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Population ecology of *Myotis daubentonii* (Mammalia: Chiroptera) in South Bohemia: summary of two long-term studies: 1968–1984 and 1999–2009

Radek K. Lučan & Vladimír Hanák

Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ–128 44 Praha 2, Czech Republic
corresponding author: rlucan@centrum.cz

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Abstract. Based on an extensive dataset (906 samples, 4175 bats captured, including 1604 recaptures of 657 individuals) obtained during two periods (1968–1984 and 1999–2009) in a model study area (South Bohemia, the Czech Republic) basic information on roosting ecology, population structure, seasonal dynamics and some aspects of reproduction of the Daubenton's bat (*Myotis daubentonii* Kuhl, 1817) was summarized. Bats roosted in an old lime kiln and tree cavities. The majority of the roosts were located a few tens up to a few hundred meters from the nearest water body and the majority were within 50 m of the edge of forest, a clearing or linear structures. Overall sex ratio of the adults was skewed toward females (mean sex ratio 3 males: 10 females) but did not deviate from 1:1 in juveniles. Seasonal dynamics of the numbers of bats differed between the two types of roosts. It was bimodal in the lime kiln and unimodal in natural roosts. In the lime kiln the maximum numbers of bats were recorded during pregnancy and post-lactation. In tree cavities, the largest aggregations occurred mostly during lactation and post-lactation. Considerable seasonal variation in the presence and numbers of different roosting aggregations was recorded. Recapture rate was generally high (33.4%) but varied both in the different roosts and research periods. The frequency of recaptures indicate a higher fidelity of bats for the lime kiln than tree cavities. Majority of recorded movements took place over distances of a few hundred meters. The data on the distances moved based on recaptures of ringed individuals were consistent with the results of a radio-tracking study conducted in the same study area. Many more movements took place between the lime kiln and tree cavities than among tree cavities, however, results may be biased, to some extent, by uneven sampling effort. These observations support the concept of the existence of discrete subpopulation units, i.e. the fission-fusion model of social organisation, reported for some other forest bats. Roughly one-third of the females reproduced in the year following their birth. Overall spatial organization of the population studied was quite unusual in the existence of a "central" roost with stable occupancy.

Key words. roosting ecology, seasonal dynamics, tree roosts, anthropogenic roosts, Mammalia, Chiroptera, *Myotis daubentonii*, Czech Republic.

INTRODUCTION

The Daubenton's bat, *Myotis daubentonii* (Kuhl, 1817), is a small (forearm length 33–42 mm, body mass 5–10 g; Bogdanowicz 1994) insectivorous bat inhabiting most of the Palearctic region (Horáček et al. 2000). It is one of the commonest species throughout most of its European range (Mitchell-Jones et al. 1999) and has increased markedly in numbers during past decades, perhaps due to favourable climatic changes and increased food supply (Kokurewicz 1995). Hence, it is listed as a species of low risk of threat by the IUCN/SSC Chiroptera specialist group (Hutson et al. 2001). During past decades, it was extensively studied, which substantially improved our knowledge of its biology. In particular research focused on its foraging activity and habitat use (e.g. Kalko & Braun 1991, Rieger et al. 1992, Ebenau 1995, Rieger 1996a, Vaughan et al. 1996, Arnold et al. 1998, Warren et al. 2000), echolocation and foraging tactics (e.g. Jones & Rayner 1988, Kalko & Schnitzler 1989, Jones & Kokurewicz 1994, Boonman et al. 1998, Britton & Jones 1999, Siemers et al. 2001) and activity at and use of hibernation sites (Roer & Egsbaek 1966, Haensel 1978, Klawitter 1980, Baagøe et al. 1988, Parsons et al. 2003, Kokurewicz 2004). Considerably less attention was paid to its roosting and population ecology in the reproductive season (Červený & Bürger 1989, Ebenau 1995, Rieger 1996b, Arnold 1998, Boonman 2000), although several excellent papers on that topic have recently been published (Encarnação et al. 2005, Kaňuch 2005, Senior et al. 2005, Encarnação et al. 2007, Kapfer et al. 2008, Encarnação et al. 2010). Despite this, there is little detailed information on the population structure and seasonal roosting dynamics, and what there is originates from a few geographically restricted areas.

During the two periods (1968–1984 and 1999–2009) intensive research was conducted in a model study area in South Bohemia in the Czech Republic, on the ecology of tree roosting bats, particulary Daubenton's bats and noctules (*Nyctalus noctula*). While some results have been published in detail (Gaisler et al. 1979, Lučan 2006, Lučan et al. 2009, Lučan & Hanák 2010, Lučan & Radil 2010), a considerable amount of data has not been analyzed and published in a scientific

