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Author: Kokurewicz, Tomasz

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Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) hibernating in natural conditions

TOMASZ KOKUREWICZ

Agricultural University of Wrocław, Department of Zoology and Ecology, Koźuchowska 5b, 51 631 Wrocław, Poland; E-mail: kokur@ozi.ar.wroc.pl

The selection of optimal hibernation temperature (T_H) was possible by bats changing both the distance at which they roosted from the mine entrance (D) (T_H versus D; $r_s = 0.73$, $n = 615$, $P < 0.001$), and the height of hibernation place (H) (T_H vs. H; $r_s = 0.16$, $n = 412$, $P < 0.01$). Bats were able to select areas of high relative humidity (RH) by roosting in low temperature (RH vs. T_H ; $r_s = -0.26$, $n = 366$, $P < 0.001$) and/or by selecting hibernation places situated lower on the mine walls (RH vs. H; $r_s = -0.61$, $n = 280$, $P < 0.001$). Sub-adult bats (identified by presence of the black chin spot) were found to hibernate at significantly lower temperatures ($Z = -3.1$, $n_1 = 164$, $n_2 = 41$, $P < 0.01$) and in places situated lower on the mine walls ($Z = -2.2$, $n_1 = 164$, $n_2 = 41$, $P < 0.05$) than adult individuals. In March sub-adults hibernated closer to the entrance than adult individuals ($\chi^2 = 8.18$, $d.f. = 1$, $P < 0.01$). The difference in average body condition index between sub-adult and adult bats recorded in March (one-way ANOVA, $F = 6.56$, error $d.f. = 51$, $P < 0.05$) made individuals in their first year of life more prone to starvation at the end of hibernation period. In this month the significantly smaller distance of hibernation place of sub-adult individuals from the mine entrance ($Z = -2.7$, $n_1 = 58$, $n_2 = 19$, $P < 0.01$), resulted in significantly lower hibernation temperature, making them more endangered by predation of mammalian and avian species than adult bats hibernating deeper in the mine. The linear ($r = 0.87$, $d.f. = 30$, $P < 0.001$) relationship between body mass at the beginning and end of hibernation (November and March) of uniquely marked individuals indicates these bats did not forage in winter and their energy use was exclusively dependent on fat reserves accumulated prior to hibernation. The significant relationship between body mass in November and total mass loss ($r = 0.59$, $d.f. = 30$, $P < 0.001$) could indicate the possibility of existence of another factor, or group of factors, that could increase the energy use in hibernating *M. daubentonii*. These may include mating and/or energy costly defence against predators.

Key words: *Myotis daubentonii*, hibernation, mass dynamics, habitat selection, predation

INTRODUCTION

During the winter the lack of flying insects, or the significant decrease of their densities (Williams, 1939), reduces the food supply for temperate insectivorous bats, leaving them insufficient energy to cover the high energetic cost of flight (Griffin, 1986; Speakman and Racey, 1991) and

increased cost of thermoregulation in low ambient temperature (Speakman, 1997). The ecological response of bats is either migration (Davis and Hitchcock, 1965; Strelkov, 1969; Petit 1998) or hibernation with its subsequent reduction in energy demands.

During hibernation, bats usually depend exclusively on fat stores accumulated prior to hibernation (Ransome, 1968; Ewing *et*

al., 1970; Kunz *et al.*, 1998; Speakman and Rowland, 1999), although foraging may occur during mild winter spells (Ransome, 1968; Avery, 1985). Large variations in over-winter weight loss, ranged from 15 to 33% of autumn body mass, have been observed in natural conditions in *Myotis sodalis* (Johnson *et al.*, 1998), suggesting that many abiotic and biotic factors may influence energy use in these mammals. Laboratory studies of bat hibernation indicate the presence of a temperature range where metabolic rate is minimised (Hock, 1951). Within this temperature range energy accumulated in white adipose tissue is used at the slowest rate, suggesting that during hibernation in natural conditions, bats would actively search for optimal temperatures to minimise fat utilisation and to maximise the potential hibernation time. Many authors have reported a positive correlation between ambient temperature and the frequency of spontaneous arousals from torpor of hibernating bats (e.g., Ransome, 1971; Daan, 1973; Twente and Brack, 1985; Twente *et al.*, 1985; Harmata, 1987; Harrie 1994). These arousals constitute ca. 75% of total energy loss in over-wintering bats (Thomas *et al.*, 1990b), suggesting that ambient temperature is the environmental factor that has the strongest effect on bats during hibernation. The large inter-specific differences in temperature range selected during hibernation in natural conditions (see Webb *et al.*, 1996 for a review) and those observed between populations (Gaisler, 1970; McNab, 1974; Kokurewicz and Kováts, 1989) indicate that thermal preference is species specific, but it could also depend on local climate and, in consequence, could be different in different geographic regions. The intra-seasonal changes of temperature selected during hibernation, observed in both *Rhinolophus ferrumequinum* (Ransome, 1968) or in vespertilionid species (Kuipers and Daan, 1970), additionally complicate

the precise description of this habitat parameter.

The relative humidity and type of microhabitats selected by bats in their hibernation sites are other factors that could influence energy use in these mammals. Body mass losses of *M. daubentonii* wintering in 100% relative humidity were up to 2.3 times lower than in individuals roosting in 80% relative humidity at the same temperature (Daan, 1973). On the other hand, many vespertilionid species hibernate in crevices (Kuipers and Daan, 1970; Daan, 1973; Bagrowska-Urbańczyk and Urbańczyk, 1983; Bogdanowicz and Urbańczyk, 1983; Twente and Brack, 1985; Lesiński, 1986; Nagel and Nagel, 1991). The ecological meaning of this behaviour is not clear. It can minimise the energy costs of the warming phase, constituting ca. 13% of the total cost of arousal (Thomas *et al.*, 1990b), by increasing insulation from the air flow, or increase it by compressing the fur insulation layer in body contact with the cold rock surface.

Sexual dimorphism observed in temperate zone vespertilionid species (Ransome, 1968; Burnett, 1983; Bogdanowicz, 1990; 1992, 1994; Speakman, 1991) leads to larger total body reserves in females than in males, and allows us to expect sex related differences in mass dynamics and habitat selection during hibernation in natural conditions. Such differences, although statistically insignificant, have been described in *Myotis myotis*, where females were hibernating in higher temperatures and in narrower temperature range than males (Harmata, 1973). From the other hand, however, expected differences may be complicated by the effect of allometry.

Between December and April the mean daily body mass losses in females and males of *M. daubentonii* hibernating in artificial caves in Holland were 16 and 14 mg, respectively (Daan, 1973), while in central

Poland they were larger (18 mg) and equal for both sexes (Lesiński, 1986). These results may suggest that climate, resulting in differences in the length of hibernation period, could also influence mass losses. It can be assumed that the hibernation strategy of bats found in severe climatic conditions, e.g. at high altitudes and latitudes, may be more oriented towards energy saving than in bats inhabiting regions where the climate is milder. Individuals in their first year of life (sub-adults), hibernating for the first time, had lower fat reserves than bats older than one year (adults) (Ransome, 1968; Ewing *et al.*, 1970; Kokurewicz, 1990; Jones and Kokurewicz, 1994; Kunz *et al.*, 1998). Premature depletion of fat reserves was the reported cause for high mortality during hibernation in sub-adults *Myotis lucifugus* (Davis and Hitchcock, 1965). Sub-adult *M. daubentonii* in western Poland wintered at significantly lower temperatures than adult individuals (Jones and Kokurewicz, 1994), which could lead to a reduction in their energy expenditure.

Human disturbance is one of the most poorly known factors that may strongly affect the mass loss and habitat selection. Bats are sensitive to the tactile (Speakman *et al.*, 1991) and nontactile human disturbance (Thomas, 1995), which may increase their energy expenditure in hibernacula frequently visited by observers. All these sources of variation in mass losses make it difficult to estimate the energy requirements of hibernating bats. Laboratory studies of the energy requirements of torpid *Tadarida brasiliensis* (Herreid, 1963) and *Pipistrellus pipistrellus* (Speakman and Racey, 1989) suggest that individuals with larger body masses at the beginning of the observation did not use more energy than individuals with smaller energy reserves. These results would predict longer potential hibernation times and higher survival of individuals with larger body reserves in the beginning

of winter. Based on these results, Speakman and Racey (1989) predicted a positive relationship between body mass at the beginning and end of hibernation period. However, these relationships were not confirmed during field studies of hibernation in both *R. ferrumequinum* (Ransome, 1968, 1971, 1985, 1990) and *P. pipistrellus* (Avery, 1985). The lack of a positive relationship between body mass at the beginning and end of the winter period, and between the body mass before hibernation and subsequent survival lead to the formulation of the homeostatic control of body food reserves hypothesis (Ransome, 1985, 1990) — this asserts that during natural hibernation bats can actively control their energy balance, primarily by winter feeding. Foraging in winter seems to be one of the most important problems involved in the studies on bat hibernation. The ability to successfully feed at low insect densities during warm winter spells, leading to increased survival, was described as an adaptive risk-prone strategy (Stephens, 1981). The reasons for winter activity in bats are still unclear. The primary function of such activity is believed to be either feeding (energy maximisation hypothesis — e.g., Burbank and Young, 1934; Krzanowski, 1961; Stebbings, 1966; Ransome, 1968; Roer, 1969; Avery, 1985; Brigham, 1987; Whitaker *et al.*, 1997) or to replenish depleted water reserves (dehydration hypothesis — Speakman and Racey, 1989; Thomas *et al.*, 1990a; Thomas and Geiser, 1997). Torpor bout duration is influenced by evaporative water loss (Thomas and Geiser, 1997), which suggests that dehydration is probably the primary stimulus for arousal from torpor, while foraging during these winter emergency flights could make them energetically neutral (Speakman and Racey, 1989; Thomas *et al.*, 1990a). The reason of winter activity could be also different in 'tree dwelling species' (*sensu* Gaisler, 1966) such as *P. pipistrellus*, hibernating in dry

hibernacula (e.g., in tree holes and attics), than in 'cave dwelling species' roosting in sites where water is usually more easily available.

This research first aimed to test the hypothesis that bats are able to regulate their mass loss during hibernation by appropriate habitat selection, without resorting to feeding in warm winter spells. The study was undertaken in a mine situated high up in the mountains, where severe climate excluded the possibility of winter feeding. Records of mass losses in uniquely marked individuals were made in the hibernation site, and changes in body mass were used to describe the relationships between body mass at the beginning and end of the hibernation period, and over-winter mass loss and survival. The second hypothesis was that sub-adult bats, having smaller energy reserves, would have significantly lower over-winter mass losses than adult individuals, as a result of a hibernation strategy primarily oriented to energy saving. *Myotis daubentonii*, a small vespertilionid species ranging from Portugal and Ireland in the west to China, Korea and Japan in the east (Bogdanowicz, 1994), was chosen to test these predictions. In temperate zone vespertilionids the somatic growth and fusion of the epiphyses are completed after 4–7 weeks (Burnett and Kunz, 1982; Anthony, 1988), which makes impossible to distinguish sub-adult bats from older ones in hibernation sites. In *M. daubentonii* forearm growth is complete within 3–4 weeks of birth (Nyholm, 1965; Kurskov, 1981), however, sub-adults retain a small black spot on their lower lip until they are one year old (Richardson, 1994; Geiger *et al.* 1996). This ageing criterion made it possible to compare the habitat selection and mass dynamics of adult and sub-adult bats during hibernation in natural conditions.

