Flexibility in habitat use, flight behaviour and echolocation of the northern bat, *Eptesicus nilssonii* and consequences for its conservation in Central Europe

Von der naturwissenschaftlichen Fakultät

der

Universität Hannover

zur Erlangung des Grades

DOKTOR DER NATURWISSENSCHAFTEN

Dr. rer. nat.

genehmigte Dissertation

von

Dipl.-Biol. Moritz Haupt

geboren am 10.12.1974, in Hannover

2005

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Korreferent: Prof. Dr. Klaus Wächtler

Tag der Promotion: 14.07.2005

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1 Abstract

The northern bat (*Eptesicus nilssonii*) though abundant in Scandinavia occurs rarely and patchily in Central Europe. In order to evaluate these contrasting patterns in regard to conservational requirements, I conducted a field study in Germany. The aim of the study was to quantify the importance of resource availability, interspecific interactions and behavioural bandwidth for abundance and geographic distribution of the species. First, I performed a transect survey to examine the importance of interspecific competition versus habitat use. *Pipistrellus pipistrellus* and *E. nilssonii* were detected most abundantly along the transect and mostly in forest and above lakes. Species morphologically similar to *E. nilssonii* (e.g. *Vespertilio murinus, Eptesicus serotinus*) rarely occurred within 2 km of the known maternity roost, the area used predominantly by radio-tracked individuals. Simultaneous hunting of these species was never observed. Next, I examined habitat use by means of radio-tracking. The tracked bats displayed flexibility: habitats were used opportunistically before the birth of the young but more selectively thereafter: forest was avoided whereas urban areas were preferred. High variability in the use of both, forest and urban habitats, suggests the use of individual strategies in this period. Finally, I quantified constraints on microhabitat use of

E. nilssonii by examining foraging skills in natural situations and in artificial clutter.

E .nilssonii displayed a higher manoeuvrability than in previous studies and was superior to morphologically similar species. However, call characteristics and foraging behaviour are very similar to the larger *E. serotinus* rendering coexistence of the two species more difficult and potentially leading to complementary distributions. To sum up, my study depicts the importance of forest and urban habitats for the conservation of northern bats on a local scale. However, the habitat preferences disclosed in the present study fail to provide explanations for large scale distribution of the species. Interspecific competition, particularly with species with morphological and ecological overlap, should provide crucial cues for the geographic distribution of the northern bat in Central Europe and should be in the focus of further studies.

Abstract

2 Zusammenfassung

Die Nordfledermaus (*Eptesicus nilssonii*) ist in Skandinavien häufig und weit verbreitet, in Mitteleuropa hingegen seltener und gefährdet. Ziel dieser Feldstudie war es, die Bedeutung von Ressourcenverfügbarkeit, interspezifischer Konkurrenz und Verhaltensbandbreite für das Vorkommen der Nordfledermaus zu quantifizieren. Zunächst untersuchte ich die Fledermausaktivität entlang eines Transekts: *Pipistrellus pipistrellus* und *E. nilssonii* wurden am häufigsten beobachtet, meist im Wald und über Gewässern. Arten, die der Nordfledermaus morphologisch ähneln, wurden innerhalb von 2 km um das bekannte Wochenstubenquartier der Nordfledermaus selten beobachtet. Gleichzeitige Insektenjagd dieser Arten wurde nie beobachtet. Anschließend untersuchte ich die Habitatnutzung der Nordfledermaus anhand von Telemetrie: diese zeigte eine flexible Habitatnutzung. Habitattypen wurden vor der Geburt der Jungtiere vorwiegend opportunistisch, nach der Geburt eher selektiv genutzt: Waldbereiche wurden vermieden, Siedlungsbereiche präferiert. Die hohe Variabilität der Habitatnutzung in dieser Periode deutet auf individuelle Strategien hin. Schließlich quantifizierte ich die Flexibilität der Art in der Ausnutzung des Mikrohabitats anhand der Untersuchung von Flug- und Echoortungseigenschaften unter natürlichen Bedingungen und im beschränkten Raum.

E. nilssonii stellte sich als weitaus manövrierfähiger heraus, als bisher vermutet und als manövrierfähiger als morphologisch ähnliche Fledermausarten. In ihren Echoortungseigenschaften ähnelt sie stark ihrer Schwesterart *Eptesicus serotinus*. Ähnliches Echoortungs- und Jagdverhalten erschwert möglicherweise ein gemeinsames Vorkommen der beiden Arten im selben Habitat und könnte auf höherer Ebene zu geographisch komplementärem Vorkommen führen. Die vorliegende Studie beleuchtet die Bedeutung von Wald- und Stadthabitaten für die Nordfledermaus auf regionaler Ebene. Habitatpräferenzen der Nordfledermaus liefern hingegen keine Erklärungen für die Verbreitungsmuster der Art in Mitteleuropa. Der Betrachtung interspezifischer Konkurrenz kommt in diesem Zusammenhang größere Bedeutung zu und sollte Inhalt zukünftiger Studien sein.

Schlagwörter: Nordfledermaus – Habitatnutzung - Flugverhalten

3 Outline and scope of the study

In terms of species diversity, bats are among the most successful mammals in the world. The number of extant species within the clade of microchiroptera amounts to at least 850 species (reviewed in Russo et al. 2004) and is thus only surmounted by the rodentia.

Echolocation as well as the ability to fly are commonly considered the two major reasons for evolutionary success in bats (Neuweiler 2003). Echolocation favours a nocturnal way of life, which enables bats to minimise competition with other vertebrates, particularly birds as well as predation pressure by diurnal, mainly visually orientated predators. The ability to fly further reduces predation risk by nocturnal avian predators such as owls (Speakman 1991) and allows bats to exploit airbound prey resources. This life style places bats at the top of the food chain.

Radiation in bats has led to a considerable diversity in morphology and body size of microchiroptera, with the smallest species (*Craseonycteris tholongyai*) weighing only 2 g and the largest ones achieving body masses of 160 g (*Cheiromeles torquatus*, Jones 1999). Along with diversity in morphology, a great dietary and behavioural diversity has evolved: most species can subsist on living prey, ranging from insects with body sizes of less than 3 mm to small vertebrates whereas others feed on pollen and nectar and three bat species from South America are specialised on vertebrate blood. In adaptation to dietary niches, bats have evolved various modes of orientation and foraging behaviour when searching for prey. Consequently, bat species can be found in a variety of habitat types and under various geographic conditions. Nevertheless, the guild of insectivores dominates most temperate and many tropical bat communities (Patterson et al. 2003).

In spite of their evolutionary success, bats have suffered from profound modifications of their environment by human beings, similar to most other mammalian species (Primack 1998). Particularly exploding urbanisation and industrialisation within the last two centuries have had serious impact on species diversity through dramatic increase of extinction rates. Current

population growth rates with numbers doubling within 80 years are complementary to species' extinction rates. Human impact is either indirect, through the influence of climate, or direct, through the change of the environment of living mammals: men have destroyed natural roosting or feeding sites, e.g. through tree logging or cave vandalism. On the other hand, men have provided new artificial resources: many extant European bat species rely on human dwellings for roosting and exploit the space around street lamps during foraging (Rydell & Baagøe 1996). Moreover, other than many ground-dwelling mammals and similar to birds, bats can react to local changes, e.g. habitat loss, by switching to the nearest appropriate environment.

European bat populations have been shown to suffer dramatically from anthropogenic changes of their environment (Racey & Entwistle 2003). One major reason for the dramatic population declines of many European bat species is the loss of roosts (i.e. trees, houses), for example through tree logging (Russo et al. 2004) or modern insulation of houses. The second important threat is the loss of habitats (e.g. Bontadina et al. 2000, Bontadina et al. 2002): as insect prey is mostly associated with either vegetation or water, the modification or loss of both will have crucial consequences for the associated bat fauna. However, consequences of anthropogenic modifications of the environment can vary depending on the species under consideration: whereas some species have gone extinct due to human impact, others may benefit from it, expand in geographic population range and increase in local population density.

Species with a limited distribution and a high degree of behavioural specialisation are commonly considered most vulnerable to extinction (Primack 1998, Racey & Entwistle 2003): the decline of trophic specialists like the barbastelle (*Barbastella barbastellus*, Rydell et al. 1996, Sierro & Arlettaz 1997) is strongly correlated to the decline of prey populations (lepidoptera), for example through use of agrocides (Wickramasinghe et al. 2004). Likewise, the decline of roost specialists like rhinolophids in Europe has been attributed to their

particular requirements concerning the microclimate in maternity roosts (Bihary 2001, Kayikcioglu & Zahn 2004). Finally, behavioural specialists such as the gleaning bat *Plecotus auritus*, are often closely bound to the occurrence of a preferred habitat, in this case deciduous woodland (Swift 1998), and hence dramatically affected by its loss.

On the other hand, populations of some generalist species are presently increasing in number and expanding in area within Europe. Populations of pipistrelle bats (*Pipistrellus pipistrellus*) have displayed a massive increase and expansion within the last decade (Arlettaz et al. 2000). The species is known for its flexibility in terms of diet, roosts and behaviour: it feeds opportunistically on small insects, makes use of a variety of habitats (Swift & Racey 1983, Blake et al. 1994) and is not confined to particular microhabitats. Moreover, it can roost in natural (e.g. tree holes) as well as artificial roosts (e.g. human dwellings) and finds abundant roost space in newly built houses. Daubenton's bats (*Myotis daubentonii*) have even been confirmed to benefit from human habitat alteration: population increase in this bat has been reported to be due to increasing pollution of water places and the correlated increase in chironomid densities (Vaughan et al. 1997). Finally, species like *Nyctalus leisleri* which display high flexibility in habitat use (Waters et al. 1999, Racey & Entwistle 2003) and are virtually unaffected by habitat fragmentation due to their wing morphology promoting fast flight, are widely dispersed and suffer low risk of extinction (Walk & Rudolph 2004).

Hence, the quantification of behavioural flexibility of a bat species as well as its adaptability to anthropogenically altered habitats is essential to predicting population trends and conservational requirements for a bat species under consideration.

However, as most European bat species are part of bat communities, population densities as well as range margins can be mutually influenced, e.g. through interspecific interactions. Competition is commonly considered an important factor affecting population densities of a given species (Guo et al. 2005). Distributions of bat species sometimes show complementary

patterns (cf. Rydell & Baagøe 1994 for *Vespertilio murinus*) and even behaviourally highly flexible species may be regionally absent due to a real competitor (Ahlen & Gerell 1989).

The northern bat, *Eptesicus nilssonii*, is widespread and common in Scandinavia. In Germany however, it is classified "critically endangered" as its occurrence is incontinuous and even patchy in some regions: evidence for reproduction has been limited to few maternity roosts within Germany (e.g. Morgenroth 2004). Though the species often occurs at elevation levels above 300 m (Morgenroth 2004, Schulenburg 2004), there has been repeated evidence for occurrence and successful reproduction in German flatlands (Steinhauser 1999). Moreover, there is indication, that German populations of the species can make good use of street lamp habitats (Skiba 1986), according to Rydell & Baagøe (1996) an indication of low risk of extinction. Thus, distribution and conservation status of the species cannot be attributed solely to geographic restriction to mountain areas and the role of street lamps as an artificial conservation tool remains doubtful.

The aim of this study was to find out, whether adaptability to anthropogenically altered habitats, competitive interactions or behavioural flexibility account for the differing distribution patterns and the conservation status of the northern bat in Northern and Central Europe.

The approach was threefold: in a first step, I wanted to assess the role of interspecific competition for small and large scale distribution of the northern bat (Chapter 1). Competition applies in particular to species within the same ecological guild (i.e. using similar foraging behaviour, Schnitzler & Kalko 2001). Distribution and abundance of a species within a given area depend on the question whether resource partitioning with competitors can be achieved (e.g. Racey & Swift 1983). This in turn depends on the behavioural flexibility and competitive strength of a species. Species similar to each other in terms of habitat use and foraging behaviour could achieve some fine-grained niche differentiation, e.g. through differences in echolocation behaviour (Siemers & Schnitzler 2004). Interestingly, some bat

species (e.g. *Eptesicus serotinus*, *N. leisleri*, Catto & Hutson 1999, Shiel 1999) that resemble the northern bat morphologically as well as behaviourally show distribution patterns complementary to the northern bat, occurring rarely in Sweden but abundantly in Central Europe. I conducted a line transect survey to document foraging activity of the northern bat and potentially competing bat species near a known maternity roost at Bad Grund (Lower Saxony).

The second step was to quantify the adaptability of the species to an anthropogenically altered environment (Chapter 2). Previous studies provided contrasting views upon habitat use of *E. nilssonii*: whereas de Jong (1994) emphasises the outstanding importance of lake and forest habitats as key habitats for the species in a Scandinavian region dominated by coniferous forest, other studies (Rydell 1992b, Rydell & Racey 1995) described the northern bat as a typical street lamp bat. However, the knowledge of habitat use is restricted to Scandinavian study areas where bats had either access to habitats with little or no human impact (natural habitats, e.g. forest with little silviculture, oligotrophic lakes) or to habitats with strong human impact (anthropogenically altered habitats, e.g. urban area, eutrophic lakes). Neither behavioural flexibility nor adaptability to anthropogenically altered habitats was therefore fully reflected. To assess both, I examined habitat use of individual northern bats from the above maternity roost through radio-tracking .

The final step was to quantify the behavioural flexibility of *E. nilssonii* in particular foraging situations (Chapter 3). The northern bat has been classified an opportunistic insect hunter (Rydell 1986b) with restricted flight capacities which prefers flight far from vertical obstacles (Baagøe 1987) and has a reduced prey capture success near clutter (Rydell 1998, reviewed in Jensen et al. 2001). Intermediate in terms of body size, aspect ratio and wing loading (Baagøe 1987), the northern bat displayed a stereotyped foraging behaviour: it circled in wide lines within the 5-10 m stratum (Baagøe 1987). However, observations of individuals occasionally diving in acoustical clutter provide evidence that the behavioural bandwidth of the species

might be greater than assumed previously. Moreover, Jensen et al. (2001) were able to show that the species tolerates a certain degree of acoustic clutter. I documented echolocation behaviour and flight style of known and radio-tracked individuals and experimentally confronted some bats with a narrow-space clutter situation in a flight tent in order to quantify manoeuvrability.

4 Chapter 1 - <u>The importance of interspecific competition and habitat use</u>

<u>to the northern bat as revealed by transect surveys</u>

4.1 Introduction

Geographic distributions of animal species are largely determined by a species' ecological niche which in turn results from a combination of abiotic (e.g. climate) and biotic conditions (e.g. competition). Both tend to be integrated in the habitat requirements of a species under consideration (Gaston 2003) with abiotic factors prevailing at high latitudes and biotic ones being more important at lower latitudes (Fortin et al. 2005).

In bats, small and large scale distribution patterns can be explained by availability of certain resources, e.g. foraging habitats, food or roosts (Fenton et al. 1992, Rautenbach et al. 1996, Arlettaz et al. 2001, Jaberg & Guisan 2001). This applies in particular to distributions of specialised species, e.g. *Barbastellus barbastella* which subsists exclusively on soft-bodied lepidopterans (Rydell et al. 1996, Rydell & Bogdanowicz 1997) or *Myotis myotis* which at times strongly depends on cockchafers (Arlettaz et al. 2001). These species are likely to depend on the occurrence of particular habitats and associated prey items, whereas distributions of more generalist species, like *Eptesicus serotinus*, are less closely related to habitat availability (Catto et al. 1996).

In this case, interspecific competition may play an important role in shaping population densities and range margins (e.g. Guisan & Zimmermann 2000). In some species, positive coexistence within the same area (Bell 1980, Swift & Racey 1983) can be achieved by means of moderate dietary specialisation or aerial stratification while foraging within the same habitat as suggested for *V. murinus* and *E. nilssonii* (Rydell 1992b) as well as *P. pipistrellus* and *P. auritus* (Swift & Racey 1983). Interspecific competition might become problematic mostly for species which overlap strongly in their ecological niches. For *E. nilssonii, N. leisleri* (Shiel et al. 1998b), *V. murinus* (Schaub, unpublished data) and *E. serotinus* are such potential competitors: they resemble the northern bat in diet or foraging styles and can often

be observed to forage in similar habitats, e.g. street lamp alleys (Rydell & Baagøe 1996, Shiel et al. 1998a). If resource partitioning cannot be achieved, this could result in competitive exclusion (Arlettaz et al. 2000) and even lead to complementary geographic distributions as suggested for *P. pipistrellus* and *Pipistrellus kuhlii* in Southern Switzerland (Haffner & Stutz 1985) or for *E. serotinus* and *V. murinus* on some Danish islands (Ahlen 1983).

As an opportunistic insectivore (Rydell 1989), *E. nilssonii* should be less clearly bound to a certain habitat though some habitats have been assigned key habitats (Rydell 1991, de Jong 1994, cf. Outline). Some of these have become regionally limited due to energetic considerations (street lamps; Rydell & Racey 1995) or improvement of water quality (eutrophic lakes). However, occurrence of *E. nilssonii* in Germany does not match distribution of these key resources and their importance for explaining distribution patterns remains speculative. Occurrence of the northern bat in Central Europe is often associated with mountain areas (Ohlendorf 1987, Rydell, 1999, Jaberg & Guisan 2001) or coniferous forests (Ahlen & Gerell 1989) of low insect density further characterised by the rarity of potential competitors of the northern bat, such as *E. serotinus.* Whereas these observations suggest competitive exclusion of the northern bat from highly productive habitats, others suggest that the species might be able to drive other bat species out of key habitats, such as the

P. pipistrellus hunting around street lamps (Rydell 1992b). However, the importance of resource availability versus interspecific competition for explaining small and large scale distribution of *E. nilssonii* has not been quantified so far.

Bat surveys haven been shown to provide an excellent window on the spatial distribution of some bats (Fenton et al. 1987): they are an appropriate method to pinpoint activity centres and thus give estimates of habitat selectivity by bats (e.g. Rydell 1992b, Blake et al. 1994). Moreover, they allow to assess habitat quality, e.g. patch size, structure or productivity, which in turn have been shown to affect species diversity (de Jong 1995, Walsh et al. 1995,

Rautenbach et al. 1996, Rachwald et al. 2002) as well as resource partitioning (Hickey et al. 1996) or mutual exclusion (Bell 1980, Holt et al. 2005) and thus give estimates of the degree of interspecific competition. However, estimates of habitat selectivity and interspecific competition from detector surveys can be biased by artefacts like dilution effects around day roosts or overestimation of bat abundance due to pseudoreplications (Rautenbach et al. 1996, Bartonicka & Zukal 2003). Surveys should therefore be coupled with radio-tracking of the species under consideration.

In the present study, I quantified the importance of resource availability versus interspecific competition in the northern bat for the first time by conducting bat surveys and comparing survey data to data obtained from radio-tracked northern bats in the same area. If interspecific competition is a main factor explaining regional distribution patterns of the species, I should find spatial or temporal segregation as well as largely unequal population densities of *E. nilssonii* and its potential competitors within a given area. Correspondingly, I should expect intensive temporal and spatial mixing and similar population densities of bat species if habitat quality was more decisive.

4.2 Material & Methods

4.2.1 Study area

The study area was located in Lower Saxony (Germany) around a known maternity roost at 51°49' N, 10°14' E. The climate is temperate with moderately warm summers. The area was situated at the edge of the Harz mountains and comprised elevation levels from 150 m a.s.l. in the west up to 600 m a.s.l. towards the east. The western flatland was dominated by fields and grassland with intensive agriculture, the eastern mountainous part comprised major fractions of deciduous and coniferous forest with coniferous forest dominating towards higher elevations.

Temperatures within the study area were measured three times per night at 150 m from the maternity roost and 1.5 m above the ground during most radio-tracking nights (n=60). Insect densities were measured in forest, grassland and urban areas on 10 occasions using a custom-made light trap (height: 1.2 m) positioned on the ground. Total numbers of insects with body sizes between 0.3 and 3.0 cm, i.e. the size classes preferred by the northern bat (Rydell 1989), were counted.

4.2.2 Bat surveys

Bat surveys were conducted during 50 complete nights from 21st May to 30th July 2003. A transect was defined starting at 10° 9' E, 51°51' N and ending at 10°14' E, 51°49' N which was 150 m from the known maternity roost of *E. nilssonii* (total length 6.88 km). Due to considerable differences in elevation along the transect, surveys along the transect were done using a modified transect method, employing 14 core measurement locations along the transect, each one 526.7 m apart from the next. Activity measurements were started at random points along the transect. One activity measurement session lasted for 25 minutes after which the observer drove to the successive sampling point (SP). Within this time, the observer walked slowly about a distance of 100m across the core location. The number of bat passes was monitored visually and acoustically. Each visual or acoustic encounter was considered a single bat pass. Bats foraging continuously at a given place were only counted once, bats flying across the observer and returning from the opposite direction within 10 sec were also counted only once. Monitoring was supported by a powerful halogen torch, or an infrared lamp and an infrared-sensitive camera (Sony DCR-PC8E) as well as a U30-bat detector (Ultrasound Advice) tuned at 35 kHz to detect all bat species. In cases where calls could not clearly be assigned to a species, calls were extended tenfold using a portable ultrasound processor (PUSP, Ultrasound Advice) and further digitised for call analysis. Frequency response of the U30 microphone was obtained by calibration of broad-band noise (0-100 kHz)

recorded by a Bruel & Kjaer microphone using a measurement amplifier (B&K type 2610). Frequency response of the U30 microphone was obtained by subtracting the actual response from the flat response of a B & K ¼ " microphone when opposed to broad-band noise. Call analysis was conducted using Bat Sound (Pettersson Elektronik AB, Ver. 1.2) and an Acer Travel Mate 223 XC. Species identification was conducted to species or genus level according to Vaughan et al. (1997), Russ (1999), Schaub (unpublished data 2001), Zingg (1990) and Obrist et al. (2004). Identification of northern bats was conducted based on recordings (about 800 calls) of radio-tracked or colour-tagged northern bats.

For seasonal considerations, the study period was subdivided into two periods of similar duration (P1: 18th May – 21st June, P2: 22nd June –30th July), referring to the date of parturition in the known roost of *E. nilssonii*, which occurred around 21st June.

4.2.3 Radio-tracking and individual time budgets

13 northern bats (ten males, three females) were captured in front of their day roost at Bad Grund (coordinates see above) from May to July in 2002 and 2003. They were equipped with radio transmitters and colour-tagged individually with reflective tape. Radio-tracking was conducted using a six-element yagi-antenna. Positions of bats as obtained by the homing-in-on-the-animal method (White & Garrot 1990) were entered into digital maps employing Gauss-Krüger coordinates using a precision of 25 x 25 m. For details on radio-tracking cf. Chapter 2. The bats' time budgets were expressed in minutes. Total observation time was the time from dusk to dawn or from the first emergence until the last arrival of a tracked bat. For considerations about nocturnal bat activity, nights were further subdivided into three thirds (T1-3) with a constant duration of T2 (0:05 to 2:35 a.m.=150 minutes) and durations slightly varying for T1,3. The bats could be observed visually most of the night (contact time). Contact time comprised the time the bats spent flying outside the maternity roost (flight time) and the time resting either within or outside the maternity roost (resting time). Flight time was

further subdivided into the time a bat spent foraging within a habitat (foraging time) and the time a bat needed to cross over between two habitats without staying at any place longer than one minute (commuting time). Resting time was further subdivided into the time a bat spent in the maternity roost (roosting time) and the time spent resting within trees (night roosting time).

4.2.4 Analysis and statistics

In order to compare results from radio-tracking and bat surveys concerning the northern bat and to decide which apparent effects might be due to dilution effects, I defined 2 km distance zones around the maternity roost. For analysis of foraging distance, I assigned each sampling point to a distance zone relative to the maternity roost of the northern bat. The occurrence of all other bat species was also monitored in relation to the known maternity roost, as I aimed at documenting the effect of the presence of other bat species, to the spatial distribution of northern bats from the maternity roost. The northern bat roost will be referred to as "the maternity roost" throughout the results section.

For analysis of habitat use through survey data, I assigned each sampling point to one of the following habitat types: forest, grassland, lakes, urban area or fields.

Analysis of foraging distances was conducted using GIS Arc View (Ver. 3.3). Foraging distances of individual animals were calculated. When visual contact was lost in commuting bats, a bat was assumed to move between habitats using direct lines. Distances calculated likewise are thus minimum distances. All spatial data from telemetry are given as medians and min/max-ranges. Time budgets were calculated using median fractions of the flight time.

I employed nonparametric tests throughout, as data were not normally distributed. Wilcoxon-matched-pair tests were used to compare differences between the night thirds T1 through T3.

I used Kruskal-Wallis-H-test with successive Mann-Whitney-U-test to analyse seasonal or individual differences. Spearman rank correlations were calculated to assess the effect of temperature on flight activity of bats and insects.

In order to describe bat activity along the transect, I used means of log transformed data, namely

$$\text{antilog } ((\Sigma \log (x+1))/n) - 1$$

where x was the number of bat passes and n the total number of sampling intervals within a period (P1 and P2, respectively; Shiel & Fairley 1998a) calculated per sampling point (SP).

I did this to normalise data as we dealt with a high number of zero-observations. For ordinary non-parametric statistics, I used original data and the tests as described above. For all multiple comparisons, the significance level was adjusted according to Bonferroni.

On the assumption of an equal distribution (random distribution) of bats throughout the transect, I compared observed abundances to expected values. For this purpose, I pooled all counts of a SP within one period (P1 and P2) and per distance zone or habitat type, then derived frequencies for the smallest number of sampling intervals within a period to get the observed frequencies. I then calculated the mean of the number of bat passes from the sampling points, frequency bands and five habitat types respectively to obtain the expected frequencies. Finally, I compared observed to expected frequencies using chi-square tests at a significance level of p=0.05.

4.3 Results

4.3.1 Bat activity along the transect

Besides the northern bat, I detected a total of 8 other species in the study area, *Myotis daubentonii*, *Myotis bechsteinii*, *Myotis mystacinus/brandtii* (no further differentiation),

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Nyctalus noctula, Vespertilio murinus, *Eptesicus serotinus*, *Pipistrellus pipistrellus* and *Pipistrellus nathusii*. I found more bat species within 3 km of the roost than at greater distances (Fig. 4.1a). Species diversity was generally highest above lakes and lowest above fields (Fig. 4.1b). I found more bat species above a highly eutrophic lake (SP 8) than above a small pond near a spring (SP 12).

