

The use of edge habitats
by commuting and foraging bats

CENTRALE LANDBOUWCATALOGUS



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2102201, 2423

The use of edge habitats by commuting and foraging bats

B. Verboom

PROEFSCHRIFT

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op dinsdag 21 april 1998
des namiddags te vier uur in de Aula.

2102201

ISBN 90-5485-838-9

Van dit proefschrift is ook een editie verschenen als Scientific Contribution 10 bij het
DLO-Instituut voor Bos- en Natuuronderzoek onder ISBN 90-76095-03-5.

BIBLIOTHEEK
LANDBOUWUNIVERSITEIT
WAGENINGEN

1. Een netwerk van opgaande vegetatieranden, zoals bosranden, houtwallen en bomenrijen, is van cruciaal belang voor het voortbestaan van populaties van de meeste in Nederland voorkomende vleermuisensoorten in agrarische gebieden.

2. Vleermuizen onderhouden akoestisch contact met opgaande vegetatieranden, ondanks het feit dat hun voorkomen bij opgaande vegetatieranden zich niet beperkt tot de zone die gedefinieerd wordt door het maximale bereik van de sonar.

contra: E.K.V. Kalko & H.-U. Schnitzler 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. Behavioral Ecology and Sociobiology 33: 415-428.

3. Door de agrarische ontwikkeling in Nederland zijn tot aan het begin van de twintigste eeuw de dichtheden van de meeste soorten vleermuizen toegenomen, hetgeen vooral samenhangt met een toename van de lengte (per oppervlakte-eenheid) van opgaande vegetatieranden.

4. De term 'echolocatie', zoals die wordt gebruikt voor vleermuizen en walvisachtigen, dient te worden vervangen door 'echoscopie'.

5. Bij zeer lage insectendichtheden is de vangefficiëntie van een vleermuis hoger dan die van een vangnet; bij zeer hoge insectendichtheden is deze lager.

6. Spierkracht kan Batman onmogelijk in de lucht houden.

U.M. Norberg & J.M.V. Rayner 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316: 335-427.

7. Bij het formuleren van onderzoekconclusies moet elke wetenschappelijk onderzoeker zich realiseren dat natuurbeleidsmakers bij de toepassing van resultaten weinig acht slaan op wetenschappelijk voorbehoud.

8. Het streven naar natuurlijkheid is in tegenspraak met het streven naar een maximale soortenrijkdom (wat vaak wordt opgevat als 'biodiversiteit').

9. De intrinsieke waarde van de natuur is een beter uitgangspunt voor natuurbeschermingseducatie dan de negatieve effecten van de achteruitgang van de natuur op het welzijn van de mens.

10. De ware wijnkenner geeft ook wijnen van minder dan een tientje per fles een kans.

11. Aan tafel zijn vorken gevaarlijker dan messen.

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1. General introduction

Bats are highly adapted animals, occupying a unique ecological niche as aerial, nocturnal hunters. To exploit the night sky, they not only developed wings to fly. Most bat species use echolocation to locate their prey in the dark and gather information on the world surrounding them.

Among mammalian orders, bats are probably unsurpassed in terms of ecological and morphological diversity. Currently, nearly one thousand species are known, one quarter of all mammals. The majority of bat species, over 800, belong to the suborder of Microchiroptera, which are more diverse and widespread than the Old World suborder of Megachiroptera, or flying foxes. According to recent insights, microchiropteran bats and flying foxes are unrelated taxa (Pettigrew et al. 1989).

Thirty-one bat species, all microchiropterans, are known to occur in Europe. In The Netherlands, 21 species have been recorded (Kapteyn 1995; Limpens et al. 1997), 19 belonging to the family Vespertilionidae and two species belonging to the Rhinolophidae. At current, 12 species are known to have one or more reproducing colonies in The Netherlands (Limpens et al. 1997). Eight species occur in good numbers, and can easily be found in their proper habitats.

Throughout the world, bats exploit a wide range of habitats, varying from hot and arid deserts to tropical rainforest, boreal forest and even alpine regions, depending on the availability of food. Microchiropteran bats feed on a wide variety of food types, such as other bats, birds, fish, reptiles, amphibians, arthropods, blood, fruit, nectar, and pollen. Most bats, including all European species, prey on insects and other arthropods.

Species diversity is greatest in sub-tropical and tropical regions. A number of insectivorous species, though, manage to survive at higher latitudes by going into torpor during the winter months. This allows them to reduce their body temperature and thus save energy. Torpor is not restricted to hibernating bats, but may also be used during the summer months whenever insect availability is low.

Among mammals, bats are unique in their ability to fly. Flight costs per unit distance are low compared to, for instance, running (Norberg 1990), and this allows bats to commute, forage and even migrate over considerable distances. Flight furthermore reduces the risk of predation (Pomeroy 1990).

Echolocation is a highly advanced acoustical information system, enabling bats to avoid obstacles and to locate and catch their prey on the wing in complete darkness. In mammals, the use of echolocation is shared only with cetaceans (whales and dolphins) and possibly insectivores (shrews and tenrecs), but it is best developed in microchiropteran bats. Although on itself energy expensive, the extra costs of echolocation to flight are reduced to near zero due to the biomechanical coupling of sound production and flapping of the wings ('wingbeat') (Rayner 1991b; Speakman & Racey 1991).

This thesis deals with how and why bats make use of vertical landscape elements, or edge habitats, in an otherwise open agricultural landscape. In this chapter, I will outline the research problem. Furthermore, I will introduce a number of relevant aspects of bat ecology, and explain some bat-related terms used in the following chapters.

Why edge habitats? A historical perspective

Ever since ultrasonic mini-detectors (which transform the ultrasonic signals of bats into sounds audible to the human ear) became available not only to professional, but also to amateur bat workers in the late 1970s, knowledge about the distribution and ecology of bats increased rapidly. Many fieldworkers learned to identify bats by their specific echolocation sounds and flight behaviour (Ahlén 1981, 1990; Helmer et al. 1987). In The Netherlands, a systematic, nationwide survey of bats in their summer habitat was conducted from 1986 till 1992. The Dutch Bat Survey not only resulted in detailed distribution maps, but revealed many aspects of the way in which different species use the landscape and landscape features (Limpens et al. 1997). Over the years, many fieldworkers became skilled, not only in identifying species, but also in tracking and mapping commuting routes and foraging areas. For several species this was rather easily performed, since travelling routes appeared to be mainly along treelines, hedgerows, forest edges and canal banks. A method was developed to locate maternity roosts by tracking down bats commuting to their foraging areas at dusk, and following them when flying back to their roost again in the morning (Helmer et al. 1987; Limpens 1993). The use by bats of edge habitats, especially as commuting corridors, became a major topic among Dutch bat workers.

Several hypotheses have been suggested to explain the relationship between bats and edge habitats (Limpens et al. 1989; Limpens & Kapteyn 1991). First, it was hypothesised that bats use their sonar to find their way through an area. It would hence be necessary for a bat to maintain acoustic contact with vertical landscape elements. The degree to which open areas apparently were avoided by small species,



Treelines and canals are heavily used by bats (photo: Ben Verboom).

was thought to be directly related to their limited sonar range. Furthermore, edge habitats were assumed to attract bats for their relative abundance of insects, and because they provide shelter from wind and predators (Limpens & Kapteyn 1991).

Although previous field studies had enlightened many aspects of the landscape use by bats, many questions about the functions of landscape elements for bats remained unanswered, and many new questions had arisen. In 1991, the Dutch Ministry of Agriculture, Nature Management and Fisheries provided funds for a study to evaluate the importance of landscape elements for bats. This thesis is the result of these studies.

General aim of this study

In this thesis, I ask whether and how density, configuration, and structural features of edge habitats affect the abundance of bats in a landscape. The main objective of this study was to obtain knowledge that can be used in landscape planning, primarily in relation to the management and creation of edge habitats for the benefit of bats.

The importance of edge habitats such as forest edges, treelines and hedgerows for bats has been demonstrated in a number of studies (Furlonger et al. 1987; Limpens & Kapteyn 1991; Grindal 1996; Krusic & Neefus 1996; Perdue & Steventon 1996; Walsh & Harris 1996a, 1996b). Landscape changes caused by humans may have a positive influence on bat species richness as long as it leads to an increase of habitat diversity, in particular of edge habitats (Estrada et al. 1992; Fenton et al. 1992). Modern land management practices such as forestry and agricultural development, however, generally lead to habitat loss and the expansion of large open areas devoid of trees, such as large clearcuttings, arable fields and 'improved' grasslands. Bat occurrence in such areas is generally low (Furlonger et al. 1987; Estrada et al. 1992; Crampton & Barclay 1996; Grindal 1996; Walsh & Harris 1996a, 1996b). Large-scale clearcutting of forest and other woody landscape elements may result in increased inter-fragment distances (isolation) and smaller forest patches. Since many bats avoid open areas, this may lead to:

- reduced feeding opportunities for species roosting outside fragments for which the open matrix between fragments forms a barrier,
- the disappearance of tree-dwelling species from fragments as a result of reduced feeding opportunities and reduced recolonization probability after extinction,
- eventually the disappearance of species from large areas.

Until the beginning of the present century, agricultural development had a positive effect on species richness in many parts of western Europe, including The Netherlands. By the conversion of natural woodland into diverse landscapes with woodlots, orchards, pastures and hayland, cereal fields, hedgerows, and treelines, man had created a small-scaled, habitat mosaic landscape, which was very rich in species. In the present century, this situation has changed substantially. Between 1900 and 1990, the total length of hedgerows, hedges and treelines, which are characteristic of old agricultural landscapes on sandy soils, was reduced by almost 60% (Dijkstra et al. 1997). This was mainly the result of land consolidation schemes

to facilitate large-scale farming, and because landscape elements, such as hedgerows, lost their original function as supply of wood. Similar processes took place in other parts of north-western Europe (e.g. Baldock 1990; Barr et al. 1993).

Over the past decades, many bat species in The Netherlands, and in the whole of north-western Europe, have declined in numbers and range (Daan 1980; Stebbings 1988; Broekhuizen et al. 1992; Limpens et al. 1997). Changes in land-use are thought to be a major cause of the decline of many species (Walsh & Harris 1996a/b; Limpens et al. 1997). In many countries, treelines, hedgerows, forest edges and vegetated banks used to form, and in some areas still form, extensive networks. Such edge habitats are often heavily used by bats. To compensate for the negative effects of the ongoing fragmentation of woody vegetation in our cultivated landscapes, protection and creation of woody landscape elements is essential.

Interactions between flight, food and echolocation

To appreciate the habitat preference, and, in particular, the use of edge habitats by different bat species, I will first give an overview of relevant aspects of the behaviour and ecology of bats in their summer habitats. There is a clear relationship between a bat's functional 'design' and its commuting and foraging behaviour. Several studies have demonstrated that flight morphology and echolocation properties of bats are strongly related to their habitat use (e.g. O'Shea & Vaughan 1980; Pye 1980; Aldridge 1986a/b; Aldridge & Rautenbach 1987; Furlonger et al. 1987; Norberg & Rayner 1987; Neuweiler 1989; Fenton 1990; McKenzie et al. 1995). Wing morphology poses energetic and mechanical constraints on a bat's flight speed and manoeuvrability (Norberg & Rayner 1987). Echolocation calls have evolved to optimise foraging efficiency in a particular habitat. Both wing morphology and echolocation call structure are believed to be interrelated parts of the same adaptive complex (Aldridge & Rautenbach 1987).

FLIGHT STYLE AND FORAGING ECOLOGY

Among insectivorous bats, the following foraging strategies can be identified (Norberg and Rayner 1987). Most insectivorous bats catch their prey on the wing in open air by 'aerial hawking'. 'Fast hawking' species often hunt in large open spaces, 'slow hawking' bats are usually found in more confined airspaces between vegetation. 'Perch-hunting' or 'flycatching' bats locate their prey hanging from a perch, then catch it by aerial hawking, and return to their post. 'Trawling' bats take their prey from water surfaces with their hind feet or tail membrane. 'Gleaning' bats take their prey from surfaces such as vegetation ('foliage gleaners') or from the ground ('ground gleaners' or 'pouncers'). Many gleaners are capable of hovering over their prey.

Many species use more than one foraging technique. All species in The Netherlands forage by aerial hawking, often in addition to one or more other techniques. The trawling species *Myotis daubentonii* and *M. dasycneme*, for instance, very frequently hawk for insects above the water surface and sometimes over land.

The flight performance (speed and manoeuvrability) and foraging behaviour

of a particular bat species are a reflection of its wing morphology (Norberg & Rayner 1987; Norberg 1990). In relation to flight style, two indices of wing morphology are especially important: 'wing-loading', which is defined as the weight divided by wing area, and 'aspect ratio', which is (wing span)² divided by wing area. Bats with high wing-loading are generally large and have relatively small wings. They are designed to fly fast. Although these bats are not manoeuvrable in confined airspaces, their flight is agile, so they can turn quickly. Large aspect ratio means that wings are long and narrow. Large aspect ratios allow greater aerodynamic efficiency because of reduced drag on the wings.

Although some bats show strong flexibility, different flight and foraging styles can be distinguished, based upon these two variables (see Norberg & Rayner 1987). Bats with high wing-loading and large aspect ratio are streamlined, fast flyers, which catch their prey on the wing in large open spaces by aerial hawking. These bats commute or migrate over long distances. In The Netherlands, *Nyctalus noctula* and *Nyctalus leisleri* have relatively high wing loadings, but average aspect ratios. Bats with low wing-loading and large aspect ratio still have a low manoeuvrability. Although they may fly long distances, their flight speed is relatively low. A number of frugivorous and nectarivorous species of the subfamily Phyllostominae, as well as several piscivorous bats, belong to this category (Norberg & Rayner 1987). Relatively few bats combine a high wing-loading with a low aspect ratio. Most of these are nectar and pollen feeders, adapted to hovering near flowers and to fly fast between patchy food supplies. Bats with low wing-loading and low aspect ratio are slow flying, highly manoeuvrable bats, adapted to hunt in confined spaces, e.g. among vegetation. The foliage gleaning *Plecotus* and several *Myotis* species fall into this category.

ECHOLOCATION

Echolocating bats produce short, high-frequency sound pulses, mostly between 20 and 120 kHz. By analysing the reflected echoes of the emitted sounds, bats create a sound-picture of the surrounding world. Although some bats produce sounds that are audible to the unaided human ear, most echolocation calls are ultrasonic, that is beyond the frequency range of human hearing. The most important reason for emitting ultrasound signals is that very small objects, such as insects, can be detected. Echolocation, furthermore, enables bats to avoid obstacles, e.g. when flying among vegetation or approaching a wall. But echolocation is more than just 'locating' objects. An echolocating bat can also recognize patterns and structures, so that, for example, it can distinguish prey from non-prey. A term analogous to visualization ('audification', Neuweiler 1990), would probably do more justice to this highly sophisticated system.

The specific echolocation pulses of bats may be of constant frequency (CF), or may include a range of frequencies (frequency modulated or FM; Fig. 1.1). CF pulses, although often starting and/or ending with a short FM component, are also called narrowband pulses. FM pulses may be termed broadband pulses. CF pulses are long, typically 10-50 ms, compared to FM pulses, which are generally 2-5 ms in duration, but in many cases even shorter. FM pulses often end, and in some cases begin, with a near CF component of variable duration. The duration of these QCF components, where QCF stands for 'quasi constant frequency' (Kalko & Schnitzler 1993), may

range 5-25 ms. The frequency of highest intensity (the peak frequency) is usually in the QCF part of the pulse.

It is generally thought that the maximum sonar ranges of most bats are in the range of 5-40 m, and that echolocation works over even shorter distances. The reason for this is that ultrasonic signals with very short wavelengths do not travel very far in air due to energy absorption, which increases exponentially with frequency and additionally increases with humidity and air temperature (Neuweiler 1990). Additionally, the travel distance of sound in air is limited by spreading loss or geometrical attenuation due to sound expansion.

Generally, FM bats avoid the overlap of a returning echo (1) with the same

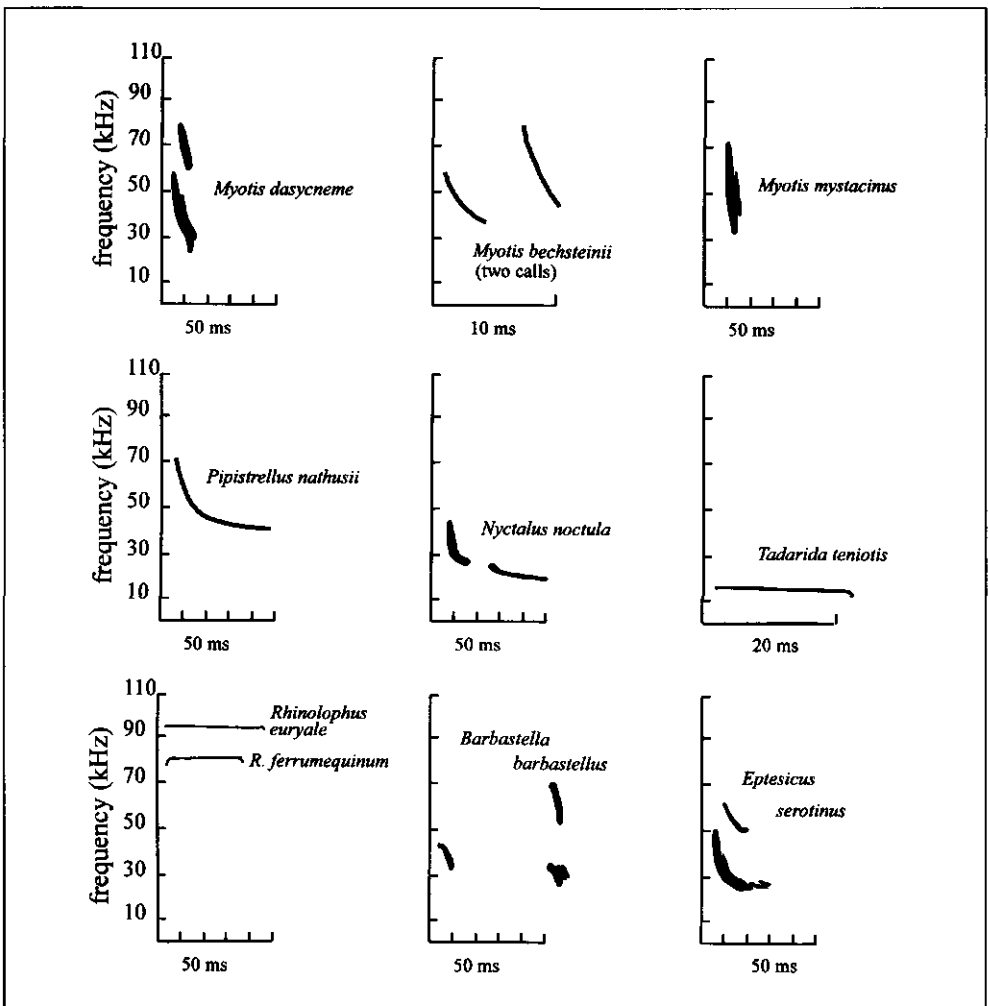


Figure 1.1.

Time versus frequency plots (sonograms) of echolocation calls, showing the variation in pulse types among nine European bat species (from Altringham 1996).

and (2) with the subsequent outgoing signal. Overlap is believed to mask information stored in the echoes, especially because of reduced hearing sensitivity during calling (Cahlander et al. 1964; Henson 1965; Suga & Schlegel 1972). For FM bats, like vespertilionids, overlap avoidance means that the duration of a pulse should be short enough when the bat-to-object distance is small. This means that prey can be detected only as long as the bat keeps a minimum distance to it. Furthermore, to avoid overlap of prey and background echo, the distance between prey and background should not be too small ('overlap-free window', Kalko & Schnitzler 1993). When the bat is echolocating a more distant object, interpulse intervals (the interval between echolocation pulses) should be long enough to allow a returning echo to be received and processed before the next pulse is emitted.

Before having detected an airborne prey, a hunting bat emits so-called 'search phase' echolocation calls. When it detects a prey and gets closer to it, the bat enters the 'approach phase' (Fig. 1.2). To avoid pulse-echo overlap, pulse duration is shortened, while more pulses per second are emitted to collect information at a faster rate. In the terminal phase preceding prey capture, the emitted pulses become even shorter and pulse-repetition rate faster. The 'terminal phase' is also called a 'feeding buzz'. This refers to the sound heard on an ultrasonic or bat detector. During the approach and terminal phases, bats often add harmonics to the fundamental frequency (Fig. 1.2b) in order to increase the signal bandwidth. This enables the

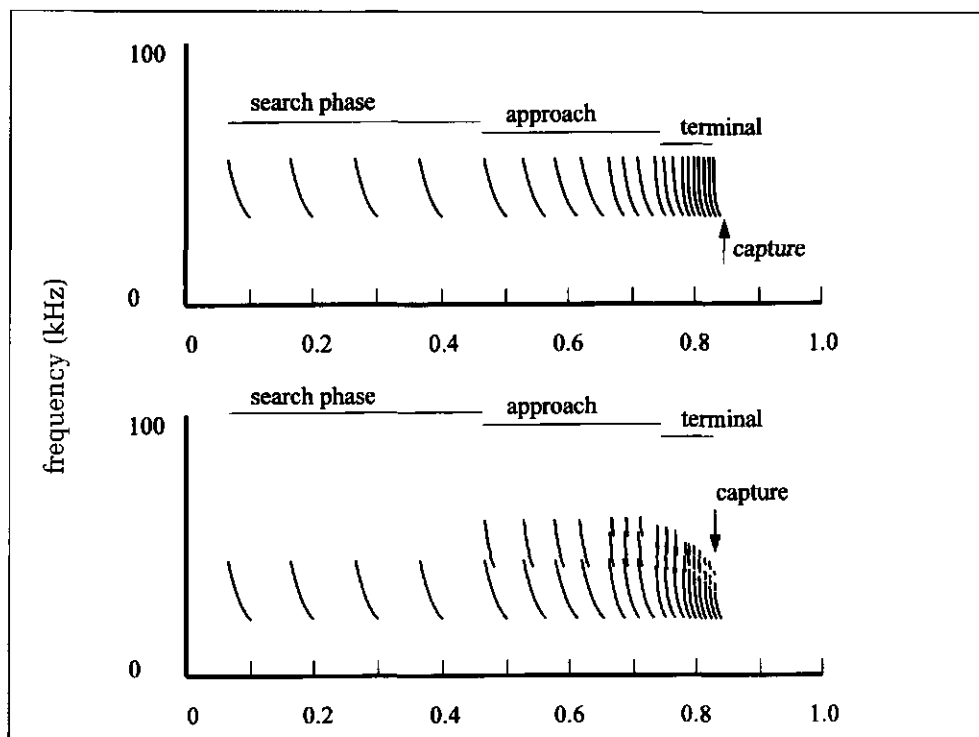


Figure 1.2.

Changes in pulse-repetition rate and pulse duration from search phase to prey capture.

(a) Fundamental frequency only, (b) with harmonics (from Altringham 1996).

animal to collect more accurate information on the exact position and structure of the target.

As illustrated by Figure 1.1, there is a wide range of echolocation pulse types among bat species, and there is much evidence that interspecific differences are strongly correlated with the habitat type in which each species occurs. Species specific differences allow the identification of many species with the use of bat detectors. However, there seems to be considerable variation on the intraspecific level (e.g. Rydell 1990; Obrist 1995), which can be a serious constraint on species identification. Individual changes in signal structure not only occur after prey is detected (approach phase, terminal feeding buzz), but may occur during the search phase as well when bats adapt their echolocation call characteristics, such as pulse duration, pulse frequency, bandwidth and interpulse intervals, in order to optimise foraging efficiency in different environments. In general, high frequency, broadband calls are better suited for the determination of target range and provide more accurate information on the texture and the structure of objects than do low frequency, narrowband echolocation signals (e.g. Simmons & Stein 1980; Saillant et al. 1993; for reviews see Neuweiler & Fenton 1988; Fenton 1990; Neuweiler 1990). Furthermore, they are more resistant to clutter (background echoes from vegetation or ground), which may interfere with prey echoes. Low frequency, narrow bandwidth calls, on the other hand are better suited for long range detection. Most of the changes seem to be related to the bats' distance to clutter-producing objects. For example, when flying from a forest lane into an open meadow, individual bats generally switch to more narrowband signals of lower frequency and longer duration. Together with flight style and foraging strategy, the variation of echolocation signal design in relation to habitat structure has been subject of many studies (e.g. Kalko & Schnitzler 1993; Obrist 1995; Fenton 1986).

There seems to be a strong relation between echolocation call design and the availability of certain categories of prey to bats. The selective feeding by a number of bat species on specific prey categories seems to be more easily explained by limitations of their echolocation system (passive selection) than by reasons of optimal foraging (active selection; Barclay & Brigham 1994).

Foraging strategies of bats (see previous section) can be characterised by their specific type of echolocation. For five species, Figure 1.3 illustrates the relationship between foraging strategy, wing-morphology and echolocation pulse design, and shows the considerable variation between species.

- Among the aerial hawking bats, species that hunt in large open spaces typically emit high intensity, low frequency, narrowband QCF or FM-QCF signals with a relatively long duration QCF component (e.g. *N. noctula*, Fig. 1.3). This enables them to detect prey over large distances, which is important since most open space hawkers are fast flyers. Once close to a prey item, they can switch to short, broadband, FM pulses which provide more detailed information. Slower flying aerial hawkers of more confined, cluttered environments tend to emit higher frequency calls (Fig. 1.3: *Pipistrellus pipistrellus*). When emitting FM-QCF pulses, the QCF components are of shorter duration, or may be absent to become FM signals.
- Trawling bats generally emit broadband FM signals (Fig. 1.3: *M. daubentonii*). Some species, such as *M. dasycneme*, emit pulses with a QCF

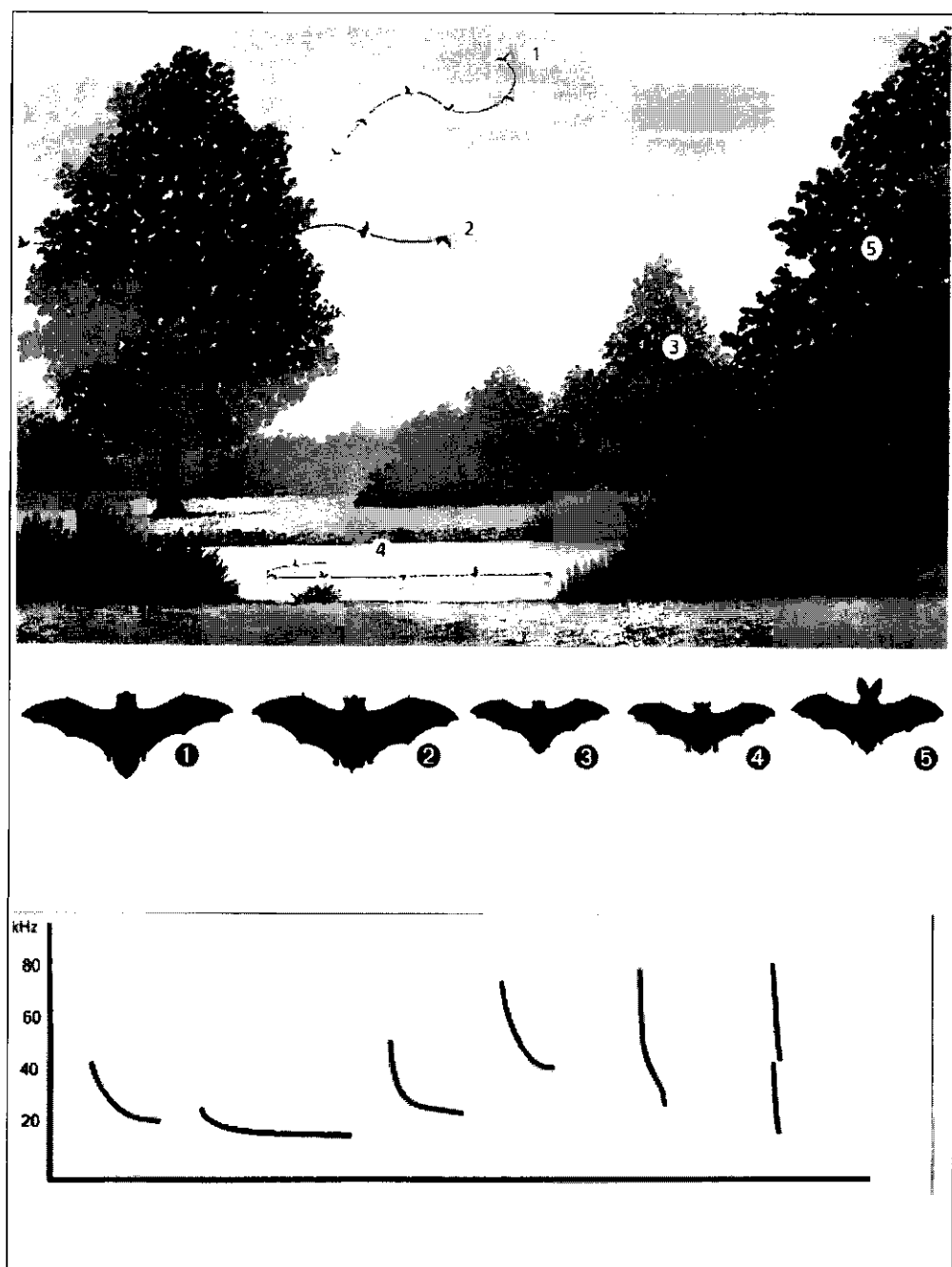


Figure 1.3.

The relationship between foraging strategy, wing-morphology and echolocation pulse design in five species from The Netherlands (drawing by P. Twisk).

1 *Nyctalus noctula* (noctule); 2 *Eptesicus serotinus* (serotine); 3 *Pipistrellus pipistrellus* (pipistrelle); 4 *Myotis daubentonii* (Daubenton's bat); 5 *Plecotus auritus* (long-eared bat)

component. This may be related to detection over long distances, but they may also be used during aerial hawking.

- Foliage and ground gleaners use FM signals of very short duration (<2 ms) and low intensity (Fig. 1.3: *Plecotus auritus*). These signals are designed to discriminate fine texture over short distances. Instead of echolocation, many gleaners use the sounds generated by their prey for detection.
- Perch-hunters such as several *Rhinolophidae* species emit CF calls, which are designed to detect fluttering insects in extremely cluttered environments.

Orientation and navigation

Bats are remarkably skilled in orientation and navigation, the former being the mechanism involved in the recognition and maintenance of direction, the latter being the mechanism involved in the identification of the direction of a given point in space (Baker 1978). A number of temperate species, for instance, undertake long-distance migrations between their summer and winter roosts, sometimes over more than 1000 km (e.g. *Pipistrellus nathusii*, Strelkov 1969; *N. noctula*, Doekemeijer 1994). Homing experiments with bats, released at varying distances from their roost, indicate that bats have very accurate navigational capabilities, especially within their home range. Although vision is poorly developed in bats, homing studies suggest that vision plays a role in navigation (e.g. Williams & Williams 1967; Davis & Barbour 1970). But in several of these experiments, blindfolded bats were as successful as their unblinded controls (e.g. Mueller & Emlen 1957; Stones & Branick 1969), suggesting a role of echolocation in navigation as well. Other possible mechanisms, such as the use of magnetic cues, have not yet been studied in bats.

There are several possible mechanisms that a bat could use to navigate through a landscape. Bat movements may be guided by information stored in cognitive maps of their environment. At least some bat species seem to possess an excellent spatial memory of the environment they are familiar with (Griffin 1988). Up till now, the role of reference landmarks in bat navigation is only speculative, but if bat movements rely on spatial memory, the information stored in cognitive maps still has to be based on acoustic and, possibly, visual cues, and reference landmarks may still be necessary for a bat's navigation.

Outline of the thesis

In Chapter 2, I ask whether and to which degree edge habitats are used by two bat species, the pipistrelle bat *Pipistrellus pipistrellus* and the serotine *Eptesicus serotinus*. On a landscape scale, the occurrence of both species is correlated to the density of hedgerows, treelines and woodlot edges and their degree of fragmentation. Four possible explanations for the assessed relationships of bats to edge habitats are discussed: (1) acoustical landmarks, (2) foraging areas, (3) shelter from wind, and (4) shelter from avian predators. In Chapters 3-5, hypothesized functions of edge habitats for bats are studied in more detail. Effects of wind and insect abundance on the occurrence of commuting and foraging pipistrelle bats near treelines are tested

in Chapter 3. Predator avoidance and acoustical landmarks are discussed as alternative explanations for the relationships found. To examine the possible function of vertical landscape elements as acoustical landmarks, the echolocation behaviour of the pond bat *Myotis dasycneme* was studied. Chapter 4 describes the flight performance and echolocation characteristics of commuting and foraging pond bats. In Chapter 5, characteristics of echolocation signals emitted by pond bats commuting over canals are related to the distance to the banks. In Chapter 6, the profitability of treelines as a feeding site for pipistrelle bats is assessed by relating the occurrence of foraging pipistrelles to treeline features (height, width, permeability). The commuting behaviour of pipistrelles was studied in relation to the distribution of potentially good feeding sites. In Chapter 7, results of the previous chapters are discussed. Practical guidelines for the application of results in the planning, conservation, and management of edge habitats are presented.

2. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*

Summary

The relation between two species of bats, the pipistrelle (*Pipistrellus pipistrellus* (Schreber, 1774)) and the serotine (*Eptesicus serotinus* (Schreber, 1774)) and linear landscape elements, in particular hedgerows and treelines, was studied in an agricultural area in The Netherlands. The pipistrelle was observed almost entirely close to landscape elements, while serotines more frequently crossed fields and meadows. Serotine activity in these open areas was, however, negatively related to the distance to a landscape element and to windspeed.

On a landscape scale the results indicate a more than proportional positive relation between the density of serotine bats and the density of linear landscape elements, whereas this relation was only proportional in the case of the pipistrelle. It is argued, that landscapes with a high density of linear elements have a surplus value for serotines.

Three possible functions of linear elements for bats (orientation clues, foraging habitat, and shelter from wind and/or predators) are discussed. Any of these may explain the results of this study.

Introduction

Studies of linear landscape elements have focused on two aspects. The first is their role as connective elements in a metapopulation concept. Several studies show the importance of corridors for the survival of a species in a landscape (e.g. Getz et al. 1978, voles; Henderson et al. 1985, chipmunks; Opdam et al. 1985 and Van Dorp & Opdam 1987, forest birds; Verboom & Van Apeldoorn 1990, red squirrels).

Secondly, the function of linear landscape elements as (daily) migration and foraging routes is emphasized by several authors (e.g. Wegner & Merriam 1979). Field studies and observations in The Netherlands during the last decade indicate that most bat species in their summer habitats prefer to fly along linear landscape elements such as hedgerows, treelines, forest lanes and edges, canals, etc. instead of crossing open areas (Limpens et al. 1989; Limpens & Kapteyn 1991). Helmer (1983) found that Daubenton's bats (*Myotis daubentonii*) used regular flight routes over distances up to 6 km, to reach their hunting grounds, following lanes, wood edges, hedgerows and water courses. A study of marked pipistrelle bats (*Pipistrellus pipistrellus*) around two colonies, revealed that the bats moved between fixed foraging sites on regular flight routes (Racey & Swift 1985). The maximum distance at which a bat was observed from its colony was 5.1 km (mean: 1.8 and 1.0 km respectively).

When commuting between colony and foraging areas Daubenton's bats only occasionally hunt for insects. Many other species, however, are frequently observed

foraging along linear landscape elements. Racey & Swift (1985) for instance, in their study of pipistrelles, found that flight routes were used for hunting as well.

Differences between species are also reflected in the degree to which they depend on linear landscape elements when moving through a landscape. In general, large species with a long range sonar, like the noctule (*Nyctalus noctula*) and the serotine (*Eptesicus serotinus*) are frequently observed in open areas. Smaller species with a short-range sonar like the pipistrelle usually keep more closely to rows of shrubs and trees and their movements are considered to be hindered by gaps in linear structures (Limpens et al. 1989; Limpens & Kapteyn 1991).