Many mammalian (e.g., Bogdanowicz, 1994; Tryjanowski, 1997; K. Kasprzyk and M. Tomaszewski, in litt.) and avian

predators (Ryberg, 1947; Radzicki *et al.*, 1999) can prey upon hibernating bats. Predation risk may influence roosting behaviour of bats (Kunz, 1982) but little is known of this influence on hibernating populations, particularly regarding differences in the sex and age of predated animals. Harmata (1985) showed that the length of time of arousal from hibernation torpor was shorter at higher temperatures than in lower ones. Consequently, it was postulated that hibernating in higher temperatures should increase probability of successful escape (Speakman *et al.*, 1991). Nevertheless, hibernating in the upper range of preferred temperature could increase the metabolic rate and make bats more prone to starvation before the end of hibernation period. The trade-off between reducing the risk of predator by hibernating at a higher temperature makes the strategy of avoiding predation by wintering bats very risky. The third hypothesis was therefore that bats in good body condition, mainly adult individuals, developed energy costly strategy of predation avoidance. To test this it was assumed that mammalian and/or avian predators, as visually oriented animals, would penetrate the part of the mine situated near the entrance more frequently than its rear part. In the locality under study, based on an analysis of median hibernation temperature, the two thermal zones (the cold one, situated close to the entrance, and the warm one, located deeper inside the mine) were selected. The conditions of hibernation, frequency of sub-adult and adult individuals and their body condition in both zones were compared.

MATERIALS AND METHODS

Study Site

Observations have been carried out in an abandoned mine shaft in Sowia Dolina Valley (50°50'N, 15°50'E; UTM WS 52), situated near the town Karpacz (50°46'N, 15°46'E) in the Karkonosze

Mountains, SW Poland (Fig. 1). The gallery is situated at an altitude of 800 m in a spruce plantation in the lower forest zone (Fabiszewski, 1985). The mine was established in 1882 to exploit silver, copper, cobalt and arsenic in gneiss and mica-flates, however all works were stopped at the beginning of 20th century. The mine has one entrance and consists of one straight adit, 223.5 m long, and side adit, 13.5 m long, situated at the distance of 65 m from the entrance. The height of the adits ranges from 2.0 to 2.5 m and they are from 1.2 to 2.2 m wide. Between 15 to 105 m from the entrance its bottom is flooded. Near the entrance and in the side adit the bottom is covered by rocks that have fallen from the ceiling, and in rear part by clay sediments (Fig. 1). The walls of the gallery are of metamorphic rocks resulting in a lack of crevices characteristic of natural limestone caves. However, drill-holes are found scattered throughout the gallery. The lack of crevices and the small size of the gallery make it ideal for observing hibernating bats. As there is only one entrance and the mine is on one level there is slow air exchange between the mine and the external environment, the microclimate in the site is static. During the winter, cold, dry air enters the mine at the lower part of the entrance. As it warms up it slowly leaves the gallery by the upper part of the entrance (Kokurewicz, 1991). In the vicinity of the locality

there are any other underground sites suitable for bat's hibernation. The nearest buildings are located 1 km away from the mine, while the nearest hibernaculum is situated 2.5 km away from it.

The mean annual temperature in Karkonosze Mts. is 5.6°C, the mean January and July temperatures are -2.9 and 14.6°C, respectively, and an annual precipitation exceeds 1,141 mm. The length of the growing period, defined as time with mean daily temperature above +5°C, ranges from 115 days in areas situated above 1,000 m a.s.l., to 160 days in regions located 400–450 m a.s.l. (Kondracki, 1981). It was assumed that the hibernation period is limited by two thermal periods of the year; pre-winter, defined as the period with daily mean temperature from 5 to 0°C, and early spring with daily mean temperature from 0 to 5°C. Based on the most recent data (Piasecki, 1997) it was estimated that at the elevation of the mine pre-winter starts in the first ten days of October and early spring starts during the last third March. Consequently, it was assumed the length of the hibernation period was between 160–180 days.

Habitat Selection

From November 1985 to March 1991, 27 inspections were made at the site. During the four winter

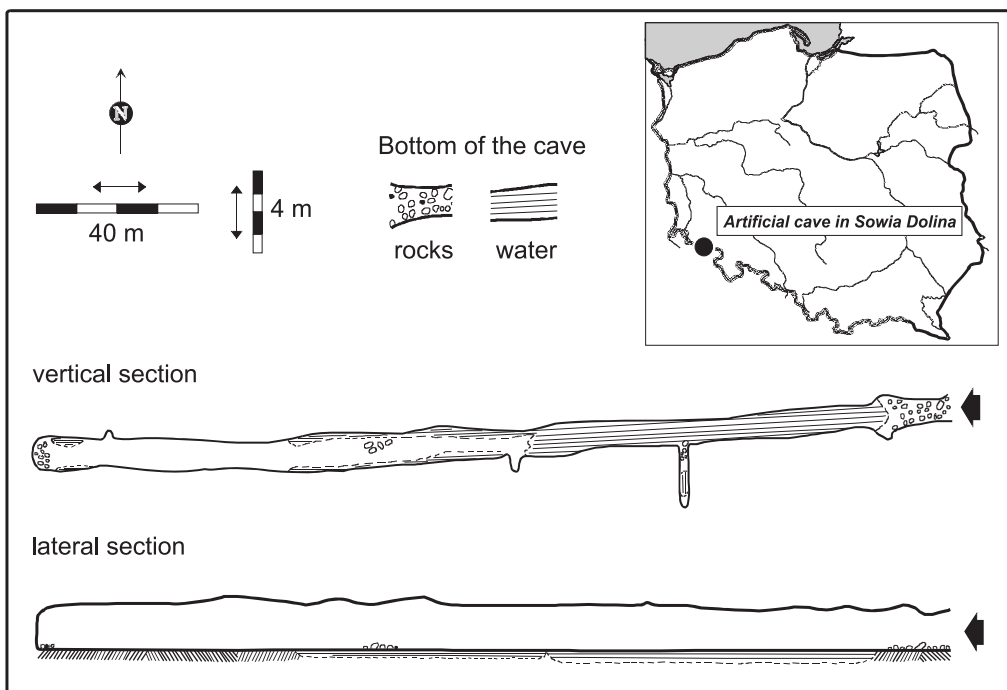


FIG. 1 The location and scheme of the mine in Sowia Dolina

seasons (1985/86–1988/89), when the majority of observations of habitat selection were undertaken, inspections were carried out every month, during the last two seasons (1989/90–1990/91), when mainly mass dynamics was studied, only twice, i.e. in November and in March.

The hibernation temperature (T_H ; $\pm 0.1^\circ\text{C}$) and relative humidity (RH; $\pm 1\%$) were measured in close vicinity to the hibernating bats by use of mercury thermometer and Assmann psychrometer. The airflow in the gallery was measured with accuracy to 0.04 ms^{-1} by use of katathermometer — special type of thermometer filled by liquid, heated to 38°C and losing heat proportionally to ambient temperature (recorded) and airflow speed (calculated). During inspections the height of the bat's hibernation place (H) and their distance (D) from the mine entrance were noted to an accuracy of 0.1 m. The type of hibernation position was coded as: 0 — individuals roosting on the wall; 1 — individuals roosting in drill-holes, referred as crevices in this paper). The frequency of bats hibernating in crevices (number of bats in crevices/total number of bats) was estimated. Hibernation in crevices and in places allowing for condensation could be a compensation mechanism allowing for increasing the relative humidity of the hibernation place. To determine the possible influence of hibernation in crevices and in places allowing for condensation of water vapour on bat's fur on sex and age-related humidity preferences, a comparison was made between the median RH, calculated separately for all individuals regardless of their hibernation place, and for bats roosting outside crevices and not covered by water drops. In the sample used to describe age related habitat selection the following sex and age classes were distinguished: adult females ($n = 101$), adult males ($n = 63$), sub-adult females ($n = 17$) and sub-adult males ($n = 24$).

Body Mass Dynamics

Bats were weighed immediately after capture using a Pesola balance ($\pm 0.1\text{ g}$). Individuals covered by water drops or having wet fur, as a result of body contact with wet walls, were not weighed. The differences in the mass of individuals between November and March were used to describe their mass losses during observation period. As it had been assumed the hibernation period finished in the last third of March, only the records of body mass made before March 20th were used. The length of right forearm ($\pm 0.05\text{ mm}$) of weighed bats was measured by use of a caliper. To investigate the relationship between hibernation temperature and condition of hibernating animals differing in size, a body condition index (BCI = body

mass/forearm length; after Speakman and Racey, 1986) was used. During four consecutive winter seasons 1987/88–1990/91 bats were banded using metal forearm rings (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn). The sample of individuals weighed in November and in March, for describing the sex and age related mass dynamics, consisted of adult females ($n = 45$), adult males ($n = 32$), sub-adult females ($n = 11$) and sub-adult males ($n = 19$). Due to the possible errors in over-winter mass losses associated with frequent inspections causing awakening of bats, those animals disturbed only twice for weighing, e.g., in November and in March, were selected. This sample consisted of 32 individually marked bats (10 adult ♀♀, 12 adult ♂♂, 5 sub-adult ♀♀ and 5 sub-adult ♂♂). The relationship between body condition in the second third of March and subsequent survival was determined using a sample consisting of 16 adult females and seven adult males whose survival was confirmed by ringing recovery records.

Statistical Analysis

Normality of distribution was tested by use of Shapiro-Wilk's W -test. For parameters having the distribution significantly different from normal ($P > 0.05$) the medians (χ) lower quartile (LQ) and upper quartile (UQ) were calculated, and the minimum and maximum values (range) were showed. Mann-Whitney U -test was used for comparisons between medians. Spearman correlation coefficient (r_s) was calculated to describe relationships between parameters that had distribution significantly different from normal. The differences of habitat parameters within and between periods selected within hibernation season were investigated by using Kruskal-Wallis ANOVA (K-W ANOVA). The effect of sex and age on body mass and mass losses were investigated by using two-way analysis of variance (ANOVA). The one-way analysis of variance was used for comparisons of differences in average body condition index of individuals hibernating in two thermal zones inside the mine. The Pearson (r) correlation coefficients and regression equations (least squares, model I) were calculated to investigate the relationships between body mass in November and in March and between body mass in November and total mass loss. For evaluation of the sex and age preferences for roosting in crevices, in places allowing for condensation of water vapour and for choosing hibernation places in the two thermal zones the $\chi^2 (2 \times 2)$ test was used. The logistic regression was used for testing the relationship between body condition in the second third of March and the survival measured by disappearance or return to

the mining shaft confirmed by ringing recovery records.

