The influence of treeline structure and wind protection on commuting and foraging common pipistrelles (*Pipistrellus pipistrellus*)

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Abstract: The influence of wind protection on the activity and distribution of commuting and foraging common pipistrelles (*Pipistrellus pipistrellus*) was examined in an area with a relatively windy climate. The wind protection provided by the treelines was quantified by their height, width, and permeability. General and feeding activities of pipistrelles were positively related to the height, width and foliage density of the treelines. The preference for commuting routes leading from a maternity roost was explained by the distribution of potentially good feeding sites close to the roost. The results highlight the importance of wind protected areas which allow bats to feed during windy conditions. This has 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.

Keywords: Chiroptera, bats, *Pipistrellus pipistrellus*, treelines, hedgerows, foraging, commuting, corridor, wind, shelter.

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. Limpens & Kapteyn 1991, Walsh & Harris 1996, Verboom & Huitema 1997, Downs & Racey 2006). The use of edge habitats as flight paths is most obvious among bats commuting between their roost and foraging areas at dusk and dawn. The edges of vertical elements are, however, also used as foraging sites. This choice seems to be common among bats that specialise in flying and hunting in semi-open situations, but also occurs in species adapted to use more confined spaces, such as members of the vespertilionid genera *Plecotus* and *Myotis*. A number of large bats, such as the noctule (*Nyctalus noctula*) and several molossid and emballonurid species, however, seem to move independently of vertical landscape features, and can frequently be observed in large open areas (e.g. Norberg & Rayner 1987, Kronwitter 1988, Ahlén 1990) or at high altitudes (e.g. Williams et al. 1973, Fenton & Griffin 1997) where they encounter less clutter (i.e. background echoes from vegetation or ground). The common pipistrelle (*Pipistrellus pipistrellus*) seems to occupy an intermediate position in this spectrum: its echolocation is not typically adapted to cluttered environments, and it frequently moves into open areas, yet also makes extensive use of edge habitats (Racey & Swift 1985, Limpens & Kapteyn 1991, de Jong 1994, Ekman & de Jong 1996, Rydell et al. 1996, Downs & Racey 2006). In previous studies this phenomenon has been related to insect distribution and wind protection on the leeside of landscape

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** *Present address:* Dutch Mammal Society, P.O. Box 6531, NL-6503 GA Nijmegen, the Netherlands elements and the possible role of shelter from avian predators (Voûte 1972, Racey & Swift 1985, Rieger et al. 1990, Limpens & Kapteyn 1991, Verboom & Huitema 1997, Verboom & Spoelstra 1999). Furthermore, it has been suggested that common pipistrelles (as well as pond bats, *Myotis dasycneme*: Verboom et al. 1999) may use vertical landscape features as reference landmarks to facilitate echo-orientation (Limpens & Kapteyn 1991).

The main question that this study addresses is whether local wind protection provided by a network of treelines influences the distribution of commuting and foraging pipistrelle bats. Exposure to wind can considerably increase the flight cost for bats and negatively influence their manoeuvrability (Schnitzler 1971, Norberg 1990). Wind protection also obviously affects the distribution of insects (Lewis & Stephenson 1966, Lewis 1969a, Lewis 1969b, Lewis 1970, Lewis & Dibley 1970). Daily variations in wind speed and direction may cause temporal variations in wind shelter patterns and hence in food abundance. Differences in treeline structure (height, width, permeability) may cause considerable spatial variations in wind shelter and hence in food abundance at night. In areas with a windy climate, such as coastal areas in western Europe, wind shelter may therefore be a primary factor affecting temporal and spatial variations in food abundance.

In this study we first examined the characteristics that determine the profitability of treelines as feeding sites. To quantify the degree of wind protection offered by treelines we characterised them in terms of their height, width and permeability. We predicted a strong relationship between the activity of foraging pipistrelles and the degree of wind protection 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, pipistrelles are believed to be generalist feeders (Bell 1980, Swift et al. 1985, Furlonger et al. 1987, Hoare 1991, Wilkinson 1992, 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, common pipistrelles commute to their feeding areas along fixed flight paths. While on route, pipistrelles may also feed on insects. An important benefit to commuting pipistrelles would be to reduce travel time and distance in order to reach their main feeding sites more rapidly; thus, bats could maximise their net rate of energy gain by taking full advantage of the exploitation of insect activity peaks at dusk. An important additional benefit would be a reduction of time exposed to potential avian predators (Speakman 1991). We therefore predict that pipistrelles select the shortest commuting routes leading to suitable feeding sites, providing that these flyways provide sufficient shelter.