From a bat's point of view, we can imagine three different functions of linear landscape elements:

1. Linear elements are used as sonar guidelines.

In addition to prey detection, bats may use their sonar for navigation and orientation (Limpens et al. 1989; Neuweiler 1990; Rieger et al. 1990; Limpens & Kapteyn 1991). Homing experiments at least suggest the existence of echo-orientation. Experiments with blindfolded bats showed no difference in homing ability, within their home range, from bats that were able to see (e.g. Mueller & Emlen 1957; Williams et al. 1966). A similar experiment with blinded as well as deafened bats, released at 50 km from their roost, resulted in successful homing by 28% of the blinded bats (controls: 31%), but by none of the deafened bats (Stones & Branick 1969). It is thought that a species with a short sonar range must keep closer to a landscape structure for navigation and orientation. Many bats traditionally use specific flight routes (Bateman & Vaughan 1974; Racey & Swift 1985; Rieger et al. 1990). Spatial memory is considered to play a role in the use of these flight routes. More efficient foraging, owing to a reduction in the costs of searching for suitable foraging areas, is assumed to be the prime benefit (Bell 1991).

2. Linear landscape elements are a suitable foraging habitat for bats.

Hedgerows, treelines and wood edges have an important influence on the distribution of insects in a landscape. Insect densities around such landscape elements are known to be relatively high compared to adjacent fields, firstly because the vegetation provides a habitat for insects (Lewis 1969a; Forman & Baudry 1984), secondly because insects from surrounding areas accumulate on the leeward side (Lewis 1969b; Lewis & Dibley 1970). In open areas, highest insect densities are found near the ground and show a steep decrease with height. In sheltered areas, such vertical gradients are less pronounced and the effects of wind and temperature are tempered (Karg & Ryszkowski 1985).

3. Linear elements provide protection against predators and/or wind.

To conserve energy and time, bats may seek shelter against wind by flying on the leeward side of trees and bushes. Predatory birds, especially owls and kestrels, now and then catch bats. According to Speakman (1991), the impact of predation by avian predators on bats and bat behaviour may be considerable in some areas. By flying on the shaded side of a linear landscape element, a bat can avoid being lighted by streetlights, moonlight or sunset glow, and decrease exposure to predators.

Although linear elements still are the predominant landscape structures in many agricultural areas in The Netherlands, they are much threatened by rural development. Yet, their importance for many species is recognized by conservation biologists. Recently, the Dutch government's nature policy has emphasised the development of an ecological infrastructure for plants and animals. In 1991, a five-year project was set up to study the role of linear landscape elements for bats. This paper deals with the relationships between bats and the landscape structure. We focused on two species, the serotine and the pipistrelle. Field observations indicated that these bats exhibit different ways of using landscape elements when moving through a landscape. Our aim was to verify whether the difference between these two species in their behaviour towards linear elements is reflected in the way they are distributed on a landscape scale. The results will help us to consider the needs of bats in landscape planning activities, e.g. land consolidation and nature development projects.

The following questions are dealt with:

1. Do pipistrelles in fact follow linear elements more closely than serotines?
2. Do bats occur along isolated fragments of linear landscape elements?
3. Do landscapes with a high density of linear landscape elements attract more bats?
4. Does fragmentation of the network of linear landscape elements negatively influence the occurrence of bats?
5. Which characteristics of linear landscape elements influence the occurrence of bats?

Questions number three and four deal with relations between bats and linear landscape elements on a landscape scale, while the other questions deal with the smaller scale of landscape elements. Whether the density of linear landscape elements influences the distribution of a bat species depends on the limiting factor for this species on a landscape scale. If we assume that linear elements indeed limit bat densities, we can summarize our expectations as follows. For the pipistrelle, being closely associated to edge habitats, we expect densities to increase in direct proportion to the amount of linear elements. The foraging habitat of a serotine is probably not confined to hedgerows, treelines and wood edges and may extend to nearby open areas. We therefore expect a less than proportional relation with linear landscape element density in serotines. Isolation effects are expected to be more important to species with a smaller sonar range like the pipistrelle.

Material and methods

STUDY AREA

The research area was in the northern part of Twente (province of Overijssel). In The Netherlands, this area represents one of the best examples of an old agricultural landscape type with many linear elements. The original agricultural landscape structure, in which meadows and fields are separated by a network of hedgerows and treelines, is still intact in parts of the area. Many small woodlots (<3 ha) are present, along with a few larger woods of 30-200 ha.



Networks of treelines and hedgerows connecting patches of wood can still be found in some old agricultural landscapes in The Netherlands, such as Twente (photo: IBN-DLO).

OBSERVATIONS

In order to detect relationships on a landscape scale as well as on the scale of the landscape element, 110 observation points were distributed over 15 1x1 km squares, each square containing 5-8 observation points. One to three of the observation points in each square were situated in open areas, in meadows, arable fields or along roadsides, 25-265 m from the nearest trees or shrubs (23 in total). The remaining 87 points were situated approximately 2 m from linear landscape elements, along single (hedgerows, tree rows) linear elements or double treelines or along woodlot edges. Observations along single elements were made on the leeward side, observations along double elements were made between the rows of trees, usually from the middle of a road or track. In order to minimise the influence of woods, there were no woodlots of more than 2 ha or woodlots with (interior) trails or roads (which may



Figure 2.1.

Diagrams of tree lanes, hedgerows and woodlots in two of the 1x1 km squares studied, illustrating the variation in density and degree of fragmentation of linear landscape elements in the study area.

be used as flight routes) in the selected squares. Two of the 1x1 km squares are shown in Figure 2.1. Data on roost sites were not collected for practical reasons.

Fieldwork was carried out between May and August 1992. At each observation point, 5 observations were made, equally divided over the investigation period and over the night. At each observation bat activity was measured as the number of bat passes per 5 minutes, using a bat detector (D-960, Pettersson Elektronik, Uppsala, Sweden). A bat pass was defined as an increase in amplitude of bat sound, followed by a decrease. The detector was tuned at 42 kHz. In the field, detection ranges seemed to be similar for both species at this tuning frequency. The (maximum) sonar ranges of both species are assumed to differ analogously with the maximum detection ranges of the bat detector when tuned at the respective peak frequencies of the bats.

Data on temperature, windspeed, cloudiness and moonlight, as well as time of the night and year were also collected.

DATA ANALYSES

Field data were analysed with Poisson regression analyses, using the statistical programming package GENSTAT (Genstat 5 Committee 1987). The number of bat passes was used as the dependent variable. Table 2.1 shows the independent variables used in the analyses. Linearity of all independent variables in relation to the logarithm of the dependent variable was assumed. The dependent variable was fitted with each of the independent variables separately. The model was extended

Table 2.1.
Independent variables used in the analyses.

LANDSCAPE SCALE (1X1 KM SQUARES)	
LLE	total length of linear landscape elements (hedgerows, tree rows, double treelines within the square (m)
LLESURR	total length of linear landscape elements in the surrounding eight 1x1 km squares
FRAG	degree of fragmentation of the linear landscape element network within the square (number of fragments divided by LLE)
FRAGSURR	degree of fragmentation of the linear landscape element network in the surrounding eight 1x1 km squares
LANDSCAPE ELEMENT	
FRAGL	length of fragment that includes observation point (m)
FRAGD	distance between the fragment of the observation point and the nearest other fragment (m)
LLETYPE	type of linear landscape element (single, double, wood edge)
WIDTH	maximum width of the element (m)
HEIGHT	maximum height of the element (m)
PERM3	visual permeability at 3 m above the ground (%)
PERM6	visual permeability at 6 m above the ground (%)
PERMMAX	maximum visual permeability (%)
OPEN AREA	
LLED	distance to the nearest landscape element (m)
WATD	distance to the nearest water (m)
OTYPE	type of open area (meadow, field, roadside)
LEVEL OF THE OBSERVATION	
TEMP	temperature (°C)
WIND	wind-speed (m/5 min)
CLOUD	cloudiness (1 - 5)
MOON	moonlight (1 - 8)
TIME	time of the night (minutes after sunset)
DATE	date (May-days)

with a second parameter if addition significantly reduced the deviance ratio (mean regression deviance divided by mean residual deviance). The level of significance used was $P=0.05$ (F-tests). The variation in the dependent variables between 1x1 km squares as well as between observation points was analysed. We also checked for possible effects of weather data and time of the night and year.

In the analyses of landscape scale parameters, we used an offset variable to correct for number of observation points per 1x1 km square. Thus the fitted values per square represent the average number of bat passes per observation point, being a measure of total bat activity.

In the calculation of the degree of fragmentation in the network of linear landscape elements (FRAGM), the length of fragments (FRAGL) and the distance between fragments (FRAGD), we (arbitrarily) used a minimum of 50 m as a distance to separate fragments, assuming that in open terrain a distance of 50 m and more forms a considerable barrier to cross, at least for pipistrelles.

Table 2.2.

Summary of bat data along linear landscape elements and in open areas.

	SEROTINE	PIPISTRELLE
LINEAR LANDSCAPE ELEMENTS (N=87)		
presence per observation point	53%	68%
mean number of passes per point	1.51	3.28
max. number of passes per point	17	24
OPEN AREAS (N=23)		
presence per observation point	52%	9%
mean number of passes per point	1.35	0.26
max. number of passes per point	6	5

Results

BAT PRESENCE

Both the serotine and the pipistrelle were observed in all 15 1x1 km squares. Table 2.2 shows presence data for both species along linear landscape elements and in open areas. The presence of pipistrelles on observation points (fraction per 5 observations) in open areas was much lower than along linear landscape elements (Table 2.2; Mann Whitney U-test: $P < 0.001$). The presence of serotines in open areas was not different from the presence along linear landscape elements (Table 2.2; Mann Whitney U-test: $P = 0.49$). However, in a Poisson regression analysis, the activity of serotines was negatively related to the distance to a linear landscape element ($n = 23$; $R^2 = 26\%$; $P = 0.01$; distances ranged 25-265 m).

Effects of isolation of fragments of linear landscape elements in which observation points were situated on bat presence were not found. Observation points were dispersed over a total of 50 fragments, meaning that some fragments contained more than one observation point. Twelve fragments lacked pipistrelle and 19 lacked serotine observations. According to certain criteria (length of fragment (FRAGL) < 1000 m and distance to nearest fragment (FRAGD) > 100 m and a maximum of five buildings along fragment), 11 relatively isolated fragments (FRAGD ranging 110-170) were selected. The presence of roosts was unlikely, as only a few buildings were situated along these fragments. Pipistrelles were observed in six and serotines in five of these most isolated fragments (FRAGD ranging 110-150 m) which demonstrates their ability to cross gaps this wide. Apparently the degree of isolation in the study area did not exclude bat movements between fragments of linear landscape elements. For both species there was no difference between the presence along isolated and non-isolated fragments (Chi-square tests: $P > 0.05$).

We also checked for effects of wind. The activity of serotines in open areas over all observations was negatively correlated with wind-speed ($n = 115$; $R^2 = 12\%$; $P < 0.001$).

Table 2.3.

Landscape scale level: Poisson regression models of the average number of pipistrelle and serotine passes per observation point. Offset parameter: number of observation points per square. R^2 = percentage of deviance accounted for by the model.

MODEL	ESTIMATE	R^2	P
pipistrelle			
LLE	-0.000034	0.3	0.845
LLESURR	-0.000338	6.8	0.350
FRAG	0.190	18.3	0.112
FRAGSURR	175.4	27.7	0.044
serotine			
LLE	0.000231	26.9	0.048
LLESURR	-0.000597	38.5	0.014
LLE + LLESURR	0.0000793	61.5	0.009*
FRAG	0.0004	0	1.000
FRAGSURR	117.2	26.9	0.049
* significance of the last variable			

LANDSCAPE SCALE

For both species, the results of the Poisson regressions are outlined in Table 2.3. In the 1x1 km squares, both pipistrelle and serotine activity were positively related to the fragmentation of the network of linear elements in the surrounding eight 1x1 km squares (FRAGSURR).

The number of serotine bat passes showed a relation with the density of linear landscape elements (LLE), and particularly with those in the surrounding squares (LLESURR). Both variables together ($r_{LLE-LLESURR}=0.105$) explained over 60% of the total deviance. The relation with LLESURR may be caused by the occurrence of many woodlots, and hence wood edges, in many of the surrounding squares, which may have attracted bats from the squares where bat data were collected. Wood edges made up 43% of the linear elements in the surrounding squares.

SCALE OF THE LANDSCAPE ELEMENT

In the regression analyses of serotines along linear elements, none of the parameters showed any significant effect. The Poisson regression analyses of the number of pipistrelle passes gave a significant positive effect of 'height of a linear landscape element' ($R^2=12.5\%$; $P=0.005$). Linear elements at the observation points were 3-25 m high. Pipistrelles were not recorded along elements less than 6 m high ($n=6$), while serotines flew along elements of all heights.

The linear landscape elements were separated into three different types: single linear elements (hedgerows, tree rows; $n=46$), double linear elements (lanes; $n=24$) and wood edges ($n=17$). T-tests revealed that neither of the species showed a preference for any of these types of landscape elements.

FORAGING ACTIVITY

Observations of feeding buzzes show that both species forage along linear elements. Only serotines were observed to hunt in open areas as well. The number of occasions with feeding buzzes was, however, very low. We recorded feeding buzzes during nine out of 550 observations for the pipistrelle as well as for the serotine. Three of these observations were in open areas for the serotine. For both species there was a strong positive correlation between the number of bat passes and the number of feeding buzzes. Three extremely high values were probably caused by bats hunting close to the observation point, flying to and from past the observer. On these occasions, we twice recorded 24 pipistrelle passes, and 17 serotine passes during a five-minutes observation period, together with 11, 4 and 1 feeding buzzes respectively.

Conclusions and discussion

DIFFERENCES BETWEEN PIPISTRELLES AND SEROTINES

We can summarise the differences between the two species with respect to linear landscape elements and the barrier effect of open areas:

1. Pipistrelles predominantly were found close to the vegetation of linear landscape elements. Serotines were observed as often in open areas as they were beside linear elements. However, the activity of serotines decreased with increasing distance from the linear element. Serotine activity in open areas was negatively influenced by wind.
2. We found a more than proportional increase of serotine activity with the density of linear landscape elements, whereas the increase of pipistrelle activity was only proportional.

BAT ACTIVITY

We recorded the number of bat passes only, which were a reflection of both bat density and individual foraging activity. It was not possible to account for bats being counted more than once during a five-minute period, which may have occurred in the case of foraging bats. In this paper we consider the number of bat passes to be an indication of bat activity.

THE FUNCTION OF LINEAR LANDSCAPE ELEMENTS

Any of the functional explanations mentioned before are capable of explaining the role of landscape elements assessed in this study:

1. Echo-orientation

The ability to use landscape elements as sonar beacons depends on the bat's maximum sonar range. Both the pipistrelle and the serotine emit relatively narrowband signals during their search flight in a more open environment (pipistrelle: Kalko & Schnitzler 1993; serotine: Miller & Degn 1981). These signals are suitable for long range detection, in contrast to the broadband signals they emit when flying close to vegetation or during prey capture (e.g. Neuweiler & Fenton 1988; Neuweiler 1990). The actual range of the narrowband signal depends on the intensity of the signal, the frequencies

emitted, the reflection properties of the target and the sensitivity of the receiver. The serotine emits longer and louder pulses at lower frequencies (appr. 27 kHz) than the pipistrelle (appr. 45 kHz for the average frequency of the narrowband pulse type). Assuming that the reflection properties of the vegetation and the sensitivity of the bats' ears for their respective peak frequencies are equal, differences in sonar range result only from energy absorption in the air, which increases exponentially with frequency. This could (partly) explain why pipistrelles on average fly nearer to landscape elements than serotines do.

2. Foraging habitat

Another important aspect to be considered is the influence of linear elements on insect-size distribution. Small and weak flying insects are more dependent on the sheltering effect of vegetation than are larger and stronger flying insects. Small insects usually swarm on the leeward side of vegetation, whereas larger insects are able to move more independently of wind (Taylor 1974). Of the two species involved in this study, the serotine hunts for larger insects such as beetles and moths (Labee & Voûte 1983; Robinson & Stebbings 1993), while the pipistrelle very often catches smaller insects, in particular Chironomidae, but also smaller dipterans (Swift et al. 1985; Hoare 1991; Sullivan et al. 1993). Differences in prey preference might explain why the pipistrelle usually keeps close to the vegetation, while the serotine is commonly observed in more open areas as well.

3. Shelter

Our analyses show two effects which might be explained by shelter of linear elements either for bats or for insects. Firstly, our data show a relation between the pipistrelle and the parameter 'height of an element'. Lewis (1969a) demonstrated that the size of the sheltered area on the leeward side of a hedgerow is related to its height. Compared to the neighbouring fields, the aerial insect fauna on the leeward side of a hedgerow was enriched up to a distance of 3-10 times the height of the hedgerow (depending on the angle between the wind and the hedgerow). Secondly, the occurrence of serotines in open areas decreases with wind-speed. Since the accumulation of insects behind linear elements increases with wind-speed (Lewis 1969b), serotines might move to more sheltered habitats in windy conditions.

Furthermore, the differences between both species can be explained by the effect of wind on their flight efficiency. As mentioned before, a bat may prefer to fly in wind-sheltered areas to diminish its flight cost. As the small pipistrelle is likely to be more sensitive to wind than the serotine, the former is expected to stay closer to trees.

The use of linear elements by bats may be affected by a combination of the above mentioned factors, depending on the species, on the configuration of different habitats in relation to the roost site and on wind direction and speed. The function of linear landscape elements may therefore vary between different parts of a landscape. Depending on the kind and distribution of foraging habitat for instance,

linear elements might be used as a main foraging area in one part of a landscape and as a commuting zone between colony and foraging area in another. Energy budgets may play a role in balancing the costs of flying in more open areas with the gain in insects.

RELATION TO LINEAR ELEMENTS

The results show a distinct difference between the two species in their relation to linear elements. The pipistrelle is largely confined to linear elements, flying close to the vegetation and infrequently crossing open areas. Pipistrelles are therefore expected to spread along the network of linear elements in an area. As stated before, it is thought that pipistrelle densities will increase proportionally to the density of linear landscape elements in an area. However, such an increase in bat density will not lead to an increase in the number of bats passing a randomly chosen observation point.

Serotines do not show a strong preference for linear elements on a small scale. The number of bat passes per observation point, however, is found to be positively related to the density of linear elements in the 1x1 km squares. Apparently, landscapes with a higher density of linear elements have higher densities of serotines. A plausible hypothesis for this is found in a possible effect of overlapping windbreak zones on the distribution of insects. In landscapes with a dense network of linear elements such an overlap of windbreak effects of different elements may occur (Forman & Baudry 1984). As large insects are able to control their flight up to a greater height than smaller insects (Taylor 1974), they will more easily respond to increased shelter. Moreover, strong flying species are less affected by temperature and are therefore a more predictable food source in sheltered habitats (Karg & Ryszkowski 1985). It is therefore possible that the serotine profits from a larger food availability in more sheltered landscapes, not only along linear elements, but also in open areas. The exploitation of open areas may be facilitated by the large sonar range of the serotine bat.

Whether the overall density of bats is indeed affected by the density of linear elements can only be confirmed by studying densities, sizes and distributions of roosts in relation to landscape characteristics. In the study area, landscape elements like woodlots and open water are not considered to play an important role as foraging habitats (open water in the area mainly refers to ditches or streams with equalized banks and little or no bank vegetation with recently planted hedgerows). Frequent visits showed us that such elements, which are rare in the area, did not attract many bats. If we want to make general statements about the relative importance of linear elements to bats, we need to do studies in areas where other potential foraging habitats play a more important role.

A major factor not included in our analyses might be the distance to a roost. Distance effects will be more important when roost density is low and distances between roosts are high compared to home range sizes. Our hypotheses are based on the assumption that roost density is high enough to exclude significant distance effects.

ISOLATION

The data show no evidence for effects of isolation of fragments of linear elements. For serotine bats, which cross open areas relatively easy, isolation effects were not expected. For pipistrelle bats, the presence in isolated, small fragments indicate that open areas of 110-150 m wide do not form a serious barrier. The influence of isolation on landscape exploitation can only be quantified when locations and sizes of roosts (including male roosts) are known.

As pipistrelles were observed at two observation points in open areas only, it seems plausible that open areas are crossed by commuting bats only on well defined flight routes. This was also suggested by Kapteyn & Verheggen (1990). They found that pipistrelles and long-eared bats (*Plecotus auritus*) were both equally abundant in small and isolated woodlots (i.e. not connected to the surroundings by linear elements) and in non-isolated woods.

In several parts of our country, we have indeed observed pipistrelle bats crossing gaps between linear structures up to 200 m on their daily flight routes. The observation points in open areas in our study area were, however, randomly distributed and the probability of coinciding with flight paths, consequently, small.

The present study area has a relatively high density of linear landscape elements. It would be interesting to know whether isolation effects will be more evident when distances between fragments increase. Furthermore, we need more information on the ecological consequences of altering the landscape structure. Especially for bats using traditional flight routes, cutting linear landscape elements may have serious implications for their possibilities to exploit an area.

3. Effects of food abundance and wind on the occurrence of pipistrelle bats *Pipistrellus pipistrellus* and serotines *Eptesicus serotinus* near treelines

Summary

I tested the hypothesis that the flying distance of pipistrelle bats *Pipistrellus pipistrellus* and serotines *Eptesicus serotinus* from treelines can be explained by food abundance and protection from wind. Foraging bats were monitored, and insect abundance and wind were measured at fixed distances up to 50 m from treelines. Different situations, with and without wind, and with low and high insect abundance in the adjacent open areas, were compared. In the presence of wind and low insect abundance in the adjacent open areas, peak occurrence of pipistrelles was closer to the treeline than insect abundance peak, and both were closer to the treeline than maximum wind shelter. At high wind-speeds or large incidence angles, pipistrelles concentrated closer to the trees. The distance distributions of pipistrelles and serotines were closely related to the insect distribution only when the treeline was bordered by insect rich grassland. In all situations, pipistrelle occurrence decreased with increasing distance to the treeline. This relation remained significant after correction for wind shelter and insect abundance. Serotine showed no decrease with distance to treeline. Pipistrelle bats commuting along a double row of trees flew mainly between the treelines, regardless of insect abundance or wind shelter. Predator avoidance is argued to be a constraint on movements of bats at relatively high light levels. At high wind-speeds and large incidence angles, the proportion of pipistrelle bats commuting on the leeward side increased. The results have implications for the conservation of bats. Treelines are important to foraging bats because they support relatively high insect abundance and protect bats from wind. For bats commuting at dusk and dawn, an essential function of tree corridors may be the protection from predators. A coherent network of tree corridors facilitates the exploitation of potential feeding areas.

Introduction

The distribution of many bat species is known to be associated with edge habitats, such as forest edges, forest lanes, treelines and hedgerows (Racey & Swift 1985; Limpens et al. 1989; Krull et al. 1990; Rieger et al. 1990; Limpens & Kapteyn 1991; De Jong 1994; Walsh & Harris 1996a/b; Verboom & Huitema 1997). Depending on the species, these landscape elements are either used as flyways by commuting bats or as feeding sites, or both. Hypothetical explanations for the use of edge habitats by bats are:

Food. Insect availability is believed to be one of the major factors determining

the distribution of insectivorous bats (Racey & Swift 1985; De Jong & Ahlén 1991). Food might be a reason for bats to forage near hedgerows, treelines, and forest edges, since insect densities are generally higher here (but not always; Ekman & de Jong 1996) than in nearby open areas (Lewis & Stephenson 1966; Lewis 1969a/b, 1970; Lewis & Dibley 1970).

Shelter from wind. The influence of wind on commuting and foraging bats has been reported in several studies (Nyholm 1965; Voûte 1972; Racey & Swift 1985; Rieger et al. 1990). To minimize flight costs, it is profitable for a bat to avoid exposure to wind (Norberg & Rayner 1987; Norberg 1990).

But what happens when there is no wind, or when insect abundance in neighbouring open areas is relatively high and differences between the treeline and adjacent open area become small? According to Ekman & De Jong (1996), pipistrelle bats still preferred the edges of forests to the open areas, although insect abundance was higher in the latter. This suggests the involvement of one or more other factors limiting the use of space by these bats.

There are two alternative explanations. First, risk of predation may explain why many bats avoid open areas and stay close to vegetation, where they are less conspicuous than in open terrain. Indeed, mortality due to predation, mainly by owls, may be considerable (Speakman 1991), and predation pressure is often thought to affect bat behaviour (Rieger et al. 1990; De Jong 1994; Rydell et al. 1996). Predation risk is believed to be highest when light levels are high (Rydell et al. 1996), that is during dusk and dawn or at high latitudes, and where many bats can be expected to be present at relatively high densities, that is near roosts or on commuting routes (Fenton et al. 1994).

A second hypothesis, suggested by Limpens et al. (1989) and Limpens & Kapteyn (1991), states that bats use landscape elements as navigational landmarks, and, consequently, maintain acoustic contact with landscape elements. The limited echolocation range of bats would then constrain bats in the use of open areas.

In this study, I tested whether the occurrence of pipistrelle bats, *Pipistrellus pipistrellus* (Schreber, 1774), and serotines, *Eptesicus serotinus* (Schreber, 1774), near treelines can be explained by (1) food abundance and (2) protection from wind. The 'food hypothesis' predicts that the bats hunt where food is most abundant. The 'wind hypothesis' predicts that bats fly where wind reduction by the treeline is highest. The distribution of foraging pipistrelles and serotines in relation to treelines was compared to insect abundance and wind (speed and direction). Different situations, with and without wind, and with low and high insect abundance in the adjacent open areas, were compared.

Study sites and methods

STUDY SITES

One study area, referred to as site "meadow-NL", was in the south-western part of The Netherlands (51°27'N, 3°38'E), approximately 2 km east of Oost-Souburg (Walcheren, province of Zeeland). In this agricultural area, with approximately 60% fields and 40% intensively managed (grazed and hay) meadows, there is a network of treelines, mainly along roads. The study site was located near a double treeline

bordering a 3-m wide, paved road. Adjacent open areas on both sides were hay meadows with some low-density grazing where *Lolium perenne* was the dominating species. The average tree height was 9 m. Tree species at the study site were *Carpinus betulus* and *Fraxinus excelsior*. Underneath the trees there was a 3-4 m (mean 3.5 m) high bush layer with *Carpinus betulus*, *Fraxinus excelsior*, *Crataegus monogyna* and *Salix alba*. Permeability of the treeline was visually estimated to be 20% at the bush layer and 70% between the bush layer and the tree crowns, between 3.5 and 5 m above the ground.

Another study area was in the Mazury district in north-eastern Poland (53°87'N, 21°66'E), north of the Urwitałt Biological Station of the University of Warsaw. Approximately 50% of agricultural land in this area are crop fields (mainly cereals) and 50% extensively managed (grazed and hay) meadows, generally rich in herbs and insects. A few woodlots are present, and a network of, mostly double, treelines border many of the roads. Measurements took place near two treelines, the first bordered by an insect rich grassland with a variety of herbs (site 'meadow-PL'), and the second bordered by cereal crop fields (*Triticum aestivum* and *Avena sativa*; site 'field-PL'). Mean tree height was 11 m at site meadow-PL and 13 m at site field-PL, with bare trunk for the first few meters above the ground. The treeline at site meadow-PL was dominated by *Tilia* species, whereas *Acer pseudoplatanus* was the main species at site field-PL.

SAMPLING METHODS AND TECHNIQUES

The study was confined to the pipistrelle bat ("46 kHz phonic type", Jones & Van Parijs 1993) and the serotine. As defined in this paper, *commuting bats* travel between their roost and foraging sites, whereas *foraging bats* remain at a particular area for some time to feed on insects. The flight of commuting bats is more straight and flight speed is higher than in foraging bats (Jones & Rayner 1989; Britton et al. 1997). Commuting bats were surveyed at dusk until 1.5 h after sunset. Foraging bats were surveyed from 1.5 h after sunset to 1.5 h before sunrise.

From May to August 1995, foraging bats at site meadow-NL were sampled at fixed points along a line perpendicular to the treelines (1) at distances of 3, 6, 9, 12, 24, and 48 m on the leeward side, (2) between the treelines, and (3) at 3 m at the windward side. At sites meadow-PL and field-PL, sample points were on the leeward side only at distances of 3, 12, 24, and 48 m. To overcome time effects, point samples were taken in random sequence.

At each point, I counted bats, measured wind-speed and sampled the aerial insect fauna. At sites meadow-PL and field-PL, bat and insect samples were collected during calm nights only (wind-speed <0.2 m/s). Passes of pipistrelle bats and serotines were scored during five-minute periods, and the amount of time bats were detected was also recorded. USA mini-2 bat detectors (Ultra Sound Advice, London, UK) were used at site meadow-NL and Pettersson D-100 detectors (Pettersson Elektronik, Uppsala, Sweden) at the Polish sites, both with headphones. To restrict the detection to the direct surroundings of the sample point, the detection was concentrated by mounting a horn (QMC mini-2) or an aluminium device (Pettersson D-100). Detectors were pointed upwards at chest height.

Wind-speeds were measured with a sensitive cup-anemometer, placed on a tripod at a height of 1.80 m. The incidence angle of the wind was defined as the

angle between the wind direction and the treeline (parallel to treeline = 0° , perpendicular = 90°). Wind-speeds in open area were measured before, half-way and after each series of samples, at 50 m from the treelines on the windward side. The relative wind-speed per sample point was defined as the the local wind-speed divided by the wind-speed in open area on the windward site.

After each bat count, insects were sampled with a hand-net (diameter 0.45 m; Bioquip, Gardena, CA, USA). Samples were taken by standardized sweepnetting along a 30 m long transect parallel to the treeline. We took 100 sweeps while walking in one direction, and another 100 while returning to the starting point. Minimum and maximum height of each sweep were 2 and 3.5 m above the ground. Contents of sweepnets were placed in ethyl-acetate jars until the insects were dead, then transferred to labelled jars with alcohol (30%) for assessment of numbers and dry weight (biomass) per sample.

At site meadow-NL, commuting pipistrelle bats were counted visually and with bat detectors at a small gap (5 m) in the treelines. The end of the commuting period was defined by the absence of commuting bats for at least 10 minutes or by increased foraging activity (feeding buzzes, bats flying into the opposite direction). Just before and just after the commuting period, insects were sampled and wind-speed was measured both between the treelines and on the leeward side at 3 m from the treeline.

DATA ANALYSES

To test whether distribution maxima of pipistrelles were equal to maxima of insect density and minima of relative wind-speed, I calculated bootstrap confidence limits on the distances between the modi in each pair of distributions. For this, I applied the bias-corrected and accelerated (BCa), nonparametric bootstrap as described by Efron & Tibshirani (1993) with 1000 iterations.

Regression analyses and bootstrap analyses were done with GENSTAT (Genstat 5 Committee 1993, 1995). For remaining statistical tests I used STATISTIX (vs. 4.0; Analytical Software, St. Paul, MN).

Results

BAT OCCURRENCE

All of the three study sites were used as commuting corridors and foraging sites as well. The pipistrelle bat was the most abundant species. Serotines occurred at sites meadow-PL and field-PL only. At site meadow-NL, pipistrelles used the treeline as one of the main commuting corridors between their roosts in the nearby village of Oost-Souburg, approximately 2 km from the site, and foraging sites along the treelines and in a woodlot approximately 1.3 km from the site.

The nearest pipistrelle maternity roosts from sites meadow-PL and field-PL were at 0.8 and 0.7 km respectively. Serotine roosts were at 0.8 km from site meadow-PL and at 1-2 km (exact location not known) from site field-PL. Foraging sites of both species were along treelines and woodlot edges, and along the edges of lakes and ponds.

BAT OCCURRENCE IN RELATION TO INSECT ABUNDANCE AND WIND

Figure 3.1 shows the distance distributions of mean pipistrelle occurrence, insect density, and relative wind-speed at site meadow-NL at wind-speed >0.2 m/s ($n=32$). Since calm nights (wind-speed <0.2 m/s, $n=7$) at this study site were scarce and bat activity during these nights very low (lower than at wind-speeds >0.2 m/s; t-test,

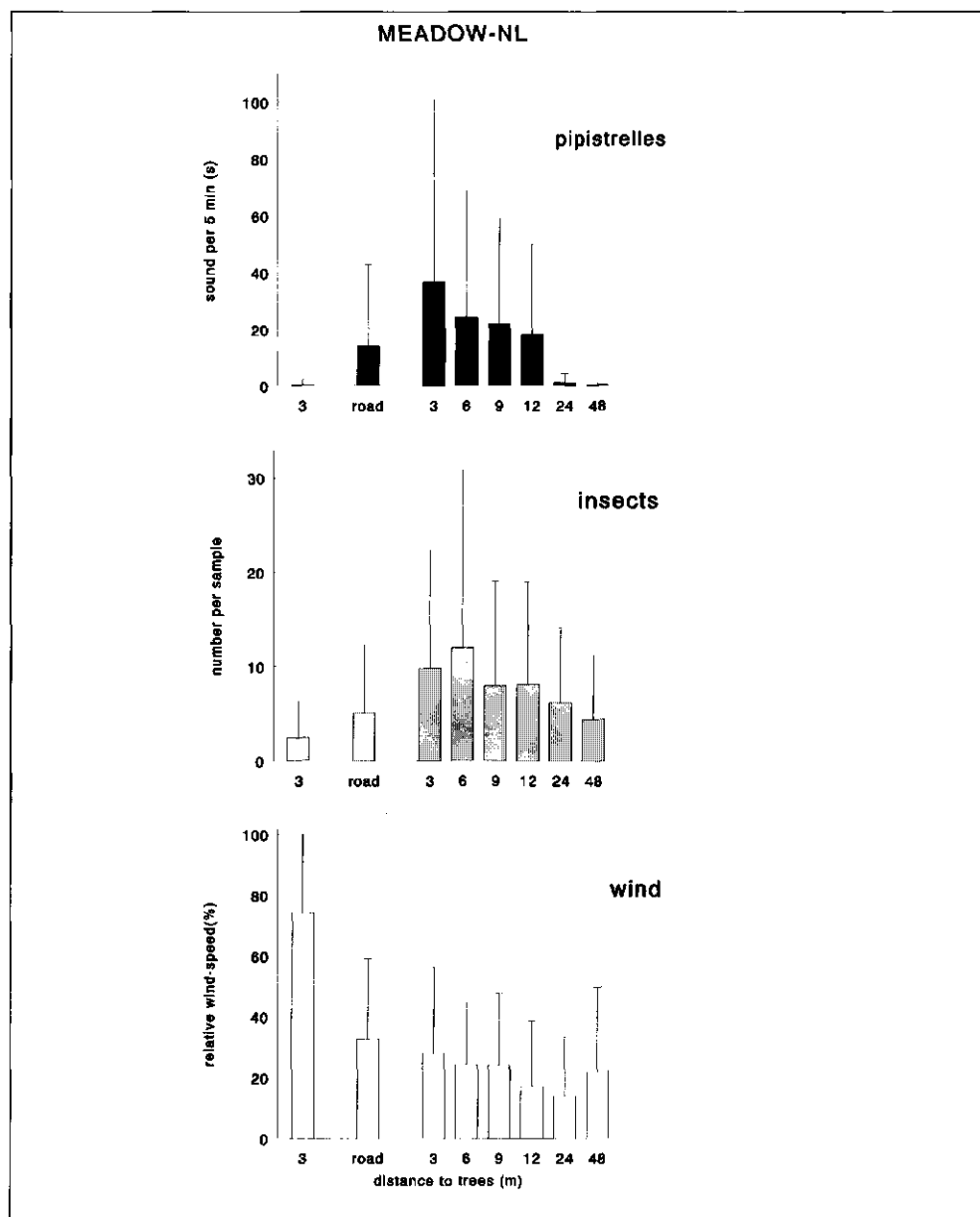


Figure 3.1. Distance distributions of pipistrelle occurrence, insect density and relative wind-speed ($n=32$, wind-speed >0.2 m/s) near a double treeline at site meadow-NL.

$P < 0.05$), data analyses at site meadow-NL were restricted to wind-speed > 0.2 m/s (see next section for analyses of data in absence of wind at Polish sites).

Figure 3.1 shows that pipistrelle occurrence on the leeward side was mainly confined to the range 3-12 m from the trees, and was significantly lower at 24 and 48 m (t-test, significant drop between 12 and 24 m, $P < 0.005$). Pipistrelle occurrence and insect numbers had maximum values at 3 and 6 m respectively; minimum relative wind-speed was at 24 m from the treeline. Bootstrap analyses show that, at the 5% significance level, maximum pipistrelle occurrence was significantly closer to the treeline than maximum insect abundance, and that both these maxima were significantly closer to the trees than the minimum relative wind-speed.

