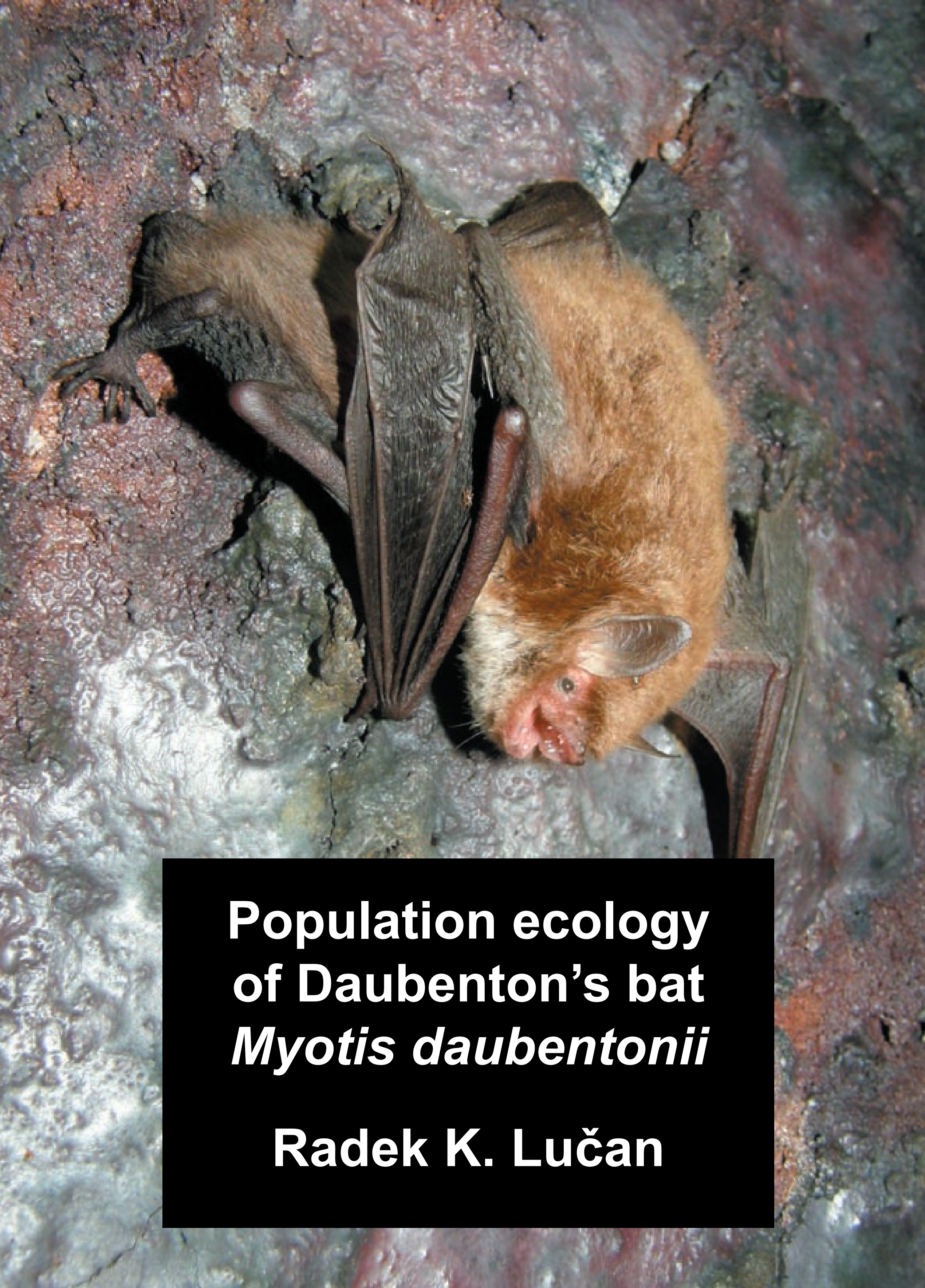

Population ecology of Daubenton's bat *Myotis daubentonii*

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Population ecology of Daubenton's bat *Myotis daubentonii*

Ph.D. Thesis

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Annotation

Various aspects of population ecology of Daubenton's bat (*Myotis daubentonii*) were analyzed based on long-term data (1968–1984 and 1999–2009) gathered in a single model study area (ca. 10 km^2) in South Bohemia, Czech Republic. Among others, population structure, roosting dynamics, movements between roosts and long-term trends in numbers of bats are described. Results of the study on patterns in reuse of tree cavities suggest that tree cavities may be reused for many consecutive seasons and that this has to be taken into consideration by conservation practices. The results of the study on microclimate of one maternity and one male colony roosting in man-made structures revealed, that microclimatic differences may be one of the key factors in roosting preference between the two sexes. Further, a profound effect of changing energetic demands in females during different phases of reproductive cycle may greatly influence their activity rhytms. In further two studies, the effect of climate on reproductive parameters of bats and abundance of ectoparasitic mites was analyzed. The results suggest that climatic variation greatly influenced reproductive parameters and parasitation of Daubenton's bats. Last but not least, the seasonal dynamics of parasitation by ectoparasitic mites and the possible effect on bats' condition was analyzed. It was found out that seasonal dynamics on abundance of parasites is adjusted to reproductive cycle and roosting dynamics of its host.

Declaration (in Czech)

Prohlašuji, že disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

Datum Podpis studenta

List of original articles

1. **Lučan R. K.** and V. Hanák: Population ecology of Daubenton's bat in the South Bohemia: summary of a long term study 1968–1984 and 1999–2009. Unpublished manucsript
2. **Lučan R. K.**, Hanák V. and I. Horáček. 2009. Long-term re-use of tree roosts by European forest bats. Forest Ecology and Management, 258: 1301–1306.
3. **Lučan R. K.**, Hanák V. and I. Horáček. Microclimate differences in two artificial roosts of Daubenton's bat (*Myotis daubentoni*) with different population structure. Unpublished manuscript.
4. **Lučan R. K.** and J. Radil. 2010. Variability of foraging and roosting activities in adult females of Daubenton's bat (*Myotis daubentonii*) in different seasons. Biologia, Bratislava, 65: in press (letter of acceptance enclosed)
5. **Lučan R.K.** 2009. 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). Lynx, n.s., 40: 71–81.
6. **Lučan R. K.** Effect of climate on the timing of reproduction and reproductive success in Daubenton's bat *Myotis daubentonii.* Unpublished manuscript.
7. **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.
8. **Lučan R. K.** and M. Weiser. Effect of climate on infestation of Daubenton's bat (*Myotis daubentonii*) by ectoparasitic mite *Spinturnix andegavinus*. Unpublished manuscript.

Author's contribution to the original articles

1. RKL collected all data in the period 1999–2010, analyzed all data and wrote the manuscript.
2. RKL collected all data in the period 1999–2008, analyzed all data and wrote the manuscript.
3. RKL collected all data in the period 1999–2008, analyzed all data and wrote the manuscript.
4. RKL conducted ca. 70% of the fieldwork, analyzed data and wrote the manuscript.
5. RKL collected ca. 90% of data, perform analyzed and wrote the manuscript
6. RKL collected ca. 80 % of data, perform analyzes and wrote the manuscript.
7. RKL collected all data, perform analyzes and wrote the manuscript.
8. RKL collected all data, perform part (ca. 20%) of the analysis and wrote the manuscript.

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I

Introduction

Bats are among the most diverse mammalian groups. With more than 1100 species they encompass roughly 20% of all recent mammals (Simmons 2005). Increasing evidence has been accumulated over last few decades on their key role in many ecosystems (Patterson et al. 2003). Simultaneously, they provide a significant ecosystem services through diverse trophic specializations. For example, they protect agricultures from detrimental effect of insect pests, control abundance of some insect vectors of diseases, pollinate important crops and disperse seeds (Kunz and Racey 2007). Further, they have enormous potential as bioindicators (Jones et al. 2009). On the other hand, they play an important role as a reservoirs and vectors of many serious diseases, such as rabies, Ebola or West Nile fever (Calisher et al. 2006). Current climate change and increasing human population pose serious threat on bats through a negative effect of habitat alteration (Medellín et al. 2000; Hayes and Loeb 2007). Furthermore, an emerging fungal disease, the White-nose-syndrom (WNS), has appeared just recently in North America, causing devastating mortality to bat populations (Blehert et al. 2009). Most recent estimates predict that it may force to extinction even the commonest Nearctic species within two decades (Frick et al. 2010). In the meantime, presence of the WNS was confirmed in Europe, yet no mass mortality has been evidenced so far (Puechmaille et al. 2010). Therefore, detailed knowledge of life-history traits has been of critical importance for successful conservation and management of bat populations (Frick et al. 2009).

Although current bat conservation efforts highlight the importance of gathering scientific data on rare and endangered species (Kunz and Racey 2007), information obtained through studies of common and widespread species may provide valuable information that can be built into broad conservation and management plans (Agosta 2002). Among European bats, a typical example of such a species may be the Daubenton's bat (*Myotis daubentonii*), one of the commonest bat throughout its European range (Mitchell-Jones et al. 1999). Given the fact, that it is originally a tree-dwelling species (e. g. Encarnação et al. 2005), it represents a group of bats that have been largely understudied. Consequently, increasing knowledge about its ecology may significantly improve conservation practices and management of all forest bats.

The aim of presented dissertation thesis is to contribute to various aspects of the population ecology of Daubenton's bat, one of the commonest as well as the most interesting bat species in Europe. Presented dissertation thesis largely benefit from a long-term study on population and roosting ecology of a tree-dwelling bat community in a model study area in the South Bohemia, the Czech Republic, that was indicated by Prof. Vladimír Hanák (Charles University in Prague) in late sixties of 20th century and later continued by the author of this thessis.

Overview of studied topics

Study species and its life-history

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) with marked increase in numbers during past decades, perhaps due to a favourable climatic changes and increased food opportunities (Kokurewicz 1995). Hence, it is listed as the species of the lower risk of threat by IUCN/SSC Chiroptera specialist group (Hutson et al. 2001).

The Daubenton's bat acts primarily as a tree dwelling bat species during the reproductive season (Rieger 1996; Boonman 2000; Encarnação et al. 2005) but it frequently uses artificial roosts (Nyholm 1965; Gerell 1985; Barva 2000) and occasionally even caves (Zahn and Hager 2005).

During past decades, it has been subjected to a vast number of studies that substantially improved our knowledge of its biology. Particular research interest has been focused on its foraging activity and habitat use (e.g. Kalko and 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 and Rayner 1988; Kalko and Schnitzler 1989; Jones and Kokurewicz 1994; Boonman et al. 1998; Britton and Jones 1999; Siemers et al. 2001) and activity in and using of hibernation sites (Roer and Egsbaek 1966; Haensel 1978; Klawitter 1980; Baagøe et al. 1988; Parsons et al. 2003). Considerably less attention has been paid on its roosting and population ecology in the reproductive season (Červený and Bürger 1989; Ebenau 1995; Rieger 1996b; Arnold 1998; Boonman 2000), although there appeared several excellent papers on that topic just recently (Encarnação et al. 2005; Kaňuch 2005; Senior et al. 2005; Encarnação et al. 2007; Kapfer et al. 2008). Despite this, detailed information on the population structure and seasonal roosting dynamics remain rather scarce and originate from few geographically restricted areas.

Recent studies have been reporting an increasing evidence of existence of a special type of social organisation , so called fission-fusion, in tree roosting bats (Kerth and König 1999; Willis and Brigham 2004). Bats with this type of social organization live in socially closed units that frequently split into subgroups which occupy different roosts. Typically, they exhibit high fidelity to particular roosting area but not so much to particular roosts (Willis and Brigham 2004). Colony members exhibit marked mixing, although individual composition of subgroups is not completely random (Kerth and König 1999). Based on observed pattern in roost use and roost switching Kapfer et al. (2008) suggested that this type of social organization may occur in the Daubenton's bat too.

In **Paper 1** we summarized basic data on the studied population of the Daubenton's bat gathered over the two study periods 1968–1984 and 1999–2009. In particular, we dealed with structure of the population, seasonal dynamics in roost occupation, movements between roosts and some aspects of reproduction.We described a rather unusual type of social organization resulting from a combined use of numerous tree cavities and an artificial roost that served as a "central" roost to which population from surrounding tree cavities was bonded.

Roosting ecology

Cavities in trees are likely the most common type of roost used by bats worldwide (Kunz 1982; Lacki et al. 2007; Kunz and Lumsden 2003). If roosts in foliage and caves represent extremes in roost permancy, then tree cavities lie somewhere in between (Kunz and Lumsden 2003). Because tree-dwelling bats frequently switch roost trees, studies suggest that rapid deterioration of suitable roosts occurs (e.g. Lewis 1995; Barclay and Brigham 2001), which suggests a relatively high turnover of tree cavity roosts. In **paper 2** we report that this might not be the case and that a significant proportion of cavities may be reused for many consecutive years.

Roost microclimate acts as one of the primary cues that bats use to base the selection of their daily roosts on (Vonhof and Barclay 1996; Sedgeley 2001; Ruczyński 2006). For example, reproductive female bats select warmer roosts during gestation and lactation to provide ideal thermal conditions for juvenile growth and stable milk production (Hutchinson and Lacki 2001; Kerth et al. 2001; Lausen and Barclay 2003; Willis and Brigham 2005). By contrast, adult males and non-reproductive females profit from using cold roosts that allow them to minimize overall energy expenditures and to attain sufficient fat reserves prior to mating and/or hibernation (Hamilton and Barclay 1994).

One of the main energy saving mechanisms commonly used by microbats is entering body torpor (Willis 2006). Lowering body temperature can provide significant energy and water savings during cold ambient temperatures and food scarcity (Webb et al. 1993). However, it may reduce rates of foetal and juvenile development through prolonged date of parturition or decreased milk production in pregnant and lactating females, respectively (Wilde et al. 1999). Therefore, reproductive females optimize development by minimizing times in torpor (Dietz and Kalko 2006).

The efficiency of entry into, and arousal from, torpor is governed by roost microclimate, primarily roost temperature (Chruszcz and Barclay 2002; Willis 2006). Consequently, thermal properties of male and female roosts should differ during period of reproduction. In **Paper 3**, we investigated the thermal properties of two artificial day roosts of Daubenton's bats with different structure of population inhabiting them. Accordingly with our presumptions, a roost occupied by male-dominated colony was colder and more fluctuant than a maternity roost with female-dominated population and this difference was most evident just during the reproductive period.

Seasonal changes in activity related to reproductive cycle

In different phases of the reproductive cycle, adult females of bats are forced to modify their activity pattern and daily time budget with respect to changing energetic demands (Speakman and Thomas 2003). Each period of reproductive cycle thus represents a unique constitution of both intrinsic and extrinsic factors that gradually change as the periods pass from one to another. For example, pregnant females are forced to substantially reduce the use of daily torpor, an energy saving physiological mechanism, in order to diminish negative impact of low body temperature on the rate of developing embryos (Racey 1973; Racey and Swift 1981; Dietz and Kalko 2007). As a consequence, they have to compensate for increased energetic demands connected with fetal development by prolonging the time they spend on foraging bouts (Barclay 1989; Rydell 1993; Catto et al. 1995; Grinewitch et al. 1995; Shiel et al. 1999; Dietz and Kalko 2007). However, as the size of embryos increases, the females' flying ability decreases and they have to use different compensatory mechanisms, such as roosting in thermally optimal roosts (McNab 1982) and/or aggregation onto large colonies in order to reduce thermal losses (Kurta et al. 1987). Lactating females, on the other hand, are confronted with dramatically increased energetic demands in consequence of milk production (Racey and Speakman 1987, Wilde et al. 1995, McLean and Speakman 1999). Moreover, their attempts to balance the negative impact of increased energy expenditures by increasing foraging activity are further constrained by the need of suckling their pups (Henry et al. 2002). This means they are bonded to maternity roosts more than in any other part of the year (Catto et al. 1996). Last but not least, after weaning of juveniles, reproductive females have to recover and to attain a good physical condition to survive the winter time (Speakman and Thomas 2003).

In **Paper 4**, we tested the influence of different reproductive state on spatial activity, roosting behaviour and roosting preference of females of Daubenton's bat. Among others, we documented a profound changes in spatial activity in response to reproduction.

The evening emergence time in bats has been suggested to be a function of dietary specialisations, foraging strategy, ability to avoid predation, energetic demands and the reproductive state of emerging individuals (Jones and Rydell 1994; Shiel and Fairley 1999; Duvergé et al. 2000). 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 and 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 and 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).

In **paper 5** we analyzed the seasonal pattern in the timing of evening emergence with respect to different periods of reproductive cycle in a maternity colony of Daubenton's bats. Overall, we observed significant changes in the timing of emergence with respect to the period of reproductive cycle.

Bats and climate

Recent climate is characterized by positive trends in global temperatures and growing incidence of climatic extremes (IPCC 2007). Behind other impacts, warming of climate has been recognized to influence the timing of life-cycle events of wide spectra of organisms. Such events as flowering and leaf unfolding dates, the timing of insect emergence or migratory bird arrival have been advanced in response to climate change (Chmielewski and Rötzer 2001; Sparks and Menzel 2002; Walther et al. 2002; Cotton 2003; Visser and Both 2005). While impact of climate on phenology has mostly been studied in plants where a long-term data from phenological gardens are available (Ahas et al. 2002), information on some other groups of organisms, such as mammals, remains very scarce (reviewed by Isaac 2009).

