are given to the right of each column. The levels of significance for deviations from the mean were applicable from the differences between the actual and average numbers using coefficients of the linear equation 1.2 a_{ij} + 4 (O b u c h 1991), and are given to the left of each column. Species exhibiting significant deviations above the mean were grouped together at a cluster. A similar method was applied previously to assess the types of the diet of owls (O b u c h 1992b). The lowest row of the tables contains the values of the Shannon index of diversity, and dominance was calculated from the total data. Relationships between diagnostic species in the community types described are indicated using following symbols:
<–> close relationship, the same significance levels of positive differences usually found in both species; –>, <– relationship between a significant and less significant diagnostic species; .. relationship less significant, only few equally significant differences found between the species.

The species considered: lesser horseshoe bat *Rhinolophus hipposideros (R. hip);* greater horseshoe bat *R. ferrumequinum (R. fer);* Mediterranean horseshoe bat *R. euryale (R. eur);* Bechstein's bat *Myotis bechsteini (M. bec);* greater mouse-eared bat *M. myotis (M. myo);* lesser mouse-eared bat *M. blythi (M. bly);* whiskered bat *M. mystacinus (M. mys);* Brandt's bat *M. brandti (M. bra);* Geoffroy's bat *M. emarginatus (M. ema);* Natterer's bat *M. nattereri (M. nat);* Daubenton's bat *M. daubentoni (M. dau);* pond bat *M. dasycneme (M. das);* northern bat *Eptesicus nilssoni (E. nil);* serotine *E. serotinus (E. ser);* particoloured bat *Vespertilio murinus (V. mur);* common pipistrelle *Pipistrellus pipistrellus (P. pip);* noctule *Nyctalus noctula (N. noc);* common long-eared bat *Plecotus auritus (P. aur);* barbastelle *Barbastella barbastellus (B. bar);* Schreiber's bat *Miniopterus schreibersi (M. sch).*

Results

A. Assemblages Found During the Winter Census (Table 1)

I. Type: *Rhinolophus* spp.
Chart: *R. eur –> R. fer <– R. hip <– M. ema*
Typical site: Jasovská cave (No. 65), Slovenský kras Mts.

This assemblage type occurs in warmer caves in the Slovakian karst. The predominant species, *R. ferrumequinum,* was considerably more numerous there as compared to the other parts of Slovakia, and it hibernated occasionally in colonies. *R. euryale* occurred irregularly, sometimes in large colonies, and it migrated during winter (*e.g.* in the Domica cave system). V a c h o l d (1955) reported this species from the Kostolík cave in the Muránska planina plateau. A broad ecological valency was characteristic to *R. hipposideros,* and this species was therefore related also to the type II. *M. emarginatus* occurs together with the latter species irregularly, even in hibernacula situated outside the Slovenský kras Mts. (*e.g.* the Michňová cave or Dubník mines).

II. Type: *R. hipposideros* and *M. myotis*
Chart: *R. hip –> M. myo <–> (M. bly?)*
Typical site: Bobačka cave (No. 46), Muránska planina plateau.

This type of assemblage occured in most caves situated in the middle and higher altitudes of Slovakia. The numbers of wintering bats were not usually high. Only one species, *R. hipposideros* and/or *M. myotis,* could predominate in numbers, respectively. The species preferring cold habitats, mainly *M. mystacinus, P. auritus, B. barbastellus,* were also sporadically found in assemblages of this type. The relationship between presence of *M. myotis* and *M. blythi* was not clear. The census results indicated a distinct decline in numbers of *M. blythi* since the fifties, but the over-wintering bats were checked individually only up to the seventies, and visual recording has largely been preferred recently so that most *M. blythi* individuals may not have been identified.

III. Type: *M. mystacinus* and *M. brandti*
Chart: *M. myo .. M. mys <–> M. bra .. E. nil <–> P. aur .. M. das*
Typical site: Dobšinská ľadová cave (No. 29), Slovenský raj Mts.

Except of the typical site, assemblages of this type were also found in certain colder caves in the Demänovská valley. The most important prerequisite to this assemblage occurrence was probably the presence of extensive forests surrounding the hibernaculum. Such habitats were preferred by the predominant species in the vegetation period. The ratio of individuals of *M. mystacinus* to *M. brandti* was 3 : 2 in mixed winter colonies (G a i s l e r 1975). The succeeding censuses were performed only visually, and the reliable distinction between both species was thus difficult. A similar problem represented the distinction between *P. auritus* and *P. austriacus.* These species, along with *E. nilssoni,* were associated with colonies of *M. mystacinus* and *M. brandti* in colder parts of the cave. The rare species of *M. dasycneme* was found regularly in the Dobšinská ľadová cave.