The relation between the distance distributions of pipistrelle occurrence, insect density (numbers per sample) and relative wind-speed (Fig. 3.1) on the leeward side was tested by multiple regression analyses. Insect density and relative wind-speed were not significant in the analyses when tested separately (Table 3.1). The factor 'distance to treeline' significantly reduced the variation in pipistrelle occurrence. This indicates that, within 50 m from the trees, the vertical distribution of pipistrelles was not associated to the distributions of insect abundance or relative wind-speed, but to one or more other, distance-related, factors.

Both the velocity and the direction of the incident wind affected the distance distribution of pipistrelles at site meadow-NL (Fig. 3.2a,b). Wind-speeds at site meadow-NL ranged from 0 to 5.6 m/s (mean 1.6 m/s, s.d.=1.3, $n=39$). There was no difference in mean pipistrelle occurrence between low (0.2-1.5 m/s) and high wind-speeds (> 1.5 m/s). At low and high wind-speeds, occurrence on the leeward side was lower at 24 and 48 m compared to 3-12 m from the trees (t-tests, significant drop between 12 and 24 m, $P < 0.005$). Mean occurrence on the leeward side at angles of incidence of 45° - 90° ($n=22$) was higher than at smaller angles ($n=10$; t-test, $P < 0.005$).

Linear regression showed that bat occurrence on the leeward side increasingly concentrated near the treeline with both increasing wind-speed and increasing incidence angle. The slope of the regression line of the distance distribution (with the total number of bats per series as a weighting variable) was positively related to wind-speed (mean per series; coeff.=0.439, s.e.=0.185, $R^2=13.2\%$, $P < 0.05$) and incidence angle (coeff.=0.036, s.e.=0.013, $R^2=17.8\%$, $P < 0.01$).

Table 3.1.

Linear regression analyses of insect abundance (numbers and biomass per sample), relative wind-speed and distance to trees on pipistrelle occurrence (recorded sound per 5 minutes) at site meadow-NL. Data were collected at wind-speeds > 0.2 m/s.

MEADOW-NL	REGRESSION COEFFICIENT	STANDARD ERROR	R^2	P
insect numbers (A1)	-0.214	0.228	-	> 0.05
insect biomass (A2)	64.083	381.930	-	> 0.05
relative wind-speed (B)	0.088	0.118	-	> 0.05
distance to trees (C)	-0.756	0.185	0.08	0.0001
A1+A2+B+C	-0.719*	0.184*	0.08	0.0001*
* last parameter only				

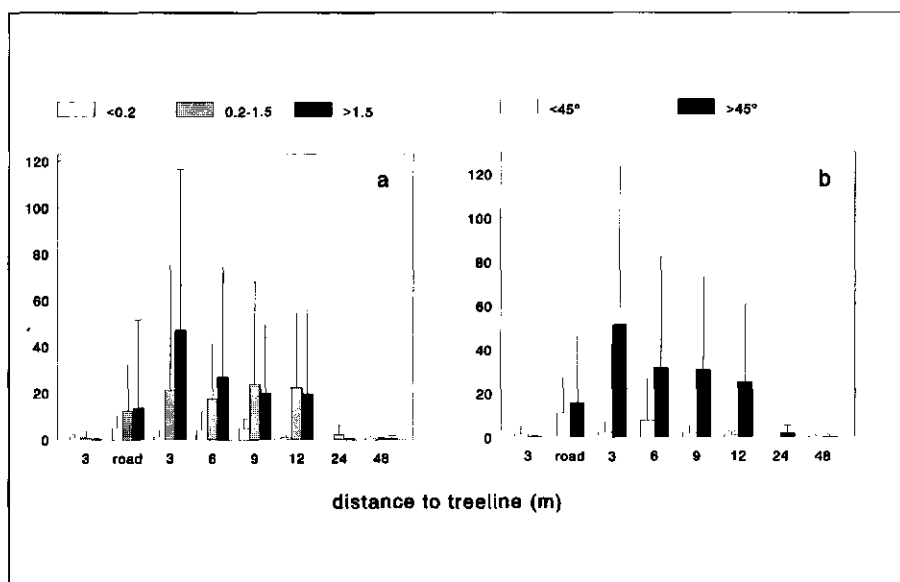


Figure 3.2.

Pipistrelle distance distributions near a double treeline at site meadow-NL (a) at different wind-speeds: <0.2 m/s ($n=7$), 0.2-1.5 m/s ($n=16$) and >1.5 m/s ($n=16$), and (b) at different incidence angles: <45° ($n=10$), >45° ($n=22$).

Pipistrelle occurrence at 3 m from the trees on the leeward side was on average higher than on the windward side (Fig. 3.1; t-test: $P<0.005$, $n=32$). However, at wind-speeds <1.5 m/s and at incidence angles <45°, differences were not significant whereas at wind-speeds >1.5 m/s (t-test, $P<0.05$) and incidence angles >45° ($P<0.005$) occurrence on the windward side was much lower (Fig. 3.2).

BAT OCCURRENCE IN RELATION TO INSECT ABUNDANCE IN ABSENCE OF WIND

Mean insect abundance at site meadow-PL exceeded that of site field-PL (Fig. 3.3; t-test, $P<0.05$ (numbers) and $P<0.005$ (biomass)). Mean insect density and biomass on the leeward side at site field-PL equalled those of site meadow-NL (t-tests, $P>0.05$). At all three sites, nematoceran Diptera made up approximately 90% of insect numbers.

Figure 3.4 shows pipistrelle, serotine and insect distance distributions at sites meadow-PL and field-PL. Absolute differences in bat occurrence between both sites were assumed to be related to the distance to the respective roosts and were not taken into account. At both sites, pipistrelle occurrence at 24 and 48 m was relatively high compared to site meadow-NL (see Fig. 3.1).

At site meadow-PL, pipistrelle occurrence was significantly related to insect numbers (Table 3.2; linear regression). At site field-PL, there was no relation to insect parameters. At both sites, the parameter 'distance to treeline' significantly decreased the variance in pipistrelle occurrence.

Serotines showed different distribution patterns at sites meadow-PL and

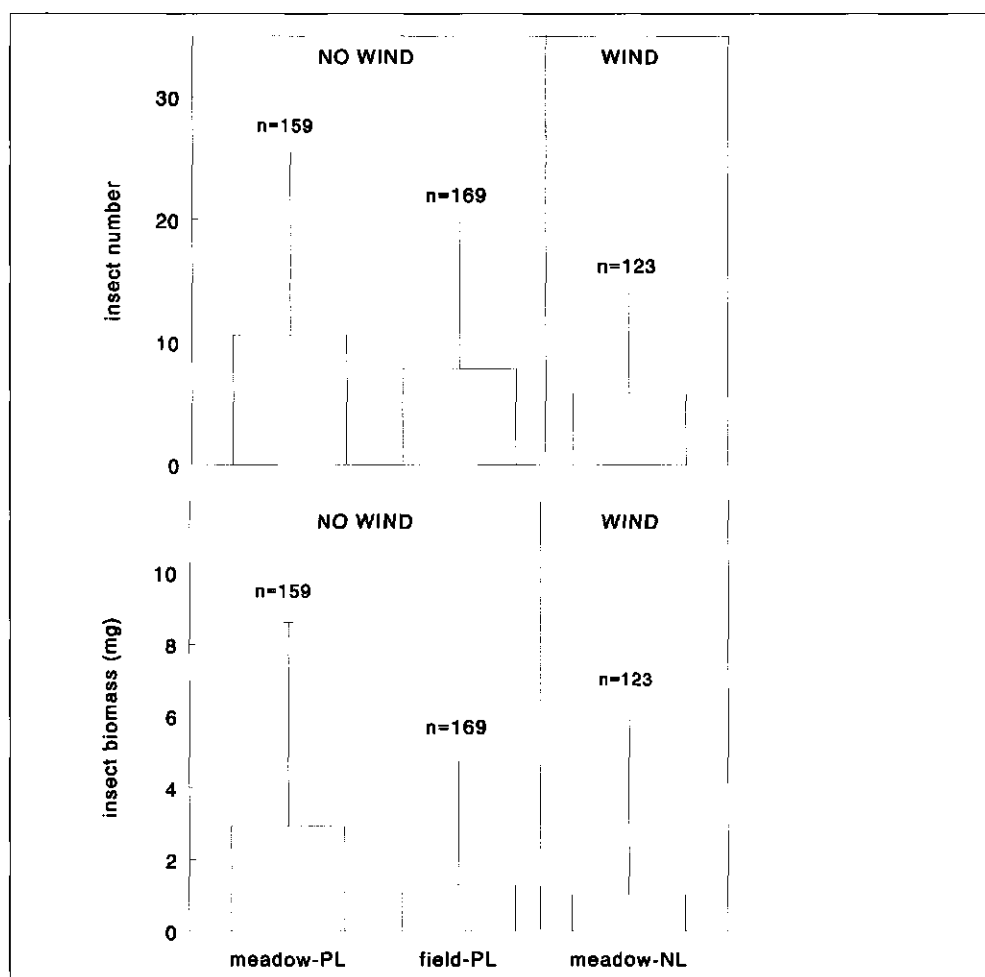


Figure 3.3.

Insect abundance (mean numbers and biomass per sample) at the three study sites.

Values \pm s.d. are averaged over distances 3, 12, 24, and 48 m from the treelines.

field-PL (Fig. 3.4). As with pipistrelles, serotine occurrence was related to insect numbers at site meadow-PL only (Table 3.3). In contrast to pipistrelles, there was no relation between serotine occurrence and 'distance to treeline'.

COMMUTING BATS

The majority of commuting bats at site meadow-NL passed between the treelines, flying in a straight line about halfway the trees at a height of 2.5-3.5 m above the road. This was just below the top of the 3.5-4 m high layer of bushes. As demonstrated by wind-speed measurements at heights of 3 and 4.5 m, there was approximately three times more wind at 4.5 m. However, at a height of 1.8 m, the average wind-speed was only 60% compared to the one at 3 m.

The number of passing bats per evening ranged from 5 to 54 (mean 23.9,

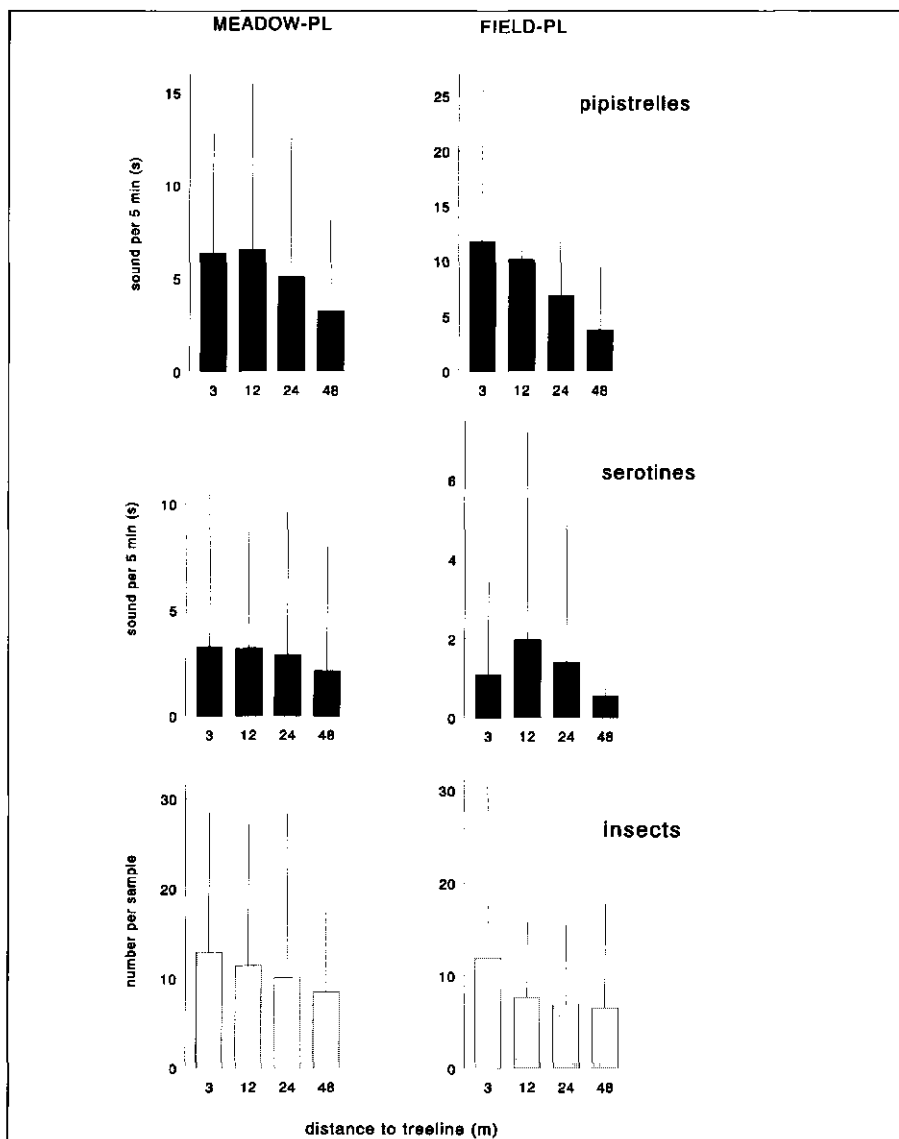


Figure 3.4.

Distance distributions of pipistrelle bat occurrence, insect density and insect biomass during calm nights near a double treeline at site meadow-PL ($n=44$) and site field-PL ($n=51$). Vertical bars represent standard deviations.

s.d.=12.2, $n=39$). An average of 81% of the bats passed over the road between the tree lanes, 2% on the windward side and 17% on the leeward side. Logit regression showed that the proportion of bats commuting along the leeward side increased with wind-speed (coeff.=0.898, s.e.=0.084, $P<0.0001$) as well as with incidence angle of the wind (coeff.=0.0281, s.e.=0.004, $P<0.0001$) at the tree lane (Fig. 3.5).

Table 3.4 shows the number of commuting pipistrelles, insect abundance and wind-speed between the treelines and on the leeward side during twelve evenings.

The large proportion of pipistrelles commuting between the treelines (84%) as compared to the leeward side during these twelve evenings, was not explained by either wind-speed or insect abundance. While bats flew more often between the treelines than on the leeward side (sign test, $n=12$, $P<0.01$), wind-speed was lower ($P=0.05$) and insect abundance was more often higher ($P<0.05$) on the leeward side than between the treelines.

Table 3.2

Linear regression analyses of insect abundance (numbers and biomass per sample) and distance to trees on pipistrelle occurrence (recorded sound per 5 minutes) at sites meadow-PL and field-PL. The parameter 'relative wind-speed' is not included as data were collected during calm weather (wind-speed <0.2 m/s).

MEADOW-PL	REGRESSION COEFFICIENT	STANDARD ERROR	R ²	P
insect numbers (A1)	0.119	0.037	0.06	<0.005
insect biomass (A2)	69.26	599.900	-	>0.05
distance to trees (C)	-0.077	0.033	0.03	<0.05
A1+A2+C	-0.067*	0.033*	0.09	$<0.05^*$
FIELD-PL	REGRESSION COEFFICIENT	STANDARD ERROR	R ²	P
insect numbers (A1)	0.053	0.061	-	>0.05
insect biomass (A2)	-220.578	210.070	-	>0.05
distance to trees (C)	-0.177	0.041	0.10	<0.0001
A1+A2+C	-0.180*	0.0414*	0.12	$<0.0001^*$
* last parameter only				

Table 3.3.

Linear regression analyses of insect abundance (numbers and biomass per sample) and distance to trees on serotine occurrence (recorded sound per 5 minutes) at sites meadow-PL and field-PL. The parameter 'relative wind-speed' is not included as data were collected during calm weather (wind-speed <0.2 m/s).

MEADOW-PL	REGRESSION COEFFICIENT	STANDARD ERROR	R ²	P
insect numbers (A1)	0.133	0.043	0.08	<0.005
insect biomass (A2)	213.075	108.200	0.04	0.05
distance to trees (C)	-0.027	0.044	-	>0.05
A1+A2+C	-0.005*	0.042*	0.10	$>0.05^*$
FIELD-PL	REGRESSION COEFFICIENT	STANDARD ERROR	R ²	P
insect numbers (A1)	0.016	0.023	-	>0.05
insect biomass (A2)	7.017	92.131	-	>0.05
distance to trees (C)	-0.023	0.018	-	>0.05
A1+A2+C	-0.02189*	0.018*	-	$>0.05^*$
* last parameter only				

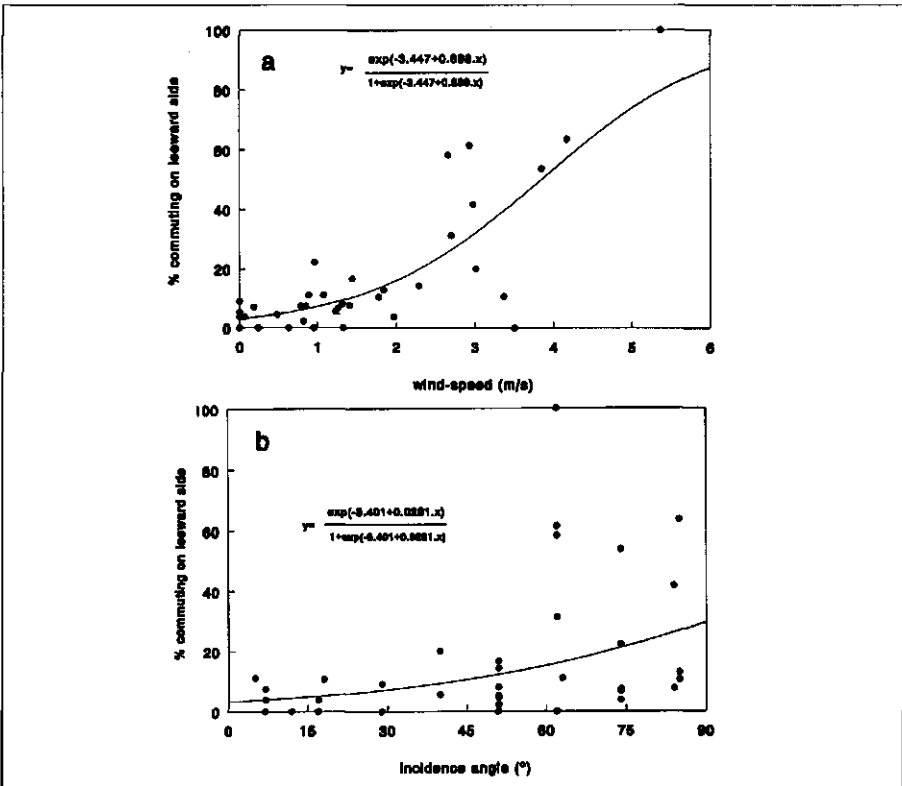


Figure 3.5.
The proportion of bats commuting along the leeward side at different wind-speeds (a) and incidence angles (b). Logit regression yield positive fits of both wind-speed ($P<0.0001$) and incidence angle ($P<0.0001$).

Table 3.4
Number of commuting pipistrelles, insect numbers (mean of samples just before and just after the migratory period) and wind-speed between the treelines and on the leeward side on twelve evenings at site meadow-NL; AOI = angle of incidence.

	PIPISTRELLES (n COMMUTING)		INSECTS (n PER SAMPLE)		WIND SPEED(m/s)		WIND AOI(°)
	ROAD	LEE	ROAD	LEE	ROAD	LEE	
June 27	6	0	81	153	0.06	0.001	51
July 3	5	2	50	5	0	0.915	0
July 4	5	5	9	51	0.73	0.89	6
July 6	25	5	14	27	1.07	0.62	85
July 10	14	2	21	51	0.89	0.63	74
July 12	24	1	46	57	0	0	-
July 17	16	1	16	16	1.08	1.03	85
July 18	4	4	2	25	1.49	1.25	85
July 20	7	0	149	64	0	0	-
July 24	17	1	19	160	0.33	0.27	40
July 25	5	5	25	83	1.23	1.12	62
July 27	18	1	12	16	0.62	0.32	51

Discussion

WIND SHELTER AND INSECT ABUNDANCE

The present study demonstrates that the distance distribution of pipistrelles near treelines is affected by both insect abundance and wind (speed and direction), and that the relative importance of these factors varies depending on the situation.

The hypotheses underlying this study predict that the occurrence of bats is maximal where insect abundance is maximal and relative wind-speed is minimal. Clearly, the distance distribution of pipistrelle bats was different from the wind shelter distribution (Fig. 3.1). The relative wind-speed at site meadow-NL showed a minimum at 24 m from the treeline, although the real minimum may have been anywhere between 12 and 48 m. This is about three times the height of the treeline, which agrees with wind shelter patterns around windbreaks found by others (e.g. Nägeli 1946; Lewis & Stephenson 1966; Lewis & Dibley 1970).

Since wind strongly affects the distribution of insects (e.g. Lewis 1970), a correlation between the distribution of insects and wind shelter is expected. This is, however, not the case in Figure 3.1 and can be explained by the fact that aerial insect distributions near treelines are the result of accumulation of insects which have passively been blown from the windward side to leeward, and from insects originating from the trees and from the grassland or field as well. The first category of insects is expected to follow the wind shelter pattern, while the second and third categories respectively will show distribution patterns which are more biased towards the treeline and which are more evenly spread across the open area (Lewis 1970). Thus, assuming that the aerial entomofauna has representatives of all three categories, maximum insect densities at site meadow-NL are expected to be found somewhat closer to the treeline than the wind shelter pattern would predict.

VERTICAL ELEMENTS AS ACOUSTICAL LANDMARKS

After correction for insect abundance and wind, a strong relationship of bat occurrence to the distance to the treelines was found. An explanation for the spatial relation of bats to treelines is that bats use treelines as acoustic landmarks and hence remain in contact with treelines by echolocation.

Insectivorous bats use echolocation to detect and approach prey and to avoid obstacles. Many members of the family Vespertilionidae seem to perform these tasks within several meters from the bat, although the function of background echoes as guideline signals may be possible (Neuweiler 1990; Kalko & Schnitzler 1993). Even so has it been suggested that bats use vertical elements as landmarks in their orientation and that echolocation range is a possible constraint on the use of open areas (Limpens et al. 1989; Limpens & Kapteyn 1991). Indications that bats maintain contact by echolocation with landscape elements come from a study on commuting pond bats, which gradually adapted their pulse durations and interpulse intervals to the distance to canal banks (Verboom et al. unpublished results).

Our data of pipistrelle occurrence in relation to vertical elements support the idea that the distribution near vertical elements is determined by echolocation range. If we assume that the duration of interpulse intervals determines the maximum distance over which bats can perceive objects while avoiding overlap between returning echoes and pulse emissions, it is possible to predict the distance

where the bat loses contact with an object. Since sound travels approximately 0.34 m in 1 ms, an average search phase interpulse interval of pipistrelle bats foraging near treelines of 80-98 ms (Ahlén 1990; Kalko & Schnitzler 1993; Vaughan et al. 1997; Verboom unpublished data) corresponds with 13.6-16.7 m. This agrees with the sudden drop in occurrence between 12 and 24 m from the treeline at site meadow-NL.

The predicted drop in pipistrelle occurrence was less obvious at the Polish sites (Fig. 3.4). This holds for the serotine as well. The serotine emits signals with an average search phase interpulse interval of 116-150 ms, although longer intervals are common (Ahlén 1981, 1990; Vaughan et al. 1997). These values would correspond with an expected drop in serotine occurrence at 20-25.5 m from the trees (or more when longer intervals are considered).

Bats are, however, frequently found commuting and foraging in open areas, well outside the range where they can perceive landscape elements by echolocation (Kalko & Schnitzler 1993; De Jong 1994; Verboom & Huitema 1997; Verboom et al. unpublished results). This was also the case at the Polish sites. Here, the occurrence levels of both species at 24 and 48 m was high as compared to site meadow-NL. This implies that constraints by echolocation are not very strict, or that vision plays a role. This raises the question whether there are benefits of staying in acoustic contact with landscape elements? Assuming that landmarks play a role in their spatial orientation, bats which are active outside the range where perception of landscape elements by echolocation is possible, may have to spend extra time in finding the way back to familiar landmarks. Staying within acoustic range would hence save time which can be allocated to other activities like foraging. When insect abundance increases, bats may be more inclined to leave contact with landmarks. Although the bat has to invest more time in orientation and navigation then, this may be outweighed by the benefits of more efficient foraging.

PREDATOR AVOIDANCE

The potential threat of predators may be another explanation for the occurrence of bats near treelines. When predation risk is increased where food is most abundant, more time may be allocated to predator avoidance (Milinski 1986). The impact of predation by avian predators on bat populations may be considerable, as suggested in a study in Britain where the annual mortality due to predation, mainly by owls, was estimated to be 11.1% (Speakman 1991). Hence, predator avoidance may be a major reason for bats to commute and forage in environments where they are less conspicuous and more likely to escape attacks, e.g. near treelines and forest edges (Rieger et al. 1990; De Jong 1994). Since owls and birds of prey hunt by vision, it is plausible that at decreasing light levels, predation risk becomes less significant. Moreover, commuting bats using regular flight routes are a more predictable prey source for predators than are hunting bats with activity patterns varying in time and space, and are therefore more vulnerable to predation (Fenton et al. 1994). In fact, behavioural changes at diminishing light levels have been observed in several species. For example, commuting lesser horse-shoe bats *Rhinolophus ferrumequinum* (Schreber, 1774) progressively increased their flight height as it became darker (H. Schofield personal communication). Other species have been observed to shift their hunting activities to more open environments as darkness

increased after dusk (*Pipistrellus pipistrellus* and *Myotis daubentonii*, Rydell et al. 1994), or in the course of summer as the nights became progressively darker (*Myotis mystacinus* and *M. daubentonii*, Nyholm 1965). A similar shift from a sheltered to a more exposed environment took place in this study, where the majority of pipistrelles commuted between the treelines, while most foraging activity was on the more exposed leeward side. Only high wind-speeds and incidence angles close to 90° supposedly forced the bats to commute along the leeward side.

FLIGHT HEIGHT OF COMMUTING BATS

Most commuting pipistrelles passed at a mean height of 2.5-3.5 m above the road between the treelines. Flying higher would be more costly, since the permeability of the vegetation between the bush layer and the tree crowns would increase from approximately 20% to 70%, and the bats would catch more wind. Flying even higher, between the tree crowns, would not allow for straight flight and would hence reduce flight speed.

But why not fly lower than 2.5 m? In spite of reduced wind-speeds bats attained a flight height just below the top of the bush layer. One explanation would be that bats keep a minimum distance when flying parallel to objects (vegetation, ground) to avoid pulse-echo overlap. The minimum distance is determined by the length of the emitted pulses. For a pipistrelle emitting pulses with an average duration of approximately 5.5 ms (wideband mode; Kalko & Schnitzler 1993), a minimum distance of $5.5 \times 0.17 \text{ m} = 0.94 \text{ m}$ from the ground and the vegetation on the sides would be required. According to Kalko & Schnitzler (1993) pulse-echo avoidance could explain why pipistrelles usually keep a distance of at least 2 m from large obstacles.

SIGNIFICANCE FOR BAT CONSERVATION

The conclusions of this study have implications for the conservation of bats and their habitats. Treelines are important to foraging bats since they support relative high insect abundance and provide shelter from wind. High insect abundance in adjacent open areas may promote the exploitation of open areas.

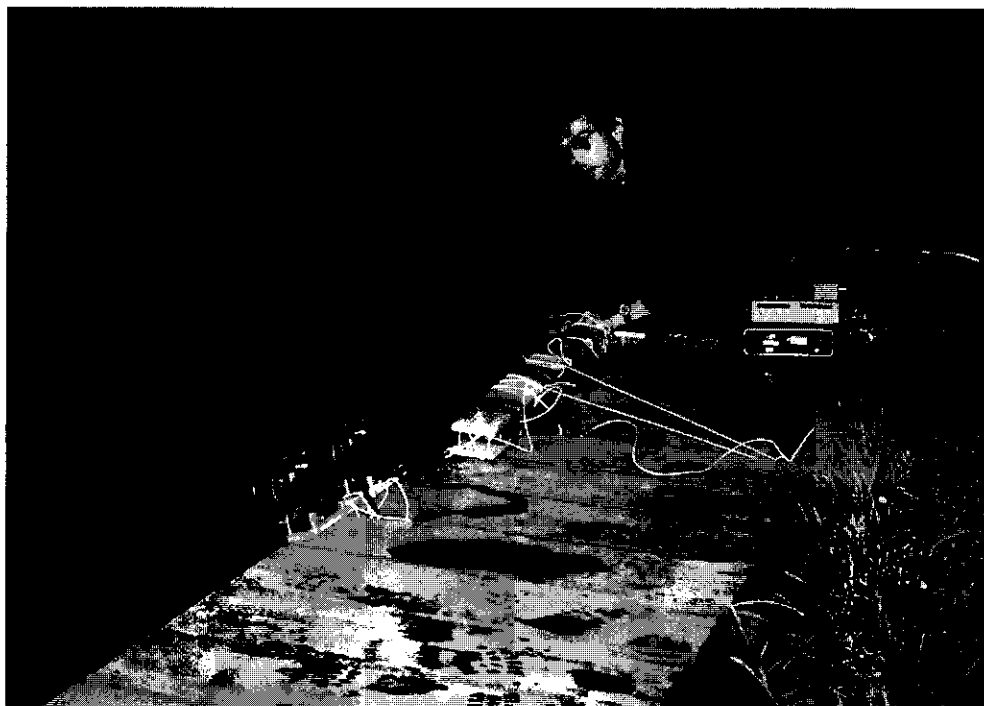
An essential function of tree corridors for commuting bats during dusk and dawn may be the protection from predators. This may be especially important in areas where bats have to travel long distances to reach good foraging sites, or at high latitudes where dusk and dawn periods are relatively long. A coherent network of tree corridors may hence help bats on their way to foraging grounds to exploit an area in an efficient way.

Furthermore, this study suggests an acoustical function of treelines for bats. Gaps in a network of linear vegetation corridors may thus become barriers and hinder bats in exploiting potentially good feeding areas.

4. Flight performance, echolocation and foraging behaviour in pond bats, *Myotis dasycneme* (Chiroptera: Vespertilionidae)

Summary

Flight performance and echolocation behaviour of the pond bat, *Myotis dasycneme* (Boie, 1825), were investigated over canals and a lake in The Netherlands. Multi-flash stereophotogrammetry, linked with synchronous recording of echolocation calls, was used to reconstruct the three-dimensional flight paths of bats and to correlate flight behaviour with changes in pulse emission during echolocation. Echolocation calls during commuting flight at the canal were sigmoidal in structure, with an initial steep frequency modulated (FM) sweep followed by a more shallow sweep, ending with a second, rapid FM sweep. Similar calls were produced during the search phase of foraging, though longer duration quasi-CF (constant-frequency) calls, with longer interpulse intervals and much reduced initial and final FM sweeps, were produced by bats hunting over a large lake. Overall, calls were



Preparing the multi-flash equipment on a canal bank (photo: Ben Verboom).

generally lower in frequency, with significantly longer pulse durations and interpulse intervals, compared with those of smaller trawling *Myotis* bats. Flight speeds were compared with predicted optima from aerodynamic models. Commuting bats exceeded predicted maximum range speed, which was considerably higher than that noted for other smaller species of trawling *Myotis*. Flight speed was significantly higher closer to the roost, at a narrower canal site. A negative correlation between wingbeat frequency and flight speed, and a facultative 1:1 link between pulse emission and wingbeat during search phase were established. During commuting, the bats flew at a height above that which would normally confer substantial power savings through ground effect. It is argued that, by flying at a lower height, bats would compromise commuting speed. Echolocation calls produced during attempted prey capture were remarkably similar in design to those produced by those other *Myotis* species that forage in a similar fashion. Prey was detected at 2 m, and reaction distance was 1.8 m. Evidence of a physiological limit on pulse duration and interpulse interval during prey capture is presented. Overlap of emitted pulse and received echo may degrade the performance of echolocation in many bats, and overlap is generally avoided in *M. dasycneme* except perhaps when the bat is very close to the prey item.

Introduction

The flight and echolocation behaviour of bats under field conditions (Fenton & Bell 1981; Jones & Rayner 1988, 1989, 1991; Acharya & Fenton 1992; Kalko & Schnitzler 1993; Schnitzler et al. 1994; Kalko 1994, 1995) has recently been studied to complement work in a controlled, artificial environment (Heblich 1986; Hartley et al. 1989; Thomas et al. 1990; Faure & Barclay 1994; Marimuthu et al. 1995). There is good reason for this, as echolocation and behaviour under relatively confined conditions may differ in comparison with natural situations (Griffin 1958; Sales & Pye 1974). Obtaining reliable information on the echolocation and foraging behaviour of free-living bats is technically difficult, however.

The few field studies on prey capture in insectivorous bats often use the technique of multi-flash photography, whereby multiple images of a single bat reveal information such as flight style and wingbeat frequency over a short time period (Schnitzler et al. 1987; Jones & Rayner 1988, 1991; Kalko & Schnitzler 1989a; Kalko & Braun 1991; Surlykke et al. 1993; Kalko 1994, 1995). Echolocation calls recorded simultaneously can be linked to specific images on the photographs, enabling correlations to be made between flight and echolocation. Stereophotogrammetry allows three-dimensional positional information of all objects within the photographic field of two cameras to be reconstructed mathematically (e.g. Wolf 1983; Spedding et al. 1984; Rayner & Aldridge 1985).

The behavioural ecology of the pond bat, *Myotis dasycneme* (Boie, 1825), has been little studied. Previous work has looked in detail at roost ecology (Voûte 1972), and more briefly at echolocation calls (Ahlén 1979, 1981, 1990; Kapteyn 1993) and flight speed (Baagøe 1987). A review of current knowledge for this species is given by Kapteyn (1995). The trawling mode of foraging of the pond bat is common to other members of the subgenus *Leuconoë* (Findley 1972). As well as taking insects

in flight by aerial hawking, the bats hunt over water, scooping insects from the surface with their feet and interfemoral membrane. Although previous studies have investigated the trawling bats *Myotis daubentonii* (Jones & Rayner 1988; Kalko & Schnitzler 1989a) and *Myotis adversus* (Jones & Rayner 1991), this is the first to detail the commuting and foraging flight of the pond bat, and to compare it with other trawling *Myotis* bats, with the aim of finding general conclusions about flight and echolocation in these bats.

Here we describe flight performance and echolocation calls of pond bats. We compare the flight and echolocation of bats flying along two canals of different widths, and over a larger lake. We compare commuting behaviour with foraging behaviour. Specific questions asked in this investigation include whether flight speed corresponds with that predicted from aerodynamic models, and whether pulse emission and wingbeat are coupled when bats are searching for prey (the search phase of echolocation) (Kalko 1994). A 1:1 link is expected in bats which hunt by aerial hawking or which emit intense, short duration echolocation calls (Jones 1994), because the coupling of calling with flapping allows the production of high-energy sound pulses at no extra cost to the energetic cost of flight (Speakman & Racey 1991). Avoidance of pulse-echo overlap seems to occur throughout interception buzzes (echolocation call sequences during attempted prey capture, where pulse repetition rate increases dramatically) in bats that emit short duration echolocation calls (Kalko & Schnitzler 1989a, 1993). Overlap is avoided because it is presumably difficult to process a faint echo while emitting an intense call, especially since muscular (Henson 1965) and neurophysiological (Suga & Schlegel 1972) mechanisms reduce hearing sensitivity during calling. We determine whether pulse-echo overlap occurs during prey capture in the pond bat.

Breeding colonies of pond bats are only known in western Europe from The Netherlands and Denmark (Daan 1980; Stebbings & Griffith 1986), and there may be as few as 3000 bats of this species remaining in western Europe (Stebbing & Griffith 1986). The pond bat is highlighted for special protection of its roosts and feeding habitats in the European Communities' Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (1992). We therefore describe the diet of pond bats in order to understand further the conservation needs of this endangered (Stebbing 1988) species, and so that echolocation behaviour can be related to diet.