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 (figure 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 a poor insect fauna in the meadows and fields. Single and double treelines border many of the roads, forming an extensive network (photos 1 and 2). The absence of forest in most of the area means the only sheltered habitat is treelines and small tree stands near farmhouses. Foraging pipistrelles were found around many of the treelines in the area in fairly high densities. Pipistrelle maternity roosts were present

Figure 1. Schematic map of Walcheren showing treelines and woodlots. M = Meliskerke, G = Grijpskerke.

in virtually all the villages in the area. 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 Grijpskerke.

Bat activity on line-transects

Bat activity 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 Grijpskerke (G1 and G2). The respective lengths of the transects were 10,760 m (M1), 11,670 m (M2), 11,080 m (G1), and 4,550 m (G2). The line-transects were representative samples of single and double treelines in the area and also crossed some open area. 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 the built-up areas. Individual (orange sodium (Na) and white mercury (Hg) vapour) street lamps were present along roads in open areas, >25 m from trees, on transects M1 (one white, one orange), M2 (one white, one orange), G1 (one orange), and G2 (two orange). Common pipistrelles were known to be present all along the transects.

Point observations along the line-transects started one hour after sunset. We assumed that by then, most bats would have reached their main foraging areas. It took between 2.5 and 4.5 hours to complete the observations along each transect (i.e. until 1.5-3 hours before sunrise). Transects were surveyed by two people cycling abreast at a constant speed of about

Photo 1. View of a single treeline in the study area. *Photograph: B. Verboom.*

Photo 2. A double treeline in the study area. *Photograph: B. Verboom.*

6 km hour^{-1}. Two, handheld, ultrasonic bat detectors (type Petterson D-960, Lars Pettersson Elektronik, Uppsala, Sweden) were used in order to detect bats flying on either side and above the road. Bat detectors were tuned at 45 kHz, which corresponds to the approximate

frequency of the highest intensity of the echolocation sounds of the common pipistrelle. This method did not allow any 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 at fixed equidistant locations 0.9 km from each other.
2. 'Feeding observation points': when a bat was detected, the observers stopped and remained at that point and a stopwatch was triggered for one minute; if a bat was detected a second time within that minute, this point was assigned as a feeding observation point. The location of these feeding observation points was variable, as opposed to fixed observation points. This method was used to select feeding sites along the transects. All the single records between feeding observation points were also noted. The minimum distance between feeding observation points was 100 m.

Each night, one transect was monitored, with either fixed observation points or feeding observation points. To account for time effects, different starting points were used each time a transect was surveyed. Fixed observation point data were collected from all four transects (eleven nights altogether). On four nights rain (which affects bat activity and equipment) prevented us from completing a fixed point transect. Feeding observation point data were collected on nine nights from transects M1 (four nights), G1 (three nights), and G2 (two nights).

At each fixed and feeding point, pipistrelle activity, relative insect density, wind speed, and wind direction were assessed. In case of a double treeline (on both sides of the road), bat activity was monitored simultaneously both from the road between the tree rows and on the leeward side. After monitoring bat activity, a sample of insects was taken from where bats were most abundant, either on the road or on the leeward side of the treeline. During a five-minute period, pipistrelle activity was logged as the total time that bat sound was recorded, with feeding activity scored as the number of feeding buzzes recorded. Insects were sampled by sweepnetting with a handnet, 0.45 m in diameter (Bioquip Products, Gardena, California, USA). At each observation point, 50 sweeps, each 4 m in length, were taken at a height of 3.5-4.5 m, while walking slowly, taking a step parallel to the treeline every two sweeps, and another 50 sweeps while returning to the starting point (i.e. circa 40 m in each direction). The contents of the sweepnet samples were placed in jars containing ethyl acetate to kill the insects, then transferred to labelled jars containing alcohol (30%) and numbers per sample were counted ('insect densities'). We used data on wind speed and direction from nearby Vlissingen, provided by the Royal Dutch Meteorological Institute (KNMI). Wind direction was expressed as the angle between the wind and treeline (incidence angle; 0-90°).