General abundance of northern bats was low and incontinuous across the transect and centered towards the known maternity roost (Fig. 4.2a top). Observed use of distance zones differed significantly from expected use in *E. nilssonii* (Table 4.1): I found a general preference of habitats within the 2 km distance zone, whereas habitats at greater distances were used as expected (2-4 km) or avoided (4-6 km). Interestingly, habitats at more than 6 km were avoided in P1 but used as expected in P2, indicating that foraging habitats at greater distances (e.g. street lamps) were used at least by some bats after parturition.

Indeed, habitat use was significantly different from expectations and gave indication for selectivity (Table 4.2): whereas activity of *E. nilssonii* in field habitats was significantly lower than expected, it was significantly higher than expected in lake habitats. Use of other habitat types matched expectations. Highest values were scored above an oligotrophic forest pond (SP 12) at 1.1 km from the maternity roost (Fig. 4.2b top). Numbers of bat passes increased slightly but not significantly from P1 to P2 (Mann-Whitney-U test, $p > 0.05$).

P. pipistrellus was detected most frequently of all species recorded and was distributed more evenly along the transect than *E. nilssonii* (Fig. 4.2a middle). Nevertheless, the distribution of pipistrelles along the transect was also slightly shifted towards the Bad Grund area with the northern bats' roost, similar to the northern bat itself suggesting the existence of pipistrelle roosts within the urban area. Moreover, I found deviations from random in the use of distance zones (Table 4.1) similar to *E. nilssonii* with a clear avoidance of habitats at 4-6 km from the northern bats' maternity roost. Other than the northern bat, pipistrelles preferred habitats at more than 6 km in P1. I found no range selectivity in P2.
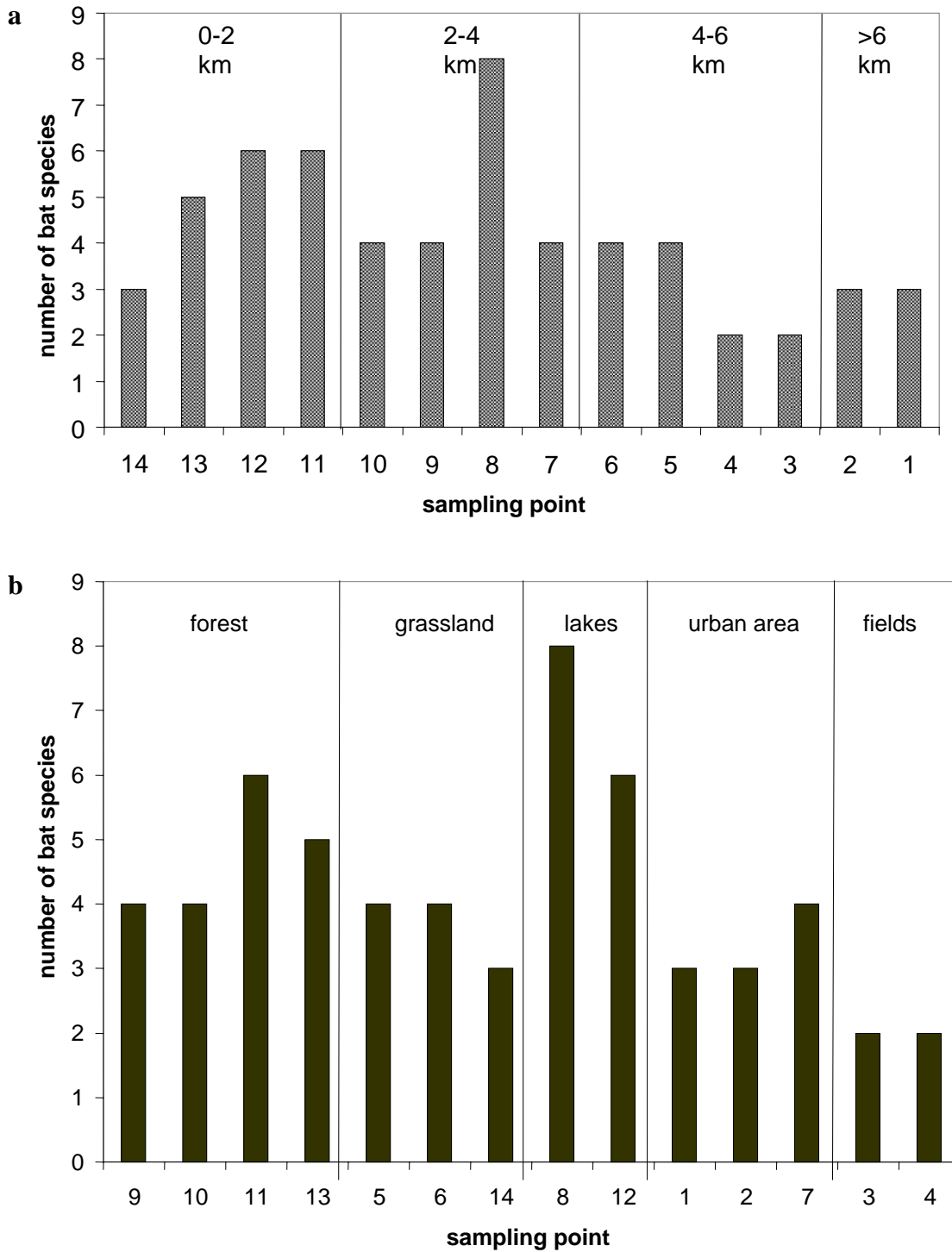
Fig. 4.1 Bat species diversity along a transect including 14 sampling points in 2003. **a** number of species in distance bands. Distances were calculated from circles centred around the day roost of radio-tracked northern bats. **b** Number of species in the 5 habitat types. Bars show minimum numbers of bat species detected and observed at each sampling point.
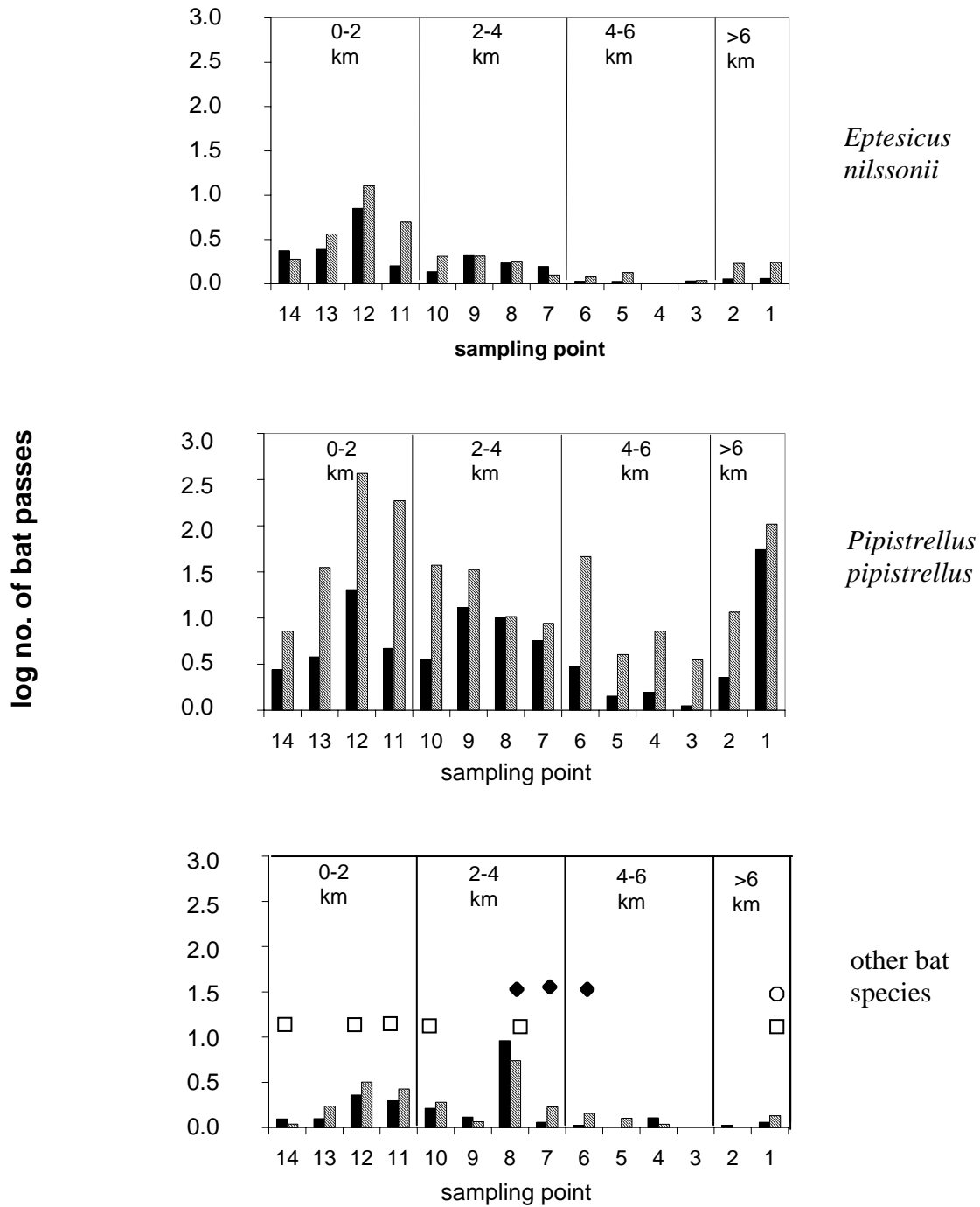
Fig. 4.2a Bat abundance along a transect including 14 sampling points in 2003. Bat counts in relation to distance from the roost. Bars show log transformed values of number of bat passes in 25 minutes (= 1 sampling period). n (minimum number of sampling intervals / sampling point)= 18. Black bars: P1, shaded bars: P2. Values for other bat species are pooled. Symbols indicate the presence of three bat species: □ *Eptesicus serotinus,* ○ *Nyctalus noctula,* ◆ *Vespertilio murinus.* For further explanations cf. Fig. 4.1.
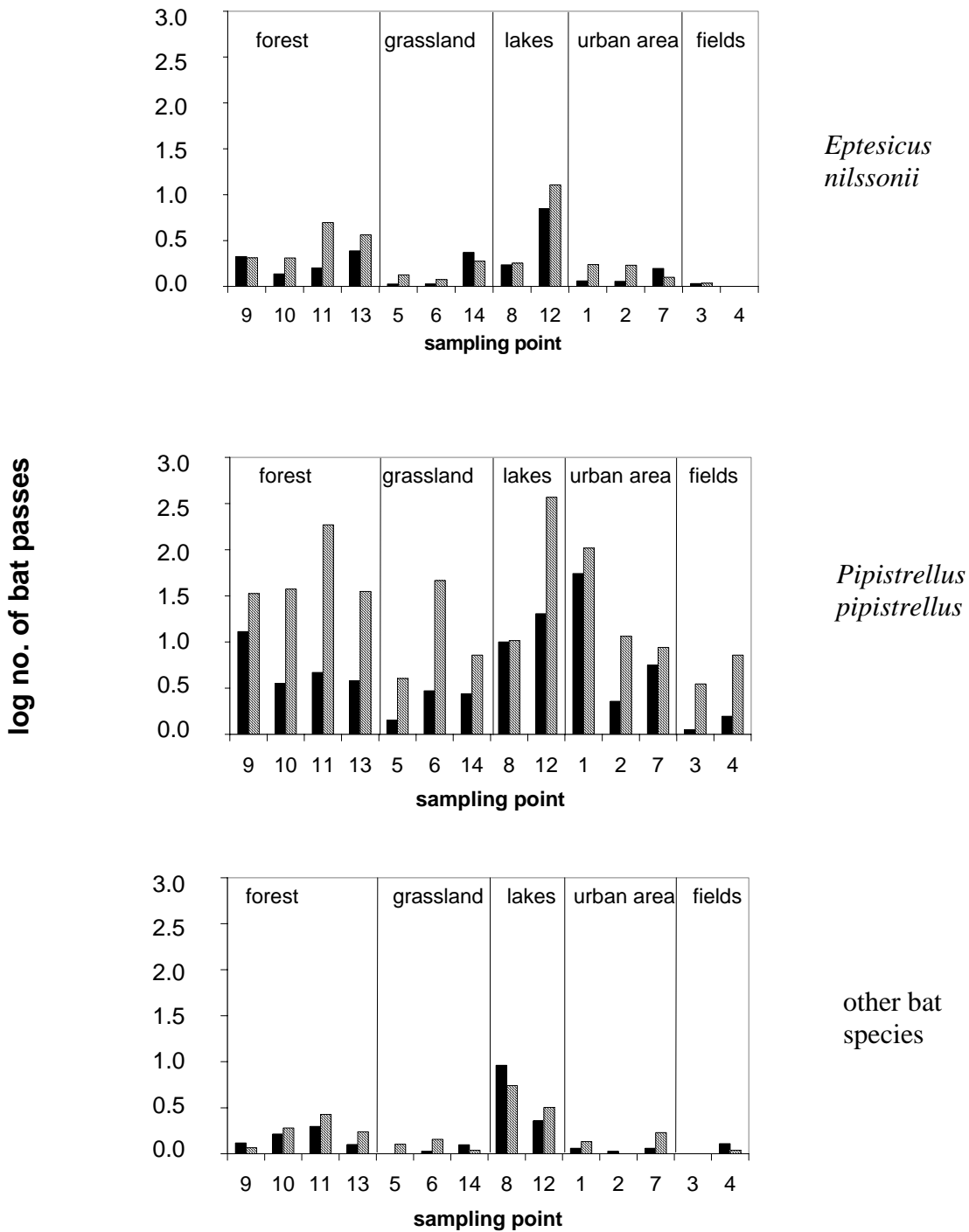
Fig. 4.2b Bat abundance along a transect including 14 sampling points in 2003. Bat counts within 5 habitat types. Bars show log transformed values of number of bat passes in 25 minutes (= 1 sampling period). n (minimum number of sampling intervals / sampling point)= 18. Black bars: P1, shaded bars: P2. top: *Eptesicus nilssonii.* middle: *Pipistrellus pipistrellus.* bottom: other bat species. For further explanations cf. Fig. 4.1.

Table 4.1 Expected and observed distribution of *Eptesicus nilssonii*, *Pipistrellus pipistrellus* and other bat species from survey data. Total observation time in period 1 (top) and period 2 (bottom) was pooled for a given distance zone. + / - indicate directions of deviations in distribution (dir.) from random. P1 (top): 18th May – 21st June. P2 (bottom): 22nd June – 1st July.

|	*Eptesicus nilssonii* χ^2=48.02 df=3 p< 0.001		*Pipistrellus pipistrellus* χ^2= 48.81 df=3 p<0.001		other bat species χ^2= 24.93 df=3 p< 0.001	
distance	χ^2	dir.	χ^2	dir.	χ^2	dir.
0-2 km	26.67	+	n.s.		n.s.	
2-4 km	n.s.		n.s.		12.43	+
4-6 km	12.07	-	25.36	-	n.s.	
>6 km	7.99	-	22.67	+	n.s.	

	Eptesicus nilssonii χ^2=35.76 df=3 p< 0.001		*Pipistrellus pipistrellus* χ^2= 13.27 df=3 p<0.01		other bat species χ^2= 16.79 df=3 p< 0.001	
Distance	χ^2	dir.	χ^2	dir.	χ^2	dir.
0-2 km	20.92	+	n.s.		n.s.	
2-4 km	n.s.		n.s.		n.s.	
4-6 km	13.24	-	n.s.		n.s.	
>6 km	n.s.		n.s.		n.s.	

Table 4.2. Habitat use along the transect by *Eptesicus nilssonii*, *Pipistrellus pipistrellus* and other bat species. P1 (top). P2 (bottom). For further explanations cf. Table 4.1.

	E. nilssonii χ^2= 59.8 df=4 p< 0.001		*P. pipistrellus* χ^2= 76.32 df=4 p< 0.001		other bat species χ^2= 73.31 df=4 p< 0.001	
habitat	χ^2	dir.	χ^2	dir.	χ^2	dir.
forest	n.s.		n.s.		n.s.	
grassland	n.s.		9.66	-	n.s.	
lakes	38.94	+	19.38	+	55.17	+
urban area	n.s.		16.30	+	n.s.	
fields	14.03	-	30.93	-	n.s.	

	E. nilssonii χ^2= 44.39 df=4 p< 0.001		*P. pipistrellus* χ^2= 21.98 df=4 p< 0.001		other bat species χ^2= 47.10 df=4 p< 0.001	
habitat	χ^2	dir.	χ^2	dir.	χ^2	dir.
forest	n.s.		n.s.		n.s.	
grassland	n.s.		n.s		n.s.	
lakes	18.27	+	n.s		31.41	+
urban area	n.s.		n.s		n.s.	
fields	16.15	-	10.63	-	9.77	-

Habitat use of pipistrelles also differed significantly from random: fields were generally avoided, whereas use of all other habitats showed seasonal variation (Table 4.2). Other than in the northern bat, urban areas were preferred in P1 and the preference of lake habitats was restricted to P1. For most sampling points, I found flight activity to be significantly increased in P2 (Fig. 4.2b middle, Mann-Whitney-U-test, U=107-175, Z=-3.2—2.3, p<0.05), when bat abundance in the area was generally increased due to the weaning of the young.

Density of all other bat species was extremely low and their distribution patchy (Fig. 2a bottom), activity values were therefore pooled. The total observed abundance in distance zones differed from expectations (Table 4.1) but did not show seasonal variation. Other than in northern bats and pipistrelles, I encountered higher activities than expected in habitats at 2-4 km from the maternity roost in P1, mainly due to the use of the above mentioned eutrophic lake (SP 8). Generally, I found significantly more bats of other species than expected above lakes (Table 4.2). *M. mystacinus/brandtii* was mainly detected in forest habitats (SP 9-SP 11), *M. daubentonii* was observed in all habitat types, though highest densities were seen in lake habitats (Fig. 4.2b bottom), other *Myotis* species were rarely detected. Thus, the occurrence of *Myotis* species seemed virtually unaffected by the occurrence of the northern bat.

In contrast, the occurrence of species with foraging styles or diets similar to *E. nilssonii* was rare as well as temporarily and spatially strongly restricted (Fig. 4.2b bottom) and simultaneous foraging with *E. nilssonii* was never observed. *V. murinus* was only observed in P2 at distances of more than 3 km to the maternity roost. *Nyctalus noctula* was only seen once in P2 at > 6 km from the maternity roost. *E. serotinus* occurred within the 2 km zone in P1, but never within 3 km of the maternity roost thereafter. Interestingly, sampling points with *E. serotinus* were never used more than expected by *E. nilssonii* (except for the pond SP12), and sometimes even avoided. Hence, my observations gave indication for spatial and temporal segregation of *E. nilssonii* and its potential competitors. Contrastingly, distribution

of *E. nilssonii* and *P. pipistrellus* along the transect was very similar and abundant observations of simultaneous hunting indicated positive coexistence.

4.3.2 Time budget of radio-tracked bats

Emergence from the roost as well as activity in T1 occurred independently of outdoor temperature or weather. Bats spent 42.5 (43.6-56.7) % of the contact time outside the roost (cf. Table 4.3). Insect densities measured within foraging habitats were positively correlated to ambient temperature (n=10, r=0.73, t=3.03, p<0.05). Flight activity was significantly and positively related to ambient temperatures only for the time after midnight (T2 and T3: r=0.33; 0.39, t=2.67; 3.18, p<0.01). Flight activity was highest in T1 and significantly lower in T2 and T3 (Wilcoxon matched-pair test, n=13, p<0.01)

Bats spent their night either foraging, resting in trees, resting within the maternity roost or commuting (Table 4.3). Intermediate resting in trees was rare (n=6 nights).

Radio-tracked *E. nilssonii* had a maximum number of four foraging bouts, but normally left the roost only once (males) or twice (females) per night. Most of the foraging time was spent hunting within habitats. However, some of the bats spent a considerable percentage of activity time commuting (Table 4.3), particularly two males tracked in P2 (m110, m081). These males were often found to commute continuously along vegetation structure, rivers, street lamps and streets without staying anywhere longer than two minutes. w080 and w223 generally commuted over long distances to reach their foraging grounds. However, commuting times did not differ significantly between animals (Kruskal-Wallis test, n=60, H=10.8, p>0.05) or between seasonal periods (Mann-Whitney U test, U=15, Z=-0,9, p>0,05).

Table 4.3 Individual time budgets of 13 northern bats radio tagged in 2002 and 2003. Minute values are given as medians and min/max-ranges per night. P1: 18th May – 21st June. P2: 22nd June – 30th July. For w180, values are given before (-1) and after (-2) parturition. m: male. w: female. * tagged in 2003. For specifications of individuals cf. Chapter 2.

Period	Bat no.	contact time	day roost	foraging breaks	foraging time	commuting time
	w084	466 (374-476)	243 (141-429)	19 (0-39)	166 (30-199)	17 (15-18)
	w084n	461 (405-463)	373 (347-384)	0	59 (40-61)	20 (18-27)
	w112*	429 (388-470)	291 (275-307)	0	122 (110-133)	17 (3-30)
	m133*	467 (416-488)	369 (308-435)	0	61 (20-108)	29 (0-50)
P1	w219	276 (217-453)	204 (21-206)	0 (0-33)	139 (60-204)	24 (10-45)
	w219n	410 (378-418)	212 (28-289)	0	155 (98-343)	19 (0-47)
	w080*	436 (361-441)	226 (160-334)	0 (0-22)	134 (63-240)	46 (8-63)
	w180-1	404 (384-422)	213 (127-338)	0	176 (49-267)	14 (0-28)
	w180-2	411 (278-424)	145 (135-290)	0	170 (112-242)	22 (10-62)
	w200	438 (253-442)	184 (88-362)	0	181 (71-252)	23 (0-67)
P2	w080n*	377 (342-412)	243 (223-262)	0	110 (92-127)	25 (23-27)
	w223	455 (393-459)	276 (190-357)	0	96 (47-160)	52 (19-88)
	m081	406 (189-491)	52 (17-399)	0 (0-75)	57 (15-331)	35 (0-157)
	m110*	362 (300-453)	143 (90-269)	0	102 (52-200)	83 (0-160)

4.3.3 Foraging distances of radio-tracked bats

After emergence from the roost, tagged bats would normally first choose forest habitats close to the maternity roost and then successively visit several other places. Median number of foraging sites per night was 4 (3.5-5.5) with no significant seasonal difference between P1 and P2 (U=17.5, z=0.5, p>0.05). Foraging sites were close to each other (Table 4.4). Sometimes, bats would come back to places visited previously during the same night. Median minimum distance travelled per night was 7.9 (5.8-9.8) km most of which was flown during the first foraging bout (6.8 (5.8-7.9) km). There were no significant differences between the distances travelled in P1 and P2 (n=13, U=10, z=-1.6). Distances covered during the second bout though were significantly higher (n=10, U=2, z=-2.2, p<0.05) in P2, when bats flew 5.1 (2.8-5.2) km per night on average, than in P1 (cf. Table 4.4).

Radio-tracked northern bats spent most of their foraging time within 2 km of their day roost (Fig. 4.3), which was tendentially more than in the 2-4 km zone (n=13, U=10, Z=2.5, 0.05>p>0.01) and significantly more than at distances of more than 6 km from the maternity roost (n=13, U=5; 0, z=2,8; 3,2, p<0.005).

Females in May were never seen further than 3 km from the maternity roost and all bats tagged until 8th July spent their foraging time within 5 km of the maternity roost, suggesting prevailing beneficial conditions within this area as to habitat productivity and competition. However, bats tagged after 8th July commuted for more than 6 km (w080, w080n, m110) in order to reach profitable foraging habitats (e.g. street lamp alleys) and were observed to forage at distances up to 7 km (m110) from the maternity roost. Habitats at intermediate distances were often avoided by these bats indicating that increased intraspecific competition through flying juveniles or decreased food availability in vicinity to the maternity roost might favour farther commuting flights.

4.3.4 Interspecific encounters of radio-tracked bats

Bat species involved in interspecific encounters with radio-tracked *E. nilssonii* were

P. pipistrellus, *Myotis myotis*, *E. serotinus*, *V. murinus* and some unidentified *Myotis* species. Encounters with species other than *P. pipistrellus* were very rare and never occurred within 2 km of the maternity roost. Only two bats were ever observed foraging simultaneously with individuals of *V. murinus* and *E. serotinus* (w080, w200). Interspecific encounters with *P. pipistrellus* occurred regularly.

Table 4.4 Individual flight records of 13 northern bats tagged in 2002 and 2003. Values are given as medians and min/max-ranges of minimum travelled distances per night in km. For w180, values are given for the time before parturition (w180 – 1) and after parturition (w180 – 2) respectively. For further specifications cf. Table 4.3.

| Period	Bat no.	distance travelled [km]	distance between two habitats [km]
	w084	5.7 (1.2-6.6)	0.7 (0.6-1.0)
	w084n	2.7 (1.2-6.2)	0.6 (0.6-0.8)
	w112	5.2 (3.2-7.1)	0.5 (0.3-0.8)
	m133	5.8 (0.1-10.6)	1.3 (0.1-1.8)
P1	w219	7.9 (1.2-8.9)	0.3 (0.1-0.7)
	w219n	10.6 (6.4-12.9)	0.8 (0.2-1.0)
	w080	9.8 (2.1-17.5)	0.7 (0.2-1.7)
	w180-1	7.7 (0.7-11.6)	0.2 (0.1-0.5)
	w180-2	9.5 (2.6-14.0)	1.5 (1.0-2.1)
	w200	8.8 (2.2-13.7)	0.8 (0.2-1.4)
P2	w080n	7.9 (7.5-8.3)	1.5 (1.1-1.9)
	w223	15.2 (7.1-25.4)	0.4 (0.1-1.3)
	m081	7.2 (0.5-27.3)	0.7 (0.6-0.8)
	m110	27.9 (8.8-56.1)	1.3 (0.1-2.3)
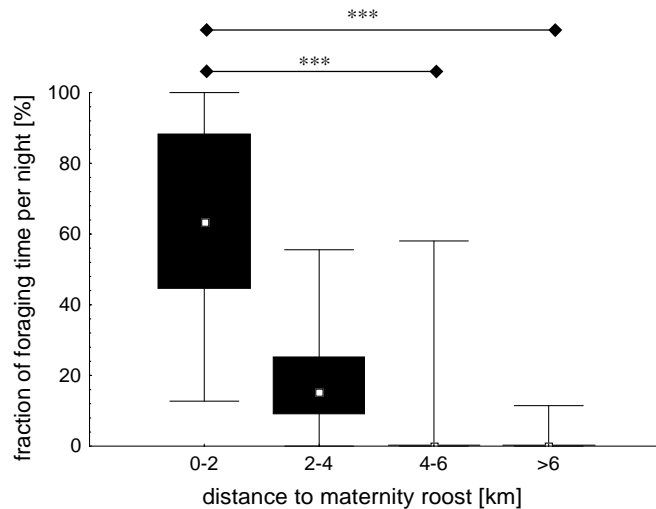
Fig. 4.3 Foraging distances from day roost of 13 northern bats tagged in 2002 and 2003. Box plots comprise medians, quartiles and min/max-ranges of fractions of foraging time per night. For further explanations cf. Fig. 4.1 and Fig. 4.2.