Methods

STUDY SITES

The study took place during July 1994 in Friesland, The Netherlands. Pond bats (*Myotis dasycneme*) from a large nursery colony (400+ individuals) in the village of Tjerkwerd used canals as flyways to commute to feeding areas on the canal and over the nearby IJsselmeer, a large man-made freshwater lake under 10 km distant. Data were collected from two canals of different width: one site (N - narrow) was 13 m wide and near the roost at Tjerkwerd, and the other (W - wide) was 4 km away at Exmorra and was 25 m wide. Commuting flight was defined as constant straight, level flight by individuals along the length of the canal soon after emergence. All commuting bats were flying in the same direction after dusk towards the IJsselmeer

from the roost. Data were collected from both sites, W and N. We assumed that no bat commuting in the same direction was being photographed twice on the same night. Data were used only from nights with negligible wind speed. Foraging flight was distinct from commuting flight in that individuals would persist around a particular area, flying low over the surface of the water, occasionally dipping or climbing to catch insects. Only sequences containing attempted prey captures were photographed. Data were collected from site W only, as regular foraging activity at site N was very rare. To increase the feeding activity around an area, small moths and caddis flies were collected from nearby light sources and placed in the water several metres in front of the cameras. Most feeding activity, however, was recorded from bats feeding on naturally occurring prey items. Additional recordings of echolocation calls were made at a c. 100 m x 50 m lake near Deventer during July 1991.

RECORDING AND ANALYSIS OF ECHOLOCATION CALLS

Heterodyned echolocation signals, used for identification purposes, were monitored in the field by using an Ultra Sound Advice S-25 bat detector. Microphone sensitivity was -57 ± 13 dB (ref. IV/ μ bar) between 20-120 kHz. Signals were also time-expanded by a factor of 10 by linking the detector to an Ultra Sound Advice S-350 time-expansion unit, and recording on to Sony Metal-XR cassette tape with a Sony WM-D6C Professional Walkman. This recording technique was also used in conjunction with stereo multi-flash photography as described below. In most cases the microphone was within approximately 2 m of the height of the bats, to minimise frequency-dependent atmospheric attenuation due to height (Jensen & Miller 1995). Vocal commentary was recorded on to an Olympus Pearlcor S906 portable Dictaphone.

Echolocation recordings were analysed on a Kay DSP Sonagraph model 5500 with 512 point fast Fourier transform size giving 400 Hz frequency resolution. Throughout the text we define interpulse interval as the duration between the onset of a pulse and the onset of a subsequent pulse. The sound of the camera shutters opening and closing, combined with the synchronisation pulses mixed from the flash sequencer, enabled echolocation calls to be accurately correlated with individual photographic images.

Echolocation calls from commuting bats were recorded on one night at each site, to minimise the chances of recording the same bat more than once. The fundamental harmonics of calls are described, as these generally contained considerably more energy than did the higher harmonics, and are at least susceptible to the effects of atmospheric attenuation. During foraging, frequency and time measurements were made for pulses at the start and end of each distinct phase in echolocation (e.g. approach phase, buzz 1 of terminal phase - as defined by Griffin (1958) and Kalko & Schnitzler (1989a)), enabling changes in pulse design to be observed both over the course of and between each phase.

MULTI-FLASH PHOTOGRAPHY

Stereo multi-flash photography was used to reconstruct the 3-dimensional flight path of bats, using field techniques similar to those described by Jones & Rayner (1988, 1991), and following calculations first described by Wolf (1983). For most

pictures, four Metz CL-3 flashguns were used in conjunction with a custom-built flash sequencer to achieve flash repetition rates of 30 Hz for a duration of one second. Flashgun intensity was modulated with Mecametz Mecablitz 45-46 sensors, and power was supplied by two Quantum Battery-2 power packs. For synchronous echolocation recording, time-expanded echolocation calls were recorded with the apparatus described above, but with output from the S-25 bat detector being first passed through a custom-built mixer, where echolocation calls were mixed with 1 ms synchronisation pulses of maximum frequency 6.25 kHz produced by the flash sequencer. These synchronisation pulses were produced in conjunction with each flashgun triggering event. The resulting mixed signal was then passed through the S-350 unit, and the time-expanded signal recorded on to cassette. In later sonographic analysis, the synchronisation pulses could be clearly seen alongside the echolocation recordings. Time delay between the bat and the microphone was corrected for assuming the speed of sound was 340 m/s, and hence echolocation calls could be linked directly to specific bat images on each stereo picture.

Two Nikon 35 mm SLR cameras (FE and FM2 models), fitted with 55 mm f3.5 Micro-Nikkor lenses, were mounted 0.2485 m apart on a machine-cut metal plate, and aligned in accordance with Jones & Rayner (1988). Both cameras were loaded with Kodak TMAX ASA 400 or ASA 3200 black and white film. A dual shutter-release cable was used to fire the two cameras synchronously. Once triggered, an electronic pulse from the FE camera was used to activate the flash sequencer. The shutters remained open for approximately one second while the sequencer fired the flashguns.

RECONSTRUCTION OF THE FLIGHT PATHS

Photographs of commuting flight were digitised from prints, by using a Summagraphics Summasketch III bitpad (resolution 1016 dots/inch) connected to an IBM-compatible computer running custom-written software (J.M.V. Rayner). Reconstruction of 3-dimensional positions was performed by using custom-written algorithms used in stereo-photogrammetry studies by Jones & Rayner (1988, 1991) and Waters & Jones (1995).

Images of foraging bats were digitised using a more time-consuming, but more accurate, method. This was necessary given the greater distance from the cameras to the bats, and because of the more variable flight paths of the bats when foraging. Errors introduced by the investigator during positional tracings and bitpad digitising were eliminated by digitising single negatives directly using a Nikon Coolscan negative scanner (resolution 2214 dots/inch) connected to an IBM-compatible computer. Corresponding left and right bitmap files were then imported into Aldus Photostyler SE, an image processing package, where the positional co-ordinates of the nose of each bat image from left and right pictures could be directly compared and recorded. These values could then be converted into a form identical to output from the bitpad digitising program, enabling 3-dimensional reconstruction to proceed. Although the scanner digitised an image 7 times smaller in linear dimensions than that used on the bitpad, the scanner was more accurate overall because of the elimination of tracing errors.

WINGBEAT ANALYSIS AND LINKAGE WITH ECHOLOCATION PULSE EMISSION

Wingbeat frequencies were measured from photographs during both commuting and foraging, at a flash frequency of 30 Hz. Additionally, at site N, a flash frequency of 60 Hz (from 8 Metz CL-3 flashguns, powered by 2 further Quantum batteries), and synchronised echolocation recordings, enabled pulse emission to be linked to the wingbeat cycle with greater accuracy than pictures taken with a lower flash rate.

DIETARY STUDIES

Droppings collected from the roost during 1993 were analysed. Fifty pellets were chosen at random, and percentage volume of prey taxa was determined following methods described by Jones (1990, 1995).

Data are given as means \pm standard deviation, unless otherwise stated.

Results

ECHOLOCATION CALLS

Myotis dasycneme echolocation calls are usually frequency modulated (FM), similar to those produced by the trawling insectivorous bats *Myotis daubentonii* (Jones & Rayner 1988), *Myotis adversus* (Thompson & Fenton 1982; Jones & Rayner 1991) and *Myotis ricketti* (A.R.C. Britton, unpublished data). All calls were classified as search, approach or terminal phase echolocation signals (Griffin et al. 1960), with terminal phase calls subdivided into buzz 1 and buzz 2 (Kalko & Schnitzler 1989a). Calls recorded from commuting bats were similar to FM signals emitted during search phase foraging. Example calls are illustrated in Figure 4.1, with descriptions in Table 4.1. For search phase calls on canals, there was a significant negative correlation between bandwidth and duration of the calls (bandwidth (kHz) = $76.1 - 3.66$ duration (ms), $r^2=38.4$, $F_{5,3}=27.73$, $P<0.001$). Mean pulse repetition rate during commuting sequences was 10.8 Hz ($n=24$ sequences of 500 ms duration). Some search phase calls contained a quasi-F portion (with a very shallow frequency modulation, but not pure CF (Kalko & Schnitzler 1993)), with an initial FM sweep (Fig. 4.1b). Very occasional calls were recorded which were almost entirely CF (Figs. 4.1c,d), producing a 'slapping' or 'plopping' noise on a heterodyne detector (Ahlén 1990).

The longer duration and narrower bandwidth calls that were recorded at the lake in Deventer were analysed separately because the diameter of the water body there was considerably larger than that at the canals. Search phase calls from the lake were sigmoidal in structure (Fig. 4.1e) with much lower maximum frequencies, shallower frequency modulation and longer durations than those recorded at the canal. Interpulse interval was longer at the lake site, resulting in a lower pulse repetition rate of 8.4 Hz ($n=20$ sequences of 500 ms) (Table 4.1). Other unusual call types recorded are shown in Figure 4.1f,g. In addition, low-intensity interference nulls were often visible in calls of lower intensity (relative to the microphone). These artefacts are characteristic of echolocating bats flying close to a reflecting surface, and are not a feature of the calls themselves (Jones & Rayner 1988; Kalko & Schnitzler 1989b).

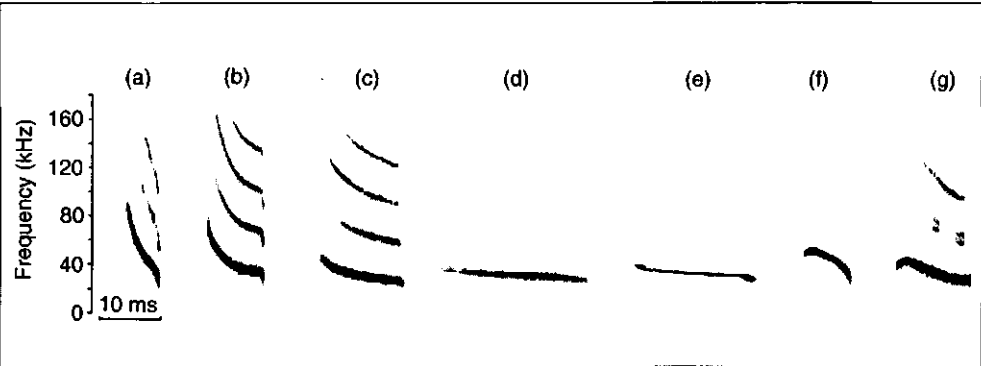


Figure 4.1.
Echolocation calls of *Myotis dasycneme*. (a-c) were recorded during commuting flight on canals, while (d) is an almost CF call recorded only occasionally in the same situation; (e) is a long duration search phase call recorded over a lake, and (f) and (g) are probably used in communication.

Table 4.1.
Description of echolocation calls of *Myotis dasycneme*. Calls described are from commuting flight at the canal (C), search phase over the lake at Deventer (L), first call of the approach phase (AF), last call of the approach phase (AL), first call of buzz 1 (B1F), last call of buzz 1 (B1L), first call of buzz 2 (B2F), last call of buzz 2 (B2L), and the first call produced after the 'post-buzz pause' (R). Frequency and time measurements are maximum frequency (FMAX), frequency of most energy (FMAXE), minimum frequency (FMIN), duration (PD) and interpulse interval (IPI - defined as the time from the start of one pulse to the start of the next). All data refer to fundamental harmonics, and are shown as means \pm standard deviations, with sample sizes in brackets at the top of the table.

CALL TYPE	C(54)	L(31)	AF (2)	AL(9)	B1F(9)	B1L(9)	B2F(9)	B2L(9)	R(8)
FMAX (kHz)	74.3 \pm 6.8	47.6 \pm 5.3	70.8 \pm 10.3	69.7 \pm 9.8	66.5 \pm 9.4	50.1 \pm 7.7	37.7 \pm 3.8	21.5 \pm 6.3	62.1 \pm 6.0
FMAXE (kHz)	35.9 \pm 2.8	34.7 \pm 1.3	36.3 \pm 4.3	33.1 \pm 1.5	39.2 \pm 12.2	30.4 \pm 5.4	25.1 \pm 1.5	20.1 \pm 6.5	36.6 \pm 2.0
FMIN (kHz)	28.1 \pm 2.2	28.1 \pm 1.5	25.2 \pm 2.0	23.4 \pm 0.7	23.2 \pm 0.5	21.2 \pm 1.5	17.7 \pm 2.4	15.6 \pm 4.4	28.6 \pm 2.6
PD (ms)	8.2 \pm 1.1	18.0 \pm 2.5	4.3 \pm 1.2	3.4 \pm 0.3	2.6 \pm 0.3	1.6 \pm 0.2	1.4 \pm 0.2	0.6 \pm 0.1	5.9 \pm 1.7
IPI (ms)	95.2 \pm 22.2	117.3 \pm 19.1	34.0 \pm 12.2	12.7 \pm 7.5	8.6 \pm 1.4	4.5 \pm 0.4	4.3 \pm 0.3	4.7 \pm 0.2	83.1 \pm 26.2

The frequency structure of approach phase calls was similar to that of search phase calls, but their durations were shorter (Table 4.1). The onset of the approach phase was characterised by a marked decrease in both pulse duration and interpulse interval, which continued over the course of the phase. The mean duration of two entire approach phases was 384.4 \pm 48.6 ms and they contained 15 \pm 15.7 pulses.

Before the onset of the terminal phase buzz, a longer interpulse interval, named here as 'pre-buzz pause', was always present, with a mean duration of 28.7 ± 15.8 ms.

The bandwidth of the fundamental harmonic began to reduce at the onset of the feeding buzz, attributable primarily to a slight reduction in the maximum frequency at the start of the call. Secondary harmonics were strongly defined, maintaining the overall bandwidth of the pulses. Over the course of buzz 1, the maximum frequency fell further, but with minimal reduction in terminal frequency. Pulse duration also reduced further over the course of buzz 1, with a continuing dramatic reduction in interpulse interval. Mean pulse repetition rate during buzz 1 was 113.1 ± 9.2 Hz. The onset of buzz 2 was characterised by a significant drop in both the maximum and minimum frequencies of the fundamental. At this point, the second harmonic became relatively more intense, maintaining bandwidth of the pulses. Towards the end of buzz 2, bandwidth of the fundamental sweep was very low (5.9 ± 2.0 kHz), with the second harmonic sometimes more intense than the fundamental. Pulse durations were reduced yet further towards the final pulses of the buzz, reaching a minimum of 0.6 ms (Table 4.1). Interpulse interval, however, appeared to reach a minimum during buzz 2. Pulse repetition rate reached a mean of 195.8 ± 3.1 Hz, the highest recorded rate being 201.2 Hz. Over the course of both buzz 1 and buzz 2, there was a noticeable decrease in pulse intensity. The mean duration of the feeding buzz, 205.0 ± 36.8 ms, was composed of 111.9 ± 33.7 ms for buzz 1 and 93.1 ± 15.1 ms for buzz 2, and the mean number of pulses in buzzes 1 and 2 was 12.4 ± 3.0 and 18.2 ± 2.9 respectively. A pause after the final pulse of buzz 2, named here as the 'post-buzz pause', lasted 76.8 ± 41.1 ms. The first pulse occurring after this pause ($n=8$) was similar in structure to a search phase call, but with a significantly ($t_{60}=5.28$, $P<0.001$) lower maximum frequency (62.1 ± 6.0 kHz) at the start of the fundamental (Table 4.1). Mean duration of this pulse was also significantly ($t_{60}=3.57$, $P<0.01$) shorter than search phase pulse duration. The frequency of maximum energy over the course of the entire feeding sequence appeared to decrease towards the end of buzz 2, except at the very start of buzz 1.

FLIGHT HEIGHT AND SPEED DURING COMMUTING

Mean flight height at site N was 0.26 ± 0.02 m ($n=17$). No comparable data were available at site W. Two models are frequently used for the calculation of V_{mp} (minimum power speed) and V_{mr} (maximum range speed): Pennycuik (1975, 1989) and Rayner (1986; Norberg & Rayner 1987). Each model relies upon different assumptions, and predicts different optimal speeds (Jones 1993a). Ground effect can have a significant effect on predicted optimal flight speeds, as it causes a reduction in induced flight power (Norberg 1991). The magnitude of ground effect is very dependent upon flight height above the surface (Aldridge 1988; Rayner 1991a). The interference coefficient (σ) can be calculated to show the magnitude of ground effect as the percentage reduction in induced power. As height above the surface decreases, the value of σ increases. For mean commuting flight height $\sigma = 0.09$, which is a 9% reduction in induced power (Norberg 1991). Morphological data used in the calculation of optimal flight speeds were taken from Schober & Grimmberger (1989) and Norberg & Rayner (1987), as data from the Tjerkwerd colony were not available.

Mean flight speed of commuting bats at site N was 9.13 ± 0.41 m/s ($n=21$),

significantly higher (Mann-Whitney $W=656$, $P<0.001$) than that at site W, which was 7.35 ± 1.26 m/s ($n=23$). A unimodal distribution of flight speeds was apparent at both sites. Predicted values for V_{mp} and V_{mr} from the Rayner model are 4.1 and 5.8 m/s, respectively. The Pennycuik model (mechanical power only) predicts V_{mp} at 5.1 m/s and V_{mr} at 8.3 m/s. Optimal speeds should be reduced in both models when ground effect is included (see Norberg 1991). The bats flew considerably faster than V_{mr} close to the roost, reducing speed to V_{mr} or slightly above it at the more distant site, depending on which model was used to calculate optimal speeds.

WINGBEAT AND PULSE EMISSION DURING COMMUTING

Mean wingbeat frequency was 9.43 ± 1.24 Hz ($n=15$) at site N, and 10.19 ± 0.76 Hz ($n=23$) at site W. The difference in frequencies between the two field sites was significant (Mann-Whitney $W=219$, $P<0.03$). Wingbeat frequency was hence close to the repetition rate of echolocation pulses (see above). A highly significant negative relationship occurred between wingbeat frequency and flight speed ($r^2=18.3\%$, $F_{35}=7.84$, $P=0.008$; Fig. 4.2).

The mean number of pulses per wingbeat during commuting flight was 1.00 ± 0.25 ($n=9$ sequences photographed at 60 Hz flash frequency). Figure 4.3 illustrates the link between wingbeat and pulse emission for a typical commuting sequence. The image of each bat image below the sonagram shows the position of the wings at progressive stages during the wingbeat cycle. The relative position of each image in the echolocation sequence indicates the period of the wingbeat cycle in which echolocation pulses were emitted. As wingbeat is cyclic, different wing positions were assigned one of eight angular positions between 0° and 360° . A Rayleigh test

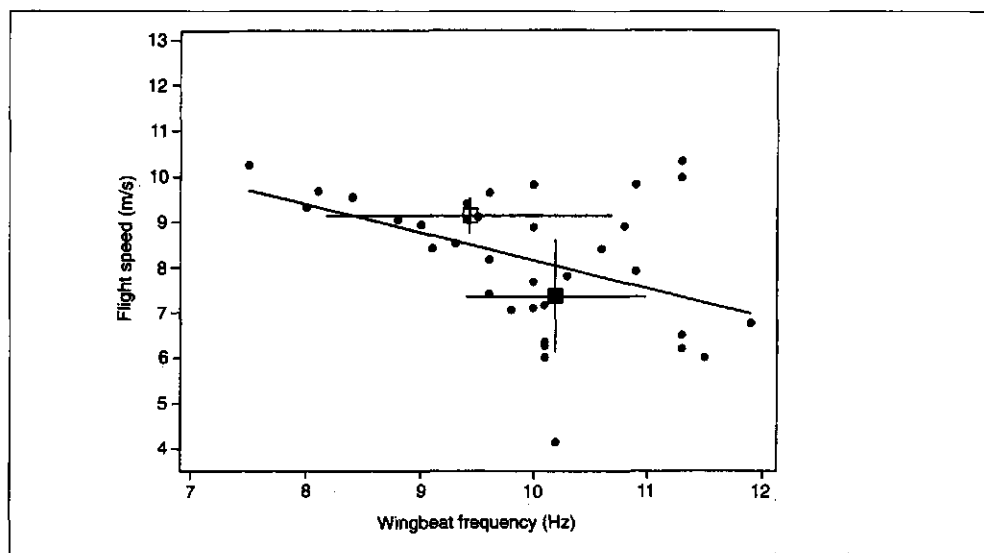


Figure 4.2.

The relationship between wingbeat frequency and flight speed during commuting. The regression equation is $y=14.2-0.6x$ ($F_{35}=7.84$, $r^2=18.3\%$, $P<0.01$). The open square shows mean (\pm standard deviations) values for site N, closed square is site W.

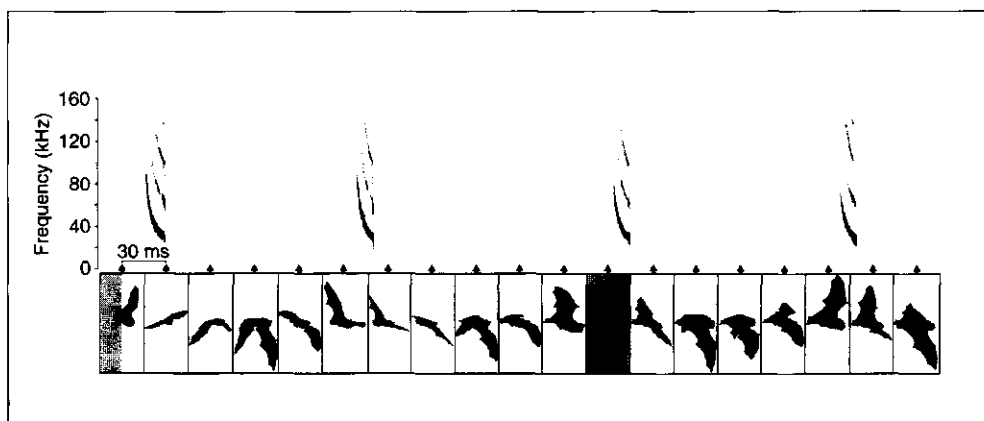


Figure 4.3.

Synchronization between wingbeat and echolocation pulse emission during commuting flight. The arrow above each bat image represents the bat's position relative to the echolocation sequence. Pulses are produced just after the top of the upstroke. The blank image represents a flashgun misfire.

shows that pulse distributions in the cycle differ significantly from random ($z_{28}=3.90$, $P<0.02$). Insufficient data were available to determine accurately the mean position of pulse emission during the wingbeat cycle, but most pulses appeared to be emitted at or just after the end of the upstroke.

FLIGHT BEHAVIOUR WHILE FORAGING

Mean flight speed during foraging flight was 3.21 ± 1.92 m/s ($n=9$). This was significantly lower than commuting flight speed ($t_{30}=18.54$, $P<0.001$), and includes sequences of prey capture. Foraging flight speed is not therefore comparable with measurements of speed while searching for prey in other trawling bats which excluded prey capture sequences (Jones & Rayner 1988, 1991). As the bat approached a potential prey item, there was a reduction in flight speed and a change in wingbeat style (Fig. 4.4). As the bat descended to the water surface, wingbeat amplitude was reduced, and wingbeat frequency dropped. Before reaching the prey, the bat entered a short glide, or a wingbeat of very low amplitude. Just after entering the glide, the bat lowered its feet and interfemoral membrane ('tail-down' stage, after Kalko & Schnitzler 1989a). Mean distance before prey at 'tail down' was 0.21 ± 0.15 m ($n=9$). Usually, as soon as the water surface was struck, the bat brought feet and head together ('head-down' stage). Mean distance after prey at 'head-down' was 0.16 ± 0.08 m. The bat then repositioned its head and feet and resumed normal flight 1.05 ± 0.77 m ($n=3$) after prey capture. There was a significant correlation between the duration of the 'head-down' stage and the duration of the post-buzz pause ($r=0.86$, $P<0.05$, $n=6$). Wingbeat style during the 'head-down' stage was much shallower than in standard, commuting flight. However, once the 'head-down' stage was over, wingbeat amplitude increased as the bat gained height. In addition to trawling behaviour, high catches were observed frequently, whereby a bat flew upwards at a steep angle in order to intercept an insect. These manoeuvres were never photographed owing to their unpredictable timing.

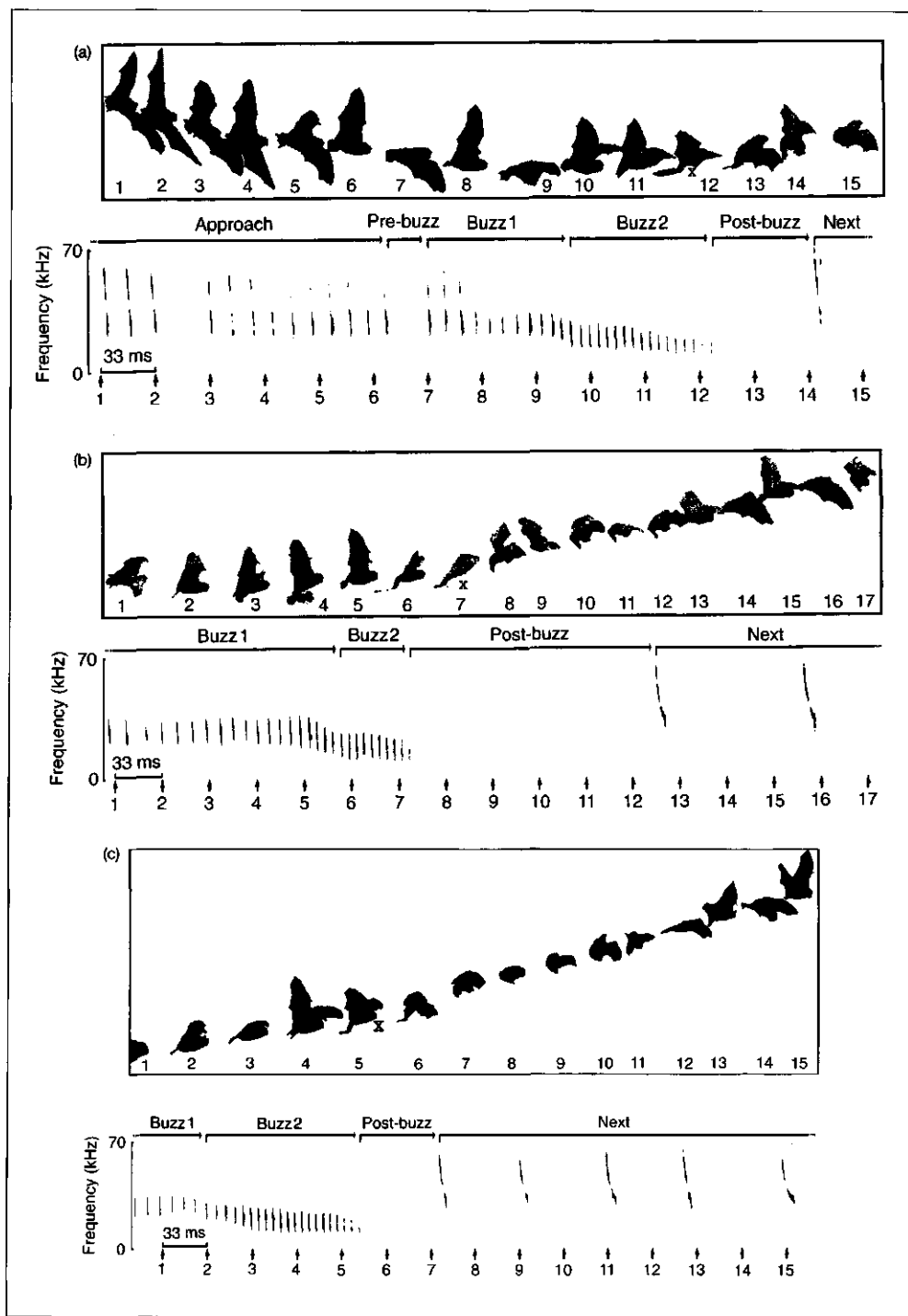


Figure 4.4.

Synchronous multi-flash sequences (30 Hz) and sonograms of echolocation calls for three attempted prey captures. Numbered bat images correspond to numbered flash synchronization pulses on sonograms. The phase of the echolocation sequence is indicated above each sonogram. Prey position is marked with a cross.

ECHOLOCATION AND BEHAVIOUR DURING PREY CAPTURE

Prey capture was linked to echolocation behaviour for nine prey capture sequences, three of which are illustrated in Figure 4.4. Two sequences contained echolocation calls emitted before the approach phase. The last search phase call before the approach phase is the assumed detection distance (Kalko & Schnitzler 1989a) and was emitted 2.03 ± 0.09 m from the prey. The approach phase began at 1.82 ± 0.10 m before prey capture, giving a measure of reaction distance (Kalko & Schnitzler 1989a). Pulse-echo overlap may be avoided during prey capture (Fig. 4.5). Calculations take into account the duration of pulses emitted by the bat, the distance from the bat to the reflecting target, and the change in flight speed of the bat during

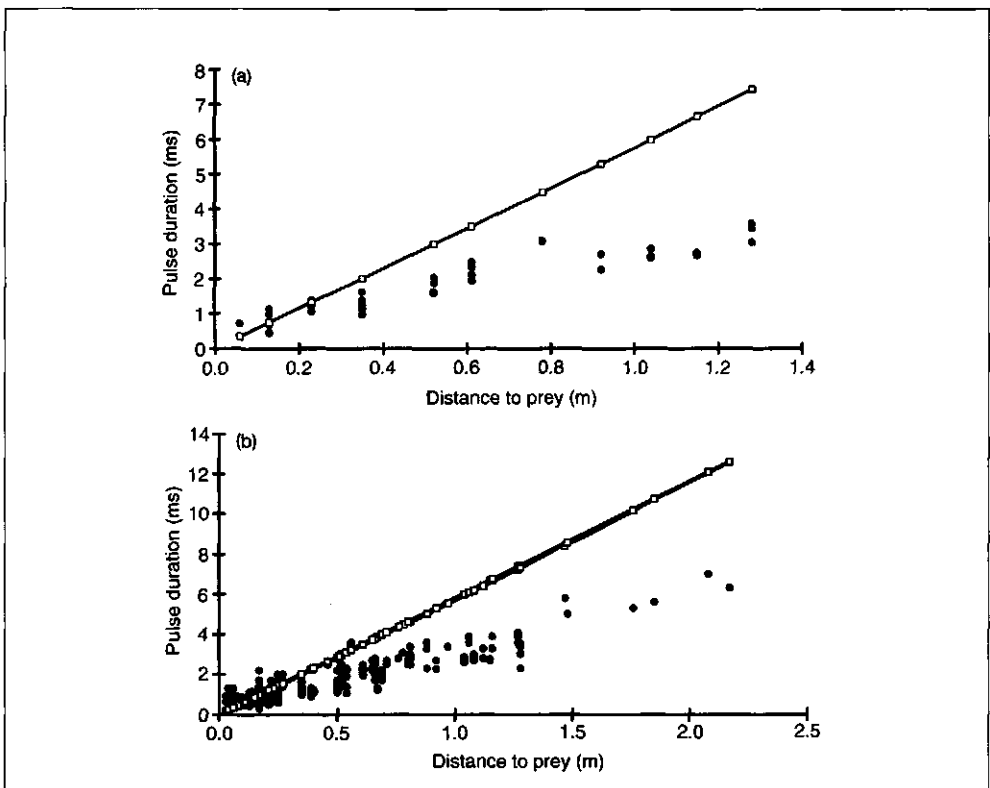


Figure 4.5.

Scatterplots of pulse duration (solid circles) as a bat approaches a prey item for (a) one feeding buzz and (b) all feeding buzzes. Connected open squares represent the maximum possible pulse duration, given the bat's flight speed and distance to the prey, before overlap with returning echo would occur. Overlap would occur if the solid circles fall above this line. Points that are grouped along the x-axis occurred between two sequential images of the foraging bat.

its approach towards the target. It is assumed the target is stationary. Two sequences showed no pulse-echo overlap. The mean distance from the prey at which there is overlap between the emission of a single pulse and the reception of that same pulse's echo ($n=7$) was 0.21 ± 0.06 m.

DIET

Pond bats ate mainly small dipterans (68% of diet by volume; Fig. 4.6). Almost all dipteran remains identified were the antennae and wings of chironomid midges. About 11% of the diet by volume consisted of beetles, 8% was chironomid pupae, 1.5% caddis flies, and one lacewing was found.

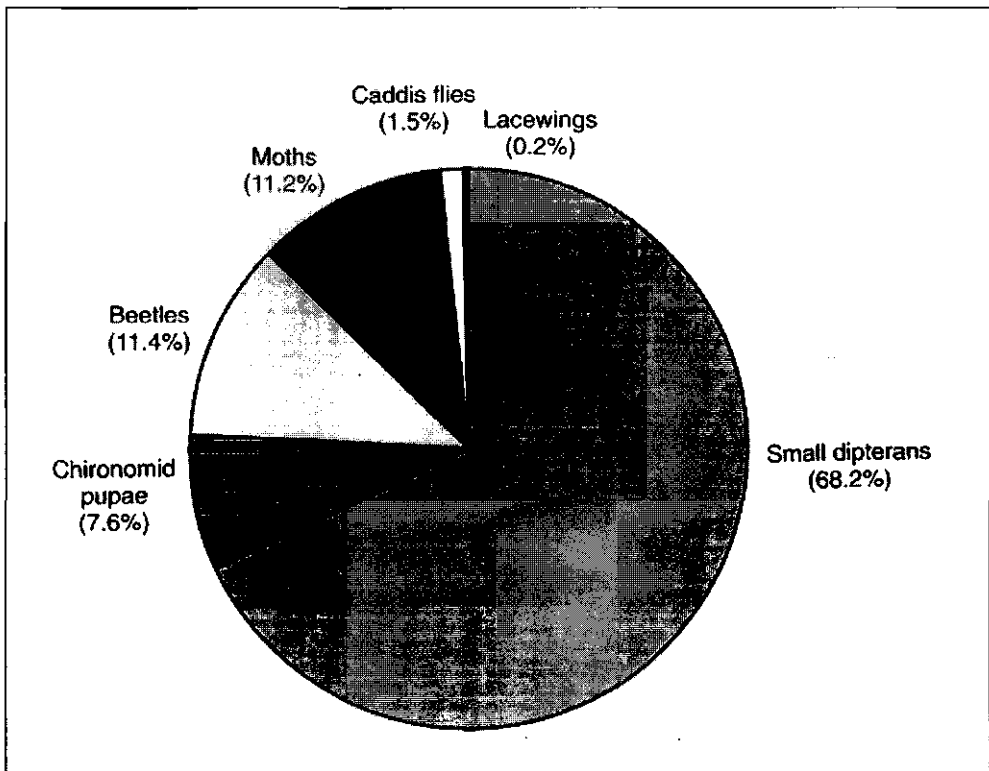


Figure 4.6.

Diet of *Myotis dasycneme* as determined by volumetric analysis of faeces.

Discussion

ECHOLOCATION CALLS

Bandwidth of the search phase calls for *M. dasycneme* was comparable to that of *M. daubentonii* during commuting flight (Jones & Rayner 1988), although both maximum and minimum frequencies were slightly lower in the pond bat - more similar to values measured of *Myotis adversus* (Jones & Rayner 1991). Frequency of maximum energy was 10 kHz lower than in the other two species. These frequency differences are probably due to the larger size of *M. dasycneme*: Barclay & Brigham (1991) showed a negative correlation between body mass and frequency of maximum intensity in bats. The interpulse interval and pulse duration of *M. dasycneme* (c. 17 g (Schober & Grimmberger 1989)) were also, as predicted, of longer duration than in *M. daubentonii* (c. 7.5 g) and *M. adversus* (c. 9.4 g) (see Jones 1994 and Waters et al. 1995, for scaling of interpulse interval and pulse duration). The negative relation between bandwidth and pulse duration is expected because bats shorten their pulses and increase bandwidth when flying in clutter (Zingg 1988).

Kalko & Schnitzler (1989a) and Jones & Rayner (1988, 1991) noted that in both *M. daubentonii* and *M. adversus* the frequency sweeps of most search phase calls were sigmoidal in shape. A sigmoidal structure is also apparent in most search phase calls of *M. dasycneme*, even in the more CF calls. A sigmoidal call structure may have a combination of different functions, making the signals Doppler tolerant (Hartley et al. 1989) while still containing target information (Simmons & Stein 1980). Most of the longer, quasi-CF calls also contained a very rapid frequency modulated sweep at the end of the pulse. This has also been noted in the calls of *M. daubentonii* (Jones & Rayner 1988) and *M. adversus* (Jones & Rayner 1991; Thompson & Fenton 1982). The latter authors noted that this low frequency component resembles a 'honk' used by some bats in social communication, but Jones & Rayner (1991) proposed that the sweeps occur too regularly for this and are more likely to be involved in height detection by trawling bats.

