

Swarming of *Myotis mystacinus* and other bat species at high elevation in the Tatra Mountains, southern Poland

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This paper reports a study of the visitation of bats to Great Litworowa Cave (1,907 m a.s.l., Tatra Mts., southern Poland) during summer and autumn 1999–2005. A total 5,608 bats representing 11 of Poland's 25 species were captured. *Myotis mystacinus* predominated. Its activity at all times was high. However, the species composition and number of other bats changed seasonally. Swarming activity lasted between July and November, peaking in late July and August. Nightly activity peaked between 22.00 and 02.00 hrs and then gradually decreased toward dawn. Strong male bias was observed. *Myotis mystacinus* showed regular changes in sex and age ratios. Rare species such as *M. bechsteinii*, *M. emarginatus*, and *Vespertilio murinus* were recorded. This cave is the highest locality of *M. bechsteinii* and *M. brandtii* in Europe. Some behavioural observations including copulation, drinking and daylight activity were recorded. The role of swarming activity is discussed in light of the findings. Some observations suggest that this activity of bats is connected with mating; some other observations provide evidence that the function of swarming is also to facilitate the location of mates and/or to assess suitable hibernacula.

Key words: elevational distribution, mountains, *Myotis*, Poland, swarming

INTRODUCTION

During summer and early autumn in the Northern Hemisphere, several months before hibernation and therefore earlier than might be expected, large numbers of bats visit caves, mines and other hibernacula (Davis and Hitchcock, 1965; Fenton, 1969; Horáček and Zima, 1978; Kiefer *et al.*, 1994; Parsons *et al.*, 2003a). This phenomenon was documented in the 1960s on the North American continent and was called 'fall swarming' (Davis, 1964) and also 'roaming movements' or simply 'summer activity' (Horáček and Zima, 1978; Bauerová and Zima, 1988; Hanzal and Průcha, 1996). Several recent and historical studies have described swarming at low elevations in Europe (Horáček and Zima, 1978; Bilo *et al.*, 1989; Harrje, 1994; Kiefer *et al.*, 1994; Degn *et al.*, 1995; Furmankiewicz and Górniak, 2002; Pugh and Altringham 2005; Rivers *et al.*, 2006) and North America (Davis, 1964; Davis and Hitchcock, 1965; Fenton, 1969; Whitaker and Mumford, 1971; Cope and Humphrey, 1977; Kurta, 1980; LaVal and LaVal, 1980; Wethington *et al.* 1996; Kurta *et al.*, 1997), and is relatively well recognized.

This activity has not been studied at high elevations in Europe. Only Magnin (1991) mentions the

capture of a few dozen bats of five different species in August and September, during the course of his research on bone remains of Vertebrata in Protoconule Cave at 1,800 m a.s.l. Studies have described this behaviour on the North American continent in the higher mountains (even at 3,048 m), but they focus on only a few aspects and are temporally incomplete (Schowalter, 1980; Goad, 1982; Navo *et al.*, 2002).

The main reason why this subject is insufficiently studied in high mountains is that the work is hampered by the terrain, the inaccessibility of caves (most of them are vertical), and variable and severe weather conditions, especially in late summer and autumn. Swarming apparently is the result of many processes and is connected with different functions. A few basic hypotheses have been offered to explain its role. They are not mutually exclusive. The first, toward which most researchers incline, posits that the function of swarming is related to mating (Thomas *et al.*, 1979). Behavioural observations of calling, chasing and copulating, noted during swarming (Fenton, 1969; Thomas *et al.*, 1979), support this, and genetic studies (Kerth *et al.*, 2003; Veith *et al.*, 2004; Rivers *et al.*, 2005; Furmankiewicz and Altringham, 2006) confirm it as well.

During swarming, bats from different summer roosts can meet (Kerth *et al.*, 2003; Rivers *et al.*, 2005).

Three other hypotheses are connected with migration and dispersal. The first assumes that the purpose of swarming is to localize mates and/or assess suitable hibernacula (Davis and Hitchcock, 1965; Hall and Brenner, 1968; Fenton, 1969; Horáček and Zima, 1978; Kiefer *et al.*, 1994; Parsons *et al.*, 2003a; Veith *et al.*, 2004). The second connects swarming with information transfer in which an adult female (mother) shows the young (born that summer) the location of the hibernaculum and/or mating places (Davis and Hitchcock, 1965; Fenton, 1969; Humphrey and Cope, 1976). The third states that swarming places can be used as pathways between summer and winter regions, and as stop-off sites (Whitaker, 1998). There is also a suggestion that the high activity of bats at entrances to caves during summer and early autumn may be connected with feeding at the caves (Whitaker and Mumford, 1971; Mumford and Whitaker, 1975).

Twenty species of bats currently occur in the Polish Tatra Mountains; of these, 12 regularly hibernate in caves (Piksa, 1998, 2006; Piksa and Nowak, 2000; Nowak, 2001; Sachanowicz *et al.*, 2006; Niermann *et al.*, 2007). The Tatras are the only area in Poland where *M. mystacinus* is the most numerous species in the caves during winter, making up over 60% of all hibernating bats. The numbers of other species are much lower.

The aims of this study were: (1) to establish whether swarming activity occurs in high-elevation caves; (2) if so, to describe features including species composition, sex and age ratios; (3) to compare activity levels and species composition at different times of the year; (4) to identify changes in activity patterns during the night as the swarming period progresses; and (5) to determine the role of these sites during that period.

