Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*

B. Verboom and K. Spoelstra

Abstract: We tested the hypotheses that the distance bats fly from tree lines depend on food abundance and protection from wind. We monitored the activity of pipistrelle bats (*Pipistrellus pipistrellus*) and measured insect abundance and wind speed and direction at fixed distances up to 50 m from tree lines. We compared bat behaviour in different situations: with and without wind and with low and high insect abundances in adjacent open areas. In all situations, pipistrelle bats' activity decreased with increasing distance from the tree line. Within nights, we found no effect of wind speed on bat activity (sound recorded per 5 min) on the leeward side of the tree lines. Between nights, however, bats concentrated their activities closer to the tree lines at high wind speeds or angles of incidence of wind from 45° to 90°. A significant relationship between bat and insect abundances was found only when the tree line was bordered by insect-rich grassland. Since wind and insect abundance only partly explained the distances bats flew from tree lines, two alternative explanations, namely predator avoidance and the use of tree lines as acoustic landmarks, are discussed. Pipistrelle bats using a double row of trees as a commuting route at dusk flew mainly between the tree lines, regardless of insect abundance or wind speed. It is argued that predator avoidance explains this behaviour, being a constraint on movements of bats at relatively high light levels. At high wind speeds and angles of incidence greater than 45°, the proportion of pipistrelle bats commuting on the leeward side of the tree lines increased.

Résumé : Nous avons éprouvé l'hypothèse selon laquelle la distance parcourue au vol par les chauves-souris depuis la bordure d'une forêt peut s'expliquer par l'abondance de la nourriture et la protection contre le vent. Nous avons observé l'activité des pipistrelles (*Pipistrellus pipistrellus*) et mesuré l'abondance des insectes, la vitesse du vent et sa direction à des distances fixes, jusqu'à 50 m de la limite d'une forêt. Nous avons comparé le comportement des chauves-souris dans diverses situations, avec ou sans vent, en présence de beaucoup ou de peu d'insectes dans les zones ouvertes adjacentes. Dans toutes les situations, les chauves-souris diminuent leur activité à mesure qu'augmente la distance de la forêt. Au cours d'une même nuit, la vitesse du vent est sans effet sur l'activité des pipistrelles (cris en registrés toutes les 5 minutes) du côté sous le vent de la limite de la forêt. Il y a cependant variation d'une nuit à l'autre et les pipistrelles concentrent leurs activités plus près des arbres lorsque la vitesse du vent est élevée ou l'angle d'incidence entre 45° et 90°. Une relation significative entre les chauves-souris et les insectes prévaut seulement lorsque la limite de la forêt longe une zone herbeuse riche en insectes. Puisque le vent et l'abondance des insectes n'expliquent que partiellement la distance parcourue par les chauves-souris depuis la limite de la forêt, nous avons envisagé deux autres explications possibles, la fuite des prédateurs et l'utilisation de la limite de la forêt comme repère acoustique. Les pipistrelles qui utilisent une double rangée d'arbres comme route de passage au crépuscule volent surtout entre les arbres, quelles que soient l'abondance des insectes ou la vitesse du vent. La fuite des prédateurs peut expliquer ce comportement, puisqu'elle représente une contrainte aux déplacements des chauves-souris à des taux d'éclairement relativement élevés. Lorsque la vitesse du vent est élevée et l'angle d'incidence de plus de 45°, la proportion des pipistrelles qui se déplacent du côté de la double rangée d'arbres sous le vent augmente.

[Traduit par la Rédaction]

Introduction

The distributions of many bat species are known to be associated with edge habitats, such as forest edges, forest tracks, tree lines, and hedgerows (Racey and Swift 1985; Limpens et al. 1989; Krull et al. 1991; Rieger et al. 1990; Limpens and Kapteyn 1991; De Jong 1994; Grindal 1996; Walsh and Harris 1996a, 1996b; Brigham et al. 1997; Verboom and Huitema 1997; Grindal and Brigham 1998). Depending on the species, commuting bats may use edge habitats as flyways, feeding sites, or both. Several hypotheses have been put forward to explain why bats use vertical,

B. Verboom. Alterra (formerly Institute for Forestry and Nature Research), P.O. Box 23, NL-6700 AA Wageningen, the Netherlands,[1] and Department of Terrestrial Ecology and Nature Conservation, Wageningen Agricultural University, P.O. Box 338, NL-6700 AH Wageningen, the Netherlands.
K. Spoelstra. Department of Terrestrial Ecology and Nature Conservation, Wageningen Agricultural University, P.O. Box 338, NL-6700 AH Wageningen, the Netherlands.

[1]Address for correspondence (e-mail: b.verboom@ibn.dlo.nl).

often linear, landscape elements. *Food*: insect densities are generally higher near vertical landscape elements than in nearby open areas (Lewis and Stephenson 1966; Lewis 1969a, 1969b, 1970; Lewis and Dibley 1970). However, Ekman and De Jong (1996) found that pipistrelle bats (*Pipistrellus pipistrellus* (Schreber, 1774)) still preferred the edges of forests to open areas, although insect abundance was higher in the latter. This suggests that one or more other factors may limit the use of open habitats by these bats. *Shelter from wind*: to minimise flight costs, it is profitable for a bat to minimise exposure to wind (Norberg and Rayner 1987; Norberg 1990). The influence of wind on the commuting and foraging behaviour of bats has been reported in several studies (Nyholm 1965; Voûte 1972; Racey and Swift 1985; Rieger et al. 1990). *Predator avoidance*: predation may have shaped bat behaviour, and predation risk may explain why many bats avoid open areas and stay close to vegetation, where they are less conspicuous than in open terrain. Although actual instances of predation on bats have only rarely been recorded, bat mortality due to predation, mainly by owls, may be considerable in some areas (Speakman 1991), and predation pressure is often hypothesised to affect bat behaviour (Rieger et al. 1990; De Jong 1994; Rydell et al. 1996). *Navigational landmarks*: Limpens et al. (1989) and Limpens and Kapteyn (1991) hypothesised that bats use edge habitats as navigational landmarks. There are indications that bats maintain acoustic contact with vertical landscape elements (Verboom et al. 1999). The limited echolocation range of bats may then constrain them to fly within acoustic range of landscape elements and thus away from open areas.

