

## Seasonal variation in nocturnal activity of male Daubenton's bats, *Myotis daubentonii* (Chiroptera: Vespertilionidae)

Jorge A. ENCARNACÃO<sup>1</sup>\*, Uwe KIERDORF<sup>2</sup> and Volkmar WOLTERS<sup>1</sup>

<sup>1</sup> Department of Animal Ecology, Justus Liebig University of Giessen, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany; e-mail: Jorge.A.Encarnacao@allzool.bio.uni-giessen.de

<sup>2</sup> Department of Biology, University of Hildesheim, Marienburger Platz 22, D-31141 Hildesheim, Germany

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**A b s t r a c t.** We studied nocturnal activity in adult male *Myotis daubentonii* from mid-May to early September of the years 1998–2003 in a male-dominated population in central Germany. Departure from roost after sunset, nocturnal activity time, time spent foraging, and return to roost before sunrise were recorded in radio-tracked animals during four observation periods (1: 14 May – 6 June, 2: 16 June – 10 July, 3: 22 July – 14 August, 4: 23 August – 2 September). Only three males (two in period 1, one in period 4) stayed in the day roost all night. The other tracked animals left their day-roost for the first time between 25 and 220 minutes after sunset, and their last arrival at the day-roost occurred between 2 and 545 minutes before sunrise. Bats spent most of their nocturnal activity time foraging (overall mean: 79.7 % of nocturnal activity time). Duration of nocturnal activity and nightly foraging time varied considerably over the four observation periods and were most extended in mid-summer (period 3). This is a time of high spermatogenic activity and steep increase in body mass (built-up of fat reserves), which leads to a particularly high food demand of male Daubenton's bats during this period of the year. Our results of an increased foraging activity during mid-summer provide evidence in support of the view that food demand of male Daubenton's bats is indeed highest during this time of the year.

**Key words:** *Myotis daubentonii*, foraging activity, seasonal variation, Germany

### Introduction

All Central European bat species are insectivorous and use hibernation as a means to overcome food shortage during winter. Hibernating bat species exhibit pronounced seasonal variation in body mass, which is lowest at the end of the hibernation period (Ewing et al. 1970, Ransome 1990, Kunz et al. 1998, Speakman & Rowland 1999). Within five to six months after leaving the hibernaculum, the animals build up new fat reserves for the subsequent hibernation period and are reproductively active in the summer habitat. During the pre-hibernal period in autumn, bats reduce their energy-expenditure by selecting cold roosting locations and depressing their body temperatures, which favors the built-up of fat stores (Krzanoski 1961, Speakman & Rowland 1999). The timing of reproductive activities and body mass increase is linked to the variation in the abundance of insect prey during the seasonal activity period. Peak energy demand in females occurs during the lactation period, while highest energy demand in males occurs later, being related to spermatogenesis and mating activity (Speakman & Thomas 2003).

In accordance with the above notion, previous studies on body mass changes and reproductive condition of adult male Daubenton's bats (*Myotis daubentonii*) suggested that their food demand is highest during mid-summer when body mass increases steeply and spermatogenic activity is high (Encarnação et al. 2004a,b). A recent study

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\*Corresponding author

(E n c a r n a ç ã o & D i e t z 2006) demonstrated that food intake and ingested energy in males are indeed highest during this time of the year. We therefore predicted that nocturnal activity, foraging activity in particular, of males is also highest during mid-summer. To test this prediction, we recorded, for the first time, the variation in nocturnal activity of free-living, male Daubenton's bats between mid-spring and late summer.

## Materials and Methods

### Study area and animal population

The study was conducted from May 1998 to September 2003 near Staufenberg (Central Hesse, Germany). The study area is used as a summer habitat by a male-dominated *M. daubentonii* population, the size and sex ratio of which have remained remarkably stable over several years (E n c a r n a ç ã o et al. 2002). Males use tree roosts singly or in groups of up to 51 individuals in a mixed forest (highest elevation 274 m) that is situated at the border of a valley and mainly consists of deciduous trees (E n c a r n a ç ã o et al. 2004b, 2005). In the valley, a brook with accompanying vegetation is used as a flight path to a pond (surface area of 16,000 m<sup>2</sup>; 170 m a.s.l.) situated a few hundred meters away. The pond and the brook are the most important foraging areas of the population. Additional foraging areas are sections of a river located at a distance of approximately 4 km from the forest. The present population was chosen for study because of the high percentage of resident males that exhibited a marked site fidelity to the two main foraging areas and which could thus be observed over the complete seasonal activity period (E n c a r n a ç ã o et al. 2002).