MATERIALS AND METHODS

Study Site

Great Litworowa Cave, located in the Tatra Mountains in southern Poland (49°13'30"N, 19°55'W), was chosen as the study site. The Tatras, spanning southern Poland and northern Slovakia, are the highest range of the Carpathian massif, the highest between the Alps and the Caucasus, and the highest between Scandinavia and the Balkan Peninsula. Although the Tatras (highest peak: Gerlach, 2,663 m a.s.l.) are much lower than the Alps, they are truly alpine in character and landscape (Mirek, 1996). The entrance to the cave is located on the northern slope of Mt. Małolęczniak at 1907 m in the alpine belt.

It is situated near Litworowa Pass (2,037 m) and Mułowa Pass (2,067 m). The cave is surrounded by rocks and high-mountain grasslands; linear landscape elements are absent. Great Litworowa Cave is a typical vertical alpine cave with spacious pitches (even over 60 m of vertical range), and chambers of large dimensions (up to 300,000 m³). This site is the highest-elevation cave of the Great Snow Cave System, which is the largest and deepest cave system in the Tatras and in Poland, over 23 km long and with a denivelation of 880 m.

Bat Captures and Hibernating Counts

Captures were made between July and the end of October or November each year. Between 2002 and 2005 the visits were limited to one per fortnight to minimize the disturbance to bats. In particular months the number of visits was constant and scheduled more or less during the same periods ($\pm 1-4$ days). It was not always possible to carry out regular surveys, especially in the latter part of October and in November, because of adverse weather conditions (intense rain and snowfall, temperatures below zero, strong foehns, difficult access to the cave entrance due to thick snow cover and the threat of avalanche, fog, etc.). Bats were captured with a mist net (7 m; Ecotone, Gdańsk, Poland), or in 2002 and 2003 with a 1.8 × 1.4 m harp trap of my own construction, placed at the bottom of a pit more than 10 m deep directly below the vertical entrance. Infrequent surveys were made using the same methods in summer and autumn between 1999 and 2001. The corridor was only partly enclosed to avoid excessive disturbance. Bats were caught on 49 occasions. In 1999 and 2003 trapping started before dusk and usually continued until dawn; in 2004 and 2005 the trapping continued until midnight.

Captured bats were identified to species and sex, and marked with different non-toxic alcohol-based colour marks. *Myotis mystacinus* and *M. brandtii* were ringed with 2.9 mm aluminium bat rings in 2005. They were also aged as adults or juveniles (born that summer) by examination of the epiphyseal joints in the finger bones (Racey, 1974; Anthony, 1988) and a combination of the following features: tooth wear, and colour of dorsal hair, ventral hair and wing membrane (author's unpublished data). Times of capture were noted. Visual observations of bat behaviour inside the cave were made using battery-powered torches and a nightscope. Hibernation counts were made in December between 1999 and 2003, and in November in 2004 and 2005. Only some parts of the cave were penetrated to about 200 m depth. All activities were carried out under permits from the Polish Ministry of Environment and Tatra National Park.

Statistical Analysis

Proportions and confidence intervals (CI) were calculated with logistic regressions (Allison, 1999). Each proportion and CI was calculated independently assuming no time trend, that is, treating a day or an hour as a categorical variable. The dashed trend curves superimposed on the proportions shown on the graphs were obtained from a semi-parametric regression method (generalized additive model, GAM — Hastie *et al.*, 1990). GAM was also used to show the seasonal dynamics of the number of individuals and of the proportion of the two sexes. A weighted least squares loss function (Neter *et al.*, 1985) was used to smooth trends. Statistical analyses employed SAS version 9.1 and Statistica version 6.1.

RESULTS

Numbers and Species Composition

A total 5,608 bats representing 11 of Poland's 25 bat species were caught (Table 1). The most numerous species, recorded at very high numbers during the whole study period, was *Myotis mystacinus*, comprising 88.0% of the captured bats. Relatively large numbers of *M. nattereri* (2.6% of the total), *M. brandtii* (2.6%) and *Plecotus auritus* (5.4%) were noted. The remaining species were found in small numbers.

On average, 45 bats were observed during hibernation counts: 28 *M. mystacinus*/*M. brandtii*, two *Eptesicus nilssonii*, single *M. nattereri* (2004) and *P. auritus* (2003), and approximately 10 bats unidentified. Hibernating *M. myotis* were observed in November 1996.

Summer and Autumnal Activity

During the study there were large seasonal and night-to-night fluctuations in the numbers of bats. Throughout the whole period the most numerous species was *M. mystacinus*. Its swarming activity was observed from July until late October or early November, peaking mid-July to the end of September. In September the activity of this and other species decreased, and in October was very low. At the beginning of November swarming ceased almost completely, and in the second half of November and in December it was not noted at all. The swarming activity of female and male *M. mystacinus* differed: males had two peaks of abundance, and females only one. The peak of female abundance coincided with the period when male abundance decreased (Fig. 1).

Temporal segregation during the course of the swarming season was evident in three other species. The number of *M. brandtii* peaked earlier than in *M. nattereri* and *P. auritus* (Fig. 2).