Variation in temperature and rainfall during the reproductive period has been recognized as a main factor governing the timing of reproduction and reproductive success in insectivorous bats (Ransome and McOwat 1994; Grindal et al. 1992; Burles et al. 2009). In general, frequent low temperatures have been singled out as the primary factor causing prolonged gestation and delayed fledging of juveniles (Racey and Swift 1981), whereas high rainfall negatively influenced overall reproductive success (Grindal et al. 1992). Nevertheless, bat species may differ in susceptibility to inclement weather in consequence of different foraging or roosting strategies. In a study of reproduction of two insectivorous bats using natural roosts during years with contrasting weather Burles et al. (2009) observed, that while adverse weather negatively influenced reproduction of *Myotis lucifugus*, it had rather positive effect on *Myotis keenii*. They hypothesized that contrasting effects of weather may have arisen from different foraging strategies of the two species. By contrast, Syme et al. (2001) found no detrimental effect of exceptionally cold summer on the timing of reproduction and reproductive success in a population of *Myotis lucifugus* roosting in buildings in the South East of U.S. The single difference they observed was changed pattern of clustering behaviour of bats in roosts. They concluded that flexible roosting behaviour and food supply ameliorated the impact of bad weather on reproduction of this species.

In **Paper 6** we analyzed the influence of temperature and rainfall on the timing of reproduction and reproductive success in a studied colony of Daubenton's bats. Overall, we proved a significant effect of temperature and rainfall on the reproductive parameters. While warm springs advanced timing of parturitions, increased precipitation reduced reproductive success. Moreover, we observed a long-term trend in advancement of parturitions in response to globally increasing temperatures.

Bats and parasites

Bat ectoparasites greatly adjusted their seasonal dynamics and reproduction to the reproduction of their hosts (Christe et al. 2000; Bartonička and Gaisler 2007; Lourenço and Palmeirim 2008). Aggregation of female bats into large colonies during reproductive period enhances transmission of ectoparasites (Rekardt and Kerth 2009), whereas juvenile bats with naive immune system and imperfect grooming skills represent ideal hosts on which the highest reproductive rate may be achieved (Christe et al. 2000). Consequently, high parasitation is a direct cost of bat sociality (Lourenço and Palmeirim 2007).

In **paper 7**, we described seasonal dynamics in abundance of ectoparasitic mite Spinturnix andegavinus infesting the Daubenton's bat. We proved that parasite abundance is, in accord with adjusted to seasonal life cycle of its hosts. Observed contrasting effects on bats' body condition are discussed in detail.

While seasonal dynamics in ectoparasite abundance and antiparasitic strategies of bats have been well described in many host-parasite systems, inter-annual variation and its causes and consequences remain poorly understood. Many authors have reported high between-year variation in ectoparasite load on bats (Deunff and Beaucournu 1981; Dietz and Walter 1985; Zahn and Rupp 2004), but no one addressed this phenomenon to a rigorous analysis, since a long term data enabling such analysis are largely missing. Given the fact, that inter-annual variation in climate has profound effect on the body condition, timing of reproduction and reproductive success of temperate bats (Ransome and McOwat 1994; Grindal et al. 1992; Burles et al. 2009), it should correspondingly affect bat ectoparasites. For example, variation in spring temperature may affect length of reproductive season of parasites (Mouritsen and Moulin 2002; Møller 2010). It is known, that spring temperature governs the time of arousal of bats from hibernation. Since reproduction of many bat parasites is reduced during bats' hibernation (Lourenço and Palmeirim 2008), high spring temperatures may advance onset of bat's activity and thereby prolong the reproductive period of their ectoparasites. Consequently, higher parasite load may occur in years following high spring temperatures. Alternatively, cold and rainy weather may result in poor condition of bats and increased their susceptibility to parasitation. While results of analyses of relationships between climatic variability and parasite abundance proved an existence of analogical scenarios in a variety of host-parasite systems (Mouritsen and Poulin 2002; Hudson et al. 2006; Poulin 2006; Møller 2010), no such study has been done on bats and their parasites.

In **paper 8** we analyzed the relationship between various climatic variables and abundance of ectoparasitic mites in a colony of Daubenton's bats over nine years. We documented a significant influence of mean winter temperature on overall parasite load recorded in the following reproductive season.

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Population ecology of Daubenton's bat in South Bohemia: summary of a long term study 1968–1984 and 1999–2009

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Abstract. Based on data obtained during two research periods (1968–1984 and 1999–2009) in a model study area (South Bohemia, Czech Republic), we summarize basic information on roosting ecology, population structure, seasonal dynamics, long term population trends and some aspects of reproduction of the Daubenton's bat (*Myotis daubentonii*). Bats roosted in two types of roosts: an old lime kiln (LK) and tree cavities. Overall sex ratio was largely skewed toward females in the sample of adult bats (mean sex ratio 3 males : 10 females) but it did not deviated from 1:1 in juveniles. Seasonal dynamics in numbers of bats differed between the two types of roosts. It was bimodal in the LK and rather unimodal in natural roosts. In the LK, maximum numbers of bats were observed during the pregnancy and the post-lactation period. In tree cavities, largest aggregations occurred mostly during the lactation and the post-lactation period. Considerable seasonal variation in presence and numbers of different roosting aggregations was recorded. Long-term monitoring of trends in numbers of bats revealed more or less stable numbers between 1968 and 1981 and ca. three-fold increase between 1999 and 2009. Recapture rate was generally high (33.4%) but it varied with respect to roost type and research period. Frequency of recaptures indicates higher fidelity of bats to the LK than tree cavities. Majority of recorded movements took place at the distance of a few hundred meters. Many more movements took place between the LK and tree cavities than among tree cavities however, results may be biased, to some extent, by uneven sampling effort. Roughly one-third of females reproduced in the year following their birth that indicates early sexual maturation in the Daubenton's bat. Overall spatial organization of the studied population was quite unusual, regarding an existence of "central" roost with stable occupancy.

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) with marked increase in numbers during past decades, perhaps due to a favourable climatic changes and increased food opportunities (Kokurewicz 1995). Hence, it is listed as the species of the lower risk of threat by IUCN/SSC Chiroptera specialist group (Hutson et al. 2001). During past decades, it has been subjected to a vast number of studies that substantially improved our knowledge of its biology. Particular research interest has been focused on its foraging activity and habitat use (e.g. Kalko and 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 and Rayner 1988; Kalko and Schnitzler 1989; Jones and Kokurewicz 1994; Boonman et al. 1998; Britton and Jones 1999; Siemers et al. 2001) and activity in and using of hibernation sites (Roer and Egsbaek 1966; Haensel 1978; Klawitter 1980; Baagøe et al. 1988; Parsons et al. 2003). Considerably less attention has been paid on its roosting and population ecology in the reproductive season (Červený and Bürger 1989; Ebenau 1995; Rieger 1996b; Arnold 1998; Boonman 2000), although there appeared several excellent papers on that topic just recently (Encarnação et al. 2005; Kaňuch 2005; Senior et al. 2005; Encarnação et al. 2007; Kapfer et al. 2008). Despite this, detailed information on the population structure and seasonal roosting dynamics remain rather scarce and originate from few geographically restricted areas.

During the two research periods (1968–1984 and 1999–2009) an intensive research was conducted in a model study area in South Bohemia, Czech Republic, on the ecology of tree roosting bats, namely Daubenton's bats and noctules (*Nyctalus noctula*). While some results have already been published in detail (Gaisler et al. 1979; Lučan 2006; Lučan et al. 2009; Lučan and Hanák 2010), a considerable amount of data has not been analyzed and presented to a scientific community so far. In the present paper, we summarize our the most important results on population ecology of the Daubenton's bat. Although some results and inferences, such as those based on ringing data, may be, to some extent, biased by uneven research effort within and between the two research periods, we believe it is still worth of publishing.

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 Třeboňsko Landscape Protected Area and Biosphere reserve (49° 9' N, 14° 42' E). It represents 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 size (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 with alders (*Alnus glutinosa*) and willows (*Salix fragilis*). A typical phenomenon in the area is the occurrence of tree rows and alleys of oaks and limes (*Tilia cordata*) growing along pond dams and roads. Trees in these alleys and rows are usually very old (>300 years) and reach 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 (LK) 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. 6×4×3.5 m (length×width×height). The brick and stone walls are very thick (~1m) and the only entrance (ca. 1.5m high×1m wide) face to an open space. There are a large number of fissures of different sizes in the walls, some of them being frequently used as shelters by Daubenton's bats. The main roosting place of bat colony represents one large (ca. 30×30 cm width and 60 cm deep) cavity in the ceiling of the LK. This cavity has been used by bats for roosting during the whole growing season whereas some smaller fissures are used only occasionally by individual bats or small aggregations, mostly during spring and autumn periods. The LK has been the only continually inhabited roost of a maternity colony in the study area, known to host Daubenton's bats at least since 1962. Only in 1987 the roof of the LK partially collapsed and only individual bats were recorded inside during that time. After restoration, bats returned back and have been roosting there each year up to now. Therefore, the LK represents, to our knowledge, the longest known inhabited roost of Daubenton's bats in Europe.

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

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 in the following periods. We fixed a nail above each tree cavity in order to be able flexibly install trapping device. We used simplified custom-made funnel traps (see Gaisler et al. 1979) to capture bats upon their

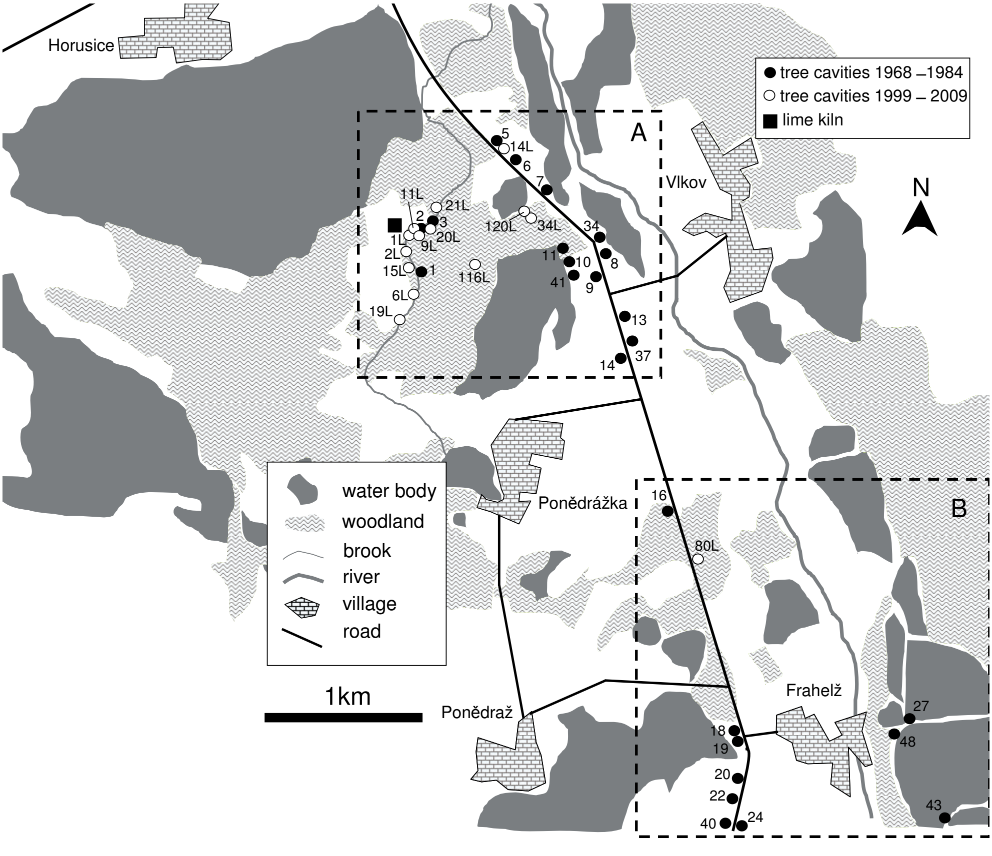

Fig. 1. Schematic map of the study area with the two study plots and locations of roosts. The numbers refer to original ID. Depicted are only roosts sampled by captures of bats.

Table 1. Total number of roost-capture events in tree cavities over the whole time of the study. For abbreviations of reproductive periods see Fig. 2.

Year	stp	p	l	pl	atp	Total
1968	–	–	–	1	–	1
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

emergence from roosts. Several cavities were usually sampled simultaneously using this technique. In some cases (N=20), we did not succeed to catch all bats from a particular tree cavity. Typically, a part of roosting group did not emerge for more than 1 hour and therefore we removed the trap from a cavity entrance to minimize disturbance. Data from these samples were not included in 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 fact allowed us to repeatedly sample bat aggregations roosting in the same cavity in different periods of the 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) markedly differ in vocalisation they produce and thus could be confidentially distinguished without capture. This method was particularly productive on warm afternoons when social vocalizations prior to flight activity were common. Noctules in particular could be heard at the distances of 30–40 m (Gaisler et al. 1979), while Daubenton's bats were audible 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 with this method. Following acoustic identification of occupied roost, we either used traps to capture emerging bats or, in some instances, we made emergence counts. Bat detector was usually used to ascertain species identification.

Overall, the research effort was unevenly distributed within and between the two phases of the research. Consequently, we got a high number of samples in some periods of the reproductive season and/or years, whereas a limited number in the others. Sampling activity in both LK and tree cavities was particularly restricted during the lactation period in order to minimize disturbance to bats. Summaries of all capture events for each year and period of reproductive cycle is given in Table l and 2.

The bats

In most captured bats we recorded their sex, age, reproductive state, weight, and forearm length. Weight was measured to the nearest 0.5 g using Pesola spring balance. Forearm length was measured to the nearest 0.1 mm using calliper. Juvenile bats were determined based on incomplete ossification of carpal joints (Brunet-Rossinni and Wilkinson 2009) and distinct black chin spot (Richardson 1994). Pregnant females were determined based on palpable embryo. Females were referred to as lactating if they had enlarged nipples and absent fur around them. The same characters (in more or less distinct extent based on the time that passed from 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, we recorded reproductive state based on state of testes. If a male had enlarged testes and *cauda epididymis*, it was regarded as sexually active (Encarnação et al. 2006; Brunet-Rossinni and Wilkinson 2009).

Between 1968 and 2004 all captured bats 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 findings by Reiter (1998) who recorded much lower incidence of wing injuries in Daubenton's bats ringed with bird rings as compared to lipped bat rings. In order to further diminish the possible negative

Table 2. Total number of roost-capture events in the LK over the whole time of the study. For abbreviations of reproductive periods see Fig. 2.

Year	stp	p	l	pl	atp	Suma
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
Suma	16	14	7	29	33	99

effects on bats, we grinded down the sharp edge of the bird ring using warding file prior its attachment to the forearm of the bat.

Evaluation of recaptures and movements between roosts

We treated all data on recaptures in two ways. (1) If the bat was recaptured in the same roost as previously, we treated is as the "same roost" recapture. If the bat was recaptured in different roost than previously, it was treated as "movement" recapture. (2) If the two consecutive recaptures were made in a single season, it was treated as "same year" recapture. If the two consecutive recaptures were made in different year, it was treated as "different year" recapture.

Monitoring the numbers of occupied tree cavities

In tree cavities, our data did not allow us to estimate the real number of bats for each year in the study area. Rather, we estimated the relative number of Daubenton's bats in cavities using total number of occupied roosts found each year in the study plot A (i.e. a plot with higher research activity and more representative data). We used only data from years when at least 18 tree cavities were inspected (either by trapping device or audio-visually) and we adjusted the number of used roosts by dividing this value by the number of total roost inspections in a given year. Total research effort (including audiovisual roost inspections) used for the analysis of temporal changes in numbers of occupied tree cavities has been published elsewhere (Lučan et al. 2009).

Periods of reproductive cycle

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

Statistical analyses

To test for deviance from 1:1 sex ratio in all samples, we used goodness-of-fit test. We used analysis of variance (ANOVA) to test for seasonal differences in the sex ratio between the LK and tree cavities. We used arcsine transformation of square-rooted values in the sex ratio data to achieve normal distribution prior to analyses (Wilson and Hardy 2002). To compare frequency of different types of recaptures, we used goodness-of-fit test. Yates correction was used in cases, where total counts were < 5. We used factorial ANOVA to test differences in movement distances between sexes, 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. To analyze the relationship between annual maximum of bats in the LK and total number of occupied tree cavities found in a given year, we used Spearman correlation. If not specified, values are given as mean±SD.

RESULTS

Total sample of bats

In total, we captured 4175 Daubenton's bats (Table 3) during 906 capture events. Of these, 2009 were individuals captured for the first time and ringed, 1604 recaptures of 657 individuals and 610 bats were not ringed at all. 2632 bats were captured in the LK and 1543 in tree cavities. We captured 3889 bats in the study plot A and 286 bats in the plot B. In 212 captures sex, age, or

Table 3. Total sample of bats captured over the whole time of the study. Ad – adults, juv – juveniles, ♀ – females, ♂ – males. For abbreviations of reproductive periods see Fig. 2.