The present study was performed in compliance with the current animal care and nature conservation laws of Germany and approved by the nature conservation authority of the administrative district of Giessen, federal state of Hesse.

### Capture of bats

Bats were caught by mist-netting at different places along the flight path to the pond at fly-off time. Sex of the captured animals was determined visually, and young of the year were distinguished from adults based on the presence of a 'chin-spot' (R i c h a r d s o n 1994, G e i g e r et al. 1996) and of unfused and translucent phalangeal epiphyses in the former (A n t h o n y 1988, R a c e y 1988). In total, 307 different individuals were captured and marked by forearm-banding over the 6 yr-study period (202 adult males, 60 juvenile males, 14 adult females, 31 juvenile females). After weighing on a digital balance (Kern EM 150-1, Ballingen-Frommern, Germany), marking, and fixation of a transmitter in some of the adult males, the animals were released at the site of capture.

### Radio-tracking

In total, 43 adult males Daubenton's bats were fitted with a radio-transmitter. Four of these males could not be located following release, reducing the number of tracked animals to 39. For radio-tracking, a transmitter weighing approximately 0.5 g (type LB-2, Holohil Systems Ltd., Carp, Ontario, Canada) was attached to the fur of the back with cyanoacrylate glue. Mass of the transmitter was on average 5.7 % of body mass of the studied individuals. Normally,

transmitters dropped off after two to five days. Radio-tracking was performed by cross-bearing, followed by the 'homing-in'-method (White & Garrot 1990). To facilitate use of the 'homing-in'-method, a small piece of reflecting foil was fixed to the tip of the transmitter's flexible aerial. This allowed a better recognition of the animal in its foraging area, using a spotlight. Bats were tracked by three observer-groups, each equipped with a VR500 receiver and an HB9CV hand-held antenna with amplifier (Wagener Telemetrieanlagen, Köln, Germany). The observation time corresponded to the local astronomical night length. During the night, the observed behavior was continuously monitored, and the following data were recorded: 1) departure time (first departure from the day roost after the period of daily inactivity), 2) arrival time (last arrival at the day roost before the period of daily inactivity), 3) flight-time over water (regarded as reflecting the time spent foraging), 4) remaining flight-time (largely commuting flights between roost and foraging area), 5) time spent resting outside the day roost; 6) time spent in the day roost, and 7) undetermined (animal location and behavior unknown). The nocturnal activity period was defined as the time between first departure from the roost after sunset and last arrival in the roost before sunrise.

Animals were tracked during the following four observation periods: period 1 (late spring, 14 May – 6 June), 7 individuals; period 2 (early summer, 16 June – 10 July), 14 individuals; period 3 (mid-summer, 22 July – 14 August), 8 individuals; period 4 (late summer, 23 August – 2 September), 10 individuals. Period 4 was shorter than the other three observation periods because adult males showed an increased mobility from early September onwards and tended to visit swarming sites and summer habitats of other populations (Ençarın et al. 2002), making continuous radio-tracking difficult. Radio-tracked individuals used between one and four different foraging sites and between one and three different tree roosts in the study area per observation period.

During the study period, we observed 122 departures from and 128 arrivals at the day-roosts. For 116 nights, nocturnal activity time of marked individuals was recorded by observing their first departure from the day roost after the period of daily inactivity and their last arrival at the day roost before the subsequent period of daily inactivity. Average contact-time was 91.5 % of the local astronomical night length. For analysis of nightly foraging time, only nights ( $n = 92$ ) in which the contact time of an individual exceeded 90 % of the local astronomical night length were included in the calculations. For analysis of the proportion of nocturnal activity time that was spent foraging, only nights ( $n = 89$ ) with nocturnal activity and a contact time over 90 % were included in the calculations. For each individual, average nightly foraging time of an observation period (up to four nights) was used as the measure of foraging activity. During radio-tracking in the foraging areas, no low temperatures were observed that, based on the findings of Dietz (2006), were likely to negatively affect the foraging activity of Daubenton's bats.

