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BODY WEIGHT PROVIDES INSIGHT INTO THE FEEDING STRATEGY OF SWARMING BATS

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ABSTRACT **-** Temperate bat species that hibernate in underground sites are known to visit hibernacula in late summer where they perform an activity known as ‘swarming’. We analysed trends in body mass-to-forearm ratio – the body condition index (BCI) - to investigate whether bats arrive at swarming sites following intensive nocturnal feeding. In a two-year study, *Myotis daubentonii, M. brandtii* and *M. dasycneme* were captured by mist-net at one swarming site from late July until early October. In late summer, the BCIs of captured males, females and subadult bats were positively correlated to the time of their capture during the night. In September, adult bats had higher BCIs than in late summer and the BCI did not increase during the night. For subadult *M. daubentonii,* the BCI was positively correlated to the time of capture in early autumn. Our results indicate that in late summer bats feed intensively during the first hours of the night before visiting swarming sites. In early autumn, subadult bats may go on feeding to complete fat accumulation.

Key words: Chiroptera, body condition index, feeding strategy*, Myotis*

RIASSUNTO - ***Deduzioni sul comportamento alimentare dei pipistrelli durante lo “swarming” a partire dall’analisi del peso corporeo***. I pipistrelli delle aree temperate che utilizzano rifugi sotterranei sono soliti visitarli a partire dalla fine dell’estate, un attività definita come “swarming”. Abbiamo analizzato la variazione nel rapporto peso corporeo – lunghezza dell’avambraccio – l’Indice di Condizione Corporea (ICC) – per verificare se i pipistrelli arrivano ai siti di swarming dopo essersi alimentati a sufficienza. Nel corso di due anni, dalla fine di luglio a inizio ottobre *Myotis daubentonii, M. brandtii* e *M. dasycneme* sono stati catturati tramite mist-net presso una cavità. Alla fine dell’estate, l’ICC di maschi, femmine e subadulti è risultato correlato positivamente all’ora di cattura. In settembre, l’ICC degli adulti è risultato maggiore e stabile nel corso della notte. All’inizio dell’autunno, l’ICC dei *M. daubentonii* subadulti è risultato correlato positivamente all’ora di cattura. I risultati ottenuti suggeriscono che in tarda estate i pipistrelli si nutrono in modo intensivo prima di raggiungere i siti di swarming, mentre, all’inizio dell’autunno, i subadulti devono ancora completare le riserve lipidiche.

Key words: Chiroptera, indice di condizione corporea, strategie alimentari*, Myotis*

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INTRODUCTION

In late summer and autumn, temperate bat species gather at underground hibernacula in large numbers to perform an activity known as 'swarming' (Fenton 1969; Kretzschmar and Heinz 1995; Parsons et al. 2003a; Piksa 2008). This behaviour has been associated with either the assessment of hibernacula prior to hibernation or information transfer from adults to subadults to familiarise them with suitable hibernation sites (Fenton 1969; Bauerová and Zima 1988; Veith et al. 2004). Swarming may also facilitate gene flow among summer colonies through mating (Kerth et al. 2003; Rivers et al. 2005).

The peak in swarming activity is observed around or after midnight (Degn et al. 1995; Parsons et al. 2003b; Berková and Zukal 2006; Rivers et al. 2006). This suggests that bats arrive at swarming sites from distant locations or after foraging. Feeding seems to be a reasonable explanation, since bats enter a state of hyperphagia before hibernation (McGuire et al. 2009a): the more the time bats spend on feeding, the more the fat they can accumulate for hibernation (Kunz et al. 1998). There may, however, be some trade-offs between longer feeding and early arriving at the swarming site, e.g. adult males may lose an opportunity to select and occupy strategic mating spots (Piksa 2008).

Gould (1955) observed that insectivorous bats are able to capture 1–3 g of insects per hour, which represents 9–51% of their pre-feeding body mass. Hence, feeding performance can be estimated by measuring individual body weights. The condition of a bat's digestive tract (full or empty) can also be evaluated by touch (Fenton 1969). To our knowledge, no study has analysed the feeding performance of swarming bats by monitoring the variation in their body mass during the night. In some studies on body mass variation (e.g. Encarnação et al. 2004), weighing wild bats after feeding was avoided, since stomach content could impair the correct assessment of body condition.