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

both categories were not recorded in field protocols and these bats were excluded from analyses and summaries shown bellow.

Roosts

During the whole research period, tree cavities were almost exclusive type of day roost used by Daubenton’s bats in the study area. Altogether, we checked more than 150 tree cavities, but only 80 of them were controlled repeatedly (Lučan et al. 2009). 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 natural rotting processes, remaining 44 cavities were originally excavated by woodpeckers, most often by the Greater Spotted Woodpecker (*Dendrocopos major*). Seven tree species were used for roosting from which willow (15), lime (14) and oak (10) were the most frequent (Table 4). All roosting trees were live exemplars from mid-age to very old ones (mainly oaks and limes) reaching sometimes immense dimensions. Most of these big trees were situated on pond dams, along forest roads and canals and, particularly, in alleys along main road. The height of the cavity entrance ranged from 1 to 15 meters, with mean value 4.6 m.

Population structure and roosting dynamics

Sex ratio

From the total sample of 4175 examined bats, 3126 were females and 1049 were males, that means sex ratio 0.25, i.e. 3 : 10 (males: females). Overall, the sex ratio largely deviated from 1:1 in all samples of adults (LK: χ^2=370.45, d.f.=121, p=0.0001; tree cavities: χ^2=276.17, d.f.=87, p=0.0001) but not in juveniles (LK: 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 prevailed at any time but the sex ratio changed with respect to the period of reproductive cycle ($F_{(4,203)}$=3.93, p=0.004). The highest

Table 4. Basic data on tree cavities occupied by Daubenton's bats over the whole time of the study. 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	3	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

proportion of males occurred during the spring and autumn transient period, when it reached up to 0.2–0.3, i.e. 0.3–0.4 males: 1 female. During the pregnancy and lactation, males contributed to the total sample by less than 10 per cent. In adult bats, the proportion of males was significantly higher in the LK than in tree cavities ($F_{(1, 203)}=4.45$, $P < 0.05$). The sex ratio between these two types of roosts particularly differed in the post-lactation and autumn transient period (Fig. 2).

Types of aggregations in roosts

In total, we obtained data on the structure of roosting groups from 99 and 162 capture events in the LK and tree cavities, respectively. However, only in 87 and 149 capture events we succeeded to capture all bats, in the LK and tree roosts, respectively, 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 the period of the season.

The LK was most frequently occupied by mixed groups composed of adult males and females during the spring transient period. However, females always greatly outnumbered males (see chapter on sex ratio). Strictly female groups prevailed during pregnancy and lactation. Because

Table 5. Sex ratio (males to all adult bats) in total sample of captured bats. Primary data are shown in Fig. 3. LK – lime kiln. For abbreviations of reproductive periods see Fig. 2.

Period	LK		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

we were not able to precisely count non-volant juveniles, our values of the number of bats in the LK 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, a typical aggregation composed of adult females, juveniles and adult males. During autumn transient period, almost all types of aggregations could be found there, except for pure male groups and groups composed only from adult males and females since juveniles were almost always admixed to adults. We have never recorded a pure male colony in the LK throughout the length of our study.

In tree cavities, we found three types of aggregations (males, females, males+females) in a similar proportion during the spring transient period. During pregnancy and lactation, female groups greatly outnumbered all other types of aggregations. In Table 6, we treated separately female groups and groups of females with juveniles, 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 composed of females and juveniles. In contrast to the LK, adult males were sometimes (21% of samples) admixed to females with juveniles in 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 the autumn transient period. The commonest were males+females, females+juveniles and pure juvenile groups.

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

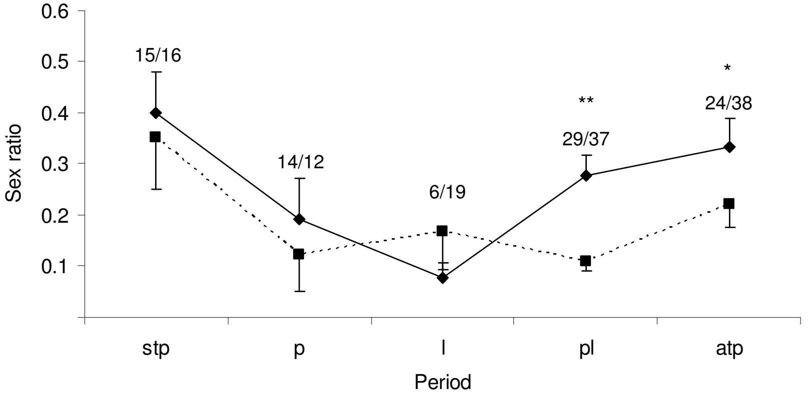

Fig. 2. Variation in the mean sex ratio in the LK (black squares) and and tree cavities (black diamonds) relative to periods of reproductive cycle. Numbers refer to sample size for the LK/tree cavities. Whiskers – S.D.; stc – spring transient period, p – pregnancy period, l – lactation period, pl – post-lactation period, atp – autumn transient period; significance: * = P<0.05, ** = P<0.01.

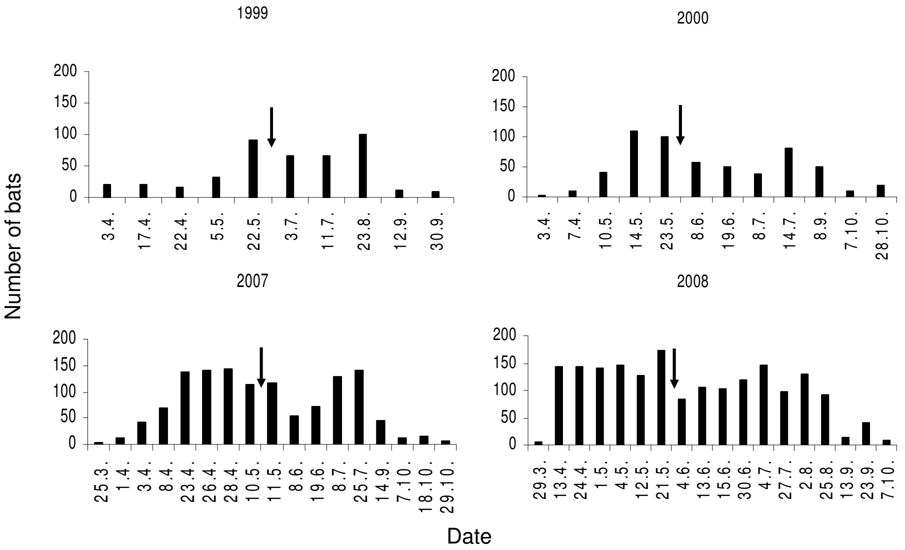

Fig. 3. Seasonal variation in numbers of bats in the LK based on emergence counts as observed in four different years. Arrows indicate time of parturitions in the roost based on observation of newborns.

Seasonal dynamics in roost occupation and size of roosting groups

In the LK, individuals or small groups up to some 20–30 Daubenton's bats usually appeared at the beginning of reproductive season (late March – end of April). Colony size rapidly increased towards the end of the spring transitional period. This increase may take just one or two weeks. We observed that formation of large colony, typically present in the LK during the

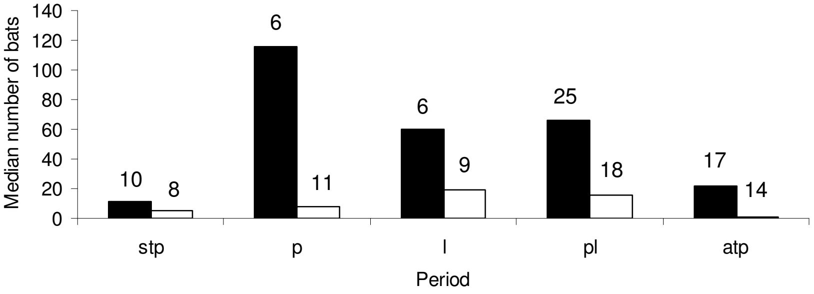

Fig. 4. Seasonal dynamics in the size of roosting aggregations based on median numbers of bats in most frequently occurring types of aggregations. Data are shown on aggregations sampled by direct captures only. Number above each column refer to sample size. Black columns – LK, white columns – tree cavities. For abbreviations of reproductive periods see Fig. 2.

Table 6. Seasonal dynamics in the occurrence and size of different types of roosting aggregations in the LK 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. For abbreviations of reproductive periods see Fig. 2.

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)	–	57(25-190) N=4	–	–	–	–
	l	60 (40-100) N=6	–	–	–	–	–	–
	pl	–	–	–	66 (19-160)	–	–	–
	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)	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

pregnancy period, advanced by 2–4 weeks during the period 1999–2009. For example, in 1999 and 2000, complete colony appeared around mid-May, whereas in 2007 and 2008 it was already in mid-April (Fig. 3). The highest number of bats was observed on April 29, 2006, when 205 individuals were counted upon evening emergence. Overall, however, 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 in the roost during that period, and almost every of those females gave birth, the real number of bats in the LK remained similar to that before parturitions. The observed decrease concerned with about half of the females present in the LK prior parturitions plus their offspring. As juveniles became volant, the number of recorded bats in the LK roughly doubled. The second peak in numbers usually occurred in the post-lactation period, but it usually did not outreach the numbers observed in the pregnancy period.

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

Long term trends in numbers of Daubenton's bats in the study area

Maximum annual counts of bats in the LK for periods 1968–1981 and 1999–2009 are shown in Fig. 5. While numbers of bats in the roost were more or less stable between 1968 and 1981, it greatly increased (ca. three times) between 1999 and 2009. Similarly, we observed 2–3 fold increase in number of occupied tree cavities in the second research period as compared to the first one (Fig. 6). Overall, number of bats in the LK was strongly correlated (r_s=0.90, n=12, P<0.001) with total number of occupied tree cavities found in a given year (Fig. 7). That means the larger was the colony in the LK, the more occupied tree cavities were found in a given year.

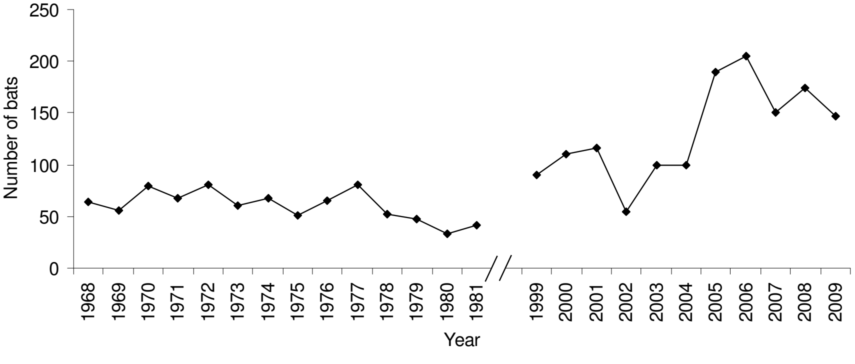

Fig. 5. Long-term trends in number of Daubenton's in the LK based on maximum annual emergence counts. For the period 1982–1998 data are not available.

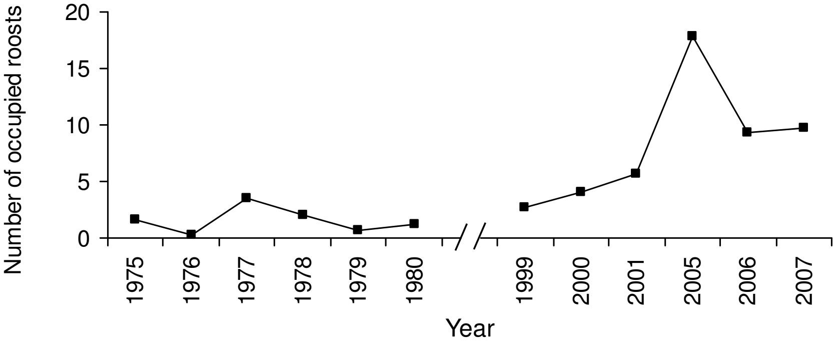

Fig. 6. Long-term trends in number of occupied tree cavities in the study plot A. Data are given for years when at lest 18 tree cavities were inspected.

Summary of ringing data

Recaptures

The time span between the first and the last capture of an individual was up to 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 first six years from ringing. Overall, we recaptured 33.4% of all ringed bats. The proportion of recaptured to all ringed individuals (recapture rate) differed between the LK and tree cavities, and varied among sex and age categories (Table 7). It was much higher in the LK than in tree cavities (49% and 19.2%, respectively). In case of bats originally ringed in tree cavities, the recapture rate was very similar among sex and age categories in the first study period, but it varied considerably in the second study period. The same was

Table 7. Numbers of ringed and recaptured individuals in the two types of roosts, separately for the two study periods.

	1968-1984			1999-2009		
	Ringed	Recaptured	% recaptured	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

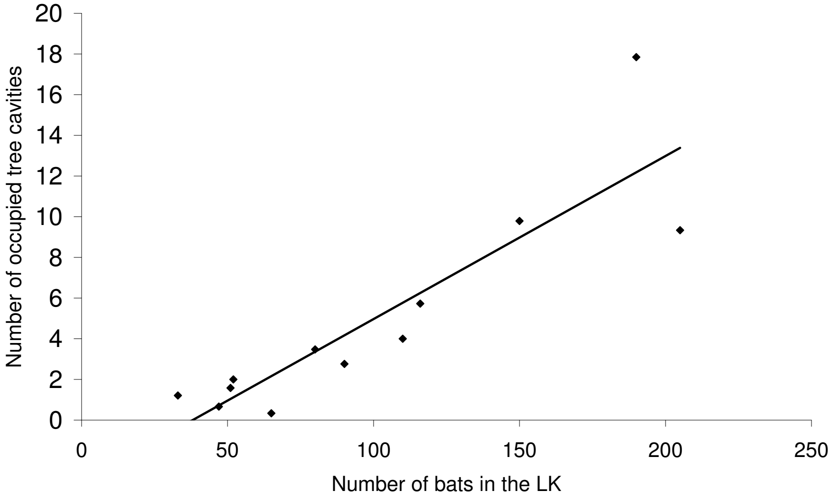

Fig. 7. The relationship between the maximum annual count of bats in the LK and total number of occupied tree cavities found in the study plot A in a given year. Line is the linear regression line.

true for bats ringed in the LK. In general, recapture rates were higher in males than in females. Between 1999 and 2009, we did not recapture any bats from the first research period.

Movements between roosts and roost fidelity

Of 1463 analyzable recaptures, 1193 were made in the LK and 270 in tree roosts. The proportion of both two 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 LK and tree cavities (χ^2=95.45, d.f.=1, P<0.0001). Much higher frequency (88.5%) of same-place recaptures were made in the LK than in tree cavities (14.1%). This trend was consistent between the two sexes. Consistently more recaptures of females were done in different years than in the same year. In males, the frequency of recaptures in the same year and in different years significantly differed between the LK and tree cavities (χ^2=17.05, d.f.=1, P<0.0001).

Almost two-thirds (66.4%) of all movements took place between the LK and tree cavities and remaining 33.6% were movements between different tree cavities (Table 9). Vast majority (over 98%) of all movements took place within the two study plots. Two of six movements between plot A and B were bats ringed in tree cavities in plot B and consecutively recaptured in the LK. Remaining four movements took place between tree cavities. Only two of these movements were recorded within a single season, remaining four were "between years" 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 impact of the period of the research and the time interval between consecutive captures on the distance to which bats moved. A summary of movement distances is given in Table 11. Overall, much shorter (Tukey post hoc

Table 8. Numbers of different types of recaptures (see Material and Methods for details) in the two types of roosts. Proportion (%) of total sample in all recaptures in particular roost type is given in parentehses.

	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)

Table 9. Summary of all recaptures relative to its 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 to which bats moved, the research period, sex, and time interval that passed from previous capture. The research period refers to first (1968–1984) or second (1999–2009) research period. Time interval refers to "same year" and "between years" 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 x T	0.576	1	0.448
P x Sex	0.772	1	0.380
T x Sex	6.705	1	0.010 **
P x T x Sex	2.068	1	0.151

Table 11. Summary of movement distances 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

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, to which different sexes moved, were related to whether it was within a single year or in consecutive years. Within years, females moved to similar distances as males ($P=0.536$), whereas between years they moved to less distant roosts than males ($P<0.01$).

Table 12. Summary of reproductive state in 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 on reproductive parameters

Maturing in females

We made 91 recaptures of 46 females that were ringed as juveniles (Table 12). In spite of limited data, we could assess 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 high (> 80%) between 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 females reproduced. We recorded 100% reproductive females in their 9th (N=2) and 10th (N=1) year of life. One 11-years old female did not reproduce in a given year.

Sexual activity in adult males

Males with enlarged testes (i.e. sexually active) were observed during the post-lactation and autumn transient period (Fig. 8). Overall, there was much higher proportion of sexually active males in the LK than in cavities during the post-lactation period while the reverse was true for the autumn transient period (Chi-square test with Yates correction; pl: $\chi^2=5.62$, d.f.=1, $P<0.05$; atp: $\chi^2=4.26$, d.f.=1, $P<0.05$). Also, we repeatedly observed mating behaviour in the LK in the post-lactation as well as in the autumn transient period (LUČAN, pers. obs.).