Commuting flight routes

Following Downs and Racey (2006), 'commuting' was defined as a direct flight along a treeline, with an occasional feeding buzz; as opposed to 'foraging', which was defined as repeated back and forth flight along a treeline by the same bat, with repeated feeding buzzes. Six different roads, all bordered by treelines on both sides, linked the village of Grijpskerke with the surrounding landscape, potentially providing commuting bats with sheltered flyways to foraging grounds. Routes 1-3 and routes 4-6 were connected with two networks of treelines, one south and one north of the village (figure 2). The two networks only interconnected in Grijpskerke. Outside Grijpskerke, the two networks were separated by more than one km of open agricultural land. During three evenings, simultaneous counts of pipistrelles leaving the village were carried out at fixed points along all six routes (n=18).

Figure 2. Commuting routes (1-6) around the village of Grijpskerke.

These counting points were located 50-100 m from the 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. The road, leeward and windward side of the 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 an 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 the treelines in Walcheren died. During the 1950s, the local government started planting treelines along roads, as part of a recovery plan. As a result of this the treelines in the study area, which consist of stretches of varying length, are rather similar in their vegetation structure and composition (photos 1 and 2). Tree species in both treelines and woodlots were European ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), field elm (*Ulmus minor*) and black poplar (*Populus* x *canadensis*). Common species in the, generally present, bush layer were common hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*) and common elder (*Sambucus nigra*).

The vegetation structure of the treelines and woodlot edges along the transects, and in both networks within 1, 2, and 3 km of the Grijpskerke built-up area (measured along treelines), was quantified by visual estimation of the height, width and foliage density. The latter was assessed during daylight by visually estimating the proportion of sky (permeability); to calculate foliage density we subtracted this percentage from 100%. All estimates were done by the same two observers. When treelines were double (that is, on either side of the road), we assumed a higher level of shelter from the wind than from single tree rows (Lewis & Stephenson 1966). Based on calculations by Lewis & Stephenson (1966), we added 10% of the density of the treeline with the lowest density to the density of 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 of 0.8 and 1.8 ha along transect G2. Foliage density at the edges of the woodlots was considered to be 100% (0% permeability).

Data analysis

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 programme GENSTAT (Genstat 5 Committee 1993, Genstat 5 Committee 1995). For the remaining statistical tests we used STATISTIX (vs. 4.0; Analytical Software, St. Paul, MN, USA).

Results

Distribution pattern

Thirty-eight fixed observation points on roads in open area were surveyed, with single passing pipistrelles recorded at four of them (mean activity 0.37 [s.d. = 1.2] s / 5 minutes). The distances to the nearest trees were 100, 175, 250, and 680 m. Pipistrelles were not observed foraging in open areas.

Bat activity in open areas was much lower than along treelines (fixed observation points; *t*-test, *P*<0.0001). Along treelines the average

Table 1. Number of observations (points and single records) and distances covered in open areas and along treelines and woodlot edges.

		feeding observation points	
	number of fixed observation points	distance monitored (m)	number of feeding observation points / single observations
open area	38	25,570	0 / 0
single treelines	9	5,534	11 / 11
double treelines	72	38,121	39 / 43
woodlot edge	0	2,093	5 / 2
treelines + woodlot edges	81	45,748	55 / 56

Table 2. Pipistrelle activity along double treelines, wind speed and wind incidence angle at fixed observation points when bats were only active over the road or over the road and on the leeside, and when bats were restricted to the leeside.

	sound recorded (s)	feeding buzzes	wind speed (m/s)	wind incidence angle (°)
road (+ leeside)				
mean ± s.d.	16.1 ± 25.5	0.5 ± 1.1	2.5 ± 2.6	33.6 ± 28.9
n	61	61	62	43
leeside only				
mean ± s.d.	66.9 ± 81.1	1.8 ± 2.7	6.1 ± 2.8	70.2 ± 16.9
n	10	10	10	10
P (*t*-test)	<0.05	not significant	0.001	<0.0001

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 1). The 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 activity was significantly overdispersed (parameter: number of observations per 1000 m, dispersion parameter = 1.85, χ^2 = 92.59, df = 45, $P<0.001$), indicating that they were patchily distributed.

