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Research Article

# The role of autumnal swarming behaviour and ambient air temperature in the variation of body mass in temperate bat species

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## Abstract

Temperate-zone bat species store fat in autumn prior to hibernation. The likelihood of surviving until the next breeding season largely depends on the resources accumulated. In addition, autumn is also a period of mating behaviour known as swarming, which is energetically expensive and may affect the body condition of bats in different ways. Our goal was to determine how swarming activity, male reproductive status, sex ratio and mean temperature influence resource deposition in six bat species. Variations in the body condition index (BCI) of bats during swarming activity mainly depended on the date of capture and, to a lesser degree, on the sex; however, it was highly species-specific and linked to the time of entering hibernation. Despite a promiscuous mating system, both species and sex significantly affected resource accumulation. Among the analysed behavioural factors, swarming activity explained a small part of BCI variation. In the foliage gleaners *Myotis bechsteinii*, *M. nattereri* and *Plecotus auritus*, an increase in male participation (higher sex ratio) was correlated with a higher BCI, while in *Myotis daubentonii* and *Barbastella barbastellus*, it led to a lower BCI in females. In turn, epididymal distension explained a significant part of BCI variation only in two species (*Myotis daubentonii* and *M. myotis*); in both with a negative correlation. Mean temperature explained BCI variation to the highest degree in *M. bechsteinii* (lower temperature implied lower body mass), but in the other gleaners, an opposite and weaker effect was found. Our findings indicate that the pattern of fat accumulation during swarming is modulated by distinct species-specific and sex-specific thermoregulatory strategies (energy-saving mechanisms) rather than by differences in mating behaviour or foraging strategies.

## Introduction

Varying availability of food resources has induced a number of adaptations in vertebrates, ranging from prolonged periods of inactivity to food collecting and seasonal migration, mainly among birds and mammals. While the first strategy is widespread among poikilothermic animals (mostly amphibians and reptiles), the other two are predominantly used by homoeothermic animals (Geiser, 2011). Seasonal changes of resource availability also affect species behaviour and requirements for reproduction and survival. A unique strategy to cope with periodic food shortages and survive until the next reproductive season is hibernation, which occurs mainly in insectivorous temperate bat species with a body mass of less than 100 g (Ransome, 1990). In hibernation, bat metabolism is reduced, with activity occurring during periodic arousals from torpor (Park et al., 2000), which accounts for the consumption of the majority of stored energy (Thomas et al., 1990). Therefore, hibernation survival is highly dependent on fat reserves (Speakman and Thomas, 2003). To some degree, resource accumulation depends on sex and age, as adult females enter hibernation with larger fat reserves and consume them more slowly than adult males and yearlings (Koteja et al., 2001; Jonasson and Willis, 2011; Šuba et al., 2011). This is linked to the fact that the reproductive success of females (entering gestation) depends on the resources accumulated at the end of hibernation (Kunz et al., 1998). Fat deposition occurs in autumn prior to hibernation, when the offspring become self-sufficient (Ewing et al., 1970; Kunz et al., 1998). During this period, bats frequently visit underground sites, and this phenomenon is known as swarming (Fenton, 1969). The function of swarming is complex, and it is mainly linked to mating behaviour (Kerth et al., 2003; Rivers et al., 2006; Furmankiewicz, 2008), although transfer of information for juveniles (Fenton, 1969), identification of suitable hibernacula (Thomas et al., 1979), and feeding (Mumford and Whitaker, 1974) should also be considered. A biphasic pattern of active mating behaviour, observed in some European bat species, swarming activity indicates temporal division as the main function: at the beginning mating, later — resources accumulation (Horáček and Zima, 1978); however, most bat species are characterised by one peak activity (Furmankiewicz and Górniak, 2002; Parsons et al., 2003a; Piksa, 2008). Therefore, the pattern of activity seems to be more dependent on the place and its function than on the bat species. Similar assemblages of swarming and wintering bats suggest that these two life periods are tightly connected (van Schaik et al., 2015).

Bat activity during swarming is highly variable, and its temporal distribution is species-specific (Parsons et al., 2003a,b). Differences in swarming patterns between species usually concern their feeding strategies, depending on the availability of preferred prey (Anthony and Kunz, 1977), of the increase in bat activity may be an effect of intensive feeding, which is partially confirmed by nightly changes in bat weight (Šuba et al., 2011). On the other hand, because flight is energetically costly (Speakman, 1991; Kerth et al., 2003), both mating behaviours observed during swarming (intense flight and social activity) and

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with diminishing feeding time can limit the accumulation of resources or/and reduce reserves accumulated earlier (Gottfried, 2009; Kohyt et al., 2016). The low number of females visiting swarming sites (Parsons et al., 2003a) would increase competition among swarming males, as pointed out by both the high number and greater diversity of social calls (Furmankiewicz et al., 2013). In terms of intraspecific behavioural differences, autumnal bat assemblages are strongly male-biased (Rivers et al., 2006; Piksa, 2008; Gottfried, 2009), and therefore, sex-specific patterns in the accumulation of resources are expected. Males have more to gain by putting more energy into courtship and mating more frequently (Ingersoll et al., 2010); therefore, their fitness might be more a function of the number of females with which they mate than the amount of prehibernation fat they can assimilate. Increased female participation in a swarming site has negative implications for fat resources in males (Kohyt et al., 2016), but this relationship appears to be species-specific (Gallant and Broders, 2015).

High male mating activity is strongly correlated with the size of their testes, which in turn corroborates the mating function of swarming (Encarnação et al., 2004; Pfeiffer and Mayer, 2013). Moreover, positive correlations between the proportion of males with distended caudae epididymides and the vocal activity of swarming bats have been found (Furmankiewicz et al., 2013). In most European swarming bat species, the size of the caudae epididymides gradually decreased throughout autumn, with one exception: *Plecotus auritus* still contained a reserve supply in spring (Furmankiewicz et al., 2013; Pfeiffer and Mayer, 2013).

Bat swarming activity can be suppressed by unfavourable weather conditions such as low temperatures and/or precipitation (Parsons et al., 2003b). Low temperatures may cause a decline in swarming behaviour due to decreased prey activity (Speakman, 1991) by triggering the onset of torpor (Humphries et al., 2006) or even hibernation (Erkert, 1982), while food shortage can induce deeper and longer torpor than decreasing temperatures (Wojciechowski et al., 2007). Frequent torpor bouts may serve as the main strategy of decreasing energy expenditure in autumn; many bat species use this mechanism of metabolism reduction during the day (McNab, 1982), regardless of whether or not they sustain it during the night (Speakman and Rowland, 1999) Higher energy expenditure can be compensated either by more frequent and deeper torpor or by increased energy (food) intake (Barclay, 1991; Cryan et al., 2000; Kerth et al., 2001; Dietz and Kalko, 2006). Fat accumulation may occur at a rapid rate, facilitated by daily torpor (Ewing et al., 1970). Because bat species differ in dietary and microclimate preferences during hibernation, some of them may be better adjusted to coping with colder conditions than others (Ingersoll et al., 2010).

Therefore, all of the above abiotic and behavioural factors may affect the variation in the body mass of bats during autumn activity, albeit to different degrees. Variation of accumulated resources can also be expected both within and between species. In this context, our aim was to assess the importance of variables as predictors in the modelling of bat resource accumulation during autumn activity.