The purpose of our study was to test the hypotheses that food abundance and protection from wind determine the distance which pipistrelle bats fly from tree lines. According to the "food hypothesis," bats will hunt where food is most abundant. The "wind hypothesis" states that bats will fly where wind reduction by the tree line is greatest. We compared the distributions of foraging pipistrelle bats in relation to tree lines with those of insect abundance and wind (speed and direction). We compared three situations: (1) with wind and low insect abundance in open areas adjacent to the tree lines, (2) no wind and low insect abundance, and (3) no wind and high insect abundance. We furthermore studied commuting behaviour at dusk in relation to food abundance and wind. Since pipistrelles only occasionally attack prey while commuting to their foraging areas at dusk (personal observation), we expected the influence of food abundance on commuting behaviour to be small. We did, however, expect commuting bats to minimise exposure to wind.

Study sites and methods

Study sites

One study area, the "meadow-NL" site, was in the southwestern part of the Netherlands (Walcheren, province of Zeeland, 51°27′N, 3°38′E). This agricultural area consists of approximately 60% fields and 40% intensively managed (grazed and hay) meadows. There is a network of tree lines, mainly along roads. The study site was located near a double tree line (i.e., two parallel rows of trees) bordering a 3 m wide paved road. Adjacent open areas on both sides were hay meadows (dominated by *Lolium perenne*) with some low-density grazing by cattle. Species in the tree line were *Carpinus betulus* and *Fraxinus excelsior*. The average tree height

was 9 m. Underneath the trees there was a 3–4 m (mean 3.5 m) high shrub layer with *C. betulus*, *F. excelsior*, *Crataegus monogyna*, and *Salix alba*. Permeability of the vegetation was visually estimated over a 100-m stretch (50 m at both sides of the sampling point). Visual permeability of the tree line was estimated to be 10–30% in the shrub layer and 60–80% between the shrub layer and the tree crowns, 3.5–5 m above the ground, and 10–20% at tree-crown height.

There were two reasons for selecting two further study sites in Poland: (1) no tree lines similar to the one at meadow-NL but bordered by insect-rich grassland were found in potentially suitable study areas in the Netherlands (i.e., with tree lines like those at meadow-NL and high densities of pipistrelle bats), and (2) calm nights were rare in these (coastal) areas in the Netherlands. The study sites were located in the Mazury district of northeastern Poland, close to the Urwitalt Biological Station of the University of Warsaw (53°87′N, 21°66′E). Approximately 50% of the land in this agricultural area consists of crop (mainly cereals) fields and 50% of extensively managed (grazed and hay) meadows, generally rich in herbs and insects. A few wood lots are present, and a network of mostly double tree lines borders many of the roads. Measurements took place near two double tree lines, one bordered by insect-rich grassland with a variety of herbs (the "meadow-PL" site) and the other by cereal-crop (*Triticum aestivum* and *Avena sativa*) fields (the "field-PL" site). Mean tree height was 11 m at meadow-PL and 13 m at field-PL, with bare trunk for the first few metres above the ground. The tree line at meadow-PL was dominated by *Tilia* spp., whereas *Acer pseudoplatanus* was the main species at field-PL. There was a layer of scattered shrubs, mainly *Sambucus nigra*. Estimated visual permeability was 80–90% up to 4–5 m high and 10–20% at tree-crown height.

Bat activity at the study sites

The study was confined to pipistrelle bats ("46 kHz phonic type"; Jones and Van Parijs 1993). A previous inventory of the study sites indicated that all sites were used as foraging sites by pipistrelle bats. Mapping of flight routes indicated that pipistrelle bats used the tree line at meadow-NL as one of the main commuting corridors between their roosts in a nearby village (approximately 2 km away) and foraging sites along the tree lines and in a wood lot approximately 1.3 km away. The pipistrelle maternity roosts nearest to meadow-PL and field-PL were 0.8 and 0.7 km, respectively, from field-PL. Foraging sites were along tree lines and wood-lot edges and along the edges of lakes and ponds.

Sampling methods and techniques

We define *foraging bats* as those remaining in a particular area for some time to feed, whereas *commuting bats* travel between roost and foraging sites. The flight of commuting bats is straighter and flight speed is higher than in foraging bats (Jones and Rayner 1989; Britton et al. 1997).

From May to August 1995, foraging bats were sampled at a fixed point for each of the three tree-line sites along a line perpendicular to the tree line. At meadow-NL, each point sample consisted of a series of eight distance samples: (1) 3, 6, 9, 12, 24, and 48 m from the tree line on the leeward side, (2) between the tree lines, and (3) 3 m from the tree line on the windward side. At meadow-PL and field-PL, point samples were taken only on the leeward side and comprised a series of five distance samples taken 3, 12, 24, and 48 m from the tree line. Foraging bats were surveyed from 1.5 h after sunset to 1.5 h before sunrise. To overcome time effects, distance samples were taken in random sequence for each point sample. We took 32 point samples over 32 nights at meadow-NL, 44 point samples over 14 nights at meadow-PL, and 51 point samples over 15 nights at field-PL.