RESULTS

Periods Selected within Hibernation Season and Thermal Zones inside The Mine

As there was no significant difference in median hibernation temperature (T_H) recorded during December, January and February (Kruskal-Wallis ANOVA, $H = 0.46$, $d.f. = 2$, $n = 350$, $P > 0.05$), data from these months (referred as mid-hibernation period) were pooled. Significant differences were recorded between November and the mid-hibernation period ($H = 11.65$, $d.f. = 1$, $n = 497$, $P < 0.001$) and between that period and March ($H = 9.76$, $d.f. = 1$, $n = 468$, $P < 0.01$). Consequently, the following periods were distinguished within observation period: early-hibernation (November), mid-hibernation (December–February) and late-hibernation period (March). In these selected periods the mine was divided into two thermal zones; a cold zone where hibernation temperature was lower than the median value, and a warm zone with $T_H \geq \text{median}$. The numbers of adult and sub-adult individuals, their body conditions and habitat parameters in both selected zones were compared.

Hibernation Temperature

The median hibernation temperature of all individuals of *M. daubentonii* observed in the gallery during six consecutive winter seasons was 6.7°C (range $0.1\text{--}9.1^\circ\text{C}$, $LQ = 6.0$, $UQ = 7.1$, $n = 615$). The differences in median value calculated for the early-hibernation period (6.9°C , $LQ = 6.4$, $UQ = 7.2$, $n = 147$), the mid-hibernation period (6.7°C ; $LQ = 6.0$, $UQ = 7.0$, $n = 350$) and late-hibernation period (6.3°C , $LQ = 5.1$, $UQ = 7.0$, $n = 118$) were statistically significant

(see above). That result indicates a strong trend of declining hibernation temperature during the course of the hibernation season (Fig. 2). Due to the positive correlation between hibernation temperature and the distance from the mine entrance ($r_s = 0.73$, $n = 615$, $P < 0.001$) hibernating animals were able to choose the optimal hibernation temperature by shifting towards or moving away from the entrance of the gallery.

The selection of hibernation temperature was also possible by changing the height of hibernation place. Over the whole length of the gallery the correlation between these parameters was positive and significant ($r_s = 0.16$, $n = 412$, $P < 0.01$), but the highest value of correlation coefficient ($r_s = 0.27$, $n = 81$, $P < 0.05$) was observed in the frontal part of the gallery ranged from the entrance up to 59 m into the mine. The airflow in the gallery measured by use of katathermometer was slower than 0.04 ms^{-1} .

Distance from The Mine Entrance and Height of Hibernation Place

The overall median distance of hibernation place from the mine entrance was 99.5 m (range $1.0\text{--}223.5$, $LQ = 61.0$, $UQ = 153.5$, $n = 615$). The median values for

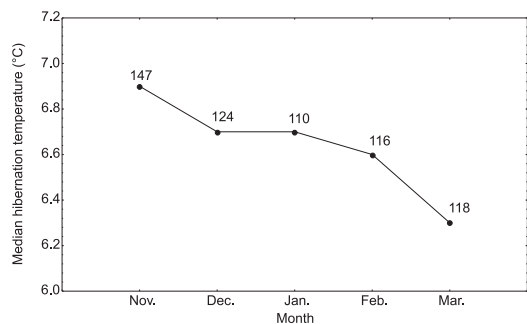


FIG 2. Median hibernation temperature of *M. daubentonii* in Sowia Dolina in consecutive months of hibernation period in winter seasons 1985/86–1990/91. Sample size is also provided

early-hibernation, the mid-hibernation and late-hibernation period were 127 m (LQ = 65.5, UQ = 173.5, $n = 147$), 105 m (LQ = 63.5, UQ = 158, $n = 350$) and 65 m (LQ = 44.5, UQ = 100.0, $n = 118$), respectively. There were no significant differences within the mid-hibernation period, however significant differences were observed between early-hibernation and the mid-hibernation period ($H = 4.60$, $d.f. = 1$, $n = 497$, $P < 0.05$), and between that period and late-hibernation ($H = 31.64$, $d.f. = 1$, $n = 468$, $P < 0.001$). In early-hibernation the hibernation places of *M. daubentonii* were situated significantly deeper inside the mine than later in hibernation season. In the mid-hibernation the distance of hibernation place from the mine entrance was stable, while a significant shift towards the entrance was observed in late-hibernation period (Fig. 3).

The overall median height of hibernation place was 1.8 m (range 0.3–2.5, LQ = 1.5, UQ = 2.0, $n = 412$). Throughout the gallery the correlation between height of hibernation place and the distance from the entrance was statistically significant ($r_s = -0.15$, $n = 412$, $P < 0.01$), but the highest value of correlation coefficient ($r_s = -0.37$, $n = 66$, $P < 0.01$) was found in the first 57 m of the mines length. For individuals roosting outside crevices this correlation was statistically insignificant in the rear part of the mine (≥ 57 m), while in the first

57 m of the its length was significant at $P < 0.001$ ($r_s = -0.64$, $n = 26$). This results indicate that the movements of bats toward the mine entrance were associated with an increase in the height of their hibernation place, which is the most probably the temperature effect, being greatest in individuals roosting outside crevices near the mine entrance.

Crevice Occupation

The average frequency of individuals hibernating in crevices, estimated for the whole observation period was 0.23 (141 individuals hibernated in crevices out of 615 observed). Significant differences were observed between early-hibernation period and the mid-hibernation ($H = 9.88$, $d.f. = 1$, $n = 497$, $P < 0.01$) and between that period and late-hibernation period ($H = 9.00$, $d.f. = 1$, $n = 468$, $P < 0.01$). This result indicates the strong trend of increasing frequency of individuals roosting in crevices during the course of the observation period (Fig. 4).

Relative Humidity

The median relative humidity of hibernation place of the individuals roosting outside crevices and not covered by condensed water vapour was 92% (range 66–98, LQ = 89, UQ = 94, $n = 366$). The median values calculated for early-hibernation, mid-hibernation and late-hibernation period were 91% (LQ = 83, UQ = 93, $n = 130$), 93% (LQ = 90, UQ = 94, $n = 177$) and 91% (LQ = 89, UQ = 93, $n = 59$), respectively. The difference between median relative humidity recorded in all individuals regardless of their hibernation place (93%, LQ = 90, UQ = 99, $n = 488$) and those roosting outside crevices (92%), excluding bats covered by water drops from compared groups, was significant (Mann-Whitney U -test, $Z = -6.29$, $P < 0.001$), but did not

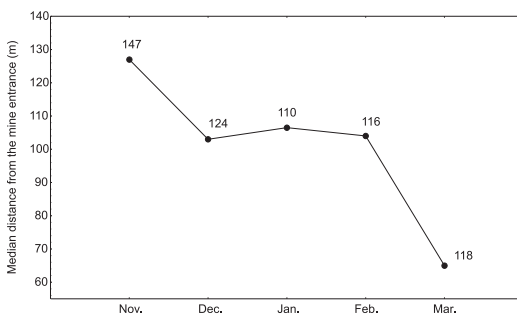


FIG. 3. Median distance of hibernating *M. daubentonii* from the entrance in Sowia Dolina in winter seasons 1985/86–1990/91. Sample size is also provided

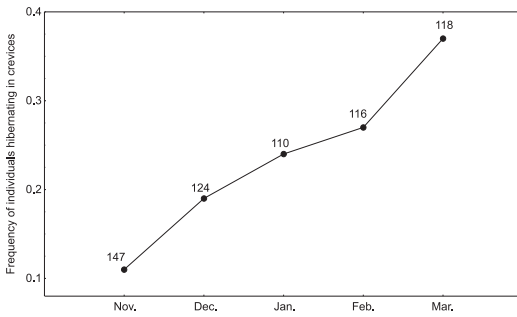


FIG. 4. Changes of frequency of *M. daubentonii* hibernating in crevices in Sowia Dolina in winter seasons 1985/86–1990/91. Sample size is also shown

exceed 1%. For individuals roosting outside crevices and not covered by water drops the relative humidity of their roosting site was negatively correlated with hibernation temperature ($r_s = -0.26$, $n = 366$, $P < 0.001$) and the height of hibernation place ($r_s = -0.61$, $n = 280$, $P < 0.001$). These relationships suggests that bats were able to choose the high relative humidity by roosting in low temperatures and/or by selecting hibernation places situated lower in the mine walls.

Sex and Age Related Habitat Selection

Between November and March the mean number of females per inspection was stable, in contrast the number of males declined between November and February (Fig. 5). Due to low average daily ambient climatic temperatures, total snow cover and the lack of any other underground sites in the vicinity of the gallery the migration to other winter shelters in the period between November and February seems unlikely. The most probable explanation of observed changes is that some males and sub-adult individuals hibernated in the rubble on the floor of the mine. The higher mean number of females than males recorded in April may indicate that males were leaving the mine earlier in spring (Fig. 5). Median hibernation temperature of *M. daubentonii* was the same in adult females,

adult males and in sub-adult females (6.5°C), but was much lower in sub-adult males (6.0°C). Difference between median hibernation temperature of adult (6.5°C , range 4.0 – 9.1 , $LQ = 6.2$, $UQ = 7.2$, $n = 164$) and sub-adult *M. daubentonii* (6.3°C , range 0.1 – 8.2 , $LQ = 5.8$, $UQ = 6.7$, $n = 41$) was statistically significant, while no significant difference between females and males was detected (Table 1).

Significant sex and age dependent differences in the height of hibernation place, probably caused by sex and age related thermal preferences, were recorded. Median relative humidity in hibernation place of individuals roosting outside crevices and not covered by water drops was significantly lower in females than in males, however taking into account all observations regardless of the place of hibernation, no sex differences were detected (Table 1). It is possible that for females *M. daubentonii* roosting in crevices and in places allowing for condensation could be a compensation mechanism allowing for increasing the relative humidity of their hibernation place. The sex and age preferences for hibernating in crevices failed statistical significance.