We expected that an increase in swarming activity, defined as bat activity, epididymis distension and participation of males, has negative impacts on bat body mass due to higher energy demand, and that decreasing air temperatures induce increasing body mass due to the suppression of activity. In addition, if swarming activity is connected with feeding, we can expect similar patterns of accumulation in species with similar diet preferences, e.g. *Myotis bechsteinii* and *Myotis nattereri*, *Plecotus auritus* and *Barbastella barbastellus*, and differences between highly specialised bats such as *Myotis daubentonii* or bat species without typical swarming behaviour, such as *Myotis myotis*. Furthermore, we hypothesised that if male and female bats differ in swarming behaviour, they should differ also in their patterns of fat accumulation at swarming sites.

### Ethics statement

All procedures were carried out under licenses from the Ministry of Environment and from the Regional Protection Agency in Poland: WPN.6401.177.2013.DC and WPN.6205.16.2013.MM. Bats were released following measurements. To minimize stress, retention time never exceeded 30 minutes.

## Materials and Methods

### Study site and species

The study was conducted in the Szachownica Cave (18°48′20″ E, 51°3′17″ N, 215 m a.s.l., a natural reserve included in the Natura 2000 network, site code PLH240004). The cave is a 1000 m long underground system partially altered by limestone exploitation, with the intact part accounting for 60% (Górny and Szelerewicz, 2010). It offers numerous micro-shelters (cracks, crevices) and a highly diverse microclimate. Currently, the cave comes fourth in Poland in terms of the number of bats hibernating (2,902 individuals in 2009), with 11 wintering bat species. Within a radius of 50 km around the Szachownica Cave, there are only several minor wintering roosts, housing a total of

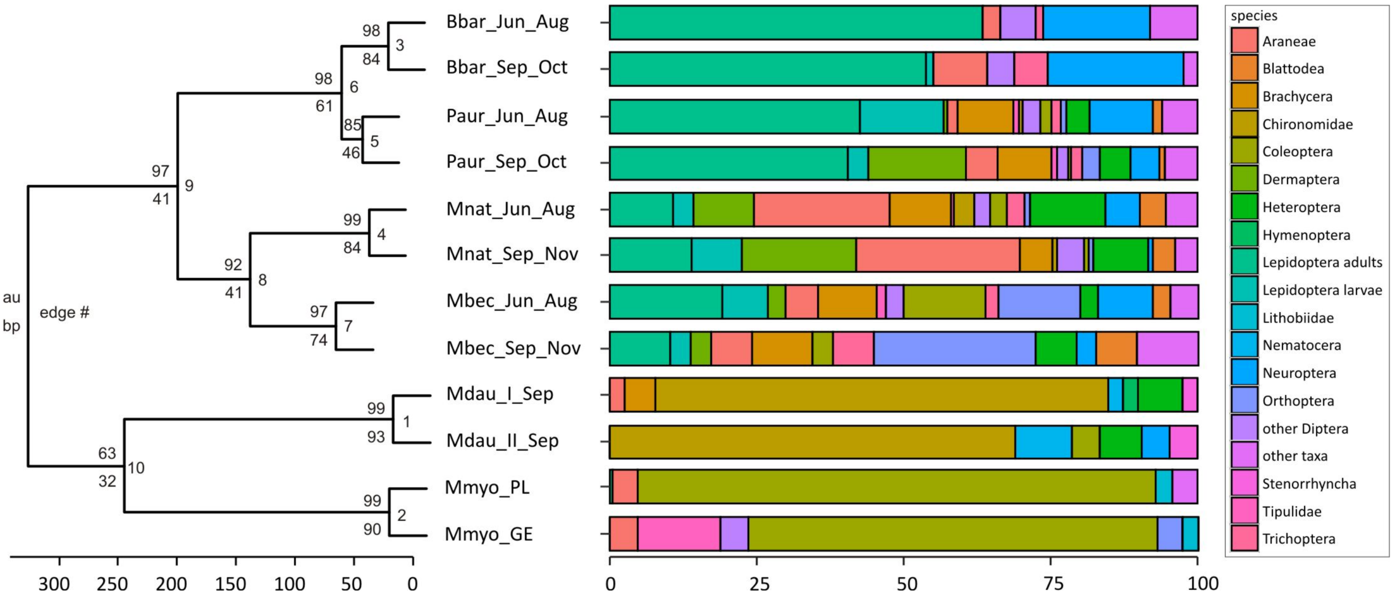

**Figure 1** – Hierarchical clustering dendrogram of diet composition (Ward's method) – similarity (left) and detailed diet composition follow Andreas et al. (2012a) for *M. nattereri* (Mnat), *M. bechsteinii* (Mbec), *P. auritus* (Paur); Andreas et al. (2012b) for *B. barbastellus* (Bbar); Pithartová (2007) for *M. daubentonii* (Mdau), Graclik and Wasielewski (2012) and Zahn et al. (2006) for *M. myotis* (Mmyo); Jun: June, Aug: August, Sep: September, Oct: October, Nov: November, PL: Poland, GE: Germany. Diet composition was described in terms of percentage occurrence of different arthropod groups. The figures presented at branches are approximate unbiased *p*-values (AU, top), bootstrap probability values (BP, bottom) and cluster labels (right).

up to 90 individuals (Lesiński et al., 2011), and they are not significant sites of swarming activity (maximum of 20 individuals per night) (W. Pawenta personal communication 2016). The Szachownica Cave is the final hibernation destination for several species of bats coming from up to 90 km (Wojtaszyn et al., 2008). Extensive chambers between the main cave entrances and the open area of the quarry (sheltered from wind) are used by the bats for intensive swarming activity.

## Bat species, body mass and reproductive status

Bats were caught in a harp trap (size: 150x200 cm) placed in the passageway between two large halls (divided into two parts by an artificially erected pillar). The halls had broad entrances from the quarry (10×4 m and 15×4 m). The harp trap closed off only one of those entrances. Bats were captured in 2013 during seven nights from sunset to sunrise, every 2 weeks from late July to late October (83 days). The activity of each bat species and their sex within the swarming season (temporal patterns) were expressed by the abundance each bat species per given night relative to the total number of captured bats.

The bats were sexed, weighed (spring balance Pesola, resolution 0.25 g), measured with a calliper (forearm length: 0.1 mm resolution) and marked temporarily with a typing correction fluid to identify recaptures on the same night (which occurred only incidentally and accounted for 1.4% of the total captures during the study period). Bats were classified either as juveniles (born in the year of capture) or adults, primarily on the basis of wing epiphyseal fusion in the finger bones, with additional age-specific characteristics, such as the degree of tooth wear, the presence and size of the chin spot and the condition of nipples in females (Haarsma, 2008). In these paper only adults was used. Body mass was characterised by means of the body condition index (BCI), defined as body mass divided by forearm length (Speakman and Racey, 1986). Sex ratio was computed as the number of males captured divided by the aggregate number of males and females captured.