4.4 Discussion

4.4.1 General observations

In the present transect survey, *P. pipistrellus* and *E. nilssonii* occurred regularly along a transect and coexisted temporarily as well as spatially. Other bat species were less abundant and can be subdivided into two groups according to their spatial distribution: small *Myotis* species occurred rarely but continuously along the transect, whereas occurrence of bat species similar to *E. nilssonii* (e.g. *Eptesicus serotinus*) was temporarily and spatially restricted, giving indication of mutual avoidance or exclusion. Results from radio-tracking further showed that tracked E. nilssonii preferred habitats within 2 km of the known maternity roost and mostly used habitats at great distances (> 6 km) after weaning.

Habitat preference and competition are two major factors that influence distribution patterns of bats and will be discussed subsequently. In order to explain activity and spatial habitat use of tagged *E. nilssonii*, the impact of abiotic factors, sex, age and reproductive state will be addressed briefly prior to the major topics.

4.4.2 Abiotic factors

General activity of tagged northern bats was negatively correlated with outdoor temperatures whereas first emergence was independent of rain and ambient temperature agreeing for example with findings of Entwistle et al. (1996) on *Plecotus auritus.* Similar to findings in other temperate zone insectivorous bat species, northern bat activity was highest in the first part of the night (Swift 1980, Barclay 1989, Shiel et al. 1998a). Minimum distances covered were highest during the first emergence. As *E. nilssonii* depends on flying insects, this pattern was likely to reflect insect abundance which peaks in the first third of the night (reviewed in Entwistle et al. 1996).

4.4.3 Effects of sex, age and reproductive state on individual kinetics

Though radio-tracked bats travelled a median distance of 8 km per night, they spent most of their time within 2 km of their known day roost, confirming an energetic model by Jones et al. (1995) who predict an average foraging range of 2 km for *E. nilssonii*. This finding is further supported by survey results of the present study which indicate highest activity of *E. nilssonii* at forest habitats within 2 km of the maternity roost. Catto et al. (1996) and Brigham (1991) postulated that at distances above five km commuting costs when travelling to a habitat, should become prohibitive but below are trivial compared to the bats' total daily energy budget: indeed, bats tracked before the middle of July in this study were never observed foraging more than 5 km from the roost hence supporting the above hypothesis. However, it is rather intriguing to ask, why those three bats tagged after weaning often travelled more than 15 km per night and were often observed foraging more than five km from the roost, thus suggesting high flight costs (Catto et al. 1996). Selection of predictable and profitable habitats at greater distances, e.g. street lamp habitats with vastly increased insect densities (Rydell 1992b), may be one explanation, but as lamp habitats exist also near the known maternity roost, other factors may be equally important, e.g. competition avoidance (see below).

Whereas flight energetics in female bats reflect constraints by the reproductive context, e.g. reduced manoeuvrability and capture efficiency during pregnancy (Rydell 1993a) and increased energetic demands during late pregnancy and lactation (Racey & Speakman 1987), energy demands of juveniles and males are less predictable. Thus, sex and age might have had different impacts on spatial habitat use: whereas all adult bats stayed within distances predicted by Jones et al. (1995), juveniles and particularly males tagged after weaning covered large distances and spent a considerable time commuting.

4.4.4 Habitat preference

General bat activity of all species in the present study was highest above water bodies supporting recent findings about the general importance of water places as hot spots of activity (Bartonicka 2002, Korine & Pinshow 2004). High bat abundance above water places is most likely due to high and predictable concentrations of swarming insects above water occurring independently of ambient temperature. This holds especially for polluted lakes with a high abundance of pollution-tolerant swarming diptera (e.g. Chironimidae) (Vaughan et al. 1996, Racey et al. 1998). Korine & Pinshow (2004) found that eutrophic water bodies support high bat abundance but low species diversity. In contrast, I found the highest diversity above a highly eutrophic lake.

General importance of water bodies was confirmed for *E. nilssonii*. A particular finding of my study was that the species occurred more abundantly above a small forest lake near the roost (SP 12) than above a eutrophic lake (SP 8) at greater distance. In view of the general lack of northern bat roosts in the western plain around the eutrophic lake, this could be based upon dilution effects from the known roost. However, preference of the oligotrophic lake may also reflect dependence on pollution-sensitive prey and the northern bat might also profit from the absence of potential competitors. Moreover, I found a general preference of adjacent forest areas, suggesting that a lake/forest combination may have been favoured by bats in my study.

Agricultural areas have been shown to be vastly depleted of insects: only few insectivorous bat species are known to subsist on such habitat types (e.g. Korine & Pinshow 2004) and negative selectivity towards agricultural areas has been confirmed for many species (e.g. Gaisler & Kolibac 1992). Not surprisingly, most bat species in the present study avoided places within the 4-6 km distance zone along the transect which comprised mainly fields.

To sum up, bat species in the present study resembled each other in terms of habitat use. Hence, contrasting distribution patterns revealed in my study are unlikely to be due to habitat preference.

4.4.5 Population density & intraspecific competition

As the study was conducted near the supposed range margin of *E. nilssonii* (Bundesamt für Naturschutz 1999), I assume the effects of intraspecific competition to be low due to low general population densities at range margins (Guo et al. 2005). Indeed, my survey data suggest low population density of *E. nilssonii* in the study area. However, I found evidence for severe intraspecific competition in street lamp habitats (for details cf. Chapter 2). Thus, greater distances travelled by bats after weaning might be an avoidance reaction to increased intraspecific competition through the weaned juveniles (Erkert 1982, Duvergé & Jones 1997). The avoidance hypothesis is further supported by the fact that urban habitats at more than 6 km from the known maternity roost were used by *E. nilssonii* after weaning, but rarely before. Indeed, my survey results revealed an increase of general bat activity within a given area through the weaning of the young, but this was significant only for pipistrelles.

Spreading effects from the known maternity roost may partially contribute to the gradient in population density of the northern bat found in the present study. However, surveys indicated that highest activities were not achieved closest to the maternity roost under study. Moreover, at least one more northern bat roost at 3.5 km from the above one was occupied during the study period. Bats from that and other roosts may have counteracted a clear spreading effect.

4.4.6 Interspecific competition

At least eight bat species were present within the study area, which I subdivided into three groups according to their abundance and distribution in relation to the northern bat: the first group comprised at least three small *Myotis* species (*Myotis daubentonii, Myotis mystacinus/brandtii, Myotis bechsteinii*). Same as *E. nilssonii*, these species were detected throughout the transect, but relatively rarely. *Myotis* species use calls of relatively weak intensity and thus their abundance must not be compared directly to the abundance of species using calls of high intensity such as the northern bat (Waters & Walsh 1994, Parsons & Obrist

2004). However, occurrence throughout the transect indicates no segregation from *E. nilssonii*. Resource partitioning with the latter was successfully achieved, even above water bodies which are limited within the study area and thus prerequisites of competition (Arlettaz 1996). Coexistence within these habitats can be realised through niche differentiation, with some members of the *Myotis*-group specialised on gleaning prey from the water surface (e.g. *Myotis dasycneme*, Britton & Jones 1997, *Myotis daubentonii*, Flavin et al. 2001) or catching prey close to adjacent vegetation (*Myotis mystacinus,* Siemers & Schnitzler 2004). Contrastingly, *E. nilssonii* is more likely to profit from swarming Diptera higher above the water surface and particularly from concentrations of non-tympanate insects that lack defence mechanisms (e.g. Jaberg et al. 1998).

The second group consisted of *Pipistrellus pipistrellus* and *Eptesicus nilssonii*, the two most abundant species which occurred regularly throughout the transect. The two species coexisted temporarily and spatially and were regularly found foraging synchronously. Aggressive interactions between the two species were never registered in radio-tracked animals and spatial distributions along the present transect were similar. Obviously, aerial stratification as observed during the present study (cf. Chapter 2) and described similarly by Swift & Racey (1983) for *Plecotus auritus* and *Myotis daubentonii,* enhances a positive coexistence of the two species within their foraging habitats.

The third group comprised species that resemble the northern bat in terms of foraging style, i.e. *Nyctalus noctula, Vespertilio murinus* and *Eptesicus serotinus*. None of these species was as abundant as the northern bat in any of the habitats although they can be as easily detected (all of these species use call intensities well above 125 dB peSPL; Holderied & von Helversen 2003). Moreover, their occurrence was spatially restricted. After parturition, none of these potential competitors were found close to the maternity roost but they occasionally occurred at distances above 4 km from the known northern bat roost. *E. nilssonii* was never observed foraging simultaneously with any of them. On one occasion, when a radio-tracked northern

bat encountered a serotine at 4 km from the maternity roost, the northern bat disappeared immediately. Hence, my findings gave indication for temporal and spatial segregation of these species from the northern bat. Due to their great dietary, morphological and behavioural overlap with *E. nilssonii* (e.g. Baagøe 1987, Rydell 1992c, Jones 1995, Harbusch & Racey 2002) the above species can be considered important competitors of the northern bat. They show great similarities in habitat use: all of them make use of forest habitats and water bodies (e.g. Kronwitter 1988, Jaberg et al. 1998) and are common around street lamps (Zingg 1988, Rydell & Baagøe 1996, Gaisler et al. 1998, Shiel & Fairley 1998a). Resource partitioning between these species is thus more difficult and sometimes even impossible, leading to mutual avoidance. Thus, for northern bats from the known maternity colony, foraging near the roost may pay off in terms of avoidance of interspecific competition. Indeed, this was a strategy chosen by many females, whereas some juvenile individuals tagged after weaning tended to visit habitats at greater distances.

To put it in a nutshell, distribution patterns of the northern bats and potentially competing species in the area are very likely to be affected by interspecific competition. Chapter 3 will address the question whether constraints of flight and echolocation in the northern bat prevent resource partitioning with potential competitors and consequently lead to competitive exclusion or mutual avoidance.

4.4.7 Effects of landscape profile, latitude and roost availability on distribution

Different use of elevation levels may have accounted for the fact that the "mountain bat" (Morgenroth 2004) *E. nilssonii* was more abundant along the transect than some "flatland species". However, distribution of the northern bat in Central Europe is not limited to mountain areas (Steinhauser 1999, Skiba in press). Rather than absolute elevation, landscape profile might affect the spatial distribution of the northern bat, e.g. the presence of slopes with appropriate habitats or sun exposition.

Catto et al. (1994) examined the influence of latitude on distribution of *E.serotinus*, noting, that the use of street lamps occurred independently of latitude. In the case of *E. nilssonii*, latitude is most unlikely to explain distribution as the occurrence within Germany is rather limited to the west, not to the north.

Availability of roosts also seems unlikely to have great impact on distribution patterns of *E. nilssonii*: during reproduction, the species can profit from many kinds of human dwellings as well as tree roosts (Steinhauser 1999) and is not specialised in certain winter roosts either (e.g. Kooj 1999).

4.4.8 Conclusions and potential implications for distribution

An important finding of the study was the complementary distribution pattern of *E. nilssonii* and its potential competitors. My results provide first evidence that interspecific competition may account for small scale distribution patterns of the northern bat. Virtually unaffected or even positively enhanced by the presence of *P. pipistrellus* or small *Myotis* species, the distribution of the northern bat seems to be considerably affected by species employing similar foraging styles (*E. serotinus, N. noctula* and *V. murinus).* For the northern bat, I thus dismiss the hypothesis by Arlettaz et al. (2000) for *Rhinolophus ferrumequinum* postulating that growing populations of *P. pipistrellus* might be able to outcompete competitively inferior species from an area. However, the increase of populations of species with ecological needs similar to *E. nilssonii* is more likely to have serious impact. Similar to *B. barbastellus* (Rydell et al. 1996, Rydell & Bogdanowicz 1997), the distribution of *E. nilssonii* is characterised by its abundant occurrence in poor mountainous or flatland regions of coniferous forest (Steinhauser 1999, Hoffmeister, 2003 pers. comm.), which could result from competitive interactions with species with similar ecological needs from adjacent highly-productive habitats. Some indication for complementary distributions of *E. nilssonii*,

E. serotinus and *N. leisleri* comes from Bavaria (Morgenroth 2004, Rudolph 2004, Walk & Rudolph 2004) and Scandinavia (Rydell & Baagøe 1996).

The northern bat thus seems vulnerable to interspecific competition and its distribution might be regionally restricted by the presence of species employing similar foraging styles. However, in order to assess the importance of interspecific competition to *E. nilssonii*, more studies are required, including the examination of interspecific competition of the northern bat to *V. murinus, E. nilssonii* and *N. leisleri* in regions of similar habitat structure.

For explaining large scale distributions of the northern bat in Central Europe, constraints other than competition have to be taken into account as well. Though habitat use failed to explain contrasting distributions of bat species along the present transect, it may well provide explanations for large scale distributions. The knowledge about habitat use in *E. nilssonii* is limited to Scandinavian environments with little habitat diversity (de Jong 1994). The importance of particular habitat types to the northern bat will therefore be further examined in Chapter 2.

5 Chapter 2 - **Flexibility in habitat use by the northern bat as revealed by radio-tracking**

5.1 Introduction

In an anthropogenically altered environment, behavioural flexibility of a species towards environmental changes may be crucial for its persistence: generalist species may be less vulnerable to modifications of their resources than more specialised ones (Primack 1998). For conservation, it is therefore essential to assess the adaptability of a species to various habitats. Bats have been recognised as excellent model taxa for conservation practice (Fenton et al. 1992, Primack 1998, Racey & Entwistle 2003). Indeed, they differ considerably in their adaptability to habitats subject to various degrees of alteration (e.g. Rautenbach et al. 1996, Vaughan et al. 1996, Robinson & Stebbings 1997, Fenton & Rautenbach 1998, Drescher & Niederfriniger 2002, Rachwald et al. 2002, Patrequin & Barclay 2003). Anthropogenically altered habitats include forests with intense harvesting (Swystun et al. 2001), orchards with diverse degrees of gardening, space above water contaminated with sewage, and anthropogenic food attractors such as street lamps (Schnitzler et al. 1987, Kronwitter 1988, Rydell 1992b, Rydell & Racey 1995, Rydell & Baagøe 1996). Bats may benefit as well as suffer from habitat alterations. For example, tree logging has been described as being beneficial to the bigger species *Lasionycteris noctivagans* but to do harm to the small gleaning species *Myotis septentrionalis* (Patrequin & Barclay 2003). Contamination of rivers by sewage leads to a different composition and amount of insects on and above the water surface (Williams & Feltmate 1992) and may thus positively affect foraging activity of some species (Racey et al. 1998) and negatively affect that of others (Vaughan et al. 1996). Orchards and gardens (Drescher & Niederfringer 2002, Goiti et al. 2002, Aihartza et al. 2003), as well as pastures (Shiel et al. 1998a), may attract insects by a high plant diversity, or faeces, and thus be beneficial to some insectivorous bats. On the other hand, the use of exotic plant species and an intensive management of grassland and arable land may lead to reduced

insect spectra and an avoidance of these habitats by bats (Goiti et al. 2002, Racey & Entwistle 2003). Streets or motorway embankments may serve as useful guidance structures between habitat fragments (Fuhrmann & Seitz 1992). However, streets can also be serious barriers to low-flying bats (e.g. Kiefer et al. 1995, Rydell & Bogdanowicz 1997, Vergari & Dondini 1998). Opportunistically feeding bat species, especially those of larger body size, with a high aspect ratio and fast flight have been shown to profit from street lamps (Rydell 1992b, Shiel & Fairley 1998b, Racey & Entwistle 2003). On the other hand, high insect density close to street lamps may not necessarily guarantee a high foraging success as street lamps attract many tympanate insects, which have evolved efficient defence mechanisms against bats (Jones & Rydell 2003).

Do particular habitat requirements of the northern bat in Germany thus account for its critical conservation status (Red List 2) within Germany? The species has been shown to exploit accumulations of insects around street lamps (Skiba 1986, Rydell 1992b) as well as eutrophic lakes (de Jong 1994). Dietary studies have revealed opportunistic feeding on diverse insect taxa, including many dipterans (Rydell 1992a, Andreas 2002). Thus, whereas the diet composition of *E. nilssonii* suggests a generalist's foraging behaviour, frequent observations of the species around street lamps and above lakes may indicate a certain degree of specialisation.

Activity measurements (Rydell 1986a, 1991, 1992b, Ekman & de Jong 1994, Rydell & Baagøe 1996) have provided indications for habitat use by the species and give important information on local concentrations of bat activity. However, activity measurements have two major limitations: First, replicative countings of bats may lead to an overall overestimate of bat abundance (Rautenbach et al. 1996, Bartonicka 2002). Thus, activity may not reliably reflect the numbers of individuals present within an area (Rautenbach et al. 1996). This applies in particular to bats patrolling along street lamp alleys. Second, activity countings do not provide data about individual habitat use. The only radio-tracking study in *E. nilssonii* (de

Jong 1994) was conducted in a sparsely populated area and suggested abundant use of lake habitats in an area dominated by coniferous forest and lakes.

In the present study, I assessed the importance of natural versus anthropogenically altered habitats for *E. nilssonii* for the first time by radio-tracking bats from a colony situated at the edge of the nature reserve Harz with access to habitats with a varying degree of human alteration. In addition, the individual habitat use of the colony members provides information about the flexibility in habitat choice. The knowledge of both may provide crucial keys for conservation and may help to explain the patchy distribution of *E. nilssonii* in Germany.

5.2 Materials and methods

5.2.1 Habitat composition within the study area

The study area was described in Chapter 1. The maternity roost was situated at 365 m a.s.l..

Potential habitats in the study area included forest (an equal mix of deciduous and coniferous trees with well developed understorey), grassland with a varying degree of agricultural usage, lakes and fields. The study area comprised a considerable amount of urban areas, including industrial areas, residential areas, streets and railway tracks. Continuous alleys of street lamps existed only in three villages within the study area. To save energy, only every third lamp in Bad Grund was lit at night. Two categorisations were made to quantify habitat composition: first, I discriminated between 5 types, i.e. forest, grassland, lakes and rivers, urban areas and fields (arable land). To quantify the importance of anthropogenic influence for habitat use in *E. nilssonii*, areas were divided into habitats with little (natural) versus strong human impact (anthropogenically altered): forest habitats, grassland without fertilising or cattle grazing and lakes unpolluted by sewage were classified as natural, urban areas, fields, lakes contaminated by sewage treatment or used for fish elevation and grassland with intensive cattle grazing were classified as anthropogenically altered. For each bat, the spatial fractions of the above

mentioned habitat types were calculated in its individual home range using GIS Arc View (ESRI, Ver. 3.3).

5.2.2 Roost, capture and marking

The maternity roost was in the attic of a house situated in a small valley in the northern part of Bad Grund. The maximum number of adult bats as estimated by countings of their emergence from the roost amounted to 22 bats. The house was surrounded by grassland which was occasionally being grazed by cattle. Bats entered and left the roost at the far ends of the house, emerging between the first top tile and a metal protective bar. Animals were captured using a mist net held up on a wooden stick. After capture, they were weighed using a 50g-PESOLA spring balance, and the forearm length of the right wing was measured using a vernier calliper. Sex and reproductive status were determined. Age was assessed by checking the degree of ossification of the forearm fissure. Animals were then equipped with armrings (Museum Alexander König, Bonn, size H). Radio transmitters (BD-2A, Holohil systems Ltd., Canada, weight 0.64 g) were fixed on the back using Sauer © medical glue. The back fur was slightly cut between the scapulae where the transmitters were fixed. Relative weight of transmitters ranged from 4.7 to 8.5 % of the bats' body mass (cf. Table 5.1). The bats were subsequently marked individually using coloured reflective tape, glued to the antenna of the transmitter or to the armring, and released in front of the maternity roost. To avoid stress on pregnant females, I conducted no captures during the supposed time of parturition in this roost, which had taken place between 12th and 24th of July in previous years (Rackow, pers. comm. 2001). We heard the first isolation calls of juvenile northern bats, denoting the time of first births (cf. Rydell 1986a), on 22nd June in 2002 and 2003. Capture, banding and radio-tracking were conducted with permission of the Bezirksregierung Braunschweig (509.42502/05-01.01) and the Niedersaechsisches Landesamt fuer Oekologie (Hildesheim / Hannover: 2.8/2.5-22203).

5.2.3 Animals and observation period

I radio-tagged 17 bats, but report data from 13 who maintained transmitters for more than 24 hours. Data of 10 female and 3 male bats, 8 tracked in 2002 and 5 tracked in 2003 (cf. Table 5.1), were analysed. These bats were radio-tracked between 18th May and 30th July. By 1st August, the number of bats in the maternity roost had decreased to less than five, thus I stopped tagging bats.

Table 5.1 Northern bats radio-tracked in 2002 and 2003. P1: 18th May - 21st June. P2: 22nd June - 30th July. Note that w219 and w219n are different bats equipped successively with the same radio-transmitter. For w180, only data obtained in P2 were included in seasonal comparisons. l: lactating. j: juvenile

bat	sex	weight [g]	forearm [mm]	transmitter fixed	nights tracked	remarks	year / period
w084	♀	7.5	40.9	21st - 24th May	3		2002 / P1
w084n	♀	10.5	41.5	25th - 30th May	3		2002 / P1
w112	♀	12.2	40.0	25th - 27th May	2		2003 / P1
m133	♂	7.5	38.3	18th - 29th May	4		2003 / P1
w219	♀	9.5	42.0	2nd - 5th June	3		2002 / P1
w219n	♀	13.0	38.0	5th - 14th June	5		2002 / P1
w080	♀	13.0	39.5	9th - 16th June	6		2003 / P1
w180	♀	10.0	40.3	11th June - 4th July	8		2002 / P1 & P2
w200	♀	13.5	41.6	24th June - 8th July	8	l	2002 / P2
w080n	♀	11.0	40.0	25th - 27th June	2	l	2003 / P2
w223	♀	10.5	38.8	9th - 16th July	5	j	2002 / P2
m081	♂	8.0	38.7	24th -30th July	5	j	2002 / P2
m110	♂	9.0	39.3	9th - 16th July	6	j	2003 / P2

5.2.4 Radio-tracking and field observation

Radio-tracking equipment consisted of a receiver and a 3-element–yagi-antenna (TITLEY electronics Regal 2000). During the initial phase of the study, a second receiver (STABO XL) and a 2-element antenna were additionally used for triangulation. These data are not included here as triangulation was soon replaced by the homing-in-on-the-animal method (cf. White &

Garrott 1990, Kenward 2000). Permissions to follow the bats within the reserve "Landschaftsschutzgebiet Harz" were granted by the district administration of Seesen (Landkreis Seesen, di 31.033) and Osterode (II.4/2303 OHA10 Haupt). Bats were followed by car or on foot. In the respective habitats, animals were individually identified by their coloured tags, using a halogen torch. In addition, an infrared digital video camera and an infrared torch were used to document the flight behaviour of tagged bats during dusk and dawn. When visual contact was lost during commuting flights, a steady change in the direction of maximum strength of the received signal (definition by Catto et al. 1996) indicated commuting. When the directional change stopped, I usually found the bat within five minutes. A bat was described as unobserved when visual contact was lost for more than five minutes. The presence of conspecifics and of bats of other species flying within the foraging areas of tagged bats was detected visually and by using a U30 bat detector (Ultrasound Advice) and further confirmed by subsequent sound analysis (cf. Chapter 1).

Fixes were entered into digital maps (Landesvermessung und Geobasisinformation Niedersachsen) using GIS Arc View (Ver. 3.3) and rounded to the nearest 25 x 25 m in the Gauss-Krüger-coordinate grid thus taking into account the typical flight path lengths of *E. nilssonii* while foraging. Outer fixes for each bat were linked resulting in 100 % minimum convex polygons (MCPs, Kenward 2000), hence forward referred to as home ranges. Two males (m081, m110) conducted long-distance commuting flights outside their regular home ranges. For these males, I used core ranges, within which they spent their regular foraging activity in all considerations concerning habitat use.

Finally, temperature within the study area was measured at the intersection of forest, grassland and urban area about 100 m from the maternity roost. Measurements were conducted 1.5 m above ground three times per radio-tracking night in sixty radio-tracking nights. Median night temperature was 12.7 (interquartile range: 10.8-15.4)°C (n=60) and dropped below 6°C only during two nights, in both cases within the final third of the night.

5.2.5 Data analysis

I determined bat activity and habitat use on a minute scale for each night. Contact time was the time an animal could be observed per night. Nightly flight time (FLT) was defined as the contact time individuals spent flying outside the roost and comprises foraging time (FT), i.e. the time a bat spent flying continuously back and forth within a restricted area per night, as well as time spent commuting, i.e. the time a bat travelled between two foraging sites (Table 2). Statistics were calculated with fractions of FLT when considering habitat use or fractions of FT when considering inter- and intraspecific encounters, respectively.

To study seasonal differences in both activity and habitat use, the entire observation period was divided into 2 periods of similar duration relative to the birth of the young bats. Period 1 (P1) lasted from 18th May until 21st June, period 2 (P2) was the time thereafter (cf. Table 5.1). For w180, data were collected during P1 and P2. For the statistical analysis of seasonal differences, I only used data obtained from this bat in P2 in order to avoid pseudoreplication.