Wind speed and wind incidence angle affected bat activity around double treelines (fixed observation points, $n=72$). In most cases, bats occurred both over the road and on the leeside, or over the road only ($n=62$); less often bat activity was restricted to the leeward side ($n=10$; table 2). When bats were active on the leeside only, wind speeds ($P=0.001$), wind incidence angles ($P<0.0001$) and bat activity ($P<0.05$) were higher.

Fixed observation points

The estimated effects of the REML and

Table 3. Estimates (± standard errors) of marginal effects on bat activity. Insect densities were skewly distributed and transformed by adding one and taking the natural logarithm. Effects may be interpreted approximately as a relative change in bat activity when the explanatory variable is increased by one unit. Asterisks mark significance in approximate Wald-tests at the 95% confidence level. Variance components (emplogit; see appendix) of bat activity, calculated with REML, are indicated by a, b, c and d, which refer respectively to transect, night within transect, observation point within transect and point observation case random effects.

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

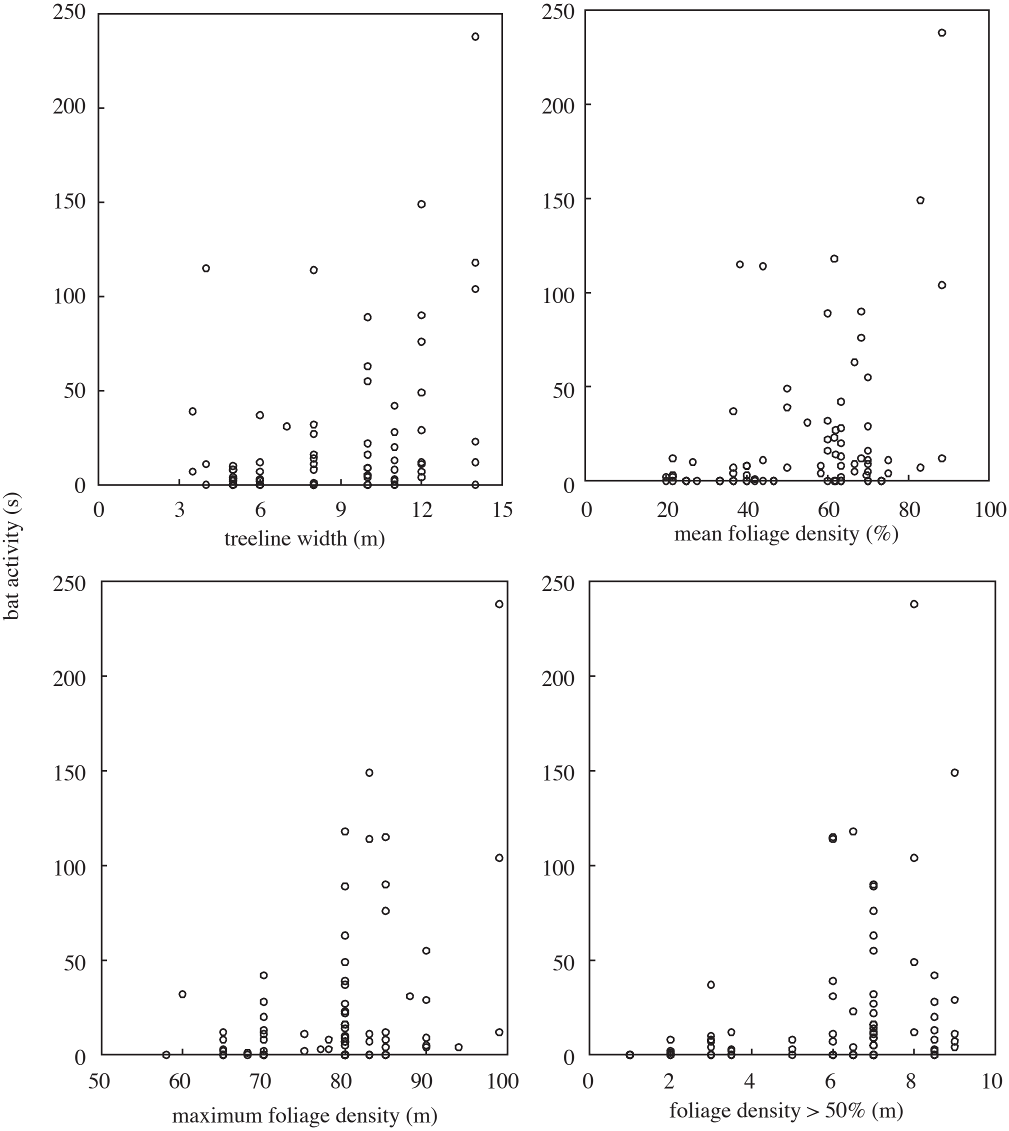

Figure 3. Bat activity on fixed observation points against four treeline parameters.

IRREML analyses show that bat activity is significantly related to treeline height, width, and foliage density (table 3). Figure 3 illustrates the marginal relation between bat activity and four of the treeline parameters.

The estimated marginal effects for bat activity (table 3) are additive on a logarithmic scale. This means that they can be interpreted as having a multiplier effect on the original bat activity scale. For not-too-large values (bat activity less than 150 s, half of the 'binomial' total 300 s), the estimates can directly be read as fractional increases. For example the coefficient 0.052 for maximum foliage density suggests a 5.2% increase in bat activity if the maximum foliage density were 1% higher. The standard error 0.026 indicates that this increase percentage may be any value between 0 and 10%.

Table 4. General and feeding activity (means ± s.d.) along treelines at 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 ± 64.9 ***	67.1 ± 62.0 ***	19.7 ± 32.9
number of feeding buzzes	2.1 ± 2.7 **	1.6 ± 2.3 *	0.6 ± 1.2

Table 5. Treeline parameter values (means ± 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

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