Most of the long duration, quasi-CF calls were recorded over the lake at Deventer. The bats here were foraging over a much larger area than on the canals, distant from the banks. Why these calls were rarely emitted by bats on the canals is not clear. Minimum detection distances (Kalko & Schnitzler 1993) correspond to about 139 cm for 8 ms calls typical of those emitted over canals, 306 cm for the 18 ms pulses recorded at the lake. Long duration, quasi-CF calls may be adapted to detecting glints from insect prey (Schnitzler 1987), and the calls recorded at the lake are clearly adapted for long-range echolocation, of objects over 3 m away. Alternatively, the bat may focus energy into a narrow bandwidth of the call, rather than spreading over a wider range of frequencies. Interpulse intervals at the lake were longer than those on the canal. Assuming that echo processing occurs before emission of the next pulse (Roverud & Grinnell 1985), then the effective maximum detection distance at the lake would be further (about 16.9 m for lake, 14.8 m for canal). Bats at the lake were able to switch to more FM calls rapidly before commencing feeding buzzes.

The unusual calls recorded as Figure 4.1 (fg) were rarely recorded. Similar calls have been recorded in *M. daubentonii* (A.R.C. Britton, unpublished data) prior to a collision with another bat, and therefore may be a warning or distress call. This

could not be confirmed here.

Comparisons with other *Myotis* bats that forage by trawling reveal a degree of similarity in both pulse design and the structure of the feeding buzz, which is not surprising given their phenetic relationship (Findlay 1972). *Myotis dasycneme*, *Myotis daubentonii* (Jones & Rayner 1988; Kalko & Schnitzler 1989a) and *Myotis adversus* (Jones & Rayner 1991) mostly produce relatively short, frequency modulated calls during search, approach and terminal phase echolocation. Therefore, all of these species presumably receive similar information about their environment, and high-bandwidth, frequency modulated calls are well suited to detecting objects on the water surface (Jones & Rayner 1988). Other trawling microchiropteran species, such as *Noctilio leporinus* (Suthers 1965) and *Noctilio albiventris* (Brown et al. 1983) also show a convergence towards rapid, linear-FM pulses during prey capture, even though these bats use a combination of FM-CF and CF pulses during search phase.

The 'pre-buzz pause' is relatively short in duration and may serve as an extended inspiratory phase just prior to the emission of the group of terminal phase pulses. Here, there is no correlation between duration of the pause and duration of, or number of, pulses during the interception buzz, despite the mean pause duration being approximately 13-14% of the whole terminal phase duration in both this dataset and data from *M. daubentonii* (A.R.C. Britton, unpublished data). There is some evidence to support a relationship between duration of the 'pre-buzz pause' and components of the terminal phase duration in *M. daubentonii* (A.R.C. Britton, unpublished data). Given the small sample for *M. dasycneme*, however, no similar conclusions can be drawn.

Buzz 1 of the terminal phase shows common trends in *M. dasycneme*, *M. daubentonii* and *M. adversus*. There is a general decrease in both the maximum and minimum frequencies of the fundamental harmonic, although Kalko & Schnitzler (1989a) note a slight increase in the minimum frequency for *M. daubentonii*. However, both *M. adversus* and *M. dasycneme* produce pulses of longer duration than *M. daubentonii* during this phase (Jones & Rayner 1988, 1991). The characteristic decrease in both pulse duration and interpulse interval continues as the bat approaches prey in all species. This serves to prevent pulse echo overlap when the bat is close to the prey (Kalko & Schnitzler 1989a). In *M. dasycneme*, the second harmonic appears to increase in intensity relative to the primary harmonic, explaining the high variability in the frequency of maximum energy (Table 4.1). As pulse intensity decreases so the relative intensity of the second harmonic appears to decrease, up to the end of buzz 1.

Buzz 2 is the period immediately before the bat attempts to catch the prey item. Maximum and minimum frequencies continue to fall, and reach their lowest values by the end of the buzz. The interpulse interval is very similar for *M. dasycneme*, *M. daubentonii* and *M. adversus* and remains virtually constant throughout buzz 2, which implies that a physiological limit to calling rate has been reached. The drop in both maximum and minimum frequencies between the final pulse of buzz 1 and the first of buzz 2 has been noted before in *M. daubentonii* (Jones & Rayner 1988; Kalko & Schnitzler 1989a), and also in other vespertilionid species such as *Pipistrellus kuhli* (Schnitzler et al. 1987) and *M. siligorensis* (Surlykke et al. 1993). Previous studies (Griffin et al. 1960) suggested the frequency drop at such

high repetition rates is an inevitable by-product of limitations in muscle physiology. However, Surlykke et al. (1993) provide evidence of its adaptive value to increase the bandwidth of the final echolocation pulses produced before prey capture, and they note that other species can maintain similarly high repetition rates without this drop in frequency. Wilkinson (1995) suggested that the drop in frequency at the end of the interception buzz allows a greater transmission range for the calls, which could signal to conspecifics that feeding is occurring.

The first pulse emitted after the 'post-buzz pause' appears to be similar to the pulses produced during search phase, although the maximum frequency is significantly lower, as is the duration. It is possible that at least the first call after a feeding buzz is affected by the events preceding it. If the bat is then carrying prey in its mouth, its echolocation ability will be temporarily impaired to some degree. This may affect the frequency, duration, intensity or number of echolocation calls produced while chewing. Preliminary data from *M. daubentonii* (A.R.C. Britton, unpublished data) suggest that echolocation calls emitted immediately after prey capture are different from normal search phase signals.

FLIGHT HEIGHT AND SPEED DURING COMMUTING

Sexual dimorphism exists in other trawling *Myotis* bats (Jones & Rayner 1991; Jones & Kokurewicz 1994). Morphological measurements used in aerodynamic models of optimal flight speeds were taken from literature. Most bats photographed in this study were probably lactating females from a nursery roost, but data on the masses of lactating females alone were not available. Hence, there are probably some slight inaccuracies in our calculations of optimal flight speeds.

V_{mp} , minimum power speed, is the theoretical speed at which the bat should fly in order to minimise power expenditure. V_{mr} , maximum range speed, is the speed at which a bat would achieve maximum flight range for a given amount of energy. While searching for insects, bats are predicted to fly somewhere between these two speeds (R.Å. Norberg in U.M. Norberg 1981; Jones & Rayner 1991) to maximise feeding efficiency. For commuting flight, in order for a bat to reach its destination in the shortest time while maximising overall energy gain, the bat should fly faster than V_{mr} (R.Å. Norberg 1981). Commuting flight speed at site N exceeded V_{mr} for both models, while flight speed at site W exceeded V_{mr} for the Rayner model, but was slightly less than V_{mr} for the Pennycuick model. Flight speeds above V_{mr} when commuting were noted by Jones & Rayner (1989) for *Pipistrellus pipistrellus*. *Leptonycteris curasoae* commuted at speeds below V_{mr} (using the Pennycuick model), however (Sahley et al. 1993). Although flights at speeds greater than V_{mr} involve increased energy expenditure, the bat reaches a foraging site more rapidly, and can begin feeding earlier. Because insect density declines rapidly after dusk (Racey & Swift 1985), any energy lost in commuting can be quickly recovered by feeding on the insects available at the destination. Arriving at a feeding site later may involve missing the dusk peak of insects, and the net energetic return of foraging gains minus energy costs while commuting may be lower than if the bat flew to the feeding site faster. Such decisions may not be applicable to *L. curasoae*, because nectar abundance may not decline rapidly after dusk. Red *Lasiurus borealis* and hoary *L. cinereus* bats both exceeded maximum range speeds even when foraging (Salcedo et al. 1995).

As the bats emerged from the roost and began commuting along the canal (site N), they flew significantly faster than bats from the same colony recorded commuting through the more distant site W. Why did flight speed decrease further from the roost? Perhaps, bats flying above V_{mr} are not able to maintain such speeds for extended periods. Maybe predation risk is greater closer to the roost, hence selecting for faster flight there. A further possibility is related to the bats' perception of linear landscape elements associated with canal width. To maintain contact with the canal banks, a bat would require an emitted pulse to be reflected back to itself before emission of the next pulse. If this were not the case, then information from this preceding echo would probably not be processed (Roverud & Grinnell 1985). Therefore, to avoid this problem, the bat could increase its interpulse interval, achieved through a decrease in wingbeat frequency and hence an increase in flight speed at a wider canal. The higher flight speed at the narrow canal is in fact opposite to that predicted by the above theory.

Mean commuting flight height at site N was such that flight power savings from ground effect would have been fairly low - certainly less of a saving than during foraging flight. The values of the interference coefficient (σ) for foraging flight in *M. adversus* and *M. daubentonii* were 0.30 and 0.25 respectively (Jones & Rayner 1991). Aldridge (1988) calculated a maximum σ value of 0.36 for *M. lucifugus* in a flight tunnel. Therefore, induced flight power savings for the above three species were around three to four times that saved during commuting flight in *M. dasycneme*. This illustrates that the main advantages of ground effect for trawling bats are usually associated with foraging flight (Rayner 1991a). Ground effect associated with the lower flight height during attempted prey capture has been noted to be significant (Jones & Rayner 1991; Rayner 1991a). Miller & Degn (1981) noted that *M. daubentonii* spends most of its time flying no more than 0.5 m from the surface of the water, whereas Baagøe (1987) noted that *M. dasycneme* generally flies and forages at slightly higher average heights than *M. daubentonii*.

LINKS BETWEEN WINGBEAT AND PULSE EMISSION

A negative relationship between flight speed and wingbeat frequency occurs in *M. dasycneme*, which is to be expected from aerodynamic theory (Rayner 1993), and indeed wingbeat frequency decreases at increasing flight speeds in laboratory studies (Schnitzler 1971; Heblich 1986). This study reports the first demonstration of the relationship between flight speed and wingbeat frequency under natural conditions. This is confirmed by the significant difference in wingbeat frequency between the two canal sites, which is reflecting the faster flight close to the roost.

Previous studies on bats (Suthers et al. 1972) have shown a facultative link between wingbeat frequency and respiration, in similar ways to those of birds. Echolocation pulses are produced in conjunction with expiration (Lancaster et al. 1995). Intense pulses can be very costly to produce at rest (Speakman et al. 1989). During flight, however, the bat must produce a regular series of pulses, for without them it will not receive sufficient information to navigate successfully (Thomas et al. 1990). Echolocation costs may be minimal for a flying bat (Speakman & Racey 1991) because bats take advantage of the link between wingbeat and respiration and produce echolocation pulses during the regular expiratory phase associated with each wingbeat (Suthers et al. 1972; Rayner 1991b). Echolocation calls are usually

produced at the top of the upstroke (Suthers et al. 1972), and this appeared to be the case in *M. dasycneme*. A 1:1 link is expected between calling and flapping for most bats (including trawling species) during the search phase (Jones 1994), deviations being due to specialised echolocation strategies, such as gleaning bats that produce low-intensity calls. Bats may occasionally produce more than one echolocation call per pulse during search flight, and may miss pulses out (Kalko 1994) or make very short glides (Thomas et al. 1990), although no gliding flight was noted here during commuting flight. This implies a greater flexibility, which is important during terminal phase echolocation, as the 1:1 link must break down when pulse repetition rate approaches 200 Hz.

PREY CAPTURE BEHAVIOUR

The significantly lower overall flight speed during capture attempts in *Myotis dasycneme* is probably partly the consequence of a lower predicted optimum flight speed during foraging compared with commuting (Jones & Rayner 1991). Moreover, lower trawling speeds are a prerequisite to successful prey capture, and extension of the wings and interfemoral membrane during the feeding sequence necessarily demand or facilitate a decrease in flight speed. Changes in wingbeat amplitude as the bat approaches the water surface would be necessary to prevent hitting the water on the downstroke and this may also enforce deceleration. Given the link between pulse emission and wingbeat frequency, and the assistance given to vocalisation by the action of beating the wings (Lancaster et al. 1995), this decrease in wingbeat amplitude may affect the relative energy cost of terminal phase echolocation. The 'pre-buzz pause' may be a time of inspiration and help to counter these effects, although the decrease in pulse intensity during terminal phase may still be necessary given the limited energy available. The frequency structure of calls may also be compromised, although the frequency drop noted in buzz 2 may not be present in some species (Surlykke et al. 1993).

The short glide seen during actual prey capture may increase the accuracy of feet placement or may result in increased lift the moment the bat strikes the water so that powered flapping can then recommence to gain height. The distance to prey at the start of 'tail down' stage is fairly constant. The bat would become aerodynamically more unstable if it adopted this position too far from the prey, yet it cannot leave the 'tail-down' stage until too late, or it would miss the prey. Low variation in the onset of the initial 'tail-down' stage would be expected, therefore. Once the bat has attempted to pick up the prey, it becomes necessary to transfer it from feet to mouth as soon as possible, lest it be dropped. The duration of this transfer stage, however, is somewhat variable, as Kalko & Schnitzler (1989a) noted with *M. daubentonii*. Data on capture success in *M. dasycneme* were not available, so its effect on the length of the 'head down' period is not known. A bat's retrieval efficiency (handling time in 'head down') may depend upon prey size. Echolocation during the 'head-down' stage generally does not occur, as implied by the significant relationship between 'head down' period and post-buzz pause duration. This relationship has also been noted in *M. daubentonii* (A.R.C. Britton, unpublished data). However, in both of these species, exceptions do occur when pulses are produced in 'head down' (e.g. Fig. 4.4a), although there seems to be little reason for the bat to produce a high-intensity echolocation pulse when its head is in this position.

The theoretical minimum detection distance from search phase calls on canals is calculated as 1.39 m for an 8.2 ms pulse, assuming avoidance of pulse-echo overlap (Kalko & Schnitzler 1989a). Calculated detection distance was 2.03 m, reaction distance was 1.82 m. These values are slightly longer than those for *M. daubentonii* (Kalko & Schnitzler 1989a), *Myotis siligorensis*, *Craseonycteris thonglongyai* (Surlykke et al. 1993) and *Pipistrellus* spp. (Kalko 1995), and this is expected given that *M. dasycneme* emit calls of a slightly longer duration. Detection distances should be greater on the lake site, given the longer pulse duration, and hence predicted minimum detection distance of about 3 m.

AVOIDANCE OF PULSE-ECHO OVERLAP

As the bat approaches an object, there is a danger of pulses being produced which overlap with their returning echo if the duration of the emitted pulse is too long (Schnitzler et al. 1987; Waters et al. 1995). This would result in a loss of information for the bat, partly due to decreased auditory sensitivity created by contraction of the middle ear muscles (Henson 1965). Avoidance of pulse-echo overlap is therefore particularly important during prey capture, and has been investigated previously in *M. daubentonii* (Kalko & Schnitzler 1989a) and *Noctilio leporinus* (Hartley et al. 1989). The bat avoids overlap by decreasing pulse duration as interpulse interval shortens prior to prey capture. In *M. dasycneme*, pulse-echo overlap generally is avoided. Indeed, two sequences showed no evidence of pulse-echo overlap. However, this may not be true for the entire terminal phase sequence. Overlap may sometimes occur just prior to prey capture (mean distance of 0.17 ± 0.10 m before prey). Kalko & Schnitzler (1989a) gave similar findings for *M. daubentonii*, but stated that this may be an artefact due to both measurement inaccuracies and the assumptions made to perform the calculation. In this study, the need for most assumptions has been minimised, although inevitable inaccuracies still exist. Unlike the study of Kalko & Schnitzler (1989a), changes in flight speed during prey capture were measured and taken into account. However, digitising inaccuracies still induce a potential source of error. Distance to prey when each pulse was produced cannot be quantified exactly, but must be equated to the nearest measurable bat-to-prey distance from the flash sequence closest in time to pulse emission. So, the final pulses in buzz 2 were assumed to end at the closest measured distance from bat to prey before capture. Given the above inaccuracies inherent in the measurement of pulse-echo overlap, the occurrence of overlap may be difficult to determine precisely, especially during the final moments of prey capture.

So, why might this short period of overlap take place, if at all? The bat will simply lose information from pulses when it is very close to its intended target. Perhaps the bat has accrued sufficient information about the target and its position that such last-minute updates are unnecessary. If this were true, however, why does the bat not terminate the echolocation pulses earlier to avoid wasting energy? It has been suggested that some species can utilise overlap beneficially (Hartley et al. 1989; Simmons et al. 1990), but there is no evidence of this in *Myotis* bats. Looking at the duration of interpulse interval and pulse duration during buzz 2, it appears that a physiological limit to call repetition rate has been reached, and such overlap may be inevitable close to a target.

DIET

The bulk of the diet of pond bats in this study comprised small dipterans, especially chironomid flies. In this respect, the diet resembles that of *M. daubentonii* (Swift and Racey 1983; Beck 1994-5), so overlap in diet of the two species may occur where they are sympatric. It has been suggested that population increases of *M. daubentonii* over much of Europe are the consequence of eutrophication of water increasing the abundance of pollution-tolerant chironomids (Daan 1980; Kokurewicz 1994-5; Vaughan et al. 1996). While *M. daubentonii* has increased in numbers in The Netherlands over the past 50 years, *M. dasycneme* has decreased (Daan 1980). It is not possible therefore to apply general arguments about diet to explain the changes in numbers of these species of trawling bats. The occurrence of pupal cases in the faeces suggests that the bats often take chironomids at the moment of adult emergence at the water surface.

Overall, in comparison with other studies, this study highlights some similarities in the flight and echolocation of trawling *Myotis* bats. Morphological differences appear to contribute to variation in flight and, to a lesser extent, echolocation characteristics between the three species discussed. Comparative investigations such as these can reveal more information than that provided by the species under study alone. This adds to the evidence which suggests that echolocation during feeding behaviour is generally similar between different species of vespertilionid bats - all of which have reached a common solution, or utilise a common solution used by ancestral forms.

5. Acoustic perception of landscape elements by echolocating pond bats *Myotis dasycneme*

Summary

The hypothesis that echolocating bats use landscape elements as acoustic landmarks was tested. If so, bats should be able to perceive distant landscape elements by echolocation and hence change their echolocation behaviour in relation to landscape elements. Echolocation parameters of commuting pond bats *Myotis dasycneme* (Boie, 1825) were related to the distance to the banks of differently sized canals. Pulse durations emitted at canals of 13, 19, and 25 m wide successively increased. Interpulse intervals were equally long at 13, 19, and 25 m wide canals, but significantly longer at a 30 m wide canal. The mean interpulse intervals at the 30 m wide canal were just sufficiently long to prevent overlap of an echo from the canal bank and a new outgoing pulse for bats flying on average halfway between the banks. The results indicate that pond bats perceive the canal banks by gradually adapting their pulse emissions to the distance to the banks. This suggests a role of the banks as acoustic cues.



A pond bat approaching prey on the water surface (photo: Zomer Bruijn).

Introduction

While moving through landscapes, many bat species follow edge habitats, such as forest lanes, forest edges, hedgerows, tree lines, river banks, and canals (Nyholm 1965; Voûte 1972; Glas 1978; Racey & Swift 1985; Limpens & Kapteyn 1990; De Jong 1994). But for what reasons? Possible explanations suggested for this phenomenon are that these landscape elements provide (1) shelter from wind, (2) shelter from predators, (3) foraging habitats, and/or are used as (4) acoustic cues for navigation and orientation (Limpens et al. 1989; De Jong 1994; Verboom & Huitema 1997).

This paper deals with the possible role of landscape elements as acoustic landmarks for commuting bats, either as orientation cues, or to stay on course. In chapter 3, we found that the distribution of pipistrelle bats relative to treelines was strongly related to the distance to the trees. Wind-speed and direction did also have an effect on the distribution of bats, and bat and insect abundance were related when insect abundance in the open area adjacent to the treeline was relatively high. When insect abundance was low, virtually all bat activity took place on the leeward side within the range perceptible by their echolocation system. This generated the hypothesis that bats are acoustically linked to landscape elements.

Previously, Limpens et al. (1989) postulated that orientational constraints with respect to long distance perception inherent in the use of echolocation, force bats to follow vertical landscape elements as guidelines. However, this idea is challenged by field observations. Commuting pipistrelle bats *Pipistrellus pipistrellus* (Schreber, 1774) sometimes cross open meadows and fields over distances up to 200 m as part of their daily flight routes (personal observations), or hunt in grasslands 50 m or more from the nearest trees or bushes (Kalko & Schnitzler 1993; personal observations). This is well beyond the maximum sonar range of this species, which may be the range of 15-20 m, as estimated from mean interpulse intervals. Nevertheless, it can still be argued that vertical landscape elements are used as reference landmarks, although bats, apparently, are not restricted to stay within acoustic reach all the time.

In this study we hypothesize that bats use vertical landscape features as acoustic navigation and orientation cues. If so, changes in the distance between a bat and surrounding landscape elements will be reflected in its echolocation. While many authors have investigated species specific sonar variation in cluttered versus uncluttered environments (e.g. Ahlén 1981; Miller & Degen 1981; Belwood & Fullard 1984; Thomas et al. 1987; Zingg 1988; Brigham et al. 1989; Zbinden 1989; Schumm et al. 1991; Kalko & Schnitzler 1993; Rydell 1990, 1993; Obrist 1995), the relation between echolocation and quantified landscape variables has not yet been examined. In most studies the bats' environment was complex and three-dimensional. In such an environment a bat's echolocation is affected by many variables, like distance to surrounding objects, height above the ground, echo-reflecting surface and prey availability.

The pond bat *Myotis dasycneme* (Boie, 1825) commutes and forages predominantly over waters (canals, ponds, lakes). While commuting between nursery roosts and hunting sites over canals, pond bats seldom hunt for insects and maintain a straight course approximately along the midline of the canal at an average height of 26 cm above the water surface (Britton et al. 1997). As its flyway is in a two-

dimensional plane, this makes a relatively uncomplicated situation to study echolocation in relation to landscape features. This paper presents a study of the relation of the echolocation of commuting pond bats to one landscape parameter, that is, distance to canal banks. Echolocation parameters were: interpulse intervals, pulse duration and peak-frequency. With increasing distance to a canal bank, we expect bats to increase interpulse intervals and to emit longer pulses of lower peak-frequency.

Study sites and methods

STUDY AREA

The pond bat nursery roost was in the church of the small village of Tjerkwerd (province of Friesland, The Netherlands), containing approximately 650 individuals in the year the study took place (pers. comm. A.M. Voûte). Bats commuted along canals to their main hunting sites at Lake IJssel. Recordings of commuting bats were made south-west of Bolsward, near Tjerkwerd and Exmorra (53°04'N, 5°27'E), at respective (straight-line) distances of 8 and 4.5 km from Lake IJssel. The area represents a typical open polder landscape with an extensive network of canals and ditches in a matrix of cattle-grazed grasslands. Canals varied between 12 and 40 m in width. The wooden sheetpiling of the canal banks protruded approximately 0.3 m above the water surface. The short vegetation on the banks was dominated by *Lolium perenne* L.

RECORDINGS OF COMMUTING BATS

Commuting bats were recorded in July and August 1994, when flying from their nursery roost in Tjerkwerd to hunting sites at Lake IJssel, using canals as flyways. Recordings were made at canals of 13, 19, 25, and 30 m wide, referred to as canal 13, canal 19, canal 25, and canal 30. At all four sites, passing bats (usually several hundreds within one hour) seldom produced terminal buzzes, indicating that the bats were actually commuting.

The microphone of a Pettersson D-980 bat detector (sampling frequency 350 kHz; resolution 8 bits) was pointed perpendicular to the bats' flyway and placed on a small, horizontal standard. Single passing bats were recorded using time-expansion by a factor 10 and heterodyning (Pettersson 1993), and both were simultaneously stored on an Aiwa HD-S100 DAT-recorder. The heterodyning circuit was tuned to the estimated peak frequency of the emitted signals: 35 kHz. Recordings were converted to digital signals with an LP900 A/D interface (12 bits; Pettersson Elektronik, Uppsala, Sweden). Sound analysis was carried out with an LP900 signal analyzer (Version 3).

ECHOLOCATION PARAMETERS

Pulse durations and peak-frequencies were obtained from the same time-expanded recordings. Recordings were digitised by computer using a sampling frequency of 50 or 100 kHz. Time-expanded signals with a signal-to-noise ratio of less than 8 dB were omitted from the analysis. Pulse durations were measured as the interval between the points where the signal amplitudes exceeded the noise level in the oscillogram.

Peak-frequency was defined as the frequency with the strongest amplitude. Peak-frequencies were calculated from Fast Fourier Transforms (FFT) over the second half (measured in time) of the pulse. We used either 2048 or 4096 points FFT, resulting in a frequency resolution of 244 and 122 Hz respectively, at a sampling rate of 50 kHz.

Interpulse intervals were measured from heterodyned recordings. Computer samples (sampling frequency 20 kHz) of these recordings were taken in an identical way for each bat. The end of each sample was defined by the abrupt fall in amplitude of the pulses which always occurred when the bat had travelled several meters past the microphone (and the microphone was no longer reached by the sound beam). An interpulse interval was defined as the interval between the peaks of two subsequent heterodyned pulses. Since the detector was tuned to 35 kHz, peak frequencies of the emitted sonar signals were well within the tuning bandwidth (± 4 kHz) of the detector. This means that the sharp peaks revealed by the signal analyser coincided (in time) with the actual peak-frequencies of the emitted pulses.

Intervals outside the range of 40-200 ms were omitted from the analyses, and were assumed to be associated with approach phases of the bats or caused by very weak, undetected, pulses. Before analysis of the recordings, a selection was made of bats that had passed the microphone while flying in 40% of the canal width bisected by the midline.

ESTIMATION OF BAT-TO-BANK DISTANCES

The distance from bats to the canal bank was estimated from polystyrene foam-markers which protruded 0.02 m above the water surface at known distances. We investigated a possible influence of these markers on the bats' echolocation or behaviour but found no effects. Only when the markers were left floating on the water surface, the majority of passing bats showed disturbed behaviour by making sudden turns or gaining height and emitting more pulses per second than usual. At canal 13, distance estimations were verified by measuring the time lapse between pulses and echoes returning from the opposite bank.

REACTION DISTANCE

Heterodyned recordings were made of commuting pond bats approaching a bridge over a canal. The position of the microphone was perpendicular to the flight-path of the bats. Loud pulses with strong echoes on the oscillogram marked the time when the bats passed the microphone. A dramatic drop in amplitude indicated that a bat had entered the space under the bridge. The time difference between these two observations was then reconciled with a flight speed of 9 m/s. Hence, each interpulse interval could be correlated to a specific distance to the bridge. It was assumed that the bats would increase their pulse repetition rate and thus shorten the duration of their interpulse intervals at the moment the bridge was detected.

To establish the distance to which pond bats react to a large clutter producing object, we used the data of commuting bats approaching a bridge in combination with data of commuting bats at the canals. Bats were hereby assumed to fly over the midline of the canals. A piece-wise linear model was fitted to estimate the break-point, that is the distance where bats started shortening their interpulse intervals: the reaction distance.

STATISTICAL ANALYSIS

For statistical analysis we used the Number Cruncher Statistical System (NCSS 5.x series, Kaysville, Utah, 1991). Data are presented as mean values \pm standard deviations, unless stated otherwise. Pairwise differences were analysed by t-tests, not by multiple procedures, with a 5% significance level per pairwise comparison (Saville 1990). We accepted a significance level of more than 5% for the total set of pairwise comparisons.

Results

BAT-TO-BANK DISTANCES

There was no difference in mean bat-to-bank distance calculated from the time-lapse between pulse and echo from the opposite bank and the estimates from foam markers at canal 13 (paired t-test, $P=0.26$, $n=14$), which shows that the latter were quite accurate. The pulse-echo measurements showed that 95% of the passing bats flew between 5.1 and 6.1 m from the opposite bank.

PULSE DURATIONS

Mean pulse durations increased from 8.22 ± 1.26 ms ($n=41$) at canal 13 to 8.71 ± 1.27 ms ($n=32$) at canal 19 and 9.83 ± 1.39 ms ($n=32$) at canal 25, and decreased again to 9.16 ± 2.28 ms ($n=38$) at canal 30 (Fig. 5.1a). There were significant differences between canals 13 and 25 (paired t-test, $P<0.001$), 19 and 25 ($P<0.005$), and 13 and 30 ($P<0.05$).

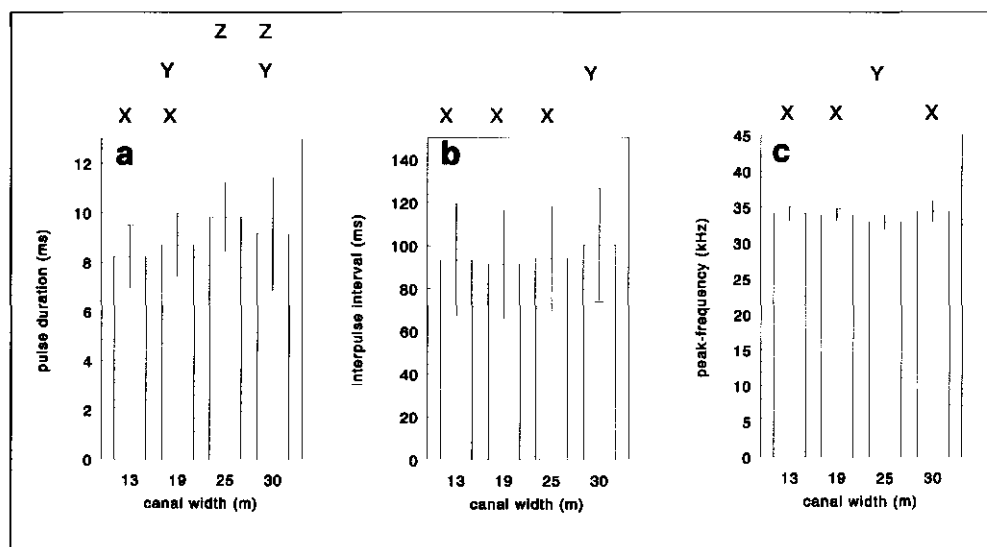


Figure 5.1.

Mean pulse durations (a), interpulse intervals (b) and peak-frequencies (c) emitted by commuting bats at four canals of different width. Error bars represent standard deviations. Non-significant differences (t-tests, $P>0.05$) are indicated by corresponding letters above bars.

INTERPULSE INTERVALS

Mean interpulse intervals were 93.17 ± 26.09 ($n=230$), 91.26 ± 25.16 ($n=201$) and 93.99 ± 24.26 ($n=209$) ms at canals 13, 19 and 25 respectively (paired t-test, differences not significant). At the widest canal, intervals increased significantly to an average value of 100.29 ± 26.45 ms ($n=209$; paired t-test, $P < 0.02$; Fig. 5.1b). As intervals were measured between the heterodyned peak-frequencies of the pulses, the (mean) pulse durations have to be subtracted in order to obtain the actual interpulse intervals.

PEAK-FREQUENCIES

Mean peak-frequencies at different canals showed an opposite trend compared to pulse durations (Fig. 5.1c). Mean peak-frequencies were 34.07 ± 0.99 kHz ($n=28$) at canal 13 and 33.93 ± 0.79 ms ($n=29$) at canal 19, then decreased to 32.84 ± 0.95 kHz at canal 25 ($n=22$; paired t-test, $P < 0.001$), and increased again to 34.33 ± 1.42 kHz ($n=27$) at canal 30 (paired t-test, $P < 0.001$).

Peak-frequency and pulse duration were negatively related (linear regression analysis, $r = -0.36$, $P < 0.001$). As the bandwidth of the fundamental is expected to reach a minimum with increasing pulse duration, we also fitted a non-linear hyperbolic model ($F(3,103) = 29423.7$, $P < 0.001$).

REACTION DISTANCE

There was a significant relation between the length of interpulse intervals and the distance of commuting pond approaching a canal bridge (linear regression, $F(1,91) = 10.74$, $n=93$, $P = 0.001$). In the piece-wise model we used data from canals 13, 19 and 25, which had equal interpulse intervals (Fig. 5.1b). The model estimated a break-point at 4.71 m (standard error = 1.07; Fig. 5.2). The results indicate that bats started reacting to the bridge by shortening their interpulse intervals at approximately 4.71 m from the bridge.

Discussion

THE PERCEPTION OF DISTANT LANDSCAPE ELEMENTS BY COMMUTING BATS

Aerial insectivorous bats use echolocation to detect and catch prey and to avoid obstacles. For many vespertilionid species, these tasks are performed within several meters from the bat. According to Kalko & Schnitzler (1993), *Pipistrellus* species only begin to react to objects at a distance of 3-5 m by switching to a pulse type with a different frequency-time course. In the present study, a similar reaction distance of approximately 4.7 m was found for commuting pond bats flying towards a bridge (Fig. 5.2). For the perception of more distant objects, e.g. landscape elements, bats need to adapt the emitted echolocation signals to receive processable and useful echoes. Our data indicate that commuting pond bats gradually adapted their echolocation signals to the distance to canal banks, which ranged from 6.5 to 15 m. With distances to the banks increasing, they emitted signals with longer pulses and interpulse intervals. It was not possible to make sound recordings from commuting bats flying further away from the bank due to low signal-to-noise ratios.

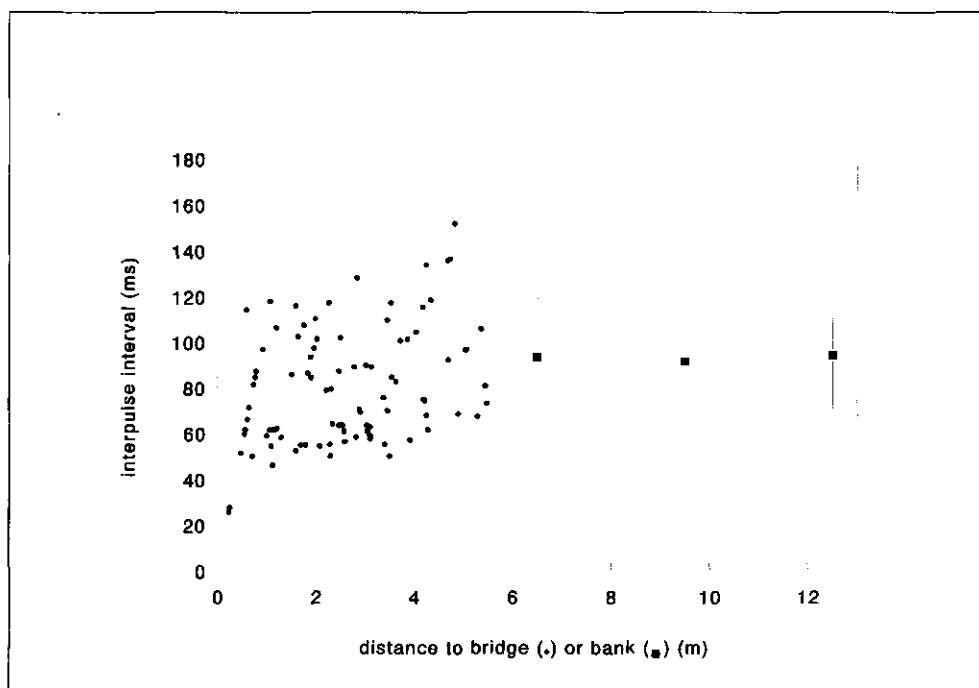


Figure 5.2.

Interpulse intervals of pond bats approaching a bridge (circles; $n=93$), and of bats commuting over canals 13 ($n=230$), 19 ($n=201$), and 25 ($n=209$) (squares; error bars represent standard deviations). Bats reacted to the bridge by shortening their interpulse intervals at an estimated distance of 4.71 m (standard error=1.07) from the bridge.

ECHOLOCATION DESIGN IN RELATION TO DISTANCE

Pulse durations

Detection and discrimination capabilities of a bat are largely determined by the frequency-time course of an echolocation signal. Vespertilionid bats using long-duration narrowband pulses usually forage in open spaces, often at high altitudes, where detection of objects is more important than structural information. Vespertilionids which hunt in dense or cluttered environments generally use short, broadband pulses. As distances to surrounding objects are short, detection is easily accomplished, whereas information about the structure of objects becomes more important (for reviews see Neuweiler & Fenton 1988; Fenton 1990; Neuweiler 1990). Similar differences in signal design are visible on the intraspecific level, where bats adapt the frequency-time structure of their pulses to the surrounding habitat (e.g. Ahlén 1981; Miller & Degn 1981; Belwood & Fullard 1984; Thomas et al. 1987; Zingg 1988; Brigham et al. 1989; Zbinden 1989; Schumm et al. 1991; Kalko & Schnitzler 1993; Rydell 1990, 1993; Obrist 1995).