In early and mid-hibernation periods there was neither sex nor age preferences

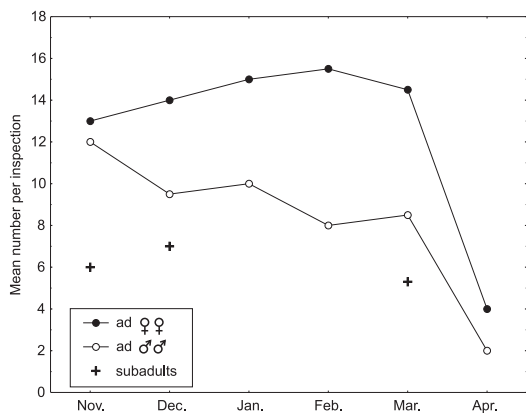


FIG. 5. Mean number of females and males of *M. daubentonii* per inspection in Sowia Dolina in winter seasons 1987/88–1990/91

TABLE 1. Sex and age related habitat selection in *M. daubentonii* in Sowia Dolina in winter seasons 1988/89–1990/91. Median (χ), sample size (in parentheses), lower quartile (LQ), upper quartile (UQ), and range are shown. Relative humidity I was calculated for all individuals, regardless of the place of their hibernation, relative humidity II – for bats roosting outside crevices and not covered by water drops. The differences were tested with the Mann-Whitney *U*-test

Parameter	Type of differences		Sex and age classes			
	Sex	Age	Adults		Sub-adults	
			♀ ♀	♂ ♂	♀ ♀	♂ ♂
Hibernation temperature (°C)	-1.57	-3.14**	6.5 (101) 6.3–7.2 4.3–9.1	6.5 (63) 6.2–7.3 4.0–8.7	6.5 (17) 6.3–6.6 0.1–7.4	6.0 (24) 5.4–6.7 4.5–8.2
Height of hibernation site (m)	-3.94***	-2.17*	1.9 (101) 1.7–2.0 0.8–2.3	1.7 (63) 1.4–2.0 0.4–2.3	1.8 (17) 1.6–2.1 1.5–2.3	1.55 (24) 1.35–1.8 0.5–2.2
Relative humidity I (%)	-1.28	-1.10	93.0 (101) 89–100 78–100	93.0 (63) 91–100 83–100	93.0 (17) 90–100 87–100	93.5 (24) 91–100 88–100
Relative humidity II (%)	-2.02*	-0.80	91.0 (68) 87.5–93.0 78–97	92.0 (43) 90–94 83–97	91.0 (11) 90–93 87–94	91.5 (14) 91–93 88–94

* — $P < 0.05$, ** — $P < 0.01$, *** — $P < 0.001$

for hibernation in the cold thermal zone in the mine. In the late-hibernation period there was no sex preference for hibernation

in the cold zone, but the strong age preference ($\chi^2 = 8.18$, $d.f. = 1$, $P < 0.01$) was recorded (Fig. 6). In March the average

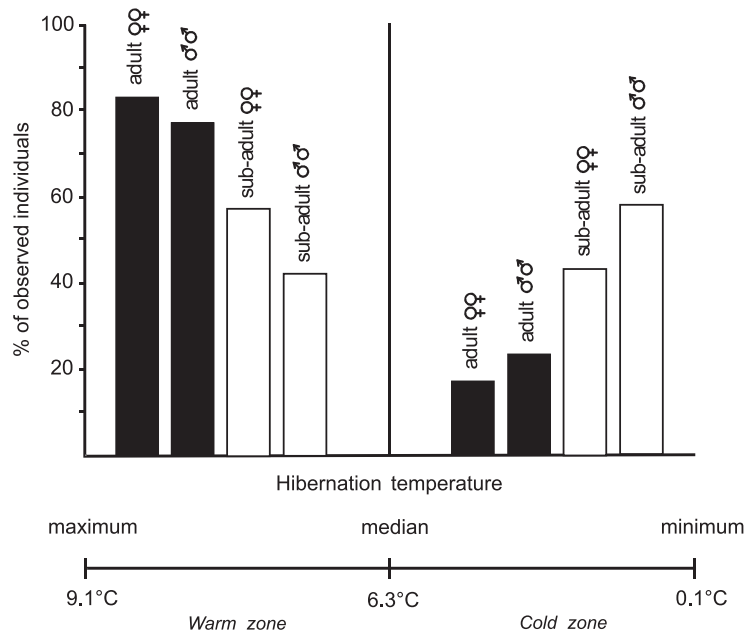


FIG. 6. Comparison of percentage of individuals from sex and age classes hibernated in March in the cold and warm thermal zones in Sowia Dolina in winter seasons 1988/89–1990/91. Median, minimal and maximal values of hibernation temperature are provided

body condition index of sub-adult bats ($\bar{x} = 0.21$, $SD = 0.012$, range 0.19–0.23, $n = 15$) was significantly lower than observed in adult individuals ($\bar{x} = 0.23$, $SD = 0.026$, range 0.17–0.27, $n = 38$; one-way ANOVA, $F = 6.56$, error $d.f. = 51$, $P < 0.05$). In this month the difference in median distance of hibernation place from the mine entrance between adult (74.5 m, range 15–215, $LQ = 64$, $UQ = 110$, $n = 58$) and sub-adult individuals (48.5 m, range 6–185, $LQ = 15$, $UQ = 65$, $n = 19$) was significant (Mann-Whitney U -test, $Z = -2.69$, $P < 0.01$; Fig. 7).

The difference in median distances from the entrance observed between age groups in March resulted in significantly higher median hibernation temperature of adult (6.6°C , $LQ = 6.3$, $UQ = 8.0$, $n = 58$) and sub-adult individuals (6.2°C , $LQ = 5.0$, $UQ = 6.6$, $n = 19$; $Z = -3.15$, $P < 0.01$). The reason for choosing lower hibernation temperature and places situated closer to the mine entrance observed in sub-adult bats in March, was probably in connection with searching for lower temperatures that could minimise their fat loss. In the part of the mine ranging from the entrance to 65 m in,

for example, to the upper quartile distance calculated for sub-adult bats, 79% sub-adult and 43% adult individuals were found. In March the statistically significant difference in average body condition index of individuals hibernating in warm ($\bar{x} = 0.23$, $SD = 0.025$, range 0.17–0.27, $n = 38$) and cold ($\bar{x} = 0.21$, $SD = 0.016$, range 0.18–0.23, $n = 15$) zone was found not only for sub-adult individuals but also across sex and age classes (one-way ANOVA, $F = 6.04$, error $d.f. = 51$, $P < 0.05$). Hibernation closer to the mine entrance made bats, first of all, sub-adult individuals more prone to predation than adult individuals roosting significantly deeper inside the gallery (Fig. 7).

A comparison of crevice occupation in the frontal (< 65 m) and rear (≥ 65 m) part of the mine showed bats were significantly more likely to be in crevices in the first 65 m of the site ($\chi^2 = 10.35$, $d.f. = 1$, $P < 0.01$). The explanation of the observed differences could be due to predation avoidance by bats hibernating near the mine entrance.

The differences in median height of hibernation place of adult (1.9 m) and sub-adult individuals (1.8 m) were statistically

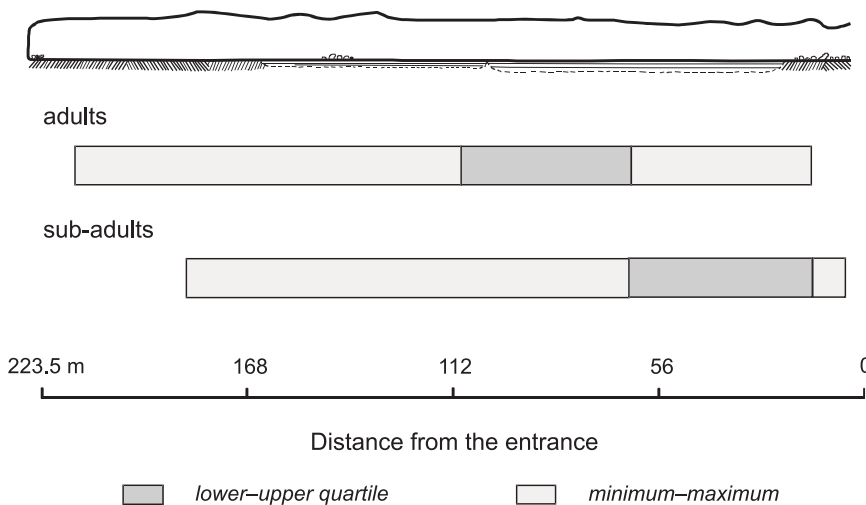


FIG. 7. Comparison of median distance of the hibernation place from the mine entrance of adult and sub-adult individuals of *M. daubentonii* hibernating in March in Sowia Dolina. Median values of the distance from the entrance; lower and upper quartiles for both age groups are shown

insignificant in March (Mann-Whitney *U*-test, $Z = -0.15$, $P > 0.05$), in contrast to the significant differences observed during the whole observation period (Table 1). The increased height of hibernation place of sub-adult individuals in March could be a result of flow of cold and dry air at floor level, or avoiding predators penetrating the frontal part of the mine by selecting roosting places situated higher on the mine walls.

Mass Dynamics

In November and in March in females and in adult individuals the average values were significantly larger than in males and sub-adult bats. The differences in mean values between sexes and age groups were not the same at the beginning and end of observation period. The difference between females and males was larger in March than in November, in contrast smaller differences between adult and sub-adult individuals were recorded at the end of observation period than at the beginning (Table 2). This result suggests that the hibernation strategy of females *M. daubentonii* is probably primarily oriented towards energy saving prior to reproduction, which occurs after the end of hibernation period. In contrast, males may sacrifice some of their mass to remain

active during mating period, which occurs during hibernation season. This could serve as an explanation for the increase in mass differences between females and males recorded at the end of observation period (Table 2). The smaller initial fat reserves of sub-adult individuals, observed in November, made their hibernation strategy primarily oriented towards energy saving ensuring survival, resulting in the smaller mass differences between adult and sub-adult bats observed in March (Table 2). The significant difference in average forearm length between females ($\bar{x} \pm SE = 39.0 \pm 0.13$, $n = 56$) and males (37.6 ± 0.12 , $n = 51$) was observed (two-way ANOVA, $F = 36.7$, error *d.f.* = 103, $P < 0.001$), while difference between adult and sub-adult individuals was statistically insignificant.

In individually marked bats disturbed twice for weighing, average values of total, relative and daily mass losses were age dependent and had significantly smaller average values in sub-adult bats than in adult individuals (Table 3). The large variations of all parameters of mass loss recorded either within selected sex and age classes or across classes indicate the large plasticity of fat loss in hibernating bats and their ability to regulate mass loss during hibernation in natural conditions. The standard deviations

TABLE 2. Relationships between sex and age, and body mass and body condition index (BCI) in *M. daubentonii* in Sowia Dolina in winter seasons 1988/89–1990/91 investigated by use of the two-way ANOVA. *F*-values, $\bar{x}$, SD, range and sample sizes in November and March, respectively (in parentheses), are shown

Parameter	Type of differences			Sex and age classes			
	Sex	Age	Sex & Age	Adults		Sub-adults	
				♀ ♀ (22/23)	♂ ♂ (17/15)	♀ ♀ (6/5)	♂ ♂ (9/10)
Body mass in November	10.1**	11.5**	2.3	11.4, 1.00 10.2–13.5	10.0, 1.10 8.4–12.2	9.9, 0.56 8.9–10.5	9.5, 0.53 8.5–10.0
BCI in November	4.6*	11.1**	1.4	0.29, 0.025 0.26–0.34	0.27, 0.028 0.23–0.33	0.26, 0.014 0.24–0.28	0.25, 0.012 0.23–0.26
Body mass in March	12.8***	4.6*	3.3	9.3, 0.93 7.8–10.9	7.9, 0.85 6.5–9.4	8.2, 0.60 7.2–8.7	7.8, 0.51 7.0–8.8
BCI in March	7.4**	4.7*	2.7	0.24, 0.023 0.19–0.27	0.21, 0.020 0.17–0.24	0.21, 0.013 0.19–0.22	0.21, 0.011 0.19–0.23

* — $P < 0.05$, ** — $P < 0.01$, *** — $P < 0.001$

of all mass loss parameters were greater in adult males than in adult females (Table 3). This result could indicate that fat loss of adult males could be more influenced by activity during mating period than in adult females.