IV. Type: *B. barbastellus, P. pipistrellus* and *M. schreibersi*
Chart: B. bar .. P. pip .. M. sch
Typical site: tunnel at Dielik (No. 38), Muránska planina plateau.
All the diagnostic species have been found wintering in the typical site. Numerous colonies of individual species were observed at other sites, e.g. the Erňa cave (*P. pipistrellus*), the gallery at Antol (*M. schreibersi*), or various accessory species were present along with the diagnostic one (the Dubník mines, Drienovecká vyvieračka cave). Cold underground spaces with large entrances were usually used as a hibernaculum. The numbers of wintering individuals often varied distinctly in such assemblages during winter as a possible consequence of human disturbance or changes in weather.

B. Assemblages Found in the Thanatocoenoses of Caves (Table 2)

Skeletal remnants have accumulated in certain parts of caves, which are then called „bat burial-grounds". The accumulation may proceed through various time periods and may result in a mixture developed in different periods when various bat assemblages occurred in the site.

Table 1. Results of winter censuses

Species/Site No.	52b	63c	52a	55	54	53b	35a	63a	63d	65	56	66a	34	33	39	47	35b	66b
R. euryale	6+ 700	4+ 103	1+ 8	1+ 9	2+ 24	2+ 20	3+ 40	3		2– 6		4–	3–	2–				1–
R. ferrumequinum	3–	3+ 49	2+ 20	3+ 80	1+ 14	1+ 14	1–	2+ 21	3+ 57	4+ 1297	1+ 9	3– 9	4–	2– 2	1		3	1– 2
M. emarginatus	1–	1+ 8	1			1				18	3+ 20	2+ 87	1–	2+ 37				5+ 120
R. hipposideros	5–	2– 3	2+ 36	2+ 75	3+106	1+ 45	1+ 39	10	2+ 30	2+ 569	2+ 26	2+ 623	4+ 1052	3+ 595	3+ 42	3+ 57	3+ 123	2+ 63
M. blythi	2–					3		1+ 7		1+ 88	1	2– 15	2– 3	2–				6
M. myotis	5–	1– 6	1–	1– 11	15	2+ 75	2– 1	10	6	1– 124	11	1– 136	2– 33	3– 6	3	1–	12	1+ 40
P. austriacius					2	2		1		3		1						
M. mystacinus	2–									3–		3– 3	2–	2–				
M. brandti	1–									3–		3–	2–	1–				1
E. nilssoni										1–		1– 1						
P. auritus												1	2		1			
M. dasycneme																		
B. barbastellus	5–	3–	2–	3– 1	3–	3–	2+103	3–	3–	6– 4	2–	2+ 1812	5– 5	5–	2–	11	36	
P. pipistrellus	7–	5–	3–	5–	4–	5–	5–	3– 4	4–	8–	3–	9–	7–	6–	3–	3–	5–	4–
M. schreibersi	5–	3–	2–	3–	3–	19	3–	2+ 53	2–	6–	2–	7–	6–	5–	1–	2–	3–	5–
E. serotinus										2		2						3–
M. daubentoni				2							2	2					1	
M. nattereri				1														
M. bechsteini																		
V. murinus																		
Total	700	169	65	179	161	179	183	109	93	2112	69	2692	1095	640	47	68	175	232
Diversity index H'	0.00	1.41	1.45	1.63	1.47	2.19	1.44	2.19	1.20	1.45	2.06	1,30	0.26	0.40	0.61	0.63	1.21	1.64

