Effect of colony size and reproductive period on the emergence behaviour of a maternity colony of Daubenton's Bat (*Myotis daubentonii*) occupying an artificial roost (Chiroptera: Vespertilionidae)

Vliv velikosti kolonie a období reprodukčního cyklu na výletové chování mateřské kolonie netopýra vodního (*Myotis daubentonii*) obývající umělý úkryt (Chiroptera: Vespertilionidae)

Radek K. LUČAN

Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ–128 44 , Czech Republic & Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 31, CZ–370 05 Czech Republic; rlucan@centrum.cz

Abstract. Emergence behaviour of a maternity colony of Daubenton's bat (*Myotis daubentonii*) occupying an artificial roost was studied between 1999 and 2009 in South Bohemia, Czech Republic. The time of emergence of the first bat (T_{FB}), rather than the median time of emergence, was used in the analysis, as these two variables were highly correlated. Daubenton's bats started to emerge from their roost 28±12 (mean±SD) minutes after sunset (min–max: 8–64). The onset of emergence had no relation to the size of the colony, but it was strongly affected by the period of the reproductive cycle. The most pronounced difference was observed between pregnancy and lactation. On average, the bats emerged by 14 minutes earlier during lactation than during pregnancy. The emergence pattern typically followed a unimodal distribution with a peak in the middle or in the second half of the exodus. The emergence rate was positively correlated with the total number of bats in the roost. The emergence length increased significantly with the increasing number of bats in the roost and varied between periods of the reproductive cycle. It was longest during lactation and shortest during autumn movements. The seasonal dynamic in the number of bats in the roost followed a bimodal pattern with a first peak occurring during spring movements and pregnancy followed by a decrease during lactation and a second peak during the post-lactation period. A comparison of T_{FB} between the studied artificial roost and tree cavities (i.e. natural roosts) located in the same study area revealed that bats roosting in tree cavities followed the same seasonal pattern as in the artificial roost but emerged significantly later.

Key words. Chiroptera, emergence counts, population dynamics.

INTRODUCTION

The evening emergence time in bats has been suggested to be a function of dietary specialisations, foraging strategy and ability to avoid predation (Jones & Rydell 1994). Bat species feeding on prey with the highest abundance around sunset, such as chironomid dipterans, tend to depart earlier from their day roosts than those specialised to feed on nocturnal insects or gleaning its prey from vegetation (Jones & Rydell 1994, Rydell et al. 1996). Furthermore, large and fast flying species with a high aspect ratio and a high wing loading emerge earlier than slow fliers

as they are more likely to better avoid attacks from potential predators relying on vision such as diurnal birds of prey (Jones & Rydell 1994). The timing of emergence may further be influenced by the roost location and the structure of the surrounding habitat. Bats inhabiting roosts located in a dense canopy or close to a forest edge may take advantage of leaving their roosts earlier than those using roosts in open habitats which do not provide protection from predators (Entwistle et al. 1996, Russo et al. 2007). Further factors constraining the timing of emergence are related to the energetic demands and the reproductive state of emerging individuals (Shiel & Fairley 1999, Duvergé et al. 2000). Although all these behavioural patterns have been known, most published data are anecdotic and there are only few European bat species that have been subject to a detailed study of the complete seasonal cycle (cf. *Pipistrellus pipistrellus* – Swift 1980, Bullock et al. 1987, Speakman et al. 1999; *Eptesicus serotinus* – Catto et al. 1995, Petrželková & Zukal 2001; *Eptesicus nilssonii* – Duvergé et al. 2000; *Barbastella barbastellus* – Russo et al. 2007; *Myotis brandtii* – Schmidt 1995). Here we present a large dataset of year-round observations on the pattern of the emergence behaviour of a maternity colony of Daubenton's bat (*Myotis daubentonii*) occupying an artificial roost in South Bohemia, Czech Republic.

MATERIAL AND METHODS

The studied roost is a small old building that originally served as a lime-kiln, and is made of bricks and stones. It is located in the northern part of the Třeboňsko basin (approximately 49° 09' N, 14° 41' E), South Bohemia, Czech Republic. The building is 5 m long, 4 m wide and 4 m high. The walls are about 1 metre thick. There are several crevices of variable size in the ceiling, the largest of them (ca. 20×20×60 cm) being the main roosting place of a colony of Daubenton's bats. A maternity colony of up to ca. 200 individuals has been using this roost for more than 40 years (Lučan & Hanák 2002). Prior to emergence from the roosting building, the bats usually leave the crevices in the ceiling and swarm for a short time inside the building. The only entrance to the room inside the building is ca. 1.5×1 m large and, therefore, the bats can easily be observed as they fly out.