We conducted a field study to investigate whether bats arrive at swarming sites following intensive feeding. Most feeding activity may occur in the first hours of the night, since aerial insect density is the highest around sunset (Racey and Swift 1985). We hypothesized that in late summer the body weight of captured bats would be positively correlated to the time of their capture, assuming that those individuals which spent more time on feeding would have increased body weight. In early autumn, when adult bats have accumulated enough fat for hibernation, subadult bats (young of the year) may be supposed to still feed intensively to complete fat accumulation (Kunz et al. 1998; McGuire et al. 2009a).

MATERIALS AND METHODS

1. Study site

Bats were captured at a semi-natural cave in the Devon dolomite (ca. 60 m in length), situated in Gauja National Park (central Latvia), ca. 5 km NE of Cēsis (57°19', 25°21'). The cave is located in woodland next to a ravine, a narrow gorge and agricultural land. Seven bat species are known to hibernate and swarm there, of which *Myotis daubentonii, M. dasycneme,* and *M. brandtii* are the most abundant (Šuba et al. 2008).

2. Trapping methods

From late July until early October 2006–2007, bats were captured by a polyester mist-net (2.5 x 3.0 m, Ecotone, Gdańsk, Poland) placed in front of the cave entrance (Kunz and Kurta 1988). We started netting just after sunset and removed the net after sunrise (netting duration varied between 5 and 12 hours across the season). Other minor entrances were covered by polythene, branches and leaves. The individuals caught flying from the inside of the cave (i.e. departing individuals) were separated from the individuals captured while trying to enter into the cave (i.e. arriving individuals). Netting (n = 7 in 2006, n = 8 in 2007) was performed fortnightly (approximately on the same dates in both years) to minimize disturbance on bats. Nights with strong wind and heavy rain were avoided.
Time of capture, flight direction, species, sex, age, forearm length and body mass of captured individuals were recorded. Age (adult or subadult) was assessed according to the degree of ossification and shape of the metacarpal-phalangeal joints (Anthony 1988). The individuals were weighed and measured within the hour of capture. We weighed bats using a 50 g Pesola balance (± 0.25 g) and measured forearm length using callipers (± 0.1 mm). Captured bats were handled with care and released at the site of capture.

3. Data analysis

Since large bats are expected to weigh more than small ones, for any captured individual we calculated the body condition index (BCI), defined as the ratio between body mass and forearm length, which allows for the effect of size on body mass (Speakman and Racey 1986; Pearce et al. 2008). The analyses covered adult males, adult females and subadults (both sexes pooled) of *M. daubentonii, M. dasycneme* and *M. brandtii.* To increase sample size, data from both years were pooled for five periods (late July, early August, late August, early September and late September). Sample size for early October was insufficient and therefore we did not include those data in the analysis.
The relationship between the BCI of captured bats and time of their capture (expressed in hours after sunset, with sunset hour = 0) was analysed by Spearman's rank correlation. We assumed that departing and arriving bats captured during the first hour after sunset had their stomachs still empty. Statistical analyses were performed by SPSS for Windows 16.0 (SPSS Inc., Chicago, Illinois).

RESULTS

In the study period, we captured and measured 746 *M. daubentonii* (380 males, 149 females, 217 subadults), 489 *M. brandtii* (200 males, 106 females, 183 subadults) and 241 *M. dasycneme* (98 males, 54 females, 89 subadults). Most bats were captured in August (N = 835) and September (N = 440). In late July and early August, most bats captured were adult males of all the studied species (71.1 %). In late August and September, captured bats were mostly subadults (41.8 %). In August, most bats captured were departing individuals (65.7%). From late July until early September 60.1– 91.7 % of departing individuals were caught during the first two hours after sunset. Individuals of all studied species (*M. daubentonii*, 56.5%; *M. brandtii*, 30.8%;

Table 1 - Mean body mass (m) and body condition index (BCI) (± SE) of arriving swarming bats captured in summer and early autumn.