Table 1. Continued

Species/Site No.	46	12	28	48	18	9	62	16	26	36	20	29	38	60	53a	50	63b	Total	(%)
R. euryale	1–	1–	1–	1–	2–	2–				3–	4–	3–	6–	7–	5–	3–	2–	913	2.12
R. ferrumeq.	6	6	1–	1–	3–	3–	2	1–		4–	4–	4–	7–	8–	6–	4–	1– 6	1598	3.71
M. emarginatus	2		5		1–	1	1			1–	2–	1–	4–	5–	3–	2–		301	0.70
R. hipposideros	3+ 120	2+ 72	2+ 78	18	2– 10	2– 18	8	19	1–	4– 3	133	5–	8–	9–	7– 1	5–	1– 20	3994	9.27
M. blythi	1	1–		2+ 20	3+ 89	4+ 301	1+ 10		1	2– 2	3+ 305	17	5– 1	7–	4– 2	3–	2– 1	873	2.03
M. myotis	2+ 58	3+ 154	2+ 105	3+ 161	3+ 516	3+ 404	2+ 31	3+ 161	3+ 67	4+ 1020	3+ 975	94	8–	7– 10	5– 13	3– 12	1– 21	4291	9.96
P. austriacus			1		2+ 9						1+ 6		1–	2–				25	0.06
M. mystacinus	2	1+ 11	1	1	2–	1– 2	1		1+ 8	2–	2+ 79	5+ 462	5–	6–	4–	3–	1–	571	1.33
M. brandti			1		1–	1–				2–	2–	5+ 373	5–	5–	4–	2–	1–	374	0.87
E. nilssoni		4		1				1	1	1	3+ 50	3+ 33	3–	3–	1–			92	0.21
P. auritus	1	2+ 11	1	2				1	1		2+ 20	3+ 37	2–	3–	1–			78	0.18
M. dasycneme			1							2		1+ 6						9	0.02
B. barbastellus	1– 16	2– 11	4–	4–	5–	5–	1+ 19	2– 5	2–	5– 2	2– 73	6–	2+ 5320	9–	8–	6–	5–	7418	17.21
P. pipistrellus	5–	5–	5–	5–	6–	7–	3–	5–	3–	7–	8–	7–	1– 2440	2+ 14545	9–	7–	6– 2	16991	39.43
M. schreibersi	3–	4–	3–	3–	5–	5–	2–	3–	2–	6–	6–	6–	5– 46	9–	3+ 3707	3+ 1200	3+ 506	5533	12.84
E. serotinus		2		4							3							11	0.03
M. daubentoni	1			1														9	0.02
M. nattereri	1				1			1				2						6	0.01
M. bechsteini		2																3	0.01
V. murinus											3							3	0.01
Total	208	273	193	208	625	726	72	188	78	1030	1647	1024	7807	14555	3723	1212	556	43093	100
Diversity index H'	1.62	1.80	1.27	1.15	0.80	1.15	2.06	0.77	0.75	0.06	1.84	1.81	0.93	0.00	0.02	0.07	0.56		

I. Type: *M. bechsteini* and *M. brandti*
Chart:

M. dau
:
M. nat –> M. bec . . M. bra . . V. mur
:
P. aur

Typical site: Stratenec chasm (No. 7), Malá Fatra Mts.

The typical site represented the largest sample of a thanatocoenosis found in Slovakia. It originated probably in the period of the so called „forest optimum" when no impairing human impact to the forest communities existed. The dominance of *M. brandti* or *M. bechsteini* was characteristic to this type, *M. nattereri* and partly also *M. daubentoni* represented the accessory species. *P. auritus* was an intermediate species between the types II and III, *V. murinus* occurred quite exceptionally in cave thanatocoenosis.

II. Type: *M. mystacinus* and *M. dasycneme*
Chart:

E. nil
:
P. aur . . M. mys <– M. das
:
B. bar

Typical site: Malá Stožka chasm (No. 31), Muránska planina plateau.

This assemblage type was usually found in colder caves and was of a subrecent origin. This type also included samples from the Dobšinská ľadová cave (No. 29), Malý Fatranský Kriváň chasm (No. 8) and Alabastrová cave (No. 25). The sample from Záskočie (No. 22) was intermediate between the types I and II. An increase in the occurrence of *M. mystacinus* was associated with findings of rare *M. dasycneme. E. nilssoni* and *B. barbastellus* were not closely related to this type.

III. Type: *M. myotis* and *R. hipposideros*
Chart: *M. bly –> M. myo .. R. hip <– M. ema*
Typical site: Žiarna cave (No. 2), Veľká Fatra Mts.

This type was represented by recent thanatocoenoses found in middle altitude caves. The composition of thanatocoenoses resembled that of over-wintering bat assemblages. *M. myotis* with mixture of *M. blythi* and/or *R. hipposideros* accompanied by *M. emarginatus* represented the dominant components of assemblages of this type.