The research was conducted between 1999 and 2009. The observation of the evening emergence started usually 10–20 minutes before sunset and lasted until the last bat had left the roost or until there was no bat emerging for at least 10 minutes. After each observation, the roost was checked to assure that all bats had left. The presence of newborns was also recorded and their numbers and age were estimated during these checks. The observer was positioned at the entrance to the roosting building, out of the flight path of the bats in order to prevent their disturbance. The roosting building is located in an open space and so the emerging bats could easily be observed against the bright sky, even in the complete darkness. In addition, the observer was equipped with a bat detector (D-240x Peterson Elektronik Ltd.). Observations were only made in the evenings, with no or weak wind and no rain. Typically, the time of emergence of the first bat (T_{FB}), the total number of emerging bats and the time of emergence of the last bat (T_{LB}) were recorded (typical observation schedule). In 2007 and 2008, the numbers of emerging bats were counted in five-minute intervals in order to estimate the emergence rate and to record the time of emergence of a median bat (T_{median}), along with T_{FB}, T_{LB} and the total number of bats (full observation schedule). We used the local astronomic sunset time data available from the Czech Hydrometeorological Service. We defined T_{FB} and T_{LB} as the number of minutes between the sunset time and the time when the first and the last bat left the roost, respectively. We calculated the emergence length by subtracting T_{FB} from T_{LB}. We defined the emergence rate as the number of bats emerging per 5 minutes.

As supplementary data, T_{FB} in tree holes (i.e. natural roosts of the Daubenton's bat) was occasionally recorded between 1969 and 2006. Monitoring of tree cavities has been conducted for more then 40 years in the same study area where our artificial roost is located (cf. Lučan et al. 2009). Typically, T_{FB} was recorded during the evening counts of bats emerging from tree cavities or during the capturing of bats using modified funnel traps (Gaisler et al. 1979).

Based on long-term observations of reproduction and population dynamics of Daubenton's bats in the study area (Lučan & Hanák 2002, Lučan 2006), we divided the reproductive season into five periods: spring movements (15 March – 10 May), pregnancy (11 May – 10 June), lactation (11 June – 10 July), post-lactation (11 July – 15 August) and autumn movements (after 15 August). Each observation was assigned to one of these five periods in order to test the effect of the reproductive state of the bats on the timing of emergence.

Prior to statistical analysis we tested the data for normality using the Kolmogorov-Smirnov test. As all variables conformed to the normal distribution criterion, we used parametric tests where applicable. We applied the Spearman rank correlation to assess the relationship between T_{FB} and T_{median}. We used a simple linear regression to analyse the effect of the size of the colony on T_{FB}, emergence rate and emergence length. We used the median value of emergence rate recorded for any given date to analyse the effect of colony size on emergence rate. We applied analysis of covariance with the total number of bats in the roost as a covariate to test the effect of the period of the year on T_{FB} and emergence length. We used the Tukey HSD test to compare T_{FB} among periods of the year. Finally, we used hierarchical analysis of variance to compare T_{FB} of the artificial roost and the roosts in tree cavities. All analyses were performed using Statistica 8.0 (StatSoft Inc.). All values are given as mean±SD.

RESULTS

A r t i f i c i a l   r o o s t

In total, 75 observations of evening emergence were made. For 36 of them the full observation schedule was followed. There was a strong correlation between T_{FB} and T_{median} (Spearman Rank correlation: $r_s=0.8$, n=36, p<0.001). Therefore, T_{FB}, instead of T_{median} was used in all analyses, which enabled us to include observations when only T_{FB} was recorded.
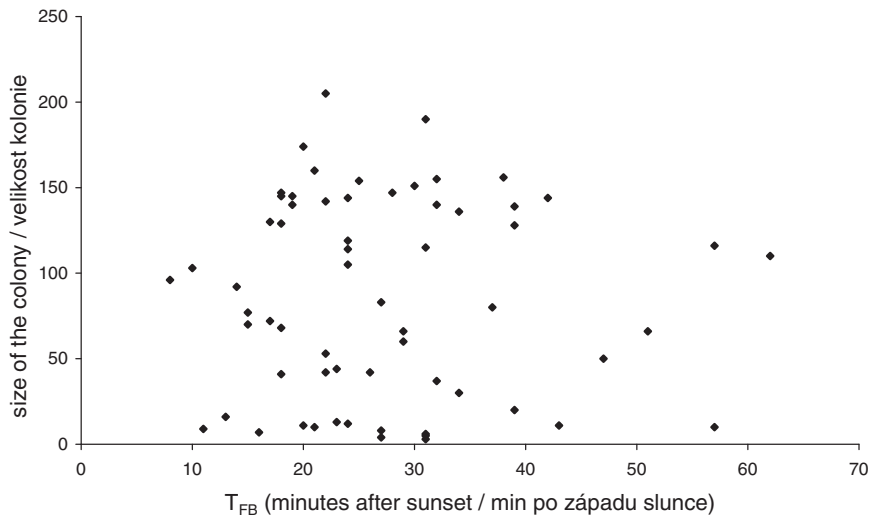

