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Ecology of Bats Hibernating Underground in Central Poland

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Bats hibernating in underground parts of a fortress in central Poland were studied over three seasons: 1979/80, 1980/81, and 1981/82. A total of 1072 individuals were marked, representing nine species. The most abundant were *Barbastella barbastellus* (48.2%) and *Myotis daubentoni* (35.3%). It has been found that the coolest and most exposed places were occupied by *B. barbastellus* and *P. austriacus*, contrary to bats of the genus *Myotis*. "Autumn" bats were distinguished, *M. myotis* and *M. daubentoni*, most abundant in October, and "winter" species occupying the fortress from late October or early November — *B. barbastellus*, *M. nattereri*, and *P. auritus*. There was a continuous exchange of individuals over the hibernation period, and the proportion of individuals noted more than once did not exceed 40%. In populations of *E. serotinus* and *B. barbastellus* males outnumbered females. The sex ratio in *M. daubentoni* and *B. barbastellus* varied over the hibernation period. The duration of hibernation, as estimated from changes in body weight, was 175—190 days for *M. daubentoni* and 140 days for *B. barbastellus*.

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1. INTRODUCTION

Ecological studies on bats hibernating underground have been in focus of scientists for many reasons. Although there are many data on this subject, the literature based on long-term studies of individually marked bats is scarce, and some large areas, for example, central and eastern Poland, were not investigated at all.

The purpose of this paper is to determine the species composition of bats hibernating underground in climatic conditions of the lowland of central Poland, and also to assess habitat preferences of different species. Changes in numbers of bats are described, also their population stability, sex ratio and its changes. An attempt was made to assess the duration of hibernation for several species.

2. STUDY AREA

2.1. Geographical Location and Climate

In northern part of the Warsaw province there is a former fortress Modlin. The central part of the fortress, located on the Narew river, is surrounded with a circle of smaller forts. The study was carried out in six abandoned forts, where hibernating bats were found during preliminary observations (Lesiński, 1980).

The forts under study are located in the Mazovian Lowland (20° 35'—20° 48' E, 52° 29'—52° 32' N), where climatic conditions are typical of extensive flats. The annual sum of precipitation is about 500 mm. Mean annual air temperature in Warsaw (at a distance of about 25 km from Modlin) is +7.8°C in October, —2.9°C in January, +7.6°C in April. Winter covers a period of 100—110 days, the number of days with frost is 40—50, and snow cover lasts for 50—60 days, on the average (Kondracki, 1969; Dylikowa, 1973).

2.2. Abiotic Conditions in the Undergrounds

The forts under study are small, and the lengths of their corridors are 150 m at Czarnowo, 160 m at Goławice II, 200 m at Janowo, 280 m at Błogosławie, 380 m at Goławice I, and 400 m at Strubiny. The forts differ in the shape and distribution of corridors, number and location of entrance holes, *etc.* "Large" corridors have been distinguished which are 3—3.5 m wide and 2—3 m high, "small" corridors, 1.5—2 m wide and 2—2.5 m high, and also chambers of different sizes (up to 10 m long).

As the number of entrance holes is high, abiotic conditions in the forts largely depends on outside conditions. In some corridors, permanent air circulation precludes stable thermal conditions. In mid-winter, the temperature of even warmest parts of some forts is below freezing point (Czarnowo, Goławice II), and the critical period is January and February. Air humidity in corridor parts most distant from the entrances varies between 80 and 100%. The corridors of forts Janowo, Strubiny and Błogosławie have two storeys, and the lower storey has more stable climate in winter. Walls of some corridors, especially in forts Janowo and Goławice I, have many crevices, and these are preferred hibernation sites for bats. Permanently submerged sections of forts Błogosławie and Goławice I, and also temporarily flooded Strubiny enhance a high relative air humidity (>90%). Forts Goławice I, Czarnowo, Błogosławie and Janowo have narrow and several-metre long ventilation shafts blocked from above. The temperature at the highest points of these shafts differs from the temperature in corridors by up to 2°C.