Due to very high numbers of swarming bats, a 3-point scale reflecting the male reproductive status was adopted, according to Encarnação et al. (2004), Furmankiewicz et al. (2013) and our data, and evaluated based on the size, shape and colour of the caudae epididymides: (1) flat, not distended; (2) distended and pale; (3) distended and dark (black or brown). Temperature was recorded hourly based on readings from the nearest official meteorological station (Katowice-Pyrzowice, Poland). Since bats visiting swarming sites i) remain there from a few hours to 2 nights (Furmankiewicz, 2008) and ii) daily temperature (Ta) cycle affects the thermoregulatory behaviour and energetics of bats (Sedgeley and O'Donnell, 1999; Russo et al., 2004; McGuire et al., 2009; Ingersoll et al., 2010), ambient temperature was pooled from three consecutive nights, with the night of capture being the last one (Fig. 2). Night-time was understood as the time between sunset and sunrise (as in the case of bat trapping). Based on a preliminary study (2012), five bat species with typical autumn swarming behaviour (promiscuous mating system) were selected for detailed analysis: *M. bechsteinii*, *M. daubentonii*, *M. nattereri*, *B. barbastellus* and *P. auritus*. In addition, we analysed *M. myotis*, a species that does not show typical swarming behaviour. Moreover, the similarities in the diets of the studied bat species were characterised based on literature data i) from the same period — swarming, ii) from the nearest geographical location and only from large data sets (Zahn et al., 2006; Pithartová, 2007; Andreas et al., 2012a,b; Graclik and Wasielewski, 2012) (Fig. 1).

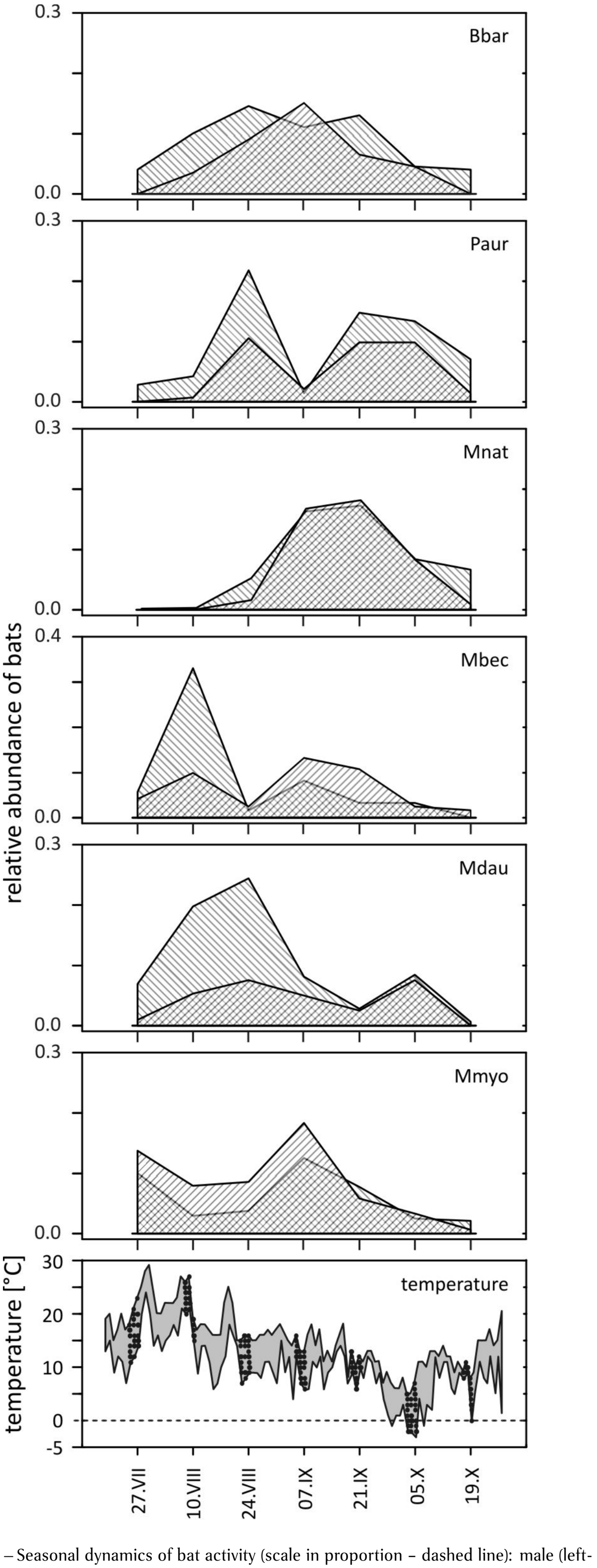

**Figure 2** – Seasonal dynamics of bat activity (scale in proportion – dashed line): male (left-skewed) and female (right-skewed) during the swarming period and temperature: solid line: hourly night temperature (20 °C), filled circles: data used for analysis. Abbreviation: Bbar: *B. barbastellus*, Paur: *P. auritus*, Mnat: *M. nattereri*, Mbec: *M. bechsteinii*, Mdau: *M. daubentonii*, Mmyo: *M. myotis*.

## Data analysis

We only included adult individuals in the analysis. In cases where less than 10 individuals were observed, they were omitted from analyses (see Fig. 2). The divergence of the measured sex ratio from a 1:1 ratio was tested with a chi-square test. Variation in epididymal distension between the bats captured during consecutive nights was tested using the nonparametric Friedman two-way ANOVA.

General Additive Models (GAM in the `mgcv` package) were performed i) to test whether the capture date, sex and interaction between these factors influenced BCI in each of the investigated bat species, ii) to determine to what extent swarming activity, sex ratio, epididymal distension and ambient temperature accounted for BCI variation. To approach normality, proportion was arcsine transformed. Before running the models, we checked for variable smoothing by calculating `gam.check` in the `mgcv` package and found that the models required no smoothing parameters; therefore, linear models were applied. The proportion of variance explained by the model is given for each sex, species and factor (R package: `calc.relimp`, bootstrap=1000).

To determine similarities of the diets between bat species, cluster analysis (Ward's method) with bootstrapping was performed using the R package `pvclust` (Suzuki and Shimodaira, 2006). Distances of objects were calculated in Euclidean space, using the average linkage method. Approximately unbiased bootstrap values (au) were computed by running 100,000 iterations.

All analyses were carried out at a significance level of $p=0.05$. Statistical computations were performed using the software package R 3.2.2 (R Core Team, 2013).

## Results

### Swarming activity of bats

A total of 2712 bats, belonging to 10 species, were captured during autumn while flying inside the cave. *Myotis nattereri*, *M. myotis*, *M. daubentonii*, *B. barbastellus* and *P. auritus* were the dominant swarming species, while *M. bechsteinii* and *M. brandtii* occurred less frequently. The remaining four bat species were observed incidentally.

Temporal distribution of swarming activity differed among species. The most abundant species at the beginning of swarming was *M. myotis*, with the first peak of activity probably occurring already in mid-July (prior to our study, although we did not observe a maternity colony in the cave). Other bat species had different onsets and distributions of autumnal activity, which gradually decreased until the end of October. The first to leave the swarming site were *M. bechsteinii*, *M. daubentonii* and *B. barbastellus*, while *M. nattereri* and *P. auritus* remained active until the end of the study period. Furthermore, females ended their swarming activity earlier than males. At the species level, *M. myotis*, *B. barbastellus* and *M. bechsteinii* females exhibited the highest activity at the beginning of September; the males and females of *M. nattereri* had the highest activity throughout September; *M. daubentonii* and *P. auritus* were characterised by bimodal swarming activity with the first peak at the end of August and the second one at the end of September or in October (Fig. 2).

The sex ratio varied significantly among the species during swarming. Four of six bat species exhibited a similar pattern: the sex ratio gradually became less male-biased during the swarming season until reaching an equilibrium and then gradually rebounded to a male bias (Fig. 3). On the other hand, by the middle of the swarming period, the *M. bechsteinii* population gradually became female-biased, followed by a return close to equilibrium. Only *M. myotis* revealed a different pattern: a female-bias gradually changed into a male-bias (Fig. 3). The sex ratio pooled for the entire swarming season was close to unity in *M. myotis*, *M. nattereri*, *M. bechsteinii* and *B. barbastellus*, while a male bias was observed in *M. brandtii*, *M. daubentonii* and *P. auritus* (Tab. 1).