	Cohort	Late July and August			September		
		m (g)	BCI (g mm^{-1})	N	m (g)	BCI (g mm^{-1})	N
M. daubentonii	Ad M.	8.46 (±0.15)	0.227 (± 0.004)	72	11.17 (± 0.28)	0.299 (± 0.007)	52
	Ad F.	9.15 (± 0.27)	0.237 (± 0.007)	15	11.74 (± 0.23)	0.307 (± 0.006)	69
	Subad.	8.31 (± 0.15)	0.218 (± 0.004)	40	9.00 (± 0.16)	0.239 (± 0.004)	80
M. brandtii	Ad M.	7.10 (± 0.15)	0.203 (± 0.004)	68	9.08 (± 0.16)	0.258 (± 0.004)	38
	Ad F.	7.39 (± 0.27)	0.208 (± 0.007)	26	9.07 (± 0.11)	0.257 (± 0.003)	30
	Subad.	6.41 (± 0.10)	0.184 (± 0.003)	65	6.47 (± 0.13)	0.185 (± 0.004)	38
M. dasycneme	Ad. M.	16.55 (±0.38)	0.362 (± 0.010)	19	20.19 (± 0.80)	0.435 (± 0.017)	20
	Ad. F.	18.96 (±1.69)	0.402 (± 0.039)	6	23.17 (± 0.44)	0.499 (± 0.009)	24
	Subad.	15.75	0.335	2	19.32 (± 0.52)	0.416 (± 0.010)	29

M. dasycneme, 12.7%) were caught leaving the cave in the evening. The proportion of arriving individuals gradually increased from early August (32.6%) until late September (92.1%).

In late July, most of the bats captured were adult males of *M. brandtii* (88.9 % of all captured *M. brandtii*), for which the BCI was correlated with the time of their capture (r_S = 0.51, p < 0.01, n = 34). In early August, the BCI of captured individuals increased significantly during the course of night for most cohorts of analysed species (Fig. 1). The increase occurred also in late August, but the BCI was not significantly correlated to the time of capture for *M. brandtii* adult males (r_S = 0.11, p = 0.46, n = 28), *M. daubentonii* adult females (r_S = 0.28, p = 0.14, n = 30) and *M. dasycneme* adult females (r_S = 0.26, p = 0.40, n = 13) and subadults (r_S = 0.05, p = 0.86, n = 17). It must be mentioned, however, that in these cases most individuals were captured during the first hours of night, hence data on later hours were insufficient or lacking.

In September, captured individuals had higher mean BCI than in late summer, except *M. brandtii* subadult individuals (Tab. 1). However, BCIs for departing *M. daubentonii* adult males and females captured during the two-hour period after sunset was low (0.198 g mm^{-1}, SD = 0.008, n = 6 and 0.218 g mm^{-1}, SD = 0.005, n = 4, respectively).

In early September, no relationship was found between the BCI and time of capture for most cohorts, except for *M. daubentonii* subadult individuals (Fig. 2). In late September, the BCI was also correlated to the time of capture for *M. daubentonii* subadults (r_S = 0.61, p < 0.01, n = 45).