Table 6. Simultaneous evening counts of pipistrelle bats commuting over roads leading away from Grijpskerke. For route numbers see figure 2; mv = missing value.

		number of passing bats (% of total) % commuting over road / on leeward / on windward						
date (d/m/yr)	wind direction and force (Bft)	route 1	route 2	route 3	route 4	route 5	route 6	n_{total} n_{roost}
24/06/1994	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
21/06/1996	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
18/07/1996	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

The variance components estimated with REML (table 3) indicate that most variability is found at the level of the observation points. There may be some relevant variability between transects and between observation points within transects, but variability between nights within transects seems unimportant or even non-existent.

Feeding observation points

At feeding observation points, we frequently found more than one, but seldom more than three, pipistrelles foraging at the same time. General activity and feeding activity were significantly higher at the feeding observation than at the fixed observation points (table 4).

For each 100 m of treeline and woodlot edge on the transects with feeding observation points (G1, G2 and M1), we estimated the average height, width, and foliage density of the vegetation. Bats were recorded all along transects G1, G2 and M1, including along most of the lowest, narrowest and most permeable treelines (usually single observations; table 5). We compared treeline parameters at feeding observation points to the overall mean values for transects M1 and G1 + G2 (excluding the 100 m tracts that included feeding observation points). In transects M1 and G1/G2, the height and foliage density of the treelines and woodlot edges at the feeding observation points were significantly higher than the overall means (table 5). No feeding observation points were recorded at places where the treelines were very low (<5-6 m), narrow (<4 m) or permeable. As expected, values at single observation points were a little lower than on feeding observation points. Many of these single animals were probably on the move between foraging sites or between foraging sites and their roost.

There were differences between transects M1 and G1/G2. The 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 along both transects (*t*-tests, $P>0.05$). This indicates that pipistrelles, although they were recorded all along transects M1 and G1/G2, selected the highest and most densely vegetated treelines as their foraging sites.