All values are generally given as medians and interquartiles. In Tables 5.2 and 5.3 and 5.5, I used min/max-ranges. As data were not normally distributed, nonparametric statistics were employed in all analyses. All statistical tests were performed using STATISTICA (Statsoft, Kernel Release 5.5 and 6.0) and SAS (Ver. 8.2, IML module).

In order to check for range selectivity, I compared the composition of habitats and elevation levels within individual circles around the maternity roost (expected) to the composition within individual MCPs (observed). The circles' radii were chosen individually according to the bats' maximum distance to the roost and thus determined the area the bat theoretically had access to. For each category, individual difference values (observed-expected) were calculated and the resulting distribution was tested against a symmetric distribution around zero using Wilcoxon-signed rank tests. Generally, two-sided tests were conducted and the significance level was adjusted according to the number of categories. Next, based on the assumption of a homogeneous habitat use by the bats, I calculated expected frequencies from

area fractions of the habitat types within each bat's home range, and compared them to the observed frequencies sampled at 15 minute intervals. Assuming a flight speed of c. 5.8 ms^{-1}, determined for a commuting bat within this study, all bats were able to cross their entire home ranges within 11 (10-13) minutes. I thus avoided temporal autocorrelation by taking a sample every 15 minutes (cf. Henry et al. 2002, Aihartza et al. 2003). As distribution of habitats and elevations within MCPs was extremely unequal, criteria for ordinary chi-statistics were not fulfilled (Horn 1977). I therefore used multinomial tests. In cases where significant deviations of observed from expected habitat use were detected, binomial tests were conducted for each category to detect the location of significant deviations setting the significance level at α/k (with k being the number of categories). Finally, I calculated confidence intervals for all bats and categories employing Pearson-Clopper values (Hartung 1993).

To test for seasonal and sex differences in habitat-use, I used bats as replicative units (medians of all nights per bat). To test for individual differences, I used nights as replicative units. I used Kruskal-Wallis-H tests and Mann-Whitney-U-Tests. Wilcoxon matched-pair tests were employed to search for differences in habitat use of an individual on the days directly following capture compared to all other days of radio-tracking.

Spearman rank correlations were performed to detect effects of temperature on habitat use in bats. In this special case, fractions of FLT per habitat type were pooled for all radio-tracking nights with median temperature measurements (n=60).

In all multiple comparisons, Bonferroni corrections were used to account for the number of categories (habitats, elevation levels). For all multiple tests, p values will be reported lower or higher than Bonferroni adjusted levels throughout the results section.

5.3 Results

5.3.1 Contact time and time budget

Visual and acoustic contact to tagged bats was kept most of the time. Average contact time (cf. Table 5.2) for the 13 bats was 93 (86–99) % of observation time and similar before (P1: 94 %) and after parturition (P2: 91 %). Long periods of up to 120 minutes without visual or acoustic contact to the observed bat occurred only at the end of July. Contact time was not significantly different between sexes (Mann-Whitney-U, $p > 0.05$).

The bats spent 43 (36-57) % of the contact time flying outside the roost (=FLT).

81 (73–90) % of FLT was spent foraging in habitats which were normally within a range of 4 km of the day roost. However, the 2 males tagged in P2 (m110, m081) showed a different pattern: in addition to regular foraging within habitats, both males displayed extended exploring flights outside the core home range normally used for foraging. They travelled up to 70 km per night following vegetation structure, rivers, street lamps and streets without staying anywhere longer than two minutes. Consequently, the percentage of commuting time was particularly high for those animals (m081: 27 (6-38) %, m110: 40 (23-68) % of FLT).

Table 5.2 Time budget of 13 observed northern bats**.** Medians and min/max values per night are given in minutes. Observation time comprises the period from dusk until dawn or from the first emergence until the last return of a bat to the day roost, when this occurred before dusk or after dawn. For detailed time budgets cf. Chapter 1.

observation time			
456 (437-494)			

contact time			
429 (362-467)			

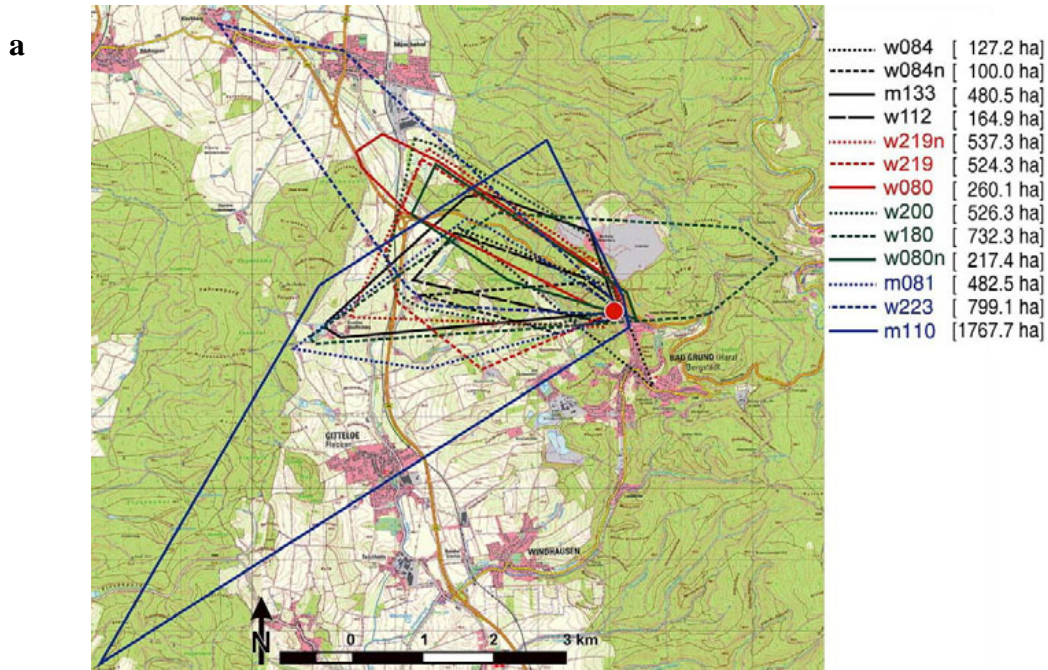| resting time		flight time (FLT)	
Roosting[a]	Foraging breaks[b]	foraging (FT)	commuting
226 (52-369)	0 (0-19)	122 (59-200)	24 (17-84)

[a] roosting was defined as the median time per night, a bat spent within the day roost
[b] foraging breaks were defined as the median time per night, a bat spent hanging in trees

5.3.2 Home ranges and habitat composition

Median home range size was 524 (217-732) ha (n = 13). Smallest home ranges were measured in May (median: 146 ha, n = 4, cf. Fig. 5.1a), largest home ranges were achieved by animals tagged after 9th July (median: 1634 ha, n = 3, cf. Fig. 5.1a and b). The home ranges of the individuals showed considerable overlap and most areas used were situated north-west of the maternity roost (cf. Fig. 5.1a).

Habitat composition was calculated based on the individual home ranges. Forest and grassland were predominant during all observation periods (forest: 62 (57-68) %, grassland: 27 (20-31) %, cf. Fig. 5.2a, top). Natural habitats prevailed over anthropogenically altered habitats (Fig. 5.2b, top) in all observation periods.

··········	w084	[127.2 ha]
- - - -	w084n	[100.0 ha]
——	m133	[480.5 ha]
— · —	w112	[164.9 ha]
··········	w219n	[537.3 ha]
- - - -	w219	[524.3 ha]
——	w080	[260.1 ha]
··········	w200	[526.3 ha]
- - - -	w180	[732.3 ha]
——	w080n	[217.4 ha]
··········	m081	[482.5 ha]
- - - -	w223	[799.1 ha]
——	m110	[1767.7 ha]

Quelle: Auszug aus Topographischen Karten © LGN Landesvermessung + Geobasisinformation Niedersachsen

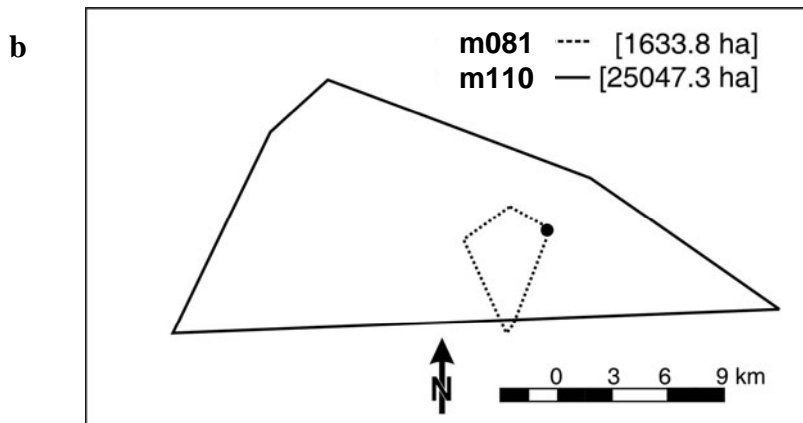| m081	- - - -	[1633.8 ha]
m110	——	[25047.3 ha]

Fig. 5.1 a Home ranges as defined by the 100% minimum convex polygons of the 13 northern bats radio-tracked in 2002 (dotted lines) and 2003 (continuous/dashed lines). Home ranges (in hectares) are shown for four periods: P1a: 18th May – 1st June (black lines). P1b: 2nd June – 21st June (red lines). P2a: 22nd June – 8th July (green lines). P2b: 9th July – 30th July (blue lines). The (red) circle indicates the position of the maternity roost. For m081 and m110, core ranges are given which do not include occasional long distance exploring flights.   (For coloured map cf. www.lgn.de). **b** Total ranges including exploring flights of m081 and m110. Note the different scale.
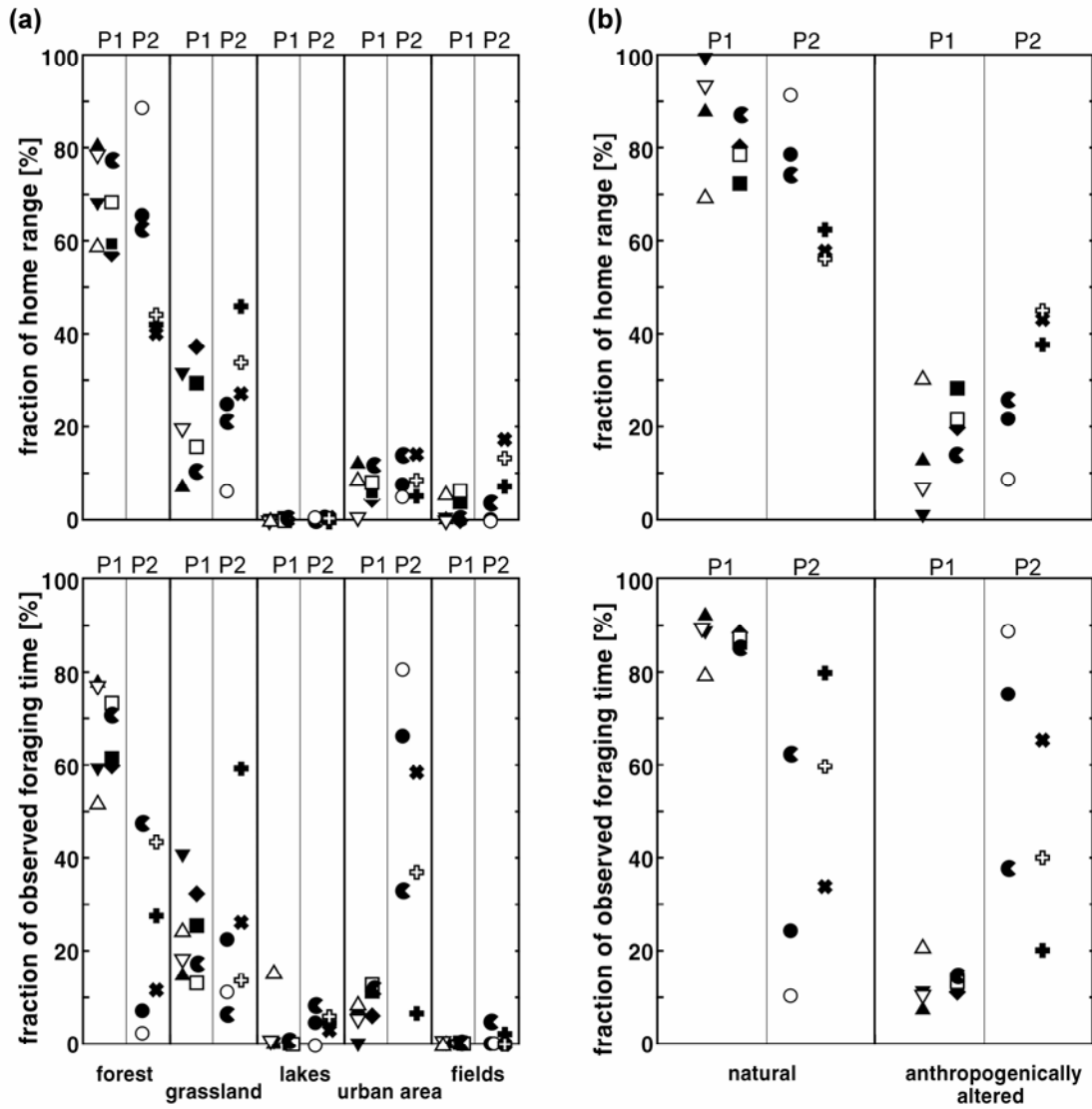
Fig. 5.2 a Habitat composition (top) within the home ranges of 13 northern bats and use (bottom) of the five habitat types. Values are given as area fractions of individual home ranges for habitat composition and as fractions of total foraging time for habitat use. For each habitat, symbols are arranged into four columns representing the four time periods (P1a, P1b, P2a, P2b). Filled symbols represent animals tagged in 2002, open symbols those tagged in 2003. **b** Habitat composition (top) within the home ranges of 13 northern bats and habitat use (bottom) of natural versus anthropogenically altered habitats. For each category, symbols are arranged into four columns (see above). For further explanations cf. Fig. 5.1.

Simultaneous comparisons of observed and expected fractions of elevation levels within home ranges and the total accessible area respectively, revealed significant differences for elevations below (200-249, 250-299, 300-349 m a.s.l.) as well as above (450-499, 500-549, 550-600, >600 m a.s.l.) roost level (Wilcoxon signed rank test, p<0.005) but no significant differences for elevations around (350-399, 400-449 m a.s.l.) roost level (p>0.005). Significance could not be confirmed for elevations below 150 m a.s.l. due to the small number of home ranges containing this level. Generally, elevations below roost level were preferred and those above roost level avoided as bats usually flew downwards in north western direction upon departure (Fig. 5.1a). I found no indication that bats selected home ranges with a habitat composition differing significantly from habitat composition within the total accessible area (n=13, p>0.01).

5.3.3 Habitat use

No significant differences in habitat use were found when comparing the night following the capture of an individual to the median of the other nights (Wilcoxon matched-pair test, n_{max} = 13, n.s.). Therefore the night following capture was included in the subsequent data analysis. No significant sex differences in habitat selection could be found, probably due to the small sample size of males (Mann-Whitney-U test, n_{males} = 3, $n_{females}$ = 10, p>0.01). Overall use of the 5 habitat types was not correlated to ambient temperatures (Spearman rank correlation, r= -0.07 – 0.18, n = 60, p>0.01).

Individual patterns in habitat use per night are given in Table 5.3. On the assumption of a homogeneous use of each habitat type, I found significant differences between the expected and the observed habitat use (cf. Fig. 5.2 and Tables 5.4a, 5.4b).

Forest habitats were used as expected by most bats, but were used less frequently than expected by three females tagged in P2 (Table 5.4a). In addition to seasonal variation, I found

indications for individual differences in the use of forest habitats in P 2 (n = 6, H = 14.1, p = 0.02). w200 and w180, radio-tracked simultaneously, differed significantly in their use of forest habitats (U = 1, p =0.008, cf. Table 5.3): while w200 was observed hunting around street lamps, w180 was found in forest habitats.

I also found seasonal variation in the use of urban habitats: whereas I detected no selectivity before parturition (cf. Table 5.3a), I found selectivity for most bats tagged after parturition which used urban habitats more than expected. Females in P2 spent a significantly higher fraction of FLT in urban habitats than those females tagged before parturition (n = 10, U = 0, p = 0.01, cf. Table 5.3). Seasonal use of urban habitats was most obvious when comparing the data obtained from w180 in P1 and P2: median use of urban areas amounted to only 6 (0-13) % of FLT in P1 but to 26 (8-37) % of FLT in P2 (cf. Table 2.3). In urban habitats, street lamps were a main attraction for the bats. Females in P2 spent 89 (78-97) % (n = 4) of their foraging time within urban areas hunting around street lamps.

Use of grassland was mostly opportunistic (cf. Table 5.4a). Lakes were used according to their availability before parturition and positively selected after parturition when included within individual home ranges (cf. Table 5.4a). Deviations from expected use were significant in bats tagged in P2 (binomial tests, p<0.01, p<0.0125 for w080n). Agricultural areas made up only tiny fractions within individual home ranges and were never used more than expected (cf. Table 5.3a). All in all, animals tagged in P1 tended to use habitats opportunistically, whereas those tagged in P2 were more selective in their habitat use. Namely, urban areas were key habitats in P2.

Natural habitats were preferred to anthropogenically altered ones by most animals in P1 (Fig. 5.2b, bottom and Table 5.4b). All females tracked in P 2, though, foraged in anthropogenically altered habitats more than expected and significantly more frequently than those bats tagged in P1 (n=10, U = 0, p=0.01).

Table 5.3 Individual habitat use of *E. nilssonii* during P1 (18th May - 21st June) and P2 (22nd June - 30th July). Median values and min/max values of flight time / night in the five habitat types and total flight time / night are given in minutes. For w180, data before (-1) and after (-2) parturition were considered.

period	bat	total flight time / night	forest	grass-land	lakes & ponds	urban area	fields
P1	w084	184 (47-214)	129 (0-178)	21 (0-37)	0	0 (0-30)	0
	w084n	79 (58-88)	30 (23-42)	19 (10-36)	0	0	0
	w112	138 (113-163)	93 (85-101)	22 (19-25)	0	7 (0-13)	0
	m133	90 (20-158)	41 (0-48)	10 (0-40)	0 (0-38)	0 (0-20)	0 (0-3)
	w219	163 (70-249)	91 (20-132)	40 (37-48)	0 (0-17)	0 (0-18)	0
	w219n	166 (126-362)	91 (35-241)	38 (18-91)	0 (0-22)	11 (0-49)	0
	w080	187 (104-274)	105 (13-202)	15 (0-44)	0 (0-5)	1 (0-91)	0
	w180-1	189 (49-295)	153 (0-174)	32 (0-52)	0	15 (0-43)	0
P2	w180-2	203 (122-281)	90 (40-110)	6 (0-32)	7 (0-47)	58 (0-111)	0 (0-32)
	w200	242 (77-281)	5 (0-63)	39 (0-77)	0 (0-38)	129 (0-204)	0
	w080n	135 (119-150)	1 (0-1)	12 (6-18)	9 (5-13)	88 (69-107)	0
	w223	163 (99-221)	0 (0-35)	17 (0-73)	0 (0-16)	50 (18-110)	0
	m081	172 (51-352)	18 (0-135)	47 (0-292)	0 (0-21)	0 (0-48)	0 (0-15)
	m110	221 (129-251)	41 (24-100)	19 (0-40)	0 (0-37)	4 (0-137)	0

Table 5.4a Observed and expected use of the five habitat types. n: total number of 15-minute intervals in which bats were observed to forage. Significant deviations of the observed from expected frequencies are indicated by asterisks. Direction of deviation from expected values is indicated by + (more than expected) and – (less than expected) respectively. For m081 and m110, calculations were based upon habitat composition in the core areas. For further specifications see Table 5.2.

bat	multinomial test	forest	grassland	lakes	urban area	fields	period
w084	n=31, k=3, p=0.19	n.s.	n.s.		n.s.		
w084n	n=13, k=3, p=0.60	n.s.	n.s.		n.s.		
w112	n=18, k=2, p=0.81	n.s.	n.s.				
m133	n=19, k=5, p=1.00	n.s.	n.s.	n.s.	n.s.	n.s.	
w219	n=28, k=4, p=0.11	n.s.	n.s.	n.s.	n.s.		P1
w219n	n=66, k=5, p=0.05	n.s.	n.s.	n.s.	n.s.	n.s.	
w080	n=43, k=5, p=0.10	n.s.	n.s.	n.s.	n.s.	n.s.	
w180 - 1	n=48, k=5, p=0.09	n.s.	n.s.	n.s.	n.s.	n.s.	
w180 - 2	n=48, k=5, p<0.0001	n.s.	*-	*+	*+	n.s.	
w200	n=102, k=4, p<0.0001	*-	n.s.	*+	*+		
w080n	n=15, k=4, p<0.0001	*-	n.s.	*+	*+		P2
w223	n=38, k=5, p<0.0001	*-	n.s.	n.s.	*+	*-	
m081	n=51, k=5, p=0.0003	n.s.	n.s.	*+	n.s.	n.s.	
m110	n=53, k=5, p<0.0001	n.s.	*-	*+	*+	n.s.	

Table 5.4b Observed and expected use of natural versus anthropogenically altered habitats. For further explanations see Tables 5.2 and 5.3a.

bat no.	binomial test	natural	anthropogenically altered	period
w084	n=31, p=1.00	n.s.	n.s.	
w084n	n=13, p=0.08	n.s.	n.s.	
w112	n=18, p=1.00	n.s.	n.s.	
m133	n=19, p=0.46	n.s.	n.s.	P1
w219	n=28, p=0.34	n.s.	n.s.	
w219n	n=66, p<0.0001	* +	* -	
w080	n=43, p=0.005	* +	* -	
w180 - 1	n=48, p=0.66	n.s.	n.s.	
w180 - 2	n=48, p=0.07	n.s.	n.s.	
w200	n=102, p<0.0001	*-	*+	
w080n	n=15, p<0.0001	*-	*+	
w223	n=38, p<0.0001	*-	*+	P2
m081	n=51, p=0.048	*+	*-	
m110	n=53, p=0.22	n.s.	n.s.	

5.3.4 Intra- and interspecific encounters

The radio-tagged individuals differed significantly in the time spent foraging (FT) with or without conspecifics, respectively (Wilcoxon-test, n = 13, T = 1, Z = 3.1, p =0.002): they spent higher fractions of foraging time hunting alone than with conspecifics. Intraspecific encounters were more frequent in females (27 % of FT with conspecifics) than in males (3 % of FT with conspecifics). Females tagged in P 2 spent a significantly higher percentage of FT hunting with conspecifics (39 (34-48) %) than the females in P1 (14 (0-24) %, n = 10, U = 0, p =0.01, Fig. 2.3, Table 5.5). This result does not persist when including the males (n=13, p =0.29). Tagged bats foraging at street lamps spent about 34-56 % of their FT with conspecifics. In this situation, agonistic behaviour, characterised by distress calls and aerial chases, occurred regularly.

Interspecific encounters were less frequent than intraspecific ones: tagged bats spent

0 (0-11) % of their FT per night hunting with other bat species, which is significantly less than the time spent foraging alone or with conspecifics (n = 13, T = 0, p =0.001).

Simultaneous foraging with other species usually occurred above lakes or close to street lamps. In most cases, *Pipistrellus pipistrellus* was hunting next to female *E. nilssonii* (cf. Table 2.5). Overlap of flight paths was avoided by stratification, with pipistrelles hunting clearly below the northern bats. Other species involved in interspecific encounters were *Myotis daubentonii, Myotis mystacinus* or *brandtii, Eptesicus serotinus, Myotis myotis* and *Vespertilio murinus*. On the rare occasion when *E. serotinus* and *E. nilssonii* were observed foraging together above an agricultural area, the tagged *E. nilssonii* disappeared immediately after the other species had arrived.
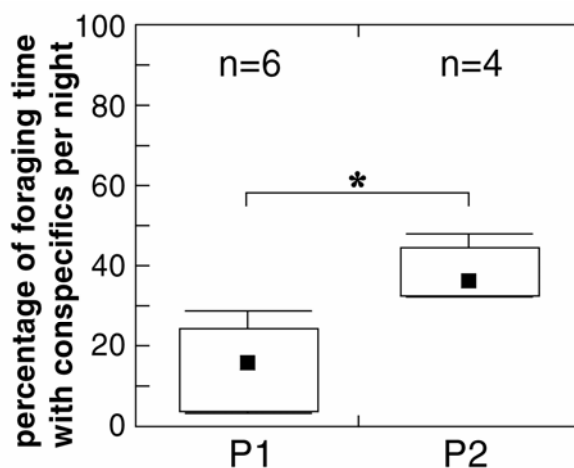
Fig. 5.3 Seasonality in the degree of intraspecific encounters for female northern bats. Medians, interquartiles and min/max-ranges are given as percentage of foraging time per night in all habitats. P1: before 21st June. P2: after 21st June.

Table 5.5 Intra- and interspecific encounters for 10 female northern bats. All minute values are given as medians and min/max ranges of the individual medians of foraging time per night. P1: 18th May - 21st June. P2: 22nd June - 30th July.

Period	foraging time (FT)	with conspecifics	with pipistrelles	with other bat species
P1 (n=6)	134 (59-166)	24 (0-36)	0 (0-9)	0 (0-0)
P2 (n=4)	140 (96-181)	61 (25-63)	9 (0-54)	0 (0-0)

5.3.5 Elevation-specific habitat use

The home ranges of all tagged bats included elevation levels between 200 m a.s.l. and 449 m a.s.l.. The home ranges of 3 bats tagged in late July (m081, m110, w223) included levels below 200 m a.s.l. and those of two bats (m110, w180) included levels above 450 m a.s.l. Generally, elevation levels from 250 m a.s.l. to 349 m a.s.l. predominated (Fig. 2.4 top). w180 differed from all other bats in including almost equal fractions of all altitude levels between 200 m a.s.l. and 449 m a.s.l. in its home range. Bats had to surpass a crest 50 m above the roost to reach their preferred habitats. Except for 2 animals tagged in P2, they avoided climbing more than that at the beginning of a foraging flight.