Fig. 1. Relation between the number of Daubenton's bats in the roost and the time of emergence of the first bat (T_{FB}) as observed during 75 occasions at the study roost (South Bohemia, Czech Republic) between 1999 and 2009.
Obr. 1. Vztah mezi velikostí kolonie netopýrů vodních a načasováním výletu prvního jedince (T_{FB}) zobrazený na základě 75 pozorování studovaného úkrytu v období 1999 a 2009.
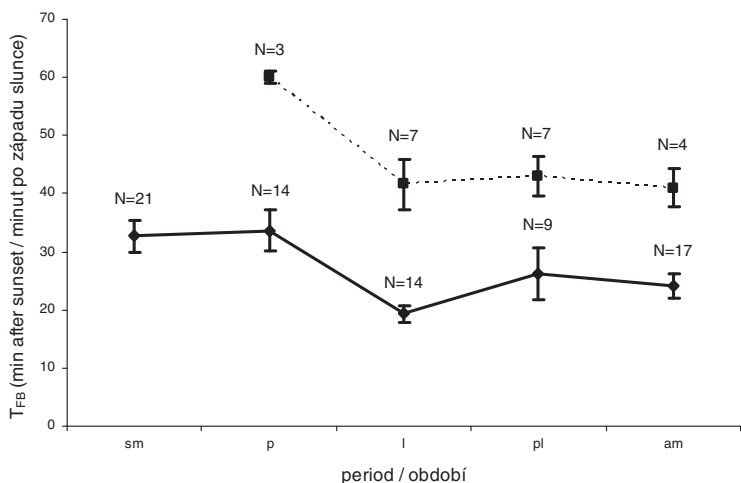
Fig. 2. Timing of evening emergence in Daubenton's bats from the studied roost (diamonds, solid line) and nearby natural roosts (squares, dashed line) in relation to the period of the reproductive cycle. The data are given as the mean emergence of the first bat (T_{FB}) in minutes after sunset±S.E. The numbers above each mark show the number of observations. Sm – spring movements, l – lactation, pl – post-lactation, am – autumn movements.

Obr. 2. Načasování večerního výletu netopýrů vodních ze studovaného umělého úkrytu (kosočtverce, plná čára) a přírodních úkrytů (stromových dutin; čtverce, přerušovaná čára) v závislosti na období reprodukčního cyklu. Uveden je průměrný čas výletu prvního jedince (TFB) v minutách po západu slunce±střední chyba průměru. Čísla nad každou značkou udávají počet pozorování. Sm – jarní přelety, p – březost, l – laktace, pl – polaktační období, am – podzimní přelety.

On average, Daubenton's bats started to emerge from their roost 28±12 min after sunset (min–max: 8–64, n=75). The mean T_{median} was 41±11 minutes after sunset (min–max: 16–64, n=36). There was no effect of the number of bats in the roost on T_{FB} (R=0.015, $F_{(1,61)}$=0.014 p<0.905, Fig. 1). However, the period of reproductive cycle significantly affected the timing of emergence ($F_{(4, 57)}$=4.167, p=0.005, Fig. 2). The most pronounced differences were observed between pregnancy and lactation (p<0.05). On average, the bats emerged by 14 minutes earlier during lactation than during pregnancy. The bats tended to emerge later during spring movements and pregnancy than during lactation, post-lactation and autumn periods ($F_{(1, 60)}$=10.770, p=0.002).

The emergence pattern expressed as the number of bats emerging in 5-minute intervals (i.e. emergence rate) is shown in Fig. 3. It typically followed a unimodal distribution with a peak in the middle or in the second half of the exodus. The emergence rate was positively affected by the total number of bats in the roost (R=0.83, $F_{(1,23)}$=51.269 p<0.001, Fig. 4). The emergence length increased significantly with the number of bats in the roost (R=0.569, $F_{(1,45)}$=21.562, p<0.0001) and varied between periods of the reproductive cycle ($F_{(4, 41)}$=4.6948, p=0.003). It was longest during lactation (37±7 min) and shortest during autumn movements (20±8 min).