## Statistical analysis

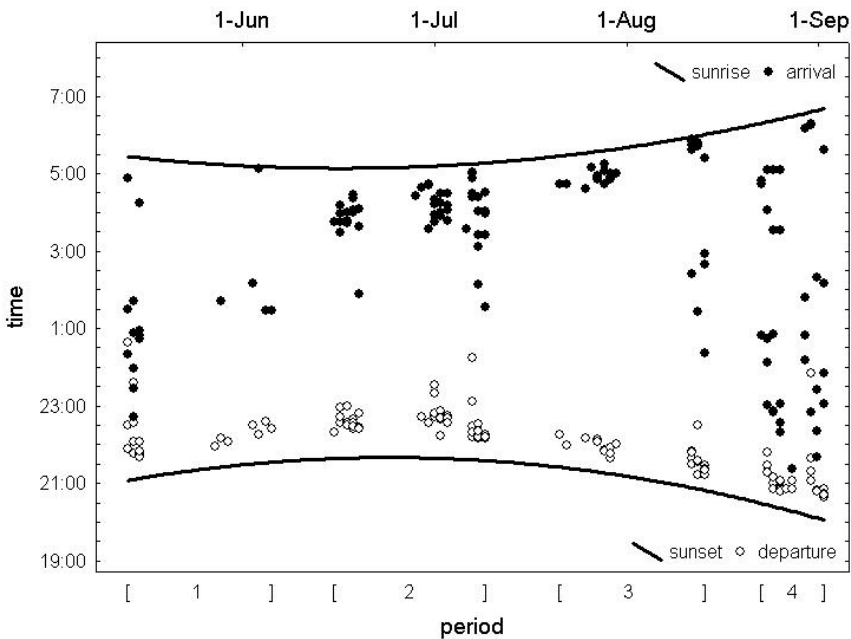
Data for the four different periods were compared by non-parametric Kruskal-Wallis ANOVA (KW-ANOVA), followed by pairwise comparisons with the Mann-Whitney-U-test. To correct for error accumulation due to replicate testing, we applied Bonferroni  $\alpha$ -adjustment for six pairwise comparisons in the U-tests (Sachs 1984). Pearson's correlation was used to test whether the duration of nocturnal activity was correlated with local astronomical night length or nightly foraging time. Statistical evaluation of the data was performed with the software package Statistica 6.0 for Windows (StatSoft). In all tests,  $p$ -values  $< 0.05$  indicated

significance. In the case of the U-tests, a Bonferroni-adjusted  $p$ -value of 0.05 equals an unadjusted  $p$ -value of 0.0083.

## Results

Length of the nocturnal activity period of individual bats ranged between 0 and 539 minutes. Values differed significantly among the four observation periods ( $H = 42.21$ ,  $df = 3$ ,  $n = 116$ ,  $p < 0.0001$ ). Nocturnal activity was more extended in early (period 2) and mid-summer (period 3) than in late spring and late summer (periods 1 and 4). During one night in period 1 with severe rainfall, two males did not leave their day-roost during the night. Despite good weather conditions, in period 4, a heavy (11.0 g) male in good reproductive condition (fully distended caudae epididymides, see En c a r n a ç ā o et al. 2006a) also stayed in the day-roost during the whole night (Table 1).

Time between last arrival of the bats at the roost and sunrise varied more strongly than time between sunset and first departure from the roost (Fig. 1, Table 1). The time interval between sunset and first departure of the tracked animals from the roost ranged between 25 and 220 minutes and varied significantly among the four observation periods ( $H = 15.89$ ,  $df = 3$ ,  $n = 122$ ,  $p = 0.0012$ ). Time to departure in period 2 was significantly longer than in periods 3 and 4 (Table 1). The time interval between last arrival at the roost and sunrise ranged between 2 and 545 minutes and also varied significantly among the four observation periods ( $H = 49.28$ ,  $df = 3$ ,  $n = 128$ ,  $p < 0.0001$ ). Time between last arrival and sunrise was significantly longer in periods 1 and 4 compared to periods 2 and 3 (Table 1). Our data show