DISCUSSION

Structure of the population

The overall sex ratio of the studied population of Daubenton's bats was highly skewed toward females. On average, females outnumbered males more than three times, and during the lactation period males were almost absent from our sample. This finding corresponds with hypothesis about

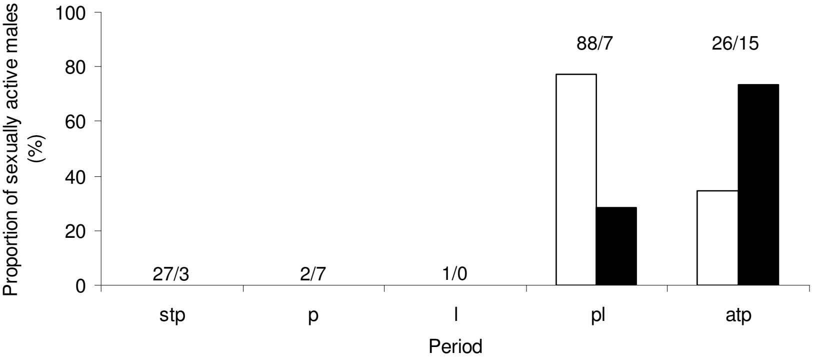

Fig. 8. Seasonal changes in the proportion of sexually active males to all adult males in the LK (white columns) and tree cavities (black columns). Numbers above each column refer to total number of adult males examined in the LK/tree cavities. For abbreviations of reproductive periods see Fig. 2.

sex segregation that is a common phenomenon in temperate zone bats (Barclay 1991; Cryan et al. 2000; Ibáñez et al. 2009). In the Daubenton's bat, it was found out that the two sexes display a different pattern in distribution based on the optimality of environmental conditions, thereby reflecting their different energy demands. While females prevail in lower situated habitats with optimal foraging areas, male-dominated populations were found mostly in higher elevations with rather suboptimal conditions (Russo 2002; Senior et al. 2005; Encarnação et al. 2006). In addition, it was proven, that a small number of males accompanying females in optimal areas largely benefit from taking advantage of easy access to mating, thereby increasing their fitness (Senior et al. 2005). The causal mechanism standing behind sexual segregation in this species has been debated and the authors suggested that behind energetic reasons, intra-specific competition for optimal food resources and access to mates in females and males, respectively, may be involved (Russo 2002; Senior et al. 2005; Encarnação et al. 2006). Our observation largely support above mentioned hypothesis. For example, our ringing data showed generally lower recapture rate in juvenile males than in adults. This may correspond to an increased emigration of young males that may be evicted from the area via territorial behaviour of resident adults. Contrastingly to juvenile males, adult males had a similar recapture rate to both adult and juvenile females, which fact indicates their fidelity to the specific area. Furthermore, the presence of sexually active males in maternity roosts was regularly recorded as early as in mid-July and our observation in the LK proved occurrence of mating directly in maternity roost. Accordingly, Encarnação et al. (2007) reported existence of mating in summer roosts.

Seasonal dynamics

In general, the size and composition of roosting groups was related to the type of roost and the period of the season. We observed different general patterns in seasonal dynamics between the two types of roosts. In the LK, number of bats steeply increased at the beginning of the pregnancy period and, typically, reached its seasonal maximum before parturitions. Few days later, about a half of all bats regularly moved away. Our ringing data and direct observation indicate that those females moved to nearby tree cavities. On the other hand, the numbers of bats in tree cavities were highest during lactation. We hypothesize, that aggregation of bats into a large colony in the LK during pregnancy may be a direct consequence of changed energetic demands of pregnant females. It was proved that female Daubenton's bats greatly reduce using of torpor during pregnancy (Dietz and Kalko 2006). Consequently, aggregation into a large colony may be beneficial to pregnant females through increased effectiveness of social thermoregulation (Willis and Brigham 2007). Our unpublished data on roost microclimate (Lučan and Nodžáková, in prep.) has proven that tree cavities are, on average, colder by 2.5°C than the LK during the pregnancy period. Therefore, females may benefit from moving to the warmer roost.

The maximum number of bats found in the LK was higher than numbers reported by most authors for natural roosts (Nyholm 1965; Rieger 1996; Červený and Bürger 1989; Lučan et al. 2009). So far, the highest reported number of bats in a single roost in a tree cavity has been 155 (Encarnação et al. 2005). Although there is only a limited information in literature, 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 and Anděra (2006) reported up to 78 Daubenton's bats occupying a summer roost in an old water tunnel at castle in South Bohemia. Therefore, using artificial roosts may be advantageous to Daubenton's bat as these can be more stable, may provide suitable microclimates and/or more space for roosting than tree cavities.

Long term trends

In general, tree and crevice-dwelling bats, among which the Daubenton's bat belongs, are known to frequently switch their summer roosts, thus making classical monitoring of numbers of bats in their roosts hardly to achieve (Weller 2007). However, it seems that if they roost in man-made structures, the colonies are faithful to these structures and using of such roosts may last for many years (e.g. Nyholm 1965; Shirley et al. 2001). Our long-term data showed that it was just the case of the LK. The occupation of the LK has been known since, at least, 1962 (Hanák, pers. obs.). Our previous study on the seasonal dynamics in numbers of bats in this roost revealed that the best time for monitoring of colony size has been the pregnancy and/or the post-lactation period when annual peaks in numbers have occurred (Lučan 2009). Using such data over periods 1968–1981 and 1999–2009 we could evaluate a long term trends in numbers of Daubenton's using this roost. Overall, we observed more or less stable numbers between 1968 and 1981, and a rapid increase (ca. three-fold) from 1999 onward. Further, we proved that changes in numbers of bats in the LK were consistent with changes of numbers of occupied tree cavities in its surrounding. Our data on long-term trends fully correspond with those reported by other authors for Central Europe (Kokurewicz 1995; Uhrin et al. 2009; Horáček 2010). However, all so far published information on trends in numbers in Daubenton's bats from Central Europe have been based on counts in hibernation sites. Our results have shown that monitoring of maternity colonies roosting in artificial roosts and/or monitoring of number of occupied roosts in the same area may be a useful monitoring method.

Recapture rates and movements between roosts

Total recapture rate recorded during our study was relatively high (33.4%) and similar to those reported by other authors. For example, Červený and Bürger (1989) recaptured 21.7% and 42.7% of all ringed males and females, 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 ringed Daubenton's bats in parkland in Slovakia. Consistently higher recapture rates in case of bats originally ringed in the LK may have arisen from 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 to be encountered than bats in the LK; (ii) the bats in the LK displayed much higher roost fidelity than bats in tree cavities. We assume that both factors contributed to observed differences. Our previous study proved that Daubenton's bats are quite faithful to particular tree cavities and may reuse them for many consecutive years (Lučan et al. 2009). However, as bats frequently switch roosts, a single cavity may be occupied for a relatively short time period within a particular season. Consequently, low and uneven sampling frequency may decrease overall recapture probability of ringed bats. Unlike tree cavities, the LK was always occupied throughout the growing season and, therefore, recapture probability in any single sampling event could be higher than in tree cavities. Indeed, we recorded high recapture rates (~30–40%, data not shown) in bats roosting in the LK even in years when a single quantitative sampling event was made, what supports our assumption of generally high fidelity to this roost.

Recorded distances that bats covered during movements between roosts were in agreement with published data obtained by ringing and radiotracking (Rieger 1996). Vast majority of movements recorded within a single season covered a few hundred meters and was restricted to a single study plot. Our own radio-tracking data on spatial activity of 15 females from the LK during different phases of reproductive cycle yielded analogical results (Lučan and Radil, in press). Our observation thus supports the concept of an existence of discrete subpopulation units reported in this species as well as many other forest bats (Rieger 1996; Kerth and König 1999; Kapfer et al. 2008; Metheny et al 2008).

The difference between the two research periods in the mean distance to which bats moved was likely affected by different spatial distribution of roost trees relative to the LK. While many more roosts were in the eastern part of the study plot A in the first research 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 LK and tree cavities, overall distances were naturally shorter in the second research period.

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

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. Regarding the fact that mating occurs during late summer and autumn (Encarnação et al. 2004), these females mated at the age of 3–5 months. Such an early sexual maturity is rather exceptional among European bats from the genus *Myotis*. In contrast, early sexual maturation is typical for bats from genera *Nyctalus* and *Pipistrellus* (Gaisler et al. 1979; Racey 1974). Similar proportion (26.7%) of one-year-old lactating juvenile females was reported in *Myotis myotis* (Horáček 1981). In the case of the Daubenton's bat, only Kaňuch (2005) mentioned that "evidence of active reproduction by these "natives" (i.e. one-year-old females) was recorded" during a study with use of ringing. Further, an evidence of early sexual maturity in male Daubenton's bats was reported by Encarnação et al. (2006). Therefore, we assume that sexual maturation by the year of their birth in a small part of juveniles may be typical for Daubenton's bats.

In general, there is lack of information how the reproductive success is influenced by the age of female bats (Brunet-Rossinni and Wilkinson 2009). Our data on recapture rates of females of known age, although limited by low sample size, suggest that they may vary considerably with age. In contrast to our findings, Horáček (1981) reported consistently high (close to 100%) reproductive success in females of *Myotis myotis* up to 11-year-old.

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2

Long term re-use of tree roosts by European forest bats

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Abstract. The few studies that have assessed the long-term patterns of reuse of tree cavities by bats all concern North American bats. We studied long term-reuse of tree cavities by two species of European bat, Daubenton's bats (*Myotis daubentonii*) and noctules (*Nyctalus noctula*). Cavities were inspected during consecutive years via direct capture of bats (more than 340 positive capture events, ca 2950 captured bats), observations of emerging bats, or by listening for bats during the early evening when bats emit typical vocalization (over 160 positive checks, over 450 observed bats). Between 1968 and 2007, we found 80 tree cavities used by bats (mostly excavated by woodpeckers) in the Czech Republic. Although more than half of the cavities were occupied for ≤4 summers, 28 cavities (35%) were reused for 5–10 years. The longest period a cavity was used was 11 and 16 years for Daubenton's and noctule bats, respectively. Sixteen tree cavities (20%) were occupied solely by Daubenton's bats and 33 cavities (41%) were occupied only by noctules. The other 31 cavities (39%) were used by both species, either at separate times or simultaneously. Our data suggest that the larger volume of a cavity, the longer duration of reuse and the greater the probability of being occupied by both species. Continuous excavation of cavities by woodpeckers prevented the overgrowth of old cavities by calluses, which keep cavities accessible to bats. We suggest that woodpeckers may be the most important providers of suitable roosts for forest bats in Central Europe. Roosts were found in both economically valuable trees (*Quercus robur* and *Tilia cordata*) and less valuable tree species (*Salix fragilis* and *Alnus glutinosa*). Economically valuable trees in our study area were long-lived and likely provide roosting habitat for longer periods but matured at a greater age. However, less economically valuable trees reached maturity and started to decay in a relatively short time, which may provide suitable cavities at a younger age. Maintaining both types of trees within forests may help provide suitable roosting oportunities for tree-dwelling bats in the Czech Republic.

Abstrakt. Všechny dosavadní práce zabývající se dlouhodobým využíváním stromových úkrytů netopýry se týkají pouze nearktických druhů netopýrů. Cílem našeho výzkumu bylo zhodnotit dlouhodobé využívání stromových dutin u dvou druhů evropských netopýrů, netopýra vodního (*Myotis daubentonii*) a netopýra rezavého (*Nyctalus noctula*). Obsazenost stromových dutin v mnoha po sobě jdoucích letech byla zjišťována na základě přímých odchytů (celkem více než 340 positivních odchytů a 2950 odchycených netopýrů), pozorování netopýrů při jejich výletu ze stromových dutin, a poslechu jejich typických akustických projevů ve vhodné denní době (celkem přes 160 positivních pozorování a více než 450 pozorovaných jedinců). Celkově bylo období 1968–2008 nalezeno 80 obsazených stromových dutin (většina z nich byla původně zhotovena šplhavci). Přestože více než polovina sledovaných dutin byla obsazena méně než 5 sezón, 28 dutin (35%) bylo opakovaně využíváno po dobu 5–10 let. Rekordní zaznamenaná délka využívání dutin byla 11 let u netopýra vodního a 16 let u netopýra rezavého. Šestnáct dutin bylo využíváno pouze netopýry vodními, 33 dutin pouze netopýry rezavými a 31 dutin oběma druhy současně a to tak, že byly

oba druhy v konkrétní dutině zjištěny současně (smíšené kolonie) nebo v časově separovaných obdobích (v různých částech roku nebo v různých letech). Z našich dat vyplývá, že prostorově objemnější dutiny byly osídleny déle a zároveň častěji oběma druhy netopýrů. Na základě našich sledování se domníváme, že šplhavci hrají klíčovou roli při vzniku úkrytových možností u středoevropských stromových netopýrů. Dutiny se nacházely jak v hospodářsky hodnotných druzích dřevin (dub letní, lípa srdčitá), tak v těch z dřevařského hlediska méně zajímavých (olše lepkavá, vrba křehká). Oba typy dřevin však mají pro lesní druhy svůj význam. Hospodářsky významné dřeviny jsou obvykle dlouhověké a mohou sloužit za úkryt po velmi dlouhou dobu. Trvá však dlouho, než dosáhnou věku, kdy v nich šplhavci tyto úkryty vytvoří. Naproti tomu krátkověké a rychle rostoucí plevelné dřeviny dozrávají do věku, kdy v nich šplhavci tvoří dutiny, nepoměrně dříve. Zachování obou typů dřevin v lesních porostech je tedy nezbytnou podmínkou při ochraně populací lesních druhů netopýrů v České republice.

Full citations

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3

Microclimate differences in two artificial roosts of Daubenton's bat (*Myotis daubentonii*) with different population structure

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Abstract. Roost microclimate plays an important role in survival, growth and reproduction in microbats. One of the main energy saving mechanisms commonly used by microbats is entering body torpor. The use of torpor is governed by roost microclimate and seasonally differs between the two sexes in relation to their reproductive condition. Consequently, thermal properties of male and female roosts should differ. To test this hypothesis, we investigated temperature parameters of two artificial day roosts of Daubenton's bats with different structure of population inhabiting them. Accordingly with our presumptions, a roost occupied by male-dominated colony was colder and more fluctuant than a maternity roost with female--dominated population. Trend towards reversed sex ratio in both roosts during post-lactation period than during pregnancy and lactation suggests changing energetic demands of both sexes during that period. Using artificial roosts may be advantageous to Daubenton's bat as these can provide suitable microclimate and/or more space for roosting than tree cavities. Further research is needed to compare the costs and benefits of the living in natural tree cavities versus artificial roosts in this species.

INTRODUCTION

Roosts are vital to the survival and successful reproduction of bats (KUNZ and LUMSDEN 2003). Although species-specific, roost selection particularly reflects energetic demands of individual bats that undergo dramatic changes based on their reproductive state. Roost microclimate acts as one of the primary cues that bats use to base the selection of their daily roosts on (VONHOF and BARCLAY 1996; SEDGELEY 2001; RUCZYŃSKI 2006). For example, reproductive female bats select warmer roosts during gestation and lactation to provide ideal thermal conditions for juvenile growth and stable milk production (HUTCHINSON and LACKI 2001; KERTH et al. 2001; LAUSEN and BARCLAY 2003; WILLIS and BRIGHAM 2005). By contrast, adult males and non-reproductive females profit from using cold roosts that allow them to minimize overall energy expenditures and to attain sufficient fat reserves prior to mating and/or hibernation (HAMILTON and BARCLAY 1994).

One of the main energy saving mechanisms commonly used by microbats is entering body torpor (WILLIS 2006). Lowering body temperature can provide significant energy and water savings during cold ambient temperatures and food scarcity (WEBB et al. 1993). However, it may reduce rates of foetal and juvenile development through prolonged date of parturition or decreased milk production in pregnant and lactating females, respectively (WILDE et al. 1999). Therefore, reproductive females optimize development by minimizing times in torpor (DIETZ and KALKO 2006).

Daubenton's bat (*Myotis daubentonii*) acts primarily as a tree dwelling bat species during the reproductive season (Rieger 1996; Boonman 2000; Encarnação et al. 2005; Lučan et al. 2009) but it frequently uses artificial roosts (Nyholm 1965; Gerell 1985; this study) and occasionally even caves (Zahn and Hager 2005). So far, it is the single European species which was subjected to a detailed study of sex-dependent seasonal changes in daily torpor patterns (Dietz and Kalko 2006). It was proven, that while both sexes became torpid during daytime, male bats used daily torpor significantly more often during reproductive period (May–June) than females. Later on, a reverse pattern was observed and post-lactating females lowered body temperature significantly more than adult males. End of lactation in and onset of sperm production in late summer most probably caused this reversed trend in thermoregulatory behaviour in females and males, respectively (Dietz and Kalko 2006). While the authors recorded both skin temperature of Daubenton's bats and ambient temperature, they did not report data on roosts and roost temperatures.