Nightly Activity

The number of bats caught during night captures fluctuated from two individuals (9 November 2002) to 382 (15 August 2001). In optimal conditions (no strong winds and/or no intense rainfall or snowfall) the pattern of overnight activity was similar throughout the swarming season. The nightly activity of *M. mystacinus* was studied in detail. Nightly activity increased to a peak between 22:00 and 02:00 hrs and then gradually decreased toward

TABLE 1. Number of bats of each species caught in the Tatras. Number of surveys is given in parentheses, sex ratio (proportion of males in total) is provided in brackets. Used symbols: * — sex ratio significantly different from unity ($P \leq 0.05$), NS — sex ratio not significantly different from unity ($P > 0.05$). G-test was performed only when > 10 individuals of a species were captured

Species	1999 (5)	2000 (7)	2001 (2)	2002 (9)	2003 (9)	2004 (7)	2005 (9)	Total (49)
<i>Myotis myotis</i>	0	2 [1.00]	1 [1.00]	3 [0.67]	1 [1.00]	3 [0.67]	4 [0.75]	14 [0.79]*
<i>M. bechsteinii</i>	2 [0.50]	0	0	0	0	0	2 [1.00]	4 [0.75]
<i>M. nattereri</i>	43 [0.77]*	28 [0.61]NS	6 [0.83]	20 [0.70]NS	11 [0.91]*	14 [0.79]*	23 [0.70]NS	145 [0.73]*
<i>M. mystacinus</i>	535 [0.76]*	833 [0.61]*	658 [0.74]*	952 [0.68]*	1,012 [0.70]*	471 [0.62]*	473 [0.59]*	4,934 [0.67]*
<i>M. brandtii</i>	5 [1.00]	13 [0.46]NS	11 [0.73]NS	44 [0.66]*	46 [0.72]*	14 [0.86]*	15 [0.73]NS	148 [0.70]*
<i>M. daubentonii</i>	4 [1.00]	10 [0.70]	1 [1.00]	8 [1.00]	9 [0.89]	0	6 [0.33]	38 [0.79]*
<i>M. emarginatus</i>	0	0	1 [1.00]	0	0	1 [1.00]	2 [1.00]	4 [1.00]
<i>Eptesicus nilssonii</i>	0	0	2 [1.00]	3 [1.00]	1 [1.00]	0	3 [1.00]	9 [1.00]
<i>Vesperugo murinus</i>	0	0	0	1 [1.00]	3 [0.33]	1 [1.00]	2 [1.00]	7 [0.71]
<i>Plecotus auritus</i>	82 [0.76]*	47 [0.60]NS	32 [0.81]*	40 [0.75]*	57 [0.61]NS	27 [0.78]*	18 [0.78]*	303 [0.71]*
<i>Barbastella barbastellus</i>	0	0	0	0	1 [1.00]	0	1 [1.00]	2 [1.00]
Total	671	933	712	1,071	1,141	531	549	5,608

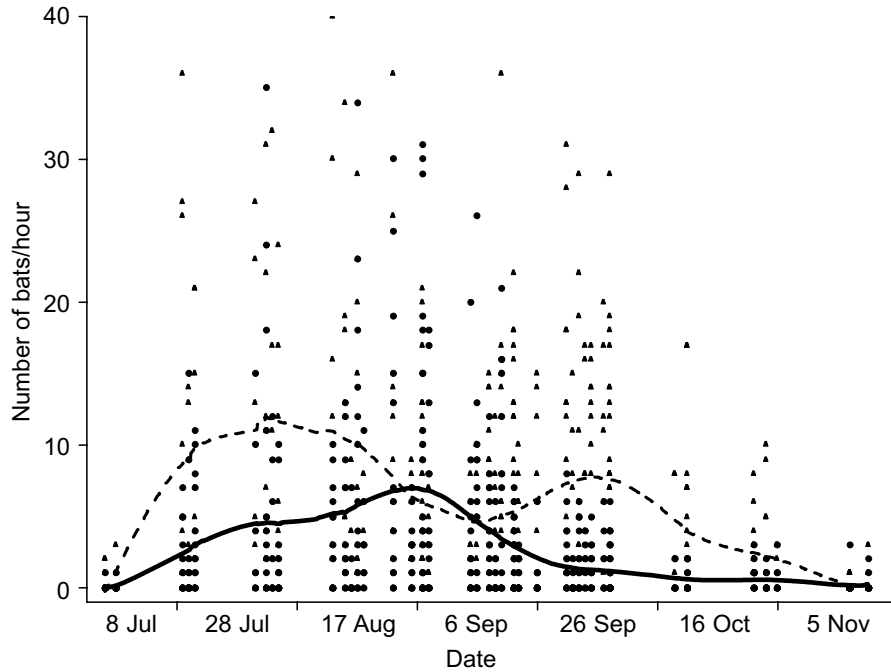


FIG. 1. Seasonal dynamics in the number of female (solid line) and male (dashed line) *M. mystacinus* during swarming in 1999–2005. Triangles indicate the number of males captured per hour. Dots indicate the number of females captured per hour

dawn. The pattern of this activity was similar in males and females, but as night progressed the proportion of females increased slightly (Fig. 3). The difference between adult females and juveniles in their activity at different night periods was not significant (Chi-square test, $\chi^2 = 4.56$, *d.f.* = 5,

$P > 0.05$). Differences in the proportion of juveniles to adult females between 2004 and 2005 were very small (Chi-square test, $\chi^2 = 0.20$, *d.f.* = 1, $P > 0.05$). On a few occasions, bats were observed to arrive during daylight. Then they were captured both before sunset (max. 1.5 hr — e.g.,