For each distance sample, we counted bats, measured the wind speed, and sampled the insect fauna. Since pipistrelle bats are aerial hawking bats (Schober and Grimmberger 1989), we only took aerial insect samples. At meadow-PL and field-PL, samples were taken on calm nights only (wind speed < 0.2 m/s). Passes of pipistrelle bats were scored during 5-min periods, and the total time (in seconds) that pipistrelle bats were detected per 5-min period was also recorded. USA mini-2 bat detectors (Ultra Sound Advice, London, U.K.) were used at meadow-NL and Pettersson D-100 detectors (Pettersson Elektronik, Uppsala, Sweden) at the Polish sites, both with headphones. Detectors were held at chest height and pointed upwards. To restrict detection at a certain distance from the tree line to a narrow column of air above the researcher, the detector sampling space was concentrated by installing a plastic (QMC mini-2) or aluminium horn (Pettersson D-100).

At each distance we measured wind speed with a sensitive cup-anemometer placed on a tripod 1.80 m high. The angle of incidence of the wind was defined as the angle between the wind direction and the tree line (parallel to the tree line = $0°$, perpendicular to the tree line = $90°$). In open areas wind speed was measured 50 m from the tree lines on the windward side before, midway through, and after each point sample. The wind reduction caused by the tree line, the *relative wind speed*, is expressed as the wind speed at a given distance from the tree line (on the leeward side) divided by the wind speed in the open area on the windward side.

After counting bats and measuring wind speed, we sampled insects with a 0.45 m diameter hand net. Distance samples were taken by standardised sweep-netting along a 30-m line equidistant from the tree line (at the same distance as the bat sample). We took 100 sweeps while walking in one direction and another 100 when returning to the starting point. Minimum and maximum height of each sweep was 2 and 3.5 m, respectively. Some sweep-netting at greater heights (up to 6 m) showed us that insect densities were lower than at the sampling heights. The contents of sweep-net samples were placed in jars containing ethyl acetate to kill the insects and then transferred to labelled jars containing alcohol (30%) for counting the insects and determining their dry mass.

The heights at which wind speed was measured and insects were sampled were within the range where most of the pipistrelle bats attacked prey. Although foraging bats generally flew at (visually estimated) heights between 1 and 7–8 m, when attempting to catch prey many bats made dives from the upper half downwards to the lower half of this range, where most of the feeding buzzes were heard. Hence, insect samples are assumed to be representative of prey availability at the height where bats were foraging. Likewise, it is assumed that the wind-shelter pattern at 1.80 m is representative of the heights at which bats flew.

Commuting pipistrelle bats were surveyed from dusk until feeding buzzes marked the onset of foraging, usually 1 h after sunset. We assessed the activity of commuting pipistrelle bats by visual counting and using bat detectors in a small gap (5 m) in the tree lines. This gap was 50 m from the place where we took (foraging) point samples at meadow-NL. Counting was done by three observers, one standing on the windward side of the tree line, one on the road between the lines of trees, and one on the leeward side of the tree line. The end of the commuting period was defined as the absence of commuting bats for at least 10 min or the onset of foraging activity (feeding buzzes, bats flying in the opposite direction). Just before and just after the commuting period, insects were sampled and wind speed was measured both between the tree lines and on the leeward side 3 m from the tree line. Flight heights of commuting bats could easily be estimated by a standing observer, since most commuting bats could be seen very well for some time when they approached the observer between the tree lines. Furthermore, we measured wind speed at heights of 3 and 4.5 m between the tree lines by standing on a ladder and holding the tripod with anemometer at the appropriate heights.

Data analyses

We used linear regression analysis to assess bat activity in relation to insect parameters and wind. Since we used only three study sites, we used t tests to specifically compare meadow-NL with meadow-PL, meadow-NL with field-PL, and meadow-PL with field-PL (rather than an F test, which would deal with site differences in general). We used a comparison-wise significance level of 95% and, as advocated by Saville (1990), did not apply more complicated multiple-comparison procedures. To test whether distribution maxima for pipistrelle bats were correlated with maxima of aerial insect density and mimima of relative wind speed, we calculated bootstrap confidence limits on the distances between the modi in each pair of distributions. For this, we applied the bias-corrected and accelerated nonparametric bootstrap (with 1000 iterations) described by Efron and Tibshirani (1993).

Regression analyses and bootstrap analyses were done using GENSTAT (Genstat 5 Committee 1993, 1995). Other statistical tests were done using STATISTIX (Analytical Software, St. Paul, Minn.).

Results

Distance distributions near tree lines

Since calm nights (wind speed < 0.2 m/s; $n = 7$) were scarce at meadow-NL and bat activity during these nights was very low (lower than at wind speeds >0.2 m/s; t test, $P < 0.05$), data analyses at meadow-NL were restricted to nights with wind speeds >0.2 m/s.

At meadow-NL, pipistrelle foraging activity on the leeward side was mainly confined to 3–12 m distance from the trees (Fig. 1), and was significantly lower at 24 and 48 m (t test, significant drop between 12 and 24 m, $P < 0.005$). However, at the calm Polish sites, pipistrelle foraging activity at 24 and 48 m was relatively high compared with that at 3 and 12 m. Absolute differences in bat foraging activity between the three sites were assumed to be related to the distances to the respective roosts and were not taken into account.

We investigated the relationship between foraging activity distributions for pipistrelle bats using regression analyses (Table 1). At all three study sites, "distance to tree line" explained a significant amount of the variation in pipistrelle activity.

### Bat foraging activity in relation to insect abundance

Mean insect abundance on the leeward side at meadow-PL exceeded that at field-PL and meadow-NL (Fig. 2; t test, $P < 0.05$ (number) and $P < 0.005$ (biomass)). Mean insect density and biomass at field-PL equalled those at meadow-NL (t test, $P > 0.05$). At all three sites, Nematocera (Diptera) made up approximately 90% of insect numbers. Particularly large insects, such as noctuid moths, were rarely caught at any site.