3. METHODS

The study was conducted during three successive hibernation periods of bats: 18 November, 1979—21 April, 1980, 2 October, 1980—7 April, 1981, and 22 September, 1981—30 April, 1982. In each fort, single censuses were made in the first and in the second half of each month of hibernation. On each census all the bats encountered were captured, identified to species, sexed, and marked with metallic rings on their forearms. The site of capture was described in terms of the way of hanging, height above the corridor floor, and utilization of crevices. Bats were weigthed to the nearest 0.5 g. From December to February, temperature was measured (mercury thermometer) and relative air humidity (hair hygrometer) in places of capture.

To estimate the significance of differences between frequencies, test χ^2 was used at $\alpha=0.05$.

To determine the stability of bat populations in the forts, the index of stability was calculated:

$$IS=\frac{\sum_{j=1}^{n-1}\frac{A_j}{j}}{\sum_{i=2}^{n}N_i}\cdot\frac{\bar{N}}{N_{max}}$$

where n is the number of censuses, N_i the number of individuals in the population during census i, $\bar{N}$ mean number of bats, N_{max} their maximum number, and A_j the sum of the j-order recaptures for all censuses ($j=1$: individuals captured on one immediately preceding census, $j=2$: individuals captured on the census made two censuses earlier, *etc.*). This index varies from 0 (no stability at all) to 1 (complete stability).

After Gaisler & Bauerová (1977), the hibernation period of bats in the forts has been divided into autumn (16 August — 31 October), winter (1 November — 15 March), and early spring (16 March — 30 April). When another division is used, this is noted in the text.

4. RESULTS

4.1. Species Composition, Numbers, and Dominance Structure

In the forts, 1072 bats were marked (Table 1), representing 9 species: *Myotis myotis* (Borkhausen, 1797), *M. nattereri* (Kuhl, 1818), *M. brandti*

(Eversmann, 1845), *M. daubentoni* (Kuhl, 1819), *M. dasycneme* (Boie, 1825), *Eptesicus serotinus* (Schreber, 1774), *Plecotus auritus* (L., 1758), *P. austriacus* (Fischer, 1829), and *Barbastella barbastellus* (Schreber, 1774). The number of bats differed from one fort to another. The highest number of bats was observed in two largest forts (Goławice I, Strubiny). Although the other forts were of similar sizes, Janowo and Błogosławie were more preferred, whereas Czarnowo and Goławice II were sparsely occupied (Table 1).

Table 1

Numbers and dominance structure (in per cent) of the bats observed in the forts. Bb — *B. barbastellus*, Md — *M. daubentoni*, Mn — *M. nattereri*, Mm — *M. myotis*, Pa — *P. auritus*, Es — *E. serotinus*, Pas — *P. austriacus*, Mds — *M. dasycneme*, Mb — *M. brandti*.

Locality	N	Bb	Md	Mn	Mm	Pa	Es	Pas	Mds	Mb
Strubiny	305	27.1	61.8	4.9	0.3	5.2	—	—	0.3	0.3
Janowo	179	24.4	52.3	14.2	4.0	3.4	0.6	1.1	—	—
Błogosławie	149	54.4	33.6	0.7	0.7	5.0	5.4	0.7	—	—
Goławice I	361	72.0	10.8	4.7	8.6	2.2	0.8	0.3	0.6	—
Goławice II	31	77.4	6.4	3.2	—	6.4	6.4	—	—	—
Czarnowo	47	53.2	10.6	2.1	15.0	10.6	2.1	6.4	—	—
Total	1072	48.2	35.3	5.7	4.3	4.2	1.4	0.7	0.3	0.1

The numerically dominant species was *B. barbastellus* (48.2%), which mostly occurred in winter. A high proportion of *M. daubentoni* (35.3%) was due to their high numbers in autumn. In forts Strubiny and Janowo, unlike in the other forts, *M. daubentoni* was more abundant than *B. barbastellus*. In all the forts, *P. auritus* was more abundant than *P. austriacus*. The least numerous bats, *M. brandti* and *M. dasycneme*, occured only in the largest forts.

