INFLUENCE OF REPRODUCTION ON THERMOREGULATION, FOOD INTAKE AND FORAGING STRATEGIES OF FREE-RANGING FEMALE AND MALE DAUBENTON’S BATS, *MYOTIS DAUBENTONII* (VESPERTILIONIDAE)

**DISSERTATION**

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SUMMARY

INFLUENCE OF REPRODUCTION ON THERMOREGULATION, FOOD INTAKE AND FORAGING STRATEGIES OF FREE-RANGING FEMALE AND MALE DAUBENTON’S BATS, *MYOTIS DAUBENTONII* (VESPERTILIONIDAE)

General Introduction

Mammals are characterized by a diverse array of life-history strategies that are strongly influenced by body size and environmental conditions. In general, larger mammals mature later, have longer gestation and lactation periods, produce lower litter size and live longer whereas small mammals tend to exhibit the opposite traits (Barclay and Harder 2003). The size of a mammal has an important effect on its energy demand for homeothermy. Small mammals have higher mass-specific metabolic rates than larger mammals to compensate for the higher rate of heat loss in relation to the larger surface area per unit mass (Speakman 2000, Speakman and Thomas 2003). In addition to the general costs of homeothermy the expensive reproduction period requires particular physiological and behavioural adaptations. Females must balance their investment in gestation and lactation to sustain the development of the young and to secure a successful reproductive period. In the temperate zone, almost all mammals breed in spring and summer when the climate is favourable and food is abundant (McDonald 1995).

In Europe, bats present nearly a quarter of all mammal species. Their life history traits reveal some remarkable adaptations to the temperate zone climate. With regard to reproduction, all European bat species except Schreiber’s bat, *Miniopterus schreibersi*, exhibit delayed fertilisation in response to the seasonal variations in climate. Furthermore, all species that have been studied so far in greater detail are characterized by seasonal monoestry (Racey and Entwistle 2000). They mate in late summer and early autumn and viable sperm is then stored
in the uterus throughout hibernation for up to six or seven months (Racey and Entwistle 2000). Fertilisation takes place in spring when females wake up from hibernation and insect availability increases. Combined with one of the lowest mass-specific foetal growth rates recorded within mammals, bats are characterized by long gestation times compared with other similar-sized mammals (Racey 1973). Reduced food supply in conjunction with low environmental temperatures can lengthen gestation by 20 percent or more (Kunz and Stern 1995). Gestation is followed by a relatively long period of lactation and post-natal care with high energetic investment of the females (Kunz and Stern 1995). Typically, only a single young or in some species twins are produced that may weigh up to 43% of their mother’s body mass as neonates (Kurta and Kunz 1987).

Unique among mammals, female bats provide their young with milk until they achieve at least 70% of adult (postpartum) body mass and 90% of adult wing dimensions (Kunz and Stern 1995). The high maternal investment and large size at the time of independence of the young may be important factors contributing to the low mortality of bats compared with other small mammals. Whereas in central Europe nearly half of the new-born females of the insectivorous bat *Myotis myotis* survive to breed (Horacek 1985, Zahn 1995) it is only 20 - 30% in the common shrew *Sorex araneaus* (Churchfield 1990). Another reason of the rather low mortality rates of bats is their nocturnal life style combined with their ability to fly which is likely to reduce predation pressure (Speakman 1991).

Furthermore, the ability of bats to fall in torpor where the animals temporarily reduce body temperature, contributes further to the differences in life histories compared with mice (Rodentia, Muridae) or shrews (Insectivora, Soricidae) both of which have a much shorter life-span of about 1 - 2 years and produce large litter size (Wang 1989). Bats reduce their daily energy expenditure (DEE) by becoming torpid not only during hibernation but also during periods of low ambient temperatures and food shortage in summer (Kurta 1990, Audet 1992, Geiser and Ruf 1995). In contrast to bats, shrews are unable to fall in torpor and have to increase metabolic rate and food intake to fuel heat production for maintenance of homeothermy when ambient temperatures are low (Speakman 2000).
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Correlation of food availability and reproduction in bats of the temperate zone

Bats that live in a temperate environment characterized by seasonal changes in climate and fluctuations in food availability require sufficiently high prey availability to satisfy their energy demands, particularly during the expensive reproductive period (Heidemann 2000). Once the development of an embryo has started, bats resemble larger mammals more than smaller mammals as they have long gestation periods and cannot react quickly to short-term environmental fluctuations. It is therefore of importance for bats to optimize timing of reproduction with seasonal changes, particularly with regard to food availability.

Synchronisation of reproduction with high food availability enhances the chances of survival for both, female and young in the temperate zone. Energy and thus food demand of females is highest during gestation and lactation to permit fast growth of the young. This is crucial so that it can rapidly be weaned to give enough time for mother and young, to fatten up for the several month-long hibernation period (Ransome 1968, Thomas et al. 1990). It has been shown for the insectivorous mouse-eared bat Myotis blythii that timing of parturition is mainly determined by food availability (Arlettaz et al. 2001). Reduced food availability for instance because of adverse climatic conditions can lengthen gestation (Racey and Swift 1981) or even lead to abortion (Roer 1962).

Energy demand of female and male bats during reproduction

Adult reproductive female and male bats underlie different physiological requirements throughout the season with regard to reproduction. Maternal investment and thus energy demand of females is highest during pregnancy and lactation (Kurta et al. 1989, McLean and Speakman 2000). This is reflected in a drastic increase in food consumption (Kunz 1974, Anthony and Kunz 1977). Because males are not involved in the development and rearing of the young their energy demand in spring and early summer is lower than that of females. It increases, however, when spermatogenesis starts in mid summer whereas the energy demand of females decreases simultaneously when the young become independent (Heidemann 2000, Speakman and Thomas 2003).

To compensate the high energy demand during reproduction, females form maternity colonies to save energy through social thermoregulation at low ambient temperatures. This strategy
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contributes to the acceleration of foetal growth and later of the young (Kunz 1973, Tuttle 1975, Audet 1992). Furthermore, females in the temperate zone select roosts with favourable temperature conditions to support reproduction (Kerth et al. 2001, Chruszcz and Barclay 2002, Lausen and Barclay 2003).

Whereas our knowledge on strategies of female bats to optimize reproduction is just starting to accumulate, we know even less about males. First evidence suggests that they differ strongly in their behaviour compared to females (Barclay 1991). In contrast to females, male bats mostly live solitarily or in small groups of only 10 - 20 individuals (e.g. Kronwitter 1988, Zahn and Dippel 1997). Because they have no offspring to care for, it has been proposed that males should thus be able to live under harsher conditions in spring and early summer than females, for instance in areas with colder climates and lower insect abundance (Barclay 1991, Güttinger 1994, Grindal, Morissette and Brigham 1999).

A main strategy of both female and male bats to balance their energy demand is the reduction of body temperature by becoming torpid (Coburn and Geiser 1998) when ambient temperatures are low and food availability is reduced. Recently, only few studies have so far linked thermoregulatory behaviour of free-ranging bats to the gender-specific energy requirements during reproduction (Hamilton and Barclay 1994, Grinevitch et al. 1995, Hosken 1997). For a better understanding of the reproductive biology of temperate zone bat species I took a comparative approach in my thesis and analysed thermoregulation, foraging strategies and food intake of sympatric free-ranging female and male Daubentont’s bats, Myotis daubentonii (Vespertilionidae), that preferably forage over water.

Objectives of the thesis, study animal and study area

Balancing the energy demand of reproduction in bats requires specific physiological and behavioural adaptations. Part of my thesis thus focussed on the use of daily torpor in M. daubentonii during colder ambient temperatures and reduced food availability, an aspect that strongly influences foetal development and probably also spermatogenesis but that has been little studied to date for free-ranging bats (Willis and Brigham 2003). This also applies for a detailed knowledge about food intake and foraging behaviour of female and male bats during different reproductive periods. I selected the insectivorous Daubenton’s bat as study species because it is rather common and its characteristic flight low over water surfaces facilitates
identification and observations of its feeding behaviour in the field. *Myotis daubentonii* is widely distributed in the Palaeartic region throughout Europe and Asia and ranges in a narrow band from Britain, France and the Iberian Peninsula to the Pacific coast and the northern islands of Japan (Mitchell-Jones *et al.* 1999). Daubenton’s bats mainly occur in landscapes with streams, ponds, and lakes. It is small with a mass of only 7 - 15 g, a wingspan of 240 - 275 mm and characteristic large feet (Roer and Schober 2001).

As all other insectivorous bats in the temperate zone, Daubenton’s bat shows a distinct reproductive periodicity that is thought to mainly follow seasonal variations in food availability. In my study area in Central Germany (Hessen), Daubenton’s bats arrive at the end of March at their feeding grounds where they also reproduce and depart to their hibernacula from mid-September until the end of October. Banded bats from my study area were found in hibernacula in several old mines at distances of about 12 - 42 km from their summer habitat. Females give birth in the first week of June and the young become volant in early July (Dietz and Fitzenräuter 1996). Mating season starts at the beginning of August when sperm production peaks and females are in oestrus (Encarnação *et al.* 2004).

The study took place from 1992 - 2003 near the City of Giessen next to the river Lahn. The study area encompasses the river Lahn and the surrounding lowlands that are used in part by intensive agriculture and in part covered with mixed deciduous forest. Nursery colonies of *M. daubentonii* were found in tree roosts including the “Philosopher’s Forest” within the city of Giessen, a small (20 ha) deciduous forest with old growth oaks and beeches. Feeding sites of Daubenton’s bats consisted of ponds and the river Lahn (Dietz and Fitzenräuter 1996, Dietz 1998).

**Hypotheses and results**

My thesis is structured in four chapters, each representing a separate publication. One chapter has already been published (chapter 1), the other three have been *submitted* (chapter 2, 3 and 4).

In **chapter 1** I analysed to which degree reproductive female and male Daubenton’s bats use daily torpor to reduce daily energy expenditure. Daily torpor can provide significant energy and water savings in bats during cold ambient temperatures and food scarcity (Speakman and
Thomas 2003). Recent studies in free-ranging Nearctic bats, particularly in *Eptesicus fuscus* (Audet and Fenton 1988, Grinevitch *et al.* 1995, Hamilton and Barclay 1994, Lausen and Barclay 2003), *Lasiurus cinereus* (Hickey and Fenton 1996), and *Myotis evotis* (Chruszcz and Barclay 2002) have shown that pregnant and lactating females partly use daily torpor in relation to fluctuating food supply induced by low ambient temperatures.

However, usage of daily torpor leads to an evident dilemma for breeding females, because foetal development and milk production decrease with lower body temperatures (Eisentraut 1937, Racey and Swift 1981, Wilde *et al.* 1995, 1999). This has been proposed also for spermatogenesis in males that might be delayed by daily torpor (Entwistle *et al.* 1998).

Therefore I hypothesized that females and males should differ in the use of torpor depending on reproductive condition. Breeding female bats should minimize their use of torpor during pregnancy and lactation whereas male bats at the same time could use torpor to reduce energy expenditure because they have no offspring to care for. In contrast, thermoregulatory behaviour of males should change accordingly in mid summer, when sperm production starts whereas post-lactating females could afford daily torpor to reduce energy expenditure.

To test these assumptions, I investigated the use of torpor in 6 female and 5 male free-ranging *Myotis daubentonii* during reproduction (gestation, lactation, and post-lactation period) with the help of temperature-sensitive radio transmitters that were attached between the shoulder-blades of free-ranging bats to measure skin temperature continuously.

While both sexes became torpid during day time, male bats used daily torpor significantly more often during spring and early summer (pregnancy and lactation period) than females. Female bats fell in daily torpor particularly in late summer when the young had been weaned. There was a significant effect of reproductive period on skin temperature in females whereas mean ambient temperature had no significant effect. However, mean ambient temperature affected mean skin temperatures in males during spring and early summer before spermatogenesis started.

The results of my study support the hypothesis that thermoregulatory behaviour of female and male Daubenton’s bats differs in relation to the reproductive status. It is likely that female Daubenton’s bats avoid torpor during pregnancy and lactation to optimize foetal development and development of the young. This assumption is reasonable because it has been shown that development of the young is strongly delayed with decreasing body temperature (McNab
Summary

1982). Furthermore, production and secretion of milk are also reduced at lower body temperatures (Wilde et al. 1999). The reduction of the usage of daily torpor during spermatogenesis in males is in line with the physiological requirements that are needed to optimize sperm production (Entwistle et al. 1998).

As a consequence of higher energy demands associated with maintenance of homoeothermic body conditions during pregnancy, lactation and spermatogenesis, intake of food should increase accordingly leading to distinct differences in flight activity between female and male bats. In chapter 2 I therefore assessed the variations in flight activity between females and males as well as within the sexes during the different reproductive periods. I expected that the foraging activity of males should be reduced in the first half of summer because their energy demand is likely to be much lower than that of the reproductively active females during the same time. In contrast, pregnant and lactating females should optimize their foraging strategy by using small, highly profitable and individual foraging areas. Furthermore, total foraging time should be longer in females than in males during this period to increase food intake. In contrast, because energy demand of male bats increases with the onset of sperm production (Racey and Tam 1974) this should result in longer foraging times for males in mid and late summer. I tested the assumptions with 16 adult females and 13 males of free-ranging Myotis daubentonii that were radio-tracked during pregnancy, lactation and post-lactation period.

Overall, average nightly flight time of females was comparable to that of males. Classification into the different reproductive periods revealed that pregnant females flew, as hypothesized, significantly longer than males during spring with nightly flight times of about six hours. Surprisingly, nightly flight time of lactating females decreased and was significantly lower than that of pregnant females but similar to that of males at the same period. Lactating females showed a bimodal activity pattern in contrast to an unimodal pattern during pregnancy and post-lactation period. They returned to the day roost once or twice, presumably to suckle their young. In mid and late summer flight activity of the females was significantly lower than during pregnancy in contrast to the males that showed long flight times as spermatogenesis had set in at this time of the year.

Ambient temperature had no notable influence on flight activity of Daubenton’s bats. However, there were distinct differences in the use of foraging areas between female and male M. daubentonii. Male bats in general tended to switch foraging areas more often during the
night than reproductive females. In contrast, females displayed a very high constancy in the use of small (< 1200 m²) foraging areas.

The results confirmed the initial proposition that flight activity of female and male Daubenton’s bats should differ in relation to reproductive period. The differences reflect the higher energy demand and nutrition requirements during the different reproductive periods for females during pregnancy and males during spermatogenesis. The results are supported further by the data from chapter 1 where I showed that females and males avoid torpor during the respective reproductive periods, probably because low body temperatures may impede foetal and juvenile development as well as spermatogenesis (Kurta and Kunz 1988, Dietz and Kalko 2005). As maintenance of higher body temperatures incurs higher energy costs, longer flights permit an increase in food intake. The shorter flight times of lactating females compared with pregnant females were at first glance surprising but they make sense as the females have to return to the young to suckle them. Moreover, total foraging time is also limited by shorter night length during this part of the year. Perhaps female Daubenton’s bats deposit surplus fat during pregnancy, which would allow them to sustain the energy demanding lactation period without an increase in flight time.

In chapter 3 I estimated food intake and ingested energy of female and male Daubenton’s bats during pregnancy and spermatogenesis based on the assumption that flight time in Daubenton’s bats over water is equivalent to foraging time. Consequently, foraging time should correlate with food intake. I expected that the differences in energy demand of reproductive females and males during the period of pregnancy and spermatogenesis should be reflected in differences in foraging time.

The estimation of food intake is based on radio-tracking results from foraging times of 14 female and 22 male bats and counts of capture attempts during foraging flights of free-ranging *M. daubentonii* marked with chemiluminescent light-sticks. Capture attempts were derived from the characteristic flight behaviour of *M. daubentonii* close to the water surface with pronounced up- and downward swoops during capture attempts that correspond to high and low catches as described by Kalko and Schnitzler (1989). Because *M. daubentonii* feeds almost exclusively on aquatic insects, primarily Chironomidae (Sullivan *et al.* 1993, Beck 1995, Vaughan 1997), the caloric content of Chironomidae collected at the study area was determined to get an estimation on ingested energy. Food intake was calculated based on two capture success rates (50 % and 92%) derived from data published for the ecological similar

In accordance to the results in chapter 2 females spent significantly more time foraging than males during pregnancy period. In contrast, during the period of spermatogenetic activity males foraged significantly longer than in spring and also significantly longer than post-lactating females. Prey attack rates per minute did not vary significantly between sexes and reproductive periods. Mean prey attack rate calculated over both periods and sexes was 8.3 (SD = 4.3) prey attacks per minute. Calculated food intake values based on a capture success rate of 92 % were more in line with literature data for other insectivorous bats than values calculated assuming a capture success rate of only 50 %.

The findings support also the hypothesis that food intake of female and male Daubenton’s bats depends on reproductive period. Food intake of male Daubenton’s bats is highest during peak spermatogenesis in mid summer and equals that of pregnant females in spring. The food intake of females during post-lactation as well as that of males during spring is considerably lower. Overall, the results of the study strongly suggest that Daubenton’s bats exploit insect availability with a high success of about 90 % to cover their energy demand. The results further suggest that reproductive active females during pregnancy and lactation and males during spermatogenesis require feeding sites with a high density of small and soft insects to optimize food intake.

Foraging sites like ponds and rivers are favourable feeding sites for bats as they provide high insect densities during the active time of bats (Taafe 1992, de Jong 1994, Grindal et al. 1999, Warren et al. 2000). As shown in chapter 3 Daubenton’s bats depend on the quality and quantity of foraging grounds for successful reproduction. This suggests a positive correlation between distribution and relative abundance of Daubenton’s bats with the amount of water surface on the landscape level. In chapter 4 I therefore analysed the distribution and relative abundance of foraging Daubenton’s bats at water bodies in the lowlands and in the surrounding uplands of my study area. I further expected an unequal distribution of female and male Daubenton’s bats especially during the energy expensive pregnancy and lactation period of females (see Leuzinger and Brossard 1994, Russo 2002). I assumed that it must be a positive correlation of the amount of feeding sites and the distribution of nursery colonies because the local concentration of pregnant and lactating females requires resource-rich feeding grounds to cover the high energy demands of the individuals.
Summary

I employed three methods to assess bat distribution and densities. Presence of Daubenton’s bats at ponds, lakes and the river Lahn was determined with standardized nightly spotlight counts. Further, the relative abundance and sex ratio of females and males were analysed by mist-netting along regularly used flight paths. Finally, nursery colonies and flight distances of females were assessed by radio-tracking.

Daubenton’s bats were present in most of the surveyed area with water bodies. The number of bats correlated positively with the area of the water surface and negatively with the distance to the nursery colonies. Nursery colonies were predominately located in the lowlands close to the river Lahn. The number of female and male *M. daubentonii* was unequal and differed significantly between the three sites where relative abundance was studied in greater detail. In the lowland I found one site clearly dominated by females and a second site with an almost balanced sex ratio. At the third site in the low mountain range, males clearly outnumbered females. These sex ratios remained largely unchanged from spring to mid summer and changed at the beginning of September when adult females left the study sites in the lowlands.