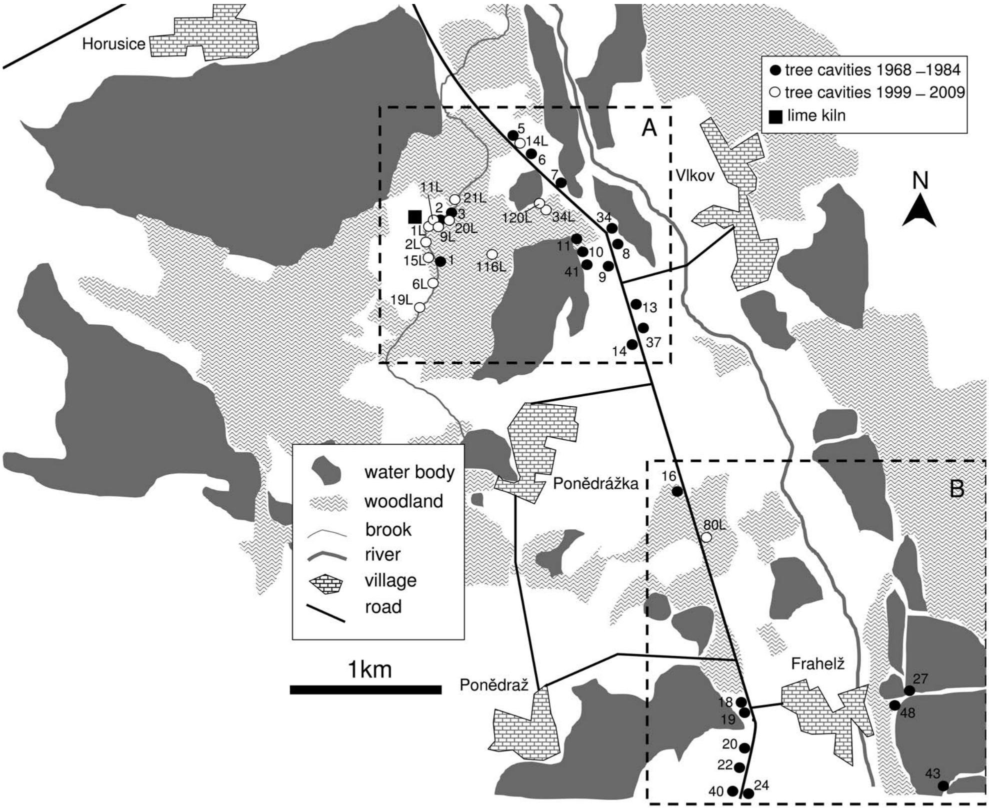

Fig. 1. Schematic map of the study area in South Bohemia showing the two study plots and locations of roosts. Numbers at each roost refer to original ID. Depicted are only roosts sampled by capturing the bats.

journal. The present paper aimed to analyze the seasonal dynamics, structure of the population, temporal variation in the use of roosts, movements between roosts and roost fidelity and present details of the reproductive parameters of the population of Daubenton's bats studied.

MATERIAL AND METHODS

Study area

The study area covered ca. 10 km^2 and included two adjacent study plots. Plot A was located in the north and plot B in the south of the study area (Fig. 1). The area was located in the northern part of the Třeboňsko Landscape Protected Area and Biosphere reserve (49° 9' N, 14° 42' E). It consists of a flat basin covered with a mosaic of semi-natural mixed forests, meadows, wetlands, peat bogs, arable land and a number of ponds of different sizes (from <1ha to >300 ha). Forests are dominated mostly by Scotch pine (*Pinus silvestris*) with oak (*Quercus robur*), aspen (*Populus tremula*), ash (*Fraxinus excelsior*) and spruce (*Picea abies*). Water bodies and streams are commonly bordered by alder (*Alnus glutinosa*) and willow (*Salix fragilis*). Typical of the area are rows of trees and alleys of oaks and limes (*Tilia cordata*) growing around ponds and along roads. Trees in these alleys and rows are usually very old (>300 years) and of immense size. The mean annual temperature reaches 6–7 °C and the mean annual precipitation is 600–650 mm (Tolasz et al. 2007).

Roosts and their sampling

Artificial roost

An old lime-kiln is a cellar-like building located at the edge of a large peat-bog and is surrounded by scattered trees. Its outer dimension is ca. 5×3×2.5 m (length×width×height). The brick and stone walls are very thick (~1m) and the only entrance (ca. 1.5 m high×1 m wide) faces an open space. There are a large number of fissures of different sizes in the walls some of which are frequently used as shelters by Daubenton's bats. The main roosting place of the bat colony is a large (ca. 30×30 cm width and 60 cm deep) cavity in the ceiling of the lime kiln. This cavity was used by the bats for roosting throughout the year whereas some smaller fissures are used only occasionally by individual bats or small aggregations, mostly during spring and autumn. The lime kiln has been inhabited by a colony of Daubenton's bats at least since 1962. In 1987 the roof of the lime kiln partially collapsed and only individual bats were recorded in in the kiln at that time. After restoration, bats returned and have roosted there each year ever since. Therefore, this lime kiln is possibly the longest inhabited roost of Daubenton's bats in Europe.

The main roosting cavity in the lime kiln could be easily inspected without seriously disturbing the roosting bats and important observations (e.g. presence of newborn, suckling behaviour, copulation etc.) more easily made than in natural roosts. The roosting bats usually start to fly about half an hour before leaving the lime kiln and swarm inside prior emergence from the kiln. After their return from foraging bouts during the night, most bats often rest on the ceiling inside the lime kiln. To capture the bats at this roost, a mist net stretched over the entrance and/or a hand net, were used. Typically, in order to obtain quantitative data as many bats as possible were sampled.

Tree cavities

Throughout the study period, we searched for tree cavities in the study area. Typically, once a cavity was found, it was labelled by an identification number and repeatedly inspected for the presence of bats. We fixed a nail above each tree cavity in order to be able install a trapping device. We used simplified custom-made funnel traps (see Gaisler et al. 1979) to capture the bats when they emerged from roosts. Several cavities were usually sampled simultaneously using this technique. In some cases (N=20), we did not succeed in catching all the bats from a particular tree cavity. Typically, part of a roosting group does not emerge for more than 1 hour and therefore the trap was removed from a cavity entrance to minimize disturbance. Data from these samples were not included in the analyses of roosting group sizes. Most tree cavities were reused by Daubenton's bats in consecutive years (up to 14 years; Lučan et al. 2009) and this allowed us to repeatedly sample bat aggregations roosting in the same cavity in different periods of a year and/or in different years.

As a supplementary method, we used audio-visual checks of tree cavities. The two bat species that occupy tree cavities in the study area (i.e. Daubenton's bats and noctules) produce markedly different sounds and thus could be confidentlly distinguished without capture. This method was particularly productive on warm afternoons when social vocalizations prior to flight were common. Noctules in particular could be heard at distances of 30–40 m (Gaisler et al. 1979) and Daubenton's bats up to 10 m. This method allowed us to reliably indentify roosts used by large groups; smaller groups or single individuals often do not produce audible vocalizations and were not commonly detected by this method. Following acoustic identification of occupied roost, we either used traps to capture emerging bats or, in some instances, we made emergence counts. The bat detector was usually used to identify the species.