IV. Type: *P. pipistrellus*
Chart: *P. pip*
Typical site: Erňa cave.

This type included recent to subfossil samples from certain smaller caves with large entrances situated in the Slovenský kras Mts. No accessory species occurred.

Table 2. Thanatocoenoses in caves

Species/Site No.	24	7	23	32	26	22	8	25	31
V. murinus	3+ 25	10		1– 5	4– 10	1+ 282	1– 32	1– 5	1– 61
M. brandti	1+ 111	1+ 1664	227	1+ 13	1+ 68	1+ 112	2– 3	5	51
M. bechsteini	3– 1	365	2+ 203	1+ 9	2+ 36	1+ 4+	1–	1	1– 1
M. nattereri	2	73	10		2	4	1		
M. daubentoni		1– 2	1+ 12			41	2– 3	2	1+ 52
P. auritus	16	1– 149	1+ 91	5	2+ 147		3+ 186	1+ 10	1+ 59
M. mystacinus	31	1– 180	2– 22	4	2– 9	1+ 114	1–	1+ 7	3+ 81
B. barbastellus	2	72	2–	1	2–	2–			2+ 24
E. nilssoni		17				2			1+ 9
M. dasycneme	2	1– 8			5			2	
M. blythi		1– 3		3					
M. myotis	2–	1– 88	2– 9		2+ 99	2– 12	1– 6	3	2– 5
R. hipposideros	2–	6– 1	4–	3	3–	4–	3–		3–
M. emarginatus		1–		2					
P. pipistrellus	2– 1	6–	4–	1–	4–	4–	3–		4–
N. noctula		3							
E. serotinus									3
M. schreibersi									
Total	195	2635	574	45	376	608	231	35	347
Diversity index H	1.76	1.84	1.95	2.81	2.15	2.09	0.96	2.67	2.72

Species/Site No.	29	16	42	34	58	59	60	Total	(%)
V. murinus					1			37	0.52
M. brandti	200	5– 2	2–	5– 2	2–	3–	6–	2605	36.58
M. bechsteini	2– 18	2– 9	1	4– 1	1–	1–	5–	850	11.94
M. nattereri	1– 4	5	1	2– 1			2–	184	2.58
M. daubentoni	1							22	0.31
P. auritus	40	3–		3– 3		1–	4–	549	7.71
M. mystacinus	2+ 215	2– 4	1	4–	1–	1–	5–	835	11.73
B. barbastellus	2– 1	1– 2	1	2– 1	1		2–	169	2.37
E. nilssoni	1		1					45	0.63
M. dasycneme	1+ 13							39	0.55
M. blythi	1+ 12	1+ 9						27	0.38
M. myotis	52	3+ 215	3+ 30	3– 2		1–	4–	521	7.32
R. hipposideros	4– 1	1+ 47		4+ 482		1–	4–	534	7.50
M. emarginatus				2+ 16				18	0.25
P. pipistrellus	4–	3–		4–	3+ 40	3+ 58	4+ 574	673	9.45
N. noctula		4						7	0.10
E. serotinus		1	1					5	0.07
M. schreibersi		1						1	0.01
Total	558	299	36	508	42	58	574	7121	100
Diversity index H	2.11	1.42	1.05	0.35	0.30	0.00	0.00		

C. Assemblages Found in the Thanatocoenoses of Rock Crevices (Table 3)

The samples were collected either directly from crevices situated in rocky faces of various height, or in the ground after dropping out of the crevices. The remnants were of a recent and subrecent origin. I also included in this type certain samples containing rich remnants of bats along with numerous mixture

of other vertebrate species (e.g. Stráňavy, Hýrov). These samples are now classified as remnants of *S. aluco* food.

I. Type: *N. noctula*
Chart: *P. pip .. N. noc .. V. mur*
Typical site: Odštiepená skala (No. 41), Muránska planina plateau.

This type was represented mainly in samples collected in sunny and warm rocky faces subdivided by large crevices. *N. noctula* dominated distinctly, and the occurrence of *V. murinus* increased at colder sites. *N. lasiopterus* was found among *N. noctula* individuals.

II. Type: *P. pipistrellus*
Chart: *N. noc .. P. pip .. V. mur*
Typical locality: Hrdzavá valley, Brestová (No. 40) Muránska planina plateau.