Expected differed significantly from observed elevation use in most bats (multinomial test, $p < 0.05$, cf. Fig 5.4, Table 5.6): I found that elevation levels below roost level (360 m a.s.l.) were mostly avoided in P2, whereas the elevation level between 350 m and 399 m a.s.l., i.e. around roost level, was significantly preferred by most bats (cf. Table 5.6).
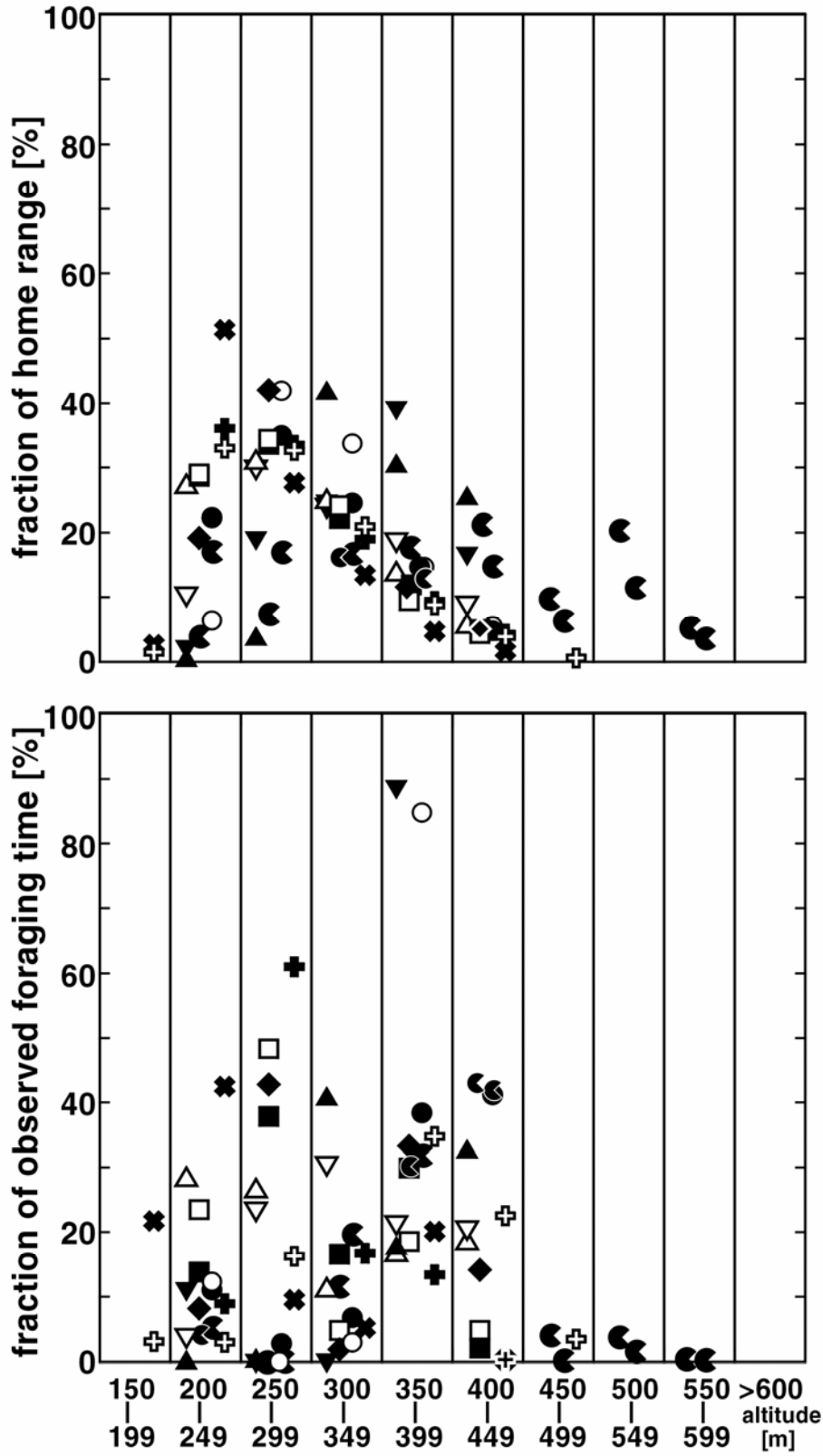
Fig. 5.4 Composition of elevation levels within the home ranges of 13 northern bats (top) and use of elevation levels (bottom). For further explanations cf. Fig. 5.2a.

Table 5.6 Observed and expected use of elevation levels. Elevation levels are given in metres a.s.l.. For further explanations see Table 5.3 and 5.4a.

bat no.	multinomial test	150-199	200-249	250-299	300-349	350-399	400-449	450-499	500-549	550-599	period
w084	n=31, k=4, p=0.04			n.s.	n.s.	n.s.	n.s.				
w084n	n=13, k=5, p=0.0004		n.s.	n.s.	n.s.	*+	n.s.				
w112	n=18, k=5, p=0.70		n.s.	n.s.	n.s.	n.s.	n.s.				
m133	n=19, k=5, p=0.07		n.s.	n.s.	n.s.	n.s.	n.s.				P1
w219	n=28, k=5, p<0.0001		n.s.	n.s.	*-	*+	n.s.				
w219n	n=66, k=5, p=0.0003		n.s.	n.s.	n.s.	*+	n.s.				
w080	n=43, k=5, p=0.003		n.s.	n.s.	*-	n.s.	n.s.				
w180 – 1	n=48, k=8, p<0.0001		n.s.	n.s.	n.s.	*+	n.s.	n.s.	n.s.	n.s.	
w180 – 2	n=48, k=8, p<0.0001		n.s.	*-	n.s.	*+	*+	n.s.	n.s.	n.s.	
w200	n=102, k=5, p<0.0001		n.s.	*-	-*	*+	*+				
w080n	n=15, k=5, p<0.0001		n.s.	*-	n.s.	*+	n.s.				P2
w223	n=38, k=6, p<0.0001	*+	n.s.	*-	n.s.	n.s.	n.s.				
m081	n=51, k=5, p<0.0001		*-	*-	*+	n.s.	*+				
m110	n=53, k=7, p<0.0001	n.s.	*-	n.s.	n.s.	*+	*+	*+			

5.4 Discussion

My study disclosed a high flexibility of *E. nilssonii* in habitat use. The bats tended to use habitats within their home ranges opportunistically before the birth of the young. Bats tagged after parturition were more selective: only then, urban habitats were key habitats to the northern bats tagged in my study. Thus, the bats displayed generalists' behaviour before and a more specialist-like behaviour after parturition. Moreover, the major habitats were used to various extents by the tagged bats revealing a high degree of individual variation.

The seasonal changes were most pronounced in the use of forest habitats: whereas before parturition, forest use of all animals matched expectations derived from home range composition, forest was avoided by some females after parturition. w180, tracked before and after parturition, used forest habitats less after parturition than before parturition. After parturition, individual strategies were obvious: 1 female (w180) continuously spent a large fraction of the night in the forest even after the birth of the young, whereas others tagged in that period hunted preferably in urban areas.

Other than in a previous study (de Jong 1994), urban areas instead of lakes were key habitats to reproducing females in the present study. In the use of urban habitats *E. nilssonii* resembled *E. fuscus* (Duchamp 2004) and *E. serotinus* (Catto et al. 1996) though use of urban habitats was less pronounced than in the latter and almost exclusively restricted to the time after parturition. Main attraction in urban habitats were illuminated areas, which fits observations of Rydell (1991) obtained by activity measurements. Agricultural areas were not selected by bats in this study, similar to observations in *E. serotinus* (Harbursch & Racey 2002).

How can one account for this habitat use of *E. nilssonii* in view of the main factors influencing habitat use in bats, i.e. ambient temperature, prey availability, predation, competition and individual energetic requirements (cf. Erkert 1982)?

Chapter 2

5.4.1 Temperature and prey availability

Temperature has been shown to influence the general activity of *E. nilssonii*, particularly when falling below a threshold of 6 ° C below which insect density becomes limiting (Rydell 1992a). In my study, these minimum temperatures reported for critical insect abundance in *E. nilssonii* were reached only twice during the observation period. Northern bats were observed hunting around street lamps while high insect densities were simultaneously measured at forest habitats (Haupt, pers. observations 2002) and other individuals (w180) were observed hunting there successfully. Thus, habitat preferences may not be explained by prey abundance in this case. In fact, Ekman & de Jong (1994) and Rautenbach et al. (1996) found that bats do not always choose habitats of highest insect abundance for nocturnal foraging.

Nevertheless, certain "key habitats" have been described that provide reliable patches of food at all times and can be crucial resources (e.g. Rydell 1991, de Jong 1994, Jaberg et al. 1998, Racey and Entwistle 2003). Lakes may be among such key habitats as they provide a great abundance of insects (Russo & Jones 2003), particularly non-tympanate ones that consequently lack defence mechanisms and are thus easier to catch for foraging bats (Jaberg & Blant 2003). In my study however, lakes were rare and were used relatively little, contrasting with findings of de Jong (1994) about the crucial importance of lake habitats to the northern bat. Instead, urban areas constituted such key habitats, particularly after the birth of the young. Mercury vapour lamps, which were used exclusively in the villages of the study area, have been shown to attract large amounts of insects (Rydell 1992b, Blake et al. 1994, Rydell and Racey 1995) but also to inhibit prey defence (Svensson & Rydell 1999, Svensson et al. 2003). Additionally, the use of visual cues (Eklöf et al. 2002) may facilitate foraging in lighted areas, and food intake by northern bats has been shown to be generally higher in street lamp than in forest habitats (Rydell & Racey 1995).

However, in view of the advantages of foraging around street lamps, why did northern bats tagged before birth spend so little time hunting there? Predation pressure as well as intra- and interspecific competition may account for this result.

5.4.2 Predation

Erkert (1982) pointed out the strong effect of predator pressure on long-lived small mammal species, such as bats, for example by owls. Density of nocturnal avian predators, namely *Strix nebulosa*, *Asio otus*, *Glaucidium passerinum* and *Bubo bubo*, is particularly high within the study area. B. bubo has been shown to roost close to the above mentioned street lamp habitats (study group owls in Osterode, pers. comm. 2004) and in one of the preferred lake habitats, S. nebulosa was regularly heard within immediate vicinity of the day roost. However, I never observed predator attacks. Being a middle-sized, fast-flying bat, *E. nilssonii* may be well-adapted to predation avoidance and thus be less vulnerable than small, slow-flying species (Baagøe 1987).

5.4.3 Competition

Interspecific competition detected in this study was low: other bat species which employ similar flight and foraging styles (*E. serotinus, V. murinus*) were but rarely observed foraging simultaneously with *E. nilssonii*. *P. pipistrellus*, the only species besides *E. nilssonii* known to have maternity roosts at Bad Grund, is a potential competitor considering the overlap in diet (Swift et al. 1985, Rydell 1986b, Arlettaz et al. 2000, Andreas 2002). However, the clear aerial stratification I observed suggests a competition avoidance (cf. Racey and Entwistle 2003) and the coexistence of the two species may better be described as a positive association (cf. Bell 1980) in my case.

Intraspecific competition is more likely to have had a considerable impact on habitat choice, especially in street lamp habitats, where general bat density can be vastly increased compared

to unlit zones (Blake et al. 1994, Rydell & Racey 1995, Jones & Rydell 2003). In my study, those northern bats that intensely used street lamp habitats regularly foraged with other conspecifics. Agonistic interaction was obvious, as reported earlier for *E. nilssonii* in other habitats (Rydell 1986, 1992a). Taking into account that frequency of conflicts depends on insect density (Rydell 1986), prey abundance may be a limiting factor for the number of northern bats hunting at street lamps. Considering street lamp alleys as a limited resource within our study area, my results suggest that the bats employed different strategies in order to optimise energetics: some bats preferred street lamps as a predictable food resource, thereby tolerating a high level of intraspecific competition, whereas others avoided intraspecific competition and rather exploited other resources (e.g. forest). For females, the choice of either strategy might be influenced by the dominance status of individuals foraging within the same area (Rydell 1986a). Also, their reproductive status and associated energetic needs (see below) may determine, whether a bat decides to risk energetically costly competitive encounters within street lamp habitats. Intraspecific competition may thus have played a major role for the individual variability in habitat use observed in my study.

5.4.4 Individual energetics

Apart from intraspecific competition, habitat use may be explained by energetic requirements. For females, the impact of pregnancy on manoeuvrability (Racey & Speakman 1987, Aldridge & Brigham 1988, Rydell 1993a), the elevated energetic needs of lactation (Wilde et al. 1995) as well as the increased flight costs due to pregnancy and the need to suckle the young may cause seasonal differences in habitat use. In my study, a strategy of most females radio-tracked immediately after the birth of the young was the extensive use of reliable urban habitats below roost altitude level and at low distances to the maternity roost, an appropriate, energy-maximising (Aihartza et al. 2003) strategy during lactation.

For males, a lower reproductive impact on flight energetics is expected and thus it is not surprising that the home ranges recorded for males were larger than those of the females. Street lamp hunting of the two males during late July may be seen as an energy compensation of high flight costs suffered during long distance exploring flights (see also Catto et al. 1996). Commuting itself may also be a foraging strategy when linked to a continuous intake of "aerial plankton" (Rydell 1992c): the two males captured in late July were both observed to commute in filter-feeder style above rivers, along street lamp alleys and forest edges during their exploring flights, and they showed frequent deviations from a straight flight course providing evidence for feeding. A positive side effect of this commuting strategy is the avoidance of competition (Erkert 1982, Swift et al. 1985), especially when intraspecific competition is increased after weaning.

5.4.5 Conclusions for distribution and conservation

In the highly diverse environment of the present study, *E. nilssonii* showed a high flexibility in habitat choice by making use of natural as well as anthropogenically altered habitats. As the habitats used in this study, and the key habitats in particular, do not occur patchily within Central Europe, habitat use fails to explain the distribution pattern of the northern bat.

A striking result of my study was that habitat use in the northern bats was coupled with a low abundance of bat species with a similar foraging behaviour.

Thus, I hypothesise that, agreeing with findings from Chapter 1, interspecific competition rather than habitat requirements accounts for the patchy distribution pattern of the species in Central Europe. However, there is indication that a combination of both factors may account for the particular distribution pattern: *E. nilssonii* is relatively abundant in regions with coniferous forest typically characterised by low insect densities and consequently the lack of competing species (Ahlen and Gerell 1989, de Jong 1994, Ohlendorf 1987). In fact, the occurrence of *E. nilssonii* is almost always coupled with either coniferous or mixed forest

habitats (Meschede & Heller 2000) which may serve as foraging grounds and provide roosting trees (Steinhauser 1999). Distribution patterns of the northern bat in Central Europe may therefore reflect the availability of suitable forest as well as the occurrence of potential competitors.

With the expansion of agricultural areas at the cost of forests and the decrease of profitable white street lamp habitats in Germany on the one hand, and a decrease in the abundance of eutrophic lakes as a result of growing environmental consciousness on the other hand, availability of forest habitats will continue to play a crucial role for the persistence of *E. nilssonii* in Germany. Conservation of woodland with understorey maintained by moderate silviculture may thus constitute a major step to protect the species.

6 Chapter 3 - <u>Constraints of echolocation and manoeuvrability on microhabitat use by the northern bat</u>

6.1 Introduction

Movement and orientation of mammals in their natural environment are largely determined by locomotor and perceptual capabilities. Nocturnal life requires particular adaptations of the latter. Diversification within the chiroptera has led to behavioural specialisation in many species in both echolocation and flight capacities. Even among aerial insectivorous bats, there is considerable diversity in echolocation and in the distance bats keep to vegetation when hunting.

As background structures within a foraging habitat directly limit the efficiency with which bats can echolocate and manoeuvre (reviewed in Sleep & Brigham 2003), Schnitzler & Kalko (1998) suggested a classification of bats into guilds according to their ability to forage close to clutter-producing background structures: species foraging close to these structures were defined as narrow-space foragers, those hunting in the open as open space foragers. Species from both guilds are potentially restricted to their habitat by flight or echolocation abilities (Korine & Pinshow 2004).

Bats hunting in the open are often characterised by fast flight, pointed wings, high aspect ratios and high wing loading (Aldridge & Rautenbach 1987, Baagøe 1987, Norberg & Rayner 1987). During search for prey, they use low-frequency calls of almost constant frequency and high intensity. Using this echolocation mode, they can achieve detection distances of up to 80 m (Holderied & von Helversen 2003). However, foraging success may be reduced in these species by their manoeuvrability (Waters et al. 1995) as they cannot manoeuvre in narrow space. Narrow-space foragers, on the other hand, are characterised by broad wings, low aspect ratio and low wing loading (Norberg 1990) resulting in a high manoeuvrability (Baagøe 1987) which enables them to hunt close to vegetation. Even during search flight, these species make use of high-frequency, broad band, frequency-modulated calls of low intensity. Consequently,

they have smaller detection ranges (Schnitzler & Kalko 1998) and are therefore confined to foraging close to vegetation (e.g. *Plecotus auritus,* Fuhrmann & Seitz 1992, Entwistle et al. 1996). Finally, edge and gap hunters as defined by Denzinger et al. (2001) represent intermediate characters in both echolocation and flight style. However, the above classifications only represent key stones within a behavioural continuum. In fact, many species show considerable deviations from predicted behavioural patterns: narrow space hunters may leave confined space and hunt in the open (Fenton & Bell 1979, Swift 1997). On the other hand, open space hunters may approach clutter, e.g. when foraging close above the ground (Helversen & Helversen 1994).

Flexibility of hunting strategies can be crucial for a species' persistence as it reflects its susceptibility to long-term changes of its environment (Obrist 1995). Specialised species such as gleaners should be most vulnerable to microhabitat loss as they depend on the existence of vegetation (Swift 1998). However, their ability to subsist on insects during the entire night may partially outbalance their vulnerability to habitat modifications (Entwistle et al. 1996). Correspondingly, fast fliers can quickly depart from unsuitable habitats (Jaberg et al. 1998) but may be unable to exploit insect accumulations close to clutter. Flexible species which can exploit microhabitats close to clutter without being clearly bound to structural guidance, might suffer least from habitat changes. Moreover, they should be able to minimise competition within a given microhabitat by a change in their behaviour (i.e. by flying closer to or farther away from background structures).

Where can we place the northern bat within this continuum of foraging strategies? Intermediate in terms of body size and wing morphology, it can be classified as an edge and gap hunter according to Schnitzler & Kalko (2001). A previous study suggests a moderate flexibility in echolocation in which call duration varied with flight altitude above ground (Rydell 1993b). According to Baagøe (1987), the manoeuvrability of the species is restricted. It has been suggested that reduced prey capture success close to clutter-producing background

is due to these constraints (Jensen et al. 2001). On the other hand, the species is resistant to a certain degree of clutter (Jensen et al. 2001) and can even make use of visual cues when foraging (Eklöf et al. 2002). However, knowledge about echolocation (Rydell 1992, Jensen et al. 2001) and manoeuvrability (Baagøe 1987) is restricted to a few conspicuous foraging situations (Rydell 1990, 1993b; Skiba 2004) and up to now, we have known little about the behavioural flexibility in a wide range of microhabitats. As shown in Chapter 1, assessing behavioural flexibility of the northern bat may be particularly crucial when evaluating the contrasting distribution patterns of *E. nilssonii* and its competitors in Central Europe and Scandinavia as it may quantify the species' ability to coexist with each other.

The aim of this chapter was therefore to determine constraints on the flight capacity and the echolocation in *E. nilssonii* in order to assess whether the behavioural flexibility of the species is sufficient to fully exploit diverse microhabitats as well as to coexist with conspecifics and potential competitors within its foraging habitats.

In a first step, I documented the foraging behaviour of radio-tracked bats in different foraging habitats to assess their behavioural bandwidth in terms of relative distance from background structures as well as echolocation call features. In a second step, I exposed captured northern bats to an experimental narrow-space situation to determine their limitations in flight capacities and echolocation behaviour. Finally, I will discuss the importance of locomotor and echolocation abilities for the persistence of the northern bat in an environment characterised by anthropogenic modifications as well as the presence of several competing bat species

6.2 Material & Methods

6.2.1 Field observations

13 northern bats (3 males, 10 females) were captured, tagged and radio-tracked as described in Chapter 2. Individual bats were identified by coloured reflective tape either glued to an arm ring or to the antenna of the transmitter. For observations, powerful halogen-torches (Osram),

a SONY DCR-PC8E digital infrared video camera and a powerful infrared torch were used. Behavioural and echolocation data were sampled only if a bat could be observed continuously foraging in one place for more than five minutes.

Flight position (i.e. altitude above ground and distance to background structures such as vegetation or house walls) was estimated in relation to reference elements within the foraging habitats with a precision of $\pm$ 1 m. Altitudes of background structures were measured using a theodolite (Landesvermessung und Geobasisinformation Niedersachsen) and are shown in Table 6.1. Visual observations took place in four habitat types: 1. forest. 2. grassland. 3. lakes. 4. urban areas. I got data from 9 radio-tracked bats in forest, 10 bats above grassland, 4 bats above the lake and 5 bats in urban areas (cf. Table 6.2).

Table 6.1 Altitude of background structures measured in reference habitats. Values are given as median and interquartiles. n denotes the number of background structures measured.

habitat type	distance from maternity roost [km]	typical structural elements	altitude [m]
grassland surrounded by trees (n=5)	0.2	beech, spruce	13.8 (13.0-17.4)
forest pond (n=7)	1.2	beech, oak, spruce	15.3 (13.7-22.3)
coniferous forest (n=7)	2.3	spruce	27.6 (25.0-30.4)
mixed forest (n=7)	2.7	beech, oak, spruce	32.4 (25.6-35.0)
light coniferous forest (n=7)	2.2	spruce	27.9 (27.2-28.9)
urban area (n=1)	0.3	street lamps	5.7

Medians of vertical and horizontal distance to background structures were calculated from medians per bat. To assess the influence of both distances on call structure, I calculated diagonal distance to background structures using simple Pytagoras geometrics (i.e. the square root from the squared vertical distance plus the squared horizontal distance).

$$d = \sqrt{(h^2 + a^2)}$$

with d being the diagonal distance, h the horizontal distance to background structures and a the flight altitude above ground.

Echolocation calls were recorded from all radio-tracked individuals, but sufficient data were gathered for 10 bats only. Search calls were recorded in three habitat types: 1. Within forest (mixed or coniferous). 2. In grassland surrounded by trees. 3. Within an urban habitat (a small street, flanked by rows of houses and lighted by mercury vapour street lamps). In addition to search calls, I recorded sequences containing final buzz calls (i.e. echolocation calls emitted immediately prior to prey capture). These short calls were used for subsequent comparison to calls recorded in the flight tent (see below).

For call recordings, I used a U30 bat detector (Ultrasound Advice) followed by a portable ultrasonic processor (PUSP). Calls were expanded tenfold and either digitised directly on an Acer Travelmate 223 XC laptop computer, or recorded on TDK SA audio tapes using a WM-D6C tape recorder and digitised thereafter with a sampling rate of 224 kHz (i.e. resolution 112 kHz). Only sound recordings from identified bats flying towards the microphone were saved for subsequent analysis.

6.2.2 Flight tent experiments

For the flight tent experiments, 8 bats were captured in front of their day roost for flight experiments in July 2002 (n=3) and 2003 (n=5). They were weighed using a PESOLA spring balance (precision 0.5 g) and forearm length was measured using a vernier calliper (precision 0.1 mm). I also determined their sex and classified them as juvenile or adult according to the degree of ossification of their forearm. The bats fed on mealworms and tap water before and after the experiments. They were not rewarded during experiments as I aimed to assess skills of naïve bats.

Experiments for manoeuvrability, agility and echolocation were conducted in a custom-made flight tent (altitude 4.0 m, length, 6.0 m, width 3.0 m; cf. Fig. 6.1). The inner tent was made of mosquito netting, to which bats could easily attach during flight breaks. The inside of the ceiling was covered with plastic sheets to prevent their landing. During the experiments, the

experimenter sat on a low chair at one end of the tent (experimenter's end). Flight behaviour during the experiments was documented using a SONY DCR-PC8E infrared sensitive video camera and a table light (OSRAM) with a 40 W red bulb. The camera was positioned at 1.0 m from the experimenter's end at 1.0 m above ground. Using a wide angle setting for the camera, I managed to view the whole opposite wall (far end) from the left to the right (3.0 m). Echolocation behaviour during the flight tent experiments was documented using the same set-up as in the field observations (cf. 6.2.1). The microphone was put at 1 m in front of the experimenter's tent end on a rack at 1.5 m above ground pointing towards the opposite end and pointing 30° in upward direction. Both camera and bat detector were placed in the centre of the experimenter's end whereas the table light was placed in one corner.