Commuting flight routes

Simultaneous counts of commuting pipistrelles at six different fixed points on three evenings ($n=18$; figure 2) showed a strong temporal and spatial variation in the numbers of bats using a specific route (table 6). In 14 out of 16 counts (for two counts we had no data on the bats’ flight position), the majority of commuting bats flew directly above the road, between the tree rows. Only twice did the majority of bats fly along the leeward side. Only once was a bat recorded commuting along the windward side.

More bats used the three routes leading to the southern network (routes 1-3 in figure 2) than the three routes leading to the northern network (routes 4-6; Poisson regression, $F_{1,14}=5.23$, $P<0.05$, after correction for effects of wind speed and wind incidence angle). There was no effect of wind force 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 7 shows the length of treelines and woodlot edges within 1, 2, and 3 km (measured along treelines) of Grijpskerke’s built-up area. It was assumed that the majority of bats foraged within 3 km of the roost, which is well above the average pipistrelle travel distances recorded in British and Dutch lowlands (Racey & Swift 1985, Limpens et al. 1997). We also assumed that the bats only commuted along treelines. Within 3 km of Grijpskerke the length of treeline and woodlot edge in the

Table 7. Length of treelines and woodlot edges (m) within 1, 2 and 3 km north and south of the built up area of Grijpskerke. Mean parameter values at feeding observation points (table 5) were used as minimum values to define 'potentially good foraging areas'.

parameter		length of treeline + woodlot edge (m)			
		0-1 km	1-2 km	2-3 km	total
total	north	4049	4085	4212	12346
	south	3858	5146	5192	14196
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	1333	4825
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

southern network was 14,069 m and in the northern network it was 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. The mean parameter values of the tree characteristics at feeding observation points (table 5) were used to define 'potentially good foraging area'. The southern network had a larger total length of treelines and woodlot edges that met these criteria than the northern network, especially within 2 km from the village (table 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 that lead to the most profitable foraging areas.

Discussion

This study shows that the general and feeding activity of common pipistrelles is positively related to the height, width and foliage density of treelines. These features strongly determine the amount of available wind protection and wind shelter patterns around windbreaks (Lewis & Stephenson 1966). Hence, our results demonstrate the significance of sheltered habitats, which provide relatively wind-free sites for pipistrelles to feed. The study was performed in a coastal area with a relatively windy climate, where the presence of landscape elements with dense vegetation that act as windbreaks may be crucial for resident bat populations. Fields and meadows in intensively used agricultural areas, such as those of north-western Europe, can be extremely poor in insects and bats may be largely dependent on woody vegetation to feed.

Furthermore, this study shows that bats prefer 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 shorter foraging flights (Racey & Swift 1985) and usually return to the roost more than once during a night to suckle their young (Swift 1980).

The landscape of Walcheren is relatively uncomplicated. Treelines and other woody vegetation are rather uniform, with a similar species composition over most of the area. Short term spatial and temporal variations in food abundance are mainly caused by a combination of wind and treeline structure. Hence, the locations and profitability of insect-rich patches can 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 leeside of the windbreaks (Lewis & Stephenson 1966, Lewis 1969a, Lewis 1969b, Lewis 1970, Lewis & Dibley 1970). These insects may originate from the windbreak itself or the meadow or field neighbouring the windbreak, but a significant proportion may be blown from elsewhere. Unfortunately, due to a strong variation in the samples, our insect sampling method proved to be inappropriate to allow us to draw proper conclusions about insect densities. More sweeps per sample at a reduced height (for instance 2.5-3 m above the ground) might have given better results.

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

Bats used all the treelines in the study areas, including the lowest, narrowest and most permeable ones, as flyways but were seldom observed in the open areas during the study. Nevertheless, common pipistrelles do sometimes traverse open areas over several hundreds of metres, as reported in earlier studies (de Jong 1994, Verboom & Huitema 1997, Simon et al. 2004) and personal observations. These observations suggest that they use well-defined flyways through fields and meadows to reach isolated feeding areas. The methods applied here may have overlooked such flyways.