Significant positive correlation between body mass in November and in March Fig. 8) indicates that *M. daubentonii* hibernating in Sowia Dolina did not forage in winter and their energy use was exclusively dependent on fat reserves accumulated prior to hibernation. Examination of that relationship within sex and age classes (Fig. 9) showed, that determination of body mass in March by body mass recorded in November was the strongest in sub-adult individuals ($r^2 = 0.83$), and the weakest in adult males ($r^2 = 0.74$). This result could indicate the presence of additional energy expenses in adult males possibly connected with activity during the mating period, which coincides with hibernation.

The significant positive relationship between the body mass in November and total mass loss found in individually marked individuals disturbed twice for weighing ($r = 0.59$, $d.f. = 30$, $P < 0.001$; $y = -0.92 + 0.291x$) suggests that bats with larger fat reserves in November had the greatest fat loss over the winter. This was probably due to them being more active, than bats that had smaller energy reserves in the beginning of

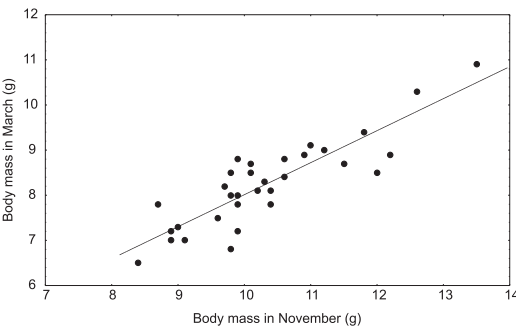


FIG. 8. Relationship between the body mass in November and in March in individually marked *M. daubentonii* disturbed twice for weighing (November and March). Mine in Sowia Dolina, winter seasons 1988/89–1990/91; $y = 0.92 + 0.709x$, $r = 0.87$, $d.f. = 30$, $P < 0.001$

winter. This result could indicate the possibility of existence of another factor, or group of factors, that could increase the mass loss and energy use in hibernating *M. daubentonii*. These could be activity during the mating period and/or energy costly defences against predators. In the bats disturbed twice for weighing there was no significant relationship between forearm length and total, relative and daily mass loss.

Relationship between Body Condition in March and Survival

The relationship between body condition in the second third of March and the

TABLE 3. Relationship between sex and age, and mass loss in individually marked *M. daubentonii* in Sowia Dolina in winter seasons 1988/89–1990/91 disturbed twice (in November and March) for weighing investigated by use of the two-way ANOVA. *F*-values, and $\bar{x}$, SD, range and sample sizes (in parentheses) are given

Parameter	Type of differences			Sex and age classes			
	Sex	Age	Sex & Age	Adults		Sub-adults	
				♀ ♀ (10)	♂ ♂ (12)	♀ ♀ (5)	♂ ♂ (5)
Absolute mass loss (g)	0.0	13.5**	0.0	2.3, 0.48 1.8–3.5	2.3, 0.63 0.9–3.3	1.6, 0.27 1.3–2.0	1.6, 0.32 1.1–1.9
Relative mass loss (%)	0.5	9.2**	0.0	20.9, 3.76 17.0–29.2	22.2, 5.18 10.3–30.6	16.1, 2.60 13.3–19.1	17.0, 3.91 11.1–21.3
Daily mass loss (mg day ⁻¹)	0.0	10.3**	0.1	20.1, 4.62 14.4–31.2	19.2, 5.71 8.0–29.5	13.6, 3.16 9.8–18.0	14.1, 3.47 8.3–17.0

** — $P < 0.01$

survival examined for adult females and males by use of logistic regression was positive but statistically insignificant. Basing on this result it can be suggested that survival rate depends closer from the trophic conditions after departure from hibernaculum than from the body mass at the end of hibernation.

DISCUSSION

Habitat Selection

The range of hibernation temperature (0.1–9.1°C) selected by *M. daubentonii* in Sowia Dolina (see Table 1) was very similar to those previously reported in old fortifications in Poznań, W Poland (0–10°C — Bogdanowicz and Urbańczyk, 1983). However, lower values were recorded in Estonia (-2°C — Masing, 1987) and in “Nietopek” Bat Reserve in W Poland (-8.4°C — Urbańczyk, 1991). In winter shelters having more than one entrance and a dynamic type

of microclimate, rapid declines in climatic temperature outside the hibernaculum, could result in bats temporarily staying in temperatures below the freezing point (author’s unpublished observations). It is not clear if the records of *M. daubentonii* hibernating at such low temperatures reflected inter-population differences or whether they were artefacts.

The range of temperatures preferred by bats in Sowia Dolina, defined in this study as the quartile range of hibernation temperature (LQ = 6.0, UQ = 7.1, $n = 615$), was narrower than that recorded by Gaisler (1970) and Urbańczyk (1991) (3–8 and 4–8°C, respectively). Gaisler (1970) made measurements over the same period as in this study (November–March), but data collection took place in different geographic regions of Europe. This may have resulted in broader range of observations. In the study by Urbańczyk (1991) data were gathered during September and April, possibly outside the true hibernation period.

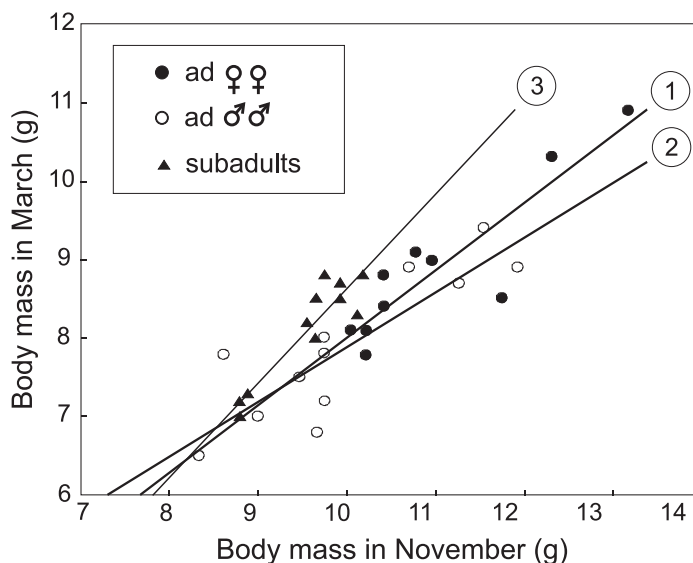


FIG. 9. Relationship between the body mass in November and in March in individually marked adult females, adult males and sub-adult individuals of *M. daubentonii* disturbed twice for weighing (November and March). Mine in Sowia Dolina, winter seasons 1988/89–1990/91; line 1 — adult ♀♀: $y = -0.26 + 0.814x$, $r = 0.90$, $d.f. = 8$, $P < 0.001$; line 2 — adult ♂♂: $y = 1.19 + 0.659x$, $r = 0.86$, $d.f. = 10$, $P < 0.001$, line 3 — sub-adults: $y = -2.92 + 1.137x$, $r = 0.91$, $d.f. = 8$, $P < 0.001$

Comparing the results of previous studies on mass dynamics of *M. daubentonii* during hibernation the large differences in estimates of mass losses are also recorded (Daan, 1973; Lesiński, 1986; Urbańczyk, 1991), while in Sowia Dolina no significant differences in average total, relative and daily mass losses between individually marked females and males were observed (Table 3). All previous were done on lowlands sites, where feeding of *M. daubentonii* in late autumn and in early spring would be expected. Individuals of *R. ferrumequinum* were able to adjust arousal frequency in accordance with insect availability by selecting proper hibernation temperature in early spring (Ransome, 1971). In regions differing in climate the differences in the composition of bat's diet could be expected, particular insect species could have different activity thresholds, which may result in different thermal preferences of bats in that period. However, the most important source of differences between previously studies of mass dynamics and thermal preferences of this species (Daan, 1973; Lesiński, 1986; Urbańczyk, 1991) was the inclusion of data from autumn (September–October) and early spring (March–April) into the analyses.

In the period of autumn fat accumulation in *Myotis lucifugus*, morphologically related to *M. daubentonii* (Findley, 1970) and inhabiting a similar trophic niche (Fenton, 1970), the increase of body mass of adult individuals was observed till the middle of September, while in sub-adult bats this increase continued until the middle of October (Kunz *et al.*, 1998). In “Nietope-rek” Bat Reserve (W Poland) in September and October and in the first ten days of March *M. daubentonii* were observed foraging and increasing their body weights (Kokurewicz, 1999). Falling into torpor in low ambient temperature in underground shelters is important for fat accumulation (Speakman and Rowland, 1999). Conse-

quently, several vespertilionid species can be observed in underground shelters in late summer and in autumn (e.g., Twente, 1955; Ransome, 1968; Ewing *et al.*, 1970; Lesiński, 1990; Kunz *et al.*, 1998). However, based on results of fat accumulation studies (Kunz *et al.*, 1998), the exact timing of the onset and end of hibernation must be known if mass losses and thermal preferences of bats inhabiting regions differing in climate are to be compared. Ransome (1990) states that hibernation begins when bats stop to wake up from daily torpor every day, and their life processes become to exclusively dependent on body reserves, and ends when bats start to forage every night in spring. This should allow for a precise comparison of all habitat parameters and mass losses in populations inhabiting different climatic regions. However, due to sensitivity of bats to non-tactile human disturbance (Thomas, 1995) it is difficult to estimate the onset and end of hibernation without equipment to automatically logging the bat's activity and required habitat parameters. As this equipment was not available during this study the duration of hibernation period was based on climatic data and on climatic periods of the year (i.e., pre-winter and early spring). Due to absence of any feeding activity in *M. daubentonii* at Sowia Dolina, in the period when the daily mean temperature had not exceeded +5°C, it is safe to conclude that hibernation of this species had started when climatic temperatures had dropped below 5°C.