My findings support the association between the distribution of Daubenton’s bats and the amount of water surface on the landscape level. Similar patterns have also been found for Daubenton’s bats in Switzerland (Moeschler and Ruedi 1995). The main factor determining this relationship is probably higher food availability in relation to larger surface areas of still water bodies. Furthermore, larger water surfaces offer more potential foraging areas for a higher number of bats. Thus it is reasonable to assume that there is a strong link between the number of foraging bats, the overall area of water surface and the proximity of nursery roosts.

As expected, the results also confirm the assumption that the distribution of male Daubenton’s bats differs from females especially during pregnancy and lactation period whereby the males use areas with lower food supply and lower ambient temperatures. These findings are in accordance to observations on Daubenton’s bats from higher mountain regions like the Bernese Jura Mountains in Switzerland (Leuzinger and Brossard 1994), the high Abruzzo mountains in central Italy (Russo 2002) and the Yorkshire Dales in the UK (Senior *et al.* 2005).
General conclusion

To conclude, the results of my thesis confirmed the proposed gender-specific, seasonal differences in foraging behaviour and habitat use of the study species *Myotis daubentonii* in relation to the energy-demanding reproductive periods. Physiological adaptations include the use of torpor. Both, female and male Daubenton’s bats only went into torpor during periods where they did not have to maintain high body temperatures to either foster the development of the foetus and subsequently the young in females or spermatogenesis in males. As I did not find a significant correlation between torpor and ambient temperature throughout the breeding season, it must be under active control of the bats in relation to their reproductive condition.

The higher costs of homeothermy especially during reproductive periods require a higher food intake. This resulted as predicted in higher foraging activities. Furthermore, females displayed a high constancy in the use of individual resource rich foraging areas over water where they mainly feed on swarming and soft insects. Foraging activity of Daubenton’s bat was not affected by air temperature. This is probably due to the buffer capacities of larger water bodies with regard to temperature that leads to higher temperatures just above the water surface and consequently to higher insect activity at ponds and rivers thus providing rich resources. This, in turn, permits high attack rates of the bats also at lower ambient temperatures compared to open landscapes or woodlands. In contrast, foraging activity of several aerial hawking bat species of the genus *Eptesicus*, *Nyctalus* or *Pipistrellus*, that mainly feed in open space decreases markedly at air temperatures below 10°C (Racey and Swift 1985, Audet and Fenton 1988, Sheal and Fairley 1998). Presumably due to reduced insect activity in open space at low ambient temperatures, both, males and females of these species fall in torpor when resource availability is low even during reproduction. Assuming that *Myotis daubentonii* feeds more successfully during low ambient temperatures compared to other species because of the higher food availability above the water surface, this may compensate for the energy required to continuously maintain high body temperature during reproductive periods.

Another aspect of the reproduction strategy of *M. daubentonii* is the unequal distribution of female and male Daubenton’s bats in the landscape (see also Senior *et al* 2005). The gender-specific distribution may be a form of resource partitioning through small scale geographic separation that has been suggested also for other bat species (Humphrey and Cope 1976, Barclay 1991). It is further likely that in order to secure sufficient food intake females become
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territorial during pregnancy and lactation (Wallin 1961, Barclay 1984, Rydell 1986, Balcombe and Fenton 1988) whereas males appear to cope well with harsher conditions during pregnancy and lactation period because they have no offspring to care for.

Implications for bat conservation strategies

Worldwide, bats are among the most endangered groups of mammals as they are strongly affected by habitat loss and degradation, pesticides and persecution (Racey and Entwistle 2003). All of the bat species in Europe are listed in Annex IV of the Habitat Directive (European Council Directive 92/43/EEC) for strict protection. Conservation-oriented research is urgently needed particularly with regard to the two paradigms of conservation ecology (Caughley 1994): the small-population paradigm that deals with the risk of extinction for species which are either low in numbers or rare or both, and the declining-population paradigm that is concerned with the external factors that lead to population decline in bats.

The results of my thesis show convincingly that the development and establishment of meaningful conservation measures require detailed monitoring data that go beyond mere distribution data of a species as areas need to be differentiated according to the role they play for females and males during reproduction. Whereas the importance of nursery sites has already been recognized quite a while ago, we hardly know anything about the numbers, locality and function of male dominated areas. This lack of knowledge goes far beyond M. daubentonii and includes all other European bat species. It is thus necessary to identify and monitor key habitats and to assess their functions, including favourable roost sites (e.g. in old growth forests) and foraging habitats with high prey densities as both strongly influence the reproductive success of female bats. Habitat quality and food supply in particular affect the distribution of sexes of bats, reproduction rate, as well as size, number and distribution of nursery colonies (Speakman et al. 1991). Therefore, to comply with the paradigms of conservation ecology, standardized, long-term population monitoring needs to be developed for areas that play crucial roles for bat reproduction. Estimations of relative abundance (population density) and colony size for bats are challenging but constitute essential elements for reliable assessments of the conservation status and provide baselines crucial for the identification of any future population decline (Racey and Entwistle 2003).
Publication of the results of this thesis and contributions from other scientists

My thesis is structured in four chapters, each representing a separate paper with its own database. One chapter has already been published (chapter 1), the other three have been submitted (chapter 2, 3 and 4) to a scientific journal with the following authorship:

**Chapter 1:** Dietz M, Kalko EKV, *published in Journal of Comparative Physiology B*

Prof. Dr. Elisabeth K.V. Kalko will be co-author in this and two other publications (chapter 2 and 4) which will arise from this thesis. She gave many excellent contributions to the manuscripts and shared her extensive experience and knowledge about bats with me.

**Chapter 2:** Dietz M, Kalko EKV, *submitted to Journal of Zoology*

**Chapter 3:** Encarnação JA, Dietz M, *submitted to Journal of Animal Ecology*

For this chapter I analysed a part of my data collection from radio-tracking (n = 13 ♀♀ and 10 ♂♂), prey-attack-rate and food intake and pooled it with data from Jorge A. Encarnação. He contributed radio-tracking Data (1 ♀♀ and 12 ♂♂), light-stick observations and analysed the caloric content of chironomides in the laboratory.

**Chapter 4:** Dietz M, Encarnação JA, Kalko EKV, *submitted to Acta Chiropterologica*

J.A. Encarnação will be co-author of this publication arising from chapter 4 because he was helpful in the very time intensive data collecting (spot-light countings, mist-netting, radio-tracking) and contributed to the interpretation of the findings.
ZUSAMMENFASSUNG

EINFLUSS DER REPRODUKTION AUF THERMOREGULATION, NAHRUNGSAUFNAHME UND FORAGIERSTRATEGIE BEI WEIBLICHEN UND MÄNNLICHEN WASSERFLEDERMÄUSEN MYOTIS DAUBENTONII (VESPERTILIONIDAE)

Die Ordnung der Fledertiere (Chiroptera) ist die zweitgrößte Säugetiergruppe und wird in ihrer Artenvielfalt nur noch von den Nagetieren (Rodentia) übertroffen. Im Gegensatz zu diesen und anderen kleinen Säugern wie Spitzmäusen (Insectivora, Soricidae) zeigen Fledermäuse jedoch eine erstaunliche Fülle an Lebenszyklus- und Reproduktionsstrategien, die in ihren Grundzügen eher mit großen als mit kleinen Säugetieren vergleichbar sind (Barclay und Harder 2003). Während für Kleinsäuger im Allgemeinen eine kurze Lebensphase von 1 - 2 Jahren, eine frühe Fertilität und eine hohe Reproduktions- und Mortalitätsrate charakteristisch ist, zeigen große Säugetiere entgegengesetzte Strategien und haben meist wenig Nachwuchs bei vergleichsweise geringer Mortalität und höherer Lebenserwartung. Einen wesentlichen Einfluss auf die Lebenszyklus- und Reproduktionsstrategie eines Säugetieres haben dabei die Körpergröße und die Körpertemperatur, wobei tendenziell kleine Säugetiere ein ungünstigeres Verhältnis der Körperfläche zu Körpervolumen und Masse aufweisen und dadurch relativ mehr Wärme über den Körper verlieren als große Säugetiere (Speakman 2000). Das Besondere an Fledermäusen ist nun, dass sie trotz der geringen Körpergröße eine sehr lange Lebensdauer erreichen, die 20 Jahre und mehr betragen kann, artspezifisch höchstens 1 - 2 Jungtiere pro Weibchen und Jahr geboren werden und die Mortalitätsrate verglichen mit anderen Kleinsäugern gering ist.

Neben reproduktionsbiologischen Besonderheiten, wie der verzögerten Fertilität (Racey und Entwistle 2000), und physiologischen Anpassungen, wie die Fähigkeit zur Absenkung der Körpertemperatur während ungünstiger klimatischer Bedingungen und Nahrungsmangel (Kurta 1990, Audet 1992, Geiser und Ruf 1995), die in Extremjahren auch zum Abort führen


Zusammenfassung


Meine Dissertationsschrift ist in eine allgemeine Einführung des Themas einschließlich einer Zusammenfassung und Diskussion der Ergebnisse gegliedert und enthält vier Kapitel, die jeweils für sich als eigenständige Publikation konzipiert und teilweise bereits veröffentlicht (Kapitel 1) bzw. eingereicht sind (Kapitel 2, 3 und 4).


Es wäre demnach zu erwarten, dass im Hinblick auf eine Optimierung des Reproduktionserfolges die Weibchen während der Schwangerschaft und Laktation Torporphasen möglichst vermieden werden sollten. Dies gilt ebenso für die Männchen während der Periode der intensiven Spermatogense. Um diese Hypothese zu testen, wurden sechs Weibchen und fünf Männchen während der unterschiedlichen Reproduktionsperioden (Schwangerschaft, Laktation und Postlaktation, letztere deckt sich weitgehend mit der Phase der Spermatogense) mit temperatursensitiven Transmittern ausgestattet und weitgehend lückenlos für 3 - 5 Tage und Nächte verfolgt, so dass für jede Stunde Messwerte der Körperoberflächentemperatur vorlagen.


Ohne nach Reproduktionsphasen zu differenzieren, ergab sich zunächst eine vergleichbare mittlere Flugaktivität pro Nacht für Weibchen und Männchen, die zwischen kaum mehr als einer Stunde und maximal acht Stunden lag. Differenziert nach den Reproduktionsphasen zeigten sich innerhalb der Geschlechter jedoch deutlich geringere Schwankungen der Flugaktivität und wie vermutet bei schwangeren Weibchen im Frühjahr signifikant längere Flugphasen als bei den Männchen.
Im Gegensatz zu den Erwartungen war die Flugzeit der laktierenden Weibchen allerdings signifikant geringer als die der schwangeren Weibchen und erreichte Werte, die mit der Flugaktivität der Männchen in dieser Periode vergleichbar waren. Auffällig war, dass die laktierenden Weibchen im Gegensatz zu den anderen Reproduktionsphasen eine ausgeprägt bimodale Flugaktivität aufwiesen und nach den ersten beiden Flugstunden in das Tagesquartier zurückkehrten, wo sie vermutlich ihre Jungtiere säugten, bevor sie erneut auszogen.

Im Mitt- und Spätsommer entsprach die Flugaktivität der Weibchen nach dem Flüggewerden der Jungtiere den Zeiten während der Laktation und war damit signifikant geringer als während der Schwangerschaft. Die Männchen dagegen zeigten in dieser Phase, die der höchsten Spermienproduktion entsprach, die längsten Flugzeiten. Ein Einfluss der Lufttemperatur auf die Flugaktivität der Wasserfledermäuse war nicht festzustellen.


Zusammenfassung

telemetrischen Bestimmung der Flugzeiten umfasste 14 reproductive Weibchen und 22 Männchen von zwei verschiedenen Untersuchungsorten im Untersuchungsgebiet. Die Quantifizierung der Beutefanghandlungen einzelner Fledermäuse erfolgte durch die Markierung der vorher gefangenen und anschließend identifizierten Individuen mit kleinen Leuchtstäbchen, die im Rückenfell mit Kleber fixiert wurden. Da Wasserfledermäuse fast ausschließlich Zuckmücken (Chironomidae) fangen, wurde neben dem Frisch- und Trockengewicht der Zuckmücken mit Hilfe eines kalorimetrischen Verfahrens (adiabatic bomb calorimetry) deren Energiegehalt bestimmt, um die pro Nacht aufgenommene Nahrungsmenge und Energie zu berechnen.

Bemerkenswert ist, dass sich die Anzahl der Beutefanghandlungen weder zwischen den Geschlechtern noch zwischen den Reproduktionsphasen unterschied, so dass sich insgesamt eine mittlere Anzahl von 8,3 (SD = 4,3, 0 - 20,8) Fanghandlungen pro Minute errechnen ließ. Die Menge der pro Nacht aufgenommenen Insekten ergibt sich dann aus der mittleren Anzahl der Fanghandlungen, einer zugrundgelegten Erfolgsquote von 50 % (nach Gould 1955, 1959) und 92 % (nach Rydell et al. 1992) sowie den mittleren nächtlichen Flugzeiten.


Aufgrund der engen Bindung der Wasserfledermäusen an Gewässer untersuchte ich in Kapitel 4, ob es eine positive Korrelation zwischen der Verbreitung und relativen Häufigkeit von Wasserfledermäusen und der Verteilung und Menge der verfügbaren Wasseroberfläche in meinem Untersuchungsgebiet gibt. Aus diesem Grund untersuchte ich die Verbreitung und
Zusammenfassung


Schlußfolgerung: Die Studie verdeutlichte einige bislang unbekannte Aspekte des Temperatur- und Foragierverhaltens der Wasserfledermaus im Hinblick auf die Vermutung, dass es bestimmte physiologische und verhaltensökologische Mechanismen gibt, die eine optimale Reproduktion während des vergleichsweise kurzen Jahresabschnitts mit hoher Nahrungsdichte fördern.

Weibchen wie Männer setzen die Fähigkeit der Thermoregulation je nach den Erfordernissen des Reproduktionszyklus ein. Torporphasen werden aktiv und in weiten
Zusammenfassung


Als weiterer wichtiger Punkt für die Reproduktion deutet sich die partielle räumliche Segregation der Geschlechter insbesondere während der nahrungsintensiven Schwangerschafts- und Laktationsphase an. Hier wäre zukünftig vertiefend zu untersuchen, ob die Segregation eine Form der innerartlichen Ressourcenaufteilung ist, die unter anderem auf einem territorialen Verhalten der Weibchen während der Schwangerschaft und Laktation aufbaut.

Neben den reproduktionsbiologischen Erkenntnissen verdeutlicht die Studie, dass zukünftige Schutzstrategien und Monitoringprogramme für Fledermäuse noch viel stärker als bisher auf einer genauen Kenntnis der Verteilung der Reproduktionszentren (Weibchen in Wochenstubenkolonien) und Männchengebiete aufbauen müssen. Der Erhalt hochproduktiver Nahrungsgebiete als Schlüsselhabitate für die Reproduktion muss eine viel stärkere Berücksichtigung als bisher finden.
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Colour plate I. The study took place in Hessen (Central Germany) and the study area encompasses the river Lahn next to the city of Giessen and the surrounding lowlands that are in part used by intensive agriculture and in part covered with mixed deciduous forest. A main part of the study area was the “Philosopher’s Forest” (PhF) at the border of the city of Giessen, the “Swan Pond” (SW), “New Pond” (NP) and the section of the river Lahn (L).
Colour plate II. The “Philosopher’s Forest” (a) is a small but favourable roosting site for *Myotis daubentonii* at the border of the city of Giessen. We found more than 500 tree holes in old grown beeches and oakes (b) concentrated of about 20 ha. I found the nursery colony of *M. daubentonii* predominate in wood-pecker holes (c). Colony structure in roosts was confirmed by catching emerging bats in the evening with custom-made funnel-shaped basket traps (d). After emergence Daubenton’s bats regularly used a flight-path along a tree-lined way (e, f) between roosting site and foraging ground.

(a, b, d – f: © Thomas Stephan; c: © Marko König).
 Colour plate III. *Myotis daubentoni* is characterized by a comparable short tragus (a), large feet and long calcars (b., typical for trawling bats) and a white fur ventral (c). To fall in torpor (d) is a strategy to save energy. Mist-netting (e) and radio-tracking (f) were important methods to gain data in my thesis. (a – d, f: © Thomas Stephan; e: © Jeroen van der Kooij).
“Trawling bats” like *Myotis daubentonii* prefer to forage over calm and open water (a). Daubenton’s bats catch emerging and swarming insects close to the water surface (b). With the help of chemiluminescent light-sticks fixed on the fur of the bats I counted prey attack rates (c). They mostly feed on *Chironomidae* (d) at the feeding grounds in my study area like the “Swan Pond” (e) and the river Lahn (f). (a: © Marko König, b – d: © Thomas Stephan, e, f: © Markus Dietz).
SEASONAL CHANGES IN DAILY TORPOR PATTERNS OF FREE-RANGING FEMALE AND MALE DAUBENTON’S BATS (*MYOTIS DAUBENTONII*)

1 ABSTRACT

Daily torpor can provide significant energy and water savings in bats during cold ambient temperatures and food scarcity. However, it may reduce rates of fetal and juvenile development. Therefore, reproductive females should optimize development by minimizing times in torpor. To test this hypothesis, the use of torpor by female and male free-ranging Daubenton’s bats (*Myotis daubentonii*) during reproduction (gestation, lactation, and post-lactation period) was investigated in 1998 and 1999. Temperature-sensitive radio transmitters were attached to the bats to measure skin temperature. Simultaneously, ambient temperature was recorded. While both sexes became torpid during day time, male bats used daily torpor (> 6 °C below individual active temperature) significantly more often during reproductive period (mean: 78.4 % of day time in May and 43 % in June) than females. Female bats went into daily torpor particularly in late summer when juveniles were weaned (mean: 66.6 % of daytime). Lowest skin temperatures occurred in a female bat with 21.0 °C during post-lactation. Skin temperatures of male bats fluctuated from 16.8 °C in torpor to 37.2 °C during times of activity. There was a significant effect of reproductive period on skin temperature in females whereas mean ambient temperature had no significant effect. However, mean ambient temperature affected mean skin temperatures in males. Our findings indicate that female Daubenton’s bats adopt their thermoregulatory behaviour in particular to optimize the juvenile development.

2 INTRODUCTION

Bats occurring in temperate zones are subject to a strong reproductive periodicity reflecting seasonal variations in food supply. They hibernate in deep torpor and give birth in summer.
Chapter 1 – *Myotis daubentonii*

when insect availability is highest (e.g. Racey and Swift 1985, Rydell 1992, Hickey and Fenton 1996). In most temperate zones, vespertilionid bats mate in late summer and early autumn when sperm production reaches a peak and females are in oestrus (Encarnação et al. 2004, Racey and Tam 1974). After mating, sperm is stored in the oviduct throughout the winter (Racey 1973). Pregnancy starts immediately after fertilisation following hibernation. During pregnancy and lactation, energy demand of females grows continuously (Kurta et al. 1989, McLean and Speakman 2000). This is reflected in higher food consumption by lactating females that increases for example by about 45 % in *Myotis lucifugus* (Anthony and Kunz 1977) and *Myotis velifer* (Kunz 1974) from pregnancy to lactation. Food availability dictates timing of parturition as shown by Arlettaz et al. (2001) for the insectivorous mouse-eared bat *Myotis blythii*.