4.2. Site Preference

The highest preference for relatively warm and humid sites was found in bats of the genus *Myotis*, most frequently using ventilation shafts and crevices of different types (Table 2). In ventilation shafts, they occupied the highest places, in contrast to *B. barbastellus*, which were found along the whole hight of the shafts, usually rather low. Almost all individuals of *M. nattereri* and *E. serotinus* occupied crevices, sometimes very deep and narrow. Bats of the genus *Plecotus* did not use ventilation shafts at all, and often they were exposed when hibernating (especially *P. austriacus*). The latter species occupied places less distant from entrance holes (to 25 m) than *P. auritus*, which hibernated even in the end sections of the corridors. *B. barbastellus* and *P. austriacus* were recorded in sites with temperatures below freezing, the former even six times. Typically, the corridors with high air circulation and without crevices were not occupied by bats, except for single *B. barbastellus*. Some shelters, for example, specified crevices, were regularly occupied by bats, and it has been found that some *B. barbastellus* and *M. daubentoni* returned to them in different years.

Table 2

Site preference of bats in the period December — February. VS — ventilation shafts, CR — crevices, EX — exposed, + — rare (1—25% of observations), ++ — average frequency (26—50%), +++ — frequent (51—100%), n — number of observations or measurements.

Species (n)	Site of capture			Height above corridor bottom (m)	Air temperature at capture sites (°C)	Relative air humidity at capture sites (%)
	VS	CR	EX			
M. myotis (14)	+++	+	+	2.2—7.0	+3.5—+6.0	86—100
M. nattereri (25)	+	+++		1.5—6.0	+1.5—+7.0	85—100
M. daubentoni (60)	+	+++	+	0.4—5.5	+0.5—+7.0	80—98
E. serotinus (12)	+	++	+	2.5—5.0	+0.5—+6.5	78—92
B. barbastellus (84)	+	++	++	1.5—5.0	—2.5—+6.5	72—98
P. auritus (22)		++	++	1.7—2.5	+1.0—+5.5	75—95
P. austriacus (8)		+	+++	1.5—2.4	—0.5—+4.5	69—90

4.3. Stability of Hibernating Populations

Changes in numbers of five species were analysed in successive hibernation periods (Fig. 1). In autumn, *M. daubentoni* and *M. myotis*, the "autumn" species, appeared earliest, reaching peak numbers in the first half of October. Then their numbers decreased. Since December only several to a dozen or so individuals of both these species were noted, and no clear increase in their numbers was observed in early spring. Much later such species appeared in the undergrounds as *P. auritus* (since mid-October), *B. barbastellus*, and *M. nattereri* (early in November) — the "winter" species. Earlier only single individuals of these species were noted. The number of *B. barbastellus* slowly declined during hibernation, and rapidly declined in March or early April. In little abundant *M. nattereri* and *P. auritus* no such tendencies were noted.

It was more difficult to determine the time when bats ultimately left the undergrounds since their numbers were very low in early spring. The species arriving to forts later, that is, *B. barbastellus*, *M. nattereri* and *P. auritus*, left the forts at the end of March, whereas *M. daubentoni* and especially *M. myotis*, were frequently noted even in April (Fig. 1).

Changes in numbers and a permanent exchange of individuals observed in most species accounted for a high instability of bat populations during the hibernation period in the undergrounds. This is indicated by the values of the index of stability *(IS)*, which did not exceed 0.2 (Table 3). Because of these low values it is difficult to make interspecific comparisons, although it may be suggested that *B. barbastellus* was more stable than *M. daubentoni* the latter species frequently showing