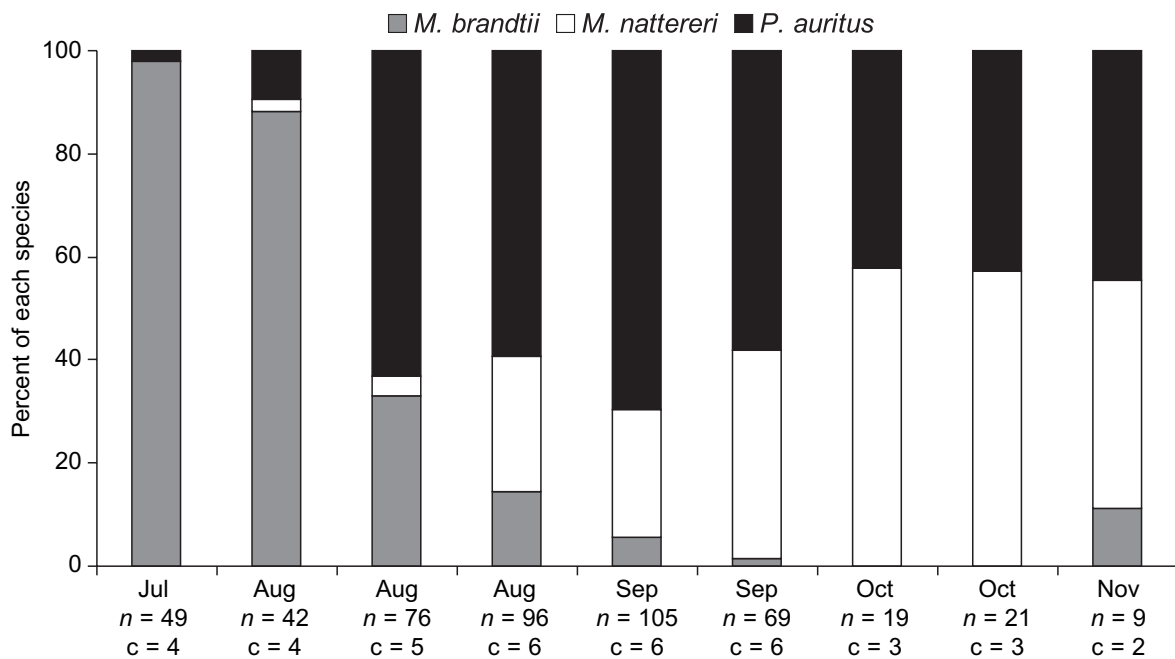


FIG. 2. Changes in the composition of *M. brandtii*, *M. nattereri*, and *P. auritus* during swarming activity at fortnight intervals between 1999 and 2005. For 1999–2001 the data used were those that matched capture dates (± 1 –4 days) from the following years. Beneath the x-axis: *n* — number of bats in sample, *c* — number of catching events

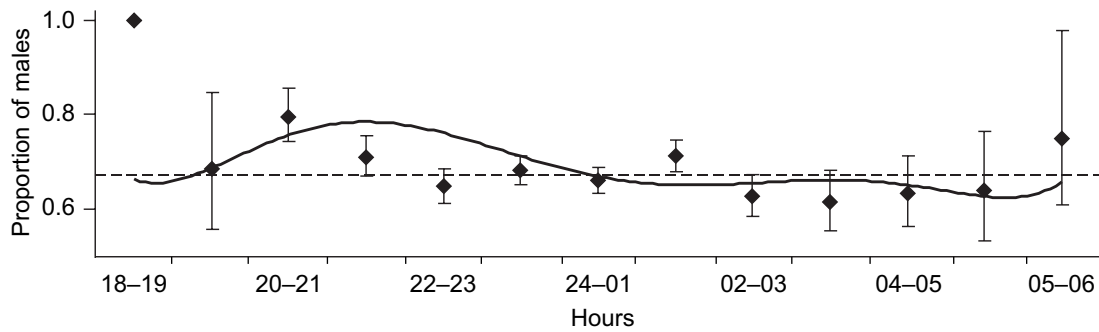


FIG. 3. Hourly changes in sex ratio (proportion of males in total) in *M. mystacinus* during night (GAM with 95% CI). Horizontal dashed line indicates the average sex ratio value for all captured individuals in 1999–2003

two males and three females of *M. mystacinus* and one male of *M. nattereri* on 4 August 2003) and after sunrise (max. 1 hr — e.g., two males and two females of *M. mystacinus* on 25 August 2001).

Sex and Age Composition

The sex ratio was highly male-biased for all species (Table 1). The sex ratio changed during the

swarming season in only one species, *M. mystacinus*; the dynamics of these changes followed similar trends in 2002–2005 (Fig. 4); the most conspicuous feature of which is the brief, marked decline in the proportion of males that recurs at the same time each year. Bats are highly social animals with a close mother-infant relationship, and adult females may be accompanied by juveniles in flights to mating and/or hibernation places. In view of this, the study was designed to include a detailed analysis of