The degree of epididymal distension differed significantly during the swarming period in three bat species: *M. daubentonii* (Friedman ANOVA chi-square test=10.3, N=6, df=2, $p=0.006$), *P. auritus* ($\chi^2=7.0$, N=7, df=2, $p=0.030$) and *M. nattereri* ($\chi^2=6.08$, N=7, df=2, $p=0.048$). In turn, no differences were found in *M. myotis* ($\chi^2=4.22$, N=7, df=2, $p=0.121$), *M. bechsteinii* ($\chi^2=3.91$, N=6, df=2, $p=0.142$) and *B. barbastellus* ($\chi^2=3.77$, N=7, df=2, $p=0.152$) (Fig. 3).

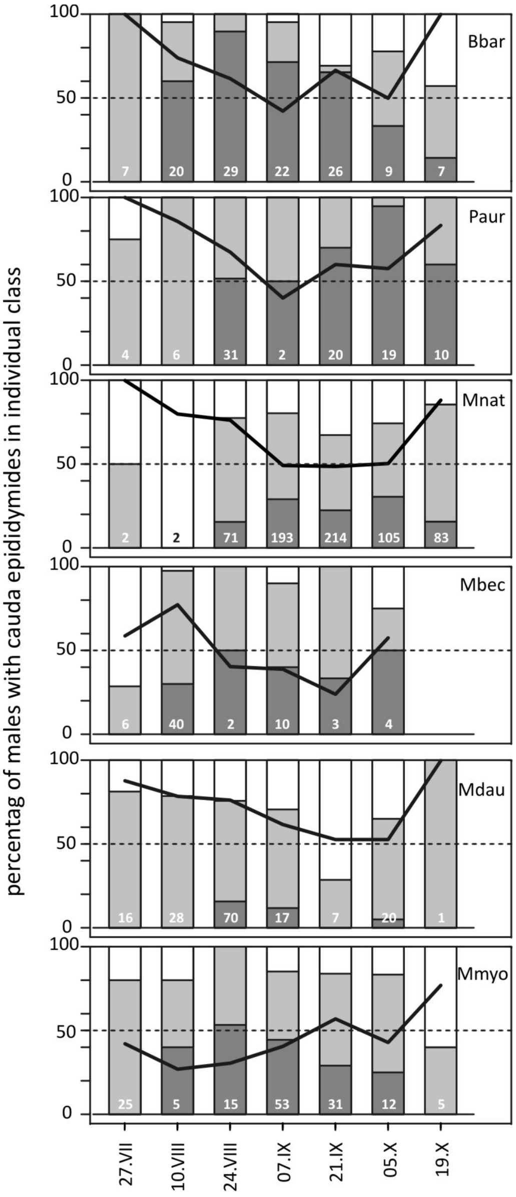

**Figure 3** – Changes in the proportions of three epididymal distension categories: flat and not distended (white bars), distended and pale (grey bars), distended and dark (dark grey) with time during swarming activity (bars) and sex ratio: male participation (solid line), Bbar: *B. barbastellus*, Paur: *P. auritus*, Mnat: *M. nattereri*, Mbec: *M. bechsteinii*, Mdau: *M. daubentonii*, Mmyo: *M. myotis*. Numbers on the bars: number of caught bats.

**Table 1** – Number of adult bats caught during swarming season (year 2013) and found during hibernation season: females/males.

| | Autumn swarming (females/males) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | 27 July | 10 August | 24 August | 07 September | 21 September | 05 October | 19 October | Total |
| *Myotis nattereri* | 0/3 | 1/4 | 22/71$^{***}$ | 227/221$^{ns}$ | 246/234$^{ns}$ | 112/114$^{ns}$ | 12/90$^{***}$ | 620/737$^{ns}$ |
| *Myotis myotis* | 66/48$^{ns}$ | 38/14$^{***}$ | 41/18$^{**}$ | 88/60$^{ns}$ | 28/37$^{ns}$ | 6/12$^{*}$ | 3/10$^{***}$ | 280/199$^{ns}$ |
| *Myotis daubentonii* | 3/22$^{***}$ | 17/63$^{***}$ | 24/78$^{***}$ | 16/26$^{ns}$ | 8/9$^{ns}$ | 24/27$^{ns}$ | 0/2 | 92/227$^{**}$ |
| *Barbastella barbastellus* | 0/8 | 7/20$^{***}$ | 18/29$^{ns}$ | 30/22$^{ns}$ | 13/26$^{*}$ | 9/9$^{ns}$ | 0/8 | 77/122$^{ns}$ |
| *Plecotus auritus* | 0/4 | 1/6 | 15/31$^{*}$ | 3/2 | 14/21$^{ns}$ | 14/19$^{ns}$ | 2/10$^{***}$ | 49/93$^{*}$ |
| *Myotis bechsteinii* | 5/7$^{ns}$ | 12/40$^{***}$ | 3/2 | 16/10$^{ns}$ | 13/4$^{***}$ | 3/4 | 2/0 | 54/67$^{ns}$ |
| *Myotis brandtii* | 6/21$^{***}$ | 7/24$^{***}$ | 1/6 | 0/0 | 0/2 | 2/0 | 1/1 | 17/54$^{***}$ |
| *Myotis dasycneme* | 0/0 | 1/5 | 0/1 | 1/2 | 0/2 | 0/1 | 0/0 | 2/11$^{NA}$ |
| *Eptesicus serotinus* | 0/0 | 3/1 | 1/1 | 0/0 | 0/0 | 0/0 | 0/0 | 2/4$^{NA}$ |
| *Myotis mystacinus* | 1/1 | 1/1 | 0/0 | 0/0 | 0/0 | 1/0 | 0/0 | 3/2$^{NA}$ |
| Total | 195 | 266 | 362 | 724 | 657 | 367 | 141 | 2712 |

Chi-square test for sex ratio: *=$p<0.05$, **=$p<0.01$, ***=$p<0.001$. ns=not significant. NA=insufficient sample size for analysis.
Test was performed only when over 10 individuals of a species were caught.

**Table 2** – Coefficients of averaged models explaining the variation in BCI in relation to sex and date of capture of bats during the swarming period. Estimate: average model coefficients, SE: unconditional standard error, Bbar: *B. barbastellus*, Paur: *P. auritus*, Mnat: *M. nattereri*, Mbec: *M. bechsteinii*, Mdau: *M. daubentonii*, Mmyo: *M. myotis*.