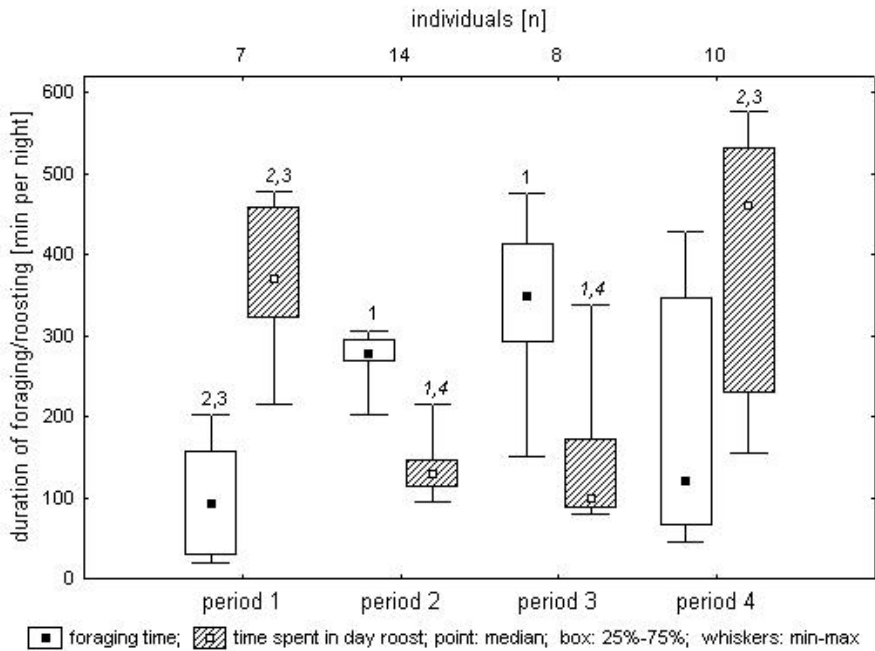


**Fig. 1.** Times of first departure from the roost and last arrival at the roost of radio-tracked male Daubenton's bats during the seasonal activity period in relation to sunset and sunrise. For definition of periods see Materials and Methods.

that the extended nocturnal activity during mid-summer was largely due to later arrival of the bats at the roosts.

The duration of nocturnal activity of male Daubenton's bats over the study period (14 May to 2 September) did not significantly correlate with local astronomical night length ( $r = -0.121$ ,  $n = 116$ ,  $p = 0.2$ ), but correlated significantly with foraging time ( $r = 0.945$ ,  $n = 92$ ,  $p < 0.001$ ).

Duration of foraging activity of radio-tracked individuals per night (averaged over up to four observation nights per individual) ranged between 20.3 and 476.0 min and varied significantly among the four observation periods ( $H = 15.25$ ,  $df = 3$ ,  $n = 39$ ,  $p = 0.0016$ ). Highest values were recorded for period 3 (mid-summer), and nightly foraging time in periods 2 and 3 significantly exceeded that in period 1. Following Bonferroni  $\alpha$ -adjustment, the difference between period 2 and period 3 was no longer significant (Fig. 2).



**Fig. 2.** Nightly foraging time and time spent in the day-roost of radio-tracked male Daubenton's bats during the four periods. Numbers above the box and whisker plots identify significant differences in the respective behavior between periods (U-tests with Bonferroni  $\alpha$ -adjustment;  $p < 0.05$ ).

Time spent resting outside the day-roosts only ranged between 0 and 25.0 minutes per night and did not differ among the four periods ( $H = 4.53$ ,  $df = 3$ ,  $n = 39$ ,  $p = 0.21$ ). Bats spent between 80.3 and 578.0 min per night in the day-roosts. Values varied significantly among periods ( $H = 24.38$ ,  $df = 3$ ,  $n = 39$ ,  $p < 0.0001$ ). During periods 1 and 4, bats spent significantly more of the night-time in the day-roost than during periods 2 and 3 (Fig. 2).

Relative nocturnal activity time in the four observation periods also showed significant variation ( $H = 47.62$ ,  $df = 3$ ,  $n = 116$ ,  $p < 0.0001$ ), with individual values ranging between 0 and 90 % of astronomical night length. Relative nocturnal activity time was highest in mid-summer (period 3), and in periods 2 and 3 significantly exceeded that in periods 1 and 4 (Table 2).

**Table 1.** Duration of nocturnal activity, first departure from the roost after sunset, and last arrival at the roost before sunrise of radio-tracked male Daubenton's bats. <sup>1</sup> Periods with significantly different values (U-tests with Bonferroni  $\alpha$ -adjustment,  $p < 0.05$ ). Note that in periods 1 and 4 some males did not leave their day roost. Numbers of departures and arrivals differ because in some cases only departure from or arrival at the roost were recorded.