The seasonal dynamic of the size of the colony followed a similar pattern across all years of the study. The number of emerging bats increased steadily during spring and reached a maximum

in April and May during pregnancy. The maximum numbers of bats observed during this period varied between 60 individuals in 2005 and 205 individuals in 2006. After parturitions, the colony size decreased by as much as ca. 50%. Typically, females in the colony gave birth during the first two weeks of June. A second peak in the number of bats appeared when juvenile bats were weaned during July and August. The number of bats in the roost observed during this second peak varied between 66 individuals in 1999 and 160 individuals in 2006. Later on, the size of the colony rapidly decreased and was between 3 and 44 individuals throughout September and
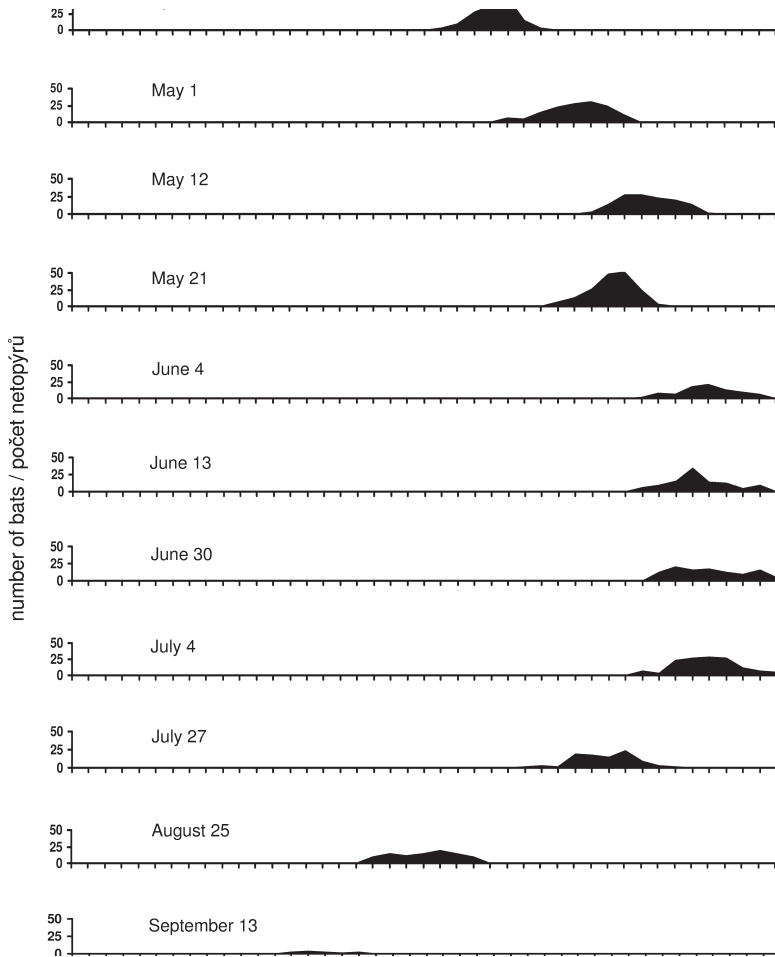

Fig. 3. The example of emergence pattern of the studied colony of Daubenton's bats in 2008. The data show emergence rates expressed as the number of bats emerging in five-minute intervals from the onset of emergence until its end.
Obr. 3. Ukázka průběhu výletu studované kolonie v roce 2008. Data zobrazují rychlost výletu vyjádřenou jako počet vyletujících netopýrů v pětiminutových intervalech od začátku výletu po jeho ukončení.
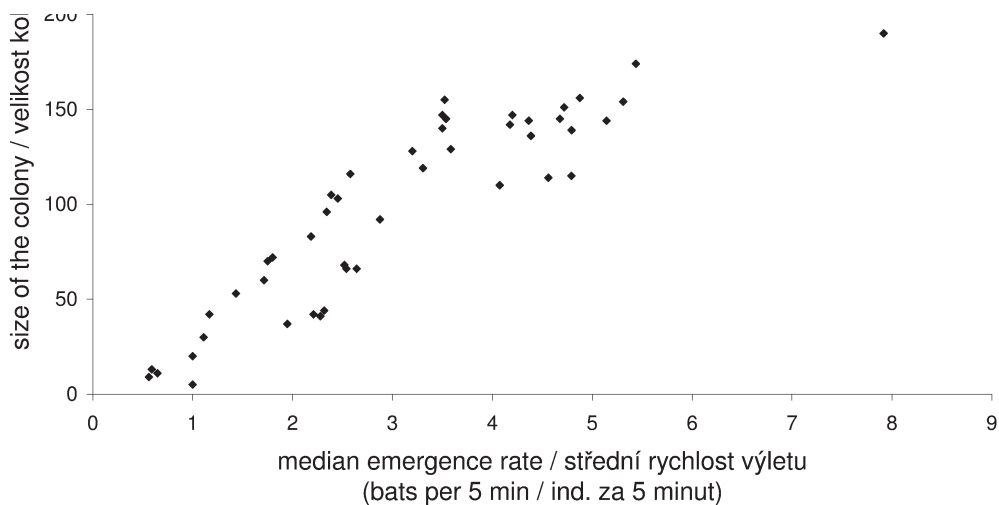
Fig. 4. The relationship between the size of the studied colony of Daubenton's bats and the median emergence rate.
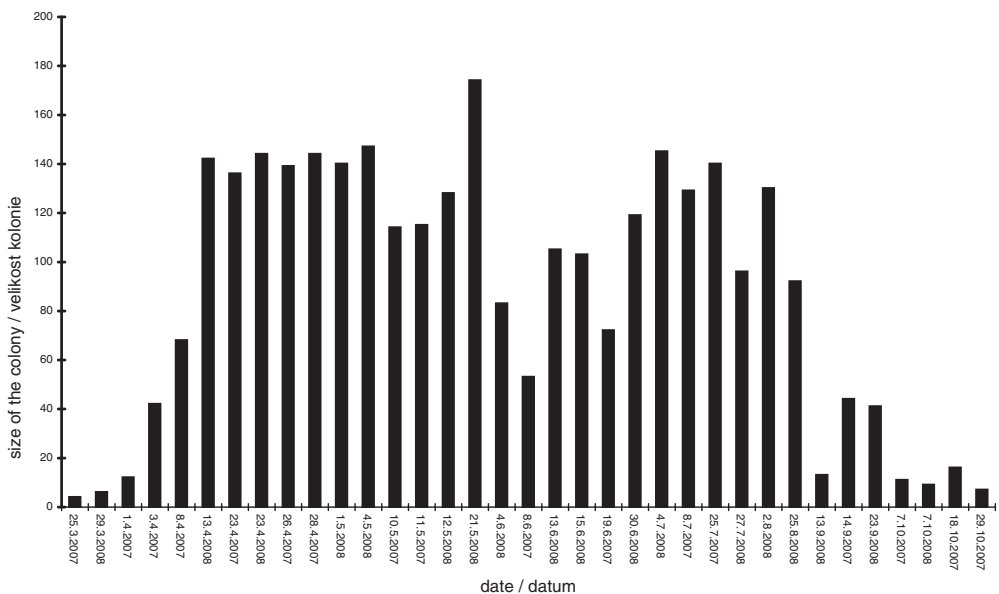Obr. 4. Vztah mezi velikostí studované kolonie netopýrů vodních a střední rychlostí výletu.