When food availability is low at low ambient temperatures, bats in the temperate zone become torpid during day time in summer to reduce daily energy expenditure (DEE) (Kurta 1990, Hosken 1997, Coburn and Geiser 1998). Such torpor patterns as a reaction of low ambient temperatures and fluctuating food supply are also known for other small mammals like lemurs (Schmid et al. 2000, Schmid 2000) and hedgehogs (Fowler 1988) as well as for birds (e.g. Prinzinger et al. 1981, Körtner et al. 2001). However, breeding females of mammals face an obvious dilemma, because milk production is less during torpor. This may considerably slow down fetal development and postnatal growth (Eisentraut 1937, Racey and Swift 1981, Wilde et al. 1995, 1999). Because of the brief gestation and the particularly short lactation period at temperate latitudes, a delay of the development of juvenile bats reduces their time to prepare for hibernation. It is therefore crucial that yearlings deposit enough fat reserves in late summer to survive the winter (Ransome 1968, Thomas et al. 1990).

So we assume that breeding female bats optimize progress of reproduction by minimizing use of torpor during pregnancy and lactation. However, current knowledge about thermoregulatory strategies of free-ranging bats during reproductive season is scarce and limited to a few Nearctic bats, in particularly to *Eptesicus fuscus* (Audet and Fenton 1988, Hamilton and Barclay 1994, Grinevitch et al. 1995, Lausen and Barclay 2003), *Lasiurus cinereus* (Hickey and Fenton 1996), and *Myotis evotis* (Chruszcz and Barclay 2002). Furthermore, skin temperature as a measure of torpor was mainly measured while the bats were in the roost but not during foraging. The purpose of this study was to investigate thermoregulatory behaviour of female and male Daubenton’s bats (*Myotis daubentonii*) during pregnancy, lactation, and post-lactation period.
We hypothesised that in order to optimize fetal development and milk production, females should maintain a constantly high body temperature during pregnancy and lactation as long as possible while deep daily torpor would be used predominantly in the post-lactation period. We expected that ambient temperatures would affect thermoregulation of reproductive active females less than actual reproductive condition. In contrast, adult male *M. daubentonii* that are not reproductive active during early summer might be expected to react more strongly to ambient temperatures by reducing body temperature more often especially at low ambient temperatures during pregnancy and parturition, because they are not involved in the development and rearing of the young. However, as sperm production starts in late summer, thermoregulatory behaviour of the males should change accordingly.

**MATERIALS AND METHODS**

**Study area and animals**

We radio-tracked 6 adult females and 5 adult males of *Myotis daubentonii* during 1998 and 1999 (Table 1). The females belong to a maternity colony in the “Philosopher-Forest”, a small deciduous forest in the city of Gießen in central Germany. Males and females live in the same place and both roost in tree holes of *Fagus sylvatica*, *Quercus robur*, and *Fraxinus excelsior*. The bats flew to their feeding grounds along a traditional flight-path. The feeding grounds consisted of two ponds at a distance of a few hundred meters to the roost, and the river Lahn at a distance of 2.5 km (Dietz and Fitzenräuter 1996). Population structure and feeding ecology of the Daubenton’s bats in the “Philosopher-Forest” have been investigated since 1992; therefore seasonality and habitat use are well known. We caught bats with mist nets set in their flight-path or at their roosts to attach radio-transmitters. The age of the bats was determined by evaluating the closure of the epiphysis (Anthony 1988) and by subsequent banding. The reproductive status was classified as pregnant, non-pregnant, lactating, and post-lactating according to the methods described by Racey (1988). Pregnancy was assessed by palpation of the abdomen directly after the emergence of the bats. A bare patch around the nipples and milk expression were used as evidence for lactation. The onset and progression of spermatogenesis in males was assessed by the size of the testes and the distension of the epididymis.
Table 1. Summary of radio-tracking data of 11 individuals of *Myotis daubentonii* sampled in central Germany during 1998 and 1999. Shown are ring number of the bat, gender (F = female, M = male), age (ad = adult), mass in grams, reproductive status of the females (preg = pregnant; lac = lactating; post-lac = post-lactating) and males (epididymal filling in %), tracking period (half of month/month of the year), recorded bat days and nights, and hourly recordings of averaged temperature measurements.

<table>
<thead>
<tr>
<th>Bat (Ring no.)</th>
<th>Sex</th>
<th>Age</th>
<th>Mass [g]</th>
<th>Reprod. Status</th>
<th>Tracking Period</th>
<th>Recorded Bat days</th>
<th>Recorded Bat nights</th>
<th>Hourly Recordings</th>
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<td>F</td>
<td>ad</td>
<td>10.7</td>
<td>preg</td>
<td>2/V</td>
<td>5</td>
<td>5</td>
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<td>F</td>
<td>ad</td>
<td>11.3</td>
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<td>M</td>
<td>ad</td>
<td>7.1</td>
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<td>5</td>
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<tr>
<td>M19545</td>
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<td>ad</td>
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<td>F</td>
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<td>120</td>
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<td>lac</td>
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<td>2/VIII</td>
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<tr>
<td>M16021</td>
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<td>ad</td>
<td>9.5</td>
<td>75 %</td>
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<td>F</td>
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<td>3</td>
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<td></td>
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<td>45</td>
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</table>

Telemetry

We used LB-2T temperature-sensitive radio-transmitters (Holohil Systems, Canada) with a weight of 0.5 g for tagging bats. The bats weighed between 7.1 - 10.7 g so that the transmitter corresponded to 4.6 - 6.8 % of their body weight which was slightly below and in a few cases slightly above the 5 % that is suggested for radio-tracking studies (see Aldridge and Brigham 1988). All transmitters were attached between the shoulder blades of the bats with Skin-Bond® (Smith & Nephew) to study skin temperature and torpor behaviour (Barclay et al. 1996). The transmitters fell off after 3 - 8 days. During this time we monitored the bats continuously by “homing-in-on-the-animal” (White and Garrott 1990) with the help of 2-element Yagi antennae and Yaesu receivers (FT-290RII) modified by Wagener, Cologne (Germany). Pulse repetition rate of the transmitters was measured 1 - 4 times per hour as long as the transmitter stayed on the bat to determine skin temperature. The pulses for three 1-minute sets were counted, and then the average of the values was determined and finally
compared with a calibration curve provided by the manufacturer. Usually, we tagged 2 - 3 bats simultaneously and monitored them with two or three observer-groups. For this study, our total sample was 1114 recorded hours distributed over 45.5 bat days and 43 bat nights. Daily ambient temperature (mean, min and max; resolution 1/10 °C) was taken from records of a station of the German Weather Service near the “Philosopher-Forest”.

The usefulness of temperature-sensitive transmitters for measuring skin temperatures of bats in the field was first demonstrated by Audet and Thomas (1996). They found that externally attached transmitters accurately reflected core temperature. The difference between measured skin and body temperature was linearly correlated with ambient temperature (Ta), but they also found differences as high as 6 °C at relatively high Ta (> 21 °C). Barclay et al. (1996) confirmed that the readings were only slightly affected by Ta. Their study revealed that skin temperature was within 2.0 °C of rectal temperature in 35 out of 44 measurements with a maximum deviation of only 3.3 °C. Willis and Brigham (2003) also showed that core body temperature is slightly higher than Ts because external transmitters were cooled by lower ambient temperatures. In our study we sometimes measured a decline of 2 - 3 °C in skin temperature for a short time when the bats emerged from their roost. This may be the influence of the cooler ambient temperature on the sensor when the bats started to fly. However, overall differences between the last Ts value measured in the roost before departure and the first value after leaving the roost were not significant (Wilcoxon Signed Rank Test, p = 0.88).

**Definitions**

“Active temperature” refers to the average skin temperature of a bat when it leaves the roost. We based our values of active temperature on temperature measurements taken about 15 min before emergence. Definition of torpor is controversial and many definitions have been proposed in different studies (Barclay et al. 2001, Geiser and Ruf 1995). We refer to Hamilton and Barclay (1994) and Grinevitch et al. (1995) for definition of daily torpor to permit direct comparison of our data with other studies on bats. As recently reviewed by Willis and Brigham (2003) differences as high as 6 °C have been observed between skin temperature and core body temperature influenced by ambient temperatures. So we defined that torpor occurs when skin temperature drops more than 6 °C below active temperature.
We further defined bat day and bat night to compare differences in thermoregulation. A “bat day” started at 6:00 am and ended at 9:00 pm in early summer during pregnancy and lactation and at 8:00 pm in late summer with shorter day length during post-lactation. A “bat night” is defined as the hours between daytimes and corresponded to the time between astronomical sunset and sunrise.

With reference to the long term studies in the research area since 1992 we divided the investigation periods (Table 1) into pregnancy, lactation and post-lactation periods. Female Daubenton’s bats give birth in the first week of June and the young become fledged at the beginning of July.

Statistical analyses

All results are given as mean ± SE. Individual skin temperatures (Ts) of females and males were calculated as mean of all average values of Ts of the recorded bat days (Table 1). Individual skin temperatures were averaged to calculate the mean skin temperature of the respective reproductive period (pregnancy, lactation, post-lactation). Influence of gender, different reproductive periods of the year and variant ambient temperatures of individual skin temperatures were tested using General Linear Model analysis (GLM). Backward stepwise selection was applied in order to exclude non-significant independent variables from the model. Active temperature is given as mean Ts for each individual bat prior to leaving the roost. Using these data we computed the individual percentage of daytime in torpor as well as the mean time for all female and male bats. Kruskal-Wallis nonparametric one-way Anova and Mann-Whitney U-test were applied to test for significant differences in mean temperature data. The Spearman rank correlations were calculated to test for significant correlations between skin and ambient temperatures. All statistical analyses were performed using Statistica v6.0 for Windows (StatSoft) and SigmaStat.
**RESULTS**

**Thermoregulation**

For Daubenton's bats GLM analysis (Table 2) revealed a significant effect of gender, reproductive period and the interaction of the two variables gender*period and period*ambient temperature (Ta) on skin temperatures (Ts) (also Figure 1).

**Table 2.** Results of a General Linear Model analysis (GLM) to test the dependence of skin temperature (mean Ts) of Daubenton’s bats from gender, daily ambient temperature (mean Ta) and reproductive period.

<table>
<thead>
<tr>
<th>Effect</th>
<th>SS</th>
<th>dF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
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<td>Intercept</td>
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<td>0.000210</td>
</tr>
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<td>0</td>
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<tr>
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<td>0</td>
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<td>0.802</td>
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</tr>
</tbody>
</table>

47
Figure 1. Mean daily skin temperature (Ts) of all 11 radio-tracked female (F, n = 6) and male (M, n = 5) *Myotis daubentonii* during different reproductive periods. Every dot represents one bat day. Values were calculated as mean of all hourly recordings of Ts during the bat days.

If we compare the individual temperature behaviour of the radio tracked bats it is obvious, that the progress in daily Ts does not follow a mechanism influenced by exogenous factors only (Figure 1). The comparison between a pregnant female and an adult male during the period of pregnancy shows that the male was heterotherm while the female remained homeotherm with constant Ts’s (Figure 2a). Those bats were radio-tracked simultaneously under similar ambient temperatures. The second example shows a second pregnant female in comparison to a post-lactating female in late summer. In both radio-tracking periods mean ambient temperature varied identically between 14 - 18 °C. During daytime the post-lactating female was regularly in torpor in contrast to the normothermic pregnant bat (Figure 2b).

Time of arousal from daily torpor varied, but both male and female raised their temperatures from low values to active temperature during the last hour before leaving the roost (Figure 2a, b). Sometimes, spontaneous arousals during the second and third daytime periods occurred (male bat in Figure 2a).
Figure 2a/b. Hourly absolute skin temperatures (°C) of a pregnant (preg) female (F) and a male (M) *Myotis daubentonii* during pregnancy period (a) with comparison of a second pregnant female and a post-lactating (postlac) female (b). Dark bars represent bat nights between dusk and dawn. Filled squares indicate the time of a bat in the day roost and open squares the time it was in flight.

It seemed obvious to us that the reduction of the body temperature is an individual behaviour which is initiated a new each day and so the daily Ts’s were independent of the Ts’s of the day before. Therefore we defined the results of individual bat days as independent data. Figure 3 shows the mean Ts of all bat days of one reproductive period for both sexes, which
was recorded daily in the same time schedule. As hypothesized thermoregulatory behaviour of the radio tracked Daubenton’s bats was different during the reproductive periods in both sexes (Figure 3, Kruskal-Wallis ANOVA: $H = 363.79, df = 5, p < 0.001$). During pregnancy and lactation, reproductive females remained active in the day roost and maintained their temperatures at a high level (pregnancy: mean $T_s$ of 34.8 °C ± 0.39 with a range from 30.7 °C - 39.5 °C; lactation: 34.3 °C ± 0.61 with a range from 27.9 °C up to a maximum of 36.3 °C). Later in the year when the young were weaned body temperature of females decreased significantly after they had entered the roost (mean $T_s$ 26.2 °C ± 0.93; Mann-Whitney U-test, $p < 0.001$) with a minimum $T_s$ of 21.1 °C.

In comparison, $T_s$ of adult males varied considerably between night and day during pregnancy and lactation period. During this time, temperature dropped immediately after the males had returned to their day roost (pregnancy period: mean $T_s$ 22.6 °C ± 1.36; lactation period: mean $T_s$ 27.1 °C ± 2.1). $T_s$ fluctuated to a much larger extent in males than in females, for example, during pregnancy period between 16.8 °C in deep torpor and 37.2 °C when the males were active. However, thermoregulatory behaviour of males changed later in the year when they maintained high temperatures during the first hours after they had entered the roost. Temperatures decreased only in the afternoon but they did not reach the low levels that we had measured in males during pregnancy and lactation period. During post-lactation period mean $T_s$ of males differed significantly from $T_s$ of females and from $T_s$ of males during pregnancy and lactation period (Mann-Whitney U-test, $p < 0.001$).
Figure 3. Mean hourly skin temperature (°C) of female (F) and male (M) *Myotis daubentonii* during different reproductive periods. Temperature values are given as mean ± standard error (SE) representing the variance between the recorded bat days. Data represent 14 bat days for three females and 8 bat days for two males during pregnancy period, 4 and 5 bat days for one female and one male during lactation period and 7 bat days each for two females and two males during post-lactation period.

Use of torpor

There was a significant difference in the use of daily torpor by females and males between reproductive and post-lactation period (Kruskal-Wallis ANOVA $H = 36.15$, df = 5, $p < 0.001$ and pairwise multiple comparison). Tagged pregnant and lactating females did not reduce their skin temperature more than 6°C below active temperature whereas in the post-lactating period, females were on average torpid for more than half of daytime (60.0 % and 73.3 %, table 3). Males were torpid during pregnancy period for about two thirds of daytime (87.99 % & 68.89 %). Later in the year, males remained mostly normothermic (Table 3).
Table 3. Individual use of daily torpor in radio-tagged Daubenton’s bats during different reproductive periods represented as percentage of daytime (F = female; M = male).

<table>
<thead>
<tr>
<th>Torpor [% of daytime]</th>
<th>Pregnancy</th>
<th>Lactation</th>
<th>Post-lactation</th>
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</thead>
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<tr>
<td></td>
<td>F1</td>
<td>F2</td>
<td>F3</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Range</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>n bat days</td>
<td>5</td>
<td>5</td>
<td>4</td>
</tr>
</tbody>
</table>

Influence of ambient temperature

The relationship between skin temperature and ambient temperature (Ta) was sex specifically assessed by calculating the Spearman rank correlations between the two variables. We found no significant influence of mean daily Ta on mean Ts of females ($r_s = -0.08$, $p = 0.7$, $n = 26$) as opposed to male Daubenton’s bats where mean Ts was positively correlated with mean Ta ($r_s = 0.67$, $p < 0.01$, $n = 20$).

We further assessed the difference of mean Ts - mean Ta and minimum Ta to assess the stability of Ts in tagged female Daubenton’s bats in comparison to ambient temperature by calculating the Spearman rank correlations between the two variables. The two variables were negatively correlated ($r_s = -0.73$, $p < 0.001$, $n = 26$). In contrast, we found a positive correlation between the two variables ($r_s = 0.64$, $p < 0.01$, $n = 20$) in male Daubenton’s bats. This indicates that body temperature of roosting female Daubenton’s bats was to a large extent constant and therefore independent of variations in ambient temperature as opposed to roosting male Daubenton’s bats where body temperature fluctuates to a large degree with ambient temperatures.

DISCUSSION

The purpose of this study was to compare thermoregulation behaviour of female and male Daubenton’s bats during different reproductive periods. It is the first study where body temperature of both sexes of a free-ranging and tree-roosting insectivorous bat in the Palaearctic region has been examined with temperature-sensitive transmitters throughout
roosting and foraging. Only Audet (1992) investigated skin temperatures of mouse-eared bats, *Myotis myotis* (Vespertilionidae) in the field, but measurements were limited to nursery colonies in attics. With our definition of torpor we take into consideration that ambient temperature slightly influences temperature measurements of external transmitters (see Willis and Brigham 2003). Compared with the possible influence of handling in captivity (e.g. physiological stress, disturbance) radio transmitters are less invasive for free-ranging bats and therefore provide a better estimate of the importance of torpor in the daily thermoregulatory behaviour of small bats (Audet and Fenton 1988, Hamilton and Barclay 1994).

The results of our study support the hypothesis that there are significant differences between the thermoregulatory behaviour of female and male Daubenton’s bats in relation to reproductive status. Female Daubenton’s bats avoided deep daily torpor during pregnancy and lactation whereas males became regularly torpid for several hours per day with lowest skin temperature of 16.8 °C. As a consequence, lower energy expenditure achieved by the use of torpor may result in reduced foraging activities. This has been confirmed for Daubenton’s bats as foraging times of male bats were significantly shorter during pregnancy period than that of female bats (Dietz and Kalko, *submitted*). As we did not find a strict correlation between torpor and ambient temperature throughout the breeding season, it must be under active control of the bats in relation to their reproductive condition.

Torpor in mammals and birds is characterized by lowering the set point for body temperature regulation to achieve a hypo-metabolic state in order to conserve energy and water (e.g. Wang and Wolowyk 1988). Recent studies have demonstrated that the onset of non-seasonal daily torpor by small mammals and birds (e.g. Schmid *et al.* 2000, Körtner *et al.* 2001) and especially by bats can be initiated by food deprivation (Racey and Swift 1981, Hickey and Fenton 1996, Audet and Thomas 1997) and by low ambient temperatures (Grinevitch *et al.* 1995). However, reproductive females have to balance energy savings through torpor with costs of decreased juvenile development. Juvenile development is depressed linearly as the body temperature decreases (McNab 1982).