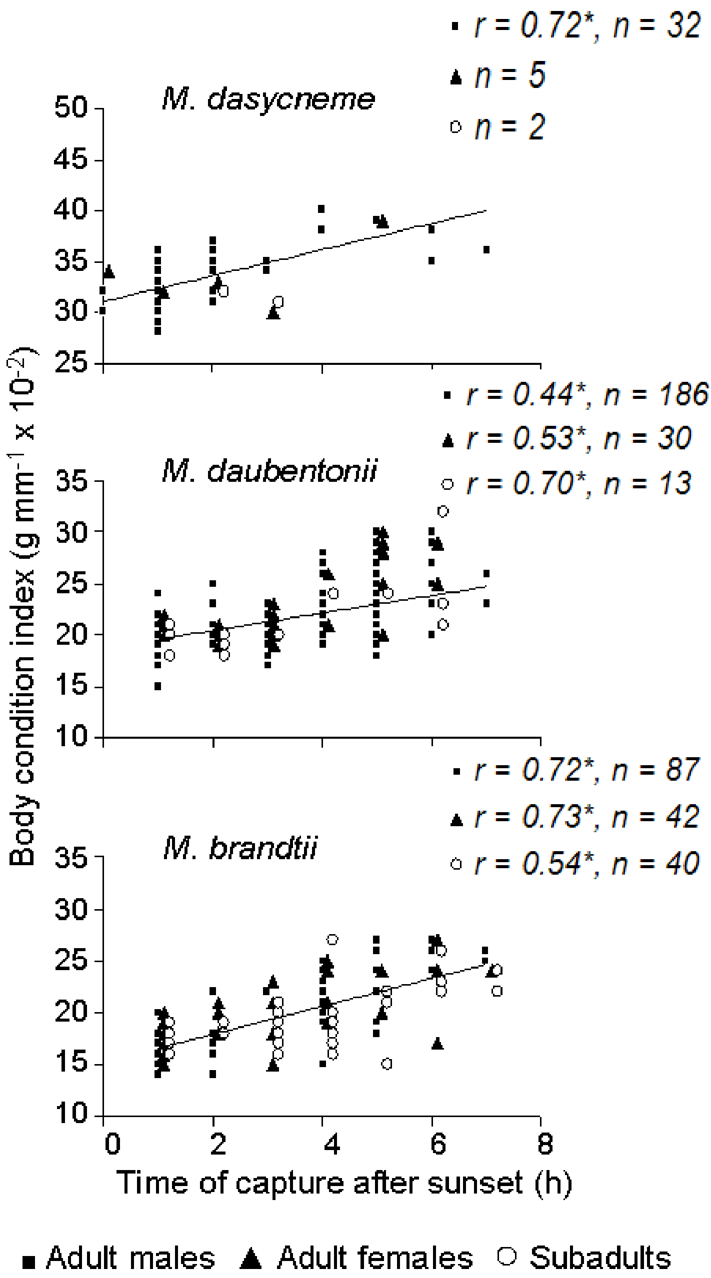

Figure 1 - Relationship between body condition indexes of captured swarming bats and time of their capture in early August. Time of capture was noted as hour after sunset (0 = sunset hour). Asterisk indicates significant correlation ($p < 0.01$, Spearman's rank correlation analysis). The line indicates the trend for all captured individuals.