Overall, the research effort was unevenly distributed within and between the two phases of the research. Consequently, we obtained a large number of samples in some periods of the reproductive season and/or years and a small number in

Table 1. Total number of times tree cavities were sampled during this study

year	stp	p	l	pl	atp	total
1969	1	1	3	–	–	5
1970	–	2	–	1	–	3
1971	1	2	–	2	–	5
1972	–	–	–	2	–	2
1973	–	–	2	5	2	9
1974	1	1	–	1	–	3
1975	10		–	17	50	77
1976	41	20	11	30	120	222
1977	22	17	21	9	12	81
1978	1	1	6	45	52	105
1979	–	–	1	4	49	54
1980	–	2	28	25	–	55
1981	–	2	–	6	–	8
1982	38	2	–	1	–	41
1983	1	1	–	–	–	2
1984	–	4	–	–	–	4
1999	13		11	2	37	63
2000	14	7	1	6	15	43
2001	–	–	–	2	6	8
2004	–	–	–	2	–	2
2007	6	–	8	–	–	14
total	149	62	92	161	343	807

others. Sampling activity in both the lime kiln and tree cavities was particularly restricted during the lactation period in order to minimize the disturbance to bats. Summaries of sampling effort for each year and period of the reproductive cycle are given in Table l and Table 2.

The bats

For most of the bats captured we recorded their sex, age, reproductive status, weight, and forearm length. Weight was measured to the nearest 0.5 g using a Pesola spring balance. Forearm length was measured to the nearest 0.1 mm using callipers. However, during the 1968–1984 research periods, we did not systematically record the reproductive status of females during the post-lactation period. Therefore, we were unable to enumerate the reproductive success (i.e. the proportion of females that gave birth in a particular year) for that research period. Juvenile bats can be distinguished by the incomplete ossification of carpal joints (Brunet-Rossinni & Wilkinson 2009) and distinct black chin spot (Richardson 1994), and pregnant females by the presence of a palpable embryo. Females were classified as lactating if they had enlarged nipples and there was no fur around them. The same characters (in more or less distinct extent depending on the time that had passed since the end of lactation) were used during the post-lactation period in order to determine whether a particular female gave birth in a given year. In males, the reproductive status was based on size and position of testes. If a male had enlarged, scrotally positioned testes and enlarged *cauda epididymidis*, it was regarded as sexually active (Encarnação et al. 2006, Brunet-Rossinni & Wilkinson 2009).

Between 1968 and 2004 all bats captured were ringed using aluminium rings. Lipped bat rings were used prior to 1999, whereas mostly bird rings were used from 1999 onwards. We changed the type of rings based on suggestions by Reiter (1998) who recorded much lower incidence of wing injuries in Daubenton's bats ringed with bird rings compared to lipped bat rings. In order to further diminish the possible negative effects on bats, we ground down the sharp edge of the bird ring using a file prior to attaching the ring to a bat's forearm.

Evaluation of recaptures and movements between roosts

The recaptures were treated in one of two ways. (1) If the bat was recaptured at the same roost as previously, it was treated as a "same roost" recapture. If the bat was recaptured in different roost than previously, it was treated as a "movement" recapture. (2) If two consecutive recaptures were made in a single season, it was treated as "same year" recapture. If two consecutive recaptures were made in different years, it was treated as a "different year" recapture.

Table 2. Total number of times the lime kiln was sampled during this study

year	stp	p	l	pl	atp	total
1968	–	–	–	1	1	2
1969	–	1	–	–	–	1
1970	–	–	–	1	1	2
1971	–	–	–	1	1	2
1972	–	–	–	1	–	1
1973	–	–	–	3	3	6
1974	1	–	–	4	4	9
1975	1	–	–	4	1	6
1976	–	–	–	1	4	5
1977	1	1	–	–	1	3
1978	–	–	1	1	3	5
1979	–	2	–	1	2	5
1980	–	–	–	1	1	2
1981	–	2	–	–	1	3
1982	1	1	–	–	1	3
1999	3	1	1	–	3	8
2000	2	1	1	1	1	6
2001	–	1	2	1	1	5
2002	1	–	–	1	–	2
2003	–	–	–	–	1	1
2004	–	–	–	1	1	2
2005	–	4	1	2	–	7
2006	–	–	–	1	–	1
2007	5	–	1	1	2	9
2008	1	–	–	1	–	2
2009	–	–	–	1	–	1
total	16	14	7	29	33	99

Periods of reproductive cycle

Each year was arbitrarily divided into five periods based on the reproductive status of bat population studied: spring (**stp**) – until May 10, pregnancy (**p**) – until June 10, lactation (**l**) – until July 10, post-lactation (**pl**) – until August 15, autumn (**atp**) – after August 15. We used this division, rather than calendar months, since it better reflects the most significant events in the bat population studied.

Statistical analyses

To test for deparure from a 1:1 sex ratio in all samples, we used a goodness-of-fit test. We used analysis of variance (ANOVA) to test for seasonal differences in the sex ratio between the lime kiln and tree cavities. We used arcsine transformation of square-root values of the sex ratio data to achieve normal distribution prior to analyses (Wilson & Hardy 2002). To compare frequency of different types of recaptures, we used a goodness-of-fit test. Yates correction was used in cases where total counts were < 5. We used factorial ANOVA to test the differences in the distances moved by the sexes, in the different research periods and time intervals from capture to recapture of individual bats. Prior that analysis, we used logarithmic transformation to achieve normal distribution of data. If not specified, values are given as mean±SD.

RESULTS

Total sample of bats

In total there were 4175 Daubenton's bats (Table 3) in the 906 samples. Of these, 2009 were captured for the first time and ringed, 1604 were recaptures of 657 individuals and 610 were not ringed. 2632 bats were captured in the lime kiln and 1543 in tree cavities. We captured 3889 bats

Table 3. Total number of bats captured during this study; ad – adults, juv – juveniles, ♀ – females, ♂ – males, stp - spring transitional period, p - pregnancy period, l - lactation period, pl - post-lactation period, atp - autumn transitional period

	ad ♀	ad ♂	juv ♀	juv ♂	Σ
lime kiln					
stp	67	30	–	–	97
p	206	25	–	–	231
l	52	4	–	–	56
pl	823	209	348	286	1666
atp	224	106	147	105	582
Σ	1372	374	495	391	2632
tree cavities					
stp	93	16	–	–	109
p	142	8	–	–	150
l	225	6	50	29	310
pl	371	26	181	113	691
atp	128	36	69	50	283
Σ	959	92	300	192	1543
total	2331	466	795	583	4175

in study plot A and 286 in plot B. For 212 samples the sex, age, or both were not recorded and these bats were not included in the analyses and summaries shown below.