The efficiency of entry into, and arousal from, torpor is governed by roost microclimate, primarily roost temperature (Chruszcz and Barclay 2002; Willis 2006). Therefore, we investigated the thermal properties of two day roosts of Daubenton's bats with different structure of population inhabiting them. We hypothesized, that a male-dominated roost should have colder microclimate than a maternity roost during reproductive period. Also, as post-lactating females use torpor more frequently (Dietz and Kalko 2006), we expected they may use the colder roost more intensively than during pregnancy and lactation. Conversely, adult males may appear in higher numbers in the warmer maternity roost during late summer and autumn when mating starts.

Material and methods

Study area and roosts

The study area was located in the central part of South Bohemia, Czech Republic. The region is dominated by two flat basins – the Českobudějovická basin and the Třeboňská basin. Both basins lie at the altitude of 380 - 420 m a. s. l. and are covered with a mosaic of semi-natural forests, agricultural landscapes and a very high number of water bodies (mostly fish ponds). The Českobudějovická basin is situated in the western part of the study area and represents a region significantly influenced by urban activities, comprising the large built up area of the regional capital city of České Budějovice, and vast areas of intensive agricultural landscapes (more than 50% of the area). The mean annual temperature is between 7–8°C and the mean annual precipitation between 550–600 mm (Tolasz et al. 2007). The local bat fauna consists of 19 bat species with Daubenton's bat being the most common (Lučan et al. 2007). Contrastingly, the Třeboňská basin in the eastern part of the study area represents a unique combination of well preserved natural habitats (wetlands, peat bogs) and semi-natural forests and agricultural landscapes (less than 30% of the area) with a low human population density. For this reason it has been established as a Biosphere Reserve under UNESCO and it is protected by the Ramsar convention. The mean annual temperature reaches 6–7° C and the mean annual precipitation is 600–650 mm (Tolasz et al. 2007) here. The local bat assemblage includes 16 bat species with Daubenton's bat being the most common (Hanák et al. 2006).

Roost A is located in the Českobudějovicko basin in the city centre of České Budějovice (approximately 48° 58' N, 14° 28' E). It is an underground water tunnel 180 m long, 2.5 m high and 5 m wide. Daubenton's bats roost in five nearby, vertically positioned crevices, up to 5 m long, 3–5 cm wide and up to 25 cm deep. Up to 80 Daubenton's bats occupy this roost on an annual basis.

Roost B is located in the northern part of the Třeboňsko basin (approximately 49° 9' N, 14° 41' E), 25 km east of roost A. It is a small abandoned cellar-like building made of bricks, formerly used as a limekiln. The building is 5 m long, 4 m wide and 4 m high. The walls are about 1 meter thick. There are several crevices of variable size in the ceiling, the largest of them (entrance 20×20 cm, depth 60 cm) being the main roosting place of a colony of Daubenton's bats. This roost has been used by a maternity colony of Daubenton's bats numbering up to some 200 individuals for more than 40 years (Lučan and Hanák 2002).

Periods of reproductive cycle and population structure of the colonies

Based on long-term observations of reproduction and population dynamics of Daubenton's bats in the study area (Lučan and Hanák 2002; Lučan 2006), we divided the reproductive season into five periods: spring movements (March 15 – May 10), pregnancy (May 11 – June 10), lactation (June 11 – July 10), post-lactation (July 11 – August 15) and autumn movements (after August 15). To obtain data on the structure of the population, we caught up to 21 individuals (median = 10, range 4–21) from colony A between 2002 and 2009 (N = 27 samples, 270 individuals). Bats were caught during the day by hand directly from crevices where they roosted. In roost B, we sampled bats using a hand net or by mist-netting in front of the entrance to the roosting building. We captured up to 140 individuals during one sampling event (median = 11, range 1–140) between 1969 and 2009 (N = 90 samples, 2441 individuals). All captured bats from both roosts were identified in terms of sex, age and reproductive state, based on the routinely used criteria for this species (e.g. Encarnacao et al. 2005; Lučan 2006). To calculate the sex ratio for a particular sampling event, we used the ratio of adult males to all the captured adult bats (Wilson and Hardy 2002). Adult bats were defined as those not born in a given sampling year. For calculations of the sex ratio, we used only samples with ≥4 and ≥10 bats captured during a single sampling event for roost A and B, respectively. Altogether, we obtained 27 and 53 such samples for roost A and B, respectively.

Roost and ambient temperatures

We used four TK-0063 (Gemini Dataloggers Ltd.) temperature dataloggers to record the temperature in both roosts and their vicinity. Temperatures were recorded in 30 min intervals from 9th March until 2nd October 2008. The in-roost temperature probes were positioned ca 30 cm from the roosting bats to avoid temperature bias via direct contact. To measure ambient temperature (T_{amb}), one temperature probe was placed ca 4 meters above ground in the vicinity of each roost, out of the reach of direct sunlight. Technical failures of dataloggers resulted in gaps in measurements between August 15–28 in roost A and between August 3–25 in roost B.

Statistical analyses

We tested differences in daily mean T_{amb} using paired t-test. We used analysis of covariance (ANCOVA) with T_{amb} as a covariate and roost and period of reproductive cycle as dependent variables to test the differences in temperature between the two roosts. Roost-days were the replication units in all analyses. We used arcsine transformation of square-rooted values in the sex ratio data to achieve normal distribution prior to analyses (Wilson and Hardy 2002). We used factorial analysis of variance (ANOVA) where roost and period were dependent variables to test the differences in sex ratio between the roosts. Tukey HSD tests were applied to compare temperatures and/or sex ratios between roosts and periods. To compare the maximum numbers of bats between the two roosts, we used two maximum counts from each year (i.e. referring to spring and summer peak, respectively) using Mann-Whitney U test. All statistical analyses were performed using STATISTICA 8.0 (Statsoft Inc.). All values are presented as mean±S.E.

RESULTS

We found significant differences in the sex ratio between the two colonies ($F_{(1, 64)} = 57.74$, $P < 0.0001$). On average, adult males greatly outnumbered females in colony A, while the reverse situation was observed in colony B (Fig. 1). However, the sex ratio varied significantly with respect to the period of reproductive cycle ($F_{(4, 64)} = 3.24$, $P < 0.05$). While the two colonies differed significantly in the sex ratio during pregnancy and lactation ($P << 0.001$), there were no differences during spring-movements ($P = 0.08$), post-lactation ($P = 0.89$) and autumn movements ($P = 0.3$) due to the high variability in the samples. Although not statistically significant, the sex ratio tended to be more skewed toward females in roost A during the post-lactation period when compared with the periods of pregnancy and lactation.

With the only exception of 2 newborn pups observed on 4 June 2009, we never found non-volant juveniles in roost A (N = 8 years). By contrast, roost B served as a maternity roost during lactation over the entire monitoring period (N > 30 years) and several tens of non-volant juveniles were observed here each year on a regular basis. In roost A, volant juvenile bats appeared as early as during late lactation (second half of June) and were present in the roost until late autumn. In roost A, juvenile bats made up 39.1% (n = 46) of total bats during post-lactation

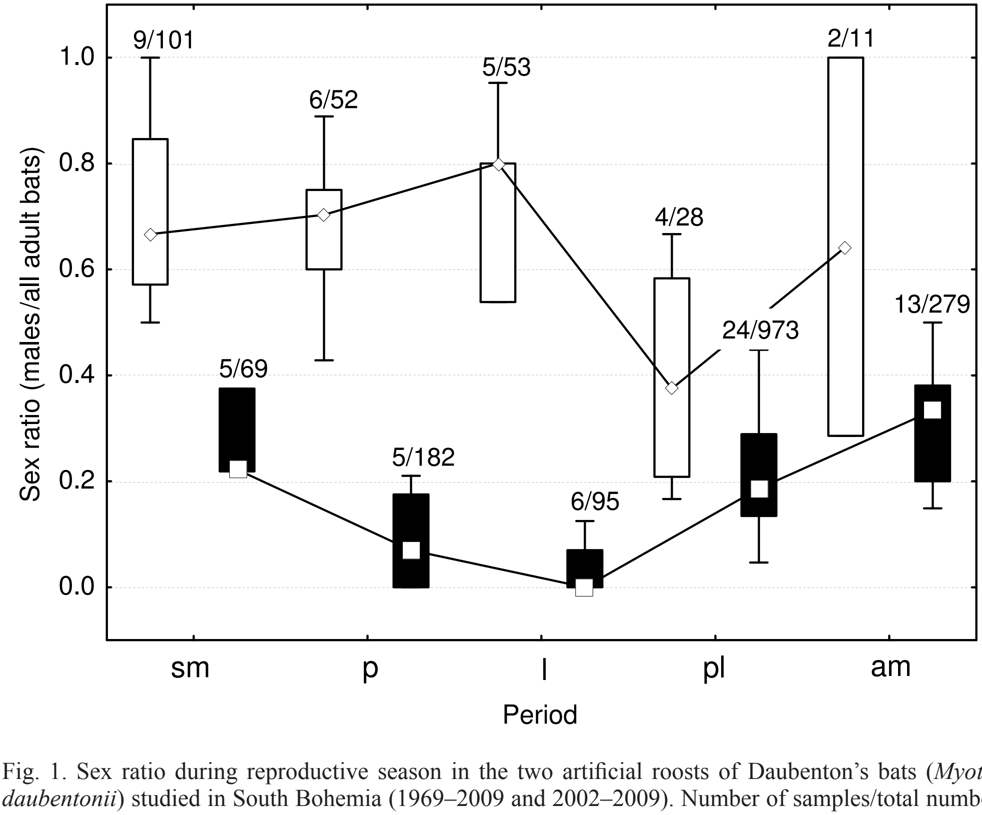

Fig. 1. Sex ratio during reproductive season in the two artificial roosts of Daubenton's bats (*Myotis daubentonii*) studied in South Bohemia (1969–2009 and 2002–2009). Number of samples/total number of examined adult bats are given for each roost and period. Abbreviations: sm–spring movements, p – pregnancy, l – lactation, pl – post-lactation, am – autumn movements. Point: median; box: 25–75%; whiskers: min–max.

Table 1. Microclimate characteristics of two artificial roosts of Daubenton's bats (*Myotis daubentonii*) studied in 2008, South Bohemia.

	Mean±SE	Min–Max (whole season)	Min–Max (pregancy–lactation)
Mean roost temperature			
Roost A	15.2±0.12	2.4–21.5	12.1–21.5
Roost B	17.1±0.13	1.8–25.5	13.4–25.5
Minimum roost temperature			
Roost A	13.2±0.13	0.3–19.5	8.3–19.5
Roos B	16.1±0.13	1.6–24.1	12.8–24.1
Maximum roost temperature			
Roost A	17.1±0.18	3.9–25.8	12.6–25.8
Roost B	18.5±0.18	2.1–34.3	13.7–34.3
Amplitude in roost temperature			
Roost A	3.9±0.11	0.5–11.8	1.4–9.3
Roost B	2.3±0.12	0.3–12.5	0.5–12.5

and 45% (n = 20) during autumn movements. In roost B, juvenile bats were present from their parturitions until late autumn. The proportion of juveniles in roost B was 38.4% (n = 1598) during post-lactation and 42.4% (n = 545) during autumn movements.

Roost temperatures

The mean, minimum, and maximum daily temperatures and temperature amplitudes in the two investigated roosts are shown in Table 1. Results of statistical analyses are given in Table 2. Mean ambient temperatures were higher at roost A than at roost B ($t_{(1, 206)} = 10.54$, $P < 0.0001$). By contrast, roost A had lower mean temperatures than roost B. The most pronounced differences in the mean temperature occurred during lactation when roost A was colder by 3.4°C on average (roost A = 18.5±0.3°C, roost B = 21.9±0.3°C). Roost A also had lower maximum temperatures than roost B. However, the maximum temperatures significantly differed only during the lactation and the post-lactation periods (Fig. 2b). Roost A cooled more than roost B throughout the season. The greatest differences occurred during the lactation period, when the minimum temperatures of roost A were higher by 4.1°C than those of roost A. The minimum roost temperatures were higher than the minimum ambient temperatures by 3.9±0.13°C and 5.6±0.13°C in roost A and B, respectively. The mean daily temperature fluctuations were higher in roost A than in roost B, but there were significant seasonal differences. Roost B had more stable temperatures (i.e. smaller daily fluctuation) than roost A during the spring, the pregnancy period and the autumn movements period and was subjected to similar temperature fluctuations during the lactation and the post-lactation periods (Fig. 2d). Daily temperature courses in the two roosts during pregnancy and lactation are shown in Fig. 3. While mean daily temperatures in roost A did not differ from mean T_{amb} throughout the season ($F_{(1, 390)} = 0.36$, $P = 0.550$), roost B kept higher mean temperatures than T_{amb} ($F_{(1, 383)} = 34.5$, $P < 0.0001$).

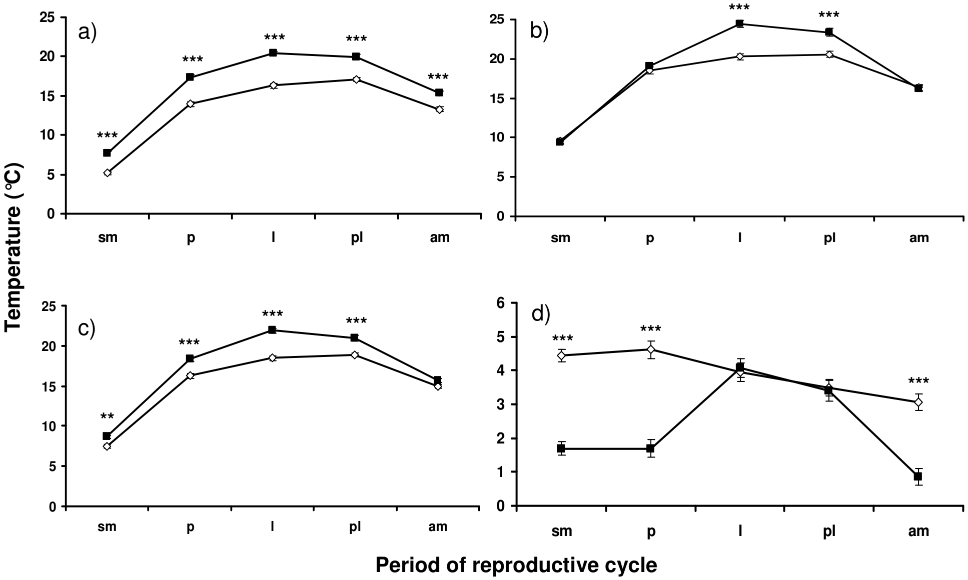

Fig. 2. Seasonal changes in microclimate characteristics of two artificial roosts of Daubenton's bats (*Myotis daubentonii*) studied in 2008, South Bohemia. Minimum roost temperatures (a), maximum roost temperatures (b), mean roost temperatures (c) and daily amplitudes in roost temperatures (d) are shown. Values are given as mean±SE. Statistically significant differences of Tukey HSD post-hoc tests are marked with asterisks (** P < 0.01; *** P < 0.001). Abbreviations: sm – spring movements, p – pregnancy, l – lactation, pl – post-lactation, am – autumn movements. Empty symbols – roost A, full symbols – roost B.

DISCUSSION

In accordance with our predictions, we observed that the colder roost with unstable temperatures was occupied mostly by males, and the warmer and more thermally stable roost served as a permanent maternity roost to a female-dominated colony. It is well known, that the two sexes of Daubenton's bat display different distribution patterns and relative abundance in relation to optimality of foraging habitats and altitude. The female-dominated populations occur mostly in the vicinity of large water bodies in lowlands whereas males prevail in suboptimal habitats located in higher altitudes (RUSSO 2002; SENIOR et al. 2005; DIETZ et al. 2006). However, both roosts in our study were located at almost the same altitude in areas that provide optimal conditions for occurrence of reproductive colonies (cf. numerous water bodies in flat landscapes) and our previous research proved the occurrence of female-dominated populations in both areas (HANÁK et al. 2006; LUČAN et al. 2007; LUČAN unpublished data). If the structure of population in the two roosts reflected regional population structure, there would be no differences in the composition of bats between the two roosts. Moreover, as the colder roost A was in a climatically warmer area (TOLASZ et al. 2007; this study) we suppose that bats had to actively select this roost based directly on roost microclimate. Therefore, we assume that the observed differences in roost use reflected primarily the energetic demands of both sexes during the reproductive

Table 2. Results of analyses of covariance describing microclimates in two roosts of Daubenton's bats (*Myotis daubentonii*) with different occupancy. Models describe mean roost temperature, minimum roost temperature, maximum roost temperature and daily amplitude in roost temperature. Roost and period of reproductive cycle was included as main effect for all temperature comparisons and T_{amb} was a covariate.

Source	F	d.f.	P
Mean Temperature			
Period	54.18	4, 368	< 0.001
Roost	156.61	1, 368	< 0.001
Roost × Period	6.21	4, 368	< 0.001
T_{amb}	852.86	1, 368	< 0.001
Minimum temperature			
Period	40.13	4, 368	< 0.001
Roost	115.09	1, 368	< 0.001
Roost × Period	1.67	4, 368	0.157
T_{amb}	772.67	1, 368	< 0.001
Maximum temperature			
Period	81.27	4, 368	< 0.001
Roost	121.67	1, 368	< 0.001
Roost × Period	18.05	4, 368	< 0.001
T_{amb}	412.16	1, 368	< 0.001
Amplitude in temperature			
Period	6.07	4, 368	< 0.001
Roost	9.28	1, 368	0.002
Roost × Period	21.72	4, 368	< 0.001
T_{amb}	170.35	1, 368	< 0.001

season (Hamilton and Barclay 1994; Grinewitch et al. 1995; Dietz and Kalko 2006). Our observations support the observation by Dietz and Kalko (2006), who reported marked differences in the thermoregulatory needs of male and female Daubenton's bats particularly during the periods of pregnancy and lactation.