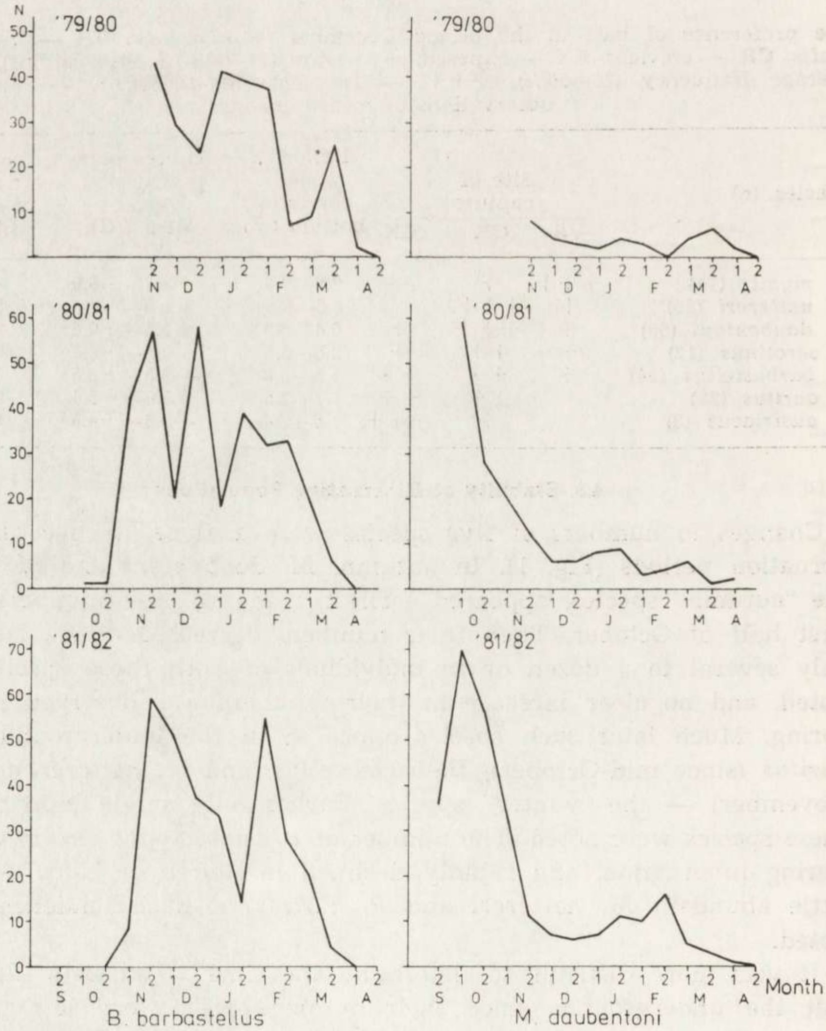

Fig. 1. Changes in numbers of bats (N) in succesive hibernation periods in all the forts. 1 — the first half of each month (1st—15th), 2 — the second half of each month (>16th). Continued on the next page.