Roosts

Except for the lime kiln, tree cavities were exclusively used as day roosts by Daubenton's bats in the study area. Altogether, we checked more than 150 tree cavities, but only 80 of them were checked repeatedly (Lučan et al. 2009, Lučan & Hanák 2010). In total, we found 48 tree cavities occupied by Daubenton's bats. While four of these cavities (8.3 %) were natural holes that originated from rotting, the remaining 44 cavities were excavated by woodpeckers, most often the Greater Spotted Woodpecker (*Dendrocopos major* Linnaeus, 1758). Seven species of trees were used for roosting of which willow (15), lime (14) and oak (10) were the most frequent (Table 4). All trees used for roosting were alive middle-aged to very old, mainly oak or lime trees, sometimes of immense size. Most of these big trees were situated on the dams around ponds, along forest roads and canals and, particularly, in alleys along main roads. The height of the cavity entrance above the ground ranged from 1 to 15 meters, with a mean value 4.6 m. The majority of the roosts

Table 4. Basic data on the tree cavities occupied by Daubenton's bats. N refers to number of tree cavities, not trees

tree species	N	entrance height above ground (m)			
		mean	SD	min	max
Alnus glutinosa	5	3.4	2.4	1.0	7.5
Malus domestica	1	2.5			
Pinus sylvestris	1	4.2	1.5	2.5	4.5
Quercus robur	9	6.1	2.3	3.0	9.5
Salix fragilis	15	4.8	1.9	3.0	10.0
Tilia cordata	14	3.8	3.5	2.5	15.0
Populus tremula	1	5.0			
total	48	4.6	2.7	1.0	15.0

Table 5. Sex ratio (males to all adult bats) of the bats captured. Primary data are shown in Table 3

period	lime kiln		tree roosts	
	adults	juveniles	adults	juveniles
stp	0.31	–	0.15	–
p	0.11	–	0.05	–
l	0.02	–	0.03	0.37
pl	0.20	0.45	0.07	0.38
atp	0.32	0.42	0.22	0.42
total	0.20	0.44	0.09	0.39

were located < 300 m from water and none were further than 1 km from the nearest water body. Over 90 per cent of all roosts were within 50 m of a forest edge, clearing or linear structure.

Population structure and roosting dynamics

Sex ratio

Of the total of 4175 bats examined, 3126 were females and 1049 males, that is the sex ratio was 0.25, i.e. 3 : 10 (males: females). Overall, the sex ratio deviated from 1:1 in all samples of adults (lime kiln: χ^2=370.45, d.f.=121, p=0.0001; tree cavities: χ^2=276.17, d.f.=87, p=0.0001) but not of juveniles (lime kiln: χ^2=66.11, d.f.=86, p=0.945; tree cavities: χ^2=27.26, d.f.=52, p=0.998, Table 5). In the sample of adult bats, females always prevailed but the sex ratio changed with the reproductive cycle ($F_{(4,203)}$=3.93, p=0.004). The highest proportion of males occurred during spring and autumn, when it reached 0.2–0.3, i.e. 0.3–0.4 males: 1 female. During pregnancy and lactation, males made up less than 10 per cent of the total sample. For adult bats, the proportion of males was significantly higher in the lime kiln than tree cavities ($F_{(1,203)}$=4.45, $P < 0.05$). The sex ratios in these two roosts differed most in the post-lactation period and autumn (Fig. 2).

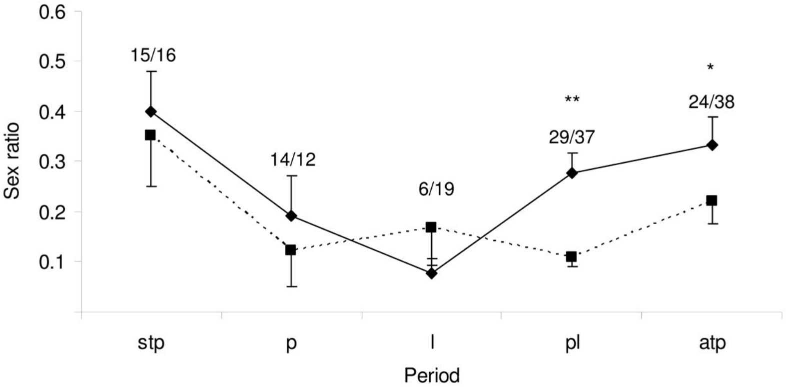

Fig. 2. Variation in the mean sex ratio in the lime kiln (LK) (black diamonds) and tree cavities (black squares) at different periods of the reproductive cycle. Numbers refer to sample size for the lime kiln/tree cavities. Whiskers – S.D.; stc – spring period, p – pregnancy period, l – lactation period, pl – post-lactation period, atp – autumn period.

Types of aggregations in roosts

In total, we obtained data on the structure of roosting groups from 99 and 162 samples for the lime kiln and tree cavities, respectively. However, only for 87 and 149 of the samples of the lime kiln and tree roosts, respectively, were all the bats captured, and these data were used for analyzes of the sizes of roosting groups (Table 6). In general, the size and composition of roosting groups was related to the type of roost and period in the season.

The lime kiln was most frequently occupied by mixed groups composed of adult males and females during spring. However, females always greatly outnumbered males (see chapter on sex ratio). Strictly female groups prevailed during pregnancy and lactation. Because we were not able to precisely count non-volant juveniles, our values of the number of bats in the lime kiln refer to the number of adult females as these could be easily counted during evening emergence. Consequently, the real number of bats in the roost was always almost two times higher due to the presence of non-volant juveniles. During the post-lactation period, a typical aggregation was composed of adult females, juveniles and adult males. During autumn, almost all types of aggregations could be found, except for pure male groups and groups composed only of adult males and females since juveniles were almost always admixed with adults. We did not record a pure male colony in the lime kiln throughout this study.