Assuming that the variance in Ts with drops of 4 - 5 °C below active temperature is not affected by Ta (pregnant females in Figure 2), reproductive female Daubenton’s bats used shallow daily torpor for short periods of time. Even such slight reduction in body temperature can already result in substantial energy savings by bats (Studier 1981, Webb *et al.* 1993). The same effect is also discussed for larger mammals like ungulates (Arnold *et al.* 2003).
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Differences in the use of daily torpor by female and male bats were also described for Nearctic *Eptesicus fuscus* where free-living bats of both sexes had been tagged with temperature-sensitive radio-transmitters, as in our study. Both sexes went regularly into torpor but males used deeper torpor and were significantly more often torpid than reproductive females (Hamilton and Barclay 1994, Grinevitch *et al.* 1995). Lactating females were torpid significantly less often than pregnant and non-pregnant females (Audet and Fenton 1988, Chruszcz and Barclay 2002). Comparable results are described for pregnant and lactating females of European hedgehogs (Fowler 1988). It is reasonable that lactating females reduce time of torpor as much as possible because synthesis and secretion of milk is reduced with decreased body temperatures (Wilde *et al.* 1999). In contrast, assimilated energy requirement for lactation is much higher than for pregnancy (Racey and Speakman 1987, Kurta and Kunz 1988).

Besides shallow torpor, another strategy to compensate for energy demands during reproductive period is to cluster in nursery colonies (Kurta *et al.* 1987). Clustered females of *Myotis lucifugus* for example consumed only 19.9 ml oxygen per hour and per individual with a high body temperature of 36.9 °C. In contrast solitary females needed 32.5 ml oxygen per hour with low body temperatures of only 32.2 °C (Kurta 1986). In our study we conclude that thermoregulation through sociality is an important factor that contributes to stable and warmer temperatures in the roosts for Daubenton’s bats. We found colonies of 20 - 40 Daubenton’s females during pregnancy and lactation whereas the males mostly lived solitarily or in very small groups.

Selecting roosts with different qualities during reproductive season can also support the thermoregulatory behaviour of female bats. For instance, reproductive females of *Myotis evotis* and *Eptesicus fuscus* roosting in rock crevices chose roosts that differed in structure and thermal characteristics (Chruszcz and Barclay 2002, Lausen and Barclay 2003). Roosts used during lactation were more thermally stable and remained warmer at night compared to the shallow roosts used by pregnant and post-lactating females. Similar results were found in *Myotis bechsteinii* (Kerth *et al.* 2001). Females preferred tree roosts on colder nights especially before parturition and after weaning whereas they favoured warm roosts in bat-boxes during the post partum period. It is likely that the development of the young benefits from the warmer roosts. Female Daubenton’s bats in the “Philosopher-Forest” also switched between different roosts during the breeding season. However, we did not find obvious
differences in the thermal properties of the tree holes used by Daubenton’s bats in our research area (unpublished data).

Thermoregulatory behaviour of female and male Daubenton’s bats changed significantly during post-lactation period after the juveniles had been weaned. During this time, females in our study used daily torpor more often and for longer time periods than males. This change suggests that males prepare for mating and therefore reduce periods of torpor to avoid the resulting negative impact on spermatogenesis (Jolly and Blackshaw 1987, Kurta and Kunz 1988, Entwistle et al. 1998). In our study area, sperm production started at the end of the lactation period. Epididymal filling continuously increased in July and August and reached its peak in the second half of September prior to the migration to the hibernacula (Encarnação et al. 2004).

We suppose that this period corresponds to the main mating season of Daubenton’s bats. Although copulations in Daubenton’s bats have only been observed in winter roosts (Roer and Egsbaek 1969, Grimmberger et al. 1987), we believe that it is likely that most copulation takes place already in late summer when the epididymes of males are fully developed and the animals are active. We found males with filled epididymes in tree roosts together with adult females at the end of July. Becoming torpid during this time would reduce copulation frequencies because adult females that have gained enough weight for hibernation already leave their breeding areas at the beginning of September to settle in the hibernation site (see Haarje 1994).

We conclude from our data on Myotis daubentonii that differences in reproductive status, in particular of females, explain the use of torpor better than exogenous factors like ambient temperature or food deprivation alone. Our results on the female bats correspond well to those of other studies where the temperature behaviour of the nearctic Eptesicus fuscus was investigated (Audet and Fenton 1988, Hamilton and Barclay 1994, Grinevitch et al. 1995). As in female Daubenton’s bats, torpor was used to the greatest extent after weaning. But female Eptesicus fuscus also used daily torpor during pregnancy in response to ambient temperatures below 9 °C.

We cannot exclude that this difference is partly due to low sample size in comparison to studies on Eptesicus fuscus that have been examined in greater numbers. However, in our opinion, it is more probable that the different results reflect the diverse feeding preferences.
and foraging strategies of the bat-species. For example, *Eptesicus fuscus* mainly feeds on *Coleoptera, Hemiptera* and *Lepidoptera* by aerial hawking in open spaces (e.g. Furlonger et al. 1987, Hamilton and Barclay 1998). For such prey, nightly availability has been shown to vary widely with ambient temperature (Lewis and Taylor 1964, Kurtze 1974). On colder nights below 10 °C prey availability decreased and also the flight activity of bats foraging in open space (Racey and Swift 1985, Hickey and Fenton 1996). As a result the energy intake on colder nights is lower than on warmer nights and so the use of torpor would be practised by individuals for whom the ratio of costs to benefits for thermoregulation was highest. In contrast to *E. fuscus* and other species, ambient temperature has no significant influence on flight duration and capture attempts of reproductive females of Daubenton’s bat (Dietz and Kalko, submitted). Moreover, tagged pregnant *M. daubentonii* still hunted at ambient temperatures below 5 °C. Daubenton’s bats mainly feed on swarming chironomids (Swift and Racey 1983, Beck 1995), capturing them close to the water surface (Jones and Rayner 1988, Kalko and Schnitzler 1989). Apparently insect density above water surfaces is less affected by short-term low ambient temperatures because of the heat saving capacity of the water.

Assuming that *Myotis daubentonii* feeds more successfully during low ambient temperatures compared to other species, this may compensate for the loss of energy to maintain high body temperature. What is remarkable is that Reynolds and Kunz (2000) found changes in the gastrointestinal tract of lactating, ecologically similar females of the Neartic *Myotis lucifugus*, which suggest that increased food intake and assimilation are the primary factors with which bats compensate for the increased energy demand during pregnancy and lactation.

Overall, we conclude that bats in the temperate zone adapt their thermoregulatory behaviour primarily to their reproductive status and the influence of ambient temperature is specifically different for gender and species.

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Chapter 1 – *Myotis daubentonii*


2 REPRODUCTION AFFECTS FLIGHT ACTIVITY IN FEMALE
AND MALE DAUBENTON’S BATS MYOTIS DAUBENTONII

ABSTRACT

Food requirements of female bats are particularly high during pregnancy and lactation and of males during spermatogenesis. Seasonal changes in energy demand and reproductive condition should therefore result in different foraging activity within and between sexes. This assumption was tested for 16 adult females and 13 males of Myotis daubentonii that were radio-tracked during pregnancy, lactation and post-lactation period. In total, average nightly flight time of females (307.2 ± 70.1 min, range: 75 - 492 min) was comparable to that of males (286.4 ± 95.3 min, range: 72 - 506 min). Divided into the different reproductive periods, pregnant females as hypothesized flew significantly longer (mean: 358.9 min; 70 % of night length) than males (mean: 228.5 min, 42.4 % of night length) during spring. In contrast to our expectation, nightly flight time of lactating females decreased and was significantly less than that of pregnant females but similar to that of males during the same period. The longest flight times of males were registered during late summer when spermatogenesis had set in. Air temperature had no notable influence on flight activity of Daubenton’s bats. However, there were distinct differences in the use of foraging areas between female and male Daubenton’s bats. Male bats in general tended to switch foraging areas more often during the night than reproductive females that displayed a high constancy in the use of foraging areas.

Overall, the results confirmed our initial proposition that flight activity of female and male Daubenton’s bats differs in relation to reproductive period. Flight activity reflects the higher energy demand and nutrition requirements in the different reproductive periods for females during pregnancy and males during spermatogenesis.
INTRODUCTION

Food requirements of bats in temperate zones are subject to significant seasonal fluctuations correlated with reproductive cycle. During reproductive period, there is an increased energy demand on pregnant females, particularly during lactation (Kurta et al. 1989). This is well reflected in higher rates of food consumption by lactating females that may increase up to 45% (Myotis lucifugus, M. velifer; Kunz 1974, Anthony and Kunz 1977) from pregnancy to lactation. In temperate zones, pregnancy and lactation of bats are synchronized with the period of highest food availability (Racey and Swift 1985, Rydell 1992, Hickey and Fenton 1996). However, food availability varies with weather conditions (Lewis and Taylor 1964, Racey and Swift 1985) that may in turn affect reproduction. As shown by Arlettaz et al. (2001) for two mouse-eared bats, parturition was synchronous in Myotis blythii and its congener, M. myotis, in years with abundant cockchafers (Melolontha melolontha; Scarabaeidea). Cockchafers are one of the main prey items early in the year for M. blythii. In years without cockchafers, M. blythii gave birth 10 days later than M. myotis, which mainly feeds on carabid beetles.

Due to its higher fat and protein content, milk of lactating insectivorous bats is considerably more nutritious than milk of frugivorous bats (Kunz and Stern 1995). This results in a notably shorter, but for females far more energy demanding lactation period (Kunz and Hood 2000). The increased physiological stress on females during reproduction has lead to mechanisms that compensate for this increased energy demand. One of these strategies is roosting in colonies where social thermoregulation is thought to improve conditions for pregnancy and post partum care (Kurta et al. 1987, Audet 1992).

Lowering body temperature is seen as the most effective way to save energy when food supply is poor. However, during reproduction lowering of body temperature is at the expense of foetal growth and development of young (Wilde et al. 1995, Wilde et al. 1999). Consequently, maximum reduction of body temperature in reproductive active female Myotis daubentonii is only 2 - 4 °C in the day roost, and deep torpor is avoided (Dietz and Kalko 2005). In contrast, male Daubenton’s bats that roost separately from females regularly enter torpor for several hours during this time similarly to other bat species like Eptesicus fuscus (Grinevitch et al. 1995). Male bats experience less physiological stress during this period than females, since they have no offspring to care for. However, in mid summer, energy
requirements of males increase with the onset of sperm production and beginning of mating period (Racey and Tam 1974).

Recent studies on body mass changes, reproductive condition and nocturnal activity of adult male Daubenton’s bats suggest that their food demand is highest in mid summer during the period of high spermatogenetic activity and steep increase in body mass (Encarnação et al. 2004a,b). From that time on, we noted distinct changes in thermoregulatory behaviour as female Daubenton’s bats became torpid during daytime after the young were fledged, whereas males remained homoeothermic (Jolly and Blackshaw 1987, Kurta and Kunz 1988, Dietz and Kalko 2005).

As a consequence of higher energy demands to reach and maintain homoeothermic body conditions during pregnancy, lactation, and spermatogenesis, intake of food should increase accordingly leading to distinct differences in flight activity between female and male bats. Individuals with a higher food intake should have longer flight times per night than individuals with a reduced energy demand. This assumption is supported by a study of free-ranging big brown bats, *Eptesicus fuscus*, where pregnant and lactating females showed a trend for longer foraging periods per night compared with males (Wilkinson and Barclay 1997). As there are no comprehensive studies so far that link nightly time and use of foraging area of sexes to different reproductive periods, we tested the assumption that males and females should differ in foraging behaviour in relation to reproduction for the trawling bat *Myotis daubentonii* and compared nightly flight time, number of foraging areas and site fidelity of free-ranging females and males. We expected for pregnant and lactating areas and site females a concentrated use of small, highly profitable and individual foraging areas to optimise energy intake. We also predicted that the bats minimize time for commuting between foraging areas. During pregnancy and lactation the nightly flight time of females should be longer than that of males. Subsequent to the lactation period, flight time of female Daubenton’s bats should be less than that of males because of the males’ increased energy demand during spermatogenesis.
MATERIAL AND METHODS

Study area and tagged bats

The study area was located in the area of the city of Giessen in central Germany (Hessen). It included the “Philosopher-Forest”, a small (20 ha) deciduous forest bordered by buildings. We radio-tracked 16 adult females and 13 adult males of *Myotis daubentonii* (Table 1). The females were part of a maternity colony in the “Philosopher-Forest”. The males roosted in tree holes in the same forest, either singly or in small groups. The feeding sites of the bats consisted of two ponds at a distance of a few hundred meters to the day roost, the brook “Wieseck” and the river “Lahn” at a distance of 2.5 km (Dietz and Fitzenräuter 1996). Population structure and feeding ecology of Daubenton’s bats in the “Philosopher-Forest” have been investigated since 1992, therefore seasonality and habitat use are well known. To attach radio-transmitters, we caught bats with mist nets set in their flight-path or at their roosts. Bats were aged (adult/juvenile) by evaluating the closure of the epiphysis (Anthony 1988) and by subsequent banding. Reproductive status of females was classified as pregnant, non-pregnant, lactating, and post-lactating according to the methods described by Racey (1982). Males were classified according to their epididymal distension (0 %, 25 %, 50 %, 75 % & 100 %) following Encarnação *et al.* (2004a).
Table 1. Summary of radio-tracking data of 16 adult female and 13 adult male *M. daubentonii* tracked in Giessen (Germany) from 1996 to 1998. Individual ring number, gender, reproductive status (females: preg = pregnant, lac = lactating, post-lac = post-lactating; males: epididymal filling in %), tracking period (half of month/month of the year), recording nights with continuous tracking and recording nights without observation gaps are given.

<table>
<thead>
<tr>
<th>period</th>
<th>bat number</th>
<th>sex</th>
<th>mass [g]</th>
<th>repro. status</th>
<th>tracking date</th>
<th>recording nights</th>
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<tr>
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<td></td>
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<td></td>
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Telemetry

We used 0.5 g LB-2 radio-transmitters (Holohil Systems, Canada) that made up between 4.6 - 6.8 % of the bat’s body mass (7.7 - 12.1 g). This is below or only slightly above the 5 % threshold suggested by Aldridge and Brigham (1988) as limit for radio-tracking. All transmitters were attached between the shoulder blades using Skin-Bond® (Smith & Nephew). The transmitters fell off after 3 - 8 days. During the tracking period we monitored the bats’ behaviour continuously by “homing-in-on-the-animal” (White and Garrot 1990). This practice combined with previous experience allowed us to locate tagged bats. We observed all radio-tracked individuals with an infrared night scope (Filin 1 BN 2.5 x 56, Kiev, Ukraine) throughout the night to document flight time as well as number and location of individual foraging areas within the feeding sites (Table 1). We visually classified about 70 % of the individual foraging areas into five size classes (< 100 m², < 300 m², < 500 m², < 1000 m², < 1500 m²) based on markings (sticks with reflecting tape) that we had set at distances of 20 m at the bank of the ponds. Our total sample for this study constituted of 132 recording nights of individuals composed of 16 tagged females and 13 tagged males. Only nights with more than 95 % contact time were used to assess nightly flight time (n = 94 nights). We tagged 2 - 8 bats simultaneously and monitored them with three to four observer-teams, each with a Yaesu receiver (FT-290RII) modified by Wagener (Cologne, Germany) and a 2-element Yagi antenna. One group recorded the nightly presence of the bats in their day roost and two teams observed the two ponds nearby. Depending on the number of tagged animals, one of the teams followed the bats when they left the ponds to the river Lahn. Daily ambient temperatures (mean, min and max) were taken from records of a station of the German Weather Service close to the “Philosopher’s Forest”.

Definitions

“Night length” includes the time interval between local astronomical sunset and sunrise.

“Feeding sites” were the two ponds (“Swan Pond”, “New Pond”) near the “Philosopher’s Forest”, the brook “Wieseck”, and the river “Lahn”. A “foraging area” in our study consisted of a small sector of the “feeding site” where radio-tracked bats flew constantly for more than ten minutes. We defined “flight time” as the time spent by a bat in flight in the foraging area.

“Nightly flight time” is the sum of the registered flight time during one night. It is represented
Foraging behaviour

as cumulative flight time per night in minutes or as percentage of night length. We argue that flight time in Daubenton’s bats over water is equivalent to foraging time because all of the bats that we observed during our visual controls at night were clearly hunting. We observed them either flying low over water where they regularly dipped at the water surface, presumably catching prey directly from the water surface (low catches) or they briefly soared up into the air above the water surface, most likely catching insects in the air (high catches) (Jones and Rayner 1988, Kalko and Schnitzler 1989). When a bat changed feeding site or foraging area or when it switched between a roost and a foraging area, we classified this as “commuting flight”. During “hanging”, bats interrupted their flight activity for more than one minute. With reference to our long-term studies in the research area since 1992 we divided the investigation periods (Table 1) into pregnancy, lactation, and post-lactation periods. Generally, female Daubenton’s bats are pregnant during May and give birth in the first week of June and the young become volant at the beginning of July (mid summer).

Statistical analyses

To avoid pseudo-replication through variations in the number of observation nights per individual, we used individual mean nightly foraging time for calculating the mean time of emergence and return, average nightly flight time and number of foraging areas of female and male M. daubentonii. All data samples were tested for normality and equal variance. Differences in flight time between the two sexes were tested with Kruskal-Wallis nonparametric one-way ANOVA followed by pairwise comparisons using the Mann-Whitney U-test. Correlations between two variables were tested with Spearman-Rank-Correlation and more than two variables were tested with a multiple comparison procedure (Dunn’s Test). Results are given as mean with standard deviation, median, and range. Statistical analyses were performed using Statistica v6.0 for Windows (StatSoft) and SigmaStat.

RESULTS

Feeding sites and foraging areas

The radio-tracked Daubenton’s bats flew directly to one of the four feeding sites after emerging from their day roost in a tree hole at the “Philosopher’s Forest”. Females and males
used similar flight paths along tree-lined walks between the “Philosopher’s Forest” and the two ponds and the brook “Wieseck” in the park. The flight path between the park and the river Lahn (Figure 1) crossed part of the city of Giessen.

Females and males used the four feeding sites with different intensity (Figure 1). Nearly all observed bats (27 from 29) foraged above the “Swan Pond” in the park that was closest to the “Philosopher’s Forest” without a significant difference in mean flight time between females and males (Mann-Whitney U-test: \( p < 0.34, n = 16 \, \♀ \, \text{and} \, 13 \, \♂ \)). In contrast, the “New Pond” was mainly used by males. Ten of the 13 tracked males foraged there and only 4 of the 16 radio-tracked females. Mean flight time of the males was significantly higher at this pond compared with females (Mann-Whitney U-test: \( p < 0.042, n = 16 \, \♀ \, \text{and} \, 13 \, \♂ \)). The brook “Wieseck” that is located between the ponds in the park was also preferred by males. We never found any of the radio-tracked females at this feeding site. In contrary the river Lahn was used by nearly one third of all females and only by a few of the males. In comparison, females had significantly higher cumulative flight times at the river Lahn than males especially during lactation period (Mann-Whitney U-test: \( p < 0.029, n = 4 \, \♀ \, \text{and} \, 4 \, \♂ \)).