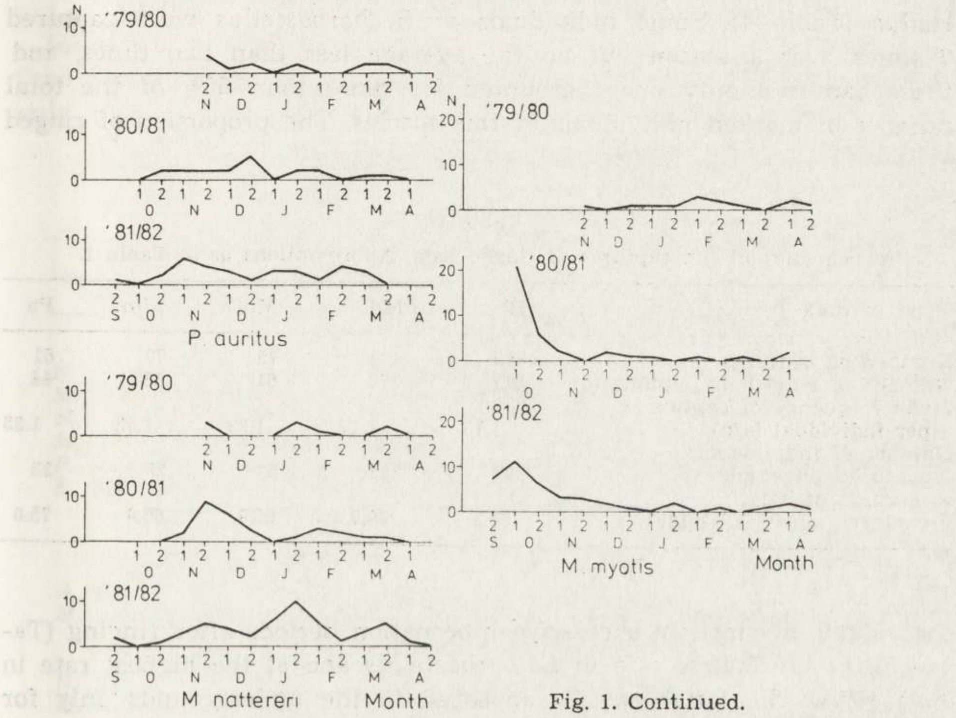

Fig. 1. Continued.

Table 3

Values of the index of stability (IS) for the *B. barbastellus* and *M. daubentoni* populations.

Species	Study period	Season	Locality			
			Goławice I	Janowo	Strubiny	Błogosławie
B. barbastellus	1st half of November — — 1st half of March	79/80	0.042	0.084	0.075	0.040
		80/81	0.042	0.161	0.081	0.084
		81/82	0.044	0.103	0.036	0.089
	2nd half of September — — 2nd half of October	80/81	0.046	0.031	0	0.125
		81/82	0	0.057	0.010	0
M. daubentoni	1st half of November — — 1st half of March	79/80	0	0.042	0.071	0.050
		80/81	0	0	0.048	0
		81/82	0.016	0.030	0	0.005

a total lack of stability ($IS=0$). There is no reason to suggest that there were differences in the stability of the *M. daubentoni* population between autumn and winter, or from one hibernation period to another.

The most frequently recaptured bats were *M. myotis* and *B. barbastellus* (Table 4). Some individuals of *B. barbastellus* were captured 7 times over a season but on the average less than two times, and those captured only once accounted for more than 60% of the total number of marked individuals of this species. The proportion of ringed

Table 4

Frequency of the captures of ringed bats. Abbreviations as in Table 1.

Type of data	Bb	Md	Mn	Mm	Pa
Number of captures (a)	880	439	75	70	61
Number of ringed individuals (b)	517	378	61	46	44
Mean frequency of capture per individual (a/b)	1.70	1.17	1.23	1.52	1.35
Number of individuals captured once (c)	327	335	53	28	33
Proportion of bats captured once (c/b×100)	63.2	89.7	86.9	60.9	75.0

individuals declined in successive hibernation periods after ringing (Table 5), at the lowest rate in *B. barbastellus* and at the highest rate in *P. auritus*. The latter species appeared in the undergrounds only for single hibernation periods.

Table 5

Percentage of recaptured individuals in relation to time after capture. A — in the same hibernation period, B — one hibernation period after ringing, C — two hibernation periods after ringing.

Species	A	B	C
B. barbastellus	28.1	20.2	18.0
M. daubentoni	8.5	3.6	2.9
M. myotis	25.8	16.5	0
M. nattereri	10.9	3.8	0
P. auritus	24.7	0	0

No relationship was found between dates of first observation of *B. barbastellus* in different years ($r=0.049$, $n=117$, $p>0.1$).

On seven occasions bats moved from one fort to another. These were *B. barbastellus* (6 cases) and *M. myotis* (1 case). Only two times this happened within the same hibernation period, and the distance did not exceed 1.5 km. The other distances were up to 4—6 km.

4.4. Sex Ratio

In seven out of nine species recorded the number of males was higher than that of females, although the difference was statistically significant only for *B. barbastellus* and *E. serotinus* (Table 6). Sex ratio varied over

Table 6

Sex ratio of first-captured and recaptured bats.