In tree cavities, we found three types of aggregations (males, females, males+females) in a similar proportion during spring. During pregnancy and lactation, female groups greatly outnumbered all other types of aggregations. In Table 6, female groups and groups of females with juveniles were treated separately, however, this is mostly due to the fact, that our data are based on capturing bats upon their emergence from roosts and juveniles were captured rather sporadically at the end of the lactation period. In fact, most, if not all, “female” groups were composed of lactating females and should be therefore regarded as nurseries

Table 6. Seasonal dynamics of the occurrence and size of different types of roosting aggregations in the lime kiln and tree cavities. Median number followed by range (in parentheses) and sample size is given for each category. ♀♀ – adult females, ♂♂ – adult males, juv–juveniles of both sexes. [a] juveniles were usually present but not counted – see text for details

period	type of aggregation						
	♀♀	♂♂	♀♀+♂♂	♀♀+♂♂+juv	♀♀+juv	♂♂+juv	juv
lime kiln							
stp	8 (1–35) N=4	–	11 (3–32) N=10	–	–	–	–
p	116 (90–190) N=6	–	57(25–190) N=4	–	–	–	–
l	60 (40–100) N=6	–	–	–	–	–	–
pl	–	–	–	66 (19–160) N=25	–	–	–
atp	1 (1–2) N=3	–	–	22 (8 –100) N=17	6 (3–16) N=5	7 (3–13) N=4	4 (5–8) N=3
tree cavities							
stp	5 (1–19) N=8	1 (1) N=3	5 (2–16) N=7	–	–	–	–
p	8 (1–51) N=11	–	–	–	–	–	–
l	7 (6–34) N=6 [a]	1 (1) N=1	6.5 (4–9) N=2	–	19 (4–44) N=9	–	–
pl	2 (1–3) N=5	–	11 (4–18) N=3	17 (4–56) N=11	16 (3–77) N=18	9 (9) N=1	1 (1–3) N=5
atp	1 (1–4) N=9	1 (1) N=2	5 (2–10) N=6	9 (4–22) N=12	7 (2–34) N=13	2 (2–3) N=3	1 (1–6) N=14

composed of females and juveniles. In contrast to the lime kiln, adult males were sometimes (21% of samples) admixed with females with juveniles in tree cavities during the lactation period. In the post-lactation period, the commonest types of aggregations were adult females with juveniles and mixed groups of adult males, females and juveniles. However, all types of aggregations were found except for pure male groups in this period. The highest diversity of types of aggregations was found in tree cavities during autumn. The commonest were males+females, females+juveniles and pure juvenile groups.

All findings of males (N=6) were of singly roosting individuals. Most of them were recorded in spring and autumn.

Seasonal dynamics in roost occupation and size of roosting groups

In the lime kiln, individuals or small groups of up to 20–30 Daubenton's bats usually appeared at the beginning of the reproductive season (late March – end of April). Colony size rapidly increased towards the end of spring. This increase may take just one or two weeks. We observed the formation of a large colony, typically present in the lime kiln during the pregnancy period, was advanced by 2–4 weeks during the period 1999–2009. For example, in 1999 and 2000, maximum colony size was recorded in mid-May, whereas in 2007 and 2008 it was in mid-April (Fig. 3). The highest number of bats was observed on April 29, 2006, when 205 individuals were counted at evening emergence. Overall, however, the maximum numbers of females occurred during the pregnancy period. In most years, a rapid decline in colony size (by ca. 50%) was observed shortly after females gave birth (see Fig. 3). However, our data are based on captures or emergence counts, i.e. only adult flying bats were registered. Given the fact that mostly reproductive females were present at the roost during that period, and almost all females gave birth, the real number of bats in the lime kiln was similar to that before parturition. The decrease amounted to about half of the females present in the lime kiln prior to parturition plus their offspring. As juveniles became volant, the number of bats recorded in the lime kiln roughly doubled. The second peak in

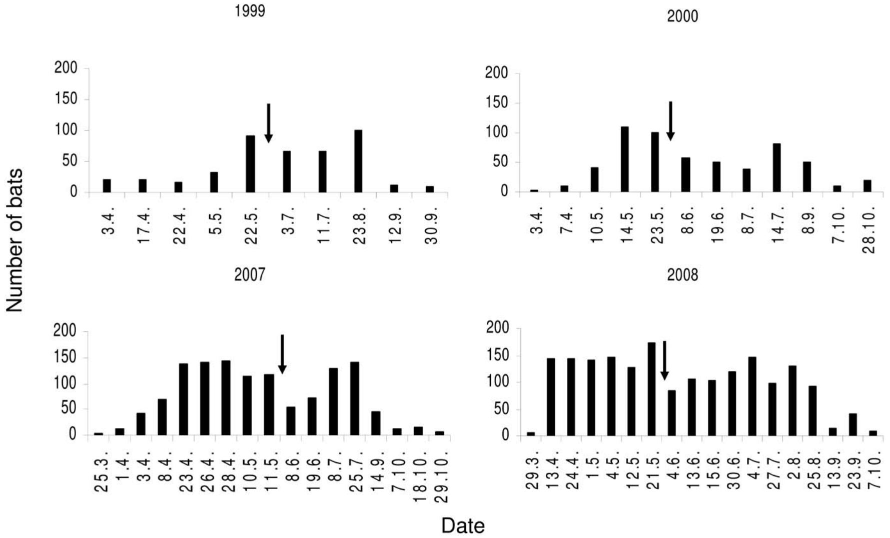

Fig. 3. Seasonal variation in numbers of bats in the lime kiln based on emergence counts in four different years. Arrows indicate times of parturition at the roost based on presence of newly born individuals.

Table 7. Number of bats ringed and recaptured at the two types of roosts, recorded separately for the two study periods

	1968–1984 ringed	 recaptured	 % recaptured	1999–2009 ringed	 recaptured	 % recaptured
tree cavities						
ad ♀	343	68	19.8	129	26	20.2
juv ♀	215	42	19.5	38	5	13.2
ad ♂	31	6	19.4	16	0	0.0
juv ♂	139	25	18.0	27	8	29.6
total	728	141	19.4	210	39	18.6
lime kiln						
ad ♀	116	69	59.5	167	86	51.5
juv ♀	195	113	57.9	74	44	59.5
ad ♂	32	18	56.3	42	13	31.0
juv ♂	161	64	39.8	72	14	19.4
total	504	264	52.4	355	157	44.2

numbers usually occurred in the post-lactation period, but it usually did not exceed the numbers observed during pregnancy.