| | Factor | Estimate (±SE) | t value | $p(>\|t\|)$ | rel imp. |
|---|---|---|---|---|---|
| Bbar | (Intercept) | $0.2714 \pm 0.0085$ | 31.8 | $<2 \times 10^{-16}$ | |
| | Sex | $-0.0275 \pm 0.0104$ | −2.66 | 0.009 | 11.7 % |
| | Date | $-0.0062 \pm 0.0021$ | −2.93 | 0.004 | 4.8 % |
| | Sex × Date | $0.0033 \pm 0.0026$ | 1.28 | 0.201 | 0.8 % |
| | | | | | 17.3 % |
| Paur | (Intercept) | $0.2198 \pm 0.0081$ | 27.3 | $<2 \times 10^{-16}$ | |
| | Sex | $-0.0144 \pm 0.0099$ | −1.45 | 0.151 | 9.8 % |
| | Date | $-0.0031 \pm 0.0017$ | −1.82 | 0.072 | 4.0 % |
| | Sex × Date | $0.0010 \pm 0.0021$ | 0.49 | 0.624 | 0.2 % |
| | | | | | 13.9 % |
| Mnat | (Intercept) | $0.1932 \pm 0.0039$ | 49.5 | $<2 \times 10^{-16}$ | |
| | Sex | $-0.0158 \pm 0.0047$ | −3.34 | 0.000 86 | 3.7 % |
| | Date | $0.0031 \pm 0.0008$ | 3.90 | 0.0001 | 6.9 % |
| | Sex × Date | $0.0019 \pm 0.0010$ | 1.93 | 0.053 35 | 0.3 % |
| | | | | | 10.9 % |
| Mbec | (Intercept) | $0.2611 \pm 0.0072$ | 36.3 | $<2 \times 10^{-16}$ | |
| | Sex | $-0.0079 \pm 0.0091$ | −0.87 | 0.386 28 | 4.3 % |
| | Date | $-0.0082 \pm 0.0024$ | −3.42 | 0.000 98 | 21.8 % |
| | Sex × Date | $-0.0006 \pm 0.0033$ | −0.19 | 0.852 46 | 0.0 % |
| | | | | | 26.1 % |
| Mdau | (Intercept) | $0.1889 \pm 0.0151$ | 12.5 | $<2 \times 10^{-16}$ | |
| | Sex | $-0.0102 \pm 0.0177$ | −0.58 | 0.564 | 5.2 % |
| | Date | $0.0189 \pm 0.0035$ | 5.44 | $1.55 \times 10^{-7}$ | 28.4 % |
| | Sex × Date | $-0.0016 \pm 0.0043$ | −0.36 | 0.718 | 0.0 % |
| | | | | | 33.6 % |
| Mmyo | (Intercept) | $0.4614 \pm 0.0067$ | 69.2 | $<2 \times 10^{-16}$ | |
| | Sex | $0.0151 \pm 0.0113$ | 1.34 | 0.183 | 0.0 % |
| | Date | $-0.0019 \pm 0.0018$ | −1.02 | 0.308 | 1.6 % |
| | Sex × Date | $-0.0041 \pm 0.0029$ | −1.38 | 0.168 | 0.5 % |
| | | | | | 2.1 % |

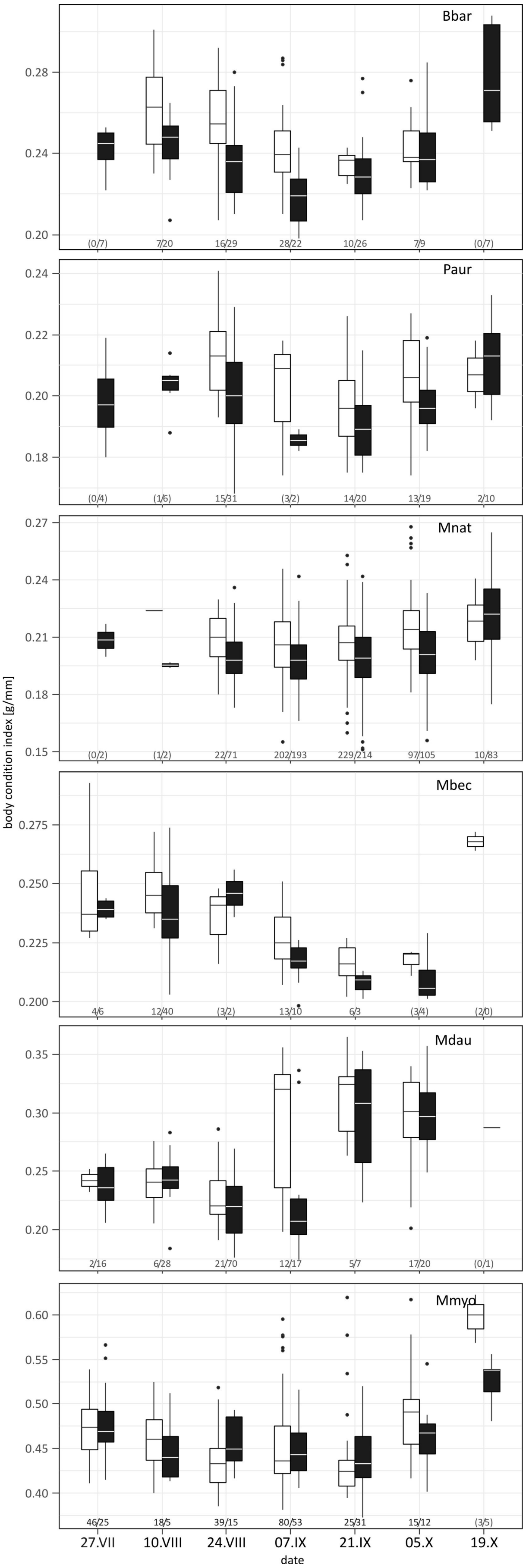

**Figure 4** – Changes in the body condition index (BCI) during swarming in females (open) and males (filled) in six bat species: Bbar: *B. barbastellus*, Paur: *P. auritus*, Mnat: *M. nattereri*, Mbec: *M. bechsteinii*, Mdau: *M. daubentonii*, Mmyo: *M. myotis*. Filled numbers: data used for analyses.

## Temporal and sex-specific patterns of resource accumulation

A generalized linear model, containing the date of capture and sex, explained the largest proportion of the body condition index (BCI) of variance during the swarming period (Fig. 4) for *M. daubentonii* (33.6%) and *M. bechsteinii* (26.1%), a moderate proportion for *B. barbastellus* (17.3%) and *P. auritus* (13.9%) and a low proportion for *M. nattereri* (10.9%) and *M. myotis* (2.1%) (Tab. 2). The date of capture significantly affected the BCI in four bat species: *M. daubentonii* (positively correlated) and *M. bechsteinii* (negatively correlated), in which it accounted for the largest amount of variance, and *M. nattereri* (positively correlated) and *B. barbastellus* (negatively correlated), with only slight effects (Tab. 2). Sex effects were significant in two species: *B. barbastellus* and *M. nattereri* — in both species, males have a lower BCI than females, although this only accounts for a small amount of variation (Tab. 2). The interaction between capture date and sex, which led to different patterns for males and females, accounted for only a minor amount of variance and was nearly significant only in *M. nattereri* (Tab. 2).