Species	Males	Females	Sex ratio M/F	Significance of differences [1]
		First-captured		
B. barbastellus	324	193	1.63	$p<0.001$
M. daubentoni	178	200	0.89	NS
M. nattereri	36	25	1.44	NS
M. myotis	25	21	1.19	NS
P. auritus	24	20	1.20	NS
E. serotinus	12	3	4.00	$0.05>p>0.01$
		Recaptured		
		Captures		
B. barbastellus	255	115	2.22	$0.05>p>0.01$
M. daubentoni	26	30	0.87	NS
		Individuals		
B. barbastellus	142	64	2.22	$0.05>p>0.01$
M. daubentoni	20	23	0.87	NS

[1] For first-captured bats in relation to 1:1 ratio, for recaptured bats in relation to the respective ratio of first-captured bats.

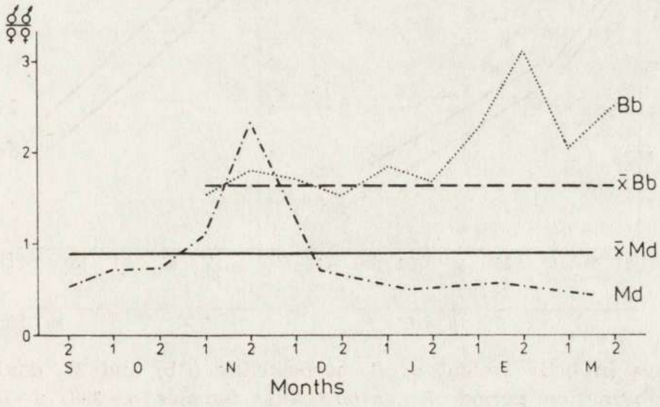

Fig. 2. Changes in sex ratio (mean values) in *B. barbastellus* (Bd) and *M. daubentoni* (Md) in hibernation periods. Symbols as in Fig. 1.

the hibernation period as shown for *B. barbastellus* and *M. daubentoni*. The proportion of males clearly increased in both these species, for *M. daubentoni* in November and early in December, and for *B. barbastellus* from early February until the end of March (Fig. 2).

Among recaptured *B. barbastellus*, the predominance of males was significantly higher than among first-captured individuals. This was not the case for *M. daubentoni* (Table 6).

4.5. Changes in Body Weight

The beginning and the end of bat hibernation were estimated from changes in their body weight. The first day of the half of a month in which the mean body weight reached a peak value was considered as the beginning of hibernation, and the last day of half of the month in which the mean body weight was at minimum was considered as the end of hibernation. Thus the hibernation period estimated in this way with a tolerance of about two weeks was 140 days for *B. barbastellus*, and 175—190 days for *M. daubentoni* (Fig. 3). For the latter species it was not possible to tell if the minimum weight was reached in the second half of February or in the first half of March, hence the above range is given.

The rate of body weight decrease in *B. barbastellus* almost did not change until mid-March, and then the body weight increased for both

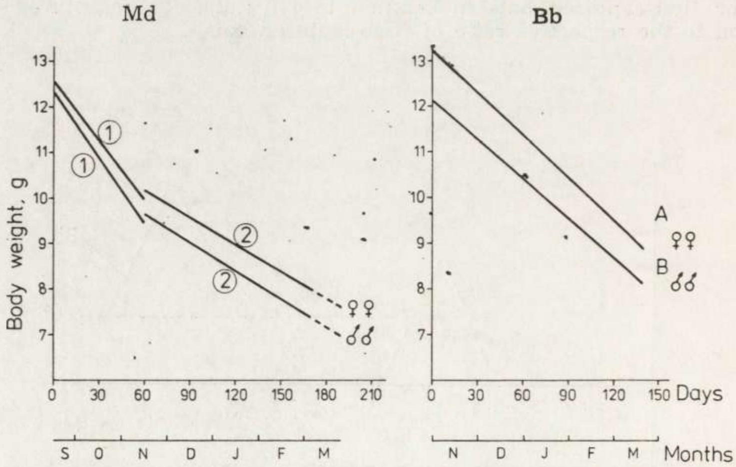

Fig. 3. Changes in body weight of *B. barbastellus* (Bb) and *M. daubentoni* (Md) during the hibernation period. *B. barbastellus:* females $n=298$, $y=13.239—0.031x$; males $n=550$, $y=12.126—0.029x$. *M. daubentoni;* females $n_1=149$, $y_1=12.598—0.048x$, $n_2=86$, $y_2=10.164—0.018x$; males $n_1=129$, $y_1=12.186—0.045x$, $n_2=69$, $y_2=9.679—0.018x$. The mean body weight of females (A) and males (B) *B. barbastellus* in the second half of March is shown ($n_A=10$, $SD_A=0.70$, $n_B=25$, $SD_B=0.54$).