From theoretical models it can be derived that range resolution, and hence discrimination performance, improves when using short, broadband pulses, and decreases when using long narrowband pulses (Cahlander 1967; Simmons & Stein

1980; Menne 1988; Zbinden 1989; Saillant et al. 1993). Theory also predicts that long narrowband pulses are optimised to solve detection problems since most signal energy is concentrated into a narrow frequency-band on which the receiver can concentrate (Simmons & Stein 1980). In laboratory experiments, Schmidt & Thaller (1994) found that *Tadarida brasiliensis* can enhance its sensitivity to echoes by increasing pulse duration within the integration time of its nervous system.

In the present study we would expect the bats to emit relatively short duration, high bandwidth pulses at short distances from the canal banks (at narrow canals) and relatively long duration narrowband calls at longer distances (at wider canals). Bandwidth, however, degrades over large distances as a consequence of atmospheric attenuation, which affects the higher frequencies more severely. Therefore, we focused on pulse duration, which is much less affected by atmospheric attenuation since the steepest frequency modulation in pond bats is at high frequencies (Britton et al. 1997). As expected, our data show longer pulses with increasing canal width.

Interpulse intervals

The distance perceptible by bats is limited by the time between two subsequent pulses. Each emitted pulse triggers a neuronal time-window which measures the range to objects by the delay of the returning echoes (Dear et al. 1993). Every new outgoing pulse triggers a time-window again, thus overriding the processing of echoes from the earlier emission (Simmons & Grinnell 1988). This means that if a bat wants to echolocate an object outside its perceptible range at that moment, it should increase the intervals to be able to receive and process the object-echoes before each subsequent emission. It has been observed in *Pipistrellus* species that interpulse intervals are significantly longer in uncluttered compared to cluttered environments (Kalko & Schnitzler 1993; Kalko 1994). It is also possible that bats flying in cluttered environments need more detailed information from their surroundings than bats flying in uncluttered environments.

Mean interval durations in pond bats in the present study were approximately 84 ms at canals 13, 19, and 25. At canal 30 an overlap between echoes and new outgoing pulses would occur at intervals shorter than 88 ms (assuming the bat's position is halfway between the banks). Thus, the mean interval length of 91 ms at canal 30 would just prevent pulse-echo overlap, and enable the bats to echolocate the canal bank.

Several studies (e.g. Schnitzler 1971; Kalko 1994) demonstrate a 1:1 relation between the bat's wingbeat frequency and pulse emission. Kalko (1994) suggests that the wingbeat frequency in pipistrelles is higher in cluttered than in uncluttered environments. This means that the longer pulse intervals at the widest canal in our study could be the result of a lower wingbeat frequency. However, in their study at two canals in the same area, Britton et al. (1997) found higher wingbeat frequencies at the widest of two canals. This would imply shorter interpulse intervals, which is contradictory to our results.

Peak-frequencies

Lower frequencies are better suited to detect objects over long distances than higher frequencies as a result of a lower attenuation coefficient of low frequencies.

However, the difference in attenuation between 34 and 32 kHz (Fig.5.1c) is only 0.08 dB/m, as calculated from Weast (1979). Consequently, the advantage of lowering the peak-frequency from 34 to 32 kHz may be negligible. The observed differences in peak-frequency can also be caused by differences in frequency-time course of pulses at the different canals. The observed correlation in the pond bat between pulse duration and peak-frequency is also found in several other species (*Eptesicus nilssonii*, Rydell 1993; *Nyctalus leisleri* and *Hypsugo savii*, Zingg 1988). It is likely that the observed differences in peak-frequency are a side-effect of different pulse durations emitted at narrow versus wider canals. At shorter pulses the peak-frequencies are somewhat raised, while longer pulses cause the opposite effect.

LANDSCAPE ELEMENTS AS ACOUSTIC CUES

The ability of pond bats to receive (processable) echoes from a bank is probably restricted to a limited range of less than 30 m. This can be demonstrated by a simple calculation. Assuming that the bat is a point source, that the atmospherical attenuation is 1.0 dB/m at 35 kHz and at 50% relative humidity (Lide 1995-1996), and that the banks reflect 100% of the incident sound, we expect the bats to receive an echo from a bank at 30 m which is about $(10 \cdot \log(1/4\pi 60^2) - 1.0 \cdot 60) = 107$ dB weaker than the emitted pulse. Under ideal circumstances (the banks reflecting all the incident energy, absence of external noise, the bat's hearing threshold at 0 dB SPL and the emitted sounds at 110 dB SPL) the bat would just be able to detect the bank. However, under normal circumstances, when not all sound energy is reflected, external noise will be present, and the bats have a higher hearing threshold, the maximum detection range will be smaller.

On the other hand, observations of pond bats foraging at their main foraging areas over Lake IJssel, sometimes at distances of more than 100 m from the bank (unpublished results), show their ability to leave echo-contact with the bank. Hence, we do not conclude that bats need acoustic contact with landscape elements.

Cognitive space maps may play a significant role in bat movements through a landscape. We can only speculate how detailed such cognitive maps are. Homing experiments have demonstrated that bats are able to return to their roost after being removed to locations which may be well outside their home range (e.g. Davis & Cockrum 1962; Mueller 1965; Barbour et al. 1966; Stones & Branick 1969). Visual cues, for instance street lamps or urban illumination, may also play an important role. Nevertheless, if movements rely on spatial memory, the information stored in cognitive maps still has to be based on acoustic and, possibly, visual cues, and reference landmarks may still be useful or even necessary for a bat's navigation and/or orientation.

6. The influence of wind protection on commuting and foraging pipistrelle bats *Pipistrellus pipistrellus* near treelines

Summary

The influence of wind protection on the occurrence and distribution of commuting and foraging pipistrelle bats, *Pipistrellus pipistrellus*, was examined in an area with a relatively windy climate. Wind protection provided by treelines was quantified by their height, width, and permeability. General occurrence and feeding activity of pipistrelles were positively related to height, width and foliage density of treelines. The preference for commuting routes leading from a maternity roost in a small village to the surrounding landscape was explained by the distribution of potentially good feeding sites at close distance from the roost. The results stress the importance of wind protected areas where bats can feed during windy conditions, and hence have implications for the conservation of bats and their habitats. It is argued that the number and distribution of sheltered feeding sites are a major constraint on bat density, especially in areas with a windy climate.

Introduction

Many bat species show a tendency to follow edge habitats such as treelines, hedgerows, forest edges, banks of rivers, canals and lakes, and drainage channels (e.g. Voûte 1972; Bateman & Vaughan 1974; Racey & Swift 1985; Rieger et al. 1990; Krull et al. 1991; Limpens & Kapteyn 1991; De Jong 1994; Walsh & Harris 1996a/b; Verboom & Huitema 1997). The use of edge habitats as flight paths is most obvious in bats commuting between their roost and foraging areas at dusk and dawn, but foraging sites too are very often situated close to the edges of vertical elements. This apparent choice seems to be widely spread among bats which are specialized to fly and hunt in semi-open situations, but also occurs in species which are adapted to use more confined spaces, such as members of the vespertilionid genera *Plecotus* and *Myotis*. A number of large bats, such as the vespertilionid *Nyctalus noctula* (Schreber, 1774) and several molossid and emballonurid species, however, seem to move independently from vertical landscape features, and can frequently be observed in large open areas (e.g. Norberg & Rayner 1987; Ahlén 1990; Kronwitter 1988), or at high altitudes (e.g. Williams et al. 1973; Fenton & Griffin 1997), where they encounter less clutter (e.g. background echoes from vegetation or ground). The pipistrelle bat, *Pipistrellus pipistrellus* (Schreber, 1774), seems to occupy an intermediate position in this spectrum: while its echolocation is not typically adapted to cluttered environments, and it may frequently move into open areas, the pipistrelle makes extensive use of edge habitats for several reasons (Racey & Swift 1985; Limpens & Kapteyn 1991; De Jong 1994; Ekman & De Jong 1996; Rydell et al. 1996). So far, our studies in The Netherlands were focused on bat occurrence in

relation to insect distribution and wind protection on the leeward side of landscape elements, and discussed the possible role of shelter from avian predators (Verboom & Huitema 1997; see also Chapters 2 and 3). Furthermore, our results suggest that pipistrelles (as well as pond bats, *Myotis dasycneme*: Chapter 5) are acoustically linked to vertical landscape features, suggesting a role of these as navigational reference landmarks (Chapter 3).

The main question in this paper is: what is the influence of wind protection on the distribution of commuting and foraging pipistrelle bats along a network of treelines? Several workers have reported an impact of wind on the commuting and foraging behaviour of bats (Nyholm 1965; Voûte 1972; Racey & Swift 1985; Rieger et al. 1990; Verboom & Huitema 1997). For the bats themselves, exposure to wind may considerably increase their flight cost and negatively influence their manoeuvrability (Schnitzler 1971; Norberg 1990). Furthermore, in addition to factors such as species composition of the vegetation and specific seasonal changes in insect peak activity, wind protection obviously affects the distribution of insects. Especially in areas with a windy climate, such as coastal areas, wind shelter may thus be a primary factor causing temporal and spatial variations in food abundance. Daily variations in wind-speed and direction may cause a temporal variation in wind shelter patterns and hence in food abundance. Differences in treeline structure (height, width, permeability; Lewis 1969b) may cause considerable spatial variations in wind shelter and hence in food abundance within nights.

In the present study I first examined which characteristics determine the profitability of treelines as feeding sites. To quantify the degree of wind protection, treelines were characterized by their height, width and permeability. I predict a strong relation between the occurrence of foraging pipistrelles and the degree of shelter provided by treelines.

In the second part of the study, the distribution of potentially good feeding sites around a maternity roost was used to predict the choice of evening commuting routes leading from the roost to the surrounding area. Like many other bat species (e.g. Bell 1980; Furlonger et al. 1987; Wilkinson 1992), pipistrelles are believed to be generalist feeders (Swift et al. 1985; Hoare 1991; Sullivan et al. 1993), adapted to exploit food patches varying in time and space in an opportunistic way (Racey & Swift 1985). After emerging from their roost around dusk, pipistrelle bats commute to their feeding areas along fixed flight paths, with hardly any feeding activity on their way (personal observations). Although the energetic cost of bat flight is relatively low (Norberg 1990), one would expect commuting pipistrelles to reduce travel time and distance in order to reach their feeding sites more rapidly and thus maximize the net rate of energy gain by maximizing the exploitation of insect activity peaks at dusk. An important additional benefit would be the reduction of time exposed to potential avian predators. In this paper I hence predict that pipistrelles select the shortest commuting routes leading to suitable feeding sites, given that these flyways provide sufficient shelter and can be used for navigation, and assuming that the bats possess information on potentially good feeding sites.

Commuting time could further be reduced by increasing flight speed. This hypothesis is supported by data from Jones & Rayner (1989) showing that flight speed of commuting pipistrelle bats is higher than foraging flight speed, even exceeding the predicted speed which minimises flight costs per unit distance

(maximum range speed) as predicted from Norberg & Rayner (1987).

Methods

STUDY AREA

The study took place in Walcheren, in the south-western part of The Netherlands (province of Zeeland), near two small villages, Meliskerke and Grijpskerke (Fig. 6.1), between May and August 1993-1996. Walcheren is a coastal area with a relatively windy climate. The area is primarily agricultural, with small villages surrounded by pastures and fields. The intensive use of agricultural land has resulted in an extremely poor insect fauna in the meadows and fields. Single and double treelines border many of the roads, thus forming an extensive network. The absence of forest in most of the area leaves only treelines and small tree stands near farmhouses as sheltered habitat. Apparently, these landscape elements offer sufficient opportunities to the local bat populations to commute and forage, given the presence

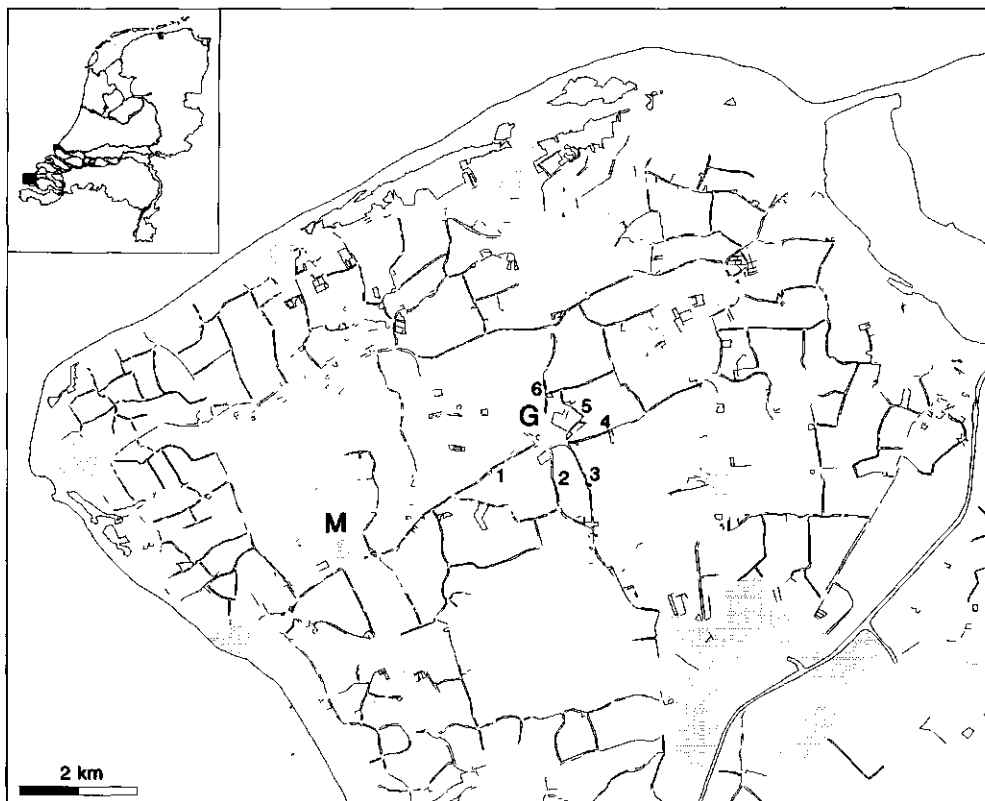


Figure 6.1.
Schematic map of Walcheren. Indicated are built-up areas (shaded) and woody vegetation (treelines and woodlots; black). M = Meliskerke, G = Grijpskerke. Numbers 1-6 refer to commuting routes.

of pipistrelle bat maternity roosts in virtually all villages in the area and the occurrence of foraging pipistrelle bats around many of the treelines in fairly high densities. There was a maternity roost of about 35 pipistrelles in Meliskerke (counts in 1994, 1995, and 1996) and one of 145 animals in 1994 and 108 in 1996 in Grijskerke.

BAT OCCURRENCE ON LINE-TRANSECTS

Bat occurrence was monitored at points on line-transects. Data were collected from four transects, two around the village of Meliskerke (transects M1 and M2), and two around Grijskerke (G1 and G2). Respective lengths of the transects were 10,760 m (M1), 11,670 m (M2), 11,080 m (G1), and 4,550 m (G2). Per night, one transect was monitored. The line-transects were representative samples of single and double treelines in the area, and partly crossed open area as well. Street lamps, which may attract pipistrelles and thus influence their distribution (e.g. Haffner & Stutz 1985-1986; Rydell 1992; Blake et al. 1994), were hardly present outside built-up areas. Single (orange sodium (Na) and white mercury (Hg) vapour) street lamps were present along roads in open area, >25 m from trees, on transects M1 (one white, one orange), M2 (one white, one orange), G1 (one orange), and G2 (two orange). Beforehand, pipistrelles had been recorded all along the transects. Point observations along line-transects took place between one hour after sunset and one hour before sunrise. It was assumed that during that period, pipistrelles would spend most of their time foraging at selected sites. Transects were surveyed by two persons driving on bicycles at a constant speed of about 6 km/h. Two ultrasonic bat detectors (type Petterson D-960, Lars Pettersson Elektronik, Uppsala, Sweden) were used in order to detect bats flying at both sides of the road and above the road. Bat detectors were tuned at 45 kHz, which corresponds to the approximate frequency of highest intensity of the echolocation sounds of *P. pipistrellus*. This method did not allow the assessment of densities, since individual bats could not be distinguished.

Observation points along transects were selected in two ways:

1. 'Fixed observation points' were established on fixed locations with fixed interpoint distances of 0.9 km.
2. 'Feeding observation points': when a bat was detected, a stopwatch was triggered for one minute; if a bat was detected a second time within that minute, an observation point was assigned. This method was used to select feeding sites along the transects. All single records in between feeding observation points were noted as well. Minimum interpoint distances were 100 m.

Fixed observation point data were collected from all four transects (11 nights altogether). In four nights I did not finish a fixed point transect due to rain (which affects the equipment). Feeding observation point data were collected in nine nights from transects M1 (four nights), G1 (three nights), and G2 (two nights). Different starting points were used for each time a transect was surveyed.

At each point, pipistrelle occurrence, relative insect density, wind-force, and wind direction were assessed. In case of a double treeline, bat occurrence was monitored simultaneously both from the road between the tree rows and on the leeward side. After monitoring bat occurrence, insects were sampled where bats were most abundant, either on the road or on the leeward side of the treeline. The

occurrence of pipistrelles was scored as the total time bat sound was recorded and as the number of feeding buzzes recorded during a five-minute period. Insects were sampled by sweepnetting with a handnet, 0.45 m in diameter (Bioquip Products, Gardena, California, USA). Per observation point, fifty sweeps, each 4 m in length, were taken at a height of 3.5-4.5 m, while walking slowly, taking a step every two sweeps parallel to the treeline, and another 50 while returning to the starting point (40 m vice versa). Wind-forces were estimated according to the Beaufort scale and transformed to wind-speeds in m/s by taking the midpoints of corresponding Beaufort classes. Wind direction was expressed as the angle between wind and treeline (incidence angle; 0-90°).

COMMUTING FLIGHT ROUTES

Six different roads, all bordered by double treelines, linked the village of Grijskerke with the surrounding landscape, potentially providing commuting bats sheltered flyways to foraging grounds. Routes 1-3 and routes 4-6 (Fig. 6.1) were connected with two networks of treelines, one lying south and one lying north of Grijskerke. Both networks were interconnected through Grijskerke only. Outside Grijskerke, the two networks were separated by more than one km of open agricultural land. During three evenings, simultaneous counts of pipistrelle bats leaving the village were carried out from fixed points along all six routes. Counting points were located 50-100 m from built-up area. Counts were made both visually and with the aid of bat detectors (Pettersson D-100; QMC-mini, QMC Instruments Ltd., London), tuned at 45 KHz, from 5-10 m breaks in the treelines. Road, leeward and windward side of treelines could be watched from these locations. Commuting flight was defined as a straight flight at a relatively high speed, and with only occasional feeding activity. The end of the commuting period was estimated by the absence of bats for at least 10 minutes or by increased foraging activity (feeding buzzes, bats flying in the opposite direction).

VEGETATION FEATURES

After a flood during World War II, all treelines in Walcheren died. During the Fifties, the local government started planting treelines along roads, as part of a recovery plan. As a result of this planting policy, treelines in the study area consist of stretches of varying length, which are very similar in vegetation structure and composition. Tree species in both treelines and woodlots were *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Ulmus minor* Miller and *Populus x canadensis* Moench. Common species in the generally present bush layer were *Crataegus monogyna* Jacq., *Acer campestre* L. and *Sambucus nigra* L.

Vegetation structure of the treelines and woodlot edges along the transects, and in both networks within 1, 2, and 3 km from Grijskerke built-up area if measured along treelines, was quantified by visual estimation of height, width and foliage density (100% - permeability). When treelines were double, 10% of the density of the treeline with the lowest density was added to the treeline with the highest density. There was one 1.7 ha woodlot along transects M1 and M2, one 0.8 ha woodlot along transect G1, and two woodlots along transect G2 with areas 0.8 and 1.8 ha along the Grijskerke transect. Foliage density at edges of woodlots was considered to be 100% (0% permeability).

DATA ANALYSES

Fixed observation point data were analysed with mixed models, in which linear modelling (regression and analysis of variance) was generalized to REML (Residual Maximum Likelihood; Patterson & Thompson 1971) and IRREML (Iteratively Reweighted REML; Engel & Keen 1994; see appendix). REML, IRREML and Poisson regression analyses were performed with the statistical program GENSTAT (Genstat 5 Committee 1993, 1995). For remaining statistical tests I used STATISTIX (vs. 4.0; Analytical Software, St. Paul, MN).

Results

DISTRIBUTION PATTERN

Thirty-eight fixed observation points on roads in open area were surveyed, on four of which single passing pipistrelles were recorded (mean occurrence 0.37 (standard deviation = 1.2) s / 5 minutes). Distances to the nearest trees were 100, 175, 250, and 680 m. The latter observation was done one hour before sunrise at relatively high light levels. During the surveys, pipistrelles were not observed foraging in open areas.

Bat occurrence in open area was much lower than along treelines (fixed observation points; t-test, $P < 0.0001$). Along treelines, the average distance between feeding observation points was 831 m (1.2 feeding observation points/km), and the average distance between pipistrelle records (including single observations) was 412 m (2.4 records/km; Table 6.1). Observations were not randomly distributed. The distribution of pipistrelle observations (feeding observation points + single observations) along treelines and wood edges (number per 1000 m) was compared to a random (Poisson) distribution. Pipistrelle occurrence was significantly overdispersed (parameter: number of observations per 1000 m, dispersion parameter = 1.85, Chi-square = 92.59, d.f. = 45, $P < 0.001$), indicating that they were patchily distributed.

Wind-speed and wind incidence angle affected bat occurrence around double treelines (fixed observation points, $n=72$). In most cases, bats occurred both over the road and on the leeward side, or over the road only ($n=62$); less often bat occurrence was restricted to the leeward side ($n=10$; Table 6.2). When bats were active on the leeward side only, wind-speeds, wind incidence angles and bat occurrence were higher.

Table 6.1.

Number of observations (points and single records) and distances covered in open areas and along treelines and woodlot edges.

	# FIXED OBSERVATION POINTS	FEEDING OBSERVATION POINTS	
		DISTANCE MONITORED (m)	# FEEDING OBSERVATION POINTS / SINGLE OBSERVATIONS
open area	38	25570	0 / 0
single treelines	95	534	11 / 11
double treelines	72	38121	39 / 43
woodlot edge	0	2093	5 / 2
treelines + woodlot edges	81	45748	55 / 56

Table 6.2.

Pipistrelle occurrence along double treelines, wind-speed and wind incidence angle on fixed observation points when bats were active over the road only or both over the road and on the leeseide, and when bat occurrence was restricted to the leeseide.

	SOUND RECORDED (s)	FEEDING BUZZES	WIND- SPEED (m/s)	WIND INCIDENCE ANGLE (°)
road (+ leeseide)				
mean \pm s.d.	16.1 \pm 25.5	0.5 \pm 1.1	2.5 \pm 2.6	33.6 \pm 28.9
n	61	61	62	43
leeseide only				
mean \pm s.d.	66.9 \pm 81.1	1.8 \pm 2.7	6.1 \pm 2.8	70.2 \pm 16.9
n	10	10	10	10
P (t-test)	<0.05	NS	0.001	<0.0001

FIXED OBSERVATION POINTS

The estimated effects of the REML and IRREML analyses in Table 6.3 show that bat occurrence is most clearly related to treeline width, height and foliage density. The estimated marginal effects for bat occurrence are additive effects on a logarithmic scale. This means that they can be interpreted as multiplicative effects on the original bat occurrence scale. For not too large values (bat occurrence less than 150 s, which is half of the 'binomial' total 300 s), the estimates can directly be read as fractional increases. E.g. the coefficient 0.052 for maximum foliage density suggests a 5.2% increase in bat occurrence if the maximum density would be 1% higher. The

Table 6.3.

Estimates (\pm standard errors) of marginal effects on bat occurrence. Insect densities were skewedly distributed and transformed by adding one and taking the natural logarithm. Effects may be interpreted approximately as relative change in bat occurrence when the explanatory variable is increased by one unit. Asterisks mark significance in approximate Wald-tests at the 95% confidence level. Variance components (emplotgit; see appendix) of bat occurrence calculated with REML are indicated by A, B, C, and D, referring to respectively transect, night within transect, observation point within transect, and observation case random effects.

	IRREML	REML	A	B	C	D
ln (insect+1)	0.08 (0.19)	0.12 \pm 0.26	0.6	0.2	0.8	2.9
height (m)	0.27 (0.17)	0.24 \pm 0.16	0.3	0.0	0.8	3.0
width (m)	0.17 (0.08) *	0.21 \pm 0.08 *	0.3	0.0	0.5	3.1
foliage density at 3 m (%)	0.050 (0.016) *	0.050 \pm 0.014 *	0.2	0.1	0.1	3.2
foliage density at 5 m (%)	0.021 (0.012)	0.022 \pm 0.011 *	0.3	0.0	0.6	3.1
foliage density at 7 m (%)	0.012 (0.008)	0.017 \pm 0.008 *	0.3	0.0	0.5	3.2
mean foliage density (%)	0.034 (0.013) *	0.043 \pm 0.012 *	0.2	-0.1	0.1	3.4
maximum foliage density (%)	0.052 (0.026) *	0.069 \pm 0.027 *	0.3	0.1	0.3	3.1
foliage density >50% (m)	0.32 (0.12) *	0.32 \pm 0.11 *	0.2	0.0	0.4	3.1
wind-speed (Bft)	-0.10 (0.23)	0.22 \pm 0.19	0.5	0.0	0.7	3.0
incidence angle (degree)	0.001 (0.008)	0.009 \pm 0.009	0.4	0.5	0.9	2.7

standard error 0.026 indicates that this increase percentage may be any value between 0 and 10%.

The variance components estimated with REML (Table 6.3) indicate that most variability is found at the level of observation points. Some relevant variability may exist between transects and between observation points within transects, but variability between nights within transects seems unimportant or even absent.

Figure 6.2 illustrates the marginal relation between bat occurrence and four of the treeline parameters. Although the relations are significant, there must be many other factors contributing to the noise in these relations. The results do not indicate

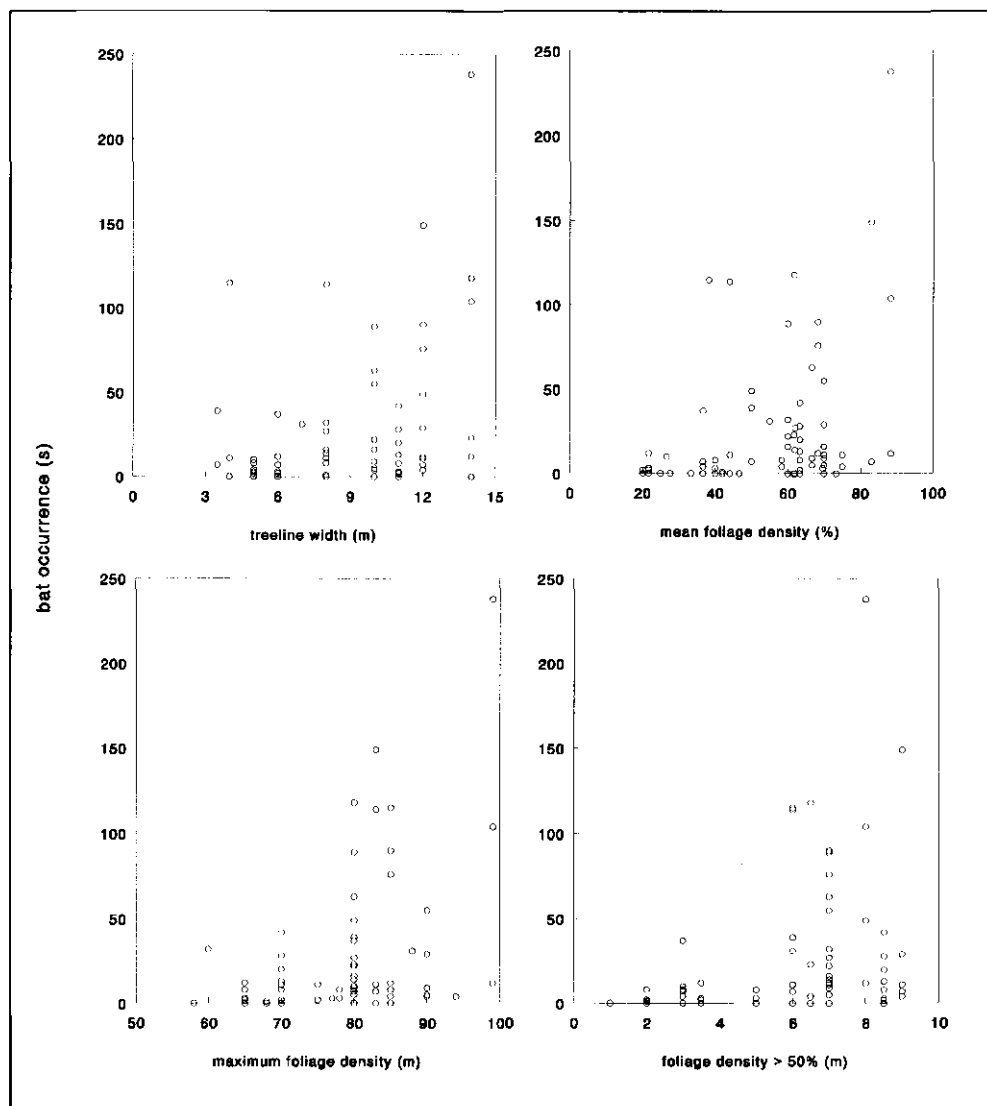


Figure 6.2.

Bat occurrence on fixed observation points against four treeline parameters.

that a relation with insect density or wind is absent. The measurements of insect density might have been too imprecise to indicate 'insect-for-bats' availability. Also the effective number of wind-force measurements (11, one per night) may have been too low, and the wind-force itself showed perhaps not enough variation to disclose the relationship.

FEEDING SITES

On feeding observation points, I frequently found more than one, but seldom more than three, pipistrelles foraging. General occurrence and feeding activity were higher than on fixed observation points (Table 6.4). Feeding observation points were hence considered to be feeding sites.

For each 100 m of treeline and woodlot edge, the average height, width, and foliage density of the vegetation was estimated. Bats were recorded all over the transects, including along most of the lowest, narrowest and most permeable treelines (usually single observations; Table 6.5). I compared treeline parameters on feeding observation points to overall mean values of both transects, that is excluding feeding observation points, each feeding observation point representing 100 m of treeline or woodlot edge. In transects M1 and G1/G2, height and foliage density of the treelines and woodlot edges were significantly higher on the feeding observation points than the overall means (Table 6.5). As expected, values on single observation points were a little lower than on feeding observation points. Many of these single animals were probably commuting between foraging sites or between foraging sites and their roost.

There were differences between transects M1 and G1/G2. Treelines in transect M1 were lower, narrower and more permeable (except for 'density at 5 m' and 'maximum density') than in transects G1/G2 (t-tests, $P < 0.05$). Nevertheless, mean values of treeline height and foliage density on feeding observation points were equal for both transects (t-tests, $P > 0.05$). This indicates that pipistrelles, although they were recorded all over transects M1 and G1/G2, selected only the highest and most densely vegetated treelines as foraging sites.

COMMUTING FLIGHT ROUTES

Simultaneous evening counts of commuting pipistrelle bats from fixed points (Fig. 6.1) showed a strong temporal and spatial variation in the numbers of bats using a

Table 6.4.

General occurrence and feeding activity (means \pm s.d.) along treelines on fixed and feeding observation points. Mann-Whitney U-tests: * $P < 0.05$ ** $P < 0.005$ *** $P < 0.0001$

	FEEDING OBSERVATION POINTS (ALONG TREELINES)		FIXED OBSERVATION POINTS (ALONG TREELINES)
	INCLUDING WOODLOTS n=39	EXCLUDING WOODLOTS n=34	NO WOODLOTS PRESENT n=81
sound recorded (s)	72.4 \pm 64.9 ***	67.1 \pm 62.0 ***	19.7 \pm 32.9
number of feeding buzzes	2.1 \pm 2.7 **	1.6 \pm 2.3 *	0.6 \pm 1.2

Table 6.5.

Treeline parameter values (means \pm s.d.) on transects (overall means), single observation points and feeding observation points. t-tests were performed to compare overall means to feeding observation points. * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$.

PARAMETER	TRANSECT M1			TRANSECTS G1/G2		
	OVERALL MEAN	SINGLE OBSERVATIONS	FEEDING POINTS OBSERVATION	OVERALL MEAN	SINGLE OBSERVATIONS	FEEDING OBSERVATION POINTS
	(MIN-MAX)	(MIN-MAX) (n=24)	(MIN-MAX) (n=22)	(MIN-MAX)	(MIN-MAX) (n=26)	(MIN-MAX) (n=27)
height (m)	5.6 (3-14)	7.0 \pm 1.7 (5-14)	7.3 \pm 2.4*** (5-14)	7.1 (3-12)	7.0 \pm 1.5 (3-10)	7.8 \pm 1.6* (6-12)
width (m)	6.8 (4-12)	8.0 \pm 1.5 (5-12)	7.5 \pm 2.2 (4-12)	9.5 (2.5-14)	7.9 \pm 3.3 (2.5-14)	9.1 \pm 2.9 (4-14)
foliage density at 3 m (%)	60.9 (26-100)	65.7 \pm 18.1 (26-100)	76.2 \pm 14.9*** (41-100)	78.7 (17-100)	79.3 \pm 9.9 (55-93)	81.8 \pm 11.0** (66-100)
foliage density at 5 m (%)	43.0 (26-100)	64.9 \pm 17.7 (26-100)	73.4 \pm 14.3*** (41-100)	39.8 (0-100)	54.6 \pm 19.3 (0-77)	65.5 \pm 18.7*** (30-100)
foliage density at 7 m (%)	14.0 (0-100)	34.0 \pm 33.2 (0-100)	42.7 \pm 39.0*** (0-100)	33.4 (0-100)	44.3 \pm 33.2 (0-77)	62.0 \pm 28.8*** (0-100)
foliage density mean of 3, 5, and 7 m (%)	44.3 (26-100)	54.9 \pm 16.5 (26-100)	64.1 \pm 18.6*** (41-100)	53.2 (28.3-100)	59.4 \pm 15.6 (28.3-80.7)	69.8 \pm 16.1** (38.3-100)
max. foliage density (%)	49.6 (26-100)	64.9 \pm 17.7 (26-100)	73.4 \pm 14.3*** (41-100)	46.6 (0-100)	57.9 \pm 19.0 (0-77)	68.5 \pm 16.9*** (30-100)
foliage density >50% (m)	4.2 (2-14)	5.9 \pm 2.6 (2-14)	6.8 \pm 2.9*** (2-14)	5.8 (0-12)	6.2 \pm 2.3 (3-12)	7.1 \pm 2.1* (3-12)

Table 6.6.

Simultaneous evening counts of pipistrelle bats commuting over exit roads of Grijskerke. For route numbers see Figure 1; mv = missing value.

DATE	WIND-DIRECTION AND WIND-FORCE (BFT)	NUMBER OF PASSING BATS (% of total) % COMMUTING OVER ROAD / ON LEEWARD / ON WINDWARD						N _{total} N _{roost}
		ROUTE 1	ROUTE 2	ROUTE 3	ROUTE 4	ROUTE 5	ROUTE 6	
24.6.94	SE 3	12 (10) 80/20/0	31 (25) 87/13/0	19 (15) mv	24 (19) 85/15/0	30 (24) 100/0/0	10 (8) 100/0/0	126 145
21.6.96	NNW 5	39 (31) 0/100/0	43 (34) 100/0/0	18 (14) 100/0/0	10 (8) 58/42/0	12 (9) 100/0/0	5 (4) 100/0/0	127 108
18.7.96	N 3	27 (23) 24/76/0	31 (27) 97/3/0	12 (10) 100/0/0	12 (10) 57/36/7	17 (15) mv	17 (15) 71/29/0	116 108

specific route (Table 6.6). In 11 out of 16 counts (for two counts I have no data), 80-100% of commuting bats passed over the road between the tree rows. Two times on route 1 only, the majority of bats flew along the leeward side. During 16 counts, only one bat was recorded commuting along the windward side.