Difference between median hibernation temperatures of adult (6.5°C) and sub-adult (6.3°C) *M. daubentonii* estimated for the whole hibernation period, however significant at $P < 0.01$ (Table 1), was very small. The highest difference was recorded in March (0.4°C), but this was still lower than estimates from “Nietope-rek” in the same month (0.7 °C — Jones and Kokurewicz, 1994). Due to the lack of

records of hibernation temperatures of sub-adult individuals in January and February (Fig. 5), it has to be stated that the age related difference in hibernation temperature were under-estimated during this study and did not reflect the real difference in thermal preferences of adult and sub-adult *M. daubentonii*. Energy costs of flight in *Plecotus auritus*, with the body mass similar to *M. daubentonii*, were estimated as $14.5 \times \text{BMR}$ (Racey and Speakman, 1987; Speakman and Racey, 1991), while the energy expenditure during one hour of flight, calculated for 7-g bat was an equivalent of 80 days of deep hibernation (Griffin, 1986). Due to mean January temperature of -2.9°C , the total snow cover and the lack of any other underground sites in the vicinity of the gallery, the migration of *M. daubentonii* hibernating in Sowia Dolina to the other winter shelters was unlikely. In terms of energy use and survival, the hibernating in the same cave all winter would be less energy costly and less risky than winter migration. It could be predicted that migrations between winter roosts are energetically possible only at the beginning and end of hibernation period, when opportunistic feeding could cover the high energy costs of flight. Some support for this prediction can be found in previous studies. In mines in Holland, situated in warm, maritime, climate most of migrations were observed in November. In the period between December and February the relative daily frequency of migration outside hibernation site in bats of the genus *Myotis* was 0.5% (Daan, 1973). The migrations between hibernation sites were also described as very rare in small vespertilionid species by Bogdanowicz and Urbańczyk (1983). The smaller fat reserves of sub-adult individuals recorded in November (Table 2), makes animals in their first year of life prone to premature fat depletion. Consequently, it is hypothesised that in January and February they were hibernating in

crevices between the rocks on the bottom of the mine. Hibernation in the rubble of the ground has only occasionally been noted in vespertilionid species (Roer, 1969; Bilke, 1978). Some support hypothesis comes from a study made in France, where hibernating bats were killed by chemicals. Twenty-one dead *M. daubentonii*, 306 *M. nattereri* and 53 *M. bechsteinii* were found, while the corresponding numbers recorded during an inspection made before the poisoning were 12, 1 and 0 respectively (Lemaire *et al.*, 1994). The significant positive relationships between the height of hibernation places and hibernation temperature suggests that sub-adult bats could probably find low temperature necessary for energy saving in the microclimate between the rocks on the mine floor. If this is so then the age related differences in hibernation temperature would probably be much larger than was actually reported.

The lack of significant sex differences in preferred temperature range (Table 1), confirms the results of previous studies. It was neither recorded in *Myotis myotis* (Harmata, 1973) nor in *M. daubentonii* (Jones and Kokurewicz, 1994), probably masked by age dependant thermal preferences.

The significant relationship between the hibernation temperature and the distance from the mine entrance indicates that hibernating animals were able to choose the optimal hibernation temperature by moving position within the hibernation site. Moving toward the entrance in course of hibernation season, called "internal migration" was previously described from mines in Holland (Kuipers and Daan, 1970). In *M. daubentonii* hibernating in Sowia Dolina the selection of hibernation temperature was also possible by changing the height of hibernation place. Changes of the distance from the entrance, or entrances, and the vertical movements inside the hibernation sites seems to be the most important ways of

selecting optimal hibernation temperature by hibernating bats. Both types of habitat selection probably allow them to actively control their energy use during natural hibernation by selecting temperatures that reduce the frequency of arousal from hibernation torpor. These mechanisms of choosing optimal hibernation temperature were previously suggested by Harmata (1973).

The lowest value of relative humidity in hibernation places of *M. daubentonii* was 70%, but in most cases hibernating individuals were observed in humidity > 85% (Bogdanowicz and Urbańczyk, 1983). In the mine in Sowia Dolina median relative humidity of *M. daubentonii* roosting outside crevices and not covered by water drops was 92%, with the preferred range from 89 to 94%, which is very close to previous estimates. The lack of significant differences in relative humidity between adult and sub-adult *M. daubentonii* (Table 1) could be an error caused by the lack of data from January and February. Due to strong significant negative correlation between relative humidity and the height of hibernation place it could be expected that sub-adult individuals hibernating probably between the rocks on the bottom of the mine were roosting in much higher relative humidity than those on the walls.

Females outnumbered males in crevices and were more often covered by condensed water vapour, but the sex preferences failed statistical insignificance. In future studies it may be interesting to investigate whether hibernating in crevices by females *M. daubentonii* is an important compensation mechanism allowing them to increase humidity of their hibernation place. Their hibernation places were situated significantly higher on the mine walls and, due to significant negative relationship between both parameters, had lower relative humidity than recorded for males (Table 1). Hibernation strategy of females of the studied

species is probably primarily oriented on energy saving before reproduction, occurring after the end of hibernation period. Due to that it is possible that females of this species could reduce the water loss by hibernating in crevices and could make the replenishing of the reduced water resources by drinking water condensed on their fur. That would allow them to save energy that would otherwise be spent during active searching for water in the hibernacula and on drinking in flight.

The other benefit of hibernation in crevices could be increasing insulation from external environment, especially from the airflow, could be important especially for sub-adult individuals having smaller energy reserves. The lack of significant age preference to hibernation in crevices observed in Sowia Dolina could be the result of slow air movement in the gallery, not exceeding 0.04 ms^{-1} . In artificial caves in Holland the airflow ranged from 0.1 to 0.4 ms^{-1} (Daan, 1973), while in "Nietoperek", the underground fortification system with many entrances, ranges from 0.0 to 3.1 ms^{-1} (Kokurewicz, 1999). The significant preference of sub-adult individuals to hibernation in crevices observed in "Nietoperek" (Kokurewicz, 1999) and its lack in Sowia Dolina, could be the result of avoiding the fast air movement, which may increase energy costs of arousals.

Body Mass Dynamics

No mass increase was observed in *M. daubentonii* wintering in Sowia Dolina and the relationship between body mass at the beginning and end of observation period was positive and linear (Fig. 8), as predicted by Speakman and Racey (1989) in their laboratory study. This is probably resulted by the lack of winter feeding in the severe climate of Karkonosze Mts. This observation also confirms Ransome's (1985, 1990)

hypothesis for the homeostatic control of body food reserves, suggesting winter feeding as the most important way of active control of energy balance in hibernating bats.

It has been hypothesised that bats are able to regulate their mass loss during hibernation not only by energetically effective feeding in warm winter spells (Ransome, 1968, 1985, 1990; Avery, 1985; Brigham, 1987; Whitaker *et al.*, 1997), but also by appropriate habitat selection. The large variation of all parameters of mass loss recorded either within selected sex and age classes or across classes (Table 3) and the significant positive relationship between the body mass in November and total mass loss seems to confirm this prediction. *Myotis daubentonii* hibernating in Sowia Dolina, actively search for low hibernation temperature and for high relative humidity of hibernation places. This must lead to a reduction in their activity, especially the frequency of spontaneous arousals, and, in consequence, would reduce their mass losses during hibernation. The ability to actively control energy expenditure was most clearly illustrated in sub-adult individuals, having significantly smaller energy reserves at the beginning of hibernation period. With appropriate habitat selection these bats were able to obtain significantly smaller average mass losses than adult individuals and were able to slow down the difference in average body mass observed between the age groups at the beginning of observation period (Tables 2 and 3). These results confirm the second prediction made during this study, assuming that bats in their first year of life would have significantly lower over-winter mass losses than adult individuals.

The decline of arousal frequency as the way of controlling energy budget by bats hibernating in severe climatic conditions was predicted by Thomas *et al.* (1990b) based on the estimate of high energy costs of arousals. In several bat species the arousal

frequency was lower in low ambient temperature (Ransome, 1971, 1990; Daan, 1973; Twente *et al.*, 1985; Harmata, 1987; Harrije, 1994). In *M. lucifugus* the decline of hibernation temperature by 1°C, in the range from 9 to 12°C, resulted in the extension of uninterrupted torpor bout on average 3 days (Twente and Brack, 1985). In *M. daubentonii* mass loss was smaller in high relative humidity (Daan, 1973). Based on those results it is predicted that sub-adult individuals, which hibernated at lower temperature (Table 1), and possibly also in higher relative humidity, than adult bats, and would consequently have significantly lower arousal frequencies. This assumption needs confirmation during a study using of thermosensitive radio transmitters.

The significant positive relationship between body mass in November and total mass loss suggests that bats that had larger fat reserves in November were probably more active and were using more energy, than bats that had smaller energy reserves at the beginning of winter. This could indicate the existence of another factor, or group of factors, that could increase the mass loss and energy use in hibernating *M. daubentonii*. These could be: (1) mating behaviour and (2) energy costly defence against predators.

Mass decline associated to mating behaviour was observed in male *Pipistrellus pipistrellus* in southern Sweden (Lundberg and Gerell, 1986) and in *Plecotus auritus* in the United Kingdom (Entwistle *et al.*, 1998). In *M. daubentonii* spermatogenesis begins in the middle of August and lasts till the middle of September (Kokurewicz and Bartmańska, 1992). Mating appears to be random, unstructured and promiscuous (Bogdanowicz, 1994). In "Nietoperek" ca. 82% of copulation were observed in September–November, ca. 6% in January–February and ca. 2% in March (Urbańczyk, 1991). In a population near the northern

border of species range, the frequency of females that have been inseminated during hibernation was 17% in September and October and reached 100% in late April (Strelkov, 1962). These results indicate that in *M. daubentonii* copulation occur during the whole hibernation period and were already reported as the cause of rapid mass decline in individuals of this species in September–November period (Daan, 1973; Lesiński, 1986; Průcha and Hanzal, 1989; Urbańczyk, 1991; Kokurewicz, 1999). In bat species having promiscuous mating systems the significant positive relationship between the number of females in winter roosts and energy expenses of males can be expected. This assumption also implies that the energy expenditure of males *M. daubentonii*, and possibly other bat species, is influenced by density of hibernating populations. This problem requires comparative study in winter colonies differing in size located in the same climatic regions.

In March *M. daubentonii* in poor body condition, predominantly sub-adult individuals (Figs. 6 and 7), were choosing low hibernation temperature by selecting hibernation places situated near the mine entrance. There could be, at least, two reasons for hibernating near the entrance to the gallery: (1) to minimise the metabolic rate by hibernating in low ambient temperature and higher relative humidity and (2) to synchronise the arousals frequency with the temperature outside hibernation site, to get information about possibility of foraging. It was shown that individuals of *R. ferrumequinum* over-wintering in natural conditions were able to detect temperature fluctuations outside the hibernation sites by choosing the roosting positions in parts of hibernation sites where temperature changes were correlated with changes of temperature outside hibernaculum (Ransome, 1971; Park *et al.*, 1999; Park *et al.*, 2000). Thus *M. daubentonii* in significantly

lower body condition were probably hibernating closer to the mine entrance for both, basically energetic, reasons. However, it has to be considered why the other bats were not benefiting from choosing the places that would allow them to decrease their metabolic rate and allow for the detection of warm weather with the possibility of successful foraging. Choosing roosting places situated close to the mine entrance could be profitable especially for adult females starting gestation just after completing hibernation. Larger fat reserves in the end of hibernation would allow females to implantation early and start gestation earlier in the year, resulting in earlier parturition and potentially increased survival of the offspring (acc. to Ransome, 1990). However, in March only 17% adult females hibernated near the entrance to the mine at Sowia Dolina (Fig. 6). One possible explanation for this is that it due to a strategy of predation avoidance used by bats not endangered by starvation.