Furthermore, we observed a tendency of the populations in the two roosts towards a reversed change in the sex ratio as the season progressed from the lactation to the post-lactation period (see Fig. 1). The proportion of adult males decreased in the colder roost A and increased in the warmer roost B. The post-lactation period corresponds with increased spermatogenetic activity in adult males of Daubenton's bats (Encarnação et al. 2004). Since the use of deep torpor is significantly reduced during spermatogenesis (Dietz and Kalko 2006), we expect that adult males may benefit from moving to warmer roosts. Moreover, apart from thermoregulatory reasons, reproductively active males may benefit from moving to the roost occupied by adult females through easy access to potential mates. In accord with this hypothesis, the findings by Encarnação et al. (2004) suggest that a large proportion of matings in Daubenton's bat occurs already in the day roosts within the summer habitat.

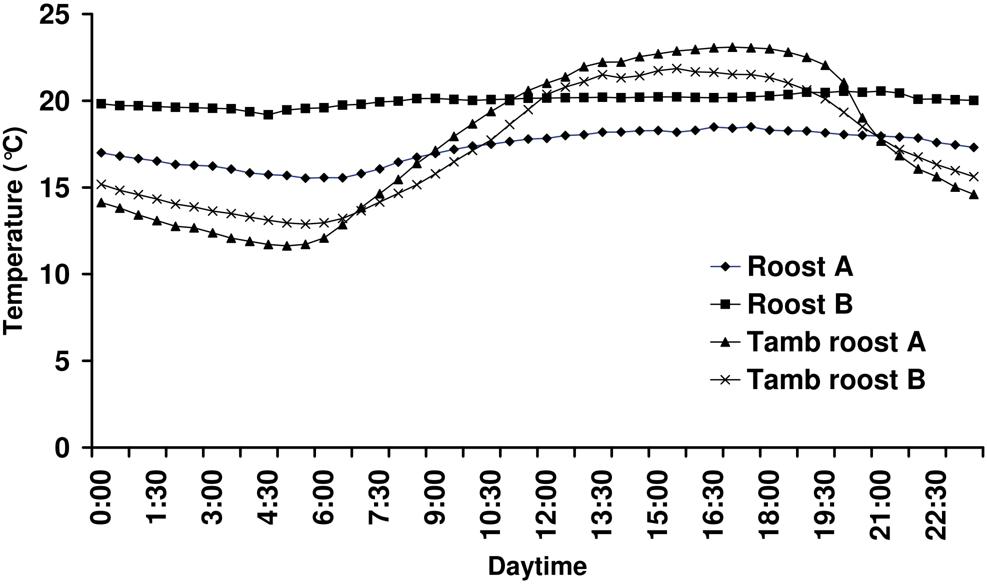

Fig. 3. Daily course of roost and ambient (Tamb) temperatures during pregnancy and lactation measured in 30 min intervals in the two artificial roosts of Daubenton's bats (*Myotis daubentonii*). Mean values are given (N = 62 days, May 10 – July 10, 2008).

Our data shows that while mean temperature in roost A was not different from T_{amb}, roost B maintained a significantly higher temperature than T_{amb} throughout the season. The differences in microclimatic parameters between the two roosts under study may arise from their location and structural characteristics. Roost A represents an underground tunnel which is not directly influenced by solar radiation, and its overall thermal changes depend solely on the ambient temperature. Also, permanent air flow through the tunnel may affect the daily temperature fluctuations. By contrast, roost B is greatly influenced by direct solar radiation. One meter thick brick, stone and concrete walls of the roosting building accumulate heat during the day and maintain a relatively high temperature during the colder parts of the day, thus minimising internal temperature fluctuations.

Majority of originally tree dwellers, such as *Myotis nattereri*, *Nyctalus noctula* and *Plecotus auritus* commonly roost in buildings and similar structures , but it appears to be rather rare in Daubenton's bat. In fact, the apparent scarcity of Daubenton's bat in man-made roosts may result from a biased research methodology. Surveys have traditionally focused on attics of buildings, which are apparently not used by Daubenton's bats. Despite the limited information, it seems likely that Daubenton's bats prefer roosts located in underground water tunnels, bridges, cellar-like structures or masonry (Barva 2000; Dietz et al. 2006; Hanák and Anděra 2006; Ceľuch and Ševčík 2008; this study). Zahn and Hager (2005) found a maternity roost occupied by up to 302 Daubenton's bats in a cave in Bavaria (Germany) with a temperature as low as 13.8 °C. This observation provides evidence that Daubenton's bats are able to exploit a variety of roosts and may use artificial roosts much more frequently than previously reported. We further assume that population increase of this species during the last decades may be, apart from trophic reasons (cf. KOKUREWICZ 1995), the result of its increasing use of artificial roosts that may be beneficial through providing enough space for large colonies and optimal microclimate. Further research is needed to compare the costs and benefits of the living in natural tree cavities versus artificial roosts in this species.

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4

Variability of foraging and roosting activities in adult females of Daubenton’s bat (*Myotis daubentonii*) in different seasons

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Abstract. We radio-tracked fifteen reproductive females (5 pregnant, 5 lactating, 5 in post-lactation) of the Daubenton’s bat in summer 2005 in order to reveal the effect of reproductive state on their foraging and roosting activity. Spatial activity of females decreased from pregnancy to lactation and increased again in the post-lactation period. Overall time spent foraging did not differ among the three study periods. However, while pregnant and lactating females spent similar proportion of the night length foraging, females in the post-lactation period were foraging for shorter part of night. The frequency of nightly visits to roosts was highest during lactation but there was a trend towards shortening of particular visits during that period. All but one roost were in tree hollows excavated by woodpeckers in spatially restricted area of ca 0.7 km^2. Tree cavities used during pregnancy were located higher on a tree trunk and had larger entrance area than the cavities used in the two later periods. Bats switched roosts every 2–3 days (range 1–8) and moved to a new roost up to 800 m apart. Pregnant females tended to switch roosts more frequently than females in the two later periods. We did not observe a significant effect of minimum nightly temperature on the activity of radio-tracked Daubenton’s bats. Therefore, we suggest that observed seasonal changes in the pattern of behaviour of Daubenton’s bat females were driven by their changing energetic demands rather than by some extrinsic factors (e.g. weather conditions).

Abstrakt. V létě roku 2005 byla za pomocí telemetrie sledována aktivita celkem 15 samic (5 březích, 5 kojících, 5 po laktaci) netopýra vodního za účelem dokumentace změn jejich prostorového a úkrytového chování v závislosti na různých fázích reprodukce. Prostorová aktivita výrazně poklesla u kojících samic. Zatímco celkový čas strávený během noci mimo úkryt byl sice ve všech třech obdobích reprodukčního cyklu zhruba stejný, v postlaktačním období trávily samice mimo úkryt výrazně kratší část noci. Frekvence návštěv denního úkrytu v průběhu noci byla nejvyšší v období laktace, průměrné trvání jednotlivých návštěv bylo však spíše kratší. Až na jednu výjimku se všechny využívané úkryty nacházely ve stromových dutinách vytvořených strakapoudy, a to v prostorově omezeném území cca 0.7 km2. Dutiny využívané v průběhu březosti se nacházely výše a měly větší vstupní otvor, než dutiny využívané v obou ostatních obdobích. Samice střídaly jednotlivé úkryty velmi každé 2–3 dny (rozsah 1–8 dní), přičemž nové úkryty ležely ve vzdálenosti až 800m od úkrytů původních. Březí samice měly tendenci střídat úkryty častěji. Celkově nebyl pozorován žádný vliv minimální teploty v průběhu noci na aktivitu netopýrů, na základě čehož soudíme, že pozorované změny v chování sledovaných samic byly důsledkem změn jejich energetických požadavků v průběhu reprodukce.

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Author's contribution: 80%

5

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

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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. 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.

Abstrakt. 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 (TFB) a časem výletu poloviny celé kolonie, byla pro všechny analýza použita první veličina, pro kterou bylo navíc k disposici 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

a anekdoticky zaznamenaných údajů o výletu z úkrytů ve stromových dutinách byla zjištěna stejná sezónní dynamika vzhledem k období reprodukčního cyklu, avšak výrazně pozdější výlet ze stromových dutin.

Full citations

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Author's contribution: 100%

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Effect of climate on the timing of reproduction and reproductive success in Daubenton's bat *Myotis daubentonii*

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Abstract. Climatic conditions, the prevailing weather patterns in an area over a long period, are a key factor affecting life history traits in mammals. We used long-term data to assess the influence of temperature and rainfall on the timing of reproduction and reproductive success of a single maternity colony of Daubenton's bat in Southern Bohemia, the Czech Republic. Mean April temperature was the best single predictor of reproductive timing. The higher was the April temperature, the earlier first newborns appeared in the studied roost. Mean date of first parturitions was July 5, but it significantly advanced by ca. 10 days between 1970 and 2010. Similarly, mean April temperature increased over the study period by ca. 2 °C. Between 1999 and 2009, mean reproductive success (proportion of reproductive females) was 75±16% but it varied between 33% (2009) and 93% (2006). It was negatively related to cumulative May and July precipitation. We hypothesize that rising spring temperatures may have beneficial influence on the population dynamics of Daubenton's bat, while increased incidence of climatic extremes, such as enormous summer rainfall, may buffer this effect. Furthermore, positive population trends observed in the past decades may have been controlled by long-term climatic trends.

Introduction

Recent climate is characterized by positive trends in global temperatures and growing incidence of climatic extremes (IPCC 2007). Behind other impacts, warming of climate has been recognized to influence the timing of life-cycle events of wide spectra of organisms. Such events as flowering and leaf unfolding dates, the timing of insect emergence or migratory bird arrival have been advanced in response to climate change (Chmielewski and Rötzer 2001; Sparks and Menzel 2002; Walther et al. 2002; Cotton 2003; Visser and Both 2005). While impact of climate on phenology has mostly been studied in plants where a long-term data from phenological gardens are available (Ahas et al. 2002), information on some other groups of organisms, such as mammals, remains very scarce (reviewed by Isaac 2009).

Climatic conditions, the prevailing weather patterns in an area over a long period, are a key factor affecting life history traits in mammals (Isaac 2009). Food availability and ambient temperature determine energy balance, and variation in energy balance is the ultimate cause of seasonal breeding in all mammals and the proximate cause in many (Bronson 2009). In temperate insectivorous bats, climatic effects on food supply are particularly important since aerial insect density is dependent on ambient temperature and precipitation (Ciechanowski et al. 2007; Fukui 2006; Racey and Swift 1985).

To meet increased energetic demands connected with reproduction, female bats can increase food intake or enter torpor (Speakman and Thomas 2004). While the former mechanism is commonly used (Barclay 1989; Clark et al. 1993; Rydell 1989; Wilkinson and Barclay 1997), the later is rather avoided since lowering body temperature negatively affects the rate of foetal development (Racey and Speakman 1987; Grinewitch et al. 1995; Dietz and Kalko 2006). For example, females of *Lasiurus cinereus* prolonged their foraging bouts at least by 73% between early lactation and fledging (Barclay 1989). However, in many species, such as Daubenton's bat (*Myotis daubentonii*), increase in flight and foraging activity from pregnancy to lactation has not been recorded and authors suggest that key factor facilitating to fulfil increased energy demands of lactation is the timing of reproduction to the periods with peak abundance of insects (Henry et al. 2002; Dietz and Kalko 2007). Furthermore, juvenile bats must learn to fly, produce and process echolocation, capture prey and store sufficient fat reserves prior to hibernation during relatively short temperate summer. Consequently, it is advantageous for parturition to occur as early as possible since it was proven that juvenile bats born earlier in the summer have a significantly higher probability of surviving their first year than young born later in the summer (Ransome 1989; Frick et al. 2010).

Variation in temperature and rainfall during the reproductive period has been recognized as a main factor governing the timing of reproduction and reproductive success in insectivorous bats (Ransome and McOwat 1994; Grindal et al. 1992; Burles et al. 2009). In general, frequent low temperatures have been singled out as the primary factor causing prolonged gestation and delayed fledging of juveniles (Racey and Swift 1981), whereas high rainfall negatively influenced overall reproductive success (Grindal et al. 1982). Nevertheless, bat species may differ in susceptibility to inclement weather in consequence of different foraging or roosting strategies. In a study of reproduction of two insectivorous bats using natural roosts during years with contrasting weather Burles et al. (2009) observed, that while adverse weather negatively influenced reproduction of *Myotis lucifugus*, it had rather positive effect on *Myotis keenii*. They hypothesized that contrasting effects of weather may have arisen from different foraging strategies of the two species. By contrast, Syme et al. (2001) found no detrimental effect of exceptionally cold summer on the timing of reproduction and reproductive success in a population of *Myotis lucifugus* roosting in buildings in the South East of U.S. The single difference they observed was changed pattern of clustering behaviour of bats in roosts. They concluded that flexible roosting behaviour and food supply ameliorated the impact of bad weather on reproduction of this species.

We used long-term data from a single maternity colony of Daubenton's bat in Southern Bohemia, Czech Republic, to assess the relationship between temperature and rainfall on the timing of reproduction and reproductive success. Daubenton's bat is a small (body mass ~ 8 g), heterothermic, insectivorous, vespertilionid bat that inhabits most of the western Palearctic (Horáček et al. 2000). It is one of the most common species in Europe, and its abundance has markedly increased over the past decades (Kokurewicz 1995). It is primarily a tree dwelling bat species during the reproductive season (Rieger 1996; Encarnação et al. 2005; Lučan et al. 2009) but it frequently uses artificial roosts (Nyholm 1965; Gerell 1985; this study) and occasionally even caves (Zahn and Hager 2005). Daubenton's bat is a typical water-surface forager, capturing insects (mostly Dipterans) both by hawking them <0.5 m above the water or gaffing them directly from the surface (Jones and Rayner 1988). Unlike aerial hawking bats, its foraging activity is not constrained by low air temperatures and it was observed foraging in temperature as low as –3.3°C (Ciechanowski 2007; Dietz and Kalko 2007). Given this fact, we hypothesized that timing of parturition should not be influenced by ambient temperatures during pregnancy. However, since activity of insects as well as detection skills of foraging bats may be limited by increased precipitation (Grindal et al. 1992), we predicted that increased rainfall during pregnancy and lactation may induce some females to forgo reproduction or lose newborn offspring, i.e. decrease reproductive success. Last but not least, we predicted, that timing of parturition may advanced during research period as a consequence of globally increasing spring temperatures.

Material and methods

The study area is located in the northern part of Třeboňská basin, South Bohemia, the Czech Republic (approximately 49° 9' N, 14° 41' E). The region lies at the altitude of 380–420 m a. s. l. and represents a unique combination of well preserved natural habitats (wetlands, peat bogs) and semi-natural forests and agricultural landscapes (less than 30% of the area) with a low human population density. For this reason it has been established as a Biosphere Reserve under UNESCO and it is protected by the Ramsar convention. The mean annual temperature reaches 6–7° C and the mean annual precipitation is 600–650 mm (Tolasz et al. 2007) here. The studied roost is a small abandoned cellar-like building made of bricks, formerly used as a limekiln. The building is 5 m long, 4 m wide and 4 m high. The walls are about 1 meter thick. There are several crevices of variable size in the ceiling, the largest of them (entrance 30×30 cm, depth 60 cm) has been serving as the main roosting place of a colony of Daubenton's bats. This roost has been used by a maternity colony of Daubenton's bats numbering up to some 200 individuals for more than 40 years (Lučan and Hanák, 2002). Numbers of bats using roosts varied with respect to the period of reproductive cycle with maximum number occurring during late pregnancy and in the post-lactation period (Lučan 2009). Owing to easy access to the roosting place of the colony, newborns and juveniles could be observed from the short distance (< 0.5 m) and therefore, their age could be estimated.

We recorded dates of first newborns in 18 of 41 years between 1970 and 2010 (1970, 1971, 1973, 1974, 1976, 1978, 1980, 1981, 1999–2002, 2004, 2005 and 2007–2010) based on direct observations of newborns in the roost or by estimating the age of juveniles using criteria given by Krátký (1981). Inspections in the roost were made in 3–14 days intervals. Although our data do not allow to analyze variation in birth timing within single season, it is well known, that most crevice- and cavity-dwelling bat species have well synchronized parturitions within a single colony (e.g. Shiel and Fairley 1999; Harbusch and Racey 2006; Hoying and Kunz 1998). In accord with published information, we observed that majority of pregnant females gave birth within 5–10 days. Therefore, our dates of first newborns are well representative in assessment of timing of parturitions.