The samples of this type were collected mainly in narrow and short crevices, situated often not high above the ground or in sites overshadowed by forest. The incidence of *V. murinus* increased in the latter sites, *N. noctula* was more numerous in high rocky faces. *E. serotinus* and *B. barbastellus* occurrence may have been incidental.

Table 3. Thanatocenoses in rock crevices

Species /Site No.	45	31	13	1b	2b	41a	41b	2a	44	5
N. noctula	1+ 146	1+ 53	1+ 41	1+ 30	1+ 35	1+ 108	1+ 111	68	1– 9	5– 1
V. murinus	2– 1	1–	5			1– 2	2– 1	1+ 29	1+ 13	2+ 62
P. pipistrellus	4–	3–	3–	2–	2– 1	2– 15	1– 41	3– 2	9	1+109
E. serotinus								1	1	5
B. barbastellus						1	1			
M. myotis	1				1			2		
M. bechsteini										
N. lasiopterus								1		
P. auritus										
M. schreibersi										
Total	148	53	46	30	37	126	154	103	32	177
Diversity index H'	0.09	0.00	0.48	0.00	0.35	0.69	0.92	1.24	1.69	1.14

Species /Site No.	4	1a	40	49b	3	14	49a	61	Total	(%)
N. noctula	2– 7	2– 4	2– 4	2– 2	2–	1– 1	84	225	929	53.36
V. murinus	1+ 15	3	4	1	1	2	1– 5	2– 6	150	8.62
P. pipistrellus	1+ 54	1+ 51	1+ 44	1+ 23	1+ 15	1+ 16	1+ 104	148	632	36.30
E. serotinus	2			1				1	11	0.63
B. barbastellus	2	1		1	3			1	10	0.57
M. myotis	1								5	0.29
M. bechsteini	1								1	0.06
N. lasiopterus									1	0.06
P. auritus	1								1	0.06
M. schreibersi			1						1	0.06
Total	83	59	53	28	19	19	193	381	1741	
Diversity index H'	1.59	0.74	0.88	1.01	0.90	0.76	1.13	1.09		

D. Assemblages Found in the Owls' Pellets (Table 4)

Samples of the food of *Strix aluco* were collected exclusively during the vegetation period. Certain owls specialise in hunting bats at the cave entrances, and the composition of their diet resembles that found in samples obtained by nettings. Other owls prey on bats roosting in crevices, and certain samples (containing less than 1 % of bat remnants) might originated from accidental hunting. *Tyto alba* only rarely hunts bats (*e.g.* the church in Necpaly), *Bubo bubo* preys on bats quite exceptionally and only 123 items of bat remnants (*i.e.* 0.37 %) were found in a total diet sample of this owl species containing 33 171 food items.

I. Type: *M. myotis*
Chart: *.. M. myo .. E. ser*
Typical sites: 1) Izbica cave, entrance hall (No. 9), *S. aluco,* recent remnants, Veľká Fatra Mts. 2) Necpaly, evangelic church (No. 15), *T. alba,* Veľká Fatra Mts.

The samples mainly included recent remnants of *S. aluco* pellets collected at cave entrances, and/or pellets of *T. alba* found in the buildings inhabited by summer colonies of bats. *M. myotis* was clearly dominate but a number of other species also occurred regularly.

II. Type: *B. barbastellus* and other species
Chart:

M. bly . . M. mys . . M. bec . . E. ser
:
P. pip . . B. bar . . P. aur . . M. bra . . E. nil
:
N. noc *R. hip* *V. mur*
:
M. sch

Typical site: Bystrická valley, cave at a tunnel (No. 10a), *S. aluco,* subfossil remnants, Veľká Fatra Mts.

The samples originated from various altitudes and their age varied (the Silická ľadnica cave, No. 57, recent remnants; the Muránska cave, No. 24, subrecent and subfossil remnants). Many bat species with various ecological strategies were represented in the samples. *B. barbastellus* was abundant at most sites, and other species varied in occurrence in samples.

III. Type: *N. noctula*
Chart:

E. ser
:
V. mur . . N noc . . M. mys

Typical site: Zbojnícka cave (No. 58), pellets of *S. aluco*, Slovenský kras Mts.