period	duration of nocturnal activity (minutes between departure and arrival)					departure from roost (minutes after sunset)					arrival at roost (minutes before sunrise)				
	mean(SD)	median	min-max	n	sig. <sup>1</sup>	mean(SD)	median	min-max	n	sig. <sup>1</sup>	mean(SD)	median	min-max	n	sig. <sup>1</sup>
1	165.1(126.3)	175.0	0-413	19	2/3	69.1(47.4)	50.5	34-215	20		232.8(109.5)	243.0	2-408	17	2/3
2	319.8(43.1)	320.5	198-401	44	1/3	56.9(23.0)	54.0	33-156	45	3/4	72.2(41.9)	67.0	12-224	49	1/3/4
3	416.0(74.1)	242.5	188-494	26	1/2/4	44.2(14.9)	43.0	25-102	26	2	72.7(87.1)	43.5	9-343	28	1/2/4
4	246.2(178.6)	159.0	0-539	27	3	48.4(35.2)	38.0	25-220	31	2	292.7(173.1)	334.0	14-545	34	2/3
1-4	298.9(135.9)	324.0	0-539	116		54.0(31.1)	46.0	25-220	122		152.2(146.9)	77.0	2-545	128	

**Table 2.** Relative nocturnal activity time, relative nightly foraging time, and nightly foraging time in percent of nocturnal activity time of radio-tracked male Daubenton's bats. <sup>1</sup> nights for which the times of first departure from and last arrival at the roost were known. <sup>2</sup> only nights with a contact time of  $> 90\%$  of the local astronomical night length. <sup>3</sup> only nights with a contact time  $> 90\%$  and flight activity of the bats. <sup>4</sup> Periods with significantly different values (U-tests with Bonferroni  $\alpha$ -adjustment,  $p < 0.05$ ).

period	relative nocturnal activity time (percentage of night length) <sup>1</sup>					relative nightly foraging time (percentage of night length) <sup>2</sup>					nightly foraging time in percent of nocturnal activity time <sup>3</sup>				
	mean(SD)	median	min-max	n	sig. <sup>4</sup>	mean(SD)	median	min-max	n	sig. <sup>4</sup>	mean(SD)	median	min-max	n	sig. <sup>4</sup>
1	33.9(26.2)	36.8	0-90	19	2/3	21.7(18.7)	17.4	0-71	19	2/3	63.9(23.2)	63.6	30-97	17	2
2	70.9(9.4)	71.5	43-88	44	1/3/4	60.9(11.0)	61.5	34-81	32	1/4	85.4(9.5)	85.1	62-98	32	1
3	78.8(14.0)	82.9	34-90	26	1/2/4	63.4(20.3)	72.0	19-87	15	1/4	82.3(15.5)	88.3	58-98	15	
4	40.4(29.3)	26.8	0-87	27	2/3	34.1(27.7)	19.3	0-86	26	2/3	81.6(16.4)	85.6	37-99	25	
1-4	59.5(26.6)	70.0	0-90	116		45.6(26.0)	54.7	0-87	92		79.7(17.4)	84.8	30-99	89	

Relative nightly foraging time ranged between 0 % and 87 % of astronomical night length and also varied significantly among the four observation periods ( $H = 35.63$ ,  $df = 3$ ,  $n = 92$ ,  $p < 0.0001$ ). Values for periods 2 and 3, during which the bats on average spent more than 60 % of the night foraging, significantly exceeded that for periods 1 and 4 (Table 2).

Foraging was the dominant nocturnal activity of the bats, with period means ranging between 63.9 and 85.4 % of nocturnal activity time (Table 2). Statistical analysis revealed significant variation among the four observation periods ( $H = 10.12$ ,  $df = 3$ ,  $n = 89$ ,  $p = 0.0176$ ), the value for period 1 being significantly lower than that for period 2 (Table 2).

## Discussion

The present study demonstrated pronounced seasonal variation in the duration of nocturnal activity, particularly the time spent foraging, of male Daubenton's bats between mid-spring and late summer. As predicted, nocturnal activity was most extended and foraging time longest in mid-summer, the period of steep increase in body mass and high spermatogenic activity (Encañón et al. 2004a,b).

Studies in *Eptesicus serotinus* (Catto et al. 1995), *E. nilssonii* (Rydell 1989) and *E. fuscus* (Wilkinson & Barclay 1997) revealed that in these species flight activity was severely reduced when air temperatures dropped below 10 °C. Such is not the case in *Myotis daubentonii*, which even at ambient temperatures of about 5 °C still shows high foraging activity (Dietz 2006). This author suggests that the insect activity over water surfaces, and in consequence the foraging activity of bats in these areas, is less affected by changes in ambient temperatures than in the case of open landscapes or woodlands. Because of the above fact, and since over the different observation periods only in very few nights ambient temperatures dropped below 10 °C, we conclude that weather conditions were probably not a major factor explaining the observed differences in nightly behavior of the Daubenton's bats during the four observation periods.