In contrast to the lime kiln, the seasonal pattern in group size in tree cavities was unimodal with the peak numbers occurring during lactation. The size of roosting groups varied greatly depending on the type of aggregation (cf. Table 6). The largest aggregation ever found, sampled on July 27, 1978, consisted of 77 individuals and was composed of adult females and juveniles. Overall, however, sizes of roosting groups were much smaller than those recorded in the lime kiln at all periods of the reproductive cycle (Fig. 4).

Summary of ringing data

Recaptures

The time span between the first and last capture was 13 and 10 years in the first and second research period, respectively. However, in both research periods, over 90% of all recaptures were recorded within the first six years of ringing. Overall, we recaptured 33.4% of all bats ringed. The proportion recaptured of all those ringed (recapture rate) differed between the lime kiln and

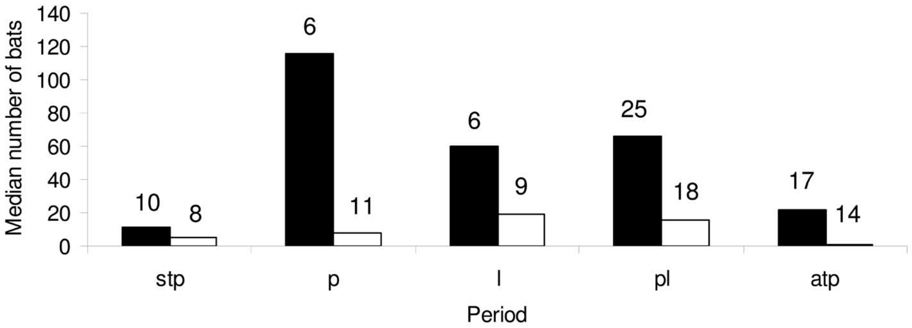

Fig. 4. Seasonal dynamics in the size of roosting aggregations based on median numbers of bats in most frequently occurring types of aggregations. Data are shown for aggregations sampled only by direct captures. Number above each column refers to sample size. Black columns – lime kiln, white columns – tree cavities.

Table 8. Number of different types of recaptures (see Material and Methods for details) at the two types of roosts. Proportion (%) of the total recaptures at particular roost types is given in parentheses

		recaptures		total
		same roost	movement	
tree roosts				
males	same year	5 (1.9)	27 (10.1)	32 (11.9)
	different year	1 (0.4)	11 (4.1)	12 (4.4)
females	same year	8 (3.0)	74 (27.4)	82 (30.4)
	different year	24 (8.9)	120 (44.4)	144 (53.3)
total	38 (14.1)	232 (85.9)	270 (100)	
lime kiln				
males	same year	105 (8.8)	11 (0.9)	116 (9.7)
	different year	170 (14.2)	7 (0.6)	177 (14.8)
females	same year	253 (21.2)	43 (3.6)	296 (24.8)
	different year	528 (44.3)	76 (6.4)	604 (50.6)
total		1056 (88.5)	137 (11.5)	1193 (100)

tree cavities, and varied among sex and age categories (Table 7). It was much higher for the lime kiln than tree cavities (49% vs. 19.2%, respectively). In the case of bats originally ringed in tree cavities, the recapture rate was very similar among sex and age categories in the first period studied, but varied considerably in the second period studied. The same was true for the bats ringed in the lime kiln. In general, recapture rates were higher for females than males. Between 1999 and 2009, we did not recapture any bats from the first research period.

Movements between roosts and roost fidelity

Of the 1463 analyzable recaptures, 1193 were for the lime kiln and 270 for tree roosts. The proportion of both types of recaptures ("same-roost" and "movement") differed between sexes and roosts (Table 8). There was a significant difference in the frequency of same-roost recaptures and movements between the lime kiln and tree cavities (χ^2=95.45, d.f.=1, P<0.0001). A higher frequency (88.5%) of same-place recaptures were recorded in the lime kiln than tree cavities (14.1%). This trend was consistent between the two sexes. There were consistently more recaptures of females in different years than in the same year. In males, the frequency of recaptures in the same year and in different years differed significantly between the lime kiln and tree cavities (χ^2=17.05, d.f.=1, P<0.0001). A higher proportion of males was recaptured in different years in the lime kiln than tree cavities.

Table 9. Summary of all recaptures relative to location. See Material and methods for explanation

type of recapture		N	% of all recaptures
movements	lime kiln → tree cavities	140	9.6
	tree cavities → lime kiln	105	7.2
	tree cavity → different tree cavity	124	8.5
same-place recaptures	lime kiln	1056	72.2
	tree cavities	38	2.6
total		1463	100

Table 10. Results of factorial ANOVA of the relationship between distance the bats moved, the research period, sex and the time to its previous capture. The research period refers to the first (1968–1984) or second (1999–2009) research period. Time interval refers to "same year" and "different year" recaptures–see Material and Methods for explanation

factor	F	d.f	p
research period (P)	79.406	1	0.001 ***
time interval (T)	12.111	1	0.001 ***
sex	1.961	1	0.162
P × T	0.576	1	0.448
P × Sex	0.772	1	0.380
T × Sex	6.705	1	0.010 **
P × T × Sex	2.068	1	0.151

Almost two-thirds (66.4%) of all movements took place between the lime kiln and tree cavities and the remaining 33.6% were movements between different tree cavities (Table 9). The vast majority (over 98%) of all movements took place within the two study plots. Two of the six movements between plot A and B were bats ringed in tree cavities in plot B and subsequently recaptured in the lime kiln. The remaining four movements were between tree cavities. Only two of these movements were recorded within a single season, remaining four were "different year" movements, i.e. bats were first captured in one study plot and recaptured in consecutive years in the other plot.

Multivariate analysis (Table 10) revealed a significant effect of the period of the research and the time interval between consecutive captures on the distance over which the bats moved. A summary of the distances moved is given in Table 11. Overall, much shorter (Tukey post hoc test: P<0.0001) movements were recorded in the second research period. Movements were, on average, shorter within years than between years (P<0.0001). The distances, over which different sexes moved, were related to whether it was within a single year or between consecutive years. Within years, females moved similar distances to males (P=0.536), whereas between years they moved to less distant roosts than males (P<0.01).