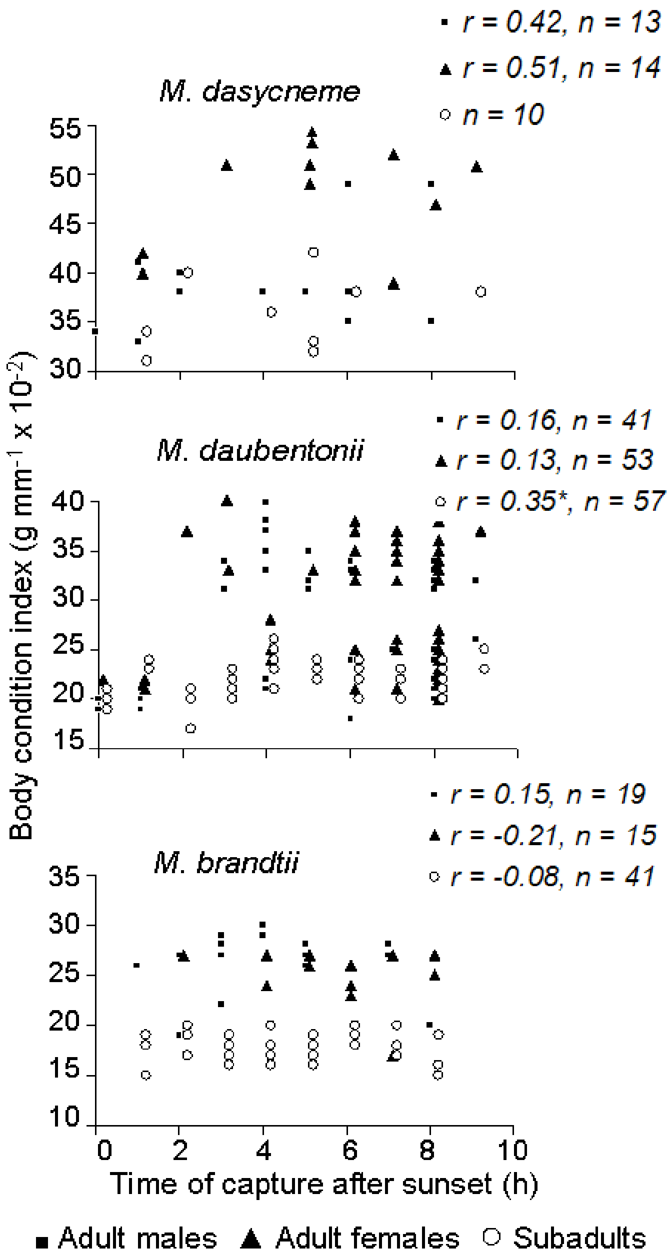

Figure 2 - Relationship between body condition indexes of captured swarming bats and time of their capture in early September. Time of capture was noted as hour after sunset (0 = sunset hour). Asterisk indicates significant correlation ($p < 0.01$, Spearman's rank correlation analysis).

DISCUSSION

In late summer, individuals captured later during the night had on average higher BCIs than individuals captured after sunset, confirming the hypothesis that bats arrive at swarming sites after feeding. Accordingly, Fenton (1969) reported that, in August, 90% of swarming bats had distended stomachs. The increasing trend suggests that bats may feed even at midnight, when insect availability is low (Racey and Swift 1985). Since flying is an energy-consuming activity that requires intensive feeding, the duration of swarming activity is likely to be restricted to a relatively short period of time, after which the bat should go on feeding. Accordingly, Sendor and Simon (2000, cited in Simon et al. 2004) found that *Pipistrellus pipistrellus* spends 3.2-13.8 minutes swarming at underground hibernacula and afterwards leaves the site. We hypothesise that in late summer individual bats spend a relatively short time on swarming and go on feeding for the rest of the night. This hypothesis is supported by recent evidence that bats become hyperphagic at the end of summer to accumulate fat for hibernation (McGuire et al. 2009a).

The high proportion of departing bats captured within two hours after sunset in late summer suggests that swarming sites may coincide with day-roosts for some bats. Such individuals probably settle down after feeding and leave the next evening, which corresponds to activity pattern observed by Degn et al. (1995). In late summer, swarming sites may function as special day-roosts that provide a suitable environment for torpor, allowing bats to convert ingested energy into fat (Krzanowski 1961; Speakman and Rowland 1999).

In September, no correlation between the BCI and time of capture was found. Fenton (1969) found that only 20% of swarming bats captured in September had distended stomachs. At this time of the year, most adults have already accumulated fat stores (Kunz et al. 1998; Encarnação et al. 2004) and arrive at underground sites to hibernate or mate (Fenton 1969; Thomas et al. 1979; Šuba, unpublished data) and insect availability is lower than in the previous month (Speakman and Rowland 1999). However, the BCIs of some *M. daubentonii* adults suggested that they had not yet completed fat accumulation or had expended stored energy reserves for mating.

In early autumn, subadult individuals of *M. daubentonii* and *M. dasycneme* also had slightly increased BCIs, compared to late summer, but this was not the case for *M. brandtii.* In September, the BCI of *M. daubentonii* subadult individuals was positively correlated to the time of capture, suggesting that subadult *M. daubentonii* may continue to feed intensively in early autumn. McGuire et al. (2009a) found that subadult *Myotis lucifugus* gradually lose mass from late summer until early autumn, probably as a consequence of their lower foraging efficiency compared to adults. Further studies on the feeding strategies of bats are needed to highlight the causes of intra- and interspecific variation in their feeding behaviour in autumn.

Our study provided new data about the feeding strategy of swarming bats. As both body mass and BCIs are not fully reliable indicators for feeding performances since bats may quickly lose ingested mass as faeces, further studies are needed, using more accurate techniques (e.g. plasma metabolite analysis; McGuire et al. 2009b).

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