Pipistrelle (Table 1) foraging activity was significantly related to insect density (number per sample), but at meadow-PL only. At meadow-NL, bootstrap analyses indicated that maximum pipistrelle activity (3 m from the tree line) occurred significantly closer to the tree line than maximum insect density (6 m).

Bat foraging activity in relation to wind

Pipistrelle foraging activity at meadow-NL was not affected by wind speed (Table 1). The maximum reduction in

Fig. 1. Activity of pipistrelle bats (*a*), insect abundance (*b*), and relative wind speed (*c*) at fixed distances from double tree lines at the three study sites, meadow-NL, meadow-PL, and field-PL. Vertical bars represent standard deviations. Data were collected at wind speeds >0.2 m/s at meadow-NL (*n* = 32) and on calm nights (wind speed < 0.2 m/s) at meadow-PL (*n* = 44) and field-PL (*n* = 51).
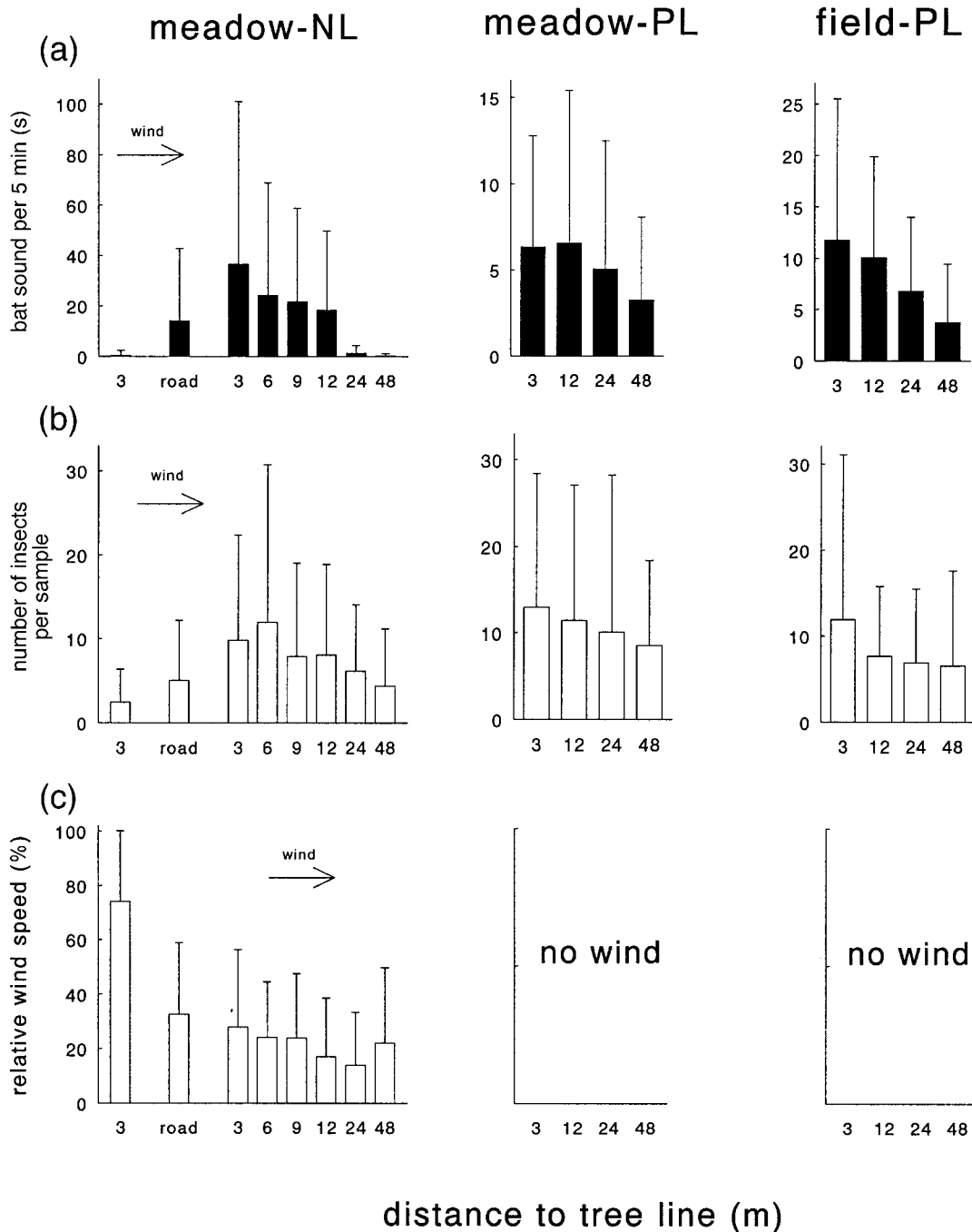
wind speed on the leeward side of the tree line occurred at 24 m. The minimum relative wind speed occurred significantly farther from the tree line than maximum pipistrelle activity (bootstrap analyses).

Both the velocity and the direction of the incident wind affected the distance distribution of foraging pipistrelle activity at meadow-NL (Fig. 3), where wind speed ranged from 0 to 5.6 m/s (mean = 1.6 ± 1.3 m/s; *n* = 39 point samples, *n* = 39 nights). There was no difference in mean pipistrelle activity during point samples at low (0.2–1.5 m/s)

and high wind speeds (>1.5 m/s). At all wind speeds, foraging activity on the leeward side was lower 24 and 48 m than 3–12 m from the trees (*t* test, significant drop between 12 and 24 m, $P < 0.005$). Mean activity 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 analysis indicated that pipistrelle activity on the leeward side was increasingly concentrated near the tree line as both wind speed and angle of incidence increased. The slope of the regression line of the distance

Table 1. Linear regression analyses of distance to trees (A), insect abundance (numbers and biomass per sample; B), and relative wind speed (C) on pipistrelle activity (sound recorded per 5 min) at the three study sites.