## Testing of competing hypotheses

The four analyzed parameters: swarming activity, sex ratio, epididymal distension, and temperature, influenced BCI to varying degrees. The higher value of adjusted R-squared was noted for *M. daubentonii* and explained nearly half of the variation (males = females), more than a quarter in *M. bechsteinii* (males = females), less in *B. barbastellus* (males > females) and *P. auritus* (males < females), but only slightly

**Table 3** – Coefficients of averaged models explaining variation in BCI in relation to swarming factors: ep dist: epididymal distension, Ta 3: mean temperature (3 days), active arcsin: activity, sex arcsin: sex ratio. Bbar: *B. barbastellus*, Paur: *P. auritus*, Mnat: *M. nattereri*, Mbec: *M. bechsteinii*, Mdau: *M. daubentonii*, Mmyo: *M. myotis*.

| | | **Females** | | | | **Males** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Factor** | **Estimate (±SE)** | **t value** | $p(>\|t\|)$ | **rel. imp** | **Estimate (±SE)** | **t value** | $p(>\|t\|)$ | **rel. imp** |
| Bbar | (Intercept) | 0.2410 ± 0.0383 | 6.2 | $3.4 \times 10^{-8}$ | | −0.0450 ± 0.0924 | −0.487 | 0.627 | |
| | ep dist | 0.0520 ± 0.0220 | 2.37 | 0.0208 | 2.9 % | 0.0680 ± 0.0247 | 2.77 | 0.007 | 5.2 % |
| | Ta 3 | 0.0020 ± 0.0009 | 2.34 | 0.0223 | 5.2 % | −0.0030 ± 0.0012 | −2.79 | 0.006 | 3.8 % |
| | activ arcsin | −0.9420 ± 0.3612 | −2.61 | 0.0114 | 3.6 % | −0.8630 ± 0.2717 | −3.18 | 0.002 | 3.3 % |
| | sex arcsin | −0.2160 ± 0.0885 | −2.45 | 0.0172 | 3.3 % | 0.2150 ± 0.0574 | 3.75 | 0.000 | 11.3 % |
| | $R^2$ adjusted | | | | 15.0 % | | | | 23.6 % |
| Paur | (Intercept) | 0.6160 ± 0.1463 | 4.21 | 0.0002 | | 0.4650 ± 0.0910 | 5.11 | 0.000 | |
| | ep dist | −0.0930 ± 0.0329 | −2.81 | 0.0077 | 9.1 % | −0.0610 ± 0.0206 | −2.96 | 0.004 | 6.4 % |
| | Ta 3 | −0.0070 ± 0.0027 | −2.71 | 0.0101 | 7.9 % | −0.0050 ± 0.0016 | −2.82 | 0.006 | 5.3 % |
| | activ arcsin | NA | NA | NA | NA | NA | NA | NA | NA |
| | sex arcsin | NA | NA | NA | NA | NA | NA | NA | NA |
| | $R^2$ adjusted | | | | 17.0 % | | | | 11.7 % |
| Mnat | (Intercept) | 0.2010 ± 0.0253 | 7.95 | $1.03 \times 10^{-14}$ | | 0.1580 ± 0.0151 | 10.47 | 0.000 | |
| | ep dist | 0.0010 ± 0.0054 | 0.197 | 0.8442 | 0.1 % | 0.0000 ± 0.0048 | 0.08 | 0.935 | 0.3 % |
| | Ta 3 | −0.0010 ± 0.0005 | −2.365 | 0.0184 | 2.5 % | −0.0020 ± 0.0003 | −6.40 | 0.000 | 2.7 % |
| | activ arcsin | 0.0160 ± 0.0501 | 0.32 | 0.7491 | 1.7 % | 0.1560 ± 0.0270 | 5.79 | 0.000 | 4.2 % |
| | sex arcsin | 0.0200 ± 0.0195 | 1.047 | 0.2957 | 0.6 % | 0.0600 ± 0.0059 | 10.25 | 0.000 | 12.4 % |
| | $R^2$ adjusted | | | | 4.9 % | | | | 19.6 % |
| Mbec | (Intercept) | 0.2270 ± 0.0173 | 13.15 | $5.42 \times 10^{-13}$ | | 0.2170 ± 0.0121 | 18.02 | 0.000 | |
| | ep dist | −0.0060 ± 0.0051 | −1.239 | 0.226 51 | 3.7 % | −0.0070 ± 0.0037 | −1.96 | 0.056 | 3.2 % |
| | Ta 3 | 0.0020 ± 0.0006 | 3.032 | 0.005 45 | 24.8 % | 0.0020 ± 0.0005 | 4.05 | 0.000 | 21.1 % |
| | activ arcsin | NA | NA | NA | NA | NA | NA | NA | NA |
| | sex arcsin | NA | NA | NA | NA | NA | NA | NA | NA |
| | $R^2$ adjusted | | | | 28.5 % | | | | 24.3 % |
| Mdau | (Intercept) | 0.4230 ± 0.0751 | 5.635 | $5.91 \times 10^{-7}$ | | 2.8420 ± 0.3580 | 7.94 | 0.000 | |
| | ep dist | 0.0220 ± 0.0484 | 0.445 | 0.6578 | 6.2 % | 0.3100 ± 0.0739 | 4.20 | 0.000 | 15.9 % |
| | Ta 3 | 0.0020 ± 0.0043 | 0.422 | 0.6747 | 9.0 % | 0.0750 ± 0.0120 | 6.25 | 0.000 | 8.8 % |
| | activ arcsin | −0.3290 ± 1.0783 | −0.305 | 0.7613 | 6.1 % | 8.3240 ± 1.3044 | 6.38 | 0.000 | 13.8 % |
| | sex arcsin | −0.2740 ± 0.1577 | −1.737 | 0.0878 | 20.5 % | −7.1410 ± 1.1132 | −6.42 | 0.000 | 15.7 % |
| | $R^2$ adjusted | | | | 41.8 % | | | | 54.2 % |
| Mmyo | (Intercept) | 0.6540 ± 0.0457 | 14.31 | $2 \times 10^{-16}$ | | 0.5990 ± 0.0395 | 15.15 | 0.000 | |
| | ep dist | −0.0380 ± 0.0076 | −5 | $1.17 \times 10^{-6}$ | 7.7 % | −0.0270 ± 0.0075 | −3.55 | 0.001 | 5.9 % |
| | Ta 3 | −0.0030 ± 0.0009 | −3.034 | 0.0027 | 1.4 % | −0.0010 ± 0.0009 | −1.13 | 0.259 | 0.8 % |
| | activ arcsin | 0.0130 ± 0.0548 | 0.242 | 0.809 37 | 0.0 % | 0.0060 ± 0.0831 | 0.07 | 0.943 | 0.1 % |
| | sex arcsin | −0.1310 ± 0.0461 | −2.849 | 0.004 81 | 1.3 % | −0.1240 ± 0.0377 | −3.30 | 0.001 | 4.8 % |
| | $R^2$ adjusted | | | | 1.4 % | | | | 10.0 % |

explained variation in *M. myotis* (males = females) and *M. nattereri* (males > females) (Tab. 3).

The amount of variation accounted for the mean size of epididymal distension, ranging from 0.1% to 15.9%. In males, the size of the epididymis explained the largest part of the variation in BCI in *M. daubentonii* (positively correlated), but only to a slight degree in *P. auritus* (negatively correlated), *M. myotis* (negatively correlated) and *B. barbastellus* (positively correlated); epididymis size was nearly significant in *M. bechsteinii* (negatively correlated). In females, the size of the male epididymis only slightly explained BCI variation and to a smaller extent than in males, namely in *P. auritus* (negatively correlated), *M. myotis* (negatively correlated) and *B. barbastellus* (positively correlated). Within individual species, similar patterns for males and females were found in all investigated species with slight differences; larger differences were only found for *M. daubentonii* (Tab. 3).

The amount of variation accounted for by temperature ranged from 0.8% to 24.8%. In males, temperature explained more variation in BCI in *M. bechsteinii* (positively correlated), while in the other species, the effect of temperature was less pronounced: *M. daubentonii* (positively correlated), *P. auritus* (negatively correlated), *B. barbastellus* (positively correlated) and *M. nattereri* (negatively correlated). In females, temperature explained more BCI variation in *M. bechsteinii* (positively correlated), while in the other species, the effect of temperature was similar compared to that in males: *M. daubentonii* (positively correlated), *P. auritus* (negatively correlated), *B. barbastellus* (positively correlated), *M. nattereri* (negatively correlated) and *M. myotis* (negatively correlated). Within individual species, similar patterns for males and females were found in all investigated species with slight differences; the opposite pattern was found for *B. barbastellus* (Tab. 3).