Two square wooden frames (light opening 3 x 3 m) were set up in the tent: the first one (F1) was at 3 m and the second one (F2) at 4.1 m from the far end of the tent (i.e. the end opposed to the experimenter). F1 was equipped with vertical strings, (diameter 1 mm), F2 with horizontal strings. Inter-string distances (ISDs) were decreased gradually. Vertical ISDs (ISD_v) were 1.5 m, 1.0 m, 0.75 m, 0.5 m, horizontal ISDs (ISD_h) were: 1.2 m, 0.8 m, 0.6 m, 0.4 m. Smaller ISDs were chosen individually for each bat (see below). Experiments started immediately after the release of a bat within the tent. Individuals started flying back and forth between the far ends of the tent turning shortly before the far walls. A bat was allowed to fly back and forth through the frames for a set ISD until it settled down, which was usually at the far tent end. After setting a new ISD, the bat was restarted by gently touching the tent wall. The number of flights through or towards the frame was counted. A flight was successful when a bat passed through both frames without touching the obstacles. When a bat detected a string, it normally initiated an avoidance reaction, i.e. it changed its call pattern and sometimes also its flight path in in order to avoid collision with strings. In the results section, I will therefore differentiate between orientation flight and avoidance reaction when assessing manoeuvrability and echolocation.
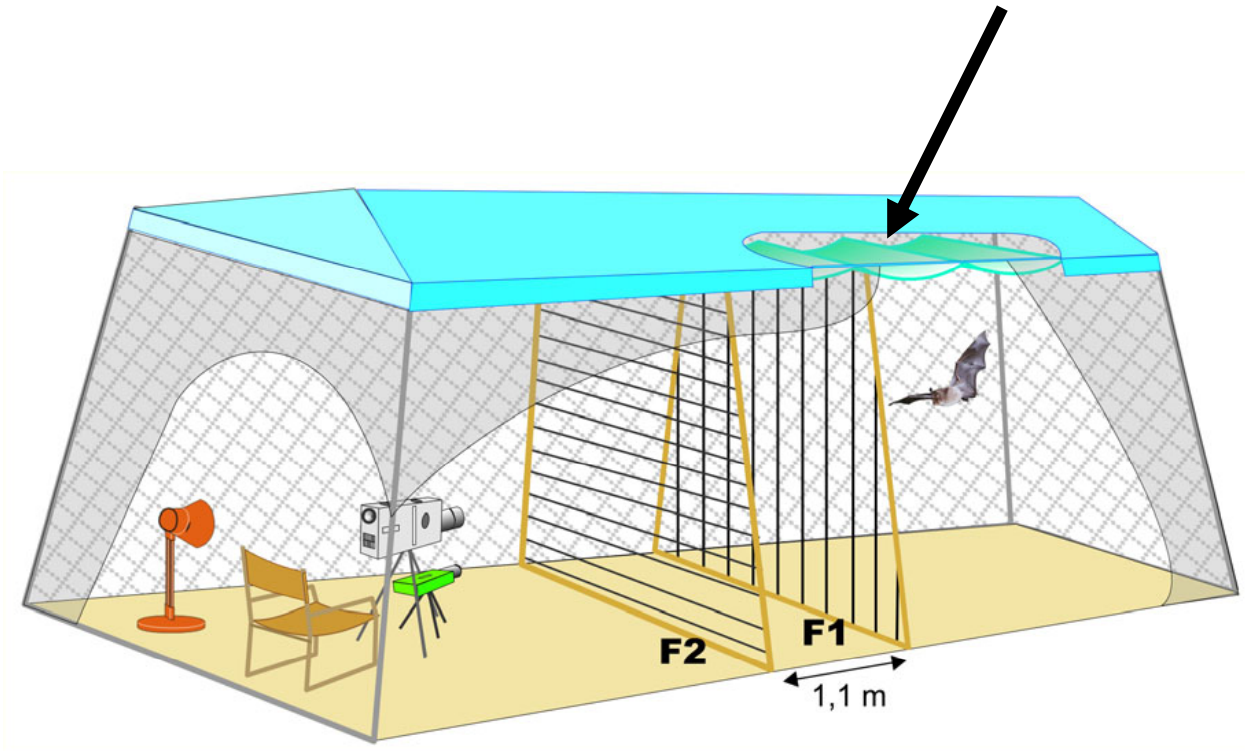
Fig. 6.1 Flight tent for behavioural experiments on manoeuvrability and echolocation in the northern bat (not to scale). The inner tent consisted of fine gaze, the outer tent of tough plastic. Further plastic sheets were fixed to the ceiling of the inner tent to prevent landing of the bats at the ceiling (see black arrow). F1: first wooden frame with strings. F2: second wooden frame with strings.

A flight was considered unsuccessful when a bat touched an obstacle during passage or when it refused to pass the frames. Touches of obstacles were revealed by subsequent video analysis (see below). The proportion of unsuccessful flights was calculated in relation to the total number of flights per bat. Experiments were stopped when the bat refused completely to fly through the frames or when it was unwilling to start again from the wall.

6.2.3 Sound analysis

Sound analysis was performed in Bat Sound (Ver. 1.2). FFT was conducted using Hanning windows with 2048 samples. Interpulse interval and sound duration [both in ms] were measured from oscillograms, duty cycle [%] was derived from these parameters. For spectral analysis, power spectra were adjusted according to the U30 microphone response (cf. Chapter 1) using a custom-made macro in Excel (Microsoft Excel 97). Parameters measured from corrected power spectra were: bandwidth at –25 dB from peak intensity and peak frequency [kHz]. Several call sequences were analysed per bat. Subsequently, I calculated median values and interquartiles of call parameters for each bat within a particular habitat (e.g. grassland) or flight situation (e.g. flying within the tent, avoiding obstacles within the tent). I obtained call sequences of five bats in forest (median number of sequences n=3), of two bats in grassland (n=7) and of five bats in urban area (n=8). Buzz calls of five bats (median number of sequences n=4) were recorded. Calls of five bats from flight tent experiments were analysed (n=5), calls during obstacle avoidance were considered for two of them (n=5).

6.2.4 Video analysis

Digital video tapes (TDK DV60) were replayed on a flat screen monitor for analysis of flight behaviour (temporal resolution: 40 ms). Manoeuvrability was defined as the radius of turning circles in front of the far tent wall. Circle diameter was determined by measuring the distance between the position where the bat started to go into a bank and the position where the bat

started to fly straight after turning. Precision was c. $\pm$ 0.1 m. Turning radius and flight speed were determined only when bats returned perpendicularly to the frames. Flight speed was calculated from the distance between F1 to the far tent end divided through the time required for this distance. The turning radius was subtracted from this distance. Speed measurements were mostly performed for flights during which the bats touched a string which allowed a precise temporal and spatial determination of its position within F1 (Fig. 6.1).

6.2.5 Statistical analysis

I used nonparametric statistics as my data were not normally distributed. I used Kruskal-Wallis tests to check for variation in flight altitude and relative distance to vertical structures between different habitat types. In order to avoid pseudoreplication, I only used data from 5 bats in forest, 3 different bats in grassland and 5 different bats in urban area in statistical tests. I also used Kruskal-Wallis tests to check for inter-individual differences in call parameters. When Kruskal-Wallis tests were used for several parameters, only the smallest value obtained for H (H_{min}) will be given in the results section. Spearman rank correlations were calculated to detect correlations between flight path position and associated call parameters as well as between distinct call parameters. In this case all single observations were pooled. Mann-Whitney U tests were used to compare short echolocation calls from the flight tent to calls recorded in the field. Wilcoxon-matched pair tests were used to compare different call types emitted by the same bat.

Relative distance of bats to the ground or to vertical background objects will either be given as median (and interquartiles) per habitat or as median per bat with n denoting the number of bats or the number of observations per bat, respectively. Echolocation call parameters will be given as medians per foraging situation (e.g. flight tent) or per bat with n denoting the number of bats or the number of observations, respectively.

6.3 Results

6.3.1 Flight corridors and search call structure in different habitats

Bats preferred the 6-9 m stratum in all habitat types examined (Table 6.2). Flight style of radio-tracked bats varied between habitat types: whereas I found no significant differences in flight altitude (Kruskal-Wallis Test, n=13 bats, p=0.22), I detected significant inter-habitat differences in distance to vertical background structures (3-10 m; n=13, H=6.14, p<0.05, cf. Table 6.2).

Hunting at street lamps was mostly confined to a corridor just above and near the lamps (Table 6.2). Flight paths of bats between two turns could be as long as 50 m. Interference with conspecifics in these flight corridors was observed at high bat densities and often resulted in aerial chases and aggressions with one or both bats leaving the flight corridor. Within street lamp habitats, pipistrelles (*Pipistrellus pipistrellus*) were often observed to hunt simultaneously but only 2-3 m above ground. Hunting in forest always took place below the canopy and often near the edge of clear-cuttings. Bats were rarely observed foraging more than 8 m from vegetation and were mostly observed at median distances of 3 m from trees and 8 m from the ground. They established elliptic flight paths with diagonals below 20 m. Foraging above grassland was most variable: sometimes bats flew as high as 15-20 m at medium speeds, in other cases they flew close to the ground or to low bushes, circling slowly and sometimes nearly hovering close to bushes (Table 6.2). I was not able to say if variable flight altitude was due to contrasting flight altitudes of bats above grassland grazed by cattle (pasture) and grassland not used for grazing (for example influenced by the presence or absence of cattle dung and associated prey), as only one bat was observed and recorded more than twice foraging above pastures. However, the fact that this bat (w223) always hunted clearly lower above pastures (7(6-7) m, n=5) than above grassland without cattle (12 (10-15) m, n=5) suggests that pasture and natural grassland might have been considered by the bat as two different habitats.

Table 6.2 Flight altitude and distance to vertical background for radio-tracked northern bats in three different habitat types. Values are given as medians and quartiles in [m]. In urban areas horizontal distance indicates flight distance to the nearest house wall or street lamp, in grassland horizontal distance is given in relation to bushes or hedge structures. n denotes the number of radio-tracked bats observed within each habitat type.

	habitat			
	forest (n=9)	grassland (n=10)	lakes (n=4)	urban area (n=5)
flight altitude [m]	8 (8-10)	9 (6-13.5)	8 (7-10)	7 (6-7)
horizontal distance [m]	3 (2.5-4.5)	10 (7.5-10)	7.3 (5-7.5)	4 (4-4)

Search call durations did not differ significantly between habitat types (Kruskal-Wallis, $p > 0.05$) and typically ranged from 7 to 15 ms. Bandwidth (-25dB) of search calls ranged from 7 to 19 kHz and peak frequency was between 27 and 34 kHz. When considering medians of all search call sequences, I found a significant negative correlation between call duration and all other call parameters (n=67 sequences, Spearman rank correlation $r < -0.7$, $p < 0.05$). The search call repertory recorded in the field is shown in Fig. 6.2.
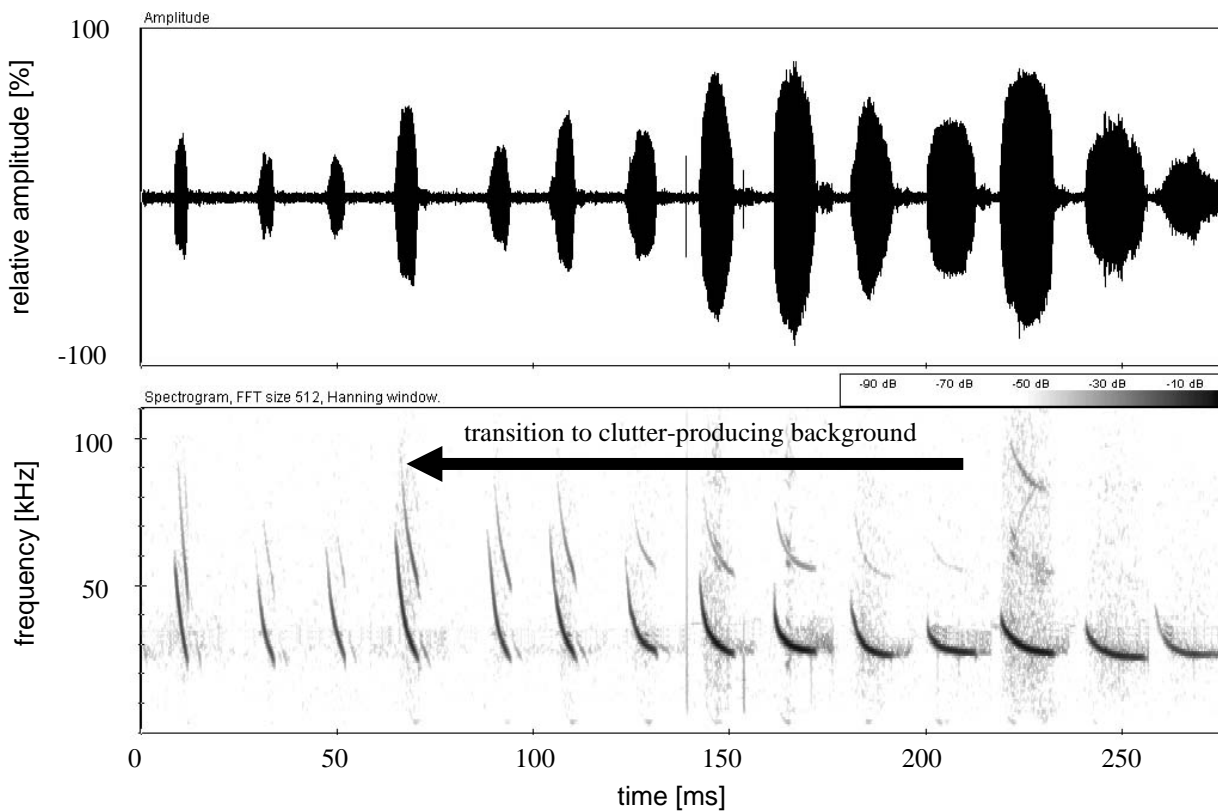
Fig. 6.2 Search calls used by the northern bat (*Eptesicus nilssonii*) during foraging flights. Oscillogram (above) and spectrogram (below). The black arrow indicates increasing proximity to clutter-producing background structures. Calls were recorded in distinct foraging situations and therefore vary in amplitude.

6.3.2 Inter-individual variation in flight behaviour and echolocation

I examined individual variation in flight and echolocation behaviour within a street lamp habitat (Table 6.3, Fig. 6.3). In spite of a general preference for flight altitudes around 6 m and horizontal distances around 5 m, bats differed in their microhabitat use: whereas I found no significant differences in the use of altitude strata (Kruskal-Wallis test, n=5, p>0.05), individuals differed significantly in the horizontal flight distance to landmark objects (house walls, street lamps; n=5, H=15, p<0.01, Fig. 6.3a).

Correspondingly, I found significant differences (Kruskal-Wallis test, n=5, H_{min}=13.5, p<0.01) between all call parameters. However, when comparing only calls with durations from 10 to 12 ms, I found no significant inter-individual differences in frequency parameters (Kruskal-Wallis test, n=5, n.s). Peak frequency was negatively correlated to call duration (n=35, r=-0.9, p<0.001; Fig. 6.3b) and call duration in turn was positively correlated to flight altitude and distance to vertical background structures (n=35, r=0.6, p<0.001; Fig. 6.2b). In two simultaneously foraging bats, I found indication that differences in peak frequencies resulting from the choice of different call durations and flight paths, respectively, might reduce acoustic interference (Table 6.3, Fig. 6.4).

Table 6.3

Intraspecific flight and call variation in a street lamp habitat. n denotes the number of call sequences analysed for each bat. For further specifications cf. Table 6.2.

bat no.	flight altitude [m]	horizontal distance [m]	pulse duration [ms]	peak frequency [kHz]
w080n (n=8)	4.5 (4-8)	4 (2-4)	6.7 (6.0-7.4)	33.8 (32.9-34.7)
w180 (n=6)	7 (7-7)	3.5 (3.5-5)	8.6 (6.9-9.4)	30.9 (30.4-32.9)
w200 (n=8)	6 (5.8-7)	5 (3.5-12.5)	11.9 (9.7-12.3)	28.8 (28.4-28.9)
w223 (n=8)	5 (3-10)	5.5 (5-7)	10.3 (8.8-12.0)	30.1 (29.0-30.3)
m110 (n=5)	6 (5-10)	7 (6-8)	8.2 (7.9-8.5)	31.7 (31.0-32.1)
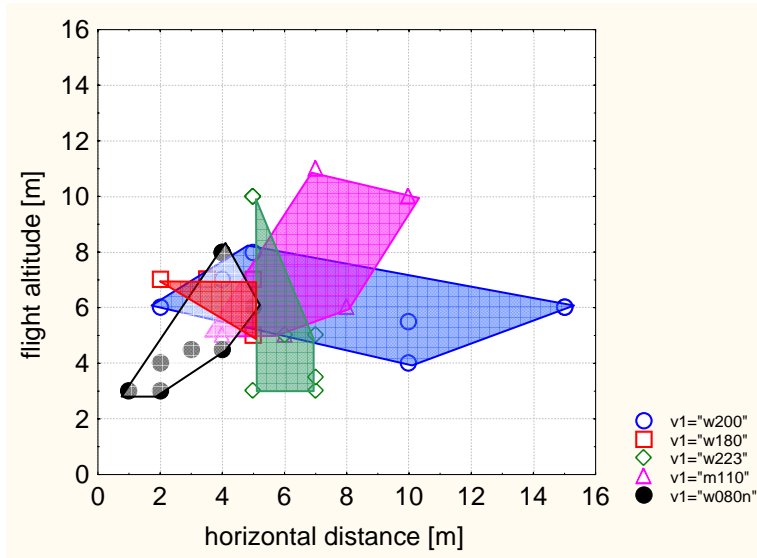
Fig. 6.3a Flight corridors of five radio-tracked northern bats within a street lamp habitat. Symbols indicate average values of single sequences. Corridors were determined using minimum convex polygons.
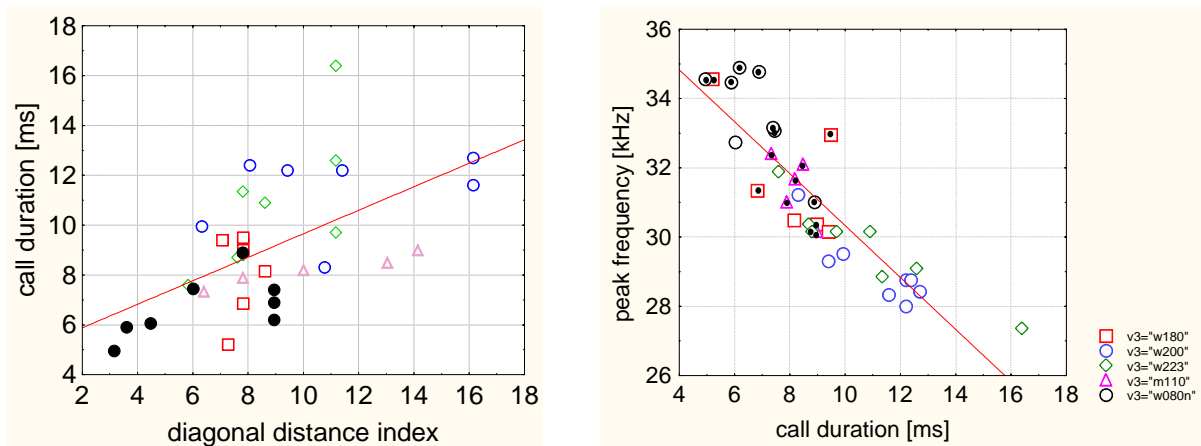

Fig. 6.3b Correlation of diagonal distance index and call duration (left) and call duration [ms] and call peak frequency [kHz] (right). Each symbol denotes the median of a single sequence (n=35), each consisting of 6 to 30 calls. Different colours denote individual bats. Black dots highlight sequences during which conspecifics occurred. For the symbol legend cf. Fig. 6.3 a.
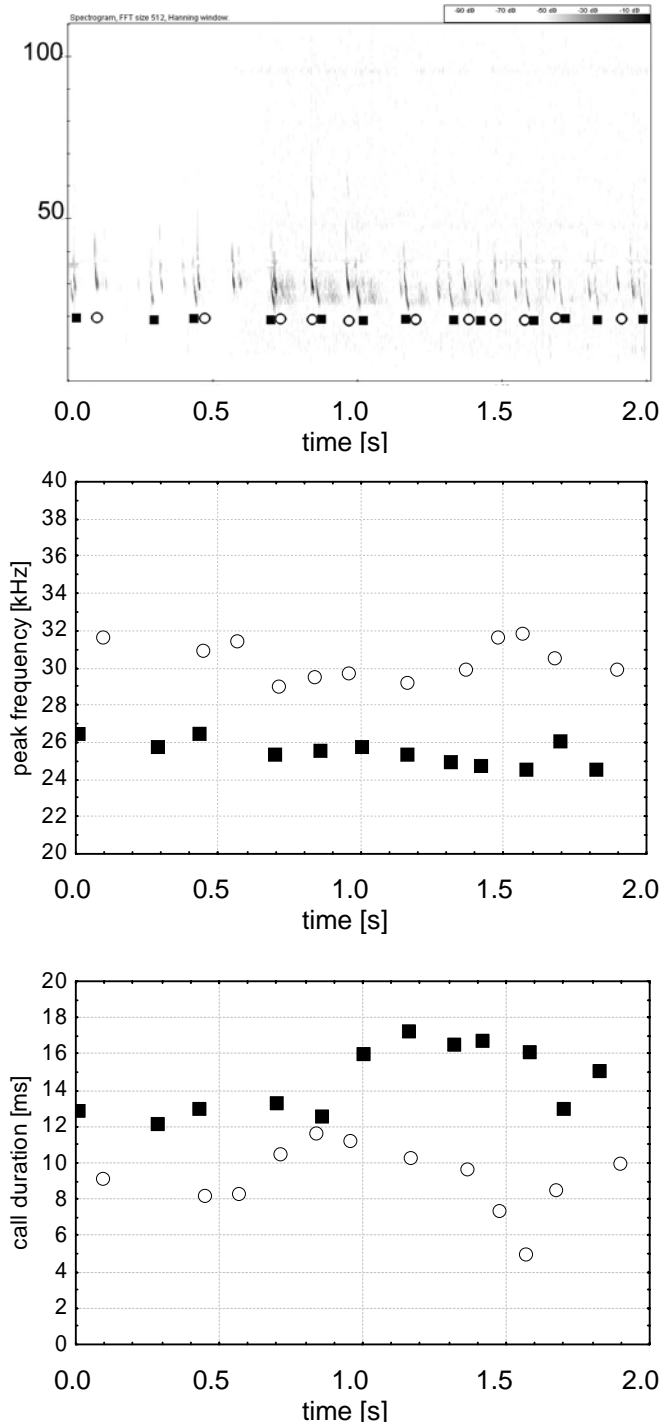
Fig. 6.4 Call features of two northern bats foraging simultaneously around a street lamp. Call spectrograms (top), peak frequency of calls (middle) and call duration (bottom) as a function of relative time [s]. Cues from the two northern bats under consideration are squares and circles, respectively. They flew at c. 6 m and 8 m flight altitude towards the microphone with a slight final turn away from it.

6.3.3 Flight and echolocation in the flight tent

I found no significant inter-individual differences in turning radius or flight speed (Kruskal-Wallis-H-test, turning radius n=5 bats, H=2.29, n.s.; flight speed n=5, H=4.27, n.s.). Median turning radius was 50 (47-55) cm, median flight speed was 3.42 (3.37-3.54) ms^{-1} (n=5). The proportion of unsuccessful flights was negatively correlated to vertical as well as to horizontal inter-string distance (n=40 trials, 40; r=-0.81, 0.79; p<0.001). It remained well below 0.5 (the proportion of misses by chance) for all ISDs above 50 cm. With vertical and horizontal inter-string distances below 50 cm, mistakes occurred significantly more frequently (n=8 trials, t=0, z=2.5, p=0.012) than with ISDs above 50 cm. The proportion of unsuccessful flights through the barrier showed highest variability for ISDs below 50 cm (Fig. 6.5). I found no significant correlation between body weight / forearm length and the proportion of unsuccessful flights through the barrier (Spearman-ranks-test, body weight r=-0.64 – 0.31, t=-1.87 – 0.73, n.s.; forearm length r=-0.77- 0.32, t=-2.4 – 0.68 , n.s.).