Predation of hibernating *M. daubentonii* by *Martes foina* has been recorded in Holland (Bekker, 1988) and in “Nietopekrek” in W Poland (Urbańczyk, 1981; Romanowski and Lesiński, 1988; Tryjanowski, 1997; R. Paszkiewicz and R. Szkudlarek, in litt.; author’s unpubl. data). The percentage of bats in the diet of martens in the Polish locality ranged from 6.2% (Tryjanowski, 1997) to 76% (R. Paszkiewicz and R. Szkudlarek, in litt.) of eaten biomass, or up to 81.3% of dry mass of the collected pellets (Romanowski and Lesiński, 1988). It is possible that, especially during severe winters, bats could be the most important element of the diet of this predator. *Myotis daubentonii* could be also occasionally eaten by *Apodemus sylvaticus*, species from the family Gliridae, and *Sorex araneus* (reviewed by Bogdanowicz, 1994). The observations recently made in Poland evidenced that *M. daubentonii* could be eaten by *Vulpes vulpes* penetrating the hibernation site up to 80 m

from the entrance (K. Kasprzyk and M. Tomaszewski, in litt.). Preying upon hibernating bats by great and blue tits (*Parus major* and *P. caeruleus*) during the exceptionally cold winter 1996, when mean night temperatures from early January to early March ranged from -10 to -15°C, was reported from Poland (Radzicki *et al.*, 1999). Tits were penetrating the cave up to 10 m from the entrance (Radzicki *et al.*, 1999) and it could be expected that they are able to prey upon bats hibernating in shallow crevices.

Some behaviours that may be related to predation defence were observed in *M. daubentonii* in Sowie Dolina. There could be: (1) significant preference to hibernation in crevices in frontal part of the mine, (2) significant differences in median distance of the hibernation place from the mine entrance of bats in good and poor body condition, and (3) the increased height of hibernation place of individuals, mainly sub-adult, hibernating in March near the mine entrance. In individuals roosting outside crevices the correlation between height of hibernation place and the distance from the entrance was highly significant in the first 57 m of gallery, while in the rear part of the mine (≥ 57 m) was statistically insignificant. The light intensity was not measured in the mine, but it seems to be possible that in frontal part of the mine it was high enough for predators to detect hibernating bats. The possible reaction of bats to increased light intensity could be the increase of the height of their hibernation place, which could explain the spatial differences in the examined relationship. The highly statistically significant difference between median height of hibernation place of females, having larger total body reserves, and males, having smaller fat deposits (see Tables 1 and 2), could be also associated with defence against predators. The value of the sex ratio in some populations of *M. daubentonii*, indicates the predominance of

females (Bezem *et al.*, 1960, Lesiński 1986, author's unpubl. data) and could be result in a higher predation pressure on male bats, especially those in their first year of life, hibernating lower on the mine walls and predominating in frontal part of hibernation sites (Table 1, Fig. 6).

In summary, it is postulated that an energy costly strategy of predation avoidance exists in hibernating populations of *M. daubentonii*. The predation pressure seems to act on population through energy budgets of hibernating individuals, and seems to concern mainly sub-adult animals who have smaller energy reserves. It is postulated that the significant relationship between the total fat loss and body mass in November, observed in adult males *M. daubentonii* is the result of the additive energetic costs of mating behaviour and energy costly defence against predators.

Survival and Effect of Disturbance

In years 1964–1987, in the region where this study was made, the increase of the population of *M. daubentonii* was estimated to reach ca. 860% (Kokurewicz, 1995). This population growth may reflect the increased availability of insect prey, notably midges (Diptera: Chironomidae), caused by eutrophication processes (Kokurewicz, 1995; Racey *et al.*, 1998). In that context the decline in the maximal number of bats observed in the mine exceeding 19% is most probably the real effect of disturbance.

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LITERATURE CITED

- ANTHONY, E. L. P. 1988. Age determination in bats. Pp. 47–58, in *Ecological and behavioral methods for the study of bats* (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington D.C., 533 pp.
- AVERY, M. I. 1985. Winter activity of pipistrelle bats. *Journal of Animal Ecology*, 54: 721–738.
- BAGROWSKA-URBAŃCZYK, E., and Z. URBAŃCZYK. 1983. Structure and dynamics of a winter colony of bats. *Acta Theriologica*, 28: 183–196.
- BEKKER, J. P. 1988. Watervleermuis *Myotis daubentonii* als prooi van steenmarter *Martes foina* in ondergrondse mergelgroeven. *Lutra*, 31: 82–85.
- BEZEM, J. J., J. W. SLUITER, and P. F. van HEERDT. 1960. Population statistics of five species of the genus *Myotis* and one of the genus *Rhinolophus*, hibernating in the caves of S. Limburg. *Archives Néerlandaises de Zoologie*, 13: 511–539.
- BILKE, P. (1978): Winterquartier von *Myotis myotis* im Bodengeröll. *Nyctalus* (N.F.), 2: 74 [not seen, cited after NAGEL and NAGEL, 1991].
- BOGDANOWICZ, W. 1990. Geographic variation and taxonomy of Daubenton's bat, *Myotis daubentonii*, in Europe. *Journal of Mammalogy*, 71: 205–218.
- BOGDANOWICZ, W. 1992. Sexual dimorphism in size of the skull in European *Myotis daubentonii* (Mammalia: Chiroptera). Pp. 17–25, in *Prague studies in mammalogy* (I. HORÁČEK and V. VOHRÁLIK, eds.). Charles University Press, Praha, xxi + 1–245.
- BOGDANOWICZ, W. 1994. *Myotis daubentonii*. *Mammalian Species*, 475: 1–9.
- BOGDANOWICZ, W., and Z. URBAŃCZYK. 1983. Some ecological aspects of bats hibernating in city of Poznań. *Acta Theriologica*, 28: 371–385.
- BRIGHT, M. R. 1987. The significance of winter activity by the big brown bat (*Eptesicus fuscus*): the influence of energy reserves. *Canadian Journal of Zoology*, 65: 1240–1242.
- BURBANK, R. C., and J. Z. YOUNG. 1934. Temperature changes and winter sleep of bats. *Journal of Physiology*, 82: 459–467.
- BURNETT, C. D. 1983. Geographic and secondary sexual variation in the morphology of *Eptesicus fuscus*. *Annals of Carnegie Museum*, 52: 139–162.
- BURNETT, C. D., and T. H. KUNZ. 1982. Growth rates and age estimation in *Eptesicus fuscus* and comparison with *Myotis lucifugus*. *Journal of Mammalogy*, 63: 33–41.
- DAAN, S. 1973. Activity during natural hibernation in three species of vespertilionid bats. *Netherlands Journal of Zoology*, 23: 1–71.
- DAVIS, W. H., and H. B. HITCHCOCK. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. *Journal of Mammalogy*, 46: 296–313.
- ENTWISTLE, A. C., P. A. RACEY, and J. R. SPEAKMAN. 1998. The reproductive cycle and determination of sexual maturity in male brown long-eared bats, *Plecotus auritus* (Chiroptera: Vespertilionidae). *Journal of Zoology* (London), 244: 1–63.
- EWING, W. G., STUDIER, E. H., and M. J. O'FARRELL. (1970). Autumn fat deposition and gross body composition in three species of *Myotis*. *Comparative Biochemistry and Physiology*, 36: 119–129.
- FABISZEWSKI, J. 1985. Szata roślinna. Pp. 191–235, in *Karkonosze Polskie* (A. JAHN, ed.). Polska Akademia Nauk, Wrocław, 566 pp.
- FENTON, M. B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. *Life Sciences Contributions Royal Ontario Museum*, 77: 1–34.
- FINDLEY, J. S. 1970. Phenetic relationships in the genus *Myotis*. *Bijdragen tot de Dierkunde*, 40: 26–29.
- GAISLER, J. 1966. A tentative ecological classification of colonies of the European bats. *Lynx*, 6: 35–39.
- GAISLER, J. 1970. Remarks on the thermopreferendum of Palearctic bats in their natural habitats. *Bijdragen tot de Dierkunde*, 40: 33–36.
- GEIGER, H., M. LECHNERT, and C. KALLASCH. 1996. Zur Alterseinstufung von Wasserfledermäusen (*Myotis daubentonii*) mit Hilfe des Unterlippenflecks ('chin-spot'). *Nyctalus* (N.F.), 6: 23–28.
- GRIFFIN, D. R. 1986. *Listening in the dark*. Cornell University Press, Ithaca, xv + 415 pp.
- HARMATA, W. 1973. The thermopreferendum of some species of bats (Chiroptera) in natural conditions. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego*, 332, *Prace Zoologiczne*, 19: 127–141.
- HARMATA, W. 1985. The length of awakening time from hibernation of three species of bats. *Acta Theriologica*, 30: 321–323.
- HARMATA, W. 1987. The frequency of winter sleep interruptions in two species of bats hibernating