sexes. In *M. daubentoni*, daily decreases in body weight in the first part of hibernation (until mid-November) were more than twice as high as in the remaining period (Fig. 3).

5. DISCUSSION

In Central Europe the undergrounds with many entrance holes and, consequently, with good air circulation, are readily and abundantly used for hibernation by *B. barbastellus* (Rybář, 1975; Sklenář, 1981; Bagrowska-Urbańczyk & Urbańczyk, 1983). In the forts under study, this species found good conditions for hibernation. It also predominated by number, selecting sites with relatively low air temperatures, this being known from the literature (Harmata, 1969; Gaisler, 1970). Temporarily, it can occupy places with temperatures below freezing, which shows that this species is resistant to freezing.

The species frequently noted and sometimes dominant also include *M. daubentoni* (Haensel, 1973; Bagrowska-Urbańczyk & Urbańczyk, 1983). It was on the second position in the forts, and this may be related to an increase in the abundance of this species in European hibernation sites in recent years (Bárta *et al.*, 1983; Daan, 1983).

Differences in numbers of some species between forts result from their specific microhabitat requirements in the undergrounds. *M. nattereri* is most abundant in the forts with many crevices available, which is confirmed in the literature (Haitlinger, 1976; Pelikan *et al.*, 1979). The distribution and numbers of *M. myotis* are rather closely related to the presence of blocked ventilation shafts. This species clearly prefers them here, like in the forts of Poznań (Bogdanowicz, 1983). Bats of the genus *Myotis* are scarce in the region of Modlin in winter, this being related to the range of their thermal preferences (typically +3 to +8°C) (Harmata, 1969; Gaisler, 1970; Gilson, 1978), which cannot be met in the study forts.

The differential occurrence of most sedentary species (*P. auritus, P. austriacus, E. serotinus*) in the forts can be related to the distribution of their summer shelters. It has been found that *P. austriacus* occupies in the forts sites closer to the entrance holes than *P. auritus* does. This can be explained by a higher preference of the former to small undergrounds (see Horáček, 1975; Haitlinger, 1976). In winter, such sites are more exposed to freezing, thus colder than those preferred by *P. auritus*, typically located deep in the forts.

The stability of bat populations hibernating in the udergrounds is generally low (*e.g.* Verschuren, 1949; Krzanowski, 1959). A similar situation was observed in this study, and a little higher stability of

B. barbastellus as compared with *M. daubentoni* shows that the former is more dependent on the wintering sites of this type.

The occurrence of the species called here "autumn" species in some undergrounds has not been explained so far, and also the hibernation places of the individuals appearing during the autumn peak numbers are not known. The "autumn" species from the study forts (*M. myotis* and *M. daubentoni*) showed similar changes in numbers in Puławy (Krzanowski, 1959) and in the region of Leningrad (Strelkov, 1971). According to Twente (1955), staying in the undergrounds in late summer, which are rather cool shelters relative to other shelter types at this time of the year, enables bats a rapid accumulation of fat before hibernation. The fact that they move from one place to another over the hibernation period suggests that they can use also other types of shelters as wintering sites, and their changes in numbers observed in the undergrounds reflect their movements from one shelter to another. Temperature falls account for a rise of bat numbers in the undergrounds (Hanák & Gaisler, 1959; Lesiński, 1983), providing evidence that they also occupy thermally less isolated shelters such as lofts and tree holes.