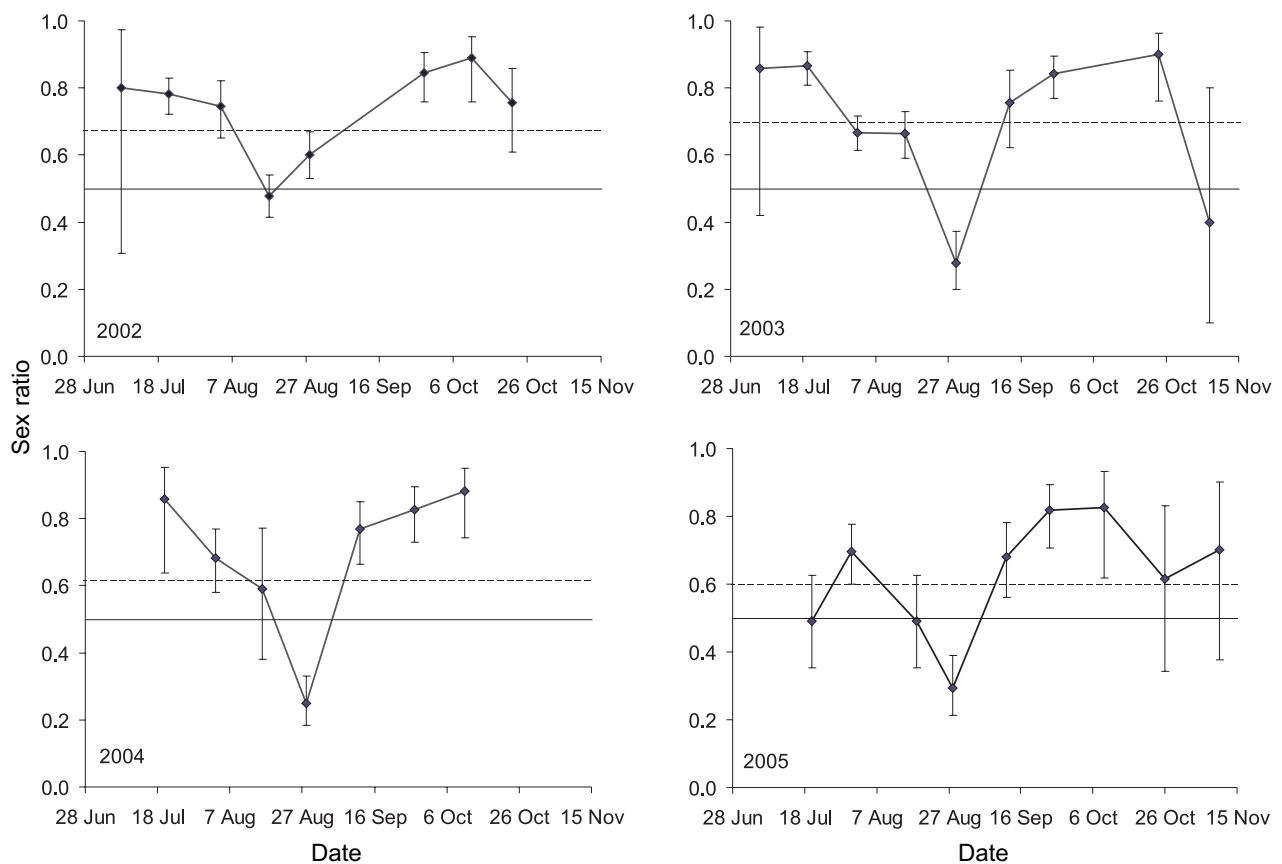


FIG. 4. Changes in sex ratio (proportion of males in total) in *M. mystacinus* in 2002–2005 (with 95% CI). Solid line indicates the balanced value (0.50). Horizontal dashed line indicates the average sex ratio value in each year, which had the following values in particular years: 2002 — 0.68, 2003 — 0.70, 2004 — 0.62, 2005 — 0.60

seasonal changes in the number of adult females and juveniles, the proportion of juveniles to females, and the juvenile sex ratio. Any form of behavioural activity testifying to this phenomenon was also noted. The age structure of *M. mystacinus* was studied in detail in 2004 and 2005; the number of juveniles changed considerably, increasing during the period of increase in the numbers of adult females and decrease in the numbers of adult males (Fig. 5). As the season progressed, the ratio of juveniles to adult females increased slightly (Fig. 6). During the peak activity of females, female-juvenile pairs were often caught in the net right next to each other (e.g., during the night of 11 September 2000 there were nine such pairs, and on 30 August there were six). In three cases an adult female made a few flights in front of the net and then fell into the bag that had already captured her struggling juvenile. The sex ratio in *M. mystacinus* juveniles fluctuated slightly (Fig. 7). Males predominated among juveniles for almost the whole swarming season, but during the peak abundance of juveniles and adult females (Fig. 6) the sex ratio in juveniles approximated unity (Fig. 7).

Behavioural Observations

Copulation (e.g., three copulating pairs observed the night of 28 September 2000) and drinking at underground pools (e.g., two drinking bats observed the night of 3 August 2005) were noted in

M. mystacinus. Copulating individuals of *M. myotis* were observed on 12 October 2005.

DISCUSSION

The study found that swarming may occur in high-elevation caves in the mountains. The following characteristics of the bat activity observed in Great Litworowa Cave qualify it as swarming: the period during which the activity was observed (a few months before hibernation), high species richness and abundance, high male bias, and behaviours such as copulation and high activity in the immediate vicinity of the cave entrance.

Number and Species Composition

The number of bats and the abundance of certain species were surprisingly large in Great Litworowa Cave. The number of bats was as high as that registered at swarming sites at much lower elevations (Kiefer *et al.*, 1994; Degn *et al.*, 1995). The high number of bats is especially surprising in view of the adverse habitat conditions: open space, lack of forest, linear landscape elements, pools of water, and severe and variable weather conditions (low temperatures, frequent winds, rain, snow).