Fig. 5. The seasonal dynamic of the size of the studied colony of Daubenton's bats in 2007 and 2008.
Obr. 5. Sezónní dynamika velikosti studované kolonie netopýrů vodních v letech 2007 a 2008.

October. As a typical example, numbers of bats in the roost as observed from spring to autumn in 2007 and 2008 are shown in Fig. 5.

Incidental observations of emergence from tree roosts

We obtained 21 records of T_{FB} from 14 tree roosts (3 records during pregnancy, 7 during lactation, 7 during post-lactation and 4 during autumn movements). On average, bats started to emerge from tree holes 45±11 minutes after sunset (min–max: 25–61). It was significantly later than in the artificial roost under study ($F_{(1, 67)}$=57.443, p<0.001). The timing of emergence followed exactly the same seasonal pattern as observed in the artificial roost, i.e. the bats emerged much earlier from pregnancy to lactation and post-lactation than in spring (see Fig. 2).

DISCUSSION

It has been suggested that T_{FB} is a less reliable indicator of the time of emergence than T_{median} in some bat species as there may be an unusually long time gap between the first emerged bat and the main emergence (BULLOCK et al. 1987) and/or that T_{FB} may be affected by the size of the colony (KUNZ & ANTHONY 1996). By contrast, our observations clearly demonstrate a strong correlation between T_{FB} and T_{median}, and no relation between the colony size and T_{FB}. Moreover, we observed that once the first bat leaves the roost, more individuals follow in a short time, typically less than two minutes. Accordingly, SHIEL & FAIRLEY (2001) suggested T_{FB} as a better predictor of the emergence time than T_{median} in *Nyctalus leisleri* in Ireland, and JONES (1995) found no relation between the colony size and T_{FB} in *Nyctalus noctula*.

Among European bats, Daubenton's bat is generally considered as a late emerger (RYDEL et al. 1996) when compared with large and/or fast flying species like noctules, serotines and pipistrelles (JONES 1995, CATTO et al. 1995, BULLOCK et al. 1987). JONES & RYDEL (1994) reported the T_{FB} and T_{median} for Daubenton's bat of 73 and 84 minutes after sunset, respectively, which is the latest emergence among the seven European representatives of the genus *Myotis* included in their study. However, these data were mostly obtained in higher latitudes (57–60°; JONES & RYDEL 1994) than those in our study (ca. 49° N), and, therefore, caution must be exercised when comparing these two datasets due to the difference in the light conditions and the length of twilight. Contrastingly, SHIRLEY et al. (2001) observed the emergence behaviour of a maternity colony of Daubenton's bats occupying a building in Northumberland, United Kingdom (ca. 55° N), and reported T_{FB} and T_{median} of 24 and 51 minutes after sunset, respectively. These values correspond well with our observations. Accordingly, DIETZ & KALKO (2007) reported emergence times of radio-tracked reproductive females between 17 and 94 minutes after sunset.