	Study site	Regression coefficient	SE	R^2	P
Distance to tree line (A)	Meadow-NL	–0.756	0.185	0.08	0.0001
	Meadow-PL	–0.077	0.033	0.03	<0.05
	Field-PL	–0.177	0.041	0.10	<0.0001
Insects (B)					
Number	Meadow-NL	–0.214	0.228	—	>0.05
	Meadow-PL	0.119	0.037	0.06	<0.005
	Field-PL	0.053	0.061	—	>0.05
Biomass	Meadow-NL	64.038	381.930	—	>0.05
	Meadow-PL	69.26	599.900	—	>0.05
	Field-PL	–220.578	210.070	—	>0.05
Wind (C)					
Relative wind speed	Meadow-NL	0.088	0.118	—	>0.05
Multiple analyses*					
B + C + A	Meadow-NL	–0.719*	0.184*	0.08	0.0001*
B + A	Meadow-PL	–0.067*	0.033*	0.09	<0.05*
B + A	Field-PL	–0.180*	0.0414*	0.12	<0.0001*

Note: "Multiple analyses" show the results of "distance to treeline" only, after correction for insect abundance (numbers and biomass) and wind speed.
   *Distance to tree line only.

distribution (with the total number of bats per series as a weighting variable) was positively related to wind speed (mean per series; regression coefficient = –0.439, SE = 0.185, R^2 = 13.2, P < 0.05) and angle of incidence (regression coefficient = –0.036, SE = 0.013, R^2 = 17.8, P < 0.01).

Pipistrelle activity 3 m from the tree lines on the leeward side was, on average, greater than on the windward side (Fig. 1; meadow-NL, t test, P < 0.005; n = 32). However, at wind speeds <1.5 m/s and angles of incidence <45°, differences were not significant, whereas at wind speeds >1.5 m/s (t test, P < 0.05) and angles of incidence >45° (P < 0.005), activity levels on the windward side were much lower (Fig. 3).

Commuting bats

The majority of commuting bats at meadow-NL passed between the tree lines, flying in a straight line at a height of 2.5–3.5 m above the road, just below the top of the 3.5–4 m high layer of shrubs. Wind speeds measured at a height of 4.5 m were approximately three times higher than at 3 m. At a height of 1.8 m, the average wind speed was only 60% of that at 3 m.

The number of commuting bats passing per evening count ranged from 5 to 54 (23.9 ± 12.2; n = 39 counts). On average, 81% of the bats flew over the road between the tree lines, 2% flew on the windward side of the tree lines, and 17% flew on the leeward side of the tree lines. Logit regression showed that the proportion of bats commuting along the leeward side increased with wind speed (regression coefficient = 0.898, SE = 0.084, P < 0.0001) as well as with angle of incidence of the wind (regression coefficient = 0.0281, SE = 0.004, P < 0.0001) at the tree line (Fig. 4).

On 12 of the 39 evenings when commuting bats were counted, we also sampled insect densities and measured

Fig. 2. Insect abundance (mean number and biomass per sample) at the three study sites, meadow-NL, meadow-PL, and field-PL. Values (mean ± standard deviation) are averaged over distances 3, 12, 24, and 48 m from the tree lines.
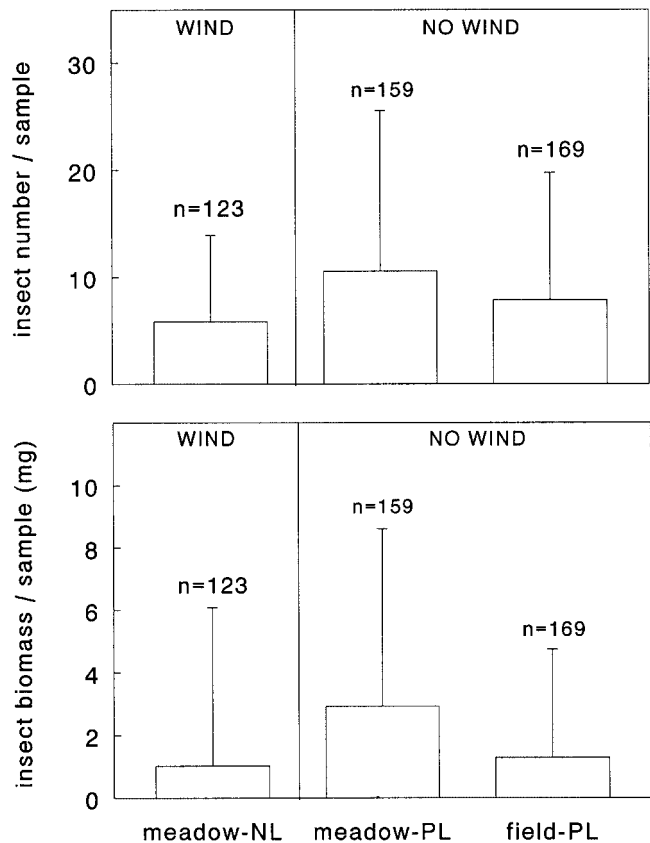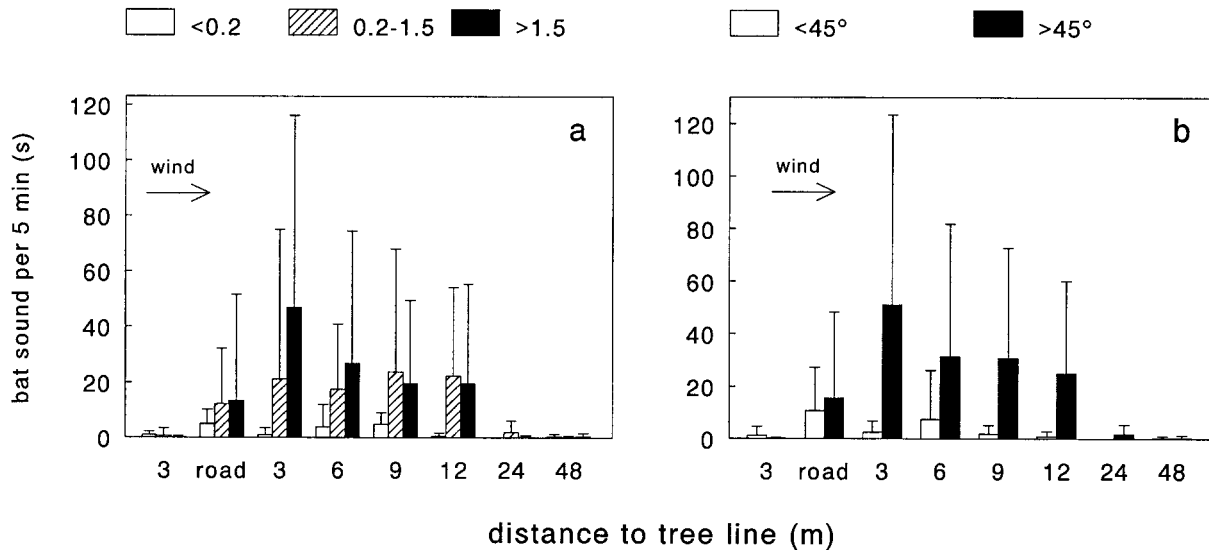
Fig. 3. Activity of pipistrelle bats at meadow-NL at different wind speeds, <0.2 m/s ($n = 7$), 0.2–1.5 m/s ($n = 16$), and >1.5 m/s ($n = 16$) (*a*), and different angles of incidence, <45° ($n = 10$) and >45° ($n = 22$) (*b*).