For such a high-elevation site, the high diversity of species is also surprising; it approximates the values from studies at lower-elevation sites where greater species abundance would be expected: for

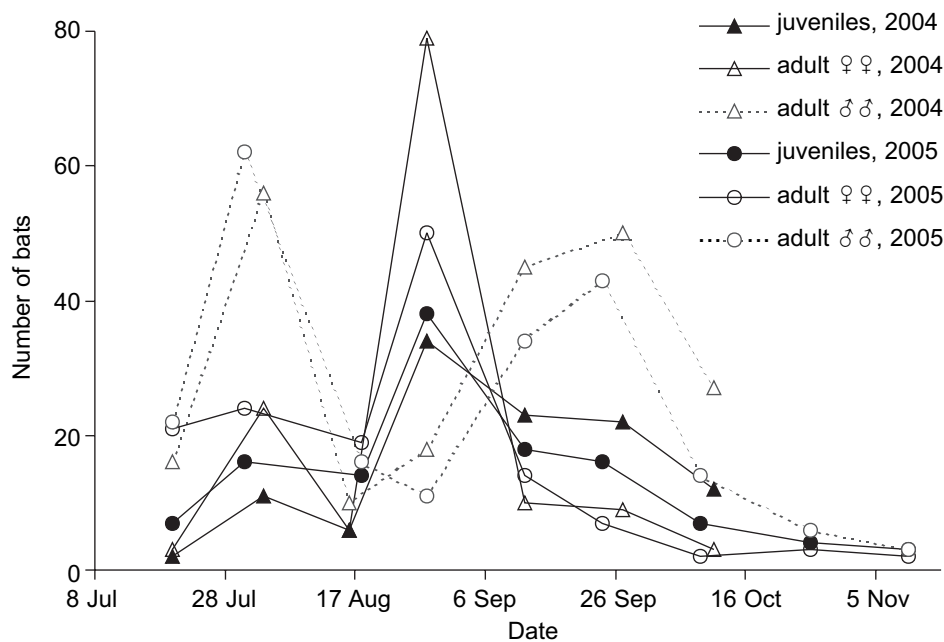


FIG. 5. Changes in the number of adult females, adult males and juveniles in *M. mystacinus* during swarming years 2004 and 2005

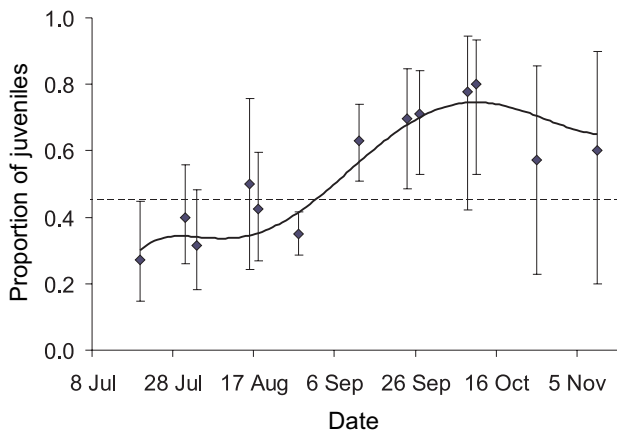


FIG. 6. Changes in the proportion of juveniles to adult females (GAM with 95% CI) in *M. mystacinus* during swarming years 2004 and 2005. Horizontal dashed line indicates the average value of this proportion (0.45)

example, 11 species captured in Great Britain (Parsons *et al.*, 2003a), 12 in Lower Silesia in Poland (Furmankiewicz and Górniak, 2002), 11 in Germany (Kiefer *et al.*, 1994), and 13 in the Czech Republic (Gaisler and Chytil, 2002). It may be, of course, that some sparsely represented species are rather occasional visitors and that their occurrence is not connected with swarming activity.

The low numbers of bats recorded hibernating in Great Litworowa Cave may seem surprising, but not when we bear in mind that only a small part of the cave was penetrated (about 1/20 of its total length). An accurate bat census was impossible in the large, vertical chambers, pits and chimneys. The high activity of bats in spring and the great numbers of bat remains (remains of more than 1,500 bats were found in a single chamber) suggest that the real numbers of bats hibernating in this cave are much higher.

Of the faunal data, an interesting finding is the presence of *M. bechsteinii* and *M. brandtii*. Great Litworowa Cave is the highest locality of these species in Europe. Until recently, in Europe they were observed only up to 1,800 m a.s.l. (Baagøe, 2001; Tupinier, 2001). This cave is also the highest hibernaculum of *M. nattereri* in Europe. Until the present study it was observed during hibernation up to 1,800 m a.s.l. (Spitzenberger and Bauer, 2001). Worthy of mention is the presence of *V. murinus*, a species never before captured in the caves of Europe during swarming (Kiefer *et al.*, 1994; Bauerová and Zima, 1998; Furmankiewicz and Górniak, 2002), except for one individual (Gaisler and Chytil, 2002).