To obtain data on reproductive success, we sampled the whole colony once a year in the post-lactation period (typically in first two weeks in August, i.e. when the number of bats in the roost was highest) between 1999 and 2009. We used a mist net stretched over the entrance to the roost together with a hand net to capture as many bats as possible. In all cases, we managed to sample 80–100% of bats present in the roost. Upon capture, we recorded sex, age and reproductive state of each bat. In adult females, we examined the nipples and its surrounding for signs of suckling during the forgone lactation period. The signs of suckling were easily visible since only some 3–4 weeks passed from weaning of juveniles. Females with enlarged nipples with absent surrounding fur were assessed as reproductive in a given reproduction period. Females with slightly enlarged but furred nipples and absent chin spot (cf. Richardson 1994) were assessed as adult but either not reproductive or they may loose their offspring prior its weanning. Those females with dark chin spot and no signs of lactation in the past were assessed as nulliparous. Nulliparous females made up to 10 percent of non-juvenile bats in the studied roost (Lučan and Hanák, in prep.). We enumerated the overall reproductive success of the colony as the proportion of reproductive females to all adult females (e.g. Burles et al. 2009).

We obtained data on monthly temperatures and rainfall from weather station in České Budějovice (ca. 25 km). Prior to statistical analyses, we transformed calendar dates of first parturitions onto Julian dates beginning from April 1. We tested all variables for normality and used data transformation to achieve normality of the distribution if necessary. We used arcsin-square-root transformation of the proportional

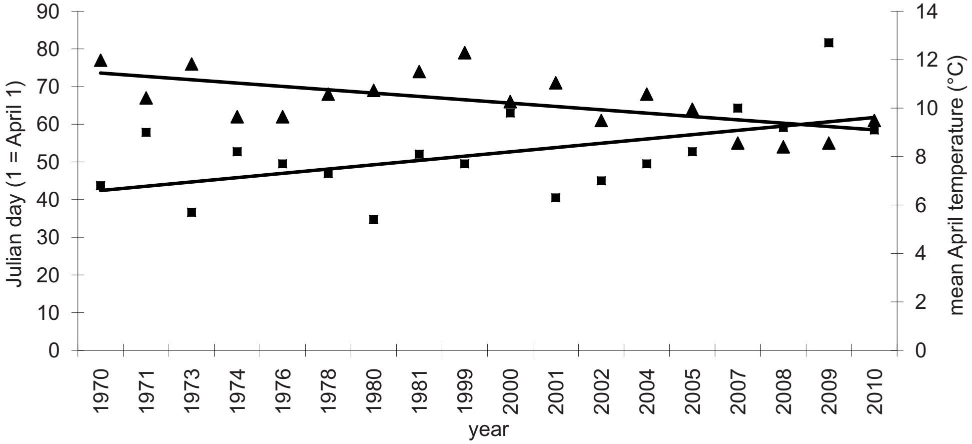

Fig. 1. Trends in dates of first parturitions (black triangles) in the studied colony of Daubenton's bats (*Myotis daubentonii*) and mean April temperatures (black squares) over the study period 1970–2010. Lines are the linear regression lines.

data on reproductive success and logarithmic transformation of the data on mean July temperatures (Zar 1999).

We used non-parametric Spearman correlation to analyze relationship between years of the study and spring temperatures and precipitation. To analyze the relationship between climate characteristics (temperature, precipitation), timing of parturition and reproductive success, we used backward stepwise multiple linear regression. We used mean April and May temperature and precipitation (data on each month separately) as explanatory variables in the analysis of the timing of parturition. We applied the same statistic procedure to analyze effect of May, June and July temperatures, and rainfall on the reproductive success. Data are shown as mean±SD.

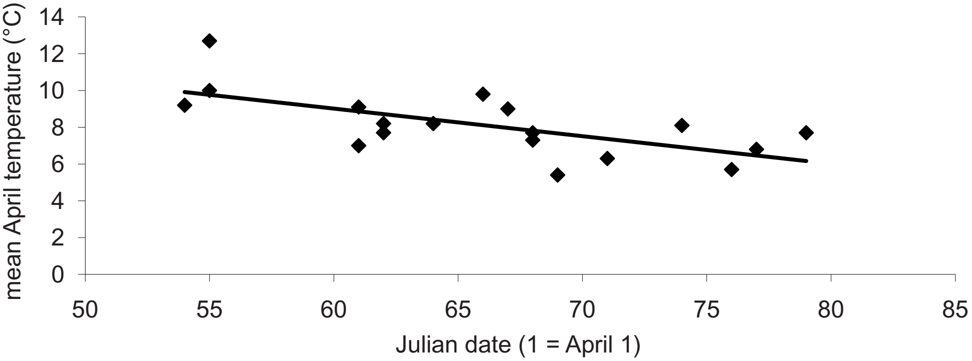

Fig. 2. Relationship between date of first parturitions in the studied colony of Daubenton's bats and mean April temperature. Line is the linear regression line.

Table 1. Numbers of reproductive (Repr.) and non-reproductive (NR) females in the LK (1999–2009). Ad ♀ – adult females, rep. success – reproductive success.

Year	NR	Repr.	Total ad ♀	Rep.success
1999	4	26	30	0.87
2000	3	28	31	0.90
2001	7	25	32	0.78
2002	7	18	25	0.72
2003	9	36	45	0.80
2004	8	31	39	0.79
2005	26	38	64	0.59
2006	4	53	57	0.93
2007	11	39	50	0.78
2008	12	37	49	0.76
2009	24	12	36	0.33

RESULTS

Mean and median date of first newborns over the whole study period was 5th June but it varied between 24th May (in 2008) and 18th June (in 1999). It was negatively correlated with the year of observation ($r_s = –0.63$, $P < 0.05$) and, on average, advanced by ca. 10 days between 1970 and 2010 (Fig. 1). Accordingly, mean April (but not May) temperatures increased over the study period by ca. 2 °C ($r_s = 0.54$, $P < 0.05$), while spring precipitation shown no significant trend (April: $r_s = 0.005$, $P = 0.98$; May: $r_s = 0.37$, $P = 0.13$). Mean April temperature was a single variable with significant effect on the timing of parturition (Fig. 2). It explained 42% of the variability in the data ($\beta = –0.64$, $F_{(1, 16)} = 11.4$, $p < 0.01$)

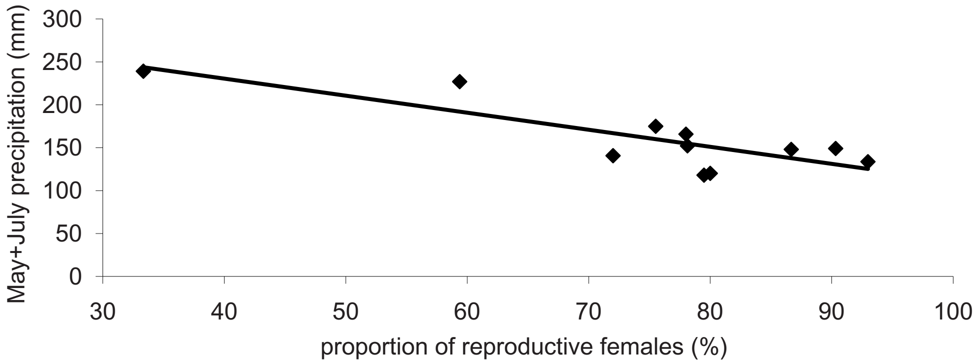

Fig. 3. Relationship between cumulative May+July precipitation and reproductive success in the studied colony of Daubenton’s bats (*Myotis daubentonii*) over 11 years (1999–2009).

Data on reproductive success are summarized in Table 1. On average, the proportion of reproductive females (i.e. reproductive success) was 75±16% but it varied between 33% (2009) and 93% (2006). While May–July temperature had no effect, May and July precipitation was negatively correlated with reproductive success (May precipitation: $\beta = -0.54$, $P < 0.05$; July precipitation: $\beta = -0.66$, $P < 0.01$, Fig. 3). These two variables explained 66% of the variability in the data ($F_{(2, 8)} = 7.7$, $p < 0.01$).

Discussion

Based on our long-term data, we proved that spring temperature and precipitation significantly influenced the timing of parturition and reproductive success in the studied colony of Daubenton's bat. While increased April temperature advanced first parturitions, increased May and July rainfall negatively affected the reproductive success. Previous studies have reported that weather plays an important role in the timing of reproduction and reproductive success. Low spring ambient temperatures may prolong gestation through its influence on the frequency of using body torpor by pregnant females (Racey and Swift 1981), it may negatively affect activity of flying insects (Hoying and Kunz 1998; Ciechanowski et al. 2007) or both. However, it was proven that Daubenton's bat is able to forage even at very low temperatures (up to –3.3°C), most probably due to its foraging strategy and predominant prey, aquatic insects, which may be less affected by low temperatures than some other groups (Ciechanowski et al. 2007; Dietz and Kalko 2007). Given this fact, we predicted no influence of spring temperatures on reproductive timing. Against our predictions, timing of parturition was positively related to April temperatures. Since April is the month when most bats leave their hibernacula, wee hypothesize, that rather then direct effect on bat's prey availability or thermoregulation (i.e. using torpor), increased spring temperature may shorten hibernation and, consequently, advance onset of pregnancy in females. It is well known, that ovulation and onset of pregnancy in hibernating bats is triggered by increase in ambient temperature and arousal from hibernation (Heideman 2000). Our long--term observation in the studied roost revealed almost one month between-year variation in the date, when first bats arrived from their hibernacula (Lučan and Hanák, in prep.) which fact well corresponds with above mentioned hypothesis. Also, observed between-years variation by up to 7.3°C in mean April temperature during 18 years of the study suggests corresponding variation in the onset of seasonal activity of Daubenton's bats.

Increased precipitation during pregnancy and lactation has been reported to delay parturition and decrease reproductive success in *Myotis lucifugus* (Burles et al. 2009), and in *M. lucifugus* and *M. yumanensis* (Grindal et al.1992). While there was no relation between precipitation and reproductive timing in our study, we documented that increased May and July precipitation adversely affected reproductive success. We hypothesize that increased May rainfall may restrict foraging activity and prey detectability by pregnant females and, consequently, induce some of them to forgo breeding (Grindal et al. 1992). On the other hand, high amount of July precipitation may increase mortality of juveniles during the onset of their volancy, i.e. during the period of their particularly vulnerability (Heideman 2000). Our data (c.f. Fig. 3) shows that a negative influence of precipitation was evident mostly during years with its enormous increase. For example, the lowest reproductive success over the study period (ca. 33% of reproductive females) was observed in 2009, when cumulative May to July precipitation was by 73% higher than long-term average, while it was higher maximally by 24% in the years with higher-than--average reproductive success.

Last but not least, our data showed overall increase in spring temperatures over the study period followed by concomitant advance of first births. Increase in spring temperatures resulting in overall prolongation of vegetative season during past decades was reported by a vast number of authors (e.g. Ahas et al. 2002; Sparks and Menzel 2002; Walther et al. 2002). Earlier onset of spring has resulted in a variable response to different organisms. For example, short-distance migratory birds advanced their arrival to breeding areas (Lehikoinen et al. 2004) and multi-brooded species may be able to increase productivity by having more nesting attempts (Jenni and Kéry 2003). Contrastingly, some long-distance migratory birds have been negatively affected by spring advancement, because the timing of their main food supply has advanced more than their breeding date (Both et al. 2006). Frick et al. (2010) reported positive influence of early parturition on 1st-year survival and breeding propensity in *Myotis lucifugus*. Given the fact, that Daubenton's bat is a Palearctic ecological equivalent of *Myotis lucifugus* (Gaisler and Zukal 2004), we assume climate may have analogical effect on its life-history traits. Consequently, rising spring temperatures may have beneficial influence on its population dynamics, while rising incidence of climatic extremes, such as enormous summer precipitation, may buffer this effect. We hypothesize, that positive population trends in Daubenton's bat observed in the past decades (cf. Kokurewicz 1995) may have been controlled by long-term climatic trends.

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7

Relationships between ectoparasitic 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 parasites on the host condition and roosting behavior

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Abstract. Host-parasite relationships between Daubenton's bat, *Myotis daubentonii* Kuhl, 1917 (Chiroptera: Vespertilionidae) and its haemathophagous ectoparasite, the mite *Spinturnix andegavinus* Kolenati, 1857 (Acari: Spinturnicidae), were subjected to analyses based on data gathered during a six-year study (1999–2004) within a single study area in the vicinity of Ruda field station of Faculty of Science, Charles University, in the northern part of Třeboňsko Protected Lanscape Area and Biosphere Reserve (49°10'N, 14°43'E, South Bohemia, Czech Republic). Seven hundred and fifty-one Daubenton's bats were inspected by screening wing membranes with an intensive light source, resulting in 4,690 recorded mites. Sex, age, weight and reproductive state were evaluated for each bat. A body condition index was calculated as a ratio of weight to forearm length. The seasonal course of mite infestation displayed distinct dynamics with the peak during the lactation and post-lactation periods coinciding with occurrence of the most numerous colonies of Daubenton's bats in the study area. Infestation rates differed between the two sexes, being higher in adult females than adult males. Juvenile bats of both sexes (with no differences between males and females) were the most infested group of all. Pregnant females had a significantly higher parasite load than non-pregnant ones while no differences in infestation rates were found between lactating and non-lactating females. The analyses of the relationship between parasite load and body condition of bats revealed no common trends for all sex and age related groups. Two possible explanations are suggested and discussed: (1)There is no true relationship between the two tested variables and, thus, the significant results were attained due to a random statistical effect, (2) Different underlying causal mechanisms may exist that influence parasite load and, especially, body condition,with respect to the particular sex and age category of bats. The seasonal roosting dynamics of Daubenton's bat are suggested to be the result not only of changing energetic demands of resident population members, but also of coevolutionary strategies within host-parasite relationships.

Abstrakt. Na základě dat získaných při studiu modelové populace v severní části CHKO Třeboňsko v období 6 let (1999–2004) byly analyzovány různé hostitelsko-parasitické vztahy mezi netopýrem vodním (*Myotis daubentonii*) a jeho ektoparasitickým roztočem Spinturnix andegavinus. Celkem bylo examinováno 751 netopýrů vodních na kterých se vyskytovalo dohromady 4690 roztočů zkoumaného druhu. U každého netopýra bylo zaznamenáno pohlaví, věk, délka předloktí a váha, na základě kterých byl spočten index tělesné kondice. Celková parasitace byla nejvyšší v období laktace a v postlaktačním období, která časově odpovídají výskytu nejpočetnějších agregací netopýrů vodních v jejich úkrytech. Početnost parasitů byla závislá na věku a pohlaví, přičemž nejvíce byla parazitována mláďata, méně dospělé samice a nejméně dospělí samci. V období březosti byly více parazitovány březí samice, zatímco během laktace se parazitace u obou skupin nelišila. Vztahy mezi tělesnou kondicí netopýrů a počty parasitů byly nejednoznačné.

Domníváme se, že buď (1) neexistuje žádný přímý vztah mezi počty parazitů a kondicí netopýrů nebo (2) existují rozdílné kauzální mechanismy, které stojí rozdílnou parasitací a jejím vlivem na kondici netopýrů. Zdá se, že sezónní dynamika velikosti netopýřích agregací není jen důsledkem měnícího se energetického rozvrhu jednotlivců v souvislosti s rozmnožováním, ale v jejím pozadí může být i koevoluce s parazity.

Full citations

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Effect of climate on infestation of Daubenton's bat (*Myotis daubentonii*) by ectoparasitic mite *Spinturnix andegavinus*

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Abstract. Based on a long term data (1999–2009) obtained from a single maternity colony of Daubenton's bat in South Bohemia, Czech Republic, we analyzed the relationship between climate, abundance of its ectoparasitic mite *Spinturnix andegavinus*, and body condition of bats. Parasite loads varied with respect to sex and age of bats and the year of observation. Minimum adequate model describing observed patterns of variation in parasitation included sex and age of the bat, number of freeze days from preceding winter, mean spring precipitation and its squared term, and two interactions. The best single climatic predictor for parasite abundance was the number of freeze days during winter and this was highly correlated with mean winter temperature. Consequently, the warmer the winter, the higher parasite abundance was in the following summer. We hypothesize that winter temperatures may control parasite load in the next growing season through their effect on the arousal of bats from hibernation and, consequently, on the length of reproductive season of parasites. We did not prove any relation between climate and body condition of bats. Moreover, we did not find any negative effect of parasite load on body condition of bats. Based on arguments from published literature, we hypothesize that such effect may exist but only during the nursing period, i.e. outside the time, when the data were sampled in our study. Last but not least, we observed an increase in the mean parasite load over the study period. Since our study showed a direct link between winter temperature and parasite load, we hypothesize that warming of climate may negatively affect bats by increased stress imposed by parasitation.

Introduction

A number of studies have demonstrated that bat ectoparasites greatly adjusted their seasonal dynamics and reproduction to the reproduction of their hosts (Christe et al. 2000; Bartonička and Gaisler 2007; Lourenço and Palmeirim 2008). Aggregation of female bats into large colonies during reproductive period enhances transmission of ectoparasites (Rekardt and Kerth 2009), whereas juvenile bats with naive immune system and imperfect grooming skills represent ideal hosts on which the highest reproductive rate may be achieved (Christe et al. 2000). Consequently, high parasitation is a direct cost of bat sociality (Lourenço and Palmeirim 2007).