wind speed between and on the leeward side of the tree lines (Table 2). The large proportion of pipistrelle bats commuting between the tree lines (84%) compared with the leeward side during these 12 evenings was not explained by either wind speed or insect abundance. While bats flew more often between the tree lines 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 tree lines.

Discussion

Why do bats fly along tree lines?

Our study demonstrates that insect abundance (density and biomass) and wind (speed and direction) have an impact on the distances foraging pipistrelle bats fly away from tree lines. However, in the absence of wind or when insect abundance is low in the nearby open area, this relation was absent.

We predicted that activity of foraging bats would be 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. 1; meadow-NL). Relative wind speed at meadow-NL was at a minimum 24 m from the tree line (although the real minimum may have been anywhere between 12 and 48 m). This is about three times the height of the tree line, which agrees with wind-shelter patterns found by others (e.g., Nägeli 1946; Lewis and Stephenson 1966; Lewis and Dibley 1970).

Since wind strongly affects the distribution of insects near windbreaks (e.g., Lewis 1970), we expected to find a correlation between the distribution of insects and wind shelter in our study, but this was not the case (Fig. 1). This can be explained by the fact that aerial insect distributions near tree lines are due to an accumulation of insects which have been passively blown from the windward to the leeward side, and 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 will show distribution patterns that are more biased towards the tree line and more evenly spread across the open area, respectively (Lewis 1970). Thus, assuming that the aerial insects include representatives of all three categories, maximum insect densities at meadow-NL are expected to occur closer to the tree line than the wind-shelter pattern alone would predict.

In all situations we investigated, a strong distance relationship existed for pipistrelle bats relative to tree lines, even after correction for insect and wind parameters (Table 1). This suggests the involvement of one or more additional explanatory factors in the relationship between pipistrelle bats and tree lines.

One explanation for the occurrence of bats near tree lines may be the potential threat of predators. Because of an increase in the predation risk, even when food is abundant, an animal may have to allocate more time to predator avoidance (Milinski 1986). Therefore, predation, being an important selective force, may explain why bats commute and forage in environments where they are less conspicuous and more likely to escape attack, e.g., near tree lines and forest edges (Rieger et al. 1990; De Jong 1994). Since owls and birds of prey hunt using visual cues, predation risk is likely to become less significant as light levels decrease. Moreover, commuting bats using regular flight routes are a more predictable prey source for predators than hunting bats with activity patterns that vary 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 horseshoe bats, *Rhinolophus ferrumequinum* (Schreber, 1774), progressively increased their flight height as it became darker (Schofield 1996). Other species have been observed to shift their hunting activities to more open environments after dusk as darkness increased (*Pipistrellus pipistrellus* and *Myotis daubentonii*; Rydell et al. 1994), or over the summer

Table 2. Numbers of commuting pipistrelle bats, insect numbers (mean of samples taken just before and just after the commuting period), and wind speed between the tree lines and on the leeward side of the tree lines on 12 evenings at meadow-NL in 1995.

| | No. of bats commuting | | No. of insects per sample | | Wind | | |
| | | | | | Speed (m/s) | | Angle of incidence (deg.) |
	Road	Leeward side	Road	Leeward side	Road	Leeward side	
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	62
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

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 our study: the majority of pipistrelle bats commuted between the tree lines, while most foraging activity took place on the more exposed leeward side. Only high wind speeds and angles of incidence close to 90° forced the bats to commute along the leeward side

Another explanation for the spatial relationship between bats and tree lines is that bats use them as acoustic landmarks and hence remain in contact with them by means of echolocation. Insectivorous bats use echolocation to detect prey and avoid obstacles. It has been suggested that vespertilionid bats use vertical elements as landmarks for orientation and that echolocation range is a possible constraint on the use of open areas (Limpens et al. 1989; Limpens and Kapteyn 1991). Recently, in a study on commuting pond bats, *Myotis dasycneme*, Verboom et al. (1999) found indications that bats maintain acoustic contact with vertical landscape elements by gradually adjusting their pulse emissions according to the distance to canal banks.