Just as in North America and elsewhere in Europe, the dominant species participating in this activity are of the genus *Myotis* (Davis and Hitchcock, 1965; Hall and Brenner, 1968; Fenton, 1969; Schowalter, 1980; Bauerová and Zima, 1988; Parsons *et al.*, 2003a; Rivers *et al.*, 2006). Of the 10 species of *Myotis* that reside in Poland (Piksa, 2006; Sachanowicz *et al.*, 2006; Niemann *et al.*, 2007), as many as eight species were noted in Great Litworowa Cave. Among them, *M. mystacinus* was the dominant species. Morphological and genetic analyses suggest that the individuals captured at this site belong to *M. mystacinus sensu stricto* (W. Bogdanowicz, K. Piksa, A. Tereba, unpublished data). This is the first study of a swarming site where *M. mystacinus* was the predominant species. In previous studies of swarming it was recorded not at all (Parsons *et al.*, 2003a) or only very rarely and in low numbers, its proportion not exceeding a few percent (Horáček and Zima, 1978; Bauerová and Zima, 1988; Ruedi *et al.*, 1989; Furmankiewicz and Górniak, 2002; Gaisler and Chytil, 2002; Rivers *et al.*, 2006). Only in three underground tunnels in the Eifel Mountains in Germany was the proportion of *M. mystacinus/brandtii* as high as 25.8%; *M. mystacinus* was clearly dominant (Kiefer *et al.*, 1994). In captures at the entrance to Protoconule Cave in Switzerland the number of these bats also slightly exceeded 20% (Magnin, 1991).

Seasonal Activity

The swarming activity of *Myotis* and *Plecotus* species is of shorter duration in Great Litworowa Cave than at lower-elevation underground sites; it starts earlier and peaks earlier as well. In most

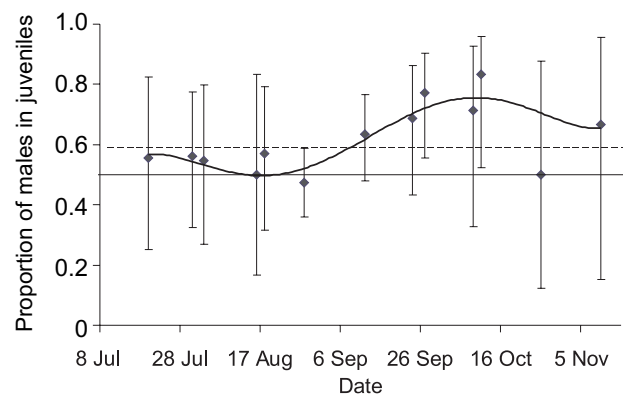


FIG. 7. Changes in juvenile sex ratio (proportion of male to total juveniles) in *M. mystacinus* through time in 2004 and 2005 (GAM with 95% CI). Horizontal dashed line indicates the average sex ratio value (0.59). Solid line indicates the balanced value (0.50)

studies on swarming at lower elevations in Europe, swarming is observed mainly between August and November, with peak activity in September, while activity in July is either low or not noticeable (Degn *et al.*, 1995; Hanzal and Průcha, 1996; Furmankiewicz and Górniak, 2002; Parsons *et al.*, 2003a, 2003b; Rivers *et al.*, 2006). In high-elevation caves in North America, as in the Tatras, bat activity was noted to be high already in mid-July (Goad, 1982). It seems that the earlier and numerous appearance of bats in caves at high elevations, and the shorter swarming period, are connected with weather conditions, which in the Tatras are definitely best in July and August. From September, especially in the alpine belt, the weather becomes more inclement. The number of windy days doubles, the wind speed rises, and the average night temperature falls markedly (Konček and Orlicz, 1974; Otruba and Wiszniewski, 1974). The ground is very often covered with snow.

Myotis mystacinus showed high activity during the whole study period. In other three species, temporal segregation was observed during the course of time. The differences in the pattern of swarming activity between *M. brandtii* and *M. nattereri* accord with results from an underground site in Britain (Parsons *et al.*, 2003a). Later-occurring and more numerous appearances of *P. auritus* were also reported by Kiefer *et al.* (1994). Similarly, Węgiel *et al.* (2004) states that such temporal segregation occurs in *P. auritus* and *M. brandtii*, but these suggestions are based on irregular, random captures carried out during one season only.

Nightly Activity

In principle this activity is no different from that observed in most such studies (Degn *et al.*, 1995; Parsons *et al.*, 2003b; Rivers *et al.*, 2006). Peak activity is observed at more or less the same time or a little earlier, around midnight (cf. Parsons *et al.*, 2003b; Rivers *et al.*, 2006). A very interesting phenomenon observed in Great Litworowa Cave is an increase in the proportion of female *M. mystacinus* as the night progressed. This has not been described in previous literature about swarming (c.f. Bauerová and Zima, 1988; Ruedi *et al.*, 1989; Furmankiewicz and Górniak, 2002; Parsons *et al.*, 2003a; Rivers *et al.*, 2006). It might be explained this way: many males arrive at swarming places earlier in order to occupy a more strategic position and thus increase their chances of meeting a partner (under the assumption that the function of swarming is mating).

These males forfeit the chance to prey longer and more effectively. At the same time, some later-arriving females have spent more time preying during the period with the highest number of insects, and in places providing better access to food. Interestingly, a difference in the pattern of nightly activity between females and males at swarming sites was also noted at lower elevations in other species (author's unpublished data); this difference in nightly activity patterns may be a general phenomenon of bat swarming behaviour.

The arrival of bats in daylight was observed only exceptionally; it is an unusual behaviour, minimized by pressure from daytime bird predators (cf. Speakman, 1991a, 1991b) and not noted in any papers about swarming (Karlsson *et al.*, 2002; Parsons *et al.*, 2003b).

