

## Community Structure and Interspecific Interactions in Bats Hibernating in Poznań

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Studies were carried out during the winter seasons of 1979—1982 in urban areas 228 km<sup>2</sup> in extent. A total of 2,393 bats belonging to 8 species, the most numerous of which proved to be *M. myotis*, were found to hibernate. There was considerable variation in the value of the index of species diversity for different shelters, due to differences in the dimensions of such hibernating places, the number of shelters available, and the variety of microclimatic conditions there. Synurbization of bats hibernating in a town was expressed by the proportion of the community formed by thermophilous species, greater than in comparable sheltering places outside towns. The hypothesis was put forward that *M. dasycneme* may be a good bioindicator of the changes which take place in a habitat under pressure of urbanization factors. The domination structure in the community and the large numbers of bats hibernating there can be explained by the presence of numerous fortifications and the peculiar geographical situation of the town. Examination was made of the character and strength of interspecific interactions at clusters level. It was found that there are statistically significant tendencies to form joint clusters between *B. barbastellus* and *P. auritus*, and between *M. nattereri* and *M. daubentoni*. The formations of clusters consisting of different species depends on the similarity of their ecological requirements.

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### 1. INTRODUCTION

The Wielkopolska region of Poland, and its chief city, Poznań, are among the most thoroughly investigated regions in Poland from the chiropterological aspect (Bogdanowicz & Urbańczyk, 1983). Historical data on the bat fauna of these areas date from 1911 (Schulz, 1911). Up to the present as many as 9 species of bats have been shown to hibernate within city limits only.

The purpose of the present study was to make detailed examination of the winter structure of the bat community under the conditions prevailing in a large town. Interspecific interactions were also traced at clusters level and their possible effect on the structure of different colonies defined.

## 2. MATERIAL AND METHODS

Observations were carried out in the city of Poznań ( $52^{\circ}24'N$ ,  $16^{\circ}56'E$ ), in which 540,000 inhabitants live within area of 228 km<sup>2</sup>. Studies were made from December to April for the 1979/80 season and from October to April for 1980/81 and 1981/82, in nineteenth century forts — groups of shelters in a system of permanent fortifications, a citadel, single separate bunkers and in several cellars in buildings (Fig. 1).

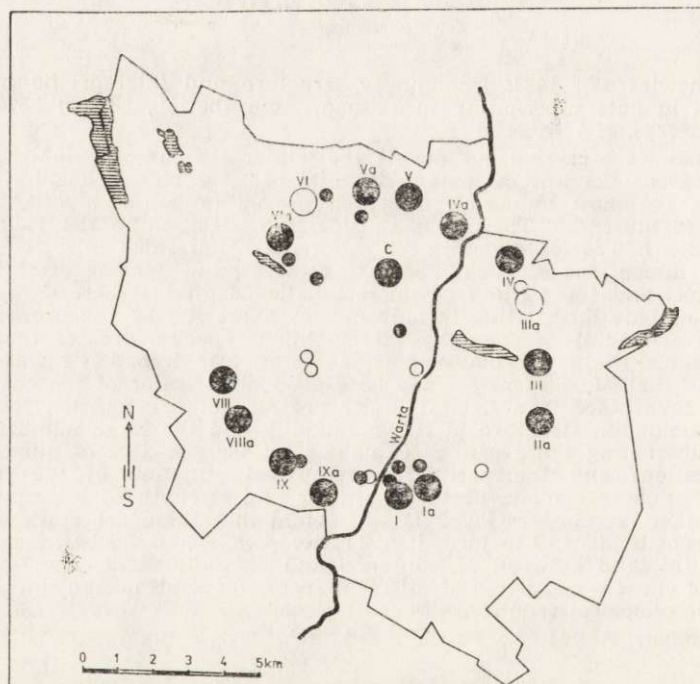


Fig. 1. Distribution of sheltering places inspected in Poznań during the winter seasons of 1979—1982.

I—IXa — fort numbers, C — citadel, bunkers and cellars not numbered. Black marks indicate sheltering places occupied by bats.