The amount of variation explained by swarming activity ranged from 0.0 to 13.8%. In males, swarming activity explained more variation of BCI in *M. daubentonii* (positively correlated) and only a small part of variation in *M. nattereri* and *B. barbastellus* (negatively correlated). In females, swarming activity explained more variation in BCI to a lesser extent than in males in *M. daubentonii*, although this finding was not significant (negatively correlated); swarming activity explained a significantly lower amount of variation in *B. barbastellus* (negatively correlated). In *P. auritus* and *M. bechsteinii*, swarming activity as a factor was excluded from GAMs. Within individual species, similar patterns for males and females were found in *B. barbastellus*; in contrast, *M. daubentonii* exhibited the opposite pattern (Tab. 3).

The amount of variation accounted for by the sex ratio (participation of males) ranged from 0.6% to 20.5%. In males, the sex ratio explained the largest part of variation in BCI in *M. daubentonii* (negatively correlated), *M. nattereri* (positively correlated) and *B. barbastellus* (positively correlated). In females, the sex ratio explained of the largest part of variation in BCI, although this result was only significant in *M. daubentonii*, while sex ratio only explained a small amount of variation in *B. barbastellus* and *M. myotis* (negative correlations for all species). Within species, similar patterns for males and females were found only in *M. daubentonii* and *M. myotis*, whereas in *B. barbastellus* and *M. nattereri*, the patterns were sex-specific. In *P. auritus* and *M. bechsteinii*, swarming activity as a factor was excluded from GAMs (Tab. 3).

## Discussion

In Europe, seasonal segregation among different species of swarming bats seems to be universal and independent of the geographic regions, elevation or weather (Parsons et al., 2003b; Piksa et al., 2011; van Schaik et al., 2015). A difference occurs, however, among species and refers to the number of peaks of activity. In *P. auritus*, unimodal (Furmankiewicz and Górniak, 2002; Piksa, 2008; Pfeiffer and Mayer, 2013), bimodal (our results) and multimodal patterns of activity have been found (van Schaik et al., 2015); in *M. bechsteinii*, both unimodal (Piksa, 2008) and bimodal patterns have been observed (van Schaik et al., 2015, our data), while in *M. myotis*, both unimodal (Pfeiffer and Mayer, 2013), bimodal (our data) and multimodal patterns were found (van Schaik et al., 2015). In *B. barbastellus*, the unimodal pattern has been observed (Gottfried, 2009, our data). Such large interspecific differences in activity patterns seem to be a result of various functions (exploring, swarming, wintering or both) rather than the division of functions into mating and accumulation phases, as suggested by some authors (Horáček and Zima, 1978).

A strong male bias in bats is considered typical in swarming species, with a universal characteristic pattern, namely a gradual increase in the proportion of females in the middle of the swarming period (Furmankiewicz and Górniak, 2002; Kerth et al., 2003; Parsons et al., 2003a; Rivers et al., 2006); this pattern is consistent with our results. However, in *M. myotis*, for the majority of the autumn period, females were slightly prevalent, and mating was not accompanied by typical swarming behaviour (Zahn and Dippel, 1997). The sex ratio for the entire period was balanced not only in *M. myotis*, as described by other authors (Pfeiffer and Mayer, 2013), but also in *M. nattereri*, *B. barbastellus* and *M. bechsteinii*, which stands in contrast to previous findings (Furmankiewicz and Górniak, 2002; Parsons et al., 2003a; Rivers et al., 2006; Gottfried, 2009). However, the other bat species, *M. daubentonii*, *P. auritus* and *M. brandtii*, exhibited a typical highly male-skewed sex ratio (Piksa, 2008). While a balanced sex ratio in *M. myotis* may result from the absence of typical swarming, this species is characterised by polygyny but not by a lek system (McCracken and Wilkinson, 2000), in other bat species, this may be attributable to the dual function of the cave, used both for swarming and wintering purposes. A balanced sex ratio would be expected, as both males and females require hibernation sites (Koteja et al., 2001), suggesting that for most species, the Szachownica cave is the destined wintering location. The similarity between swarming and hibernating bat assemblage indicates the use of swarming sites as hibernation sites (Furmankiewicz and Górniak, 2002; Piksa, 2008; van Schaik et al., 2015).

Variations in body conditions usually change seasonally with a sex-dependent pattern during the pre-hibernation period in temperate bat species (Entwistle et al., 1998; Kunz et al., 1998; Encarnação et al., 2004; Rughetti and Toffoli, 2014). A seasonal variation in bat body condition can be a response to changes in food availability (Kunz et al., 1998; Wojciechowski et al., 2007); in turn, sex-specific patterns should reflect differences in timing of maximum energy allocation (Entwistle et al., 1998; Encarnação et al., 2004; Jonasson and Willis, 2011). In the two bat species *P. auritus* and *B. barbastellus*, characterised by a similar diet (Andreas et al., 2012a,b), the sex was the most influential factor, whereas the capture date was a less significant factor. In turn, the second pair of species with a similar diet, *M. bechsteinii* and *M. nattereri* (Andreas et al., 2012a), differed in resource accumulation patterns. In contrast to other species, in *M. myotis*, variance of resources is not determined by either capture date or sex, although this could be expected due to food preferences and mating behaviour (Zahn and Dippel, 1997; Zahn et al., 2006). Therefore, diet preferences (Fig.1) only explained species-specific patterns of resource accumulation to a certain degree. The hypothesis that the species-specific differences in activity are mainly determined by diet was not corroborated — species-specific patterns seem to be more complex and may also depend on swarming behaviour, thermoregulatory (torpor ability Encarnação et al., 2012; Becker et al., 2013; Matthias et al., 2013 or hibernation strategy (Ingersoll et al., 2010)). It has also been hypothesised that the purpose of differences in the activity of species with similar diets is to avoid competition, although this theory is controversial.

### Competing hypotheses

Flight activity is energetically costly and may reduce body mass (Lundberg and Gerell, 1986), especially during migration or chasing flight. Bats arriving from the surrounding areas to swarm for several hours and then depart before sunset (Parsons et al., 2003b) use shelters such as trees or, occasionally, caves for daylight alternatives (Parsons and Jones, 2003). Energy expenditure depends on the distance between the foraging area and roost or swarming site (Parsons and Jones, 2003; Hillen et al., 2011), and therefore, species-specific differences should be expected. Among the examined bat species, the largest distances between daily roosts and swarming sites were found for *M. myotis* (Zahn and Dippel, 1997) and *M. nattereri* (Parsons and Jones, 2003; Rivers et al., 2006), followed by *M. daubentonii* (Parsons and Jones, 2003) and the sedentary species *M. bechsteinii* (Kerth et al., 2003), *B. barbastellus* (Gottfried, *pers. comm.* 2016) and *P. auritus* (Furmankiewicz, 2008). In all these species, females travelled longer distances than males. Surprisingly, the obtained effect of swarming activity was considerably lower than expected and did not occur in all species; actually, *M. nattereri* males exhibited a slight but significant increase in BCI during high activity. Among the studied species, males and females differed in terms of the influence of specific factors on BCI, except for *M. bechsteinii*, in which that impact was almost the same. It may be assumed that fat accumulation occurs during periods of lower swarming activity of bats in proximity of the cave. Nightly activity has a similar pattern throughout the swarming season: it is low after dusk, with a peak in the middle of the night (Parsons et al., 2003b), indicating intensive feeding before mating (Šuba et al., 2011). Hence, energy depletion during mating or migration flights may be compensated by ongoing prey intake. As flight cost increases with weight, the absence of fat accumulation during peak activity seems to be an adaptive feature regulating energy expenditure. In turn, sex-specific differences may result not only from different patterns of foraging activity and mating behaviour, but also from a thermoregulation strategy: females use daily torpor more frequently and for longer periods of time than males (Dietz and Kalko, 2006).