Several findings of recent remnants from various mountain ranges in Slovakia were included here. The roosting site of an owl was usually situated in the vicinity of a colony of *N. noctula.* Numerous mixtures of other species (*V. murinus, E. serotinus, M. mystacinus*) were sometimes recorded.

Table 4. Bats in the food of owls

Species / Site No.	28	15	51	9	27	67	29	57	6	30	24	10a	37
M. myotis	3+ 146	2+ 32	2+ 29	2+ 73	1+ 12	1+ 23	2+ 42	10	3– 2	1– 1	4– 4	3– 4	3
E. serotinus	1–		3	2	2	2+ 29		3	21	2+ 18	1– 18	1– 12	2
M. mystacinus				3		5	2+ 13	2+ 14	1+ 19	3	25	2–	
M. blythi	1	1	1	4	1	2		1+ 8			2–	1	
M. bechsteini	1			6		6	1	1+ 5	4	1+ 6	2– 2	13	
M. brandti	2			5	1	1		3	2–	2+ 15	1+ 68	1– 8	
E. nilssoni				1	1				1	3	1+ 40	1– 2	
B. barbastellus	1– 2			11		10	2	3	2+ 100	2+ 28	4– 1	1+ 50	1
P. auritus	2	1		3	2	3		1	1– 5	4	2– 8	2+ 74	1+ 7
R. hipposideros					3	1		1	2–	2	3–	2+ 67	2
M. schreibersi											1–	2+ 15	
N. noctula	3–	1	3	1– 3	2	14	1–	1–	3– 4	2– 1	180	1+ 113	
V. murinus	4–	2– 1	2–	3– 4	1–	1– 19	3–	2– 3	114	2– 5	1+ 904	176	1–
P. pipistrellus	4–	2–	1–	2– 4	1–	1– 9	2–	2–	1+ 158	2– 1	7–	1– 101	1
M. nattereri						1	2	1		4	1	1	1
M. dasycneme				3				1			2		
P. austriacus		3											
M. daubentoni	1								1	3			
M. emarginatus												2	
R. ferrumequinum													
N. lasiopterus											1		
Total	155	39	36	122	24	123	60	53	429	94	1254	639	17
Diversity index H'	0.44	1.03	0.97	2.28	2.31	3.02	1.24	3.00	2.17	2.98	1.38	2.85	2.40

Table 4. Continued

Species / Site No.	64	11	40	43	41	58	19	21	10b	36	59	Total	(%)
M. myotis	1	1– 2	6		6	5	3–	5	4	3– 2	4–	412	9.77
E. serotinus	1	1+ 7	2		3		1– 1	1	1+ 7	6	1– 3	141	3.34
M. mystacinus	1	1				1+ 8			1	1– 1	2–	94	2.23
M. blythi	2	1	2							2	2	28	0.66
M. bechsteini			1		3				3	7	1–	58	1.38
M. brandti							1–			4	2–	107	2.54
E. nilssoni		1				1				1	1–	51	1.21
B. barbastellus		4		2		1	2–		3	19	3–	237	5.62
P. auritus	2	1			3		1–		1	1– 4	2–	121	2.87
R. hipposideros	1+ 6	2							1	3	1– 1	89	2.11
M. schreibersi											1	16	0.38
N. noctula		1+ 21	1+ 10	2+ 38	1+ 8	2+ 25	2+ 82		5	2– 12	3– 3	525	12.45
V. murinus	1– 1	20	1–	2–	1– 1	2–	1+ 84	1+ 12	1– 11	2– 20	4– 5	1380	32.73
P. pipistrellus	7	10	1–	2–	1–	1– 3	4–		1+ 29	2+ 230	2+ 366	919	21.80
M. nattereri		1				1						13	0.31
M. dasycneme									1			7	0.17
P. austriacus	1	1				1						6	0.14
M. daubentoni												5	0.12
M. emarginatus		1								1		4	0.09
R. ferrumequinum						2						2	0.05
N. lasiopterus												1	0.02
Total	22	73	21	40	24	47	167	18	66	312	381	4216	100
Diversity index H'	2.65	2.79	1.85	0.28	2.32	2.13	1.03	1.12	2.57	1.57	0.30		

IV. Type: *P. pipistrellus*
Chart: . . *P. pip* . . *E. ser*
Typical site: Ohnište cave (No. 59), recent remnants, *S. aluco,* Slovenský kras Mts.