During each inspection all bats found and accessible were ringed (or their ring number noted), recording the species and sex, and data on their distribution in the shelters. These results were supplemented by data on conditions prevailing within the hibernating place. Temperature was measured with a mercury thermometer with accuracy  $\pm 0.1^{\circ}C$ . An Assmann psychrometer was used for measuring relative atmospheric humidity.

The total number of bats was defined as the sum total of all individuals ringed and inaccessible individuals capable of identification. Bats recaptured were omitted from these calculations.

Structural relations in the community of hibernating bats in Poznań were described on the basis of the following biocenotic parameters;



## 1) index of dominance (D)

$$D = (N_i/N) \cdot 100$$

where  $N_i$  — number of individuals of the species ( $i$ )  
 $N$  — number of individuals of all species

2) Shannon-Wiener index of species diversity ( $H'$ )

$$H' = - \sum_{i=1}^s p_i \cdot \log_2 p_i$$

where  $p_i = N_i/N$   
 $s$  — number of species

3) Sheldon's equitability index ( $E$ )

$$E = H'/H_{\max}$$

where  $H_{\max} = \log_2 s$  — theoretically greatest diversity for ( $s$ ) species

The coefficient of mean square contingency ( $c$ ) was used to estimate tendency to joint formation of clusters between pairs of different species:

$$c = \pm \sqrt{\frac{\chi^2}{n + \chi^2}}$$

where  $n$  sum total of single- and multispecies clusters  
 Correlation tables  $2 \times 2$  were used for calculating  $\chi^2$ .

## 3. RESULTS

## 3.1. Description of the Bat Community

A total of 2,393 individuals of 8 species of bats were found to hibernate within city administration limits during the period 1979—82: *Myotis myotis* (Borkhausen, 1797), *Myotis nattereri* (Kuhl, 1818), *Myotis mystacinus* (Kuhl, 1819), *Myotis daubentoni* (Kuhl, 1819), *Eptesicus serotinus* (Schreber, 1774), *Plecotus auritus* (Linnaeus, 1758), *Plecotus austriacus* (Fischer, 1829) and *Barbastella barbastellus* (Schreber, 1774).

In order to define the importance of different species in the community their domination was examined, i.e. the percentages they formed were compared (Table 1). A dominating species, that is, consisting of at least 30% of the individuals included in the composition of the community, proved to be *M. myotis*. In each of the study seasons this species was characterized by a high index of dominance, from 36.6 to 50.7% (Table 1). The mass hibernation of individuals of *M. myotis* in the tall (up to 8.5 m) and narrow (up to 0.5 m) ventilation chimneys in fort I had a decisive influence on this domination structure. There was no draught in these places and at the turning point between autumn and winter temperature

of up to  $+10.5^{\circ}\text{C}$  was recorded. *M. myotis* was also encountered relatively frequently in other forts in the city, but their numbers were far smaller than in fort I. This species was found practically not to hibernate in the single separate bunkers, or in cellars of dwelling houses (Table 2). A similar situation, but less sharply defined, was also observed in the case of co-dominating species (*B. barbastellus* and *M. daubentoni*) and accessory species (*M. nattereri* and *P. auritus*) (cf. Fig. 2). As a rule these species predominated numerically in one or two shelters. This distribution of numbers was determined by the different ecological requirements of these species and differences in microclimatic conditions and number of specific sheltering places accessible in hibernation sites. *M. nattereri*, for instance, dominated in quarters well isolated from the

Table 1

Structure of the bat community hibernating in Poznań from 1979—1982.  
n — numbers, D — index of dominance,  $H'$  — index of species diversity, E — Sheldon's equitability index.