The emergence time varied substantially with respect to the period of the reproductive cycle. The bats tended to emerge later during spring than during the summer and autumn periods, with the most pronounced differences between pregnancy and lactation. Earlier emergence from pregnancy to lactation was also reported for *Myotis brandtii* (SCHMIDT 2005), *Nyctalus noctula* (JONES 1995), *Nyctalus leisleri* (SHIEL et al. 2001), *Eptesicus nilssonii* (DUVERGÉ et al. 2000), *Eptesicus serotinus* (CATO et al. 1996), *Rhinolophus ferrumequinum* (DUVERGÉ et al. 2000), *Plecotus austriacus* (SCHEUNERT et al. 2009) and *Barbastella barbastellus* (RUSSO et al. 2007), *Lasiurus cinereus* (BARCLAY 1989). Thus, it seems to be a common pattern in many temperate bats. In contrast to our observations, DIETZ & KALKO (2007) did not record significant differences in the timing of emergence between pregnancy, lactation and post-lactation in reproductive female Daubenton's bats. It has been suggested that pregnant females tend to depart later as a consequence of an

increased body weight and wing-loading that negatively affect manoeuvrability and increases predation risk (Duvergé et al. 2000). Lactating females, on the other hand, have dramatically increased energetic demands and thus are forced to emerge earlier to exploit the dusk peak in insect activity (Duvergé et al. 2000, Russo et al. 2007). Our observations strongly support the above mentioned hypotheses. Furthermore, the later emergence of females in the spring period may be the consequence of a high insect density. Lučan (2004) recorded the highest biomass of dipterans, the dominant prey of Daubenton's bats, during late spring in water habitats of the South Bohemian basin. Consequently, female Daubenton's bats may afford to leave their roost later to avoid predation, but without risking insufficient food gain.

In general, the size of the colony and the configuration of the roost exit may affect the emergence rate, the clustering pattern and the emergence length (Swift 1980, Kunz & Anthony 1996, Shiel & Fairley 1999). Likewise, the emergence rate as well as the length of emergence in the studied colony were highly correlated with its size. However, there was no bottleneck effect of the roost entrance on the emergence rate because of its large dimensions (see Material and Methods). The emergence pattern followed a unimodal distribution with the maximum rate of emergence half way through the exodus. An analogical pattern in the emergence behaviour was observed in *Pipistrellus pipistrellus* (Swift 1980), *Myotis emarginatus* (Boldogh et al. 2007), *Myotis blythii* (Boldogh et al. 2007) and *Nyctalus leisleri* (Shiel & Fairley 1999). By contrast, a maternity colony of Brandt's bat roosting behind window shutters emerged fastest at the beginning of emergence (Schmidt 2005).

The length of emergence varied with the number of bats in the roost, but it was also dependent on the period of the reproductive cycle when corrected for colony size. Although lactating females emerged earlier than pregnant females, some of them may have delayed their emergence in order to suckle or groom their pups prior to departure from the roost (Lučan, pers. obs.). Also, the onset of volancy of juvenile bats during late lactation further increased the emergence length in this period. Accordingly, a prolonged emergence during late lactation and early post-lactation was observed in *Myotis brandtii* (Schmidt 2005), *Plecotus austriacus* (Scheunert et al. 2009).

Bats tend to emerge earlier from roosts located in more protective habitats such as those surrounded by trees or situated within a dense canopy (Entwistle et al. 1996, Duvergé et al. 2000, Russo et al. 2007). In this study, Daubenton's bats emerged significantly earlier from a putatively less sheltered artificial roost than they did from tree cavities situated in forest stands or along the edge of a forest. As there may exist sex-based differences in the emergence time (e.g. Lee & McCracken 2001), one could argue that the observed pattern may arise from a different population structure in the two types of roosts. However, the vast majority of tree cavities in the study area were occupied by a female-dominated population, i.e. of the same or at least similar structure as in the studied artificial roost (Lučan & Hanák 2002). Therefore, it is not likely that the observed differences were related to a different population structure. We assume that the earlier emergence from the artificial roost may be facilitated by a faster re-warming from daily inactivity due to a warmer microclimate imposed by the building itself, as well as by the effect of a larger number of bats living inside (social thermogenesis) compared to smaller group sizes in tree cavities (usually <20 individuals, cf. Lučan et al. 2009). This hypothesis is in accord with the observation of Shirley et al. (2001) who recorded earlier emergence of Daubenton's bats from a building relative to a much later emergence time observed in bats roosting under natural conditions in nearby regions (Jones & Rydel 1994). Furthermore, the entrance to the building through which the bats in this study emerged was ca. 1 m above ground and faced to a meadow

with scattered trees and bushes which the emerging bats used to fly along. Therefore, they may have been even less conspicuous to potential diurnal predators than bats emerging from tree cavities located high on the tree trunk and thus clearly visible against the sky. Consequently, the bats emerging from the artificial roost may take benefit from an earlier emergence without the risk of falling victim to diurnal predators relying on vision.