More bats used the three routes leading to the southern network (routes 1-3 in Fig. 6.1) as compared to the three routes leading to the northern network (routes 4-6; Poisson regression, $F_{1,14}=5.23$, $P<0.05$, after correction for wind-speed and wind incidence angle). There was no effect of wind-speed and wind incidence angle on the number of pipistrelles using a particular commuting route ($F_{1,16}=0.05$ and 0.04 respectively, $P>0.05$). Table 6.7 shows the amount of treelines and woodlot edges within 1, 2, and 3 km from Grijskerke built-up area. It was assumed that the majority of bats foraged within 3 km of the roost and that they travelled along treelines only. Within 3 km, the length of treeline and woodlot edge in the southern network was 14,069 m and in the northern network 12,569 m. The significance of both networks as foraging areas for pipistrelles was quantified by calculating the amount of 'potentially good foraging area' at 0-1, 1-2, and 2-3 km. Mean parameter values at feeding observation points (Table 6.5) defined 'potentially good foraging areas'. In the southern network, the total length of treelines and woodlot edges meeting these criteria was higher than in the northern network, especially within 2 km from the village (Table 6.7). This shows that there were more potential foraging areas available at closer distance in the southern network, which supports the hypothesis that pipistrelles use the shortest commuting routes leading to the best foraging areas.

Table 6.7.

Amount of treelines and woodlot edges (m) within 1, 2, and 3 km north and south from Grijskerke built-up area. Mean parameter values at feeding observation points (Table 6.5) were used as minimum values to define 'potentially good foraging areas'.

PARAMETER		AMOUNT OF TREELINE + WOODLOT EDGE IN m			
		0-1 KM	1-2 KM	2-3 KM	TOTAL
total	north	4049	4085	42121	2346
	south	3858	5146	51921	4196
height >7.8 m	north	2270	1788	1443	5501
	south	2715	2730	1460	6905
mean foliage density >70%	north	1286	1382	1958	4626
	south	1334	2158	133	34825
maximum foliage density >69%	north	1477	2271	3212	6960
	south	1572	3460	5097	10129
foliage density >50% >7.1 m	north	2667	1551	2577	6795
	south	3001	3143	2445	8589
height >7.8 m and mean foliage density >70%	north	1286	1191	491	2926
	south	1334	2158	730	4222



Example of a treeline in Walcheren, showing variation in foliage density at different heights (photo: Ben Verboom).

Discussion

This study demonstrates the significance of sheltered habitats where bats can find relatively wind-free sites to feed. The study was performed in a coastal area with a relatively windy climate, where the presence of landscape elements with dense vegetation as windbreaks is believed to be crucial for resident bat populations. Especially in the intensively used agricultural areas of north-western Europe, fields and meadows can be extremely poor in insects, and bats may be largely dependent on woody vegetations to feed.

Furthermore, this study shows that bats preferably choose commuting routes to areas where good foraging patches are relatively close to the maternity roost. The presence of such patches at close distance to the roost may be of critical importance, especially to lactating females which, on average, make short foraging flights (Racey & Swift 1985) and usually return to the roost more than once during a night to suckle their young (Swift 1980).

In Walcheren, the landscape is relatively uncomplicated. Treelines and other woody vegetation are rather uniform in species composition over most of the area. Spatial and temporal variations in food abundance are mainly caused by wind in combination with treeline structure. Hence, the locations and profitability of insect-rich patches may vary from day to day or even change within a night. In areas with,

for instance, riparian woodland, patches rich in insects may be less affected by weather conditions, and persist for longer periods. Here, the distribution of predictable, high density food patches may allow bats to adopt a different optimal foraging strategy with longer commuting flights (Charnov 1976: marginal value theorem), in spite of increased predation risk.

Protection from wind may affect bats in two ways. First, small insects concentrate on the leeward side of the windbreaks (Lewis 1969a/b, 1970; Lewis & Stephenson 1966; Lewis & Dibley 1970). The origin of these insects may be in the windbreak itself or in the meadow or field neighbouring the windbreak, but a significant proportion may be the result of accumulation of small insects which have been blown from elsewhere. Unfortunately, due to strong variation in the samples, our insect sampling method proved to be inappropriate to allow proper conclusions with respect to insect densities. More sweeps per sample at a reduced height (for instance 2.5-3 m above the ground) might give better results.

Wind furthermore affects the flight performance and energy expenditure of the bats themselves. The groundspeed of a flying animal decreases with increasing headwind strength, and a small and relatively slow flying animal such as the pipistrelle bat, is strongly affected by wind (e.g. Pennycuik 1969; Norberg 1990). At a headwind of 7 m/s or more, a pipistrelle would not be able to fly in a forward direction at all (Pennycuik 1969). Tailwinds have the opposite effect of headwinds, and winds from besides the animal have an intermediate effect: when the angle between flight direction and wind direction is greater than 90°, flight costs increase (Pennycuik 1969; Norberg 1990). Furthermore, wind affects the manoeuvrability of bats (Schnitzler 1971), thus decreasing feeding efficiency.

Bats used all treelines in the study areas near Meliskerke and Grijskerke as flyways, including the lowest, narrowest and most permeable ones, but were seldom observed in the open areas during the study. Nevertheless, pipistrelle bats are able to traverse open areas over several hundreds of meters, as reported from earlier studies (De Jong 1994; Verboom & Huitema 1997; Chapter 2) and personal observations. These observations suggest that they use well-defined flyways through fields and meadows to reach isolated feeding areas. With the methods applied here, such flyways may have been overlooked.

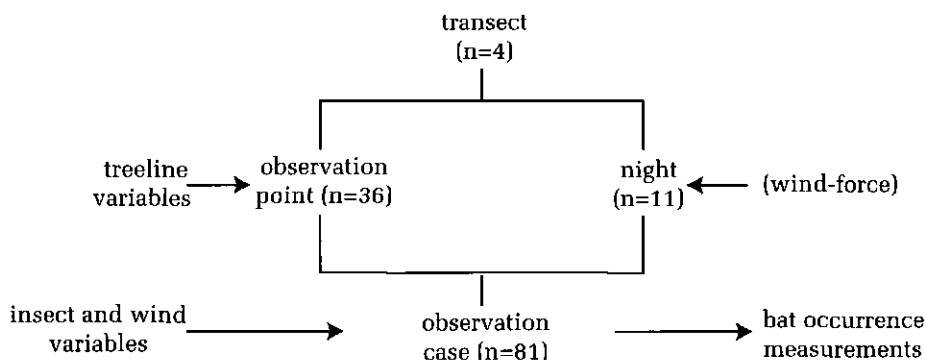
SIGNIFICANCE FOR BAT CONSERVATION

The conclusions of this study have implications for the conservation of bats. In particular in insect poor agricultural areas with a windy climate, bats may largely be dependent on windbreaks providing shelter to both bats and the insects they feed on. Land management and development should hence focus on the conservation and creation of wood patches and linear vegetations, such as hedgerows and treelines which are sufficiently high, wide, and densely vegetated, and hence provide sufficient shelter in windy conditions, to be useful as feeding sites. Double treelines are more suitable as commuting corridors than single ones. Furthermore, potential feeding sites should be close to roost sites, and interconnected and connected to roosts by vegetation corridors.

Appendix

Application of REML and IRREML in modelling relations between bat occurrence and environmental variables

The statistical analysis should respect the structure of the 81 observation cases. Observations were made in four transects, during 11 nights, and at 36 different fixed observation points. Nights and observation points are nested within transects, observations are made at certain combinations of night and observation point. A schematic representation is as follows:



The direction of the arrows indicates the intention to model bat occurrence as a function of the other variables.

Standard tools for the statistical analysis of relations between variables are linear and generalized linear models (GLMs, McCullagh & Nelder 1989). Examples of GLMs are logistic regression (appropriate when the response variable is a fraction, such as recorded bat sound per 5 minutes), and Poisson regression (appropriate when the response variable is a count). If the data are not really from a binomial or Poisson distribution, which is the case for the bat data, a standard option is to estimate one extra dispersion factor (quasi-likelihood method; see McCullagh & Nelder 1989, chapter 9). However, all these models assume that the structure in the set of observation cases is modelled via the explanatory variables, so that the random (error) terms are independent. To account for dependence between observations the models should be extended with extra random terms representing the structure of the data. The resulting models are known as mixed models, i.e. models with mixed fixed and random explanatory variables. In this way, linear modelling (regression and analysis of variance) has been generalized to REML (Residual Maximum Likelihood, Patterson & Thompson 1971), and, more recently, generalized linear modelling to IRREML (Iteratively Reweighted REML, Engel & Keen 1994). See Engel (1997) for a recent overview. Computations are easily performed with the statistical

program Genstat (Genstat 5 Committee 1993, 1995). REML is a standard feature of the program, IRREML is available as a procedure (Keen 1996).

For analysis of the bat data (sound recorded per 5 minutes), use of IRREML seems the most rational approach. No analysis of number of feeding buzzes has been undertaken, as there seemed to be too little information in the values (mostly 0 or 1). For our problem, the specification of the random terms is easy if one considers the scheme above. There are four levels of random variation: transect, observation point within transect, night within transect, and observation case.

In Genstat, REML and IRREML will estimate variance components (with standard errors) for each of the four random terms. These components may be compared to see which random terms are most important. However, in IRREML the unit level variance component is estimated at a completely different scale than the other ones, so that the direct comparison of variance components is restricted to the higher-level estimates. Mainly for this reason the IRREML analyses were supplemented with REML analyses on transformed data: the empirical logit (emplogit) transformation for recorded sound per 5 minutes (t_{sound}):

$$\text{emplogit}(t_{\text{sound}}) = \ln \{ (t_{\text{sound}} + 0.5) / (300 - t_{\text{sound}} + 0.5) \}$$

This data transformation implies a certain variance function (variance as a function of the level) for t_{sound} . This function is not compatible with the variance function in the IRREML model. However, REML on the transformed data is a relatively standard approach for analyzing this type of data, so large differences between the results from both approaches would be a reason to be more concerned with the precise form of the variance function for these data. In this sense, performing both analyses provides a protection against important misspecification of the model.

The fixed effects can be included in the model either each on its own (marginal effects) or together (conditional effects). In the problem presented here, many of the explanatory variables were approximately measuring the same treeline characteristics. Hence it is not sensible to estimate effects of changing one variable while keeping all others fixed (as is done with conditional modelling). Therefore all analyses have been performed with only one explanatory variable as a fixed term in conjunction to the four random terms mentioned above. For t_{sound} and an explanatory variable x the (quasi-binomial) IRREML model can be written as:

$$\begin{aligned} \ln \{ E(t_{\text{sound}}) / [300 - E(t_{\text{sound}})] \} &= \mu + \alpha_i + \beta_{ij} + \gamma_{ik} + \delta x_{ijk} \\ \text{var}(t_{\text{sound}}) &= \sigma^2 \frac{E(t_{\text{sound}}) [300 - E(t_{\text{sound}})]}{300} \end{aligned}$$

where α_i , β_{ij} , γ_{ik} are the random effects of transect i , observation point ij , and night ik , respectively. μ and δ are the fixed effects: the constant and the marginal effect of variable x , respectively. σ^2 is the dispersion factor which has to be estimated from the data.

7. Summary and general discussion

The significance of edge habitats to bats has been demonstrated in several studies (Furlonger et al. 1987; Grindal 1996; Krusic & Neefus 1996; Walsh & Harris 1996a, 1996b). This thesis deals with the use of edge habitats, in particular hedgerows, treelines, forest edges, and canal banks by commuting and foraging bats. The results are applicable in semi-natural and natural habitats as well. The studies were aimed to separate the effects of different factors explaining the association of bats with edge habitats, in order to point out their relative importance. Indications were found that all factors considered, i.e. food abundance, shelter from wind, shelter from predators, and the use of vertical landscape elements as acoustic navigational landmarks, play a role in the assessed relations between bats and edge habitats, and that their relative importance varies depending on the situation.

This chapter starts with a general discussion of results. After that, the implications of this study for bat conservation are discussed and a number of recommendations are provided to implement the results into the management and creation of bat habitats in agricultural areas.

Predators, food and wind

COMMUTING ROUTES

Predation risk is often emphasized as an important factor controlling the movements of bats (e.g. Rieger et al. 1990; De Jong 1994; Rydell et al. 1996). Unfortunately, the impact of this factor is hardly testable in the field, and for much of the observed behaviour in relation to vertical elements, predation risk can be put forward as an alternative explanation. However, predation on bats is likely to take place mainly when light levels are high (Rydell et al. 1996), that is during dusk and dawn or at high latitudes, and near roosts or on commuting routes, where bats can be expected at relatively high densities (Fenton et al. 1994). This hypothesis is supported by the data (Chapter 3): pipistrelle bats mainly commuted over the road between the treelines, in spite of stronger wind and lower insect abundance as compared to the leeward side.

FORAGING AREAS

Food abundance clearly is a major factor affecting the movements and distribution of bats (e.g. Racey & Swift 1985; De Jong & Ahlén 1991). From an optimal foraging perspective, it can be predicted that bats avoid open areas where insect abundance is lower than near landscape elements. Ekman & De Jong (1996), however, argue that the energetic cost of crossing insect poor open areas is relatively low and that the avoidance of open areas with low insect densities by commuting bats cannot be explained by energetic constraints due to scarcity of food. They conclude that another factor, such as predator avoidance, must be responsible for the low presence of many species in open areas. In support of this conclusion, Ekman & De Jong found that pipistrelle bats preferred forest edges in spite of higher insect abundance in the adjacent open areas. In the present study areas (Chapter 3), insect abundance was

found to decrease with distance to treelines. Insect abundance in open areas, however, apparently does influence the distribution pattern of bats near treelines. When insect abundance in the open area adjacent to the treeline was relatively high, there was a strong correlation between bat and insect abundance, and bat activity only slightly decreased with distance from treeline (Chapter 3). When the open area was poor in insects, a bat-insect relation was absent, and bats stayed close to the treeline.

An experiment to test the hypothesis that pipistrelle bats exploit patches of prey in an open area with, normally, relatively low insect abundance was carried out (H. Huitema & B. Verboom, unpublished results). The response of pipistrelle bats to artificially induced insect patches at 25 m from a (double) treeline on the leeward side was examined. Insect concentrations were attracted by ultraviolet light. Soon after turning on a UV-light, a dense cloud of insects was formed close to the lamps. During the four on/off sessions, pipistrelle foraging activity increased rapidly around the light, and a maximum of 17 feeding buzzes per 5 minutes were recorded.

The same experiment was carried out at 3 m on the windward side of the treeline. During one out of 10 on/off sessions, a pipistrelle reacted by feeding around the lamp. During all sessions, both on the leeward and the windward side, pipistrelles passed or foraged close to the treeline on the leeward side or over the road between the treelines. The results prove that pipistrelle bats are capable and willing to forage in open areas once insect abundance is high. The poor reaction on the windward side may be explained by the conservative searching behaviour of the bats, which may have constrained them to locate insect concentrations outside their regular foraging routes between the treelines and on the leeward side.

Shelter from wind affected the occurrence of foraging bats as well (Chapters 3 and 6). Wind and insect abundance are interrelated effects on bat distribution near vertical elements, since wind strongly affects the distribution of insects as well (e.g. Lewis 1970). This explains why bats mainly forage on the leeward side of vertical elements during strong winds (Chapter 3). This also explains the strong influence of wind-protection on the activity of foraging pipistrelles along treelines (Chapter 6). Furthermore, the distribution of wind-protected feeding sites proved to influence the use of commuting routes to foraging sites (Chapter 6).

In conclusion, both food abundance and shelter from wind affect the foraging behaviour and distribution of the bats studied near landscape elements. However, the results furthermore suggest the involvement of one or more additional explanatory factors for the relationship between bats and treelines (Chapter 3). Firstly, because a distance relation of pipistrelle bats to treelines remained significant after the effects of wind and insects were ruled out. Secondly, when insect abundance was low, the average peak of pipistrelle occurrence on the leeward side was significantly closer to the treeline than both the average peaks of insect abundance and wind reduction. There are two alternative explanations:

Predation risk. For bats, the risk of being caught by owls and other avian predators that hunt by vision, may be considerable (Speakman 1991). However, predation risk is likely to become less significant when light levels decrease. This might explain why bats commuting between the treelines at dusk shifted to the more exposed leeward side after the commuting period (Chapter 3). It is assumed that predator avoidance played a less significant role then. Similar behavioural responses

to decreasing light levels were found in previous studies (Nyholm 1965; Rydell et al. 1994).

Echolocation contact seems a plausible explanation. Support for this hypothesis is given in Chapter 3, where pipistrelle occurrence in the insect-poor situation was almost entirely restricted to a zone where acoustical perception of the treeline was possible. Hence, the logical step was taken to further examine the possible role of echolocation contact to vertical landscape elements.

Echolocation: landscape elements as navigational landmarks

Although echolocation studies have demonstrated that many bat species are very flexible in their echolocation behaviour (e.g. Rydell 1990; Obrist 1995), it is commonly accepted that the design of echolocation pulses emitted by bats is adapted to characteristics of their specific environment, and hence to an optimal flying distance from clutter producing objects. In this study it was hypothesized that bats use vertical landscape elements as landmarks when navigating through an area. The first step was to prove that bats maintain contact with vertical landscape elements by echolocation. The pond bat study (Chapter 5) indeed provides evidence that landscape elements are perceived by these bats over long distances. They adapt echolocation signals to increasing distances to canal banks to enable acoustic perception over long distances. A next step would be to prove that bats actually need landscape elements as navigational landmarks. This study provides no evidence for this. There are many observations of commuting and foraging bats in open areas, far from vertical landscape elements, where perception of these elements by echolocation is not possible. For instance, the presence of pipistrelles and serotines along relatively isolated forest fragments in Twente (province of Overijssel), strongly suggests that open areas of 150 m or more are frequently crossed (Chapter 2). During a mapping of flight routes in Walcheren (province of Zeeland), two daily pipistrelle commuting routes appeared to bridge open areas of 140 and 170 m respectively (B. Verboom, unpublished data). The latter crossing even included a four-lane motorway. These observations at least imply that bats do not need landscape elements for acoustical reasons.

Vision might play a role here. Previous studies have demonstrated that in some bat species vision is involved in orientation over long distances (Davis 1966; Williams et al. 1966), or obstacle avoidance (Chase & Suthers 1969), or even in finding prey on the ground (Bell 1985). Vision may especially be important in commuting bats around dusk and dawn, when light levels are relatively high.

Nevertheless, many bats still seem to prefer to stay close to vertical landscape elements, rather than to cross open areas. Mostert & Van Winden (1989) describe an example of commuting *Myotis daubentonii*, which, to reach their feeding grounds over a canal, made a considerable detour along a well developed hedgerow, instead of flying a shorter route along more sparsely vegetated hedgerows with a 100 m wide gap. In Walcheren, bats crossed the 170 m open area which included the motorway at the narrowest point only, that is where the distance between woody elements was smallest (see also De Jong 1995). To reach the point of crossing, the bats first had to make a

significant detour along a treeline. Apparently, they were aiming to reduce the travel time and distance in open area, which indicates that the latter is a barrier to pipistrelle bats.

To examine whether or not commuting bats would use a newly created (artificial) vertical structure as an acoustical guideline to a patch rich in insects, I conducted a brief experiment in Walcheren in 1995. Bamboo sticks were used to exclude possible effects of shelter from wind (to bats and insects) and from predators. The structure was placed in a grassland between the treeline and an insect rich patch, and consisted of a 100 m long row of 3 m high bamboo sticks. The treeline was used as a daily commuting corridor by ca. 30 pipistrelle bats. The angle between the row and the treeline was 45° and the direction of the row corresponded with the direction of evening commuting flight. Distances between the bamboo sticks varied from 0.5 m close to the treeline to 1 m further away from it.

During evening commuting periods and the first two hours of darkness over a period of eight days, bat activity was monitored by two persons, one close to the treeline, the other walking along the row of sticks. On two occasions only, a pipistrelle commuting along the treeline obviously responded to the sticks by making several turns around the first 5 m of the row. No bats were recorded flying along the line of sticks. If pipistrelle bats had followed the line of bamboo sticks, the conclusion would have been that the sticks were acting as an acoustic guideline, and that this feature was sufficient to attract the bats. The negative response by the bats, however, does not allow for conclusions. Firstly, the element might have been unattractive to bats due to the absence of shelter from predators (commuting bats), and/or the lack of food and shelter from wind (foraging bats). Secondly, the duration of the experiment might have been too short. If information about their environment is stored in cognitive maps, this may result in conservative behaviour in the use of flight routes. Hence, the bats may need a longer period to respond to a new situation. This agrees with the outcome of the experiment with UV-lamps, which suggested that conservative commuting and foraging behaviour prevented bats to detect and exploit insect patches on the windward side of a treeline.

In Chapter 3, the duration of interpulse intervals is assumed to be a measure for the maximum sonar range. For species intolerant of pulse-echo overlap, this interval indeed sets the maximum of sonar range. Under field conditions, however, the effective distance over which echolocation signals and their reflected echoes are perceived may be smaller, because the perception of sound through air is limited by geometrical spreading loss and by energy absorption (Neuweiler 1990). Since the latter increases with frequency, maximum sonar ranges estimated from interpulse intervals will be better approximated by bats emitting low frequency QCF signals than by bats emitting high frequency FM signals.

A further test of the 'acoustical link hypothesis' for other species would be to correlate their interpulse intervals with their flying distance from landscape elements. Table 7.1 shows average search phase interpulse intervals of several vespertilionid species recorded in The Netherlands, the corresponding maximum sonar range, and data by Baagøe (1987) of estimated flying distances from large vertical objects (trees, walls, etc.). Although the distance-to-object estimations in Table 7.1 are rather crude to draw conclusions, all species listed seem to fly mainly within their presumed maximum sonar range from large objects. To further establish this relation, more detailed investigations are needed.

Table 7.1.

Average durations of search phase interpulse intervals, corresponding maximum sonar ranges, and estimated flying distances from large vertical objects (trees, walls, etc.) of vespertilionid species recorded in The Netherlands. ¹ Intervals between search phase calls (range of means) given by different authors: Ahlén (1981, 1990), Zingg (1988), Jones & Rayner (1988), Kalko & Schnitzler (1989a, 1993), Schumm et al. (1991), Vaughan et al. 1997, Verboom (unpublished data) and Chapters 4 and 5). ? no data. ^{1*} when flying in buildings; ² Data from Baagøe (1987). Distances to large objects e.g. vegetation were roughly divided into three classes: <1 m, 1-8 m, and >8 m. The most important class is presented in the table.

SPECIES	INTERPULSE INTERVAL ¹ (ms)	MAXIMUM SONAR RANGE (m)	DISTANCE TO OBJECTS ² (m)
<i>M. daubentonii</i>	65-79	11-13	1-8
<i>M. dasycneme</i>	90-110	15-19	1-8
<i>P. auritus/austr.</i>	45 / 190	8 / 32	1-8
<i>M. emarginatus</i>	26-91	4-15	?
<i>M. nattereri</i>	77-80	13-14	1-8
<i>M. bechsteinii</i>	85 ^{1*} -96	14-16	1-8
<i>M. myotis</i>	?	?	?
<i>M. myst./brandtii</i>	88-95	15-16	1-8
<i>B. barbastellus</i>	64-115	11-20	?
<i>P. pipistrellus</i>	80-98	14-17	1-8
<i>P. nathusii</i>	134	23	>8
<i>E. serotinus</i>	116-150	20-26	>8
<i>E. nilssonii</i>	200	34	>8
<i>N. leisleri</i>	177-350	30-60	?
<i>V. murinus</i>	210	36	>8
<i>N. noctula</i>	300-336	51-57	>8
<i>N. lasiopterus</i>	?	?	?

Habitat fragmentation

The apparent importance of edge habitats for many bat species (Furlonger et al. 1987; Limpens & Kapteyn 1991; Grindal 1996; Krusic & Neefus 1996; Walsh & Harris 1996a/b) explains why a low or moderate degree of forest fragmentation may have a positive effect on bat abundance (Perdue & Steventon 1996). This positive effect may exist as long as the habitat fragments are sufficiently interconnected by woody landscape elements to allow bats to travel between them. When the process of fragmentation proceeds, discontinuities in connective landscape elements may become larger. For commuting bats, a newly created open gap in a fixed flight route of less than twice its maximum sonar range, may not be a problem. But when distances between fragments become larger, barriers may arise and fragments may become isolated. This situation is expected to decrease bat abundance. Eventually, due to large-scale clearcutting of forest and other woody landscape elements, landscapes with large open areas, devoid of significant vertical elements, may be left. In large open areas, bats generally occur in low numbers or are even absent (Furlonger et al. 1987; Estrada et al. 1992; Crampton & Barclay 1996; Grindal 1996; Walsh & Harris 1996a/b; Chapter 2). Large open areas may simply be unattractive to

bats because there are no suitable feeding areas. Close to vertical elements, bats generally find more food and shelter from wind and predators. This may explain why many species use fixed commuting and foraging routes. Furthermore, in the light of optimal foraging, it seems less efficient to search for food in open areas, even when rich patches of insects are present.

For many bat species, there will be an optimal situation, in which the amount of continuous edge habitats reaches a maximum. It is likely that the degree of fragmentation established in old agricultural landscapes used to promote bat abundance as compared to the former natural situation of continuous forest. In several parts of Twente, for instance, the old configuration of woody landscape elements is still intact, and discontinuities in the network of treelines and hedgerows are generally small. In many other areas in The Netherlands and north-western Europe, however, fragmentation has reached a more advanced stage and has become, or is likely to become, a major constraint on the occurrence of bats.

The use of edge habitats by bats in The Netherlands

Bats show specific adaptations in flight morphology and echolocation signal design to a particular habitat type (e.g. Norberg & Rayner 1987; for reviews see Neuweiler 1989; Fenton 1990; see also Chapter 1). Hence, interspecific differences in the use of edge habitats are expected. The relationship between a bat's functional "design", and its commuting and foraging behaviour may help us to make predictions about the use of landscape elements by particular bat species.

Morphological and perceptual (echolocation) differences between species appear to be related to the bats' flying distance to large objects, e.g. vegetation, walls or the ground, in their preferred habitat type. In Table 7.2, the species recorded in The Netherlands (Kapteyn 1995; Limpens et al. 1997) are tabulated according to their main foraging habitat and foraging technique. Most species in The Netherlands occur in closed habitats, whereas fewer species are typical for edge or open habitats. Species from closed habitats include the *Rhinolophus* and *Plecotus* species, and the gleaning *Myotis* species. The remaining species are all aerial hawkers. Edge species are slow-hawking species, and at least include both *Pipistrellus* and *Eptesicus* species, although the latter are frequently found in more open situations. Species from open habitats are fast aerial hawkers, and include *Vespertilio murinus* and *Nyctalus* species. On average, species of closed habitats are smaller than species of open habitats.

There are clear differences in wing-morphology and the types of echolocation used between species from open, edge and closed habitats (see also Chapter 1). Jones (1993b) grouped British bat species (all of which are in Table 7.2 as well) according to their wing morphology. Principal Component Analysis (PCA) was used to correct for size-effects (see Norberg & Rayner 1987). When wing-loading components were plotted against aspect ratio component, this revealed three clusters which mainly differed in their wing-loading components (low, average and high; Jones 1993b: Fig. 1).

Species with low and high wing-loading components roughly contained species of closed and open habitats, respectively. Species with intermediate wing-loading components consisted of edge species and several species of more closed

habitats. The positions of the small *P. pipistrellus* and the much larger *E. serotinus* in the scatter plot are very close (Jones 1993b: Fig. 1), indicating similar wing shapes. Thus, flight performance, that is after controlling for body size, cannot explain the assessed differences between these species with respect to their flying distance from vertical landscape elements (Chapters 2 and 3).

There is, however, evidence that specific foraging and echolocation behaviour can be predicted from a bat's size. In general, flight speed increases with body size, and with wing-loading (Norberg & Rayner 1987). Large and fast flying bats are likely to be less sensitive to wind, and less vulnerable with respect to predation, which may explain differences between *E. serotinus* and *P. pipistrellus*.

A bat's size is also correlated to echolocation features. Signal frequency, for instance, is negatively correlated to body size (Barclay & Brigham 1991). Furthermore, many large species emit signals of higher intensity and longer duration (due to a longer QCF component) than small species. These features should result in a longer echolocation range, and, assuming that bats keep acoustic contact with vertical landscape elements, this may explain why large bats, such as *E. serotinus*, generally fly at greater distance from vertical objects than small ones, such as *P. pipistrellus*. Furthermore, signal frequency seems to be negatively correlated to dietary niche breadth (Barclay 1986). *E. serotinus* has a larger dietary niche breadth than *P. pipistrellus* and includes large insects in its diet as well. Since large insects occur in more open areas than small insects, this may explain the frequent occurrence of *E. serotinus* in open environments.

In conclusion, the conservation and creation of edge habitats in cultivated areas is expected to influence the occurrence of virtually all species in The Netherlands in a positive way, but the response to conservation measurements is expected to differ between species. Small species of closed environments strongly avoid open areas, and stay close to vegetation during both commuting and foraging. In fragmented landscapes, the presence of continuous and dense vegetation corridors connecting woods is essential for these species.

In The Netherlands, several species, especially *M. daubentonii*, *M. dasycneme*, and *P. pipistrellus*, often have commuting routes over several kilometers along hedgerows, treelines and forest edges, and several edge species also find feeding areas along these elements. For them, a cohesive network of edge habitats over a wide area is of major importance, especially in cultivated areas where travel distances are relatively long.

According to Fenton (1990), the occurrence of bats in particular habitat types is constrained by their ability to deal with narrow spaces and clutter. Consequently, bat species cannot forage effectively in habitats which are more closed (cluttered) than the habitat they are specifically adapted to. Practically, this means that species of closed (cluttered) habitats can be expected along edges as well, and that open air foragers are expected to be absent from edge habitats. For large species which are adapted to open habitats, edge habitats may be less important as foraging areas or as connective elements. However, for those

species that feed on large insects, the presence of windbreaks may increase foraging opportunities in open areas (Chapter 2).

Table 7.2.

Wing morphology, echolocation features, and habitat use of bat species recorded in The Netherlands. * known to reproduce in The Netherlands. Foraging techniques: *ah* aerial hawking, *ph* perch-hunting, *fg* foliage gleaning, *gg* ground gleaning, *tr* trawling (main technique(s) in bold). Use of commuting corridors: + follows commuting corridors, ++

SPECIES	WING MORPHOLOGY		FORAGING TECHNIQUE(S)	ECHOLOCATION	
	WING LOADING	ASPECT RATIO		PULSE-TYPE(S) PEAK FREQUENCY	PULSE DURATION
greater horseshoe bat <i>Rhinolophus ferrumequinum</i>	12.21 10.63 ²	6.1 ¹ 5.15 ²	ph, ah, fg, gg	fm 80-85	30-40
lesser horseshoe bat <i>Rhinolophus hipposideros</i>	7.1 ¹	5.7 ¹	ah, fg, gg, ph	fm-CF-fm 105	50
Daubenton's bat * <i>Myotis daubentonii</i>	7.0 ¹ 8.26 ²	6.3 ¹ 6.15 ²	tr, ah	FM 45	3-5
pond bat * <i>Myotis dasycneme</i>	10.4 ¹	6.8 ¹	tr, ah	FM 35 fm-QCF 35	5-7 15-25
long-eared bat * <i>Plecotus auritus</i>	7.1 ¹ 5.89 ²	5.7 ¹ 5.98 ²	fg, ah	FM 50-35	1-2
grey long-eared bat * <i>Plecotus austriacus</i>	7.9 ¹	6.1 ¹	fg, ah	FM 50-35	1-2
Geoffroy's/notch-eared bat * <i>Myotis emarginatus</i>	7.1 ¹	5.91	fg, ah (gg, ph)	FM 45-55 (no clear peak)	1-3
Natterer's bat * <i>Myotis nattereri</i>	6.1 ¹ 6.02 ²	6.4 ¹ 6.32 ²	fg, ah, tr, gg	FM 50 (no clear peak)	2-3
Bechstein's bat <i>Myotis bechsteinii</i>	9.0 ¹ 9.51 ²	6.0 ¹ 5.57 ²	fg, gg, ah?	FM 50	2-3
mouse-eared bat <i>Myotis myotis</i>	11.2 ¹	6.3 ¹	gg, fg, ah	FM 35	?
whiskered bat * <i>Myotis mystacinus</i>	7.1 ¹ 6.41 ²	6.0 ¹ 6.53 ²	ah, fogl	FM 45	2-3
Brandt's bat <i>Myotis brandtii</i>	6.47 ²	6.21 ²	ah, fg	FM 45	2-3
barbastelle <i>Barbastella barbastellus</i>	9.1 ¹	6.0 ¹	ah	CF-FM 32-35	4-5
pipistrelle * <i>Pipistrellus pipistrellus</i>	8.1 ¹ 5.97 ²	7.5 ¹ 6.47 ²	ah	FM-qcf 45-50 fm-QCF 42-45	5 7
Nathusius' pipistrelle * <i>Pipistrellus nathusii</i>	7.2 ¹ 9.13 ²	9.8 ¹ 6.56 ²	ah	FM-qcf 38-40 fm-QCF 35-37	5-7 5-10
serotine * <i>Eptesicus serotinus</i>	12.2 ¹ 11.09 ²	6.5 ¹ 6.57 ²	ah, fg	FM-QCF 25-30	5-8
northern bat <i>Eptesicus nilssonii</i>	8.1 ¹	6.6 ¹	ah	FM-QCF 27-32	10
Leisler bat * <i>Nyctalus leisleri</i>	19.3 ¹ 15.24 ²	7.9 ¹ 7.02 ²	ah	FM-QCF 28 fm-QCF 25	8-10 14
parti-coloured bat <i>Vespertilio murinus</i>	10.2 ¹	7.0 ¹	ah	fm-QCF 25-27 FM-QCF 27	?
noctule * <i>Nyctalus noctula</i>	16.1 ¹ 17.28 ²	7.4 ¹ 8.21 ²	ah	QCF and FM-QCF 20 FM 20-30	18->20 2-5
greater noctule <i>Nyctalus lasiopterus</i>	?	?	ah	QCF and FM-QCF <20	?

strongly follows commuting corridors, - no well defined commuting corridors.

Data on wing morphology: 1 Norberg & Rayner (1987), 2 Jones (1991);
echolocation: Weid (1988), Schumm et al. (1990), Limpens et al. (1997), Verboom
& Huitema (unpublished results); habitat use: Limpens et al. (1997), Sierro &
Arlettaz (1997), H.J.G.A. Limpens (pers. comm.).

HABITAT USE			
MAIN FORAGING HABITAT	OPEN, EDGE, CLOSED	USE OF COMMUTING CORRIDORS	COMMUTING DISTANCE (km)
close to vegetation in open, broad-leaved woodland	closed	?	max. 2 (?)
hedgerows, treelines, banks, riparian woodland	closed	++ hedgerows, treelines	mean 2-3
(sheltered) ponds, ditches, canals, slow-flowing streams, forest openings	'closed/edge'	++ hedgerows, treelines, wood edges	max. 5
lakes, ponds, wide canals	'closed/edge'	++ treelines, hedgerows, canals	max. >15
forest, forest lanes/ openings, double treelines, wooded banks	closed	forest lanes/edges, treelines	max. 1.5, mean <1
treelines, hedgerows, orchards, forest edges, buildings	closed	?	?
forest edges, among tree crowns, buildings	closed	+ treelines, hedgerows, banks	max. >10
riparian woodland, sheltered streams and ponds	closed	+ forest lanes/ edges, treelines	?
edges of forest and woodlots	closed	+ forest lanes	?
forest lanes/openings/ edges	closed	+ forest lanes, over forest canopy	max. >10
forest clearings/openings/ lanes/edges, open woodland	closed	+ forest lanes, treelines	max. <1.5
forest clearings/openings/ lanes/edges/ponds	closed	+ forest lanes ?	?
above forest canopy, forest edges/lanes	closed/edge	?	?
treelines, hedgerows, forest edges, vegetated banks, gardens, street lamps	edge	++ treelines, hedgerows, wood edges, buildings	max. 5
forest edges/openings, treelines, above waters	edge	+	?
grassland with treelines/ hedgerows, woodlot edges, open marshland	edge/open	+ treelines, hedgerows, banks	mean <1 max. 3-4
forest and woodlot edges/ openings, marshland	edge/open	?	?
open spaces in forest, forest edges, over forest canopy, above waters, street lamps	open	-	?
open spaces in forest, marshland, above waters, street lamps	open	-?	?
marshland, above lakes, rivers, canals, meadows, fields	open	-	mean 3-6, max. 20
open spaces ?	open	-	?