Species	1979/80		1980/81		1981/82		Total	
	n	D	n	D	n	D	n	D
<i>M. myotis</i>	370	44.1	214	36.6	493	50.7	1,077	45.0
<i>B. barbastellus</i>	153	18.3	122	20.9	137	14.1	412	17.2
<i>M. daubentoni</i>	115	13.8	108	18.5	138	14.2	361	15.1
<i>M. nattereri</i>	151	18.1	69	11.8	136	14.0	356	14.9
<i>P. auritus</i>	38	4.5	67	11.4	66	6.8	171	7.1
<i>P. austriacus</i>	8	1.0	3	0.5	2	0.2	13	0.6
<i>M. mystacinus</i>	—	—	2	0.3	—	—	2	0.1
<i>E. serotinus</i>	1	0.1	—	—	—	—	1	0.0
$H'$	2.08		2.24		1.97		2.10	
E	0.74		0.80		0.76		0.63	

effect of weather conditions (e.g. fort VIa and the bunker near fort I), whereas *M. daubentoni* preferred sheltering places flooded with rainfall (some of the chambers in forts I and VIa, citadel) (cf. Table 2).

The remaining species, i.e. *P. austriacus*, *M. mystacinus* and *E. serotinus*, hibernating within the city limits, proved to be random species and their proportion in domination structure did not exceed 1% (Table 1). In the case of *P. austriacus* such small numbers were connected, *inter alia*, with the occurrence of this species near the northern limits of its range (Ruprecht, 1983).

In the study bat community there was no group of species consisting of 1—5% of individuals (sporadic species). This distribution in domination structure suggests that a special winter chiropteroфаuna is connected with fortifications as an independent type of sheltering place. It follows from this that the composition and domination relations in the bat community are to a great extent conditioned by the presence of specific

Table 2  
 Numbers (n), index of species diversity ( $H'$ ) and Sheldon's equitability index ( $E$ ) in sheltering places most numerously occupied by bats.

Species	I	IIa	III	Forts Via	VIIIa	IX	Cit.	Bunker near F.I	F.VI	Bunkers and cellars	Forts
<i>M. myotis</i>	909	9	13	20	11	66	47	—	1	1	1,076
<i>B. barbastellus</i>	254	3	91	—	5	1	15	—	4	5	407
<i>M. daubentonii</i>	144	13	36	68	5	—	66	1	21	23	338
<i>M. nattereri</i>	89	9	25	90	38	—	54	19	8	43	313
<i>P. auritus</i>	112	5	4	—	5	—	22	1	5	15	156
<i>P. austriacus</i>	—	—	5	—	6	—	—	—	—	1	12
<i>M. mystacinus</i>	—	—	1	—	—	—	—	—	1	1	1
<i>E. serotinus</i>	—	—	—	—	1	—	—	—	—	—	1
Total, n	1,508	39	175	178	71	67	204	21	40	89	2,304
$H'$	1.71	2.17	1.91	1.38	2.09	0.11	2.14	0.55	1.93	1.89	2.05
$E$	0.74	0.93	0.68	0.87	0.74	0.11	0.92	0.35	0.75	0.67	0.68



hibernation sites, and that they are also affected by the absolute proportions between different species.

No direct correlation was found between the numbers of bats and the diversity of the community. The greatest indices of species diversity were obtained for fort IIa and the citadel (Table 2). These sheltering places were distinguished by considerable spatial differences, expressed by the wealth of different types of sheltering places and microclimatic conditions. At the same time very high values for Sheldon's equitability index were found for these hibernation sites (Table 2), forming evidence of the balanced proportions in the numbers of different species, and consequently of the absence of a decided preference for any of them as the result of the conditions prevailing in a given hibernation site. In turn the lowest index of species diversity — only 0.11 — from among the winter quarters examined was obtained for fort IX (Table 2). This was connected with the unfavourable conditions for hibernation — low atmospheric humidity (50—55%) and lack of fissures and gaps — which exposed the bats to great fluctuations in ambient temperature. More favourable conditions were present only in the ventilation chimneys and it was there that all individuals of *M. myotis* hibernating on this fort were found.

The picture of qualitative and quantitative relations in particular shelters had a considerable influence on the value of the biocenotic indices in the community. The highest value of species diversity and equitability indices were found during the 1980/81 season (Table 1), although in each of the study seasons these values were relatively high and comparable with those obtained for other hibernating sites (cf. Gaisler, 1975, 1979).