The seasonal dynamic of the number of bats in the roost followed a bimodal pattern with a first peak during spring movements and pregnancy followed by a decrease during lactation and a second peak during the post-lactation period. In accordance with our observations, Shirley et al. (2001) observed almost identical seasonal changes in numbers of a colony of Daubenton's bats roosting in an old priory in Northumberland, UK. A similar seasonal pattern was also observed in *Pipistrellus pipistrellus* (Webb et al. 1996, Feyerabend & Simon 2000), *Nyctalus leisleri* (Shiel & Fairley 1999) and *Myotis brandtii* (Schmidt 2005). We assume that adult bats tend to aggregate into large colonies for thermoregulatory reasons during spring when mean roost temperatures are low. This holds particularly for pregnant females that may benefit from sustaining a high body temperature through social thermogenesis (Willis & Brigham 2007). As roost temperatures increase during pregnancy and lactation, aggregating may become less beneficial and the bats may scatter over many roosts. In accord with that, we observed such a pattern over many years in the studied roost where a part of the colony moved to nearby tree cavities shortly after parturitions (Lučan & Hanák 2002). It has been observed that, in contrast to pregnant females, lactating female Daubenton's bats save energy via entering torpor (Dietz & Kalko 2006). Based on our own unpublished data, tree cavities are generally colder than the studied artificial roost and therefore may enable the lactating females to enter daily torpor. Furthermore, the decrease in the size of the colony may be due to the departure of adult males and non-reproductive females that may constitute up to ca. one third of all bats in the roost during spring movements and early pregnancy (Lučan, unpubl. data). Apart from thermoregulatory reasons, bats are also forced to change their roosts due to an increased parasitation (Lewis 1995). This may be the case, as the highest numbers of ectoparasites in Daubenton's bats in the studied roost were found during pregnancy (Lučan 2006). Last but not least, the obtained data on the seasonal population dynamic suggest that the emergence counts made in May and/or late July provide the most reliable information on maximum numbers of Daubenton's bats roosting in buildings for monitoring purposes.

SOUHRN

V rozmezí let 1999 a 2009 bylo sledováno chování během večerního výletu u mateřské kolonie netopýra vodního (*Myotis daubentonii*) obývající umělý úkryt (bývalá vápenka) v oblasti jižních Čech. Vzhledem k vzájemné vysoké korelaci mezi časem výletu prvního jedince (T_{FB}) a časem výletu poloviny celé kolonie, byla pro všechny analýza použita první veličina, pro kterou bylo navíc k dispozici více údajů. Výlet prvního jedince probíhal 28±12 (průměr±SD) minut po západu slunce (min–max: 8–64 minut). Načasování výletu nebylo nijak ovlivněno velikostí kolonie, významný vliv však mělo období reprodukčního cyklu. Největší rozdíly byly pozorovány mezi obdobím březosti a laktace: v období kojení vyletovali netopýři ven z úkrytu v průměru o 14 minut dříve. Množství jedinců za jednotku času bylo největší zhruba v polovině délky výletu. Rychlost a délka výletu byly positivně korelovány s velikostí kolonie. Na délku výletu mělo vliv i období reprodukčního cyklu, přičemž nejdéle trval výlet v období laktace, nejkratší dobu naopak v období podzimních přeletů. Sezónní dynamika velikosti kolonie byla následující: po rychlém nárůstu početnosti během dubna dosahovala sledovaná kolonie prvního vrcholu v počtu jedinců v úkrytu během období březosti, následovaného poklesem počtu jedinců v období po porodech mláďat. Druhý vrchol v průběhu sezóny se vyskytoval v postlaktačním období v souvislosti s přítomností tohoročních mláďat.

Srovnáním načasování výletu dlouhodobě sledované kolonie ve vápence s anekdoticky zaznamenanými údaji o výletu z úkrytů ve stromových dutinách v blízkém okolí byla zjištěna stejná sezónní dynamika vzhledem k období reprodukčního cyklu, avšak výrazně pozdější výlet ze stromových dutin.

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REFERENCES

Barclay R. M. R., 1989: The effect of reproductive condition on the foraging behaviour of female hoary bats, *Lasiurus cinereus*. *Behavioural Ecology and Sociobiology*, **24**: 31–37.

Boldogh S., Dobrosi D. & Samu P., 2007: The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, **9**: 527–534.