Within the feeding sites the radio-tracked Daubenton’s bats used small foraging areas. We classified 33 foraging areas of females and 18 foraging areas for males. More than half of the foraging areas of the females covered between 100 and 300 m² (\( n = 19; \, 57.7 \% \)). The largest foraging area covered by a female was about 1200 m². Classifying the foraging areas of the males resulted in the same pattern where half of the sites (50 %) covered areas of 100 - 300 m² (\( n = 9 \)). In some cases we noted that tagged bats were engaged in chasing each other when another bat came into their foraging area and flew too close. The chases usually did not last longer than 10 sec.
Foraging behaviour

Figure 1. Distribution of 74 (33 ♀, 41 ♂) foraging areas of radio-tracked Daubenton’s bats at four feeding sites at the border of the city of Giessen, Central Germany (SP: “Swan Pond”, NP: “New Pond”, W: the brook “Wieseck”, RL: the river “Lahn” and the roosting site, PhF: “Philosopher’s Forest”).

Time of emergence and return

There was no significant difference between tagged female or male Daubenton’s bats in emergence time from the roost in the evening and return in the morning throughout the study period (Figure 2). Time of emergence in females was a few minutes earlier after local sunset (mean: 46.4 ± 13.6 min; median: 44.5 min, range: 17 - 94 min after sunset) than that of males (mean: 50.0 ± 10.7 min; median: 46.0 min, range: 28 - 89 min after sunset). In both sexes, time of emergence correlated significantly with time of local sunset (♀: n = 16; r = 0.82; p < 0.001 and ♂: n = 13; r = 0.9; p < 0.001). The earliest and latest emergences were found in females at 17 and 94 min after sunset, respectively.

The final return to the day roost differed between females and males with respect to reproduction periods. Pregnant and lactating females returned late about ¾ hour before sunrise (mean: 43.0 ± 16.0 min, median: 44.1 min, range: 7 - 91 min before sunrise). Post-lactation females often returned in mid summer already in the first part of the night without leaving again (mean: 201.4 ± 171.1 min, median: 130 min, range: 14 - 453 min before sunrise,
Figure 1). Male Daubenton’s bats showed the opposite behaviour. They returned earlier during May (mean: 122.5 ± 104.6 min, median: 54.5 min, range: 32 - 324 min before sunrise) and finished their last flights in mid summer later (mean: 38.16 ± 37.1 min, median: 37 min; range: 14 - 85 min before sunrise).

![Figure 2](image.png)

**Figure 2.** Mean time of emergence and return of female and male *M. daubentonii* (♀: n = 16 individuals; ♂: n = 13 individuals).

**Nightly flight time and activity patterns of females**

There was a significant difference in nightly flight time of females during different reproductive periods (Kruskal-Wallis-ANOVA: H = 10.5, p = 0.005). During pregnancy, females mostly flew almost three quarters of the night (median: 70 % of night length, range: 64.1 - 88.4 %). Nightly flight time decreased during lactation when percentage of flight time per night was lowest with about half of the night (median: 52.1 % of night length, range: 50.6 - 53.8 %, Figure 3).

Cumulative nightly flight time in minutes per night was highly variable and ranged from 75 min to 492 min (mean: 307.2 min ± 70.1 min, median: 319.4 min, Table 2). It differed
Foraging behaviour

significantly between pregnancy and lactation (Mann-Whitney U test: p < 0.004, n = 8 ♀ and 4 ♀, for individual nights see Table 1). Cumulative nightly flight time dropped by about a third from pregnancy (mean: 358.9 ± 50.6 min, median: 340.2 min, range: 295 - 455 min) to lactation (mean: 234.3 ± 6.7 min, median: 236.7 min, range: 174 - 285 min). After the young became volant in mid and late summer, total flight time of post-lactating females was also significantly lower than during pregnancy (Mann-Whitney U test: p = 0.016, n = 8 preg ♀ and 4 post-lac ♀, for individual nights see Table 1) but slightly higher than during lactation (Table 2).

Flight activity patterns of females during the night were also different between the reproductive periods. In accordance to the high cumulative nightly flight time, pregnant females showed a high activity in flight time per hour throughout the night. Individual means ranged from 88.5 - 100 % flight time per hour from the second hour after emergence until the second hour before return to the day roost. Overall, flight activity decreased only slightly throughout the night (Figure 4).

Lactating females showed a bimodal activity pattern with significantly shorter flight time in the third hour after emergence compared with the same night time during pregnancy and post-lactation period (Kruskal-Wallis ANOVA: H =11.45, p = 0.003). Lactating females returned to the day roost for 20 - 48 min, presumably to suckle their young. After weaning, females flight activity became unimodal and flight time per hour of night reached a maximum in the second hour after emergence with a steady and significant decrease afterwards (Figure 4).

Nightly flight time and activity patterns of males

Males also showed significant differences in flight time per night [%] during different reproductive periods (Kruskal-Wallis ANOVA: H = 8.21, p < 0.005), but the seasonal pattern was opposite to that of females (Figure 3). The longest flight time occurred during mid summer with almost 70 % of the night, whereas the shortest flight time was recorded in May when the males flew only less than half of the night (median: 42.8 % of night length, range: 32.5 - 60.3 %, Figure 3). Accordingly cumulative flight time of males increased from May (median: 220.5 min per night, range: 72 - 330 min) to mid summer (median: 401.3 min per night, range: 274 - 506 min, Table 2).
Male Daubenton’s bats exhibited the opposite seasonal pattern as females with regard to variations in nightly activity patterns (Figure 4). During spring they showed an unimodal activity pattern with highest flight times per hour in the first part of the night and a distinct decrease in the second part of the night. In July and later in the year, flight times per hour remained even with high activity throughout the whole night (Figure 4).

**Comparative flight times of females and males**

Our results showed a significant difference in cumulative flight time between the sexes during pregnancy period when females had much longer flight times than males (Mann-Whitney U-test: p < 0.002, n = 8 ♀ and 5 ♂, for individual nights see Table 1). During lactation, flight time remained more or less the same between sexes. However, during the post-lactation period, males displayed a significantly higher flight time than females (Mann-Whitney U-test: p < 0.03, n = 4 ♀ and 4 ♂, for individual nights see Table 1).

Particularly in mid summer, both sexes displayed considerable variation between individuals in the second half of the night as indicated by the high standard deviation. While at the end of July one of the females already returned to the day roost after 2 - 3 hours of flight time without re-emergence, a second female was still active for the whole night with high variability in flight times in subsequent nights in spite of similar weather conditions.

We did not find a significant relation between night length and nightly flight time of female and male Daubenton’s bats throughout the study period (♀: r = 0.15; n = 16; p < 0.36; ♂: r = 0.2; n = 13; p < 0.31). However, flight time of pregnant females tended to slightly increase with increasing night length. Flight time of males only correlated significantly with night length in late summer (n = 10; r = 0.7; p < 0.008).
Figure 3. Flight time represented as percentage of night length by adult female (F) and male (M) *M. daubentonii* during pregnancy (♀ = 8; ♂ = 5), lactation (♀ = 4; ♂ = 4) and post-lactation period (♀ = 4; ♂ = 4).
Figure 4. Flight time represented as percentage per hour after sunset (mean ± SD) by reproductive females and adult males of *M. daubentonii* during pregnancy: (8 ♀; 5 ♂), lactation (4 ♀; 4 ♂) and post-lactation period (4 ♀; 4 ♂).

**Influence of temperature on flight time**

Ambient temperature had no discernible influence on flight time of females (*r* = 0.05; *n* = 16; *p* = 0.97). Even at ambient temperatures below 10 °C the tagged animals continued foraging. One pregnant female foraged continuously at an air temperature as low as 3 °C at the beginning of May. As for females, we did not find a clear relationship between flight activity and air temperature in males (*r* = 0.25; *n* = 13; *p* = 0.15). There was a tendency for males to fly less in cooler nights during early summer in May and June.
**Number of foraging flights and foraging areas**

The registered flight time of Daubenton’s bats was reciprocal to the time spent in the day roost during the nights. Nightly presence of females at the day roost increased significantly from pregnancy to lactation, thereafter it remained about the same (Kruskal-Wallis ANOVA: H = 16.52, p < 0.001). Lactating females returned to the day roost at least once, sometimes two or three times per night (Table 2). As a consequence, time spent in the day roost (mean: 39.2 min) each night was about twice as high as during pregnancy (mean: 19.3 min). In most cases, pregnant females did not return to the day roost after they had emerged in the evening. Consequently, average number of emergences per night was low (1.1 ± 0.3 emergences per night). This was also the case in mid summer after the young were weaned. Post-lactating females often did not leave the roost for a second foraging flight. In contrast, most males returned to the day roost and flew out a second time per night. During July and September we registered up to five flight periods for each male with several resting phases (mean: 2.4 ± 1.0 flight periods per male, Table 2).

After leaving the day roost, the females displayed a high constancy in the use of foraging areas and remained for several hours each night in the initially chosen foraging area (Table 2). Pregnant females usually stayed in one foraging area per night and during the tracking period and seldom visited another foraging area. In contrast, lactating females often switched to a second foraging area during their second activity period in the night. For females, we could not establish a relationship between flight time and number of chosen foraging areas (r = 0.18, n = 16, p > 0.27) compared to males that tended to visit more foraging areas (mean range: 2.7 - 3.2 areas per night) from pregnancy to post-lactation period. The number of switches was higher than the number of foraging areas, i.e. males switched often several times per night between a small set of foraging areas. As in females, there was no obvious connection between length of flight time and number of chosen foraging areas.

**Cumulative flight distances per night**

Compared with the time used for commuting flights, female and male Daubenton’s bats spent similar proportions of their flight time in the foraging areas. In females, cumulative mean flight time needed for commuting flights between day roost and foraging areas (Figure 1) as well as between different foraging areas encompassed a total of 14 min per night. This
Chapter 2 – *Myotis daubentonii*

constitutes less than 5% of overall flight time per night. Males spend slightly more time (mean: 15 min) in commuting flights. Average distance between day roost and visited foraging areas at the different feeding sites was 1.5 km for females and 1.1 km for males, with a maximum of 3.9 km for females and 4.7 km for males.

We calculated cumulative flight distances of individual Daubenton’s bats per night in their foraging habitat by using mean cumulative flight time at their feeding sites and flight speeds ranging from 3.4 - 4.1 m/s (Baagøe 1987, Jones and Rayner 1988, Kalko and Schnitzler 1989) (Table 2). Pregnant females covered the longest distances with about 85.1 km per night (mean ± 12.5, range 75.9 - 111.4 km) and an added 2.5 - 3 km for commuting flights. As total flight time of females was reduced during lactation, cumulative distance decreased to 53.3 km per night (mean ± 3.1, range 42.6 - 69.8 km). Males covered the longest flight distances in mid summer (mean: 90.7 ± 3.1 km, range 67.1 - 123.9 km per night) that were comparable to pregnant females.
Table 2. Comparable flight time, flight activity, foraging flights, commuting flights and flight distances of female and male Daubenton’s bats per night \([n^{-1}]\) during the three reproduction periods. Significant differences \([p]\) were calculated with MW-U-Tests.

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* Estimated by the mean nightly flight time and the flight speed given in Jones and Rayner (1988), Baagøe (1987) and Kalko and Schnitzler (1989).
DISCUSSION

Time of emergence and return

We did not find any difference in the timing of emergence between female and male Daubenton’s bats. Both sexes emerged on average about ¾ hour after local sunset. This is slightly different to another study in our region, where male Daubenton’s bats emerged from their day roost only a few minutes later (mean: 54 min after sunset, Encarnação 2005). In both studies Daubenton’s bats emerged in relation with the time of sunset.

A correlation of emergence time with the time of sunset is in accordance to other studies on insectivorous bats in the temperate zone (Jones and Rydell 1994, Speakman 1995) that also did not find gender-specific differences (Wilkinson and Barclay 1997). The emergence time of both, male and female Daubenton’s bats coincided with the period of highest nightly insect density in the first hour after sunset (own unpubl. data, Williams 1939, Lewis and Taylor 1964, Rydell et al. 1996) suggesting that both sexes performed similar foraging strategies by exploiting in particular the evening insect peak.

Flight activity

In total average nightly flight time of females was comparable to that of males and both showed similar short commuting times below 20 min per night. However, divided into the different reproductive periods, pregnant females flew significantly longer than males during spring combined with an intensive and continuous use of small foraging areas of about several hundred square-meters. The spatial use combined with long nightly flight times exhibited by pregnant females are likely to reflect higher energy demands than males during this reproductive period (Kurta et al. 1987, McLean and Speakman 2000). Our continuous monitoring of the radio-tracked bats throughout the night combined with visual controls indicates that flight time over water is equivalent to foraging time.

The short commuting times below 20 min and the long time outside the roosts each night for many foraging bats were also recorded in another study on Daubenton’s bats in Yorkshire Dales, UK (Senior et al. 2005). However, in contrast to our study no detailed data about flight-times outside the roosts were given in relation to the different reproductive periods. The
authors suggested that females and males within the same downstream foraging area did not differ in foraging times compared to males in an upstream area.

Despite the fact that energy demand reaches its maximum during late lactation (Kurta and Kunz 1988, Wilde et al. 1995), lactating females in our study reduced foraging time compared with pregnant females. Flight times of lactating females were equal to that of male Daubenton’s bats and to that of post-lactating females. At first glance, the comparable short flight times of lactating females contradicts our initial hypothesis that higher energy demands during lactation should lead to longer flight times compared with post-lactation. However, there are at least two factors that limit foraging time for lactating females. First, lactating females have to suckle and probably also briefly warm their young and thus have to return from time to time to the roost thus shortening foraging time. Furthermore, as night-length during lactation period is shorter in our study area than during pregnancy and post-lactation, overall time potentially available for foraging was shorter. In contrast to E. fuscus, which saves energy by sporadically entering torpor during lactation after cool nights (e.g. Audet and Fenton 1988, Grinevitch et al. 1995) we did not find this strategy in Daubenton’s bats (Dietz and Kalko 2005). Perhaps female Daubenton’s bats deposit surplus fat during pregnancy, which would allow them to sustain the energy demanding lactation period without increasing flight time.

Another mechanism that could lead to higher energy gain during reproduction may include a higher efficiency in digestion during pregnancy and lactation as it has been found in females of the Nearctic Myotis lucifugus (Reynolds and Kunz 2000) that feeds on small insect orders comparable to M. daubentonii. Distinct changes in the gastrointestinal tract of lactating females are interpreted as a means to increase assimilation with increased food intake. This, in turn, would permit bats to compensate at least in part for increased energy demand during pregnancy and lactation. If this was the case also in M. daubentonii, reproductive female bats could use the seasonal insect maximum over calm water bodies (Morris and Brooker 1981, Titmus and Badcock 1981) with a hitherto unappreciated efficiency. This assumption is supported by the very high rate of terminal phases (every 3.7 sec) that were monitored for foraging Daubenton’s bats over calm waters (Kalko and Braun 1991) and that indicate capture attempts.

In our study area, the duration of foraging flights of male Daubenton’s bats steadily increased from spring to mid summer, probably linked to the onset of sperm production (Höglund and
Sheldon 1998, Rose and Bradley 1998) that begins in June (lactation period in females) and reaches its maximum in late summer (Encarnação et al. 2004a). This is supported further by observations that males enter torpor less often during this period, probably because low body temperatures may impede spermatogenesis (Kurta and Kunz 1988, Dietz and Kalko 2005). As maintenance of higher body temperatures incurs higher energy costs this requires higher food intake that can be achieved by longer flights as seen in the males.

During mid and late summer, foraging times of females in our study were significantly shorter than those of males at the same period, presumably because the young were already weaned at that time and because the females used daily torpor phases more frequently than during pregnancy and lactation (Dietz and Kalko 2005). Both aspects lead to reduced energy expenditure.

**Influence of temperature on flight time**

In our study ambient temperature had no discernible influence on foraging times of individual *M. daubentonii*. This contrasts with observations of other aerial insectivores including the Palaearctic *Eptesicus serotinus* (Catto et al. 1995) and *E. nilssonii* (Rydell 1989) as well as the Nearctic *E. fuscus* (Wilkinson and Barclay 1997), where flight activity ceased to a large extent when air temperatures dropped below 10 °C. The high foraging activity of Daubenton’s bats even at low ambient temperatures about 5 °C may be linked to a higher quality of the feeding patch in particular higher food availability over water. In general, insect activity at ponds and rivers is less affected by changes in ambient air temperatures in comparison to open landscapes or woodlands. Insect density at calm water bodies already peaks in spring (Morris and Brooker 1981, Titmus and Badcock 1981) and constitutes mainly of mass emerging chironomids, which form the main prey of Daubenton’s bats (Swift and Racey 1983, Beck 1995).

**Usage of foraging areas**

An important characteristic of the hunting strategy of reproductive female Daubenton’s bat is their high site fidelity. Particularly during pregnancy, the tagged females in our study consistently used individual foraging areas of only a few hundred square meters throughout
the night from emergence to return and in subsequent tracking nights. Male Daubenton’s bats in our study tended to switch foraging areas more often during the night than reproductive females and they preferred hunting at the “New Pond” and the brook “Wieseck” with significant higher flight times than females.

A distinct difference in the use of foraging areas between female and male bats has also been shown for *E. fuscus* (Wilkinson and Barclay 1997) and brown long-eared bats, *Plecotus auritus* (Entwistle *et al.* 1996). Males of *E. fuscus* foraged over larger (about 5 km²) areas than females (mean: 2.75 km²) and spent significantly more time away from the main feeding sites (Wilkinson and Barclay 1997). Males of *P. auritus* foraged further from the roost than females (Entwistle *et al.* 1996). The authors concluded that males often forage in less favourable foraging areas and have to make a larger effort compared to females to obtain enough food. A high constancy in temporal and spatial usage of individual foraging areas has also been described for females of other bat species in the temperate zone (Rydell 1986, Audet 1990, Kerth *et al.* 2001) and in the Neotropics for the trawling bat *Macrophyllum macrophyllum* (Meyer *et al.* 2005) which is rather similar in body mass and foraging behaviour to *M. daubentonii* but with a different phylogenetic affiliation.

Because most European bats live in maternity colonies (Altringham 1996) which may lead to potential competition at feeding sites close to the day roost, it could be an advantage for reproductively active females to defend their small-scale, high quality individual foraging areas against other individuals to ensure continuously high hunting success (Barclay 1984, Rydell 1986, Balcombe and Fenton 1988). First observations on individual *M. daubentonii* in our study area suggest territorial behaviour as we occasionally saw individuals chasing each other across the foraging area accompanied by audible vocalisations (see Wallin 1961). Usually, one animal retreated in the course of those pursuits.

**Conclusion**

To summarize, the results of our study show clear differences in flight activity, namely foraging times of female and male Daubenton’s bats in association with different stages in reproduction. Female bats covered their elevated energy demands during pregnancy and lactation through long foraging times in small, individual foraging areas in conjunction with
high site fidelity. The pattern was reversed after the young had been weaned and in males after they entered spermatogenesis.