Ectoparasite abundance may be directly influenced by both the host behaviour and the environmental condition (Giorgi et al. 2001; Reckardt and Kerth 2006; Bartonička and Gaisler 2007). There are several ways how bats' behaviour may control ectoparasite load. Ectoparasites completing entire life cycle on their hosts, such as mites, may be effectively reduced by grooming (Giorgi et al. 2001; Hofstede and Fenton 2006). Those ectoparasites that spend part of their life-cycle outside host's body (e.g. bat flies or bat bugs) may be reduced by grooming and roost switching (Lewis 1995; Reckardt and Kerth 2006; Bartonička and Gaisler 2007).

Additionally, abundance of both types of parasites may be controlled by decreased aggregation (Lourenço and Palmeirim 2007; Rekardt and Kerth 2009).

While seasonal dynamics in ectoparasite abundance and antiparasitic strategies of bats have been well described in many host-parasite systems, inter-annual variation and its causes and consequences remain poorly understood. Many authors have reported high between-year variation in ectoparasite load on bats (Deunff and Beaucournu 1981; Dietz and Walter 1985; Zahn and Rupp 2004), but no one addressed this phenomenon to a rigorous analysis, since a long term data enabling such analysis are largely missing. Given the fact, that inter-annual variation in climate has profound effect on the body condition, timing of reproduction and reproductive success of temperate bats (Ransome and McOwat 1994; Grindal et al. 1992; Burles et al. 2009), it should correspondingly affect bat ectoparasites. For example, variation in spring temperature may affect length of reproductive season of parasites (Mouritsen and Moulin 2002; Møller 2010). It is known, that spring temperature governs the time of arousal of bats from hibernation. Since reproduction of many bat parasites is reduced during bats' hibernation (Lourenço and Palmeirim 2008), high spring temperatures may advance onset of bat's activity and thereby prolong the reproductive period of their ectoparasites. Consequently, higher parasite load may occur in years following high spring temperatures. Alternatively, cold and rainy weather may result in poor condition of bats and increased their susceptibility to parasitation. While results of analyses of relationships between climatic variability and parasite abundance proved an existence of analogical scenarios in a variety of host-parasite systems (Mouritsen and Poulin 2002; Hudson et al. 2006; Poulin 2006; Møller 2010), no such study has been done on bats and their parasites.

The purpose of this study was to analyze the relationship between climate and abundance of ectoparasitic mite *Spinturnix andegavinus* infesting the Daubenton's bat (*Myotis daubentonii*). *Spinturnix andegavinus* is the only species from the genus *Spinturnix* infesting the Daubenton's bat (Bruyndonckx et al. 2009). It is haematophagous mite occurring on wing membranes of bats and completing its entire life-cycle on hosts's body (Rudnik 1960). It has profound seasonal dynamics with maximum abundance during reproductive period of Daubenton's bat (Zahn and Rupp 2004). Highest numbers of mites were recorded on females and juvenile bats, whereas males host fewer mites (Lučan 2006).

Material and methods

The present study was carried out in the northern part of Třeboň Basin Protected Landscape Area and Biosphere Reserve (49°10'N, 14°43'E), South Bohemia, Czech Republic, from 1999 until 2009. We used data from a single colony of Daubenton's bats roosting in an abandoned lime-kiln. The colony of up to 200 Daubenton's bats has been using this roost as a maternity at least since 1962 (Hanák, pers. com.). To obtain data on numbers of mites, we sampled the whole colony once a year in the post-lactation period (typically in the first two weeks in August, i.e. when the number of bats in the roost was highest – cf. Lučan 2009). We used a mist net stretched over the entrance to the roost together with a hand net to capture as many bats as possible. In all cases, we managed to sample 80–100% of bats present in the roost. Upon capture, we recorded sex, age and reproductive state of each bat. The number of mites was counted by screening wing membranes of the bats with an intensive light source (Lučan 2006). In total, 900 bats were examined from which 3154 mites were recorded. In 2000 and 2001, the sampling of data on bats and mites was done in the first half of July, when numbers of parasites were much higher then in first half of August, i.e. the sampling period in all other years (Lučan 2006). Therefore, we excluded this data from analyses. We counted body condition index for each bat as the proportion of body weight

Table 1. Variables used for the construction of regression models.

Parameter	Description
NFD	number of days with mean temperature <0°C from November 1 to April 30
msprT	mean monthly temperature from April 1 to July 31
JanAprT	mean monthly temperature from January 1 to April 30
MayJunT	mean monthly temperature from May 1 to June 30
JunJulT	mean monthly temperature from June 1 to July 31
MayJulprec	cumulative precipitation from May 1 to July 31
MWT	mean monthly temperature from November 1 to April 30
sumwinT	sum of mean monthly temperatures from November 1 to April 30
meanSpringPrec	mean monthly precipitation from April 1 to July 31
spring PrecSuma	cumulative precipitation from April 1 to July 31
numbats	number of Daubenton's bats in the roost during particular sampling event

to the length of forearm (e.g. Lourenço and Palmeirim 2007). Due to a missing data, we counted body condition index for 868 of 900 examined bats.

We used climatic data (temperatures and precipitation) from weather station in České Budějovice (25 km distant). A non-parametric Spearman correlation was used to analyze relationship between the year of the study and overall parasite load. We used 11 explanatory variables (Table 1) for the construction of regression models. If not specified, in all analyses a replication unit was an individual bat. Number of parasites per individual (= parasite load) were log-transformed (using ln(number of parasites +1) transformation) prior analyses to improve data homoscedascity. Statistical modelling was performed using R (R Development Core Team 2008). Models of relationship between climatic variables and parasite load in general were constructed and tested as linear mixed effects models, using R package lme4 with year of the study as the random effect. We used maximum likelihood fitting method to allow us to compare models with different fixed effects and to decrease the estimated variance of random effect (year of sampling) by the fit of fixed effects. Variability in the parasite load attributable to the annual changes (random effect) was estimated using restricted maximum likelihood fitting method. After fitting minimal adequate model with climatic variables, we added sex and age and eliminated terms included into the minimal adequate form. In all steps, we used significance level of 5%. We used the same procedure to analyze the effect of climatic variables on body condition of bats. Finally, we used non-parametric Spearman correlation to analyze relationship between body condition of bats and parasite load.

Results

Parasite loads for each sex, age and year are summarized in Table 2. Overall, there was a positive trend in the mean parasite load over the study period ($r_s = 0.75$, N = 9, $P<0.05$).

Overall, 18.5 % of variation in parasite load was attributed to the random effect of the year. Number of frost days (NFD) was the best single predictor for the number of ectoparasites (Chi-square = 4.64, d.f. = 1, p = 0.031; Fig. 1). The second best single predictor was the mean winter temperature (MWT; Chi-square = 4.33, d.f. = 1, p = 0.037), any other predictor was not significant at p = 0.05. Since NFD and MWT were highly correlated ($r_s = 0.98$, $P < 0.0001$), we used NFD in model building. Minimum adequate model included sex, age, number of freeze days, mean spring precipitation and its squared term, and two interactions (Table 3). Overall, parasite load decreased in following order: juvenile females>juvenile males>adult females>adult males. Increase in overall winter temperature and mean spring precipitation positively affected parasite load. As indicated by the two significant interactions, the correlation (slope of

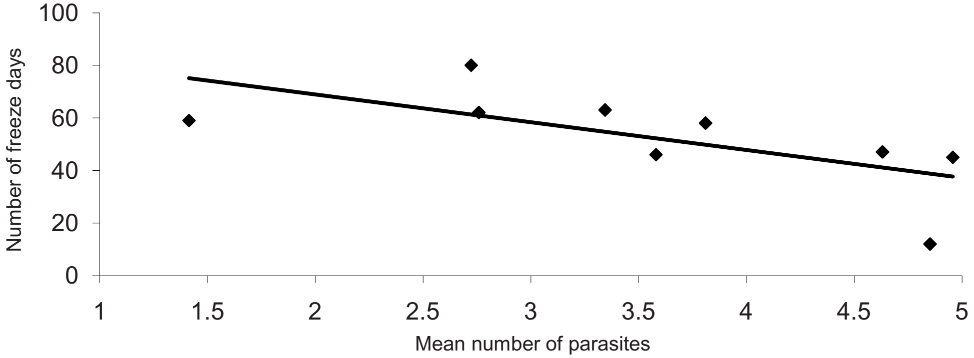

Fig. 1. The relationship between the number of frost days in the winter preceding the sampling of parasites and mean parasite load (number of parasites) in Daubenton's bats.

Table 2. Summary of parasite loads in bats of different sex and age over the study period.

	1999		**2002**		**2003**		**2004**		**2005**	
	± SD	N	± SD	N	± SD	N	± SD	N	± SD	N
Adult females	1.5±1.4	40	2.9±1.9	32	2.7±2.3	53	3.8±3.1	50	2.4±1.8	77
Adult males	1.1±1.2	7	4.0±3.6	4	2.1±1.8	11	3.8±2.4	5	3.1±2.5	10
Juvenile females	1.3±0.8	10	4.2±3.0	9	1.7±1.3	18	4.5±3.0	13	3.5±2.3	25
Juvenile males	1.7±1.3	10	5.4±2.4	8	1.9±1.5	16	3.7±1.9	14	3.0±1.9	16
Total	1.4±1.3	67	3.6±2.5	53	2.3±2.0	98	3.9±2.8	82	2.8±2.0	128

	2006		**2007**		**2008**		**2009**		**Total**	
	± SD	N	± SD	N	± SD	N	± SD	N	± SD	N
Adult females	2.2±1.8	66	4.3±3.1	60	4.4±2.6	57	3.8±4.3	43	3.1±2.7	478
Adult males	2.2±1.9	17	2.3±1.6	14	2.6±1.3	13	3.7±3.5	11	2.6±2.2	92
Juvenile females	4.0±2.4	35	6.5±3.7	30	7.0±4.2	27	6.1±2.7	19	4.7±3.4	186
Juvenile males	2.5±1.8	22	5.7±3.7	24	5.3±2.4	21	5.7±3.5	13	3.9±2.9	144
Total	2.7±2.1	140	4.9±3.5	128	4.9±3.2	118	4.6±3.9	86	3.5±2.9	900

Table 3. Parameter estimates in the best fitted minimum adequate regression model on parasite load. Overall fit of the model: χ^2= 84.347, d.f.=7, P<0.0001. B – slope.

Parameter	B	SE	p
Sex	-0.117	0.046	0.01
Age	-0.072	0.184	0.0001
Number of freeze days (NFD)	-0.01	0.002	0.0001
Mean spring precipitation (MSP)	0.047	0.018	0.0001
MSP^2	-0.0002	0.0001	0.05
Sex x NFD	-0.006	0.002	0.01
Age x MSP	0.009	0.002	0.001

Table 4. Parameter estimates in the best fitted minimum adequate regression model on body condition of bats. Overall fit of the model: χ^2=226.85, d.f.=2, P <0.0001. B – slope.

Parameter	B	SE	p
Sex	-0.011	0.002	0.0001
Age	-0.017	0.001	0.0001

Table 5. Results of non-parametric (Spearman) correlation between body condition of bats and parasite load. r_s – Spearman correlation coefficient.

	N	r_s	P
Adult females	453	0.019	NS
Adult males	91	-0.042	NS
Juvenile females	182	-0.062	NS
Juvenile males	142	0.092	NS

regression curve) between NFD and parasite load differed between sexes and the correlation between MSP and parasite load differed between adults and juveniles.

Overall, 12.1 % of variation in body condition index (BCI) was attributed to the random effect of the year. Minimum adequate model for the relation between BCI and eleven explanatory variables included only sex and age of examined bats (Table 4). No other variable significantly contributed to a decrease in variance in the data. Finally, we found no significant relationship between parasite load and BCI in any sex- and age-group of bats (Table 5).

Discussion

Our long-term data showed direct influence of climatic factors on abundance of ectoparasites. Increase in winter temperature and spring/mid-summer precipitation positively affected parasite load. Daubenton's bats spend winter time hibernating in temperatures below 10°C in underground shelters with a very stable microclimate and limited influence of fluctuation of external temperatures (Kokurewicz 2004). Therefore, we assume that direct effect of winter temperature on ectoparasites is of limited value. Moreover, it is known, that reproduction of spinturnicid mites is ceased during hibernation period (Lourenço and Palmeirim 2007). We hypothesize that mean winter temperatures (or number of frost days) may control parasite load in next growing season through its effect on the length of bat's hibernation. The warmer the winter, the shorter is hibernation and, consequently, the earlier onset of parasites's reproduction. Prolongation of reproductive period may thus result in higher parasite abundance observed in mid-summer. Similarly, changes in parasite loads as a consequence of prolonged reproductive season due to increased temperatures were reported in some other host-parasite systems (e.g. barn swallows – Møller 2010; molluscs – Poulin 2006).

Increased spring/mid-summer precipitation may negatively affect body condition of bats through its influence on availability of their prey (Grindal et al. 1992) and, consequently, they may be more susceptible to parasitation. Furthermore, it was proven that increased May and July precipitation negatively affect reproductive success in the studied colony of Daubenton's bats (Lučan and Hanák, in prep.). In contrast to these facts, we found no effect of climatic variables on body condition of bats. Despite this, we hypothesize that a negative effect may exist only during the pregnancy and nursing period, when energy demands of reproductive females are particularly high and inclement weather conditions may cause a significant stress (Lourenço and Palmeirim 2007). Since our sampling of bats and parasites was conducted in the post-lactation period, decrease in body condition from preceding reproduction period may have not been detectable, whereas high parasite load may persisted.

Parasites are costly to bats since they have influence on their immune response, energy budget, behaviour, and body condition (Giorgi et al. 2001). The effect of parasitism on the condition of bat hosts has been subjected to many studies. However, while under some circumstances authors found a significant effect (Lourenço and Palmeirim 2007), others concluded that the body condition was not related to parasite load (Zahn and Rupp 2004). Similarly, we found no significant relationship between parasite load and body condition. Lourenço and Palmeirim (2007) studied the effect of abundance of *Spinturnix psi* on the body condition of *Miniopterus schreibersii* during the whole growing season and observed a significant negative relationship only during nursing period when mites were most abundant. Our previous study on bat-parasite relationship in the same study area revealed contrasting results – while adult and subadult females with higher body condition hosted more parasites, a negative relationship was proven in juveniles (Lučan 2006). However, we used the data from bats sampled in different types of roosts (building and tree cavities) and there may have existed differences in parasite load and the body condition. Given the fact that maximum abundance of *Spinturnix andegavinus* has occurred much earlier than was our sampling period in this study (cf. Lučan 2006), we could not prove the possible negative effect of high parasite load on body condition of bats in the studied colony.

Last but not least, we observed an increase in the mean parasite load over the study period. Since this trend was related solely to climatic variables, we suggest these changes to be directly linked with current change of global climate (IPCC 2007). It has been proved that rising spring and winter temperatures over last few decades greatly affected the phenology, reproduction and distribution of a large number of organisms (Sparks and Menzel 2002; Walther et al. 2002). Prolongation of reproductive season may result in increased number of parasite generations per year and, consequently, to overall increase in population size (Møler 2010). Since our study showed a direct link between winter temperature and parasite load, we hypothesize that warming of climate may negatively affect bats by increased stress imposed by parasitation.

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1. An old lime kiln (LK) – an artificial roost used by Daubenton's bats for more than four decades.

2. Small part of maternity colony of Daubenton's bats in main roosting space in the LK.

3. Female of the Daubenton’s bat suckling its non-volant pup in the LK.

4. Non-volant juvenile Daubenton’s bats was observed frequently roosting apart separately from their mothers during daytaime.

5. A radio-tracked female of the Daubenton's bat nigh-roosting in the cluster of other individuals on the ceiling of the LK.

6, 7. – 6 (left) A typical tree cavity occupied by Daubenton's bats in the study area. – 7. Locating tree roost with use of radio-tracking.

8. Inspection of occupied tree cavity.

9. Underground water channel in České Budějovice. A roosting place of studied male roost of Daubenton's bats. Location of roosting fissures is shown woth white arrow.

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CV

Curriculum vitae

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Bc. 1998–2001, thesis: Population biology of Daubenton's bat, *Myotis daubentonii*, in the Třeboň basin (supervisor prof. Ivan Horáček).
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Current position: research asistent at Department of Zoology, Faculty of Science, Charles University in Prague

Research interests: population ecology of European forest bats, historical biogeography of Mediterranean fruit bats (*Rousettus aegyptiacus*)

Language skills and other information: English language – actively, Spanish and French – passively. Secretary of the Czech Bat Conservation Trust, well trained in field work in bat research, including zoological expeditions to other countries (Venezuela 2003, 2004 and 2006, Syria 2001 and 2004, Cyprus 2005, 2009, 2010, Egypt 2005, 2010, Lebanon 2006, 2007, 2008, 2009, Turkey 2009).

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August 5, 2010

Dear Dr. Lučan,

I am pleased to inform you that your manuscript entitled “**Variability of foraging and roosting activities in adult females of Daubenton’s bat (*Myotis daubentonii*) in different seasons**“ has been accepted for publication in journal Biologia.
Your MS will be scheduled for publication in volume 65 (2010) of the journal.

Looking forward to further co-operation.

Sincerely yours,

Mária Kazimírová
Managing editor