Application of results in landscape planning

Since bats generally use a mosaic habitat landscape with spatially separated feeding grounds, summer roosts and winter roosts, bat abundance provides a good indication of the spatial connectivity of different landscape parts. Therefore, conservation efforts should especially focus on the management, restoration and creation of bat habitat and landscape elements connecting habitat patches in agricultural areas. This is especially important because of the recent attention to multifunctional areas with nature outside the reserve network (e.g. Ministry of Agriculture, Nature Management & Fisheries 1990, 1995).

Currently, there is a need for tools to evaluate and improve the quality of natural habitats in agricultural landscapes. Guidelines for bat conservation should form a part of the tool kit of landscape planners. In this study, several multivariate models were derived which can be used to predict the numerical response of bat occurrence to changes in the density and configuration of edge habitats (Chapter 2), and in the structural features of treelines (Chapter 6). These models are, for example, useful in scenario comparisons. The following recommendations, extracted from this thesis, are directly applicable to the management, restoration, and creation of treelines and hedgerows for the benefit of bats:

- (1) On a landscape scale, increasing the density of woody elements will positively influence bat abundance (Chapter 2). Continuity of edge habitats is essential for an optimal exploitation of feeding habitats. Maximum allowable gaps in hedgerows and treelines are species-specific. A distance of twice the maximum sonar range (Table 7.1) provides a safe measure which can be used to minimise effects of habitat fragmentation.
- (2) For commuting bats, edge habitats are important not only as connective corridors (Chapter 6), but also provide shelter from predators (Chapter 3). So double treelines are more effective than single ones.
- (3) When planning a hedgerow or treeline, it is best orientated perpendicularly to the prevailing wind direction in order to provide maximum wind protection (Chapter 3). When planning several of these elements, it is important that different orientations are represented.
- (4) The suitability of a treeline or hedgerow as a feeding site depends on its structural features (Chapters 2 and 6). Increased foliage density, width, and height improves the suitability as a feeding site. This is especially important in areas with a windy climate. For example, from Table 6.3, it can be derived that an increase of mean foliage density of 1% would correspond with an average increase in bat activity of 3.4%. To enhance wind protection, treelines should have a dense bush layer to increase shelter below the tree crowns. For small bats, such as pipistrelles, the minimum height of treelines and hedgerows should be 6 m (Chapters 2 and 6).
- (5) Open areas adjacent to treelines should be rich in insects to facilitate the exploitation of open areas outside the bats' acoustical range from treelines.

Data on habitat use by bats in The Netherlands have always been very scarce. Recently, this situation changed. This thesis provides important information on the use of edge habitats by bats and the barrier effect of the open matrix in agricultural areas. The recently published results of the Dutch Bat Survey (Limpens et al. 1997)

provide detailed distribution maps of species on a national scale. Both information sources should be combined to develop models which can be powerful tools in landscape management and planning. Effects of guidelines presented above will not be restricted to bats alone, but will generally affect biodiversity in agricultural landscapes, and may positively affect species typical of hedgerows and treelines (e.g. ortolan bunting *Emberiza hortulana*), forest species using hedgerows and treelines as connective corridors between forest patches (e.g. European nuthatch *Sitta europea* L., red squirrel *Sciurus vulgaris* L., carabid beetles) and species using edge habitats in small-scaled, mosaic habitat landscapes (e.g. amphibians, European badger *Meles meles* L.).

Samenvatting en discussie

Vleermuizen hebben als enige zoogdieren het vermogen ontwikkeld om zich vliegend voort te bewegen. Daarnaast maken zij gebruik van een hoog ontwikkeld akoestisch waarnemingssysteem, echolocatie. Door deze combinatie van eigenschappen zijn ze in staat zich in het nachtelijk luchtruim te begeven en er hun prooien te bejagen. Sinds het einde van de jaren zeventig maken handzame, draagbare vleermuis-detectors het mogelijk de nachtelijke vliegbewegingen van vleermuizen door het landschap te bestuderen. Zonder deze apparatjes, die de ultrasone echolocatiesignalen van vleermuizen omvormen tot hoorbare geluiden, had dit proefschrift niet tot stand kunnen komen.

Waarom dit onderzoek?

Dit proefschrift gaat over het gebruik van lijnvormige, opgaande elementen in het landschap door vleermuizen. In het moderne, versnipperde cultuurlandschap zijn verblijfplaatsen en foerageergebieden van vleermuizen vaak kilometers van elkaar verwijderd. Veel soorten overbruggen deze afstanden via vaste vliegroutes langs lijnvormige landschapselementen, zoals boslanen, bosranden, bomenlanen, bomenrijen, houtwallen, rivieroeveren en kanalen. Dergelijke routes worden soms jarenlang achtereen gebruikt en vormen belangrijke verbindingen voor vleermuizen. Genoemde landschapselementen zijn voor een aantal soorten tevens foerageergebieden.

Lijnvormige elementen zijn van oudsher typerend voor het Nederlandse cultuurlandschap. Ontwikkelingen in de landbouw hebben, vooral in de laatste decennia, drastische veranderingen tot gevolg gehad, waardoor natuurwaarden in het agrarisch gebied sterk achteruitgingen en veel diersoorten in hun verspreiding werden teruggedrongen tot opgaande landschapselementen. Door het verdwijnen van de behoefte aan 'boerengeriefhout', en als gevolg van schaalvergroting en ruilverkavelingen verdween tussen 1900 en 1990 bijna 60% van de houtwallen, heggen en bomenlanen in ons land. Bovendien zijn lijnvormige begroeiingen steeds meer onderbroken geraakt. Deze ontwikkelingen kunnen een negatieve invloed hebben op de aantrekkelijkheid van gebieden voor vleermuizen, enerzijds op grond van de verminderde hoeveelheid foerageerhabitat, anderzijds doordat verbindingen tussen foerageergebieden worden aangetast of wegvallen, waardoor de bereikbaarheid van delen van het landschap, en daarmee de hoeveelheid exploiteerbaar foerageerhabitat, afnemen.

Het hier gepresenteerde onderzoek is uitgevoerd om gegevens te verzamelen over de manier waarop vleermuizen houtwallen, bomenlanen en bosranden gebruiken. Zo kunnen adviezen worden gegeven bij de aanleg en het beheer van landschapselementen ten behoeve van vleermuizen. In hoofdstuk 2 wordt de vraag gesteld in hoeverre het voorkomen van enkele soorten vleermuizen gerelateerd is aan lijnvormige landschapselementen. Tevens worden gezocht naar een functionele verklaring voor de gevonden relaties. In de daarop volgende hoofdstukken (3-5) worden verschillende potentiële functies van lijnvormige landschapselementen voor vleermuizen in detail bestudeerd. In hoofdstuk 6 wordt het voorkomen van foerage-

rende dwergvleermuizen in verband gebracht met structuurkenmerken van houtsin-gels, en wordt de keuze van vliegroutes gerelateerd aan de verspreiding van poten-tieel goede foerageerplekken over het landschap. Tenslotte worden aanbevelingen gedaan, waarmee de onderzoekresultaten toepasbaar kunnen worden gemaakt voor het natuurbeheer (hoofdstuk 7).

Verschillen tussen soorten

Elke vleermuizensoort wordt gekenmerkt door een bepaalde combinatie van eigen-schappen die maakt dat hij optimaal is aangepast aan een bepaalde foerageerstrate-gie in een bepaald habitat (Hoofdstuk 1). Morfologische kenmerken, met name de vorm van de vleugels en de lichaamsgrootte, geven aan wat zijn optimale (meest energiezuinige) vliegsnelheid is en hoe wendbaar hij is. Kenmerken van de echolo-catiesignalen (puls lengte, pulsduur, frequentie) en de duur van de intervallen tussen pulsen, duiden aan of een soort voorkomt in een open omgeving, of juist in de beslo-tenheid van bijvoorbeeld vegetatie. Deze aanpassingen maken het mogelijk voor-spellingen te doen over het gebruik van opgaande landschapselementen, zoals hout-wallen, bomenlanen en bosranden, door vleermuizen.

Bij in Nederland voorkomende vleermuizen kunnen we twee uitersten onder-scheiden. Enerzijds zijn er soorten die hun prooien bejagen in een besloten omge-ving, dicht bij vegetatie, gebouwen of de grond. Open terrein wordt door hen zoveel mogelijk gemedend. Vliegafstanden zijn doorgaans niet groot, routes lopen vaak via open plekken in het bos, zoals boslanen en -paden. Voorbeelden zijn de gewone grootoorvleermuis (*Plecotus auritus*) en een aantal soorten van het geslacht *Myotis*. Aan de andere kant van het spectrum bevinden zich de soorten die een open jacht-omgeving prefereren. Deze vleermuizen kunnen in de loop van een nacht relatief grote afstanden afleggen. De binding met vegetatie en opgaande landschapselemen-ten lijkt niet of nauwelijks aanwezig. Voorbeelden zijn de rosse vleermuis (*Nyctalus noctula*) en de tweekleurige vleermuis (*Vespertilio murinus*). Daarnaast is er een middengroep, waartoe de gewone dwergvleermuis (*Pipistrellus pipistrellus*), de ruige dwergvleermuis (*P. nathusii*), de laatvlieger (*Eptesicus serotinus*), de water-vleermuis (*Myotis daubentonii*) en de meervleermuis (*M. dasycneme*) kunnen wor-den gerekend. In het algemeen vertonen deze soorten aanpassingen aan een halfopen omgeving, waarbij enige afstand wordt gehouden tot grote objecten. Vooral deze soorten maken gebruik van opgaande, lijnvormige landschapselementen in cultuur-landschappen.

Verschillen tussen soorten in het gebruik van landschapselementen hangen dus samen met verschillen in morfologie, voedsel-ecologie en echolocatiegedrag. In het kleinschalige houtwallenlandschap van Twente bleek de gewone dwergvleer-muis vrijwel uitsluitend op korte afstand (<25 m) van houtwallen en bomenrijen te foerageren, terwijl de laatvlieger geregeld op tientallen meters of meer in het open terrein vloog (hoofdstuk 2). Toch vertoonde ook de laatvlieger een binding met opgaande elementen, gezien de dichtheidsafname van deze soort in open terrein bij een toenemende afstand tot het landschapselement.

Er zijn verschillende functies van lijnvormige landschapselementen voor vleermuizen denkbaar, waarmee de gevonden relaties kunnen worden verklaard:

1. *foerageerhabitat: verschillen in voedselkeuze*

De insectenrijkdom rond opgaande landschapselementen is in het algemeen groter dan in het aangrenzende open terrein. Enerzijds vormen deze landschapselementen voor veel insecten een geschikt voortplantingshabitat, anderzijds worden vooral kleine insecten op passieve wijze door de wind meegevoerd en aan de beschutte lijzijde van de elementen geaccumuleerd. De laatvlieger jaagt in het algemeen op grotere insecten dan de dwergvleermuis. Grote insecten zijn krachtige vliegers, die bij sterkere wind - en dus verder van opgaande elementen - nog actief kunnen vliegen. De kleine insecten, het voedsel van de dwergvleermuis, bevinden zich vooral in de meest tegen wind beschutte delen, d.w.z. dicht bij opgaande elementen.

2. *beschutting tegen wind: verschillen in windgevoeligheid*

Door in de windluwte van opgaande landschapselementen te vliegen, kunnen vleermuizen hun energieverbruik beperken. De relatief kleine dwergvleermuis is gevoeliger voor wind dan de veel grotere laatvlieger. De eerste moet dan ook uit energetische overwegingen meer in de beschutting van, dus dicht bij, opgaande elementen blijven.

3. *beschutting tegen predatoren: verschillen in predatiekans*

Opgaande begroeiingen kunnen dekking tegen predatoren verschaffen. Brits onderzoek geeft aan dat predatoren, zoals uilen, verantwoordelijk zijn voor ca. 10% van de jaarlijkse sterfte onder vleermuizen. De laatvlieger is een snellere vlieger dan de dwergvleermuis, en is daardoor beter in staat te ontsnappen aan een aanval van, bijvoorbeeld, een uil. De laatvlieger kan zich daarom beter permitteren in het onbeschutte open terrein te vliegen.

4. *navigatiebakens: verschillen in sonar-reikwijdte*

Opgaande landschapselementen zouden een functie kunnen vervullen als geleidende structuren voor vleermuizen. Indien vleermuizen hun sonar gebruiken om via deze structuren hun weg door het landschap te zoeken (te navigeren), dan dienen zij hiermee contact te houden ('sonar' is de afkorting van 'sound navigation and ranging' en wordt vaak in de plaats van het begrip 'echolocatie' gebruikt). De dwergvleermuis zendt minder luide echolocatiesignalen met een hogere frequentie uit dan de laatvlieger. Hoge frequenties doven sterker uit, en reiken daardoor minder ver, dan lage frequenties. Daardoor heeft de sonar van de dwergvleermuis een kleinere reikwijdte dan die van de laatvlieger. De dwergvleermuis moet dus dicht bij opgaande landschapselementen blijven om hiermee contact te kunnen houden.

Op landschapsschaal zijn er ook verschillen tussen beide soorten. De dichtheid (per vierkante kilometer) van dwergvleermuizen nam evenredig toe met de dichtheid aan houtwallen en bomenlanen. De dichtheid van laatvliegers daarentegen nam meer dan evenredig toe met de dichtheid van lijnvormige landschapselementen, hetgeen betekent dat ook per lengte-eenheid lijnvormig element meer laatvliegers werden waargenomen. De grote waarde van landschappen met een hoge dichtheid aan houtwallen voor de laatvlieger kan verklaard worden uit het feit dat in dergelijke landschappen de windbeschuttingszones van de opgaande elementen elkaar

in het tussenliggende open terrein overlappen. In deze overlappingsgebieden ontstaan luwtes waarin de wind voldoende getemperd worden om actief vliegen van grote insecten mogelijk te maken, terwijl kleinere insecten hier nog steeds niet in staat zijn te vliegen. Hiervan profiteert de laatvlieger.

Voedsel, wind en predatoren

In het voorafgaande is duidelijk geworden dat er plausibele verklaringen zijn voor het gebruik van opgaande, al dan niet lijnvormige, landschapselementen door vleermuizen, en voor de verschillen tussen soorten (hoofdstuk 2). Voor een nadere analyse van de functies van deze elementen voor vleermuizen en hun relatieve belang, is een gedetailleerd onderzoek uitgevoerd naar dwergvleermuizen en laatvliegers rond houtsingels in relatie tot voedsel, wind en predatoren (hoofdstuk 3).

VLIEGROUTES

Vleermuizen die de afstand tussen verblijfplaats en foerageergebieden overbruggen, vliegen doorgaans sneller en rechtlijniger dan foeragerende vleermuizen. Sommige soorten, zoals de watervleermuis, jagen onderweg niet. Dwergvleermuizen foerageren onderweg slechts in geringe mate.

In de avondschemering, op een vliegroute tussen verblijfplaats en foerageergebieden, bleek 81% (gemiddeld over 39 avonden) van de dwergvleermuizen boven de weg tussen de bomenrijen te vliegen. De loefzijde werd slechts incidenteel gebruikt. Dit gedrag kan niet verklaard worden uit de verdeling van voedsel en wind: insectendichtheden waren gemiddeld genomen lager en windsnelheden hoger tussen de bomenrijen dan aan de lijzijde. Anti-predatiegedrag lijkt in deze situatie een plausibele verklaring voor de vliegroute van de vleermuizen. Uit onderzoek van anderen is gebleken, dat predatierisico's het grootst zijn rond de avond- en ochtendschemering, wanneer het relatief licht is. Het risico is ook groot nabij verblijfplaatsen en nabij regelmatig gebruikte vliegroutes.

Ook wind beïnvloedde de vliegroute: het aandeel aan de lijzijde langsvliegende dieren nam toe bij toenemende windsnelheid en wanneer de wind onder een grote hoek (45°-90°) inviel.

FOERAGEERGEBIEDEN

Voor foeragerende vleermuizen lijkt de verdeling van voedsel een voor de hand liggende factor. De invloed van voedsel en wind werd onderzocht in drie situaties: aanwezigheid van wind én een relatief insectenarm open terrein (situatie 1), windstilte én een relatief insectenarm open terrein (situatie 2) en windstilte én een relatief insectenrijk open terrein (situatie 3). Het onderzoek richtte zich op de dwergvleermuis (situaties 1, 2 en 3) en de laatvlieger (situaties 2 en 3) en leverde de volgende resultaten op:

Het voorkomen van foeragerende vleermuizen rond houtsingels bleek samen te hangen met zowel voedsel als wind:

- Tussen de bomenrijen werd minder gefoerageerd dan aan de insectenrijkere en meer windluwe lijzijde.
- In het geval van een insectenrijk open terrein (situatie 3) was de verdeling

van dwergvleermuizen en laatvliegers over verschillende afstanden (3-48 m) tot de bomenlanen significant gecorreleerd met die van insecten.

- De vleermuizen concentreerden zich zowel bij toenemende windsnelheid als bij toenemende invalshoek dicht bij de bomenlaan (situatie 1; invalshoek 0° = evenwijdig aan bomenlaan, 90° = loodrecht op bomenlaan). Bij een grote invalshoek ($> 45^\circ$) was de totale vleermuisactiviteit aan de lijzijde groter dan bij een kleine invalshoek ($< 45^\circ$).

Echter, de samenhang tussen vleermuizen, insecten en wind ontbrak in insectenarme situaties:

- In situatie 1 vlogen dwergvleermuizen aan de lijzijde significant dicht bij de bomenlaan dan de aanwezige insecten (maxima op respectievelijk op 3 en 6 m van de bomenlaan) en wind (maximale windluwte op 24 m van de bomenlaan).
- In situaties 1 en 2 was er geen relatie tussen de verdeling van dwergvleermuizen over verschillende afstanden tot de bomenlaan en de afstandsverdelingen van insecten (dichtheden en biomassa) en windluwte. Hier bepaalde een andere factor, de 'afstand tot de bomenlaan', waar de dwergvleermuizen vlogen. Bij laatvliegers was dit afstandseffect afwezig.

Naast voedsel en wind, duiden de resultaten dus op het bestaan van een of meer andere factoren, die de binding van de vleermuizen aan bomenlanen verklaren. Er zijn twee mogelijkheden:

Predatie. Omdat de jacht op vleermuizen voor zichtjagers als uilen in het nachtelijk duister, naar verwachting, veel minder kans op succes biedt dan tijdens de schemering, is het risico om geïpreed te worden voor foeragerende vleermuizen rond bomenlanen vermoedelijk veel kleiner dan voor vleermuizen die tijdens de avond- en ochtendschemering tussen verblijfplaats en foerageergebieden pendelen. Bovendien zijn foerageerplekken van vleermuizen voor een predator minder voorstelbaar (in ruimte en tijd) dan vliegroutes.

Echolocatiebinding met landschapselementen. Dit zou een verklaring kunnen zijn voor het feit dat vleermuizen in de insectenarme situatie 1 dicht bij de bomenlaan vlogen, onafhankelijk van voedsel en windbeschutting.

De resultaten gaven aanleiding om het verdere onderzoek te richten op het bestaan van een echolocatiebinding van vleermuizen met landschapselementen.

Echolocatie in relatie tot het landschap

De variatie in echolocatiesignalen onder vleermuizensoorten is groot. Deze variatie lijkt vooral samen te hangen met de openheid van het habitat waarin de soort voorkomt. Individuen kunnen daarnaast op flexibele wijze hun echolocatiesignalen aanpassen aan veranderende situaties, bijvoorbeeld wanneer zij uit de beslotenheid van een boslaan een meer open omgeving invliegen.

Indien vleermuizen met hun sonar navigeren en daarbij landschapselementen gebruiken als geleidende structuren, dan moeten zij hiermee contact onderhouden. Dit zou tot uiting moeten komen in een geleidelijke aanpassing van echolocatiesignalen aan de afstand tot landschapselementen. Deze hypothese is getoetst bij de meervleermuis (hoofdstuk 5). Omdat over de meervleermuis weinig literatuur

bestaat, is vooraf een studie gemaakt van het vlieg-, foerageer- en echolocatiegedrag van deze soort (hoofdstuk 4).

De meervleermuizen in het studiegebied in Friesland gebruiken kanalen om de afstand tussen verblijfplaats en foerageergebieden te overbruggen. Geluidsoptnamen maakten duidelijk dat de vleermuizen hun echolocatiegeluiden aanpassen aan de afstand tot de kanaaloever. Bij toenemende afstand werden langere pulsen uitgezonden. Lange pulsen zijn beter geschikt voor detectie van objecten over grote afstand dan korte pulsen, omdat de kans op waarneembare echo's toeneemt. Het uitzenden van langere pulsen is dus een manier om het sonarbereik te vergroten. Het tijdsinterval tussen pulsen kan worden beschouwd als een maat voor het maximale sonarbereik (zie ook hoofdstuk 1). De duur van dit interval dient lang genoeg te zijn om de echo van het uitgezonden signaal terug te kunnen ontvangen. In het onderzoek bleek dat de vleermuizen bij toenemende afstand tot de kanaaloever de intervallen verlengden op het moment dat, bij een toenemende afstand tot de kanaaloever, deze niet meer toereikend waren om de geluidssignalen de afstand tot de kanaaloever (heen en terug) te laten overbruggen.

Uit de resultaten mag worden afgeleid dat meervleermuizen contact houden met kanaaloevers. Verdere ondersteuning voor deze hypothese kwam uit het onderzoek naar de afstandverdeling van vleermuizen in Walcheren. Dwergvleermuizen bleken zich hier vrijwel uitsluitend op te houden in een zone waar contact met de bomenlaan via echolokatie mogelijk was, d.w.z. op afstanden tot de bomenlaan die kleiner waren dan hun maximale sonarbereik van ca. 15 m.

Afweging van kosten en baten

Uit dit onderzoek blijkt dat opgaande (lijnvormige) landschapselementen om verschillende redenen van belang zijn voor vleermuizen. Het gebruik van landschapselementen varieert, en blijkt te worden bepaald door de situatie met betrekking tot voedselaanbod, wind en predatierisico.

Al kan op grond van de resultaten, niet direct worden geconcludeerd dat vleermuizen landschapselementen gebruiken, of zelfs nodig hebben, als akoestische navigatiebakens, er zijn toch duidelijke aanwijzingen dat vleermuizen contact houden met opgaande landschapselementen. Hiervoor zijn goede redenen te bedenken. Het onderhouden van sonarcontact met bekende structuren, kan de efficiëntie waarmee een vleermuis een gebied exploiteert, verhogen. Mogelijk speelt hierbij een in zijn ruimtelijk geheugen opgeslagen 'cognitieve kaart' van vliegroutes en foerageergebieden in het gebied een rol. Referentiepunten, bijvoorbeeld in de vorm van opgaande landschapselementen, kunnen een belangrijke rol spelen bij het totstandkomen van dergelijke kaarten.

Vleermuizen zijn in staat het sonarcontact met landschapselementen los te laten. Dit hoeft echter niet te betekenen dat opgaande elementen geen betekenis zouden hebben als akoestische bakens. Wanneer bijvoorbeeld de voedseldichtheid in open terrein hoog is en/of het windstil is, zou het lonend kunnen zijn om de foerageeractiviteiten meer in de richting van het open terrein uit te breiden (hoofdstuk 3). Dit weegt wellicht op tegen mogelijke extra navigatiekosten en een hoger predatierisico.

Evenzo hoeft het feit dat vleermuizen zo nu en dan open terreinen van tientallen of zelfs enkele honderden meters oversteken, niet te betekenen dat open terreinen of onderbrekingen in landschapselementen geen barrières vormen. De voedselsituatie aan 'de overzijde' kan voldoende compensatie vormen voor eventuele kosten en risico's die de oversteek met zich meebrengt. Daarnaast speelt mogelijk het gezichtsvermogen een rol bij de oriëntatie en navigatie, naar verwachting vooral in de schemering.

Geconcludeerd kan worden, dat opgaande elementen in het cultuurlandschap, zoals houtwallen, bomenlanen en bosranden, een belangrijke rol vervullen voor een aantal soorten vleermuizen. Dit gegeven is van belang voor het beheer van landschappen en landschapselementen ten behoeve van vleermuizen. Uit het voorgaande is echter nog niet duidelijk geworden wanneer een opgaand landschapselement aantrekkelijk is voor vleermuizen. Dit is een van de vragen die worden gesteld in hoofdstuk 6.

De structuur van houtsingels

De geschiktheid van een gebied voor vleermuizen hangt voor een belangrijk deel samen met de aanwezigheid van geschikte foerageergebieden, alsmede met de bereikbaarheid daarvan via corridors. In hoofdstuk 6 wordt allereerst de vraag gesteld welke eigenschappen van een opgaand landschapselement zijn geschiktheid als foerageerplek bepalen. In Walcheren, waar houtsingels vrijwel de enige vorm van opgaande begroeiing vormen, blijkt de geschiktheid van houtsingels als foerageerplek voor dwergvleermuizen gecorreleerd te zijn met de hoogte, breedte en vegetatiedichtheid (permeabiliteit) van de singels. Deze structuurkenmerken bepalen de mate van windbeschutting, een belangrijke eigenschap in een winderig kustgebied als Walcheren.

De verspreiding van potentieel geschikte foerageerplekken in het studiegebied bleek bepalend voor de keuze van vliegroutes tussen een verblijfplaats van dwergvleermuizen in een klein dorp en het omliggende landschap. Het meest gebruikt werden routes die leidden naar die delen van het landschap waar (potentieel) hoogkwalitatieve foerageerplekken op relatief korte afstand van de verblijfplaats gelegen waren.

Toepassing

Door hun mobiliteit zijn vleermuizen in staat grote afstanden af te leggen tussen hun ruimtelijk gescheiden dagverblijven en foerageergebieden. Connectiviteit tussen deze deelhabitats is dus een belangrijke voorwaarde voor de overlevingskansen van vleermuispopulaties. Het zijn juist de landschappelijke veranderingen in de afgelopen decennia, met name in het agrarisch gebied, die een belangrijke rol hebben gespeeld bij de achteruitgang van veel soorten vleermuizen.

Voor een effectieve bescherming van vleermuizen en hun habitats zijn richtlijnen noodzakelijk. Dit onderzoek levert daar een belangrijke bijdrage aan in de vorm van een aantal concrete adviezen voor de inrichting en het beheer van land-

schappen en landschapselementen in agrarische gebieden ten behoeve van vleermuizen. Juist deze agrarische gebieden, die buiten de Ecologische Hoofdstructuur vallen, staan momenteel in de belangstelling bij beleidsmakers. De in hoofdstuk 7 gegeven aanbevelingen hebben betrekking op de dichtheid, configuratie en structuurkenmerken van lijnvormige, opgaande begroeiingen, de (soortspecifieke) maximaal toelaatbare grootte van open 'gaten' in lijnvormige elementen, en de insectenrijkdom van open terreinen. De regressiemodellen met betrekking tot vleermuizen in relatie tot dichtheid, mate van fragmentatie en structuurkenmerken van lijnvormige landschapselementen (hoofdstuk 2 en 6) kunnen een toepassing vinden in studies waarin inrichtingsscenario's met elkaar worden vergeleken. De toepassingswaarde van de gegevens zou echter belangrijk kunnen worden vergroot door de ontwikkeling van een modelinstrumentarium, waarin alle kennis wordt samengebracht. In combinatie met het omvangrijke databestand van het Vleermuis Atlas Project (Limpens et al. 1997), dat gegevens bevat over de verspreiding en habitatkeuze van soorten op nationale schaal, dient een 'decision support system' te worden ontwikkeld voor beheerders en inrichters van landschappen en landschapselementen.

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Dankwoord

Toen mij in de zomer van 1991 in een Zweedse telefooncel een promotieonderzoek aan vleermuizen in het vooruitzicht werd gesteld, moest ik wel even slikken. Ik realiseerde mij dat mijn kennis van deze dieren bleef steken bij die van de gemiddelde Nederlander, of ten hoogste van een gemiddelde bioloog. Mijn definitie van vleermuizen luidde: vliegende zoogdieren, die zich in het nachtelijk duister oriënteren met behulp van echolocatie. De meest kenmerkende en essentiële aspecten van hun levenswijze had ik hiermee weliswaar te pakken, ik bevroedde echter nog nauwelijks hoe fascinerend deze dieren werkelijk zouden zijn. Vooral hun uitgebreide scala aan echolocatiegeluiden opende voor mij een nieuwe wereld. Gedurende de eerste zomermaanden na mijn aanstelling heb ik vele nachten buiten doorgebracht, waarbij mij de kneepjes van het determineren op geluid met behulp van de 'bat detector' werden bijgebracht door onder meer Herman Limpens, Kees Kapteyn en Minne Feenstra. Als verwoed vogelaar ging mij dit vrij gemakkelijk af.

De ideeën die ten grondslag hebben gelegen aan dit onderzoek, waren afkomstig van Nederlandse pioniers op het gebied van vleermuisonderzoek met bat detectors, met name Herman Limpens, Wouter Helmer, Kees Kapteyn, Kees Mostert, Ludy Verheggen en Alphons van Winden. Dat dit onderzoek van de grond kon komen is daarnaast te danken aan de inzet van Wim Bongers (LUW), Paul Opdam en Jan Veen (beiden IBN-DLO), en Peter Lina (Vleermuiswerkgroep Nederland).

Vooral in de beginperiode van mijn onderzoek vormden de kennis en ervaring van Herman Limpens op het gebied van vleermuizen een belangrijke bron van informatie en advies, in algemene zin, en in het bijzonder voor de opzet van hoofdstuk 4. Herman, op jouw krappe zolderkamertje hebben we geregeld gebrainstormd over wilde, al dan niet uitvoerbare ideeën. Na Hermans vertrek naar Duitsland diende vooral mijn co-promotor Jan Veen als inhoudelijk klankbord op het IBN-DLO. Jan, door discussies met jou is de structuur van enkele hoofdstukken belangrijk verbeterd. Daarnaast waren de discussies met, en het opbouwend commentaar van Wim Bongers, Arend Brunsting en, in het begin van mijn onderzoek, Paul Opdam van groot belang. Prof. dr. Herbert Prins wil ik bedanken dat hij als promotor wilde optreden, en voor zijn stellige en inspirerende commentaar op manuscripten. Herbert, jij wees mij er telkens en terecht op [to] "keep it simple" en "not [to] clutter [my] message". Dit kwam de helderheid van enkele stukken zeer ten goede.

Hans Huitema kwam in 1992 als gewetensbezwaarde aan het onderzoek meewerken. De samenwerking met Hans heb ik als bijzonder inspirerend ervaren. Hans, onze brainstormsessies tijdens nachtelijke fietstochten in het veld hielpen mij (en jou) om ook na drieën het hoofd erbij te houden. Twee veldseizoenen op Walcheren was je erbij. Door 'Lyme' gevelde, moest je helaas het veldseizoen in Twente grotendeels missen. Hans heeft een wezenlijke bijdrage geleverd aan hoofdstuk 2; ideeën van hem vinden hun weerslag in hoofdstuk 3 en 6.

Zonder de hulp en inzet van studenten en stagiairs was dit proefschrift niet tot stand gekomen. Arjan Boonman verrichtte zijn onderzoek aan de LUW als doctoraalstudent van de Universiteit Utrecht. Zijn kennis van en ervaring met echolocatie waren onontbeerlijk voor het welslagen van het complexe onderzoek aan de meervleermuis in Friesland (hoofdstuk 4). Martijn Boonman wil ik bedanken voor

zijn hulp in het veld. *Adam Britten and Gareth Jones, I thank you both for our pleasant and fruitful collaboration, and for introducing to me this wonderful technique of 'multi-flash stereophotogrammetry', which unravelled many aspects of pond bat behaviour.*

Erik Gorter en Kamiel Spoelstra waren studenten van de vakgroep Terrestrische Oecologie en Natuurbeheer van de LUW. Tijdens hun verblijf van drie maanden in Polen hebben zij met veel inzet en improvisatievermogen een mooie dataset verzameld en bewerkt, en zodoende hun stempel gedrukt op hoofdstuk 3. *Dr. Michael Kozakiewicz (Warsaw University), thank you for helping us to organise our stay in Poland. Dr. R. Halba (Warsaw University), Elzbieta and Maćiek Fuszara, and Grzegorz Lesinski (Institute of Ecology, Łomianki), many thanks for your hospitality and for sharing with us such a good time on this wonderful spot at the Urwitaf Field Station.* Liesbeth Brussen, Marian van Lieshout, Bert Oude Egbrink, Bas Slatman, Vera Streutker, Bianca de Vos en Eva Willems hebben als assistent of stagiaire een belangrijke bijdrage geleverd aan veldwerk in Twente, Walcheren en Friesland. Cor Berrevoets, Coos Ettema, Aylin Erkman, Anton van Haperen, Jan en Daniël Goedbloed, Jan Hengst, Marcel Klootwijk, Luud Persijn, Leo Santbergen, Joop Scheijbeler, Bert van Staveren en Fred Twisk hielpen mee aan simultaantellingen op Walcheren.

Het IBN-DLO heb ik altijd als een zeer inspirerende werkplek ervaren. Ik dank mijn collega's en afdelingsgenoten voor de prettige sfeer. Zowel vanuit de LUW als het IBN-DLO heb ik altijd voldoende ruimte bij de uitvoering van mijn onderzoek gekregen.

Ludy Verheggen, Kees Kapteyn en Rombout de Wijs dank ik voor het kritisch doornemen en becommentariëren van manuscripten. Hilko van der Voet dank ik voor zijn statistische ondersteuning. Thom van Rossum wil ik bedanken voor de eindredactie van het proefschrift.

Jana wil ik bedanken voor haar morele steun en flexibiliteit tijdens mijn onderzoek. Jana, wanneer ik voor veldwerk tijdens zomermaanden langdurig afwezig was, wist jij de opvoeding en verzorging van Lukas en Simon in hun eerste levensjaren op energieke en creatieve wijze te combineren met jouw eigen drukke baan.

Tot slot wil ik mijn moeder bedanken, voor het feit dat zij, al in mijn prille jeugd, mijn belangstelling voor biologie heeft gestimuleerd en mij alle ruimte heeft gegeven mijn kennis van plantjes en beestjes te vergroten.

Curriculum vitae

Ben Verboom werd geboren op 8 oktober 1962 te Amsterdam. Na het behalen van het diploma Gymnasium-B op de Christelijke Scholengemeenschap Overvoorde in 1981, studeerde hij biologie aan de Rijksuniversiteit Leiden, waar hij in 1987 het doctoraalexamen aflegde. Het hoofdvak dieroecologie werd gevolgd op de Katholieke Universiteit Nijmegen (bij dr. J.J. van Gelder), en bestond uit een studie van kolonisatie-kansen van nieuwe poelen door amfibieën in Zuid-Limburg, alsmede van de effecten van poelgrootte en isolatie op deze diergroep. Daarnaast werd een vangst-terugvangst onderzoek gedaan van de geelbuikvuurpad *Bombina variegata*. Aan de RUL werd het bijvak plantenecologie gedaan (bij dr. A.H. Prins). Onderwerp was de relatie tussen de vlinder *Ethmia bipunctella* en hondstong *Cynoglossum officinale*, waarbij vooral gekeken werd naar de door vraat geïnduceerde afweer door de plant. In 1988 en 1989 was Ben Verboom volontair onderzoeker op de afdeling Landschapsecologie van het Instituut voor Bos- en Natuuronderzoek (IBN-DLO), het toenmalige Rijksinstituut voor Natuurbeheer (RIN), waar hij de effecten van habitatfragmentatie op de eekhoorn, en op evertrebraten-populates in schraalgraslanden in Zuid-Limburg, onderzocht. In 1990 werkte hij als freelance onderzoeker aan twee projecten. In opdracht van Heidemij Adviesburo B.V. voerde hij een ecologische inventarisatie uit van insecten in een bos/heide-terrein. Daarnaast werd, in opdracht van de toenmalige Directie Natuur-, Milieu- en Faunabeheer (NMF) van het Ministerie van Landbouw, Natuurbeheer en Visserij, populatie-dynamisch onderzoek verricht aan de geelbuikvuurpad in Zuid-Limburg. In 1991 trad hij in dienst van de vakgroep Terrestrische Oecologie en Natuurbeheer (TON) van de Landbouwniversiteit Wageningen. Als DLO-AIO was hij gedetacheerd op de afdeling Dieroecologie van het IBN-DLO. Dit proefschrift is hieruit voortgekomen. Hij is getrouwd met Jana Vasiljev en is vader van twee kinderen, Lukas (1993) en Simon (1994).