The samples were found in various mountain ranges and their age varied. A high number of species and the dominance of *P. pipistrellus* were typical of this type. *E. serotinus* was found frequently in any type of bat records ascertained in the food of the owls. This species was probably rather frequent in several habitat types.

Table 5. Comparison of four data sets informing on the occurrence of bats

Species / Total of data	A	B	D	C	Total	(%)
Pipistrellus pipistrellus	16991	2– 673	1– 919	632	19215	34.21
Myotis myotis	4291	1– 521	412	5– 5	5229	9.31
Rhinolophus hipposideros	3994	534	2– 89	6–	4617	8.22
Myotis emarginatus	301	1– 18	2– 4	2–	323	0.58
Barbastella barbastellus	1+ 7418	3– 169	2– 237	4– 10	7834	13.95
Miniopterus schreibersi	1+ 5533	8– 1	5– 16	6– 1	5551	9.88
Rhinolophus ferrumeq.	1+ 1598	6–	5– 2	4–	1600	2.85
Rhinolophus euryale	1+ 913	5–	5–	3–	913	1.63
Myotis blythi	1+ 873	2– 27	1– 28	3–	928	1.65
Myotis brandti	3– 374	3+ 2605	1– 107	5–	3086	5.49
Myotis bechsteini	7– 3	3+ 850	58	3– 1	912	1.62
Myotis nattereri	4– 6	3+ 184	13	1–	203	0.36
Myotis mystacinus	1– 571	2+ 835	94	4–	1500	2.67
Myotis dasycneme	2– 9	2+ 39	7		55	0.10
Myotis daubentoni	1– 9	2+ 22	5		36	0.06
Plecotus auritus	3– 78	3+ 549	1+ 121	3– 1	749	1.33
Eptesicus nilssoni	1– 92	1+ 45	2+ 51	1–	188	0.33
Eptesicus serotinus	3– 11	2– 5	3+ 141	1+ 11	168	0.30
Vespertilio murinus	8– 3	3– 37	4+ 1380	2+ 150	1570	2.80
Nyctalus noctula	9–	4– 7	2+ 525	4+ 929	1461	2.60
Plecotus austriacus	25		6		31	0.06
Nyctalus lasiopterus			1	1	2	0.00
Total	43093	7121	4216	1741	56171	100
Diversity index H'	2.56	2.83	2.84	1.41		

A: winter censuses, B: thanatocoenoses in caves, C: thanatocoenoses in rock crevices, D: bats in the food of owls.

A Comparison of Synoptical Data

Synoptical data on 22 bat species obtained by four methods described above were arranged in a contingency table (Table 5). The comparison of significant deviations from the mean resulted in four clusters of species:

1. Highly dominant species without significant deviations above the mean were *P. pipistrellus, M. myotis, R. hipposideros* and *M. emarginatus*. They were the dominant species in certain recent hibernacula.

2. Species frequently occurring in over-wintering assemblages but rarely found amongst skeletal remnants were *M. schreibersi, R. ferrumequinum, R. euryale, B. barbastellus* and *M. blythi.*

3. Species distinctly dominant in the cave thanatocoenoses and occurring moderately or frequently in the diet of *S. aluco* were *M. brandti, M. bechsteini, M. nattereri, M. mystacinus, M. dasycneme, M. daubentoni, P. auritus* and *E. nilssoni.* These species were numerous in caves in the period of the oceanic climate and low human impact to the landscape in the lower Holocene.

4. Species occurring frequently in the thanatocoenoses of rock crevices and in the food of owls, but sporadically represented in caves, were *N. noctula, V. murinus,* and *E. serotinus.*

There were few data in the materials studied to evaluate precisely the position of *P. austriacus, N. lasiopterus, N. leisleri* and *P. nathusii.*

Discussion

The bats represent a specific mammalian order characteristic by rapid and extensive changes in time and space. Therefore, different methods often yield controversial information on the numbers and species represented, and the actual status of populations and communities is documented in only a fragmentary record. Certain types of species composition are, however, recorder repeatedly in spite of the different size of samples evaluated. The patterns in species composition have been formed by a complex of factors, and it is difficult to determine the essential influences. Every quantitative record is unique and unrepeatable but its specificity may be evaluated only after comparison with other data collected in a similar manner. The reliability of classifying species into particular types of assemblages is largely dependent on the amount of such comparative data.

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