Main factors affecting emergence time in echolocating bats are foraging strategy and predation risk (Erkert 1982). Bats that feed on small aerial insects have to forage for a long time to meet their food demands (Kurtá et al. 1989). Thus, they leave their roosts relatively early and extend their foraging activity until dawn. Emergence well before dark and foraging at dusk, however, exposes the animals to an increased predation risk by diurnal predators. Daubenton's bats feed mainly on aquatic Diptera, primarily Chironomidae (Swift & Racey 1983, Beck 1991, Taake 1992, Sullivan et al. 1993, Vaughan 1997) and forage over most of the nocturnal activity period (Arnold et al. 1998, Dietz 2006, this study). The evening emergence of *M. daubentonii* correlates with the peak in flight activity of small insects at dusk (Rydell et al. 1996, Dietz 2006). In contrast, several bat species that feed independently of the dusk peak of dipterans emerge later (Swift 1980, Racey & Swift 1985, Swift et al. 1985, Rydell et al. 1996), thereby reducing their predation risk (Jones & Rydell 1994).

Energetic aspects related to their age, reproductive state and body condition (Düvergé et al. 2000) also affect emergence time of insectivorous bats. Shiel & Fairley (1999) observed that during the nursery period, female *Nyctalus leisleri* leave their roosts earlier than during other times of the year. Compared with the present investigation, other studies on *M. daubentonii* reported earlier emergence from (between 5 and 44 min after sunset) and later arrival at the roosts (between 31 and 54 min before sunrise) (Helmer 1983, Dietz & Fitzenräuter 1996, Rydell et al. 1996, Rieger 1997, Arnold et al. 1998).

However, most of the observed individuals in the latter studies were gravid or nursing females that according to Hill & Smith (1984) leave their roosts earlier than males. For a single gravid female Daubenton's bat, Dietz (2006) calculated a mean foraging time of 465 min per night.

The relatively higher constancy of departure compared to arrival dates observed in the present study may be explained by assuming that the bats try to take advantage of the high prey availability during the dusk peak of the insect emergence and the fact that after the daily inactivity period the animals are hungry.

Although nights were longer in periods 1 and 4 than in periods 2 and 3, nocturnal activity times and foraging times were shorter. In addition to the increased energy demand during the latter periods, probably also other factors contributed to this difference in nocturnal activity. Interestingly, in period 1 on average a much lower percentage of the nocturnal activity time was used for foraging than in the other three periods. It may be hypothesized that a large part of the non-foraging activities outside the day-roost during this period were related to the occurrence of non-resident males in the study area that had been forced out of more productive areas by gravid females. The occurrence of both, resident and non-resident males in the study area has been demonstrated in a previous study (Ençarnação et al. 2002).

Emergence times and relative nocturnal activity times similar to those reported in the present study were also recorded for radio-tracked male Daubenton's bats ( $n = 8$ ) in the Yorkshire Dales, England (Senior et al. 2005). However, these authors give no detailed data about the duration of nightly foraging activity by the bats, and temporal variation of the activity pattern during summer was not studied.

The marked increase from period 3 to period 4 in the time spent in the day-roost during the night could be related to the existence of mating roosts occupied by adult males. Evidence in support of the existence of such mating roosts in the summer habitat of *M. daubentonii* has recently been obtained (Ençarnação et al. 2006b). The findings from that study indicate that matings in Daubenton's bats occur not only at swarming sites and in hibernation roosts from autumn to spring, but also at summer sites, which suggests a 'resource-defense-polygyny' strategy by males during late summer. Senior et al. (2005), who studied Daubenton's bats in England, arrived at a corresponding conclusion.

In conclusion, the findings of the present study suggest that nocturnal activity, foraging activity in particular, largely reflects the varying food demand of male Daubenton's bats over the seasonal activity period. During mid-summer, the high energy requirements of male Daubenton's bats, which are caused by intense spermatogenic activity and the built-up of fat reserves, are mainly met by an increased foraging activity. This is possible, because at that time of the year prey availability is generally high. During autumn, a time of lower prey availability, which was not covered by the present study, a further increase in fat reserves can be achieved by a reduction in energy expenditure. Such energy saving mechanisms include the selection of cold roosting sites and an active lowering of body temperature (Krzanowski 1961, Speakman & Rowland 1999).

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