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3 ESTIMATION OF FOOD INTAKE AND INGESTED ENERGY IN DAUBENTON’S BATS (MYOTIS DAUBENTONII) DURING PREGNANCY AND SPERMATOGENESIS

ABSTRACT

We studied food intake and estimated ingested energy in female and male Myotis daubentonii during the periods of pregnancy (observation period 1: 8 May – 4 June) and of intense spermatogentic activity (observation period 2: 24 July – 22 August) during eight years (1996 - 2003) in central Germany. Time spent foraging was recorded in radio-tracked animals and prey attack rate was determined in animals marked with chemiluminescent light-sticks. Body-length, body-mass, moisture content and caloric content of Chironomidae, the main prey of Daubenton’s bats, were measured to estimate the nightly food intake and, in consequence, energy intake of females and males during the periods of pregnancy and intense spermatogenesis, respectively.

Pregnant females spent significantly more time foraging (period 1: mean = 359 min) than males during late spring (period 1: mean = 161 min) and females during the post-lactation period (period 2: mean = 221). In contrast, during the period of highest spermatogentic activity in mid summer males foraged significantly longer (period 2: mean = 363 min) than during late spring and also significantly longer than post-lactating females. Prey attack rate during foraging flights did not vary significantly between gender and reproduction period. Based on a mean number of 8.3 prey attacks per minute, the time spent foraging, and a capture success rate of either 50 % or 92 % that were published for the ecological similar Myotis lucifugus, we calculated two models for food intake of female and male Daubenton’s bats during late spring and mid summer. Calculated intake values with a feeding rate of 7.6 insects per minute (= 92 % capture success rate) were more in line with literature data for other insectivorous bats than values calculated assuming a capture success rate of only 50%.
Chapter 3 – *Myotis daubentonii*

Estimates of food intake were based on mass and energy values of chironomids, the main prey item of Daubenton’s bats. In the model assuming the higher capture success rate, calculated food intake of female Daubenton’s bats ranged between 4.9 g of insects per day during post-lactation period (period 2) and 8.0 g during pregnancy (period 1), providing the animals with 3.0 to 5.0 kJ of ingested energy per gram body mass and day. Calculated food intake of male Daubenton’s bats ranged between 3.6 g insects per day during late spring (period 1) and 8.0 g during period of intensive spermatogenesis in mid summer (period 2), providing the animals with 2.6 to 5.7 kJ of ingested energy per gram body mass.

The findings of the present study suggest that the food intake of female and male Daubenton’s bats requires a high capture success linked to feeding grounds with a high density of small and soft membranous insects to cover the energy demand during energy demanding periods of the reproductive cycle.

INTRODUCTION

All Central European bat species are insectivorous and their reproductive cycles are adapted to the seasonal fluctuations in prey availability. In females, pregnancy and lactation are synchronized with the period of highest food availability in late spring and early summer. In males, spermatogenesis takes place in mid summer when insect density reaches a peak. Pregnancy, lactation and spermatogenesis are energy demanding processes and require an increase in food intake (Kunz 1974, Anthony and Kunz 1977, Racey and Speakman 1987, Heidemann 2000, Speakman and Thomas 2003, Dietz and Kalko 2005).

However, thus far no quantitative data on seasonal variation in food intake of female and male bats are available. We therefore investigated the European trawling bat *Myotis daubentonii*, whose foraging behaviour is adapted to hunt insects above water surfaces (Jones and Rayner 1988, Kalko and Schnitzler 1989, Siemers *et al.* 2001). The preferred foraging strategy of Daubenton’s bats above waters and the characteristic flight close to the water surface enables a rather easy and reliable observation of capture attempts.

Daubenton’s bats feed nearly exclusively on aquatic insects, primarily Chironomidae (Swift and Racey 1983, Sullivan *et al.* 1993, Beck 1995, Vaughan 1997) with a mean body-length of 7.2 mm (Taake 1992). The caloric content of chironomids ranges from 19.1 to 25.3 kJ per
gram dry mass (Tubb and Doris 1965, Wissing and Hassler 1968, 1971, Cummins and Wuycheck 1971, Driver et al. 1974, De la Noüe and Choubert 1985) and is similar to values reported for other aquatic invertebrates (Armitage 1995).

A first estimation of food consumption for a pregnant female Daubenton’s bat indicated an energy demand of 43.1 kJ d\(^{-1}\) and an amount of 7.2 g d\(^{-1}\) insects to provide this energy (Dietz 1998). In the present study we investigated comparable food intake and ingested energy of female and male Daubenton’s bats at different reproductive periods. We hypothesized that the energy demand and, therefore, the food intake of pregnant females in late spring is higher than that of males at the same time and also higher than that of females after fledging of the young in mid summer. Furthermore, we assumed that the energy demand of male Daubenton’s bats is highest during the period of maximum spermatogenetic activity and steepest increase of body mass in mid summer (Encarnação et al. 2004a, b).

In order to test the hypothesis of seasonal differences in energy demand between the two sexes, we calculated for the first time food intake and ingested energy of Daubenton’s bats during the periods of pregnancy and spermatogenesis. For this we determined the body mass and caloric content of chironomids from the study area as a basic for the calculation of food intake and energy ingestion.

If energy demand and food intake differ between female and male Daubenton’s bats, we assume different foraging activities in the feeding grounds to meet nutritional requirements (see Dietz and Kalko, submitted). Because Daubenton’s bats feed mainly on small and soft membranous insects, the capture attempts, success rate and subsequent the insect consumption should be high to compensate the energy demand. First estimations published by Kalko and Braun (1991) and Dietz (1998) support this assumption. To test the hypothesis that most of the capture attempts are successful we calculated the daily food intake and energy demand assuming a success rate of either 50 % or 92 %. Both estimates are available for *Myotis lucifugus* (Gould 1955, 1959, Anthony and Kunz 1977, Rydell et al. 2002), a closely related Nearctic species with a similar body mass that feeds on comparable prey items.
Chapter 3 – Myotis daubentonii

MATERIALS AND METHODS

Field site

The study was conducted from 1996 to 2003 in Central Hessen (Germany). The study area is located around the city of Giessen and is used as a summer habitat by Daubenton’s bats with highest elevation of 274 m. Animals use predominantly tree roosts in mixed forests that mainly consist of deciduous trees. Several ponds and the river Lahn are the most important feeding sites, mostly situated within 2 - 4 km of the roosting sites. Tree-lined brooks and tree rows were regularly used as flight paths to the feeding grounds (Dietz and Fitzenräuter 1996, Encarnação et al. 2002).

Capture of bats

Bats were caught by mist-netting along the flight paths between roosts and feeding sites during emergence in the evening. Sex of the captured animals was determined by visual inspection, and young of the year were distinguished from adults based on the presence of unfused and translucent phalangeal epiphyses (Anthony 1988, Racey 1988) and a ‘chin-spot’ (Richardson 1994, Geiger et al. 1996) in the former. Body mass was measured with a digital balance (Kern EM 150-1, Ballingen-Frommern, Germany) to the nearest 0.1 g. Reproductive status of females was classified as pregnant, non-pregnant, lactating, and post-lactating according to the methods described by Racey (1982). The reproductive condition of males was classified based on to their epididymal distension following Encarnação et al. (2004a). After marking, the animals were released at the same location.

Radio-tracking

Radio-tracking data from 14 adult females and 22 adult males of Daubenton’s bats were analysed for this study. For radio-tracking we used transmitters weighing between 0.4 and 0.6 g (type LB-2, Holohil Systems Ltd., Carp, Ontario, Canada). They were attached to the fur between the shoulder blades using skin-bond (Smith & Nephew™). Transmitters fell off after about 3 - 8 days. Radio-tracking was performed by cross-bearing followed by the ‘homing-in-on-the-animal’-method (White and Garrot 1990). This practice allowed us to locate tagged
bats within an area of 50 m. To increase the exactness of the ‘homing’-method, a small piece of reflection foil was fixed to the tip of the flexible antenna. This enabled an easier observation of the bat in its foraging area using a spotlight or a night-vision binocular (Filin 1 BN 2.5 x 56, Kiev, Ukraine).

The bats were tracked by three to four observer-groups, each equipped with a VR500-receiver and an HB9CV-hand-held antenna with amplifier (Wagener Telemetrieanlagen, Cologne, Germany). The observation time corresponded to the astronomical night length. During the night, the behaviour was continuously monitored, and the following data were recorded: 1) departure time (first departure from day roost after the period of daily inactivity), 2) arrival time (last arrival at day roost before the period of daily inactivity), 3) flight-time over water (most likely equivalent to time spent foraging), 4) remaining flight-time (e.g. commuting flights between roost and foraging area), 5) time spent resting outside the day roost, 6) time spent in the day roost, and 7) undetermined (animal location and behavior unknown).

Eight females and 11 males were tracked during the pregnancy period (observation period 1: 8 May – 4 June). For comparisons, 6 females and 11 males were tracked during the period of high spermatogenetic activity (observation period 2: 24 July – 22 August). For analysis of the nightly foraging time (= flight-time over water), only nights with a contact time over 90 % were taken into consideration (102 nights).

**Observations with light-sticks**

To determine the prey attack rate of Daubenton’s bats we marked 91 bats with small, chemiluminescent snap light-sticks, similar to methods applied by Buchler (1976a) and Barataud (1992). Light-sticks were attached to the fur of the back with a drop of skin-bond (Smith & Nephew™). During the first observation period, we marked 24 adult males and 13 pregnant females, and during the second period 26 adult males and 28 post-lactating females.

The light-sticks (size of 12 × 2 mm, weight about 0.2 g) were visible from a distance of about 50 m with the naked eye and from about 80 - 100 m using a night-vision binocular (Filin 1 BN 2.5 x 56, Kiev, Ukraine). Adult females were marked with blue and adult males with green light-sticks. The sticks remained visible for one night and mostly fell off the following day.
After releasing, the animals were monitored at the feeding grounds for the whole night until sunrise. The number of prey attacks per animal was recorded using night-vision binoculars, a mechanical counter and a micro-chronometer (Casio HS 50W, Norderstedt, Germany). As prey attacks we counted all visible ‘low catches’ and ‘high catches’ according to Kalko and Schnitzler (1989).

**Body mass and caloric content of Chironomidae**

We analysed the caloric content of Chironomidae, the main prey item of Daubenton’s bats in the study area (Dietz, unpublished data). Insects were sampled at the feeding sites by nightly light trapping during the radio-tracking periods using the method of Taake (1992). Insects were sampled at the feeding sites by nightly light trapping during the radio-tracking periods using the method of Taake (1992). Insects were trapped in a glass container (height x length x width: 20 x 30 x 20 cm) containing water with detergent. It was placed at the bank of the pond of about 40 cm above the water surface. The light beam was aimed at a mirror that then reflected the light towards the water surface. Insects that were attracted by the light fell into the detergent of the light trap and thus collected in the morning. Afterwards, they were transferred in grimp-top vials with pure water and frozen at -21°C until analysis. Insects were determined at the family level based on Schaefer (1994).

Body-length, wet mass, moisture content and dry mass were measured for 354 sampled chironomids with a body-length between 4.5 and 15 mm. Body-length was determined by measuring the dorsal surface from the anterior edge of the head capsule to the posterior tip of the abdomen using a binocular (Leica MS 5, 15 - 100 x, Bensheim, Germany) with the use of an ocular micrometer (± 0.1 mm) and illumination (Halolux 150, Streppel oHG, Wermelskirchen, Germany). After measuring, individuals were transferred to pre-weighed aluminium pans, air-dried at 25°C for 60 min and weighed (wet mass, WM) on a microbalance (Sartorius BP 110S, ± 0.0001 mg, Göttingen, Germany). Subsequently the insects were oven-dried at 105°C for 3 h and weighed again to obtain their dry mass (DM). Moisture content was calculated as the difference between wet and dry mass.

For determination of the caloric content of the chironomids, five pre-weighed aluminium pans were filled with a sample weighing between 1.4 - 4.9 g (WM). The five samples were then oven-dried at 105°C for 3 h and compressed to form tightly-packed pellets of 0.3 to 1.1 g.
DM. Subsequently the caloric value of each sample was determined by adiabatic bomb calorimetry using an IKA calorimeter C 4000 (Janke and Kunkel, Staufen im Breisgau, Germany). Data are expressed as kJ per g DM.

**Calculation of food intake and energy ingestion**

Food intake was calculated as the product of 1) the time spent foraging revealed by radio-tracking, 2) the mean prey attack rate recorded using light-sticks, 3) an assumed capture success rate of either 50% (Gould 1955, 1959, Anthony and Kunz 1977) or 92% (Rydell et al. 2002) and 4) the average WM per insect gained from this study (see results). The values for the capture success rates used in the calculations had been obtained for *M. lucifugus*, a closely related species of similar body mass as the Daubenton’s bat and with a comparable preference for small and soft membranous insects (Gould 1955, Findley 1972, Whitaker 1972, Belwood and Fenton 1976, Buchler 1976b, , Anthony and Kunz 1977, Frenckell and Fenton 1987).

Ingested energy per night was calculated as the product of the amount of food taken up by the bat and the determined caloric content of per gram of chironomid prey. Nightly ingested energy per gram body weight of *M. daubentonii* was calculated based on the recorded body mass of the radio-tracked individuals.

To assess the nightly ingested energy and food intake of the bats, we also estimated the field metabolic rates (FMRs, kJ d⁻¹) for males and females based on the mean body mass (BM) of the radio-tracked *M. daubentonii*, using the formula (Speakman and Thomas 2003):

\[
\log_e \text{FMR} [\text{kJ d}^{-1}] = 1.87 + 0.732 \log_e \times \text{BM} [\text{g}].
\]

Because of the consistency of body mass data for both females and males in the two observation periods, we pooled data from individuals of the same sex. Applying the conversion factors for the energetics of *M. lucifugus* used by Kurt et al. (1989, see below) and the analyzed caloric content of chironomids gained from this study, ingested energy (FMR × 1.32) as well as assimilated energy (FMR × 1.11) were calculated.
Chapter 3 – *Myotis daubentonii*

**Statistical analysis**

To compensate for variation in the number of observation nights per individual (range: 2 - 5 nights), we used individual mean nightly foraging time for calculating the mean number of prey attacks by the bats per period. No significant differences in mean prey attack rate could be observed between the two periods and the two sexes (non-parametric Kruskal-Wallis-ANOVA by ranks (KW-ANOVA)). Therefore we used mean prey attack rate averaged over all observation intervals for calculation. Data on nightly foraging time and number of prey attacks of female and male Daubenton’s bats during the two periods were compared by KW-ANOVA, followed by multiple pairwise comparisons with the Mann-Whitney-U-Test (MW-U). To correct for error accumulation due to replicate testing, we applied Bonferroni $\alpha$-adjustment (Sachs 1984). Using body length and wet and dry mass data of Chironomidae, linear regression models were calculated to estimate the wet mass of chironomids with a body length of 7.2 mm, the size which is preferred by Daubenton’s bats (Taake 1992). Pearson’s Product-Moment-Correlation was used to test the correlation of wet mass and dry mass of the chironomids with body length. For all tests, p-values < 0.05 were considered to indicate significance. The mean caloric content of one gram fresh chironomits was calculated based on the analyzed data of mean caloric content of oven-dried insects and the determined moisture content. Statistical evaluation of the data was performed with the software package Statistica v6.0 for Windows (StatSoft).

**RESULTS**

**Foraging time and prey attack rate of Daubenton’s bats**

Nightly foraging time of Daubenton’s bats ranged from 20.3 to 462.7 min (Table 1) and varied significantly between the four groups (period 1: pregnant females, males with low spermatogenetic activity; period 2: postlactating females, males with intense spermatogenetic activity; $H(df = 3, n = 36) = 22.22, p < 0.0001$). Nightly foraging time of pregnant females during period 1 (mean (SD) = 359 (51) min, median = 338 min) was significantly higher than that of males during the same period (mean (SD) = 161 (91) min, median = 161 min, $p < 0.01$) and also higher than that of post-lactating females during period 2 (mean (SD) = 221 (76) min, median = 225 min, $p < 0.05$).
Male Daubenton’s bats spent significantly more time foraging during period 2 (mean (SD) = 363 (87) min, median = 351 min) than females during the same period (p < 0.05) and males in period 1 (p < 0.01). Foraging time of females during period 1 did not differ from foraging time of males in period 2 (p = 0.27) and also by females during period 2 and males in period 1 (p = 0.23) (Figure 1).

Over the whole study period, 1587 prey attacks of Daubenton’s bats were observed in 146 observation intervals during a total monitoring time of 3.3 h. Prey attack rates ranged from 0 to 20.8 attacks per minute and did not vary significantly between the four groups (H(df = 3, n = 146) = 2.56, p = 0.47) (Figure 1). Mean prey attack rate calculated over both periods and sexes was 8.3 (SD = 4.3) prey attacks per minute.

**Figure 1.** Box plots of foraging time per night and prey attack rate of female and male Daubenton’s bats during the two observation periods (n = individuals / observation intervals). Nightly foraging time varied significantly among all groups (Kruskal-Wallis-ANOVA by ranks: H(df = 3, n = 36 individuals) = 22.22, p < 0.001). No significant differences of prey attack rates could be observed (Kruskal-Wallis-ANOVA by ranks: H(df = 3, n = 146 observation intervals) = 2.56, p = 0.47). Groups identified by the same lower case letters are significantly different (Mann-Whitney U-tests with Bonferroni correction: p < 0.05).
Chapter 3 – *Myotis daubentonii*

**Body mass and caloric content of Chironomidae**

Body-length of chironomids correlated significantly with their wet mass (PMC: \( r = 0.81, p < 0.001, n = 354 \)) and dry mass (PMC: \( r = 0.82, p < 0.001, n = 354 \)). The equation for the linear regression of wet mass \( [y] \) on body length \( [x] \) of chironomids was \( y = -1.929 + 0.66637 x \) \((r^2 = 0.66)\), the respective equation for dry mass was \( y = -0.4302 + 0.15 x \) \((r^2 = 0.67)\). Based on these regression equations, a chironomid with a body-length of 7.2 mm, the size preferred by Daubenton’s bats (see Taake 1992), has a calculated wet mass of 2.9 mg, a moisture content of 77 % and a calculated dry mass of 0.7 mg. The determined mean caloric value for Chironomidae is 24.97 kJ per gram dry mass \((SD: 0.53, \text{range: 24.35 - 25.59} \text{ kJ g}^{-1} \text{ DM}, n = 5)\). Given a moisture content of 77 %, the mean caloric value for fresh chironomids is 5.75 kJ g\(^{-1}\) WM.

**Food intake and energy ingestion of Daubenton’s bats**

Calculated number of prey attacks per bat and night (calculated as mean individual foraging time per night \([\text{min}] \times 8.3 \text{ prey attacks min}^{-1}\)) ranged between 169 and 3840. Highest values were estimated for males during period of intense spermatogenesis (period 2: mean \((SD) = 3011 (723) \text{ prey attacks per night}\)), followed by pregnant females during period 1 (mean \((SD) = 2979 (420) \text{ prey attacks per night}\)). In accordance with the reduced nightly times spent foraging, lower values resulted for post-lactating females in period 2 (mean \((SD) = 1835 (629) \text{ prey attacks per night}\) and males during period 1 (mean \((SD) = 1333 (758) \text{ prey attacks per night}\) (Table 1).