Females that have successfully mated may visit swarming sites less frequently than males or for less time (Senior et al., 2005; Furmankiewicz, 2008; Gottfried, 2009). In turn, to maximise their reproductive success, males should visit swarming sites and mate as often as possible (Kerth et al., 2003; Kerth and Morf, 2004; Veith et al., 2004). Therefore, a skewed sex ratio reflects mainly behavioural differences between the sexes, and, according to previous results, we expected that higher male activity should be negatively correlated with their fat reserves (Entwistle et al., 1998; Encarnação et al., 2004; Gottfried, 2009; Kohyt et al., 2016), while in females, those variables should be independent (Jonasson and Willis, 2011). In our study, sex ratio variation was linked to BCI dynamics and exhibited mainly sex-specific patterns: in foliage gleaners (*M. nattereri*, *M. bechsteinii* and *P. auritus*), a higher proportion of males correlated with a higher BCI, while in *M. daubentonii* and *B. barbastellus*, it correlated with a lower female BCI. A greater presence of females could reduce foraging time for males and/or increase their energy expenditure on mating behaviour; however, this applies to species with remarkable ecological flexibility, including high seasonal variability of diets (Andreas et al., 2012a). In contrast, in species with a narrow trophic niche, namely *M. daubentonii* (Pithartová, 2007) and *B. barbastellus* (Andreas et al., 2012b), the peak of the male presence correlated negatively with female BCI. Species-specific differences probably indicate foraging-specific compensation of energetic expenditure during swarming (mating effort) and thermoregulatory balance and were also partly associated with sex-specific differences in the arrival at the swarming site (but this issue requires further research).

The reproductive condition of males is closely linked to their physical condition (Speakman and Racey, 1986; Entwistle et al., 1998): males in good body condition will have a higher reproductive status than those in poor body condition. On the other hand, a high reproductive activity of males has no effect on body condition in some of the swarming bat species (Gallant and Broders, 2015). The findings of the present study provided only weak evidence for a relationship between the reproductive condition (epididymal size) and BCI in males. Moreover, the effect of epididymal distension on fat resources was different from that of male activity, although the two parameters were closely related (Pfeiffer and Mayer, 2013). Among typical swarming bat species, increased epididymal size entailed a high decline in BCI only in *M. daubentonii* males, which stands in contrast to a previous study of Encarnação et al. (2006). Differences between these findings are probably attributable to the fact that the study was carried out in August, while ours was conducted until the end of October. In the remaining species, the reproductive condition of males either had no or a slightly positive effect on their BCI. The changing frequency of visits or distance from the mating site could compensate the energetic expenditure during swarming, but these factors did not produce a straightforward correlation with BCI (Gallant and Broders, 2015). In turn, a small negative correlation between the reproductive status of males and female BCI was found in *P. auritus*. *Plecotus* is the only European genus of bats in which swarming begins in autumn and extends into spring (Furmankiewicz, 2008; Pfeiffer and Mayer, 2013), and this physiological adaptation for long-term sperm storage may have contributed to a different pattern of fat deposition. Similar negative effects were identified in both sexes of *M. myotis*, probably resulting from a reproductive strategy other than swarming. In autumn, members of this species form small harems, consisting of one male and one to several females and lasting for one to several days, with both sexes often giving up foraging (Zahn and Dippel, 1997). In this strategy, some sex-specific differences can be expected. In the studied cave, large, periodic aggregations of *M. myotis* were observed, but not typical harems. It is possible that both sexes came to the cave after the harems had disintegrated, and the negative impact on body condition may have resulted from both mating completion and migration.

Last but not least, temperature can also significantly contribute to variations in body mass due to diminished prey activity. Temperature affects flying and ground insects to different degrees (Anthony and Kunz, 1977; Šuba et al., 2011), which should be reflected in bat BCI: open-foraging bats, which feed on flying insects, could be expected to complete fat accumulation earlier than gleaning bats, which capture prey from surfaces. However, in our study, larger differences were obtained between different gleaning bat species than between gleaners and aerial hawkers: lower temperature resulted in a considerable BCI reduction in *M. bechsteinii*, but an opposite, albeit weaker, effect was noted for *M. nattereri* and *P. auritus*. In turn, the diet of *M. bechsteinii* is more similar to that of *M. nattereri* than that of *P. auritus* (Andreas et al., 2012a) (Fig. 1), which largely excluded its interaction with temperature and the impact on resource accumulation. Furthermore, *M. daubentonii* bats can forage even at very low temperatures (Dietz and Kalko, 2006; Ciechanowski et al., 2007), but their body mass started to decline earlier than that of other bat species. On the other hand, lower temperature often induces bat torpor, limiting swarming behaviour (Rivers et al., 2006). Torpor use is also influenced by food availability (Wojciechowski et al., 2007), which indicates that this energy-saving mechanism is especially important under variable conditions. However, regardless of its induction mechanism, torpor precipitates fat accumulation or its efficient assimilation (Speakman and Racey, 1986), and therefore, lower temperatures may considerably enhance BCI. Inter-specific differences in response to different temperature conditions could also result from physiological adaptations: according to a previous study, minimum skin temperature during the active period in three bat species is lowest in *P. auritus*, intermediate in *M. nattereri* and highest in *M. bechsteinii* (Matthias et al., 2013). Minimum skin temperature in *M. daubentonii* is similar to that in *M. nattereri*, but is highly variable depending on habitat characteristics (Encarnação et al., 2012). For most species, our results indicate a compromise: accumulation occurs at a lower temperature (with less available prey), but with the use of torpor. In turn, species-specific minimum skin temperature may, to some extent, explain differences in the use of energy-saving mechanisms and fattening. The species *M. bechsteinii* is unique in that temperature variations probably shortened its foraging times due to a distinct thermoregulatory behaviour, whereas fat accumulation occurred outside of the swarming site to a much greater extent than in other species.

Our study shows that the studied species differ considerably in the effects of the analysed factors on the pattern of fat accumulation during the swarming season: in some species, BCI is mainly dependent on the sex ratio (*M. daubentonii* and *B. barbastellu*), while in others, it depends on the male epididymal distension (*M. daubentonii* and *M. myotis*) or on temperature (*M. bechsteinii*). Unexpectedly, swarming activity, generally regarded as a factor negatively correlated with fat reserves (Gottfried, 2009; Šuba et al., 2011), had only limited explanatory power. Patterns of resource accumulation are sex-specific in bat species exhibiting typical swarming behaviour. Furthermore, the analysed factors affecting BCI are somehow interrelated: swarming activity is negatively correlated with temperature and epididymal distension, which are in turn positively correlated with each other. Despite similarities in swarming behaviour, the studied factors are associated with different energy-saving mechanisms and hibernation strategies and thus exert different effects on fat accumulation.

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