The higher number of males than females recorded for *B. barbastellus* and *E. serotinus* in Modlin, has frequently been noted in the undergrounds (*e.g.* Davis, 1959; Gauckler & Kraus, 1963; Feldmann, 1973). Also changes in the sex ratio during hibernation are known from the literature (Krzanowski, 1959; Gaisler, 1963; Daan, 1973), but they are not consistent with the results of this study.

Taking into account that numbers of bats in the undergrounds vary and that there is a permanent exchange of individuals, it is difficult to estimate the duration of the hibernation period. Typically, in the literature the time of the occurrence of bats in the undergrounds is given. The method described here, based on the analysis of changes in body weight, seems to be more appropriate. Its accuracy can be increased by distinguishing shorter time periods. *B. barbastellus* occur in the forts even after reaching the minimum body weight, thus after the ending of hibernation.

M. daubentoni belongs to the species with longest hibernation period (Strelkov, 1971; Daan, 1973), in contrast to *B. barbastellus* (Rybář, 1975), and this is confirmed in the present study. Bats beginning hibernation in early autumn, *e.g. M. daubentoni*, loose weight at a much higher rate in the early period of hibernation than in winter (similar observations are reported by Strelkov, 1971; Daan, 1973; Funakoshi & Uchida, 1978). This may be explained by the fact that air temperatures in the undergrounds at that time of the year are too high in relation to the optimum, and they accelerate metabolic rate.

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EKOLOGIA NIETOPERZY HIBERNUJĄCYCH W PODZIEMIACH W ŚRODKOWEJ POLSCE

Streszczenie

Badania prowadzono w podziemiach fortów twierdzy modlińskiej w ciągu 3 okresów hibernacji nietoperzy (1979/80, 1980/81, 1981/82). Podziemia kontrolowano dwukrotnie w ciągu miesiąca, odławiając i znakując wszystkie dostępne nietoperze. Zanotowano obecność 1072 osobników należących do 9 gatunków, spośród których dominującymi liczebnie są: *B. barbastellus* (48.2%) i *M. daubentoni* (35.3%). Przedstawiono charakterystyki miejsc wybieranych przez poszczególne gatunki w okresie zimowym: w najchłodniejszych występują *B. barbastellus* i *P. austriacus*, a w najcieplejszych nietoperze z rodzaju *Myotis* (Tabela 2).

Wyróżniono gatunki „jesienne" *(M. myotis* i *M. daubentoni)*, których szczyt liczebności przypada na początek października oraz gatunki „zimowe", które w większej liczbie przylatują do podziemi w listopadzie *(B. barbastellus, P. auritus, M. nattereri* i prawdopodobnie *P. austriacus* i *E. serotinus)*. W ciągu całego okresu hibernacji następuje stała wymiana osobników w podziemiach (wartości wskaźnika stabilności $IS<0.2$ — Tabela 3), która nie jest efektem przelotów pomiędzy fortami. Największą stabilność wykazują populacje *B. barbastellus* (Tabele 3, 4 i 5). Udział osobników odławianych częściej niż raz najwyższy jest u *M. myotis* — 39.1%

i *B. barbastellus* — 36.8%. *P. auritus* już w następnym po oznakowaniu okresie hibernacji nie powraca do fortów.

Populacje *B. barbastellus* i *E. serotinus*, zasiedlające badane podziemia, charakteryzuje istotna statystycznie przewaga samców, przy czym stosunek płci ulega wahaniom w okresie hibernacji (Tabela 6, Ryc. 2). Wśród znakowanych *B. barbastellus* odławianych powtórnie istotnie częstsze są samce (Tabela 6).

Średnie dobowe spadki ciężaru ciała *M. daubentoni* w pierwszej części hibernacji (0.045—0.048 g) są ponad dwukrotnie większe niż w zimie (0.018 g). U *B. barbastellus* tempo spadku ciężaru ciała jest w całym okresie przebywania w fortach w przybliżeniu równe (0.029—0.031 g na dobę) (Ryc. 3). Czas trwania hibernacji, określony na podstawie analizy zmian ciężaru ciała, jest dłuższy u *M. daubentoni:* 175—190 dni, niż u *B. barbastellus:* 140 dni.