The low-success model for food intake and ingested energy of Daubenton’s bats based on a capture success rate of 50 % estimated for *M. lucifugus* (Gould 1955, 1959, Anthony and Kunz 1977). This assumed capture success rate corresponds to an uptake of 4.2 insects per minute by a bat. In this model mean food intake of females ranged between 2.7 g d\(^{-1}\) during post-lactation (period 2) and 4.3 g d\(^{-1}\) during pregnancy (period 1). Mean daily ingested energy per female was calculated to range between 15.3 and 24.8 kJ d\(^{-1}\), corresponding, respectively, to 1.6 and 2.7 kJ d\(^{-1}\) per gram body mass. Mean food intake of males ranged between 1.9 g d\(^{-1}\) in period 1 and 4.4 g d\(^{-1}\) during spermatogenesis in period 2. Calculated mean ingested energy ranged from 11.1 kJ d\(^{-1}\) to 25.1 kJ d\(^{-1}\) respectively 1.4 - 3.1 kJ d\(^{-1}\) per gram body mass (Table 1).
Food intake

The high-success model based on a capture success rate of 92% as determined by Rydell et al. (2002) for *M. lucifugus*, corresponded to an uptake of 7.6 insects per minute by a bat. In this model mean food intake of females ranged between 4.9 g d\(^{-1}\) (period 2) and 8.0 g d\(^{-1}\) (period 1) and mean ingested energy ranged from 28.2 kJ d\(^{-1}\) to 45.7 kJ d\(^{-1}\) (3.0 - 5.0 kJ d\(^{-1}\) g\(^{-1}\)). Mean values of food intake of males ranged between 3.6 g d\(^{-1}\) (period 1) and 8.0 g d\(^{-1}\) (period 2). This resulted in a mean of ingested energy ranging from 20.5 to 46.2 kJ d\(^{-1}\) (2.6 - 5.7 kJ d\(^{-1}\) g\(^{-1}\)) (Table 1).

Based on the mean body mass of the radio-tracked females over both study periods (9.4 g) an average FMR of 33.5 kJ d\(^{-1}\) (3.6 kJ d\(^{-1}\) g\(^{-1}\)) was calculated using the formula of Speakman and Thomas (2003). Applying the conversion factors used by Kurta et al. (1989), this corresponds to 37.2 kJ d\(^{-1}\) (4.0 kJ d\(^{-1}\) g\(^{-1}\)) of assimilated energy and 44.0 kJ d\(^{-1}\) (4.7 kJ d\(^{-1}\) g\(^{-1}\)) of ingested energy. This energy demand is met when 7.7 g of insects are consumed per day. Based on the mean body mass of the radio-tracked male Daubenton’s bats over both study periods (8.3 g) an average FMR of 30.4 kJ d\(^{-1}\) (3.7 kJ d\(^{-1}\) g\(^{-1}\)) was calculated. This value corresponds to 33.8 kJ d\(^{-1}\) (4.1 kJ d\(^{-1}\) g\(^{-1}\)) of assimilated and 40.0 kJ d\(^{-1}\) (4.8 kJ d\(^{-1}\) g\(^{-1}\)) of ingested energy and is provided at an insect consumption of 7.0 g d\(^{-1}\).
### Table 1. Body mass, nightly foraging time, number of prey attacks, number of captured insects, food intake and ingested energy of radio-tracked female (f) and male (m) Daubenton’s bats during the two observation periods. Values were calculated based on the recorded foraging time (min) multiplied by 8.3 prey attacks per minute, a capture success rate of 50 % (Gould 1955, 1959, Anthony and Kunz 1977; corresponding to an uptake of 4.2 insects per minute) and, alternatively, a capture success rate of 92 % (Rydell et al. 2002; corresponding to an uptake of 7.6 insects per minute), a calculated insect weight of 2.9 mg, and a calculated energy content of 5.75 kJ per gram of fresh insect prey.

<table>
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<th>period</th>
<th>sex</th>
<th>body mass [g]</th>
<th>foraging [min d⁻¹]</th>
<th>prey attacks [n d⁻¹]</th>
<th>succ. captures [n d⁻¹]</th>
<th>food intake [g d⁻¹]</th>
<th>ing. energy [kJ d⁻¹]</th>
<th>ing. energy [kJ d⁻¹ g⁻¹]</th>
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<td>1</td>
<td>f</td>
<td>9.3 (1.4)</td>
<td>359 (51)</td>
<td>2979 (420)</td>
<td>1489 (210)</td>
<td>4.3 (0.6)</td>
<td>24.8 (3.5)</td>
<td>2.7 (0.6)</td>
</tr>
<tr>
<td>1</td>
<td>m</td>
<td>8.2 (1.0)</td>
<td>161 (91)</td>
<td>1333 (758)</td>
<td>667 (379)</td>
<td>1.9 (1.1)</td>
<td>11.1 (6.3)</td>
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<tr>
<td>2</td>
<td>f</td>
<td>9.5 (1.2)</td>
<td>221 (76)</td>
<td>1835 (629)</td>
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<tr>
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<td>3011 (723)</td>
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<td>4.4 (1.1)</td>
<td>25.1 (6.0)</td>
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</table>

1) Ingested energy per gram body mass of bats.
DISCUSSION

The present study revealed pronounced seasonal changes in foraging activity, food intake and ingested energy of female and male Daubenton’s bats during different periods of the reproductive cycle.

Foraging activity

The results confirmed our initial proposition that foraging activity of female and male Daubenton’s bats should differ in relation to reproductive condition and related energy demand. As shown in the study of Dietz and Kalko (submitted) ambient temperature had no notable influence on foraging activity of Daubenton’s bats. Visual observations of radio-tracked bats with a night-vision binocular confirmed that flight time over water is equivalent to foraging time. Therefore, it is reasonable to assume that the differences in foraging activity of *M. daubentonii* reflects differences in energy demand and nutrition requirements during the different reproductive periods, in particular the higher energy demand of females during pregnancy (McLean and Speakman 1999) and of males during spermatogenesis (Entwistle *et al.* 1998).

The differences in foraging time of female and male Daubenton’s bats are also in line with observations showing that males enter torpor less often during the period of spermatogenesis, probably because low body temperatures may impede spermatogenesis (Entwistle *et al.* 1998). However, as maintenance of higher body temperatures incurs higher energy costs and thus requires higher food intake, males need to fly longer than females. In contrast, during spring pregnant females do not use daily torpor and forage significantly longer than males that regularly fall in torpor, presumably to reduce their energy expenditure (Dietz and Kalko 2005).

Capture rates

As assumed, we found no significant differences in prey attack rates between females and males throughout the observation periods. Both sexes show similar prey attack rates (about
8.3 per minute) in late spring and mid summer. This corresponds to an average time interval of 7.2 seconds between two attacks. Comparable capture attempt rates were estimated by Kalko and Braun (1991) who counted terminal phases at time intervals of about 6.5 seconds. This high rate of capture attempts suggests that Daubenton’s bats are able to effectively exploit high insect densities.

The number of terminal phases and capture attempts are not identical with success rates (Kalko and Braun 1991). Misses and unsuccessful attempts are also accompanied by terminal phases that often cannot be reliably distinguished from terminal phases emitted during successful catches (Britton and Jones 1999). To estimate the success rate of Myotis daubentonii in the field we therefore compared our estimated feeding rates with data of M. lucifugus (see also Kalko and Braun 1991, Dietz 1998). Mean difference in body mass of female M. lucifugus between first leave and first return to the roost was 1.6 g in pregnant and 2.3 g in lactating individuals (Anthony and Kunz 1977). Unlike the present study, an average weight of 2.2 mg per insect (Griffin et al. 1960) was taken to calculate the feeding rate of the bats, which encompassed 7 insects per min in the study by Anthony and Kunz (1977). This compares well with the feeding rate of 8 insects per min calculated by Gould (1955, 1959) for this species.

In our study, feeding rates of 7.6 insects per minute were calculated for Daubenton’s bats with an assumed capture success rate of 92 % (high-success model, Table 1) that has been proposed for M. lucifugus (Rydell et al. 2002), whereas the values of the low-success model with a capture success rate of 50 % were much lower (4.2 fed insects per minute). Based on these results it can be hypothesized that the energy demand of Daubenton’s bats during energy demanding periods of the reproductive cycle can only covered by a high capture success linked to feeding grounds with a high density of small and soft membranous insects.

**Food intake and ingested energy of Daubenton’s bats**

Assuming capture success rates of either 50 % (low-success model) or 92 % (high-success model) we calculated average daily food intake of Daubenton’s bats. Pregnant females in period 1 consumed either 4.3 g d⁻¹ or 8.0 g d⁻¹ of insects. The value calculated with a capture success rate of 92 % is more comparable with the values cited in the literature than the values of the low-success model with a capture success rate of 50 %. For M. lucifugus, Kurta et al.
(1989) calculated an insect consumption of 5.5 g d\(^{-1}\) for a pregnant female of 9 g body mass and of 6.7 g d\(^{-1}\) for a 7.9 g lactating female, while Dietz (1998) calculated a food consumption of 7.2 g d\(^{-1}\) for a pregnant female of \textit{M. daubentonii} weighing 9.5 g.

Using the data on the wet mass and energy content of fresh insects obtained in our study, calculated daily ingested energy in female \textit{M. daubentonii} in the low-success model ranged from 15.3 kJ (1.6 kJ g\(^{-1}\), period 2) to 24.8 kJ (2.7 kJ g\(^{-1}\), period 1) and in the high-success model from 28.2 kJ (3.0 kJ g\(^{-1}\), period 2) to 45.7 kJ (5.0 kJ g\(^{-1}\), period 1). Converting these values into field metabolic rates (FMRs), using the conversion factors used by Kurta \textit{et al.} (1989), the high-success model is again more comparable with data previously published by other authors. Thus, Speakman and Thomas (2003) calculated FMRs for insectivorous bat species of between 1.7 and 4.4 kJ d\(^{-1}\)g\(^{-1}\). Using their equation, a FMR of 3.6 kJ d\(^{-1}\)g\(^{-1}\) was calculated for female and of 3.7 kJ d\(^{-1}\)g\(^{-1}\) for male Daubentons’ bats (all females and males pooled over both periods). This energy is provided at an insect consumption of 7.7 g d\(^{-1}\) for females and of 7.0 g d\(^{-1}\) for males. These values correspond well with the calculated food intake in the high-success model for pregnant females in period 1 and males with high spermatogonetic activity in period 2 (both 8.0 g of insects per day). However, mean food intake of post-lactating females during period 2 (high-success model: 4.9 g d\(^{-1}\)) and males during period 1 (high-success model: 3.6 g d\(^{-1}\)) was considerably lower.

In conclusion, the results of the present study support the hypothesis that energy demand and, in consequence, food intake of Daubentons’ bats is highest during reproductive processes. This is in accordance to Reynolds and Kunz (2000) who documented distinct morphological changes in the gastrointestinal tract of lactating \textit{M. lucifugus}. This suggests that increased food intake and assimilation are the primary factors with which bats compensate for the increased energy demand during pregnancy and lactation.

To conclude, the capture success rate of \textit{M. daubentonii} should be between 85 % and 95 % to cover their energy demand. Additionally, Daubentons’ bats require feeding grounds with a high insect density of swarming and soft membranous insects to optimize their food intake especially during reproduction.
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SMALL SCALE DISTRIBUTION PATTERNS OF FEMALE AND MALE DAUBENTON’S BATS (*MYOTIS DAUBENTONII*) - IMPLICATIONS FOR BAT MONITORING AND CONSERVATION STRATEGIES

ABSTRACT

We analysed the distribution and relative abundance of foraging Daubenton’s bat (*Myotis daubentonii*) in the lowlands and uplands around the river Lahn near the city of Giessen (Hessen, Central Germany). As a trawling bat, *M. daubentonii* relies mostly on water bodies for foraging. Therefore we assumed a positive correlation between distribution and relative abundance of Daubenton’s bats with the amount of water surface in our study area. We further expected an unequal distribution of female and males Daubenton’s bats especially during the energy demanding pregnancy and lactation period of females.

We investigated a total of 64 ponds and lakes and a 42.3 km long section of the river Lahn in the summertime 2001 with standardized nightly spotlight counts for the presence of Daubenton’s bats. Relative abundance and sex ratio of females and males were assessed in three detailed studied sites from 1992 - 2003 by mist-netting along regularly used flight paths (n = 1771 caught individuals). 30 reproductively active females were radio-tracked to localize nursery colonies and to determine flight distances between roost and foraging areas.

Daubenton’s bats were present in 75 % of the surveyed waters. The number of Daubenton’s bats correlated positively with the area of the respective water surface and negatively with the distance to the nursery colonies. Nursery colonies were predominately located in the lowlands close to the river Lahn (distance: < 1.8 km). Mean flight distance between nursery colonies and foraging areas was 2.3 km (mean ± 1.4 km, range: 0.64 - 6.3 km).

The number of female and male *M. daubentonii* was unequal and differed significantly between the three sites where we studied relative abundance and sex ratio in greater detail. In
the lowland we found one site clearly dominated by females (79.8 % ♀ : 20.2 % ♂, n = 168 ind.) and a second site with an almost balanced sex ratio (49.3 %♀ : 50.7 % ♂, n = 864 ind.). At the third site in the uplands males outnumbered females (13.6 %♀ : 86.4 ♂, n = 739 ind.). These ratios remained largely constant from spring to mid summer and changed at the beginning of September.

The study revealed that a detailed knowledge of the spatial distribution of gender specific roost sites and key foraging habitats is necessary for the establishment of meaningful monitoring and conservation measures.

**INTRODUCTION**

Daubentons’s bat (*Myotis daubentonii*) is one of the three European trawling bats (*M. dasycneme* and *M. capaccini*). It is mainly adapted to hunt for insects above water surfaces (Jones and Rayner 1988, Kalko and Schnitzler 1989, Siemers et al. 2001). Daubentons’s bats feed mostly on Chironomidae (Swift and Racey 1983, Beck 1995) that are caught when they emerge or swarm just above the water surface. Because of their feeding habits, riverine areas with extensive still water surfaces represent key foraging habitats for this species (Warren et al. 2000). The importance of those foraging areas is further supported by radio-tracking studies, where *M. daubentonii* has been documented to spend well over 90 % of their nightly activity time (Dietz 2000, Dietz and Kalko submitted, Encarnação et al. 2004). The high preference of waters leads to the presumption that the abundance of Daubentons’s bats across the landscape is positively correlated with the amount of water surface. Therefore, in a first step, we examined the distribution and relative abundance of Daubentons’s bats in our research area in relation to the available water surface.

Results of previous studies led to the second assumption that spatial distribution of *M. daubentonii* should differ depending on gender and time of year. This assumption is based on differences in foraging activity and thermoregulation of females and males, especially during the period of pregnancy and lactation (Dietz and Kalko submitted). Pregnant females showed significantly longer flight times than males. At the same time, males fell in torpor during the day significantly more often than females (Dietz and Kalko 2005). Female Daubentons’s bats avoided a reduction of body temperature to save energy presumably because a decrease would negatively affect foetal development and milk secretion (Wilde et al. 1995 and 1999). This
leads to a higher overall energy demand of reproducing females, particularly during pregnancy and lactation period (Kurta et al. 1989). Studies on *Myotis lucifugus* and *M. velifer* have shown that food consumption of females increases by about 45% from pregnancy to lactation period in temperate zone (Kunz 1974, Anthony and Kunz 1977). Therefore, reproducing female *M. daubentonii* should choose parts of waters with a high insect abundance combined with short commuting distances to roosting sites to compensate the higher energy requirements.

As a consequence of these differences in energy demands and thus needs for nutrient rich foraging habitats we hypothesize that the higher nutritional requirements of pregnant and lactating females compared to males may lead to intra-specific competition if both sexes feed in the same foraging area. A previous study has shown that pregnant and lactating female Daubenton’s bats show high site fidelity and hunt within small, individual foraging areas in conjunction with long foraging times (Dietz and Kalko, submitted). We assume that reproductively active females should defend those small-scale, high quality and individual foraging areas against other individuals to ensure continuous high feeding success and thus enough energy gain to cover the cost-intensive pregnancy and lactation period (see Barclay 1984, Rydell 1986, Balcombe and Fenton 1988). First observations on individual *M. daubentonii* in our study area suggest territorial behaviour because we occasionally saw individuals chasing each other across the foraging area, accompanied by audible vocalisations (see Wallin 1961). Usually, one animal retreated in the course of those pursuits.

As a consequence of an increased energy demand and increased territoriality of reproductive females we expect small scale variation in the distribution of female and male Daubenton’s bats across a landscape. We assume that the distribution of nursery colonies and therefore a higher portion of females should be related to short commuting distances to favourable feeding sites. This assumption is further supported by observations in previous studies where distinct differences in the distribution patterns of male and female Daubenton’s bats were noted in the valleys of the Bernese Jura Mountains in Switzerland. Only males were present in the valleys from May until August, while adult females and juveniles were mist-netted exclusively at lower altitudes, presumably because of more favourable climatic conditions (Leuzinger and Brossard 1994). Similar observations were reported for *M. daubentonii* in the hilly countryside of the Yorkshire Dales, England (Senior et al. 2005) and in the high Abruzzo mountains in Central Italy (Russo 2002). However, except those studies in mountain
ranges, possible differences in the distribution patterns of *M. daubentonii* on local scales in the lowlands are not known.

We therefore assessed the distribution patterns and relative abundance of female and male Daubenton’s bats in our study area along the river Lahn and adjoining areas with still water bodies. We tested the assumption that the relative abundance of females and males differs seasonally whereby females should forage mostly next to nursery colonies and in climatically favoured lowland areas at the river Lahn during pregnancy and lactation compared to males. This pattern should change in mid summer after the young become volant.

In addition to important base-line data, the main goal of our study is to provide scientifically data for conservation (see Caughley 1994) and monitoring strategies in line with international agreements like the Habitat Directive (European Council Directive 92/43/EEC), which lists all bats in Annex IV for strict protection. Meaningful recommendations require detailed knowledge about regions of reproduction, population structures, and key habitats.

**MATERIALS AND METHODS**

**Study area**

The study area close to the city of Giessen (Hessen, central Germany) consisted of a hilly landscape with forests and a basin area that is mainly used for agriculture (Klausing 1988). The climate varies markedly depending on elevation (144 - 498 m a.s.l.). Mean ambient temperature is higher (16 °C – 17 °C in June) in the lowland areas along the river Lahn compared to the surrounding upland areas (15 °C). In contrast, means of rainfalls are lower (600 - 650 mm versus 700 mm in June) (Kalb and Vent-Schmidt 1981). About a third (34 %) of the study area is covered with forest, consisting predominantly of old grown (> 100 years) broadleaf trees. Water bodies in the area include the Lahn river (width ≥ 10 m), about 64 ponds of varying size (range: 0.08 - 34.2 ha), and brooks with a width of less than 5 m. The study area encompassed an area of about 1092 km² including 6.5 km² (0.6 %) of water surface (Figure 1).

We monitored foraging activity of Daubenton’s bats at the 64 ponds and along a 42.3 km-long stretch of the river Lahn between the Cities of Marburg and Wetzlar that represented a characteristic part of the landscape. We selected three sites within the study area with nursery
colonies known since 1992 - 1995 to investigate sex ratio and seasonal relative abundance of female and male Daubenton’s bats in greater detail: Allendorf, Giessen, and Staufenberg.