- in limestone tunnels. *Acta Theriologica*, 32: 331–332.
- HARRJE, C. 1994. Etho-ökologische Untersuchung der ganzjährigen Aktivität von Wasserfledermäusen (*Myotis daubentoni* Kuhl, 1819) am Winterquartier. *Mitteilungen Naturwissenschaftlichen Gesellschaft Schaffhausen*, 39: 15–52.
- HERREID, C. F. 1963. Survival of a migratory bat at different temperatures. *Journal of Mammalogy*, 44: 431–433.
- HOCK, R. J. 1951. The metabolic rates and body temperatures of bats. *Biological Bulletin*, 101: 289–299.
- JOHNSON, S. A., V. BRACK, and R. E. ROLLEY. 1998. Overwinter weight loss of Indiana bats (*Myotis sodalis*) from hibernacula subject to human visitation. *The American Midland Naturalist*, 139: 255–261.
- JONES, G., and T. KOKUREWICZ. 1994. Sex and age variation in echolocation calls and flight morphology of Daubenton's bats *Myotis daubentonii*. *Mammalia*, 58: 41–50.
- KOKUREWICZ, T. 1990. Hibernation of two age classes of *Myotis daubentoni* (Kuhl, 1819) in the nature reserve "Nietoperek" (W Poland) and effect of microclimate on cluster formation. *Bat Research News*, 31: 43.
- KOKUREWICZ, T. 1991. Materiały do chiropterofauny Polskich Karkonoszy. *Prace Karkonoskiego Towarzystwa Naukowego*, 53: 104–116.
- KOKUREWICZ, T. 1995. Increased population of Daubenton's bat *Myotis daubentoni* (Kuhl, 1819) (Chiroptera: Vespertilionidae) in Poland. *Myotis*, 32–33: 155–161.
- KOKUREWICZ, T. 1999. Hibernation ecology of Daubenton's bat *Myotis daubentonii* (Kuhl, 1817). Ph.D. Thesis, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, 141 pp.
- KOKUREWICZ, T., and J. BARTMAŃSKA. 1992. Early sexual maturity in males of Daubenton's bat (*Myotis daubentoni* (Kuhl, 1819) (Chiroptera: Vespertilionidae); field observations and histological studies on the genitalia. *Myotis*, 30: 95–108.
- KOKUREWICZ, T., and N. KOVÁTS. 1989. Interpopulation differences in thermopreferendum of the lesser horseshoe bat, *Rhinolophus hipposideros* Bechstein, 1800 (Chiroptera: Rhinolophidae) in selected areas of Poland and Hungary. *Myotis*, 27: 131–137.
- KONDRACKI, J. 1981. *Geografia fizyczna Polski*. PWN, Warszawa, 464 pp.
- KRZANOWSKI, A. 1961. Weight dynamics of bats wintering in the cave at Puławy (Poland). *Acta Theriologica*, 4: 249–264.
- KUIPERS, B., and S. DAAN. 1970. "Internal migration" of hibernating bats: response to seasonal variation in cave microclimate. *Bijdragen tot de Dierkunde*, 40: 51–55.
- KUNZ, T. H. 1982. Roosting ecology. Pp. 1–46, in *Ecology of bats* (T. H. KUNZ, ed.). Plenum Press, New York, 425 pp.
- KUNZ, T. H., J. A. WRAZEN, and C. D. BURNETT. 1998. Changes in body mass and fat reserves in pre-hibernating little brown bat (*Myotis lucifugus*). *Ecoscience*, 5: 8–17.
- KURSKOV, A. N. 1981. *Rukokrylye Belorussii*. Nauka i Technika, Minsk, 136 pp.
- LEMAIRE, M., J. J. CHAUT, and L. ARTHUR. 1994. 400 cadavres dans un site d'hibernation pollue. Pp. 129–133, in *Actes des Cinquièmes Rencontres Nationales 'Chauves-Souris'*. Muséum d'Histoire de Bourges et Société Française pour l'Étude et la Protection des Mammifères, Bourges.
- LESIŃSKI, G. 1986. Ecology of bats hibernating underground in Central Poland. *Acta Theriologica*, 31: 507–521.
- LESIŃSKI, G. 1990. Changes in numbers of *Myotis daubentoni* (Kuhl, 1819) in autumn shelters and the effect of disturbance. *Acta Theriologica*, 35: 364–368.
- LUNDBERG, K., and R. GERELL. 1986. Territorial advertisement and mate attraction in the bat *Pipistrellus pipistrellus*. *Ethology*, 71: 115–124.
- MASING, M. 1987. Zimnee peredviženie rukokrylych meždu ubežiščami. *Učonye Zapiski Tartuskogo Gosudarstvennogo Universiteta* 769, *Trudy po Zoologii*, 15: 41–60 [not seen, cited after BOGDANOWICZ, 1994].
- MENAB, B. K. 1974. The behavior of temperate cave bats in a subtropical environment. *Ecology*, 55: 943–958.
- NAGEL, A., and R. NAGEL. 1991. How do bats choose optimal temperatures for hibernation? *Comparative Biochemistry and Physiology*, 99 A: 323–326.
- NYHOLM, E. S. 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *Myotis daubentoni* (Leisl.) (Chiroptera). *Annales Zoologici Fennici*, 2: 77–123.
- PARK, K. J., G. JONES, R. D. RANSOME. 1999. Winter activity of a population of greater horseshoe bats (*Rhinolophus ferrumequinum*). *Journal of Zoology* (London), 248: 419–427.
- PARK, K. J., G. JONES, R. D. RANSOME. 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Functional Ecology*, 14: 580–588.
- PETIT, E. 1998. Population structure and post-glacial history of the noctule bat *Nyctalus noctula*

- (Chiroptera, Mammalia). Ph.D. Thesis, Friedrich-Alexander-Universität Erlangen-Nürnberg, 105 pp.
- PIASECKI, J. 1997. Thermal periods of the year (1951–80). Map no. 48, in *The atlas of Silesia*. Wrocław University, Wrocław, 117 maps.
- PRŮCHA, M., and V. HANZAL. 1989. Some aspects of hibernation of bats wintering in the Bohemian Karst (central Bohemia, Czechoslovakia). *Acta Universitatis Carolinae, Biologica*, 33: 315–333.
- RACEY, P. A., and J. R. SPEAKMAN. 1987. The energy costs of pregnancy and lactation in heterothermal bats. *Symposia of the Zoological Society of London*, 57: 107–125.
- RACEY, P. A., S. M. SWIFT, J. RYDELL, and L. BRODIE. 1998. Bats and insects over two Scottish rivers with contrasting nitrate status. *Animal Conservation*, 1: 195–202.
- RADZICKI, G., HEJDUK, J., and J. BAŃBURA. 1999. Tits (*Parus major* and *Parus caeruleus*) preying upon hibernating bats. *Ornis Fennica*, 76: 93–94.
- RANSOME, R. D. 1968. The distribution of the greater horseshoe bat, *Rhinolophus ferrumequinum*, during hibernation, in relation to environmental factors. *Journal of Zoology (London)*, 154: 77–112.
- RANSOME, R. D. 1971. The effect of ambient temperature on the arousal frequency of the hibernating Greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. *Journal of Zoology (London)*, 164: 353–371.
- RANSOME, R. D. 1985. Homeostatic control of body food reserves in hibernating greater horseshoe bats. *Bat Research News*, 26: 70.
- RANSOME, R. D. 1990. The natural history of hibernating bats. Christopher Helm, London, xxi + 235 pp.
- RICHARDSON, P. W. 1994. A new method of distinguishing Daubenton's bats (*Myotis daubentonii*) up to one year old from adults. *Journal of Zoology (London)*, 223: 307–344.
- ROER, H. 1969. Zur Ernährungsbiologie von *Plecotus auritus* (L.) (Chiroptera). *Bonner Zoologische Beiträge*, 20: 378–383.
- ROMANOWSKI, J., and G. LESIŃSKI. 1988. Kuny polują na nietoperze. *Wszechświat*, 89 (9): 210.
- RYBERG, O. 1947. *Studies on bats and bat parasites*. Bokförlaget Svensk Natur, Stockholm, 330 pp.
- SPEAKMAN, J. R. 1991. Daubenton's bat *Myotis daubentonii*. Pp. 108–111, in *The handbook of British mammals* (G. B. CORBET and S. HARRIS, eds.). Blackwell Scientific Publications, Oxford, 588 pp.
- SPEAKMAN, J. R. 1997. Factors influencing the daily energy expenditure of small mammals. *Proceedings of Nutrition Society*, 56: 1119–1136.
- SPEAKMAN, J. R., and P. A. RACEY. 1986. The influence of body condition on sexual development of male brown long-eared bats (*Plecotus auritus*) in the wild. *Journal of Zoology (London)*, 210: 515–525.
- SPEAKMAN, J. R., and P. A. RACEY. 1989. Hibernation ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. *Journal of Animal Ecology*, 58: 797–813.
- SPEAKMAN, J. R., and P. A. RACEY. 1991. No cost of echolocation for bats in flight. *Nature*, 350 (6317): 421–423.
- SPEAKMAN, J. R., and A. ROWLAND. 1999. Preparing for inactivity: how insectivorous bats deposit a fat store for hibernation. *Proceedings of Nutrition Society*, 58: 123–131.
- SPEAKMAN, J. R., WEBB, P. I., and P. A. RACEY. 1991. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology*, 28: 1087–1104.
- STEBBINGS, R. E. 1966. A population study of bats of the genus *Plecotus*. *Journal of Zoology (London)*, 150: 53–75.
- STEPHENS, D. W. 1981. Logic of risk-sensitive foraging preferences. *Animal Behaviour*, 29: 628–629.
- STRELKOV, P. P. 1962. The peculiarities of reproduction in bats (Vespertilionidae) near the northern border of their distribution. Pp. 306–311, in *Proceedings of the International Symposium on Methods of Mammalogical Investigation*, Brno, Czechoslovakia, 1960 (J. KRATOCHVÍL and J. PELIKÁN, eds.). Československá Akademie Věd, Praha, 383 pp. [not seen, cited after BOGDANOWICZ, 1994].
- STRELKOV, P. P. 1969. Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. *Acta Zoologica Cracoviensia*, 14: 393–439.
- THOMAS, D. W. 1995. Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy*, 76: 940–946.
- THOMAS, D. W. and F. GEISER. 1997. Periodic arousals in hibernating mammals: is evaporative water loss involved? *Functional Ecology*, 11: 585–591.
- THOMAS, D. W., D. CLOUTIER, and D. GAGNE. 1990a. Arrhythmic breathing, apnea and non-steady state oxygen uptake in hibernating little brown bats (*Myotis lucifugus*). *Journal of Experimental Biology*, 149: 395–406.
- THOMAS, D. W., M. DORAIS, and J. M. BERGERON. 1990b. Winter energy budgets and cost of

- arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy*, 71: 475–479.
- TRYJANOWSKI, P. 1997. Food of the stone marten (*Martes foina*) in Nietoperek Bat Reserve. *Zeitschrift für Säugetierkunde*, 62: 318–320.
- TWENTE, J. W. 1955. Some aspects of habitat selection and other behaviour of cavern dwelling bats. *Ecology*, 36: 706–732.
- TWENTE, J. W., and V. BRACK. 1985. The duration of the period of hibernation of three species of vespertilionid bats. I. Field studies. *Canadian Journal of Zoology*, 63: 2952–2954.
- TWENTE, J. W., J. TWENTE, and V. BRACK. 1985. The duration of the period of hibernation of three species of vespertilionid bats. II. Laboratory studies. *Canadian Journal of Zoology*, 63: 2955–2961.
- URBAŃCZYK, Z. 1981. Fledermäuse (Chiroptera) in der Nahrung des Marders (*Martes* sp.). *Säugetierkundliche Mitteilungen*, 29: 77–79.
- URBAŃCZYK, Z. 1991. Hibernation of *Myotis daubentoni* and *Barbastella barbastellus* in Nietoperek bat reserve. *Myotis*, 29: 115–120.
- WEBB, P. I., J. R. SPEAKMAN, and P. A. RACEY. 1996. How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology*, 74: 761–765.
- WHITAKER, J. O., JR., R. K. ROSE, and T. M. PADGETT. 1997. Food of the red bat *Lasiurus borealis* in winter in the great dismal swamp, North Carolina and Virginia. *The American Midland Naturalist*, 137: 408–411.
- WILLIAMS, C. B. 1939. An analysis of four years captures of insects in a light trap. Part 1. *Transactions of the Royal Entomological Society of London*, 89: 79–132 [not seen, cited after RANSOME, 1968].

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