Sex Ratio

Males outnumber females in most studies on swarming (Davis and Hitchcock, 1965; Humphrey and Cope, 1976; Bauerová and Zima, 1988; Kerth *et al.*, 2003; Parsons *et al.*, 2003a; Rivers *et al.*, 2006). Similarly, in Great Litworowa Cave the sex ratio was highly male-biased in all species. The most frequently caught species, *M. mystacinus*, showed significant changes in the sex ratio over time. Before this study there were no reports of such a phenomenon in bats of the genus *Myotis* or *Plecotus* (Davis and Hitchcock, 1965; Fenton, 1969; Bauerová and Zima, 1988; Parsons *et al.*, 2003a; Rivers *et al.*, 2006). It is true that changes in the sex ratio have been reported in the little brown bat *M. lucifugus* (Davis and Hitchcock, 1965), but they differed from those in *M. mystacinus*. In *M. lucifugus* the sex ratio was highly male-biased in late July and August (similarly to *M. mystacinus*) and gradually approached unity until the numbers of males and females were equal during hibernation between November and March. In *M. mystacinus* in Great Litworowa Cave, for almost the whole season it was male-biased, and only in the latter part of August and early September was the number of females significantly greater. The dominance of females in this period may be associated with the dispersal of reproductive colonies and their synchronized arrival at potential hibernacula and/or mating places. Initial observations in the surroundings of the nearest mountain passes seem to confirm this conjecture. During this period, one of the females ringed at Litworowa Pass was caught in the cave.

In addition to the high female bias at a certain period during swarming, the very presence of females at this elevation is a surprising finding. General observations across bat populations show rather the contrary: the absence or very rare occurrence of females at higher elevations (Grindal *et al.*, 1999; Cryan *et al.*, 2000; Russo, 2002; Neubaum *et al.*, 2006).

Age Composition

One theory explaining swarming activity suggests that the function of swarming is to introduce, gather and record information concerning the location of optimal winter roosts and/or mating places. Bats are highly social animals with a close mother-infant relationship, and this theory implies that adult females (mothers) are accompanied by juveniles (born that summer) on flights to these places (Fenton, 1969; Humphrey and Cope, 1976). Some observations from Great Litworowa Cave seem to support this: (1) a considerable increase in the number of juveniles in the period of mass arrival of adult females; (2) the proportion of juveniles to adult females, approximating unity in that period; and (3) the netting of adult females paired with juveniles. Indirect evidence is seen in the sex ratio among juveniles, which in this period is closest to unity, and therefore approximates that observed among juveniles in a reproductive colony.

Another phenomenon observed in *M. mystacinus* during this study was a small, gradual increase in the proportion of juveniles. This is consistent with the observations of other authors who noted an increase in the number of juveniles in the latter phase of swarming (Fenton, 1969; Horáček and Zima, 1978; Thomas *et al.*, 1979; Schowalter, 1980).

Behavioural Observations

The observations of copulating bats show that this cave is used as a mating place. It is widely known that the basic function of swarming is for mating (Davis, 1964; Fenton, 1969; Thomas *et al.*, 1979; Kerth *et al.*, 2003; Parsons *et al.*, 2003a; Rivers *et al.*, 2005), but copulations have very rarely been observed in this period (Fenton, 1969; Thomas *et al.*, 1979; LaVal and LaVal, 1980; Harrje, 1994; Kurta *et al.*, 1997). In the Tatras as well, long studies yielded only a few records of this behaviour, and only in two species, *M. mystacinus* and *M. myotis*. The observations of *M. myotis* reported in this paper, as well as those of Harmata (1994) and Kretzschmar

and Heinz (1995), who recorded copulating *M. myotis* in caves, in September and October, showed that bats copulated not only in the attics of buildings (Zahn and Dipel, 1997) but also in hibernacula during the pre-hibernation and hibernation periods (Ittermann, 1991).

The availability of water may be essential to the presence of the numerous bats in this cave. Karstic terrain, especially at such elevations, has no or very scant surface water resources (e.g., Pulina, 1999). Bats that reach high elevations travel great distances, both horizontally and vertically, over areas devoid of water. Those flights entail great effort and consequently increased demand for water. To quench their thirst, they must visit the only places where water is present — caves.

The present results show that swarming may occur at high-elevation caves in mountains. Despite the unfavourable location and severe climatic conditions there, swarming activity differs only slightly from that noted at lower elevations in respect of, for example, the number of bats, species richness, and temporal segregation of bat species. There are bigger differences in the seasonal dynamics of the numbers of males and females, juvenile individuals, etc. This study also shed new light on the causes behind swarming. Some observations suggest that this activity of bats is connected with mating, hence the cave is a place for meeting potential partners. Other observations, such as the appearance of a great number of adult females together with accompanying juveniles, provide evidence that swarming is not only for mating but also for facilitating the location of mates and/or assessing suitable hibernacula. There are many factors that may be related to the increased bat activity in this cave, such as its proximity to mountain passes and therefore to flight passages, the presence of pools in the cave while none exist on the surface, and stable conditions inside the cave allowing survival during adverse weather. These results support a number of explanations for swarming, a phenomenon still incompletely understood despite much research.

ACKNOWLEDGEMENTS

I thank three anonymous referees for their useful comments and suggestions. I would also like to thank members of the Caving Club of the University of Science and Technology in Cracow and the Cracow Caving Club for their help on catch nights. I also thank Tatra National Park staff: Paweł Skawiński, Zbigniew Krzan, Wojciech Gąsienica Byrcyn, Jan Chmiel, Wiesław Siarzewski for their help and patience, and for enabling the research. Special thanks to Bartosz Jenner for invaluable help with statistical analyses and Bradley Bergstrom

and Michael Jacobs for comments and corrections in the English text. The project was undertaken with funding from the State Committee for Scientific Research (2 P04F 048 27).

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