Table 11. Summary of the distances moved (in meters) among roosts recorded in the two study periods

		N	mean	median	minimum	maximum
1968–1984						
females	within one year	71	807	500	50	2400
	consecutive years	155	1042	1200	50	6500
males	within one year	32	747	950	20	1900
	consecutive years	14	1314	1300	300	3250
total		273	954	1100	20	6500
1999–2009						
females	within one year	44	168	70	40	750
	consecutive years	21	151	70	40	600
males	within one year	6	118	50	40	450
	consecutive years	4	555	575	70	1000
total		78	182	70	40	1000
grand total		351	783	450	20	6500

Table 12. Summary of the reproductive status of females ringed as juveniles and recaptured in consecutive seasons. Repr. – reproductive, NR – non-reproductive

year of life	repr.	%	NR	%	total
2	10	35.7	18	64.3	28
3	18	90.0	2	10.0	20
4	13	92.9	1	7.1	14
5	10	83.3	2	16.7	12
6	2	28.6	5	71.4	7
7	5	83.3	1	16.7	6
9	2	100.0	0	0.0	2
10	1	100.0	0	0.0	1
11	0	0.0	1	100.0	1
recaptures					91
individuals					46

Details of reproductive parameters

Maturing of females

We made 91 recaptures of 46 females that were ringed as juveniles (Table 12). In spite of limited data, we could assess the reproductive success of females of known age. More than 35 % of recaptured females reproduced in the year following their birth. Proportion of reproductive females was highest (> 80 %) in their third and fifth year of life. Almost two thirds of 6-years-old females were non-reproductive. In their 7th year of life, >80% of the females reproduced.One hundred percent of the females in their 9th (N=2) and 10th (N=1) year of life reproduced. One 11-year old female did not reproduce in that year.

Sexual activity of adult males

Males with enlarged testes (i.e. sexually active) were observed during the post-lactation period and autumn (Fig. 5). Overall, there was a much higher proportion of sexually active males in

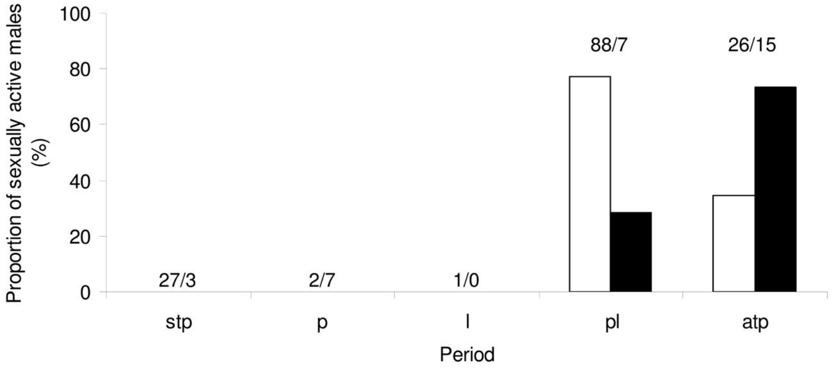

Fig. 5. Seasonal changes in the proportion of the males that were sexually active in the lime kiln (white columns) and tree cavities (black columns). Numbers above each column refer to total number of adult males examined in the lime kiln / tree cavities.

the lime kiln than in tree cavities during the post-lactation period while the reverse was true in autumn (Chi-square test with Yates correction; pl: χ^2=5.62, d.f.=1, P<0.05; atp: χ^2=4.26, d.f.=1, P<0.05). Also, mating behaviour was repeatedly observed in the lime kiln in the post-lactation period and in autumn (Lučan, pers. obs.).

DISCUSSION

Roosts

Daubenton's bat was originally a tree-dwelling bat (Červený & Bürger 1989, Rieger 1996, Boonman 2000, Encarnação et al. 2005, Lučan et al. 2009), although it may roost in man-made structures such as tunnels, bridges, domestic dwellings, abandoned houses (Nyholm 1965, Gerell 1985, Barva 2000, Shirley et al. 2001, Lučan & Hanák 2011; this study) and even caves (Zahn & Hager 2005). In the area studied the majority of tree roosts were in cavities excavated by woodpeckers. This fact stresses the importance of primary excavators in providing roosting opportunities for Daubenton's bats (Lučan et al. 2009). The vast majority of all roosts were located close to forest edges and within a few tens or a few hundred meters of the nearest water body. Our data fully correspond with the findings of Racey (1998), Boonman (2000) and Encarnação et al. (2005). This location of roosts most probably enables bats to minimize flight costs and/or may be prefereable for thermoregulatory reasons (Boonman 2000).

Structure of the population

The overall sex ratio of the population of Daubenton's bats studied was highly skewed toward females. On average, females outnumbered males more than three to one and during lactation there were almost no males in the samples. This finding corresponds with hypothesis that sex segregation is a common phenomenon in temperate zone bats (Barclay 1991, Cryan et al. 2000, Ibáñez et al. 2009). In the Daubenton's bat the two sexes display different distribution patterns, which reflect their different energy demands. While females prevail in lower situated habitats with optimal foraging areas, males dominate habitats that are situated higher up where the conditions are suboptimal (Leuzinger & Brossard 1994, Russo 2002, Senior et al. 2005, Encarnação et al. 2006). In addition, the small number of males accompanying females in optimal areas benefit from taking advantage of easy access for mating and thereby increasing their fitness (Senior et al. 2005). The causal mechanism of the segregation of the sexes in this species are still a matter of debate and authors suggest intra-specific competition for food resources and access to mates may be involved (Russo 2002, Senior et al. 2005, Encarnação et al. 2006). Our observations support the above hypotheses. For example, the ringing data revealed a lower recapture rate for juvenile males than for adults. This may correspond to an increased emigration of young males, which may be evicted from the area by the resident adults. In contrast to juvenile males, adult males had a similar recapture rate to both adult and juvenile females, which indicates their fidelity to a specific area. Furthermore, the presence of sexually active males in maternity roosts was regularly recorded as early as mid-July and mating occurred in the maternity roosts in the lime kiln. Similarly, Encarnação et al. (2007) report mating in summer roosts.