When flying in the tent, bats emitted stereotyped short fm-calls (1.8 (1.7-1.8) ms; n=5; Fig 6.6) consisting of a strong first and a weaker second harmonic (difference in intensity >15 dB SPL). Calls were emitted either as single or double pulses, resulting in a slightly bimodal distribution of IPI frequencies. I found no indication of significant individual variation (Kruskal-Wallis test, p>0.05): calls were typically downwards modulated from 56 to 25 kHz, duty cycle was very low (Table 6.4). In their duration, these orientation calls resembled buzz I calls recorded from radio-tracked bats in the field (c. 2 ms, Fig. 6.6, Table 6.4). However, peak frequency was significantly higher in orientation calls than in buzz I calls (Mann-Whitney U, U=0, Z=2.6, p<0.01) whereas duty cycle was significantly lower (U=0; z=2.6, p<0.01).
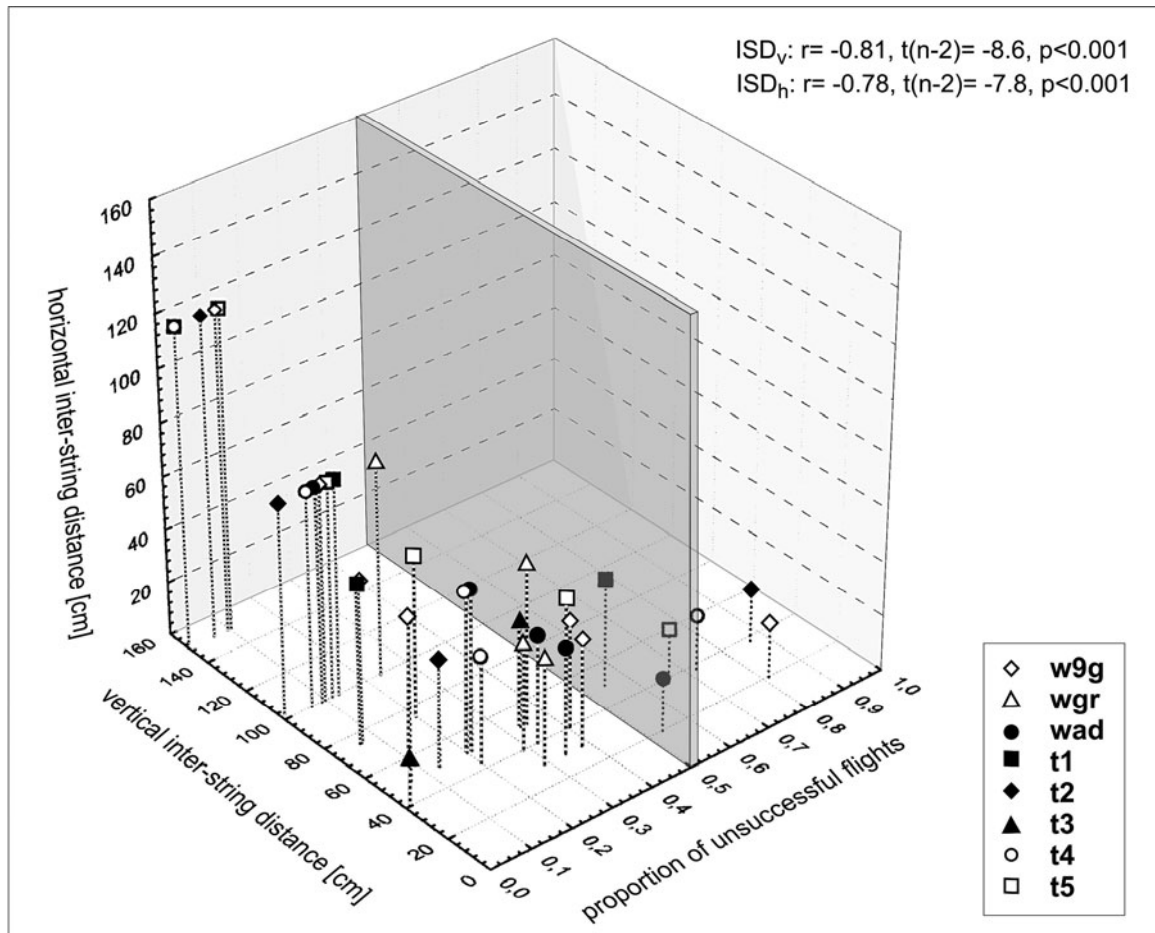
Fig. 6.5 Manoeuvrability of the northern bat in artificial narrow-space. Manoeuvrability is expressed as the proportion of unsuccessful flights through obstacle barriers in relation to vertical inter-string distance (ISD_v) and horizontal inter-string distance (ISD_h). Results for associated Spearman rank analyses are given above, including five ISD_v/ISD_h combinations for each bat (n= 8 * 5 = 40). The transparent barrier denotes the 50-percent-error proportion a bat would be expected to display by chance.
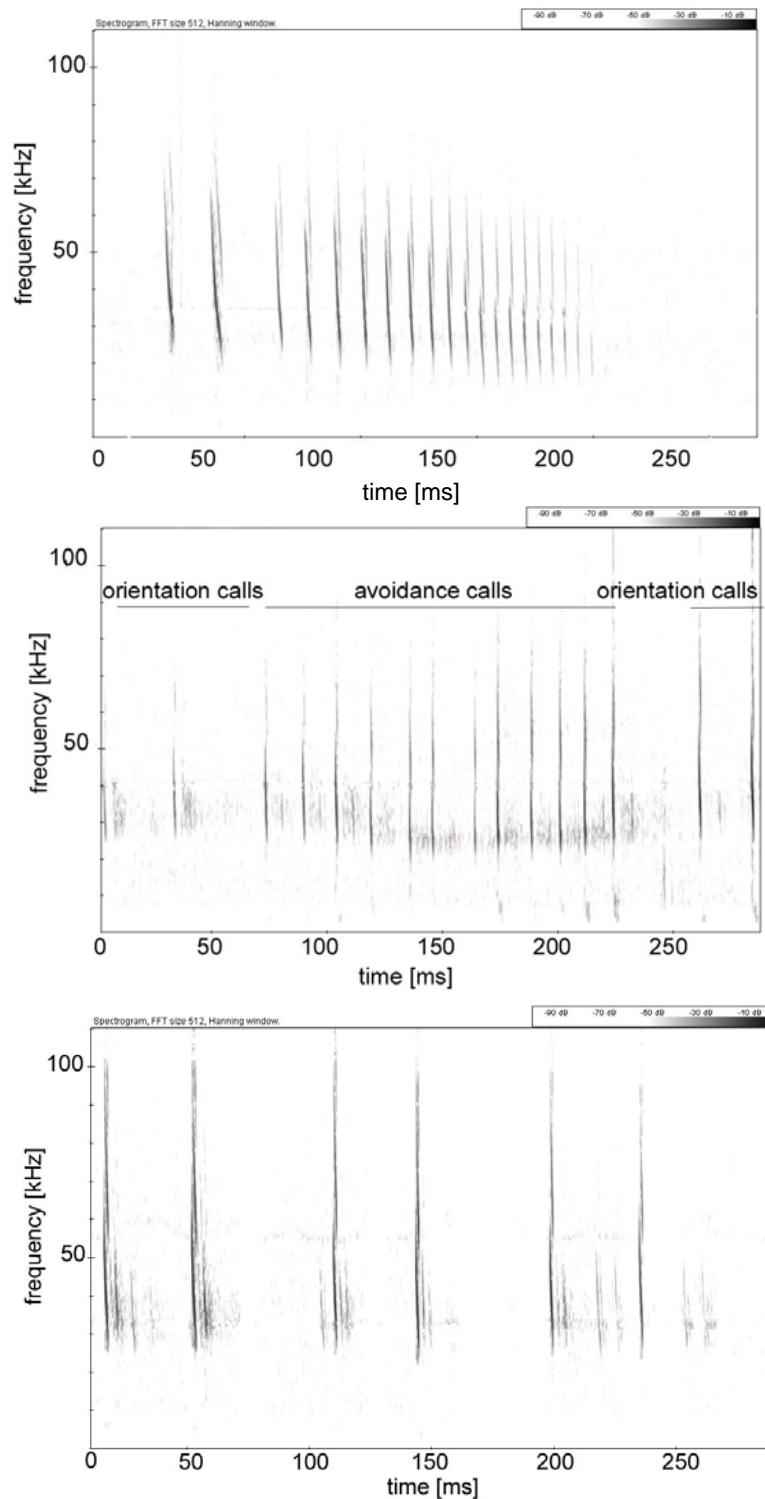
Fig. 6.6 Echolocation calls of *E. nilssonii* recorded when the bats approached a prey item or an artificial clutter-producing background, respectively. Buzz in the field (top). Orientation and avoidance calls recorded in a flight tent (middle). Orientation calls emitted in the flight tent (bottom). All calls are shown as spectrograms, different shadings of grey indicate differences in sound intensity [dB].

When approaching the vertical and horizontal strings, the bats initiated an avoidance reaction and call duration was shortened abruptly. Though bandwidth of avoidance calls remained unchanged, the frequency band was shifted downwards, duty cycle increased and peak frequency was lowered. However, these changes were significant in only one of the two bats in which calls were recorded while they approached the string array (Wilcoxon matched pair test, T=0, Z=2.0, p<0.05). In terms of duration, avoidance calls were very similar to buzz II calls recorded in the field (Fig. 6.6, Table 6.4). However, I found considerable variation in call parameters: in buzz II calls, the frequency band was shifted downwards (Fig. 6.6), duty cycle was increased (Table 6.4). Bandwidth however, was similar to avoidance calls. Due to small sample sizes though, these differences were not significant (Mann-Whitney-U, p>0.05). Assuming the onset of avoidance calls at the moment of detection of a string, mean detection distance was 0.78 m before reaching the first obstacle, based on a mean flight speed of 3.4 ms^{-1}. Median duration of avoidance reactions in the flight tent was 180 ms, which was shorter than median duration of feeding buzzes recorded from radio-tracked bats.

Table 6.4 Comparison of short echolocation calls used during prey capture in the field (above) and calls emitted during flight in the flight tent (below). n denotes the number of individual bats for which call data were obtained within the respective behavioural context. For each bat, a median number of 5 sequences was analysed. Values are given as medians and interquartiles, except for obstacle avoidance which is given as median and min/max-range. OC: calls emitted during orientation flight in the tent. AC: calls emitted during obstacle avoidance (i.e. avoidance of vertical or horizontal strings) in the flight tent.

behavioural context		n	call duration [ms]	IPI [ms]	duty cycle [%]	peak frequency [kHz]	band-width at – 25 dB [kHz]	slope [kHz/ms]
field	buzz I	5	2.2 (2.0-2.3)	9.5 (9.2-10.2)	22.5 (22.5-23.1)	25.2 (23.0-25.3)	19.0 (18.2-19.3)	9.4 (8.5-10.1)
	buzz II	4	0.93 (0.88-1.02)	5.9 (5.7-6.1)	16.3 (15.1-17.2)	22.9 (22.4-23.3)	14.2 (12.8-20.3)	14.8 (12.0-23.2)
flight tent	OC	5	1.79 (1.69-1.83)	52.0 (45.8-73.0)	3.2 (3.1-3.4)	34.5 (33.5-34.9)	23.1 (22.6-23.6)	12.9 (12.1-13.4)
	AC	2	0.91 (0.74-1.07)	19.5 (15.6-23.4)	4.6 (4.5-4.7)	26.9 (26.4-27.3)	18.0 (17.9-18.0)	19.9 (16.1-23.7)

6.4 Discussion

I found considerable behavioural flexibility of the northern bat in both flight and echolocation behaviour. Flexibility was displayed in terms of both intra- or inter-individual flexibility. However, echolocation performance showed little inter-individual variation when considering calls of similar duration only, indicating that bats actively select particular call designs from a continuum to achieve acoustic niche differentiation. Selection of a particular call design might in turn be due to individual skills in obstacle avoidance and flight paths chosen by the individuals. Below, I will address the question whether the widely varying distances to vertical background structures as well as the considerable repertoire of echolocation calls displayed by the northern bat enables the species to effectively use its microhabitat and whether competition might be reduced through this flexibility. Results will be discussed with respect to vulnerability to extinction.

6.4.1 Foraging near to and far from clutter-producing background structures

Foraging near vegetation which provides shelter from predators (Patrequin & Barclay 2003) or acts as windbreak accumulating insects can be very advantageous for bats. Accumulations of flying prey are often associated with either water bodies or vegetation structures. This is particularly true for the time of flowering when large quantities of swarming insects can be found close to trees (e.g. de Jong 1994). Additionally, vegetation structures often provide a comfortable guideline for bats during foraging flights as well as during commuting flight (Limpens & Kapteyn 1991). Finally, a stable microclimate in cluttered habitats (e.g. below tree tops) provides good conditions for temporarily as well as spatially persistent and predictable insect densities compared to more open habitats.

Foraging close to vegetation generally poses two major problems to an echolocating bat: the risk of physical collisions as well as the difficulty in finding prey due to clutter echoes from

the vegetation (Sleep & Brigham 2003). Hence successful foraging near clutter-producing background depends on flight and echolocation skills of a species.

When bats approach clutter-producing background, they shorten their calls with call frequency parameters being inversely correlated to pulse duration. In *E. nilssonii*, I found a similar correlation between distance to background structures, call duration and associated frequency parameters, agreeing with Rydell (1993b) and Jensen et al. (2001) who found variation in duration, peak and end frequency according to flight altitude and distance to clutter (Rydell 1990). However, duration of typical search calls has been said to typically lie between 7 and 9 ms (Jensen et al. 2001), with shorter calls only being used in exceptional situations (e.g. emerging from the roost, Rydell 1991). My study revealed that shorter call durations are regularly used by *E. nilssonii* even in relatively open foraging situations, similar to *E. serotinus* (Miller & Degn 1981). Search call durations ranged from 5 to 20 ms and were associated with dramatic variations in call bandwidth and frequency parameters.

Often, the negative correlation between call duration and frequency parameters is inverted for call durations below 4 ms, which normally characterise final buzz calls emitted during prey capture in the field (Surlykke & Moss 2000). Interestingly, though call duration of orientation calls recorded in the flight tent was similar to final buzz calls, the inverted correlation between call duration and frequency parameters did not hold true for these calls: bandwidth of orientation calls remained high and also peak frequency was higher in these calls than in the buzz calls recorded in the field. Thus, bats in the flight tent might have acted in the buzz and approach phase as suggested by Surlykke & Moss (2000), but only in terms of call duration, whereas frequency call features resembled more typical search calls emitted in the field. This supports findings about the low frequency properties of the final buzz being mainly due to physiological limitations at high repetition rates.

Bandwidth of search calls is a measure for a species' ability to hunt successfully close to clutter (Siemers & Schnitzler 2004). Northern bats flying in the flight tent used 2ms-fm-calls

with maximum bandwidths (-25dB) of the first harmonic well above 23 kHz. They may even achieve higher bandwidths when making use of the second harmonic, which however, similarly to findings in *E. serotinus* (Jensen & Miller 1999), is less intense than the first one. Though maximum frequencies as well as bandwidth are below those of narrow space foragers (e.g. *Myotis* spp., Siemers & Schnitzler 2004), both are well above values known for other species of the gap hunter guild, e.g. *N. leisleri* (Zingg 1988). Considerable bandwidth found in *E. nilssonii* could explain a certain degree of clutter-tolerance found by Jensen et al. (2001). Indeed, high bandwidth of echolocation calls should guarantee a considerable degree of fine resolution and enable the species to cope with acoustic clutter.

However, capture success near to structural clutter is much reduced for *E. nilssonii* (Rydell 1998) and Jensen et al. (2001) attributed this to restrictions in manoeuvrability. Indeed, Baagøe (1987) found that *E. nilssonii* was mostly foraging more than 8 m away from obstacles flying in straight lines and wide curves and seldom employing curves with a radius below 1.5 m. This contrasts with my findings from the flight tent, where the bats had a turning radius of only 50 cm. Moreover, naive northern bats could negotiate inter-string distances below 60 cm with error rates below 30 %. This finding is supported by observations of Ahlén (1991) who demonstrated that the northern bat is able to successfully fly and echolocate in narrow space as well as by observations of the author of individuals circling very near to clutter (bushes in grassland, roost loft). However, flight performance of studied individuals became much worse at ISDs below 50 cm, but also much more variable indicating that minimum negotiable distance is being approached (Aldridge 1986) and that individuals vary most in their ability to cope with these gap sizes. Indeed, recent studies (e.g. Sleep & Brigham 2003) suggest that even small bat species with low wing loadings, aspect ratios and therefore high manoeuvrability avoid ISDs below 50 cm when hunting under natural conditions. Moreover, with intermediate aspect ratio and wing loading (Rayner 1987), foraging in narrow space could be energetically more expensive for the northern bat than for typical narrow-

space hunters. Nevertheless, my findings suggest, that *E. nilssonii* displays manoeuvrability capacities well above previous estimates.

6.4.2 Foraging near conspecifics

If *E. nilssonii* is sufficiently manoeuvrable to exploit microhabitats with a complex spatial structure, it should theoretically also be able to use its flight and echolocation skills to avoid interference with other bats. However, flight path selection and distance to clutter should primarily be based upon distribution of prey items (Sleep & Brigham 2003). For the northern bat, a regular street lamp forager (Rydell 1991), it should be most advantageous to forage close to the lights, as insects are typically highly concentrated within a few metres of the lamps (Hickey & Fenton 1990). However, particularly at foci of insect concentrations such as street lamps, a bat seldom forages on its own when several conspecifics can subsist simultaneously on a sufficiently large amount of prey. Thus the selection of a particular flight path might also reflect the necessity to avoid collision with a conspecific or, conversely, the need to follow a conspecific in cases of kleptoparasitism or cooperative hunting (Reddy & Fenton 2003). Typically, simultaneous foraging of several bats is observed in fast-flying species often flying in straight lines along widely spaced structures (e.g. street lamp alleys) and thus easily avoiding collisions by using separate areas within a patch. *E. nilssonii* has been reported to use this wide-space foraging style (Baagøe 1987, Rydell 1991). However, with decreasing distance of insect concentrations and decreasing prey abundance, the presence of conspecifics can become a serious problem. Some species have been shown to do group hunting (Barak & Yom-Tov 1989) or forage simultaneously without apparent signs of aggression or interaction (Hickey & Fenton 1990). At lower insect densities, though, interspecific competition often occurs in the northern bat (Rydell 1986a) and group hunting is generally less common than in other European species, such as the pipistrelle (Racey & Swift 1985). Aggression between northern bats was regularly observed by the author (cf. Chapter

2), particularly at high bat densities. In this case, foraging within these activity centres is energetically profitable only, if foraging space is successfully partitioned. In the present study, I found indication that bats actively established flight paths within the same street lamp habitat: whereas some individuals never approached house walls or street lamps closer than 6 m, others were regularly observed as close as 2-3 m. Interestingly, they all used similar flight altitudes.

Apart from physical interference, acoustic interference may be a serious problem for bats hunting with conspecifics: with many conspecifics foraging close to each other, individuals must differentiate between echoes of their own calls, calls of conspecifics and echoes of calls of conspecifics (Barclay & Brigham 1994, Moss & Surlykke 2001). As individuals of the same species normally use calls of similar spectral properties, a frequency shift in response to the presence of conspecifics would be a way to avoid jamming: For *E. nilssonii*, Rydell (1993b) stated the general use of slightly higher frequencies in the presence of conspecifics but found no indication for the use of exclusive frequency bands, in the latter finding agreeing with findings of the present study. However, proper recognition of a bat's own calls might not necessitate the use of exclusive frequency bands, a shift in peak frequency might be sufficient (cf. Ulanovsky et al. 2004). My study revealed that while hunting simultaneously within a street lamp habitat, individual bats chose flight paths that differed in their distance to vertical background structures. Moreover, I found a wide range of peak frequencies (28 to 34 kHz) and call durations (6 to 12 ms) of search calls in these bats. This contrasts with findings of Obrist (1995) in *E. fuscus* who found most intraspecific variability in peak frequency but least variability in call duration. Interestingly, I found no inter-individual differences when considering only calls of the same duration and bats did not change their call design in situations when they hunted with conspecifics compared to lonely foraging flights.

I conclude that bats chose distinct flight paths in relation to clutter that allowed them to minimise risk of mid-air collisions, similar to findings of Adam & Simmons (2002) on bats

flying above a water hole. Contrasting call designs are due to various distances to clutter-producing background and might allow individuals to reduce acoustic jamming at moderate bat densities. Manoeuvrability as well as dominance in relation to bats from the same or other colonies will determine, whether an individual can exploit the space of highest insect density.

6.4.3 Foraging near other bat species

Insectivorous bat species often coexist by means of behavioural specialisation: *Myotis auriculus* and *M. lucifugus* though morphologically similar can coexist as the former species can temporarily feed on resting insects (Fenton & Bell 1979), *Plecotus auritus* and *Myotis daubentonii*, roosting in the same house, coexist within the same area by using different foraging habitats (Racey & Swift 1985). Even within the same ecological guild, coexistence can be achieved, e.g. in the case of lasiurines through temporal avoidance (Hickey et al. 1996). However, when key habitats become increasingly patchy through anthropogenic influences such as silviculture, agriculture and urbanisation, interspecific competition can locally become a serious problem and again, the behavioural flexibility of a given species may determine whether two ecologically similar species can coexist. Within the study area, there are at least seven other insectivorous bat species apart from *E. nilssonii*, ranging from species with low wing-loading and aspect ratio (e.g. *M. mystacinus, M. daubentonii, P. auritus*) to species with medium or high wing-loading and aspect ratio (e.g. *P. pipistrellus, N. noctula, N. leisleri, E. serotinus, V. murinus*) similar to *E. nilssonii* (Baagøe 1987, Russ et al. 2003).

With measured flight speeds between 3.4 ms^{-1} in the flight tent and 5.8 ms^{-1} during foraging flights, *E. nilssonii* was slower than estimated by Baagøe (1987) for relatively straight search flight and resembled to small-curve circling *E. serotinus* and to *P. pipistrellus* (cf. e.g. Hughes and Rayner 1993) *V. murinus, N. noctula* and *N. leisleri* on the other hand seem more adapted to fast straight-line, almost completely avoiding curves and displaying poor manoeuvrability

(Baagøe 1987, Shiel et al. 1999, Schaub, unpublished data 2001). Prevailing flight speed gives indication of preferred microhabitats, with fast-flying species often foraging at greater distances from background structures. Hence, for *E. nilssonii*, synchronous foraging within a habitat is facilitated with the fast-flying *N. noctula, N . leisleri* and *V. murinus* but rendered more difficult with the medium-speed *P. pipistrellus* and *E. serotinus*. This might lead to mutual exclusion of species from a habitat: Rydell & Baagøe (1996) noted that the latter two species predominated around street lamps in Sweden only in the absence of *E. nilssonii*. My field observations suggest that coexistence of *E. nilssonii* and *P. pipistrellus* is facilitated by vertical stratification (cf. Chapter 2). However, considering the great similarity in flight speed and spectral call features with *E. serotinus* (Miller & Degn 1981, Jensen & Miller 1999), physical and acoustic interference should represent a serious problem for the two species. In this case, competitive strength will determine population densities and spatial area use.

6.4.4 Conclusions

Northern bats in my study displayed high flexibility in echolocation and microhabitat use: the species can hunt close to or far from clutter. It showed considerable inter- and intra-individual variability in echolocation within a given habitat, suggesting a potential for the use of various foraging strategies, e.g. to avoid acoustic interference. Thus, the northern bat should be able exploit a complex microhabitat to a high degree using the space far from as well as close to clutter-producing background. The species may thus be less susceptible to changes in its habitats than smaller bat species that depend on the proximity of guidance structures during regular foraging flights (e.g. *Myotis nattereri*, Swift 1997). I therefore assume that the behavioural flexibility of *E. nilssonii* is sufficient to prevent extinction due to habitat loss. However, I doubt whether its plasticity is high enough to enable a temporal and spatial coexistence with morphologically similar species, particularly *E. serotinus*. Hence, the results of this chapter support the conclusions of previous chapters that it is more likely that the

persistence of *E. nilssonii* in Central Europe is strongly affected by the regional abundance of potential competitors.

7 Conservation, distribution and perspectives for future research in the northern bat

Flexibility of the northern bat in habitat use, flight skills and echolocation is considerable and indicates a low degree of vulnerability to extinction. On the other hand, my findings suggest that human habitat modification, particularly elimination of forest in favour of agricultural areas, may negatively affect populations. Thus conservation actions should concentrate on the protection of forest habitats within 2 km of northern bat colonies. Decreased abundance of predictable anthropogenic habitats (e.g. street lamps with white light, eutrophic lakes) further emphasises the importance of preserving natural habitats. However, my study revealed that interspecific competition with bat species employing similar foraging styles (e.g. *E. serotinus*) rather than habitat availability may account for the contrasting distribution patterns and population densities of the northern bat in Europe. Similarity in the use of macro- and microhabitats might prevent coexistence of these species at high population densities.

It has to be taken into account that distribution and habitat use of *E. nilssonii* were assessed in an area where such potential competitors were not abundant. Previous studies suggest that when these species occur sympatrically, the most abundant species might take over key resources (Blake et al. 1994). Further studies should therefore focus on population densities of these species with similar foraging behaviour in regions where they coexist, such as in some parts of Southern Germany (Harbusch 2004, pers. comm.) and examine, whether they can establish resource partitioning, particularly in respect to foraging habitats. Future studies should also examine the diet of these species: *E. nilssonii* and *E. serotinus* are generally opportunistically feeding (Andreas 2002). Nevertheless, they might achieve some trophic differentiation (e.g. with *E. serotinus* feeding mainly on beetles, cf. Harbusch & Racey 2002). To sum up, interspecific mechanisms might be particularly important in determining distribution patterns and population densities of highly flexible bat species and render the quantification of direct human contributions to a population decline more difficult. Hence,

conservation actions for a particular species should be based on its behavioural flexibility and the competition scenario at a given location.

8 Acknowledgements

9 References

Adam, R.A. & J.A. Simmons (2002): Directionality of drinking passes by bats at water holes: is there co-operation? Acta chiropt. 4: 195-200.

Ahlén, I. (1983): The bat fauna of some isolated islands of Scandinavia. Oikos 41: 352-358.

Ahlén, I. (1991): Identification of Scandinavian bats by their sounds. Sw. Univ. Agric. Sci. Rep. 6: 1-56.

Ahlén, I. & R. Gerell (1989): Distribution and status of bats in Sweden. *In* European Bat Research 1987. *Edited by* V. Hanak, J. Horacek and J. Gaisler. Charles University Press, Prague. pp. 319-325.

Aihartza, J.R., Garin, I., Goiti, U., Zabala, J. & I. Zuberogoitia (2003): Spring habitat selection by the Mediterranean Horseshoe Bat (*Rhinolophus euryale*) in the Urdaibai Biosphere Reserve (Basque Country). Mammalia 67 (1): 25-32.

Aldridge, H. (1986): Manoeuvrability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*M. yumanensis*) bats (Chiroptera: Vespertilionidae). Can. J. Zool. 64: 1878-1882.

Aldridge, H.D.J.N. & I.L. Rautenbach (1987): Morphology, echolocation and resource partitioning in insectivorous bats. J. Anim. Ecol. 56: 763-778.

Aldridge, H.D.J.N. & R.M. Brigham (1988): Load carrying and manoeuvrability in an insectivorous bat: a test of the 5% -rule of radio-telemetry. J. Mammal. 69: 380-382.

Andreas, M. (2002): Feeding ecology of A bat community. PhD thesis, Czech Agriculture University in Prague, Faculty of Forestry. Prague.

Arlettaz, R., Godat, S. & H. Meyer (2000): Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). Biol. Conserv. 93: 55-60.

Arlettaz, R., Jones, G., & P.A. Racey (2001): Effects of acoustic clutter on prey detection by bats. Nature 414: 742-745.

References

Baagøe, H.J. (1987): The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. *In* Recent advances in the study of bats. *Edited by* Fenton, M.B., Racey, P. & J.M.V. Rayner. Cambridge University Press. Pp. 57-74.

Barak, Y. & Y. Yom-Tov (1989): The advantage of group hunting in Kuhl's bat *Pipistrellus kuhli* (Microchiroptera). J. Zool. (Lond.) 219: 670-675.

Barclay, R.M.R. (1989): The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behav. Ecol. Sociobiol. 24: 31-37.

Barclay, R.M.R. & R.M. Brigham (1994): Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. Anim. Behav. 48: 1013-1021.

Bartonicka, T. (2002): Habitat use of four bat species in Jablonec n.N. revealed by bat detector. Przyroda Sudetow Zachodnich. Supplement 2: 79-87.

Bartonicka, T. & J. Zukal (2003): Flight activity and habitat use of four bat species in a small town revealed by bat detectors. Fol. Zool. 52, 2: 155-166.

Bell, G.P. (1980): Habitat use and response to patches of prey by desert insectivorous bats. Can. J. Zool. 58: 1876-1883.

Bihary, Z. (2001): Characteristics of the northernmost population of Rhinolophus ferrumequinum in the Carpathian Basin. Acta theriologica 46 (1): 13-21.

Blake, D., Hutson, A.M., Racey, P.A., Rydell, J. & J.R. Speakman (1994): Use of lamplit roads by foraging bats in southern England. J. Zool. (Lond.) 234: 453-462.

Bontadina, F., Schofield, H. & B. Naef-Daenzer (2002): Radio-tracking reveals that lesser horseshoe bats (Rhinolophus hipposideros) forage in woodland. Journal of Zoology (London) 258: 281-290.

Bontadina, F., Arlettaz, R., Fankhauser, T., Lutz, M., Mühlethaler, E., Theiler, A. & P. Zingg (2000): The lesser horseshoe bat Rhinolophus hipposideros in Switzerland: present status and research recommendations. Le Rhinolophe 14: 69-83.