However, bats are frequently found commuting and foraging in open areas, well outside the range where they can perceive landscape elements by echolocation (Kalko and Schnitzler 1993; De Jong 1994; Verboom and Huitema 1997). If we assume that the duration of interpulse intervals determines the maximum distance over which bats can perceive objects while avoiding overlap between outgoing pulse emissions and returning echoes, it is possible to predict the distance at which a pipistrelle bat loses contact with an object. Since sound travels approximately 0.34 m in 1 ms, an average search-phase interpulse interval of 80–98 ms for pipistrelle bats foraging near tree lines (Ahlén 1990; Kalko and Schnitzler 1993; Vaughan et al. 1997) corresponds to 13.6–16.7 m. This agrees with the sudden drop in activity between 12 and 24 m from the tree line at meadow-NL. At

Fig. 4. Proportions of pipistrelle bats commuting along the leeward side of tree lines at different wind speeds (*a*) and angles of incidence (*b*) at meadow-NL.
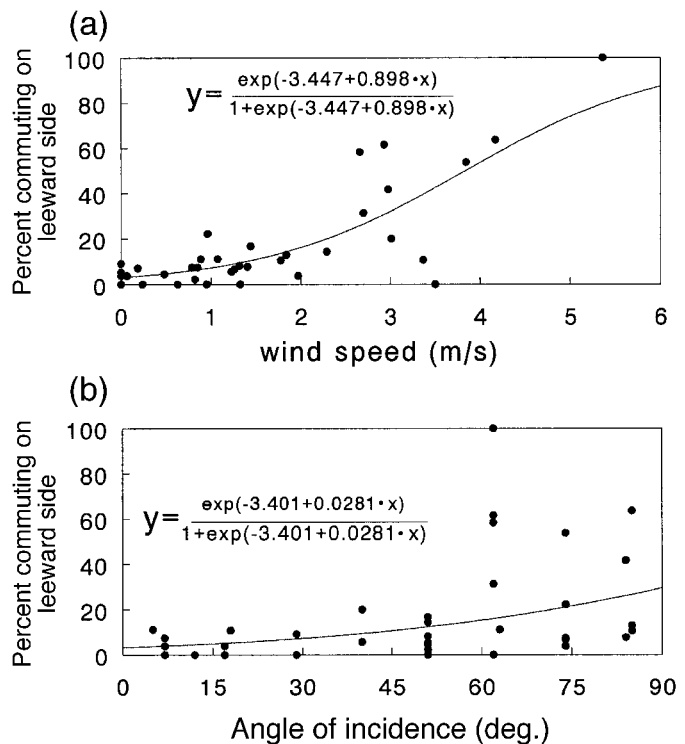
the Polish sites, however, pipistrelle activity at 24 and 48 m remained relatively high (Fig. 1).

These observations imply that constraints possibly imposed by the interpulse interval are not very strict and this raises the question of whether there are benefits to staying in acoustic contact with landscape elements. If we assume that

landmarks play a role in their spatial orientation, bats which are active outside the distance range where landscape elements can be perceived by means of echolocation may have to spend extra time finding their way back to familiar landmarks. Hence, staying within acoustic range would save time that could be allocated to other activities like foraging. When insect abundance increases, bats may be more inclined to forgo contact with landmarks. Although bats then have to invest more time in orientation and navigation, this may be outweighed by the benefits of more efficient foraging. It is also possible that bats use vision to maintain contact with vertical elements such as trees.

Flight height of commuting bats

The vast majority of commuting pipistrelle bats passed at a height of 2.5–3.5 m above the road, between the tree lines. Flying higher would be more costly, since the permeability of the vegetation would increase from approximately 20% at the shrub layer to approximately 70% between the shrub layer and the tree crowns, and the bats would be more affected by wind. Flying even higher, where the crowns of both tree lines approach each other closely, would not allow for straight flight and hence would 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 shrub layer. One explanation is that bats keep a minimum distance when flying parallel to objects (vegetation, ground) in order to avoid pulse–echo overlap. The minimum distance can be calculated from the length of the emitted pulses. For a pipistrelle bat emitting pulses with an average duration of approximately 5.5 ms (wideband mode; Kalko and Schnitzler 1993), a minimum distance of 5.5×0.17 m = 0.94 m from the ground and the vegetation at the sides would be required. According to Kalko and Schnitzler (1993), pulse–echo avoidance could explain why pipistrelle bats usually remain at least 2 m from large obstacles.

Significance for bat conservation

The conclusions drawn from our study have implications for the conservation of bats and their habitats. Vegetation corridors such as tree lines are important to foraging bats, since they support a relative high insect abundance and provide shelter from wind. A high insect abundance in adjacent open areas may promote the exploitation of the open areas.

An essential function of tree corridors for commuting bats at dusk and dawn may be 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 the dusk and dawn periods are relatively long. A network of contiguous tree corridors may therefore help bats on their way to foraging grounds to exploit an area efficiently.

Acknowledgements

References

Ahlén, I. 1990. Identification of bats in flight. Swedish Society for Conservation of Nature and the Swedish Youth Association for Environmental Studies and Conservation, Stockholm.

Brigham, R.M., Grindal, S.D., Firman, M.C., and Morissette, J.L. 1997. The influence of structural clutter on activity patterns of insectivorous bats. Can. J. Zool. **75**: 131–136.

Britton, A.R.C., Jones, G., Rayner, J.M.V., Boonman, A.M., and Verboom, B. 1997. Flight performance, echolocation and foraging behaviour in pond bats, *Myotis dasycneme* (Chiroptera: Vespertilionidae). J. Zool. (Lond.), **241**: 503–522.

De Jong, J. 1994. Distribution patterns and habitat use by bats in relation to landscape heterogeneity, and consequences for conservation. Rep. No. 26, Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala.

Efron, B., and Tibshirani, R.J. 1993. An introduction in the bootstrap. Chapman & Hall, London.