### 3.2. Interspecific Interactions

The character and strength of reciprocal relations were examined by means of estimating the co-occurrence of different species of bat in mixed clusters. The coefficient of mean square contingency was used to estimate tendency to joint formation of clusters between pairs of different species. This coefficient showed values from  $-1$  to  $+1$ . The coefficient of mean square contingency reaches a value of  $+1$  when two species always occur together, and  $-1$  when pairs of species never form joint groups. When co-formation of clusters is of a random character coefficient  $c$  shows values in the interval from  $-0.11$  to  $+0.11$  (for  $n=335$  with 95-percentage limit of confidence) (Table 3).

It was found that two pairs of species have a statistically significant tendency to co-occurrence in clusters: 1) *B. barbastellus* and *P. auritus*,

Table 3

Values of the coefficient of mean square contingency  $c$  on left-hand side of table and number of multi- and single-species clusters of bats on right side of table. The sum of clusters is greater than (n) on account of the presence of clusters containing more than two species.

	<i>B.b.</i>	<i>P.a.</i>	<i>M.d.</i>	<i>M.n.</i>	<i>M.m.</i>
<i>B.b.</i>	42	19	14	14	1
<i>P.a.</i>	+0.17	16	8	10	1
<i>M.d.</i>	-0.10	-0.07	31	35	5
<i>M.n.</i>	-0.14	-0.06	+0.16	42	4
<i>M.m.</i>	-0.37	-0.25	-0.33	-0.38	108

2) *M. nattereri* and *M. daubentoni*. In the first case this is due to the greater tendency to clustering of *B. barbastellus*, which forms the clusters with *P. auritus*, and in the second case with the greater tendency to clustering of *M. nattereri* than of *M. daubentoni*. The following species do not exhibit tendencies either to co-occurrence in clusters or to avoiding same: *M. daubentoni* and *P. auritus*, *M. nattereri* and *P. auritus*, *M. daubentoni* and *B. barbastellus*, Pairs of species which mutually avoid each other in clusters are: *B. barbastellus* and *M. nattereri*, *B. barbastellus* and *M. myotis*, *P. auritus* and *M. myotis*, *M. daubentoni* and *M. myotis*, *M. nattereri* and *M. myotis*. Differences connected with age and sex of the individuals belonging to the species, examined were not taken into consideration.

Table 4

Ranges of preferred temperatures, selectivity of crevices and fissures (%) and tendency to form clusters for 5 species of bats hibernating at Poznań (years 1979-82).

+ = distribution more frequent than random, 0 = random distribution, - = distribution less frequent than random.

Sp.	Preferred temp. °C	Selectivity of crevices	Tendency to form clusters				
			<i>B.b.</i>	<i>P.a.</i>	<i>M.d.</i>	<i>M.n.</i>	<i>M.m.</i>
<i>B.b.</i>	0.0-3.0	82.3		+	0	-	-
<i>P.a.</i>	0.5-4.0	82.1			0	0	-
<i>M.d.</i>	1.5-6.0	71.4				+	-
<i>M.n.</i>	2.0-6.5	84.9					-
<i>M.m.</i>	3.5-10.0	3.1					

The results obtained correspond to the thermopreferendum and preferences for sheltering places of the different species of bat (cf. Bogdanowicz & Urbańczyk, 1983). Species with a similar range of preferred temperatures and character of hibernation (*B. barbastellus* and *P. auritus*, *M. nattereri* and *M. daubentoni*) exhibit a tendency to co-occurrence in



clusters, but in the case of species of which the thermopreferendum and preference for sheltering places greatly differ from each other, co-formation of clusters is random in character and sometimes gives the impression that these species quite simply avoid each other (this being particularly clear in the relation of *M. myotis* with the remaining species) (Table 4). This points to the absence of interspecific interactions on the structure of winter colonies of bats.