References

Brigham, R.M. (1991): Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*): Can. J. Zool. 69: 117-121.

Britton, A.R.C. & G. Jones (1997): Echolocation behaviour and prey capture success in foraging bats: laboratory and field experiments on *Myotis daubentonii*. J. Exp. Biol. 202: 1793-1801.

Bundesamt für Naturschutz (1999): Bats and Bat Conservation in Germany. Landwirtschaftsverlag. Münster-Hiltrup.

Catto, C.M.C. & A.M. Hutson (1999): Eptesicus serotinus (Schreber, 1774). *In* The Atlas of European Mammals. *Edited by* Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & J. Zima. T & A D Poyser Natural History.

Catto, C.M.C., Racey, P.A. & P.J. Stephenson (1994): Activity patterns of the serotine bat (Eptesicus serotinus) at a roost in southern England. Journal of Zoology (London) 235: 635-644.

Catto, C.M.C., Hutson, A.M., Racey, P.A. & P.J. Stephenson (1996): Foraging behaviour and habitat use of the serotine bat (*Etpesicus serotinus*) in southern England. J. Zool. (Lond.) 238: 623-633.

Denzinger, A., Siemers, B.M., Schaub, A & H.-U. Schnitzler (2001): Echolocation by the barbastelle bat, *Barbastella barbastellus*. J. Comp. Physiol. A 187: 521-528.

Drescher, C. and O. Niederfringer (2002): Habitat use of *Myotis myotis*. *In* Proceedings of the IXth European Bat Research Symposium, Le Havre [online]. 19. Available from www.vleermuis.net.

Duchamp, J.E. (2004): Foraging-habitat selection by bats at an urban-rural interface: comparison between a successful and less successful species. Can. J. Zool. 82: 1157-1164.

References

Duvergé, P.L. & G. Jones (1997): Greater Horseshoe Bats – Activity, foraging behaviour and habitat use. British Wildlife 6: 69-77.

Eklöf, J., Svensson, M. & J. Rydell (2002): Northern bats, *Eptesicus nilssonii*, use vision but not flutter-detection when searching for prey in clutter. Oikos 99 (2): 347-351.

Ekman, M. & J. de Jong (1994): Local patterns of distribution and resource utilisation of four bat species (*Myotis brandti, Eptesicus nilssoni, Plecotus auritus* and *Pipistrellus pipistrellus*) in patchy and continuous environments. J. Zool. (Lond.) 238: 571-580.

Entwistle, A.C., Racey, P.A. & J.R. Speakman (1996): Habitat exploitation by a gleaning bat, *Plecotus auritus*. Phil. Trans. R. Soc. Lond. B 351: 921-931.

Erkert, H.G. (1982): Ecological aspects of Bat Activity Rhythms. *In* Ecology of Bats. *Edited by* T.H. Kunz. Plenum Press, New York. Pp. 201-242.

Fenton, M.B., & G.P. Bell (1979): Echolocating and feeding behaviour in four species of *Myotis* (Chiroptera). Can. J. Zool. 57: 1271-1277.

Fenton, M.B., Tennant, D.C. & J. Wyszecki (1987): Using echolocation calls to measure the distribution of bats, the case of *Euderma maculatum*. J. Mammal. 68 (1): 142-144.

Fenton, M.B., Acharya, L., Hickey, M.B.C., Merriman, C., Obrist, M.K. & D.M. Syme (1992): Phyllostomid Bats (Chiroptera: Phyllostomidae) as indicators of Habitat Disruption in the Neotropics. Biotropica 24 (3): 440-446.

Fenton, M.B. & I.L. Rautenbach (1998): Impacts of Ignorance and Human and Elephant Populations on the Conservation of Bats in African Woodlands. *In* Bat Biology and Conservation. *Edited by* Kunz, T. H. & P.A. Racey. Pp. 261-270.

Flavin, D.A, Biggane, S.S., Shiel, C.B., Smiddy, P. & J.S. Fairley (2001): Analysis of the diet of Daubenton's bat *Myotis daubentonii* in Ireland. Acta theriol. 46 (1): 43-52.

Fortin, M.-J., Keitt, T.H., Maurer, B.A., Taper, L., Kaufman, D.M. & T.M. Blackburn (2005): Species' geographic ranges and distributional limits: pattern analysis and statistical issues. Oikos 108: 7-17.

References

Fuhrmann, M. & A. Seitz (1992): Nocturnal activity of the brown long-eared bat (*Plecotus auritus* L., 1758): data from radio-tracking in the Lenneberg forest near Mainz (Germany). *In* Wildlife telemetry: remote monitoring and tracking of animals. *Edited by* I.G Priede. Ellis Horwood, New York. Pp. 538-548.

Gaisler, J. & J. Kolibac (1992): Summer occurrence of bats in agrocenoses. Folia zool. 41 (1): 19-27.

Gaisler, J., Zukal, J., Rehak, Z. & M. Homolka (1998): Habitat preference and flight activity of bats in a city. J. Zool. (Lond.) 244: 439-445.

Gaston, K.J. (2003): The Structure and Dynamics of Geographic Ranges. Oxford University Press.

Goiti, U., Aihartza, J.R. & I.Garin (2002): Habitat changes: the mediterranean horseshoe bat *Rhinolophus euryale* in Peril. *In* Proceedings of the IXth European Bat Research Symposium, Le Havre: 19 [online]. Available from www.vleermuis.net.

Guisan, A. & N.E. Zimmermann (2000): Predictive habitat distribution models in ecology. Ecol. Model. 135: 147-186.

Guo, Q., Taper, M., Schoeneberger, M. & J. Brandle (2005): Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108: 47-57.

Haffner & Stutz, (1985): Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at street lamps. Myotis 23-24: 167-168.

Harbusch, C. & P.A. Racey (2002): Aspects of the ecology of serotine bats, *Eptesicus serotinus* in contrasting landscapes. Proceedings of the IXth European Bat Research Symposium, Le Havre. 19.

Hartung, J. (1993): Statistik. Lehr- und Handbuch der angewandten Statistik. 9th edition. R. Oldenbourg Verlag. München Wien.

Helversen, O.v.. & D.v. Helversen (1994): The "advertisement song" of the lesser noctule bat (*Nyctalus leisleri*). Folia zool. 43 (4): 331-338.

References

Henry, M., Thomas, D.W., Vaudry, R. & M. Carrier (2002). Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). J. Mammal. 83 (3): 767-774.

Hickey, M.B.C. & M.B. Fenton (1990): Foraging by red bats (*Lasiurus borealis*): do intraspecific chases mean territoriality? Can. J. Zool. 68: 2477-2482.

Hickey, M.B.C., Acharya, L. & S. Pennington (1996): Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. J. Mammal. 77 (2): 325-334.

Holderied, M.W. & O.v. Helversen (2003): Echolocation range and wingbeat period match in aerial-hawking bats. Proc. R. Soc. Lond. B 270: 2293-2299.

Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A. & M.L. Taper (2005): Theoretical models of species' borders: single species approaches. Oikos 108: 18-27.

Horn, S.D. (1977): Goodness-of-fit tests for discrete data: a review and an application in a health impairment scale. Biometrics 33: 237-248.

Hughes, P. & J.M.V. Rayner (1993): The flight of pipistrelle bats *Pipistrellus pipistrellus* during pregnancy and lactation. J. Zool. (Lond.) 230: 541-555.

Jaberg, C. & J.-D. Blant (2003): Spatio-temporal utilisation of roosts by the parti-coloured bat *Vespertilio murinus* L., 1758 in Switzerland. Z. Säugetierkd. 68: 341-350.

Jaberg, C. & A. Guisan (2001): Modelling the distribution of bats in relation to landscape structure in temperate mountain environment. J. Appl. Ecol. 38: 1169-1181.

Jaberg, C., Leuthold, C. & J.-D. Blant (1998): Foraging habitats and feeding strategy of the particoloured bat *Vespertilio murinus* L., 1858 in Western Switzerland. Myotis 36: 51-61.

Jensen, M.E. & L.A. Miller (1999): Echolocation signals of the bat *Eptesicus serotinus* recorded using a vertical microphone array: effect of flight altitude on searching signals. Behav. Ecol. Sociobiol. 47: 60-69.

References

Jensen, M.E., Miller, L.A. & J. Rydell (2001): Detection of prey in a cluttered environment by the northern bat *Eptesicus nilssonii*. J. Exp. Biol. 204: 199-208.

Jones, G. (1995): Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. J. Zool. (Lond.) 237: 303-312.

Jones, G. (1999): Scaling of echolocation call parameters in bats. J. Exp. Biol. 202: 3359-3367.

Jones, G., Duvergé, P.L. & R.D. Ransome (1995): Conservation biology of an endangered species: field studies of greater horseshoe bats. Symp. zool. Soc. Lond. 67: 309-324.

Jones, G. & J. Rydell (2003): Attack and Defence: Interactions between Echolocating Bats and Their Insect Prey. *In* Bat Ecology. *Edited by* Kunz, T.H. & M.B. Fenton. The University of Chicago Press. Pp. 301-345.

Jong, J. de (1994): Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssonii* in a hemiboreal coniferous forest. Mammalia 58 (4): 535-548.

Jong, J.de (1995): Habitat use and species richness of bats in a patchy landscape. Acta theriol. 40 (3): 237-248.

Kayikcioglu, A. & A. Zahn (2004): High temperatures and the use of satellite roosts in Rhinolophus hipposideros. Mammalian biology 69, 5: 337-341.

Kenward, R. (2000): A manual for wildlife radio-tagging. London: Academic Press.

Kiefer, A., Merz, H., Rackow, W., Roer, H. & D. Schlegel (1995): Bats as traffic casualties in Germany. Myotis 32-33: 215-220.

Korine, C. & B. Pinshow (2004): Guild structure, foraging space use, and distribution in a community of insectivorous bats in the Negev desert. J. Zool. Lond. 262: 187-196.

Kooij, J.V. de (1999): Nordflaggermus *Eptesicus nilssonii* funnet i steinroys. Fauna 52(4): 208-211.

References

Kronwitter, F. (1988): Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. Myotis 26: 23-85.

Limpens, H.J.G.A. & K. Kapteyn (1991): Bats, their behaviour and linear landscape elements. Myotis 29: 63-71.

Meschede, A. and K.G. Heller (2000): Ökologie und Schutz von Fledermäusen in Wäldern. *Edited by* Bundesamt für Naturschutz. Landwirtschaftsverlag, Münster-Hiltrup.

Miller, L.A. & H.J. Degn (1981): The Acoustic Behavior of Four Species of Vespertilionid Bats Studied in the Field. J. Comp. Physiol A 142: 67-74.

Morgenroth, S. (2004): Nordfledermaus *Eptesicus nilssonii* (Keyserling et Blasisus, 1839). *In* Fledemäuse in Bayern. *Edited by* Bayerisches Landesamt für Umweltschutz, Landesbund für Vogelschutz in Bayern e.V. and Bund Naturschutz in Bayern. Pp. 314-321.

Moss, C.F. & A. Surlykke (2001): Auditory scene analysis by echolocation in bats. J. Acoust. Soc. Am. 110 (4): 2207-2226.

Neuweiler, G. (2003): Evolutionary aspects of bat echolocation. J. Comp. Physiol. A. 189: 245-256.

Norberg, U. (1990): Vertebrate flight. Mechanics, Physiology, Morphology, Ecology and Evolution. Springer Verlag. Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong.

Norberg, U.M. & J.M.V. Rayner (1987): Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Phil. Trans. R. Soc. Lond. B: 336-427.

Obrist, M.K. (1995): Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. Behav. Ecol. Sociobiol. 36: 207-219.

References

Obrist, M.K, Boesch, R. & P.F. Flückinger (2004): Variability in echolocation call design of 26 Swiss bat species: consequences, limits and options for automated field identification with a synergetic pattern recognition approach. Mammalia 68 (4): 307-322.

Ohlendorf, B. (1987): Zur Verbreitung und Biologie der Nordfledermaus, *Eptesicus nilssonii* (Kayserling , Blasius, 1839), in der DDR. *In* European Bat Research 1987. *Edited by* Hanak, V., Horacek J. and J. Gaisler. Charles University Press, Prague. Pp. 609-615.

Patrequin, K.J. & R.M.R. Barclay (2003): Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40: 646-657.

Parsons, S. & M.K. Obrist (2004): Recent Methological Advances in the Recording and Analysis of Chiropteran Biosonar Signals in the Field. *In* Advances in the Study of Echolocation in bats and dolphins. Proceedings of the Biosonar Conference 1998. Chicago University Press.

Patterson, B.D., Willig, M.R. & R.D. Stevens (2003): Trophic strategies, niche partitioning, and patterns of Ecological Organization. *In* Bat Ecology. *Edited by* Kunz, T.H. & M.B. Fenton. The University of Chicago Press. Pp. 536-579.

Primack, R.B. (1998): Essentials of Conservation Biology. Sinauer Associates Inc. Sunderland, Massachusets.

Racey, P.A. & A.C. Entwistle (2003): Conservation Ecology of Bats. *In* Bat Ecology. *Edited by* Kunz, T.H. & M.B. Fenton. Chicaco University Press. Chicago.

Racey, P.A. & J.R. Speakman (1987): The energy cost of pregnancy and lactation in hetherothermic bats. Symp. R. Soc. Lond. 57: 107-125.

Racey, P.A. & S.M. Swift (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J. Anim. Ecol. 54: 205-215.

References

Racey, P.A., Swift, S.M., Rydell, J. & L. Brodie (1998): Bats and insects over two Scottish rivers with contrasting nitrate status. Anim. Conserv. 1: 195-202.

Rachwald, A. , Wodecka, K. & L. Kluzinski (2002): Bats in the forest areas of different level of air pollution. *In* Proceedings of the IXth European Bat Research Symposium. 20. [available online].

Rautenbach, I.L., Fenton, M.B. & M.J. Whiting (1996): Bats in riverine forests and woodlands: a latitudinal transect in southern Africa. Can. J. Zool. 74: 312-322.

Reddy, E. & M.B. Fenton (2003): Exploiting vulnerable prey: moths and red bats (Lasiurus borealis; Vespertilionidae). Can. J. Zool. 81: 1553-1560.

Robinson, M.F. & R.E. Stebbings (1997): Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. J. Zool. (Lond.) 243: 117-136.

Rudolph, B.-U. (2004): Breitflügelfledermaus *Eptesicus serotinus* (Schreber, 1774). *In* Fledemäuse in Bayern. *Edited by* Bayerisches Landesamt für Umweltschutz, Landesbund für Vogelschutz in Bayern e.V. and Bund Naturschutz in Bayern. Pp. 305-313.

Russ, J. (1999): The bats of Britain and Ireland. Echolocation calls, Sound Analysis and Species Identification. Alana Books.

Russ, J., Briffa, M. & W.I. Montgomery (2003): Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. J. Zool. (Lond.) 259: 289-299.

Russo, D. & G. Jones (2003): Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. J. Zool. (Lond.) 258: 91-103.

References

Russo, D., Cistrone, L., Jones, G. & S. Mazzoleni (2004): Roost selection by barbastelle bats (*Barbastella barbastellus,* Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. Biol. Conserv. 117: 73-81.

Rydell, J. (1986a): Feeding territoriality in female northern bats, *Eptesicus nilssonii*. Ethology 72: 329-337.

Rydell, J. (1986b): Foraging and diet of the northern bat Eptesicus nilssoni in Sweden. Holarct. Ecol. 9: 272-276.

Rydell, J. (1989): Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. Oecologia 80: 562-565.

Rydell, J. (1990): Behavioural Variation in Echolocation Pulses of the Northern Bat, *Eptesicus nilssonii*. Ethology 85: 103-113.

Rydell (1991): Seasonal use of illuminated areas by foraging northern bats, Eptesicus nilssoni. Holarct. Ecol. 14: 203-207.

Rydell, J. (1992a): Occurrence of bats in northernmost Sweden (65° N) and their feeding ecology in summer. J. Zool. (Lond.) 227: 517-529.

Rydell, J. (1992b): Exploitation of insects around streetlamps by bats in Sweden. Funct. Ecol. 6: 744-750.

Rydell (1992c): The diet of the parti-coloured bat Vespertilio murinus in Sweden. Ecography 15: 195-198.

Rydell, J. (1993a): Variation in foraging activity of an aerial insectivorous bat during reproduction. J. Mammal. 74, 2: 503-509.

Rydell, J. (1993b): Variation in the Sonar of an Aerial-hawking Bat (*Eptesicus nilssonii*). Ethology.

Rydell, J. (1998): Bat defence in lekking ghost swifts (*Hepialus humuli*), a moth without ultrasonic hearing. Proc. R. Soc. Lond. B (1998) 265: 1373-1376.

<center>References</center>

Rydell, J. (1999): *Eptesicus nilssonii*. *In* The Atlas of European Mammals. *Edited by* Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, Bl, Rejjnders, P.J.H., Spitzenberger, F., Stubbe, M., Thisssen, J.B.M., Vohralik, V. & J. Zima . Pp. 140-141.

Rydell, J. & H.J. Baagøe (1994): Vespertilio murinus. Mamm. spec. 467: 6.

Rydell, J. & H.J. Baagøe (1996): Bats & Streetlamps. Bats 14 (4): 10-13.

Rydell, J. & W. Bogdanowicz (1997): Barbastella barbastellus. Mamm. spec. 557: 1-8.

Rydell, J., Natuschke, G., Theiler, A. & P.E. Zingg (1996): Food habits of the barbastelle bat *Barbastella barbastellus*. Ecography 19: 62-66.

Rydell, J. & P.A. Racey (1995): Street lamps and the feeding ecology of insectivorous bats. Symp. Zool. Soc. Lond. 67: 291-307.

Schaub, A. (2001): Das Echoortungsverhalten von *Vespertilio murinus* (Linnaeus, 1785). Diplomarbeit. Freie Universität Berlin.

Schnitzler, H.-U., Kalko, E., Miller, L. & A. Surlykke (1987): The echolocation and hunting behavior of the bat, *Pipistrellus kuhli*. J. Comp. Physiol. A 161: 267-274.

Schnitzler, H.-U. & E. K. Kalko (1998): How Echolocating Bats Search and Find Food. *In* Bat Biology and Conservation. *Edited by* Kunz, T.H. & P.A. Racey. Smithsonian Institution Press. Washington and London. Pp.183-195.

Schnitzler, H.-U. & E.K. v. Kalko (2001): Echolocation by insect-eating bats. Bioscience 51 (7): 557-569.

Schulenburg, J. (2004): Kurzbeitrag zum Vorkommen und zur Ökologie der Nordfledermaus (*Eptesicus nilssonii*) im Landkreis Freiberg (Osterzgebirge). Mitt. f. sächs. Fledermausfr. 1: 46-50.

Shiel, C.B. (1999): Nyctalus leisleri (Kuhl, 1817). *In* The Atlas of European Mammals. *Edited by* Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & J. Zima. T & A D Poyser Natural History.

References

Shiel, C.B. & J.S. Fairly, MRIA (1998a): Activity of Leisler's Bat *Nyctalus leisleri* (Kuhl) in the field in south-east county Wexford, as revealed by a bat detector. Biology and Environment: Proc. R. Ir. Soc. 98B (2): 105-112.

Shiel, C.B., Duvergé, P.L., Smiddy, P. & J.S. Fairley (1998b): Analysis of the diet of Leisler's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. J. Zool. (Lond.) 246: 417-425.

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

Siemers, B. & H.-U. Schnitzler (2004): Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 229: 657-661.

Skiba, R. (1986): Verbreitung und Verhalten der Nordfledermaus, *Eptesicus nilssonii*, im Westharz. Beitr. Natkd. Nds. 39: 35-44.

Skiba, R. (2004): Europäische Fledermäuse. Westarp Wissenschaften. Neue Brehm Bücherei.

Skiba, R. (in press): Zum Vorkommen der Nordfledermaus, *Eptesicus nilssonii* (Keyserling & Blasius 1839) im Südlichen Harzvorland. Mitt. AG Zool. Heimatf. 10: 1-9.

Sleep, D.J.H. & R.M. Brigham (2003): An experimental test of clutter tolerance in bats. J. Mammal. 84 (1): 216-224.

Sierro, A. & R. Arlettaz (1997): Barbastelle bats (*Barbastella* spp.) specialise in the predation of moths: implications for foraging tactics and conservation. Acta Oecologica 18 (2): 91-106.

Speakman, J.R. (1991): The impact of predation by birds on bat populations in the British Isles. Mammal Reviews 21(3): 123-142.

Steinhauser, D. (1999): Erstnachweis einer Wochenstube der Nordfledermaus (*Eptesicus nilssonii*) im Land Brandenburg mit Hinweisen zur Ökologie dieser Fledermausart. Nyctalus (N.F.) **7** (2): 208-211.

References

Surlykke, A. & C.F. Moss (2000): Echolocation behavior of big brown bats, Eptesicus fuscus, in the field and the laboratory. Journal of the Acoustic Society of America 108 (5): 2419-2429.

Svensson, A.M. & J. Rydell (1999): Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera* spp.; Geometridae). Anim. Behav. 55 (1): 223-226.

Svensson, A.M., Eklöf, J., Skals, N. & J. Rydell (2003): Light dependent shift in the anti-predator response of a pyralid moth. Oikos 101 (2): 239

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

Swift, S.M. (1997): Roosting and foraging behaviour of Natterer's bats (*Myotis nattereri*) close to the northern border of their distribution. J. Zool. (Lond.) 242: 375-384.

Swift, S.M. (1998): Long-eared Bats. A D Poyser Ltd, London.

Swift, S.M. & P.A. Racey (1983): Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. J. Zool. (Lond.) 200: 249-259.

Swift, S.M., Racey, P.A. & M.I. Avery (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. J. Anim. Ecol. 54: 217-225.

Swystun, M.B., Psyllakis, J.M. & R.M. Brigham (2001): The influence of residual tree patch isolation on habitat use by bats in central British Columbia. Acta Chiropt. 3 (2): 197-201.

Ulanovsky, N., Fenton, M.B., Tsoar, A. & C. Korine (2004): Dynamics of jamming avoidance in echolocating bats. Proc. R. Soc. Lond. B 271: 1467-1475.

Vaughan, N. , Jones, G. & S. Harris (1996): Effects of sewage effluent on the activity of bats (Chiroptera: Verspertilionidae) foraging along rivers. Biol. Conserv. 78 (3): 337-343.

Vaughan, N., Jones, G. & S. Harris (1997): Identification of British Bat Species by multivariate analysis of echolocation call parameters. Bioacoustics 7: 189-207.

References

Vergari, S. & G. Dondini (1998): Causes of death in two species of bats (*Pipistrellus kuhli* and *Hypsugo savii*) in urban areas of north-central Italy. Myotis 36: 159-166.

Walk, B. & B.-U. Rudolph (2004): Kleinabendsegler *Nyctalus leisleri.*(Kuhl, 1817). *In* Fledemäuse in Bayern. *Edited by* Bayerisches Landesamt für Umweltschutz, Landesbund für Vogelschutz in Bayern e.V. and Bund Naturschutz in Bayern.Ulmer Verlag. Stuttgart. Pp. 253-261.

Walsh, A.L., Harris, S. & A.M. Hutson (1995): Abundance and habitat selection of foraging vespertilionid bats in Britain: a landscape-scale approach. Symp. zool. Soc. Lond. 67: 325-344.

Waters, D.A. & A.L. Walsh (1994): The influence of bat detector brand on the quantitative estimation of bat activity. Bioacoustics 5: 205-221.

Waters, D.A., Rydell, J. & G. Jones (1995): Echolocation call design and limits on prey size: a case using the aerial-hawking bat *Nyctalus leisleri*. Behav. Ecol. Sociobiol. 37: 321-328.

Waters, D., Jones, G., & M. Furlong (1999): Foraging ecology of Leisler's bat (Nyctalus leisleri) at two sites in southern Britain. Journal of Zoology (London) 249: 173-180.

White, G.C. & R.A. Garrott (1990): Analysis of wildlife radio-tracking-data. Academic Press, London.

Wilde, C.J., Kerr, M.A., Knight, C.H. & P.A. Racey (1995): Lactation in vespertilionid bats. Symp. Zool. Soc. Lond. 67: 139-149.

Williams, D.D. & B.W. Feltmate (1992): Aquatic insects. CAB International, Wallingford.

Wickramasinghe, L.P., Harris, S., Jones, G. & N. Vaughan Jennings (2004): Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. Cons. Biol. 18 (5): 1283-1292.

Zingg, P.E. (1988): Search calls of echolocating Nyctalus leisleri and Pipistrellus savii Mammalia: Chiroptera recorded in Switzerland. Z. Säugetierkd. 53: 281-293.

References

Zingg P.E .(1990): Akustische Artidentifikation von Fledermäusen (Mammalia: Chiroptera) in der Schweiz. Rev. Suisse Zool. 97: 263-294.

10 Glossary

AC	avoidance calls; echolocation calls bats emitted after detection of strings in flight tent experiments
a.s.l.	above sea level
E	eastern longitude
F1	first obstacle frame in flight tent experiments
F2	second obstacle frame in flight tent experiments
f_{min}	minimum frequency of an echolocation call
f_{max}	maximum frequency of an echolocation call
FFT	fast fourier transformation
FLT	flight time; the time radio-tracked spent either commuting or foraging
FT	foraging time; the time radio-tracked bats spent flying back and forth within a restricted area searching for insects
IPI	inter pulse interval [ms]; temporal distance from the beginning of one echolocation call to the beginning of the next one
ISD	inter-string distance in flight tent experiments
ISD_v	vertical inter-string distance
ISD_h	horizontal inter-string distance
m	stands for "male" in radio-tracked bats. m110: male bat carrying transmitter 110 (frequency emitted by the transmitter)
MCP	minimum convex polygon; expression used to describe home range sizes of bats
N	northern latitude

Glossary

OC   orientation calls; echolocation calls bats emitted when flying in the flight tent

P1   the observation period before the birth of the young northern bats as indicated by the first occurrence of isolation calls, i.e. before 21st June

P2   the observation period after the birth of the young, i.e. from 22nd June – 30th July

SP   sampling point along a transect

T1 , 2 , 3   first, second and third third of the night. Duration of T2 was always 150 minutes. Duration of T1 and T3 varied with the time of dusk and dawn

w   stands for "female" in radio-tracked bats. w180: female bat carrying transmitter 180 (frequency emitted by the transmitter)