Ekman, M., and De Jong, J. 1996. Local patterns of distribution and resource utilization of four bat species (*Myotis brandti*, *Eptesicus nilssoni*, *Plecotus auritus* and *Pipistrellus pipistrellus*) in patchy and continuous environments. J. Zool. (Lond.), **238**: 571–580.

Fenton, M.B., Rautenbach, I.L., Swanepoel, C.M., Grosell, J., and van Jaarsveld, J. 1994. Raptors and bats: threats and opportunities. Anim. Behav. **48**: 9–18.

Genstat 5 Committee. 1993. Genstat 5 Release 3 reference manual. Clarendon Press, Oxford.

Genstat 5 Committee. 1995. Genstat 5 Release 3.2 reference manual supplement. Numerical Algorithms Group, Oxford.

Grindal, S.D. 1996. Habitat use by bats in fragmented forests. *In* Proceedings of the First International Bat–Forest Interactions Symposium, 19–21 October 1995. *Edited by* R.M.R. Barclay and R.M. Brigham. B.C. Ministry of Forests, Victoria. pp. 260–272.

Grindal, S.D., and Brigham, R.M. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. J. Wildl. Manage. **62**: 996–1003.

Jones, G., and Rayner, J.M.V. 1989. Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. *In* European bat research 1987. *Edited by* V. Hanak, I. Horacek, and J. Gaisler, Charles University Press, Prague. pp. 247–253.

Jones, G., and Van Parijs, S.M. 1993. Bimodal echolocation in pipistrelle bats: are cryptic species present? Proc. R. Soc. Lond. B Biol. Sci. **251**: 119–125.

Kalko, E.K.V., and Schnitzler, H.-U. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. Behav. Ecol. Sociobiol. **33**: 415–428.

Krull, D., Schumm, A., Metzner, W., and Neuweiler, G. 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behav. Ecol. Sociobiol. **28**: 247–253.

Lewis, T. 1969a. The distribution of flying insects near a low hedgerow. J. Appl. Ecol. **6**: 443–452.

Lewis, T. 1969*b*. The diversity of the insect fauna in a hedgerow and neighbouring fields. J. Appl. Ecol. **6**: 453–458.

Lewis, T. 1970. Patterns of distribution of insects near a windbreak of tall trees. Ann. Appl. Biol. **65**: 213–220.

Lewis, T., and Dibley, G.C. 1970. Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. Ann. Appl. Biol. **66**: 477–484.

Lewis, T., and Stephenson, J.W. 1966. The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Ann. Appl. Biol. **58**: 355–363.

Limpens, H.J.G.A., and Kapteyn, K. 1991. Bats, their behaviour and linear landscape elements. Myotis, **29**: 63–71.

Limpens, H.J.G.A., Helmer, W., van Winden, A., and Mostert, K. 1989. Vleermuizen (Chiroptera) en lintvormige landschapselementen. Lutra, **32**: 1–20.

Milinski, M. 1986. Constraints placed by predators on feeding behaviour. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Croom Helm, England. pp. 236–252.

Nägeli, W. 1946. Weitere Untersuchungen über die Windverhältnisse im Bereich von Windschutzstreifen. Mitt. Schweiz. Anst. Vorstl. Versuchswes. **24**: 659–737.

Norberg, U.M. 1990. Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Springer-Verlag, Berlin.

Norberg, U.M., and Rayner, J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philos. Trans. R. Soc. Lond. B Biol. Sci. **316**: 335–427.

Nyholm, E.S. 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). Ann. Zool. Fenn. **2**: 77–123.

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

Rieger, I., Walzthöny, D., and Alder, H. 1990. Wasserfledermäuse, *Myotis daubentonii*, benutzen Flugstrassen. Mitt. Naturforsch. Ges. Schaffhausen, **35**: 37–68.

Rydell, J., Bushby, A., Cosgrove, C.C., and Racey, P.A. 1994. Habitat use by bats along rivers in north east Scotland. Folia Zool. **43**: 417–424.

Rydell, J., Entwistle, A., and Racey, P.A. 1996. Timing and foraging flights of three species of bats in relation to insect activity and predation risk. Oikos, **76**: 243–252.

Saville, D.J. 1990. Multiple comparison procedures: the practical solution. Am. Stat. **44**: 174–180.

Schober, W., and Grimmberger, E. 1989. Bats of Britain and Europe. Hamlyn, London.

Schofield, H.W. 1996. The ecology and conservation biology of *Rhinolophus hipposideros*, the lesser horseshoe bat. Ph.D. thesis, University of Aberdeen, Aberdeen, Scotland.

Speakman, J.R. 1991. The impact of predation by birds on bat populations in the British Isles. Mammal Rev. **21**: 123–142.

Vaughan, N., Jones, G., and Harris, S. 1997. Identification of British bat species by multivariate analysis of echolocation call parameters. Bioacoustics, **7**: 189–207.

Verboom, B., and Huitema, H. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecol. **12**: 117–125.

Verboom, B., Boonman, A.M., and Limpens, H.J.G.A. 1999. Acoustic perception of landscape elements by the pond bat *Myotis dasycneme*. J. Zool. (Lond.), **248**: 59–66.

Voûte, A.M. 1972. Bijdrage tot de oecologie van de meervleermuis *Myotis dasycneme* (Boie, 1825). [Contribution to the ecology of the pond bat, *Myotis dasycneme* (Boie, 1825).] Ph.D. thesis, University of Utrecht, Utrecht, the Netherlands.

Walsh, A.L., and Harris, S. 1996*a*. Foraging habitat preferences of vespertilionid bats in Britain: land-use relations and conservation management priorities. J. Appl. Ecol. **33**: 508 518.

Walsh, A.L., and Harris, S. 1996*b*. Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. J. Appl. Ecol. **33**: 519–529.