#### 4. DISCUSSION

##### 4.1. Structure of Bat Communities during the Winter Season in Towns in Central Europe

Despite the approximation of certain data based on information in literature and the results of the authors' own studies, it was possible to carry out a quantitative analysis of the structure of bat communities hibernating in large towns (from 125 to 480 km<sup>2</sup>) densely populated (from 150,000 to 2,500,000 inhabitants): Pilsen (Húrka, 1973, *in litt.*, 1983), Brno (Gaisler, 1979), Poznań (author's data), Berlin (German Democratic Republic; Haensel, 1967, 1972, 1982) and West Berlin (Klawitter, 1975, 1976). Data on the "urban" chiropteroфаuna of these centres were compared with observations carried out in the external ring of fortifications at Modlin (52°27'N, 20°43'E) (Lesiński, 1982, *in litt.*, 1983) and in the fortifications of the Międzyrzecki Fortified Region (MFR) (52°23'N, 15°28'E) (Bagrowska-Urbańczyk & Urbańczyk, 1983) (Fig. 2). For purposes of comparison use was also made of the results of studies in an artificial cave at Puławy [11,700 inhabitants (1956) (Krzanowski, 1959)]. These hibernating places are situated at a considerable distance from large towns. In this way a system was obtained for analysis in which bats hibernating in sheltering places of anthropogenic origin were at most exposed to the effect of urbanization factors to a slight degree only.

A combination was distinguished of species with the highest, at least 50%, indices of dominance. In hibernation sites in which fortifications formed the dominating type of sheltering places, *i.e.* at Modlin and in the Międzyrzecki Fortified Region, West Berlin and Poznań, the characteristic combination of species differs only slightly from each other. In West Berlin and Poznań the largest number of bats hibernated in Spandauer Zitadelle and fort I respectively. There are, however, certain differences in the domination structure of the community, which should be considered as due to the effect of urbanization factors. In short the proportion in the community of thermophilous species (chiefly *M. myotis*, fewer *M. nattereri*), in West Berlin and Poznań is greater than in areas



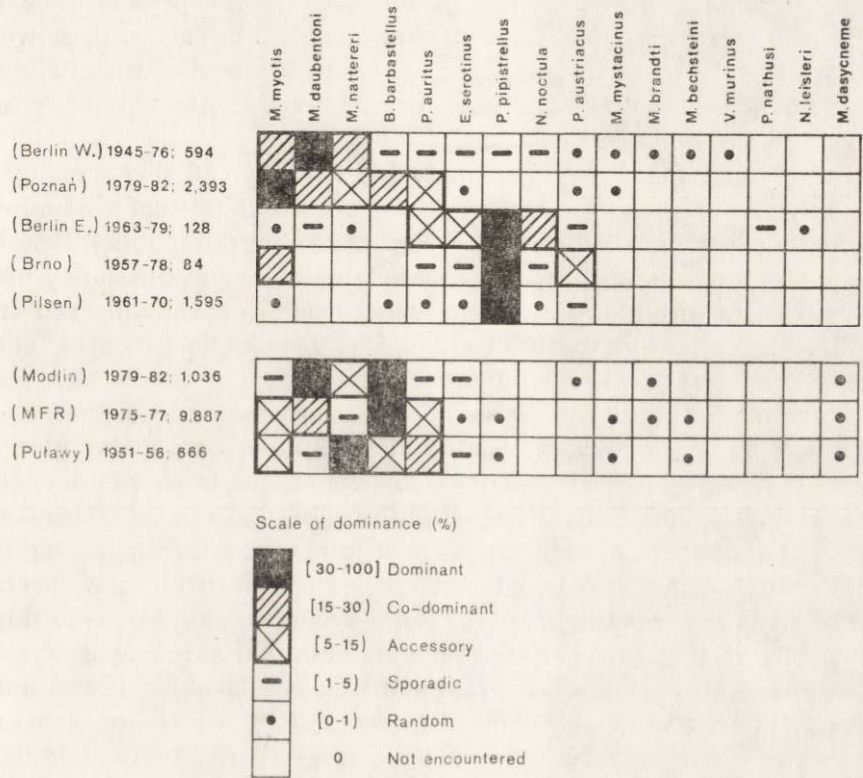


Fig. 2. Comparison of the structure of bat communities in selected winter quarters in Central Europe (for references see text).