Seasonal dynamics

In general, the size and composition of roosting groups was related to the type of roost and the season. We observed different general patterns in seasonal dynamics between the two types of roosts. In the lime kiln, there was a steep increase in the number of bats at the beginning of pregnancy, which typically reached its seasonal maximum before parturition and a few days later about a half of the bats moved away. Our ringing data and direct observation indicate that females moved to cavities in nearby trees. On the other hand, the numbers of bats in tree cavities were highest during lactation. We hypothesize, that the large aggregation of bats in the lime kiln during pregnancy may be a direct consequence of changed energetic demands of pregnant females. The female Daubenton's bats greatly reduce their energy requirements by undergoing torpor during pregnancy (Dietz & Kalko 2006). Consequently, aggregation in a large colony may be beneficial for pregnant females because of the increased effectiveness of social thermoregulation (Willis and Brigham 2007). Our unpublished data on the microclimate in roosts (Lučan & Nodžáková, in prep.) indicates that tree cavities are, on average, colder by 2.5 °C than the lime kiln during the pregnancy period. Therefore, females may benefit from moving to the warmer roost.

The maximum number of bats recorded in the lime kiln was higher than that reported by most authors for natural roosts (Nyholm 1965, Rieger 1996, Červený & Bürger 1989, Lučan et al. 2009). So far, the highest number of bats reported at a single roost in a tree cavity is 155 (Encarnação et al. 2005). Although there is little information in the literature, the numbers of Daubenton's bats in artificial roosts tend to be higher than in tree cavities. For example, Shirley et al. (2001) found up to 269 Daubenton's bats roosting in an old priory in the UK. Barva (2000) found a maternity colony of 110 individuals in an underground water tunnel in Central Bohemia and Hanák & Anděra (2006) report up to 78 Daubenton's bats occupying a summer roost in an old water tunnel at a castle in South Bohemia. Therefore, using artificial roosts may be advantageous to Daubenton's bat as these can be more stable, provide suitable microclimates and/or more space for roosting than tree cavities.

Recapture rates and movements between roosts

Total recapture rate recorded during this study was relatively high (33.4%) and similar to those reported by other authors. For example, Červený & Bürger (1989) recaptured 21.7% and 42.7% of all males and females ringed, respectively, during their study on a community of tree-dwelling bats in an old castle park in Western Bohemia. Similarly, Kaňuch (2005) recaptured 32% of all Daubenton's bats ringed in parkland in Slovakia. The consistently higher recapture rates of bats originally ringed in the lime kiln may be due to two not mutually exclusive reasons: (i) our sampling effort was unevenly distributed over the periods and roosts and, consequently, bats in tree cavities had different probabilities of being encountered than bats in the lime kiln; (ii) the bats in the lime kiln displayed much higher roost fidelity than bats in tree cavities. We assume that both factors contributed to the observed differences. Our previous study proved that Daubenton's bats are quite faithful to particular tree cavities and may reuse them for many years (Lučan et al. 2009). However, as bats frequently switch roosts, a single cavity may be occupied for a relatively short period of time within a particular season. Consequently, low and uneven sampling frequency may decrease overall recapture probability of ringed bats. Unlike tree cavities, the lime kiln was continuously occupied throughout the growing season and, therefore, the probability of recapture there was higher than for those bats that occupied tree cavities. Indeed, high recapture rates (~30–40%, data not shown) of bats roosting in the lime kiln were recorded even in years when this roost was only sampled once, which supports our assumption of a generally high fidelity to this roost. Ngamprasertwong (2008) reports the use of both tree cavities and buildings by maternity colonies in Scotland. He found a situation quite similar to that recorded here – bats frequently switched between roosts in buildings and trees but displayed much higher fidelity to roosts in buildings.

The distances that the bats covered during movements between roosts are similar to those obtained by ringing and radio-tracking in Switzerland (Rieger 1996). Most of the movements recorded within a single season covered a few hundred meters and were restricted to a single study plot. Our own radio-tracking data on the spatial activity of 15 females from the lime kiln during different phases of their reproductive cycle provided analogous results (Lučan & Radil 2010). Our observation thus supports the concept of the existence of discrete subpopulation units in this species and many other forest bats (Rieger 1996, Kerth & König 1999, Kapfer et al. 2008, Metheny et al. 2008).

The difference between the two research periods in the mean distance the bats moved was possibly affected by the different spatial distributions of roost trees relative to the lime kiln. While there were many more roosts in the eastern part of study plot A in the first period, there were only a few in the second period (see Fig. 1). Since a large proportion of all recorded movements took place between the lime kiln and tree cavities, overall distances were naturally shorter in the second period.

Overall, the observed pattern in roost occupation and movements among roosts in the study area deviated from the situation typical of forest-dwelling bats (Barclay & Kurta 2007). While the lime kiln served as a stable and permanently occupied "central" roost for the population studied the use of tree cavities by bats was more dynamic. Consequently, we assume that the lime kiln played a key role in the social organization of the population of Daubenton's bats studied.

Sexual maturity and reproductive success in females

We proved that roughly one third (35.4%) of female Daubenton's bats reproduced in the year following their birth. As mating occurs during late summer and autumn (Encarnação et al. 2004), these females mated when they were 3–5 months old. This is rather exceptional for European bats of the genus *Myotis*. Sexual maturation by the end of the first summer is typical of bats of the genera *Nyctalus* and *Pipistrellus* (Gaisler et al. 1979, Racey 1974). A similar proportion (26.7%) of one-year-old lactating juvenile females is reported for *Myotis myotis* (Horáček 1981). In the case of the Daubenton's bat, Kaňuch (2005) mentions that "evidence of active reproduction by these 'natives' (i.e. one-year-old females) was recorded" during a study based on ringing. Evidence of age at sexual maturity of male Daubenton's bats in the season of birth is reported by Kokurewicz & Bartmanska (1992) and Encarnação et al. (2006). Therefore, sexual maturation within a year of birth of a small proportion of individuals may be typical of Daubenton's bat.

In general, there is a lack of information on how reproductive success is influenced by the age of female bats (Brunet-Rossinni & Wilkinson 2009). Our data on the reproductive rates of females of known age, although based on a small sample, suggest that it may vary considerably with age but that it is generally high in first 5 years of life. In contrast to our findings, Horáček (1981) reports consistently high (close to 100%) reproductive success of females of *Myotis myotis* up to 11-years-old.

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