**Recording of foraging *M. daubentonii* with spotlight counting**

Hunting Daubenton’s bats can be rather easily monitored because of their characteristic foraging behaviour. They mostly fly low over water (< 20 cm) and take food from the water surface either in a brief dip (low catch) or by briefly rising up into the air (high catch) (Jones and Rayner 1988, Kalko and Schnitzler 1989). In order to count foraging *M. daubentonii* above the water we used a strong portable spotlight (12V/50W, halogen reflector). We scanned the water surface continuously from the left to the right from fixed points on the shore. All *M. daubentonii* flying at a height up to 1 m above the water surface were recorded. We reiterated the counting for three times each after a break of one minute. The spot light enabled us to recognize flying bats at a distance of 60 - 70 m. This corresponded to a semicircular area of about 8000 m² centered on our fixed points at the shore. In 2001, two spotlight counts (June and August) were conducted at each of the 64 still water sites between 45 and 140 minutes after sunset. During this time Daubenton’s bats show the highest flight activity at night (Dietz and Kalko, submitted). The weather conditions at all countings were favourable (> 15°C ambient temperature at dusk) and without rainfall and strong wind.

At large ponds we counted simultaneously from several locations at distances of about 150 - 200 m to avoid double-counting from the same individuals. Finally, the relative abundance of foraging *M. daubentonii* for the entire still water bodies was extrapolated from the number of individuals within the areas illuminated by the spot light (number of counting locations x 8000 m²). Analyses were done with the mean relative abundance of foraging *M. daubentonii* from both countings.

Several observers in canoes assessed the distribution and relative abundance of Daubenton’s bats along a 42.3 km stretch of the river Lahn during the first half of the night. We counted the whole stretch during one night with five teams starting at the same time in different subsections of similar length. The canoes were kept close to a bank of the river, while the spotlight was directed towards the other bank. To avoid double-counting only *M. daubentonii* that crossed in upstream direction and were flying close to the water surface were recorded.
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The relative abundance for the complete 42.3 km section of the river Lahn in the study area was examined only once (June) because of the huge effort involved.

**Presence/absence recordings and estimates of relative abundance**

The counting at the still water bodies and the river Lahn were used for presence/absence controls and in a further step to estimate relative abundance. To compare the counting at the river Lahn with the results from the 64 still water bodies we divided the 42.3 km section into 33 sections of about 1.4 km.

We derived relative abundance of foraging *M. daubentonii* at still water habitats from the counted number of individuals within the illuminated area of each water body. For a graphically presentation of the distribution and relative abundance of *M. daubentonii* in the research area in relation to the amount of water surface we divided the research area in 1 km²-grids (n = 1200). The study area contained 91 x 1 km²-grids with examined water bodies or parts of it. In many cases a water body like the river Lahn or large ponds covered parts of two or more grids. The relative abundance of Daubenton’s bats was calculated proportional to the water surface within a 1 km²-grid.

To illustrate the overall distribution of Daubenton’s bats across the landscape, we assigned the relative abundance of foraging *M. daubentonii* at still water bodies and along the section of the river Lahn to one of four categories (0, < 5, < 25, ≥ 25 individuals, Figure 1) within a 1 km²-grid.

**Radio-tracking**

During the years 1996 - 2003, thirty reproductively active (pregnant or lactating) females were radio-tracked in the study area during the reproduction season (May 15 until July 31) in order to find nurseries, foraging areas and to determine commuting flight distances. The animals were caught with mist-nets on known flight routes and fitted with a transmitter weighing about 0.5 g (LB-2, Holohil, Ontario, Canada). This is below or only slightly above the 5 % threshold suggested by Aldridge and Brigham (1988) as limit for radiotracking. We used VR500 receivers (Wagener Telemetricanlagen, Cologne, Germany) with 2-element
hand-held antennas (HB9CV). The searches for the locations of the colonies and the foraging areas were done with the “homing-in-on-the-animal”-method (White and Garrott 1990). We followed individual bats for 2 - 8 nights to locate individual foraging areas (Dietz and Kalko, submitted). Direct distances between roosts and individual foraging areas were measured on the monitor of a PC with a mapping program (TOP25, Hessen). We classified the mean flight distance of all radio-tracked females as the average distance between roost and individual foraging area within a feeding site. The maximum flight distance was based on the greatest measured distance between roost and foraging area. Colony structure in roosts was confirmed by catching emerging bats in the evening with custom-made funnel-shaped basket traps (Mitchell-Jones and Mc Leish 1999).

**Recording the sex ratio composition through mist-netting**

We determined sex ratio of foraging *M. daubentoni* at three sites of the study area (Allendorf, Giessen, and Staufenberg) with nursery colonies nearby. Sex ratio is expressed as the ratio of adult females to adult males (n ♂ : 1 ♀) caught at evening emergence along the regular used flight routes between roost site and foraging habitat (Dietz and Fitzenräuter 1996, Encarnação et al. 2002). Bats were caught with mist-nets (8 x 3 m, 70 Denier, mesh width 16 mm) that were placed within the flight path of the bats. Data collecting encompassed 3 - 8 seasons depending on the study area. It started in April and ended in October each year. 253 trapping actions were performed between 1992 and 2003 (Allendorf: n = 13, Giessen: n = 116, Staufenberg: n = 124). Trapping started at sunset and ended 2 - 3 hours after bat emergence.

The age of the bats was determined by epiphyseal closure (Anthony 1988) and by documenting band numbers. Bands with individual numbers were provided by the Museum Alexander Koenig (Bonn, Germany). The reproductive status of females was classified as pregnant, non-pregnant, lactating, non-lactating, and post-lactating following Racey (1982).

**Statistics**

Data analysis and presentation were done using Statistica v6.0 for Windows (StatSoft). All data samples were tested for normality and equal variance. The correlation between relative abundance of *M. daubentonii* and water surface area was analyzed using the Pearson-Product-
Moment-Correlation and linear Regression Analysis. Differences in sex ratios between the three sites Allendorf, Giessen, and Staufenberg were tested for significance using Kruskal and Wallis H-Tests, followed by pairwise comparisons with the Mann-Whitney U-Test. Significance levels were adjusted using the Bonferroni-method.

RESULTS

Distribution and relative abundance of Daubenton’s bats

Daubenton’s bats were widely distributed in the study area. We found them at three quarters (n = 48) of the 64 still waters and also at about 75 % (n = 25) of the 33 sections at the river Lahn. In reference to the grid-system, we recorded foraging Daubenton’s bats in 82 of the 91 1 km²-grids with water bodies (Figure 1). Number of counted bats varied widely within the 1 km²-grids. Only a few bats were monitored in about one third of the grids (n = 30, < 5 individuals). In another third (n = 31) between five and < 25 foraging Daubenton’s bats were found and in about a quarter of the grids (n = 21) we counted high numbers with 25 or more Daubenton’s bats. The number of counted Daubenton’s bats increased significantly with increasing water surface per 1 km²-grid ($r^2 = 0.78; r = 0.89$, p < 0.001).

Distribution of Daubenton’s bats along the river Lahn was unequal. We counted a total of 856 Daubenton’s bats during our nightly survey with canoes along the 42.3 kilometers of the river. Mean abundance was 2.02 individuals per 100 m section of the river, ranging from 0 - 10.8 Daubenton’s bats.
Figure 1. Relative abundance of foraging Daubenton’s bats and nursery colonies along the river Lahn and adjoining regions given in four classes (0, < 5, < 25, ≥ 25 ind.) relative to the area of the water surface in 1km² - grid cells (n = 91 cells with water bodies).

**Distribution and flight distances of female bats**

We compared the distribution of Daubenton’s bats foraging over water with the distribution of colonies in the study area. Radio-tracking of lactating females revealed six nursery colonies in the study area (Figure 2). Four of the six colonies included more than 40 adult females and were located less than two kilometers away from the river Lahn. The results of radiotelemetry revealed continuous use of the river for foraging by females of the nursery colonies.

We found one colony (< 10 individuals) that was further away in the uplands of the study area and a sixth colony that was more than ten kilometres away from the river Lahn in the
lowlands without any relation to the river Lahn. Females of this colony were found at ponds and a small brook nearby the roost.

Mean flight distance of the 30 radio-tracked pregnant or lactating females between day roost and foraging area was 2.3 km (±1.4 km, range: 0.64 - 6.3 km). Only two females had a maximum commuting distance of more than four kilometres between nursery roost and individual foraging area with a maximum distance of 6.3 km.

Projecting the mean and maximum flight distances of the pregnant and lactating females as potential activity range around the nursery colonies, indicates a complete distribution of reproducing females for the study area along the river Lahn (Figure 2). Densities of foraging Daubenton’s bats per 1 km²-grids determined with spotlight-counting was significant higher within the radio-tracked range of the mean flight distance around the nursery colonies than beyond (Kruskal-Wallis H = 6.02, p < 0.05)

**Figure 2.** Distribution of six nursery colonies of *Myotis daubentonii* in the research area surrounded with a circle that represents the potential activity ranges around the nursery colonies based on the mean (2327 m) and maximum (6296 m) flight distance revealed by radio-tracking of 30 pregnant and lactating females of different colonies.
Distribution patterns

Relative abundance and sex ratio of females and males

We caught 1771 Daubenton’s bats (Table 1) with mist-nets along the flight-path at the three selected sites (Allendorf: 168 ind., Giessen: 864 ind., Staufenberg: 739 ind.). Reproducing females occurred at all three sites. However, number of individuals at the nursery sites differed. Whereas at the two study sites in the lowland areas nearby the river Lahn (Allendorf and Giessen) nursery colonies contained more than 40 adult females during pregnancy and lactation period, the nursery colony in the upland area (Staufenberg) consisted of less than 10 females that roosted together with adult males (3 - 6 ind.). In Allendorf and Giessen males lived in the same roosting area of small deciduous forests nearby the females but roosted mostly singly or in small groups with 10 individuals or less. We also documented all-male colonies containing up to 51 males in Staufenberg. At each of the three study sites, both sexes used the same feeding grounds and the same flight routes along tree-lined ways and brooks between the roosting site and feeding grounds.

The ratio of adult females to males varied significantly at the three study sites (Kruskal-Wallis H-Test; $H = 15.66$, $p < 0.001$, Figure 3). The highest proportion of females was found in Allendorf, where the female/male ratio was 5.3 : 1. In Giessen, the sex ratio was almost balanced ($♀ : ♂ = 0.97 : 1$) and the proportion of females in percentage of mist-netted individuals was significantly lower than in Allendorf (Mann-Whitney U-Test with Bonferroni adjustment: $p < 0.05$). The significantly lowest proportion of females was recorded in Staufenberg with a female/male ratio of 0.2 : 1 (Mann-Whitney U-Test with Bonferroni adjustment: $p < 0.01$).

Analysing the monthly relative abundance of females and males in the three study sites supported the initial hypothesis that the sex ratio remains constant throughout pregnancy and lactation period from spring to mid summer (Table 1, Figure 4). During this time the number of females in Giessen was slightly higher than those of the males (range of means: 52.1 % - 63.1%). It decreased distinctly in September to 36.1 % (SD: 7.7) (Figure 4). A similar trend was observed in Allendorf with a somewhat higher monthly percentage of females that ranged between 72.7 % - 90.9 % and decreased to 57.1 % in October. In Staufenberg, we did not observe any seasonal variations. The percentage of females was with less than 20 % for all months much lower than at the other sites (mean $= 13.5 \pm 3.5$ %).
Table 1. Monthly numbers and sex ratio of adult female and male Daubenton’s bats caught at regularly used flight routes between roost site and foraging ground in the three study sites.

<table>
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<td>6</td>
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<td>20.2</td>
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Figure 3. Sex ratio of adult Daubenton’s bats at three study sites given as mean number of females in relation to a male (n♀ : 1♂; mean ± SD; Allendorf: n = 168 ind., Giessen: n = 864 ind., Staufenberg: n = 739 ind.).
Figure 4. Monthly variation in relative abundance of adult females at the three selected sites represented as percentage of mist-netted individuals (Allendorf: n = 168 ind., Giessen: n = 864 ind., Staufenberg: n = 739 ind.) (SD = Standard Deviation).

DISCUSSION

Distribution and relative abundance of Daubenton’s bats

Daubenton’s bats are widely distributed in the study area and were found in 75% of the ponds and river sections with spotlight countings. As predicted based on the foraging behaviour of *M. daubentonii* (e.g. Jones and Rayner 1988, Kalko and Schnitzler 1989, Dietz 2000, Dietz and Kalko, submitted, Encarnação et al. 2004) we found a significant increase in relative abundance of Daubenton’s bats with increasing amount of water surface per 1 km²-grid. This result is in accordance to a study in Switzerland, where a similar correlation between the distribution of Daubenton’s bats and the amount of water surface was found (Meoschler and Ruedi 1995). The main factor determining this relationship is probably an increasing amount of food supply with an increasing water surface area by a comparable quality of most of the still water bodies. Furthermore, an increased water surface offers a higher range of foraging areas for an increased number of bats.
Our results also indicate a strong link between number of foraging bats, the overall area of water surface and the proximity of nursery roosts. This applies in particular for the river Lahn with nearby nursery colonies of more than 40 females. The slow-flowing river with a smooth surface offers favourable conditions for Daubenton’s bats (see Warren et al. 2000, Siemers et al. 2001) and is intensively used by females with high nightly flight times particularly during lactation period (Dietz and Kalko, submitted). This intensive use is likely due to the higher energy demand of lactating females (Racey and Speakman 1987, Kurta et al. 1989) coupled with profitable hunting grounds. Custom-made emergence traps placed at four locations on the water surface from April to September revealed high numbers of insects that are preferably consumed by *M. daubentonii*, particularly chironomids at this period of the year at the Lahn compared with still water bodies (unpublished data). A limited period of reduced insect-mass production at ponds and lakes during summer is a common phenomenon (Jonasson and Kristiansen 1967) and raises the meaning of streams as feeding ground in the home range area of Daubenton’s bats.

**Distribution of females and males**

Our results confirm the assumption that distribution of male Daubenton’s bats differ from females especially during pregnancy and lactation period as they use areas with lower food supply and severe climatic conditions. We recorded significant differences in the sex ratio between the three detailed studied sites Allendorf, Giessen, and Staufenberg. The portion of females in the nursery colonies in Allendorf and Giessen close to the river Lahn and in the climatically favourable lowland was significantly higher than in the upland areas of Staufenberg. This may be influenced by the smaller amount of water surface in Staufenberg that translates into a reduced offer of potential feeding areas. Furthermore, weather conditions are more unpredictable in Staufenberg. Mean ambient temperature in the study sites with more females is higher (16°C - 17°C versus 15°C in June) and rainfalls are lower (600 - 650 mm versus 700 mm in June) than in the hilly countryside of Staufenberg. Both the smaller amount of water surface and the severe weather conditions are leading to a reduced food availability which could be crucial for the high nutritional requirements of reproducing females. In contribution, warmer ambient temperatures resulted in favourable roost conditions and this is one of the most important factors influencing growth and development of the young (Kunz 1973, Tuttle 1975, Lausen and Barclay 2003).
The assumption is supported by studies in the Swiss Jura Mountains (Leuzinger and Brossard 1994), in the Italian Abruzzo landscape (Russo 2002) and in the Yorkshire Dales (UK) (Senior et al. 2005) where pregnant and lactating females occurred significantly more often in lower altitudes than males. It is concluded that insect density in general declined with increasing elevations and lower temperatures and therefore only male Daubenton’s bats were found at higher elevations. Barclay (1991) found comparable results for the ecologically similar *Myotis lucifugus* in the Rocky Mountains and also concluded that insect abundance is a major factor influencing the distribution of adult males and females.

That, in reversal, males get along quite well in habitats with lower productivity compared to the lowland areas near the river Lahn, was shown by our banding results in Staufenberg where we monitored a population of adult males from April to September. Comparable to females in nursery areas they showed a high fidelity in roosting sites over the years and were of good physical and reproductive condition (Encarnação et al. 2004).

The colonization of males to habitats with lower productivity does not seem to be of any obvious disadvantage. The reproductive advantage for males in habitats with lower productivity might become most obvious in late summer during mating period. At this time adult females suddenly appear in these areas, when nursery colonies in resource rich habitats break up (Leuzinger and Brossard 1994, Russo 2002). This coincided with the time when energy demand of females decreased and they left their nursery colonies close to the river Lahn (Allendorf, Giessen) after the young became independent. In contrast to the migration of females the volant young remained in the resource rich feeding areas near the nurseries and left them later in the year. In the first time after they became independent juvenile insectivorous bats feed at shorter distances to the nursery colonies than in late summer and early spring (Audet 1990, Jones et al. 1995, Adams 1997). This trend is supported by other studies where adult females such as *Myotis myotis* (Vespertilionidae) migrate in late summer presumably to search for reproductively active males (Zahn and Dippel 1997). For Daubenton’s bats we found first evidence for this assumption at the study site of Staufenberg (Encarnação et al. 2005a). Males in good body condition indicated by rather high weight and pronounced distension of the caudae epididymides occupied tree roosts for most of the night. They were accompanied by adult females and matings were observed in individuals that had been captured and were kept together with adult females in a cage for a couple of hours.
In our investigation we found no evidence that females visited the mating sites for more than one night. We assume that besides mating, females already prepare for hibernation in late summer and that they leave the summer habitats shortly after mating. There is evidence that adult females already settle in hibernaculas in the first half of September, before adult males or juveniles appear for hibernation (Haarje 1994). This is supported by mist-netting captures at the entrances of hibernation sites where we caught banded females from the nursery colonies at the river Lahn already in the first half of September. We further conclude from the increased weights of those females (about 11 g and more) that they are already prepared for hibernation. Furthermore, swarming behaviour of Daubenton’s bats at the entrances of hibernaculas that takes place mid-August has just finished at this time of year (Kallasch and Lehnert 1994).

Implications for conservation and monitoring strategies

Our results support unequal distribution of adult female and male *Myotis daubentonii* on the landscape level which is mainly linked to habitat factors, namely presence of foraging areas (water surfaces), productivity of foraging grounds, presence of roost sites, and climatic conditions (see also Encarnação *et al.* 2005b). Habitat quality and food supply in particular have a possible influence not only on the distribution of males and females but also on the number of females that give birth (reproduction rate), the size of nursery colonies and the spatial distribution (density) of nursery colonies on the landscape level (Speakman *et al.* 1991).

The results of this study have important implications for the development of robust long-term monitoring-programs and strategies for bat conservation. In particular, in reference to *M. daubentonii*, conservation-oriented monitoring programs combined with the implementation of conservation measures require reliable mapping data that permit differentiation into reproduction areas with nursery colonies and, as the opposite, male dominated regions. Furthermore it is necessary to identify key habitats for the respective species like favourable roost sites and nearby foraging grounds with high prey densities necessary to foster reproductive success of pregnant and lactating females.

To conclude, management strategies aimed at conservation need to develop well designed and standardized population monitoring of the reproduction areas to identify factors crucial for
survival of the bats and as an early-warning system regarding population declines (Racey & Entwistle 2003).

REFERENCES


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