The study years and size of sample (n) are given by the name of the winter quarter. The winter season was counted from October 1st to 31st March.

outside towns (Modlin together with the MFR), and there is at least a similar proportion of species preferring lower temperatures (*B. barbastellus*, *P. auritus* and *M. daubentoni*) (Fig. 2). On the other hand, however, it is known that atmospheric temperature in a town is higher than outside it (Schmuck, 1969) and bats' hibernation period lasts a shorter time there than in regions devoid of urban buildings (author's unpublished data). Thus changes in the structure of a bat community in urban areas, with which there is increased importance of more thermophilous species, may be considered as synurbic changes characterizing the life of a population under the specific conditions formed for it by a town. It would appear that in the future certain towns may prove to be attractive places for hibernation for other thermophilous species, e.g. for such typical cave-dwelling bats as *Rhinolophidae*, synanthropi-

zation of the life of which can be observed at the present time (e.g. Issel, 1950; Gaisler, 1963; Horáček & Zima, 1979). This will, however, be possible only when these species increase the range of their tolerance to lack of peaceful quiet (cf. Issel & Issel, 1960; Saint Girons & Saint Girons, 1968; Stebbings 1970, etc.).

Distinct relations were found between the kind of sheltering places characteristic of given towns and the structure of the bat communities hibernating in them. In Berlin (German Democratic Republic), Brno and Pilsen fortifications are almost entirely absent and the majority of the bats hibernate in buildings and churches. This has a very marked effect on the composition of the bat communities present in this area, and as a rule dominating or co-dominating species during the winter season play a similar role during the summer season also. An exception to this is formed by *M. myotis* at Brno, which found a convenient place for hibernation in the galleries on the outskirts of this town (Gaisler, 1979).

The typical community of species from Berlin (German Democratic Republic) contains not only fully synanthropic species, i.e., *E. serotinus* and *P. auritus*, but also two forest species (*P. pipistrellus*, *N. noctula*), which in this case proved to be semi-synanthropic. An even higher proportion of *P. pipistrellus* in the community (related to decrease in importance of *N. noctula*) was found in Czechoslovakian towns and at Pilsen it was completely dominant ( $D=97.3\%$ ), while the remaining species were not even accessory species (Fig. 2). A situation similar to this was observed in these towns in summer, when *P. pipistrellus* occurred in such large numbers, and simultaneously in such varied sheltering places, that the situation took on the character of an "invasion" (Palášthy & Gaisler, 1965; Grummt & Haensel, 1965; Hürka, 1966). This phenomenon was not observed in either West Berlin or in Poznań. In both these cities, as was the case at Modlin and MFR, the structure of the community and the large numbers of hibernating bats were to a great extent determined by the presence of numerous and relatively extensive fortifications. At Puławy the artificial cave played a similar role. It must be assumed that any changes in the use made of these sheltering places (including their renovation) will lead to an absolutely catastrophic decrease in the numbers of bats, which is to be expected in Kraków, where the wide-scale renovation of historic buildings threatens the destruction of the summer sheltering places of these mammals (Kubisz, 1983).

The geographical situation of hibernating sites is also of importance to community structure. In the northern and central parts of Poland there are no natural winter quarters for bats (this including mining galleries and stone quarries), of which there is an abundance in the



southern part of the country. This is most certainly conducive to even better use of such artificial shelters such as forts, bunkers, underground tunnels etc. by bats hibernating in northern and central Poland. In the case of Berlin (German Democratic Republic) and West Berlin, alternative winter shelters are provided by the galleries at Rüdersdorf (Haensel, 1972) and at Brno, the caves in the Moravian Karst (Gaisler, 1975, 1979). In turn the more southerly situation of Czechoslovakian towns ensures that the proportion of *P. austriacus* is greater than in other hibernating sites (Fig. 2), which corresponds with the situation observed in regions with a relatively warm climate.

The place of *M. dasyncneme* in the bat communities examined is exceptional. In Central Europe this is one of the rarer species of bats, which usually everywhere occurs in very small numbers (cf. Hanák & Gaisler, 1965). Certain general regularities can, however, be observed in the choice made by *M. dasyncneme* of winter quarters — this species clearly avoids greatly urbanized areas (Fig. 2) (cf. also Hanák & Gaisler, 1965; Sluiter *et al.*, 1971). It occurs at Modlin, MFR and at Puławy, and at one time it was recorded from Poznań (Schulz, 1911). In this connection the hypothesis may be put forward that within the limits of its range *M. dasyncneme* is a bioindicator of the changes taking place over a period of years in a habitat subjected to urbanization pressure.