Bullock D. J., Combes B. A. & Eales L. A., 1987: Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrellus*). *Journal of Zoology*, *London*, **211**: 267–274.

Catto C. M. C., Racey P. A. & Stephenson P. J., 1995: Activity patterns of the serotine (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, *London*, **235**: 635–644.

Dietz M. & Kalko E. K. V., 2006: Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiology*, **176**: 223–231.

Dietz M. & Kalko E., 2007: Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentonii*. *Canadian Journal of Zoology*, **85**: 653–664.

Duvergé P. L., Jones G., Rydell J. & Ransome R. D., 2000: Functional significance of emergence timing in bats. *Ecography*, **23**: 32–40.

Entwistle A. C., Racey P. A. & Speakman J. R., 1996: Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philosophical Transactions of the Royal Society of London*, *Series B*, **351**: 921–931.

Feyerabend F. & Simon M., 2000: Use of roosts and roost switching in a summer colony of 45 kHz phonic type pipistrelle bats (*Pipistrellus pipistrellus* Schreber, 1774). *Myotis*, **38**: 51–59.

Gaisler J., Hanák V. & Dungel J., 1979: A contribution to the population ecology of *Nyctalus noctula*. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae*, *Brno*, *n. s.*, **13**: 1–38.

Jones G., 1995: Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *Journal of Zoology*, *London*, **237**: 303–312.

Jones G. & Rydell J., 1994: Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society of London*, *Series B*, **346**: 445–455.

Kunz T. H. & Anthony L. P., 1996: Variation in the timing of nightly emergence behaviour in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Pp.: 225–235. In: Genoways H. H. & Baker R. J. (ed.): *Contributions in Mammalogy*: *a Memorial Volume Honoring Dr. J. Knox Jones*, *Jr*. Museum of Texas Tech University Press, Lubbock, 315 pp.

Lee Y.-F. & McCracken G. F., 2001: Timing and variation in the emergence and return of Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Zoological Studies*, **40**: 309–316.

Lewis S. E., 1995: Roost fidelity of bats: a review. *Journal of Mammalogy*, **76**: 481–496.

Lučan R. K., 2006: Relationships between parasitic mite *Spinturnix andegavinus* (Acari: Spinturnicidae) and its bat host, *Myotis daubentonii* (Chiroptera: Vespertilionidae): seasonal, sex- and age-related variation in infestation and possible impact of parasite on the host condition and roosting behaviour. *Folia Parasitologica*, **53**: 147–152.

Lučan, R. & Hanák V., 2002: A long term study of population of Daubenton's bat, *Myotis daubentonii*. *Bat Research News*, **43**: 96.

Lučan R. K., Hanák V. & Horáček I. 2009: Long-term re-use of tree roosts by European forest bats. *Forest Ecology and Management*, **258**: 1301–1306.

Petrželková K. & Zukal J., 2001: Emergence behaviour of the serotine bat (*Eptesicus serotinus*) under predation risk. *Netherlands Journal of Zoology*, **51**: 395–414.

Russo D., Cistrone L. & Jones G., 2007: Emergence time in forest bats: the influence of canopy closure. *Acta Oecologica*, **31**: 119–126.

Rydell J., Entwistle A. & Racey P. A., 1996: Timing of foraging flights in three species of bats in relation to insect activity and predation risk. *Oikos*, **76**: 243–252.

Scheunert A., Zahn A. & Kiefer A., 2009: Phenology and roosting habits of the central European grey long-eared bat *Plecotus austriacus* (Fischer 1829). *European Journal of Wildlife Research*. DOI 10.1007/s10344-009-0333-9

Schmidt C., 2005: Emergence behaviour of a nursery colony of *Myotis brandtii* (Eversmann, 1845) in Saxony. *Myotis*, **43**: 55–62.

Shiel C. B. & Fairley J. S., 1999: Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland. *Journal of Zoology*, *London*, **247**: 439–447.

Shirley M. D. F., Armitage V. L., Barden T. L., Gough M., Lurz P. W. W., Oatway D. E., South A. B. & Rushton S. P., 2001: Assessing the impact of a music festival on the emergence behaviour of a breeding colony of Daubenton's bats (*Myotis daubentonii*). *Journal of Zoology*, *London*, **254**: 367–373.

Speakman J. R., Irwin N., Tallach N. & Stone R., 1999: Effect of roost size on the emergence behaviour of pipistrelle bats. *Animal Behavior*, **58**: 787–795.

Swift S. M., 1980: Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology*, *London*, **190**: 285–295.

Webb P. I., Speakman J. R. & Racey P. A., 1996: Population dynamics of a maternity colony of the pipistrelle bat (*Pipistrellus pipistrellus*) in northeast Scotland. *Journal of Zoology*, *London*, **240**: 777–780.

Willis C. K. R. & Brigham R. M., 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioural Ecology and Sociobiology*, **62**: 97–108.