#### 4.2. Interspecific Interactions

According to Ryberg (1947) the majority of bats from northern Europe tolerate — at least during winter — the presence of individuals of other species in their colonies. This author considers that only *E. serotinus*, like *M. myotis* in Central Europe, would appear to be less tolerant in relation to other species of bats. Krzanowski (1955) has also referred to the low degree of gregariousness (or tolerance) of *E. serotinus* in relation to other species. Tatarinov (1956) draws attention to competition in winter hiding places such as exists between *B. barbastellus* and *P. auritus* in respect of numbers. Brosset & Caubère (1959) consider that relations between some species, and particularly between *M. emarginatus* and *Rhinolophidae*, *M. schreibersi* and *M. myotis*, and *R. euryale* and *R. ferrumequinum*, are conditioned by interspecific social ties ("liens sociaux interspécifiques"), the so-called "facteur psychologique" determining this in *R. euryale*. Relations between *M. emarginatus* and *Rhinolophidae* (particularly *R. ferrumequinum*) are defined by Brosset (1974a) by the term "parasitisme écologique". Fairon *et al.* (1982) have also drawn attention to the strong character of the relations between *M. emarginatus* and *R. ferrumequinum*.

In the light of the studies presented above it was found that co-occurrence of *M. myotis*, *M. nattereri*, *M. daubentoni*, *P. auritus* and *B. barbastellus* in winter clusters depends on similar ecological requirements, while such factors as preferences, tolerance or avoidance of one species by another in the pairs of species examined is of no practical importance. It is probable that in other European species of bats also co-formation of multispecies clusters or mixed colonies during the winter season depends chiefly on the similarity in the range of the thermopreferendum, preferences for shelters, clustering strategy etc. (see also Brosset, 1974b).

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STRUKTURA ZESPOŁU I INTERAKCJE MIĘDZYGATUNKOWE  
U NIETOPERZY ZIMUJĄCYCH W POZNANIU

## Streszczenie

Badania prowadzono w sezonach zimowych w latach 1979—82 na terenach miejskich o powierzchni 228 km<sup>2</sup> (Ryc. 1). Stwierdzono zimowanie 2393 nietoperzy należących do 8 gatunków, z których najliczniejszym okazał się *M. myotis* (Tabela 1). Strukturę dominacyjną oraz wysoką liczebność zimujących tutaj nietoperzy tłumaczy się obecnością licznych i stosunkowo rozległych fortyfikacji oraz położeniem miasta w regionie Polski, gdzie brak naturalnych kwater zimowych. Zaobserwowano dużą zmienność w wartościach wskaźnika różnorodności gatunków dla poszczególnych kryjówek (Tabela 2) co związane było z różnymi rozmiarami zimowisk oraz z różnicami w liczbie dostępnych schronień i różnorodności warunków mikroklimatycznych. Synurbizacja zimujących w mieście nietoperzy wyrażała się większym niż w porównywalnych kryjówekach pozamiejskich udziałem w zespole gatunków termofilnych (Ryc. 2). Fakt ten tłumaczy się specyficznymi warunkami jakie panują na terenie miasta. Postawiono hipotezę, że *M. dasycneme* w granicach swojego zasięgu może być cennym bioindykatorem zmian jakie zachodzą w środowisku pod presją czynników urbanizacyjnych. Zbadano charakter i siłę interakcji międzygatunkowych na poziomie skupisk. Stwierdzono, że statystycznie istotne tendencje do współtworzenia skupisk istnieją pomiędzy *B. barbastellus* i *P. auritus* oraz *M. nattereri* i *M. daubentoni* (Tabela 3). Tworzenie różnogatunkowych skupisk zależy od podobieństwa wymagań ekologicznych, głównie termopreferendum i wybiórczości schronień (Tabela 4). Uznano, że interakcje międzygatunkowe w sezonie zimowym nie mają wpływu na strukturę poszczególnych kolonii nietoperzy.