Commuting pipistrelles in our study mainly flew over the road between double treelines. This is in line with Verboom and Spoelstra (1999), who found the majority of pipistrelles commuting between treelines, irrespective of insect abundance and wind speed. They suggested predator avoidance as a possible explanation for this behaviour, which represents a constraint on movements of bats at relatively high light levels. In their study, feeding activity after dark took place both over the road and on the leeside of double treelines, which is in line with the results from this study. Similar bat activity shifts at decreasing light levels from sheltered to more exposed environments were found by others, e.g. Rydell et al. (1994) (common pipistrelle and Daubenton's bat, *Myotis daubentonii*) and Schofield (1996) (lesser horseshoe bat, *Rhinolophus hipposideros*).

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 that provide them, and the insects they feed on, with shelter. Land management and development should focus on creating and conserving patches of wood and linear vegetations, such as hedgerows and treelines. In order to provide sufficient shelter in windy conditions and be useful as feeding sites these need to be sufficiently high (at least 5-6 m), wide (at least 4 m) and densely vegetated. 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.

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Samenvatting

Effecten van windbeschutting op het landschapsgebruik door gewone dwergvleermuizen (*Pipistrellus pipistrellus*)

De gewone dwergvleermuis (*Pipistrellus pipistrellus*) maakt veelvuldig gebruik van bomenrijen en andere opgaande, lintvormige, vegetaties, als foerageergebied en als verbindingsroute tussen verblijfplaats en foerageergebied en tussen foerageergebieden onderling. Windbeschutting speelt naar verwachting een belangrijke rol bij de keuze van vliegroutes en foerageerplaatsen. In het windrijke kustgebied Walcheren (Zeeland) onderzochten we daarom de invloed van structuureigenschappen van houtsingels op foeragerende dwergvleermuizen. De hoogte, breedte en vegetatiedichtheid (permeabliliteit) van de singels bleken bepalend voor de mate waarin vleermuizen langs de bomenrijen foerageerden. Zeer lage (<5-6 m), smalle (<4 m) en wind-doorlatende bomenrijen werden niet gebruikt als foerageerplek. De verspreiding van potentieel geschikte foerageerplekken in het studiegebied bepaalden de keuze van vliegroutes tussen een verblijfplaats van dwergvleermuizen in een kleine bebouwingskern 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.

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Appendix

The application of REML and IRREML in modelling relations between bat activity and environmental variables

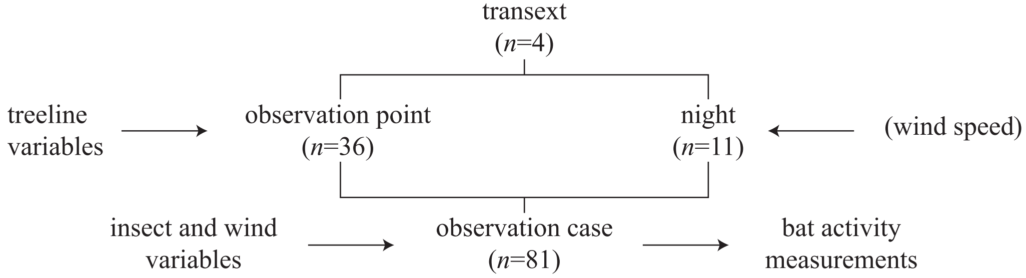
An appropriate statistical analysis was required that took into account the structure of the 81 observation cases. Observations were made along four transects, over 11 nights, and at 36 different fixed observation points. Thus the nights and the observation points are nested within transects, each observation was made at a certain combination of night and observation point. This is schematically represented below.

The direction of the arrows indicates ways in which the survey was structured so as to model bat activity as a function of the other variables.

The standard tools to statistically analyse relations between variables are linear and generalised 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 thse 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 of the set of observation cases is modelled via the explanatory variables and 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 a mixture of fixed and random explanatory variables. In this way, linear modelling (regression and analysis of variance) is generalised to REML (Residual Maximum Likelihood; Patterson & Thompson 1971), and generalised linear modelling to IRREML (Iteratively Reweighted REML, Engel & Keen 1994. See Engel (1997) for an overview). Computations are easily performed with the statistical programme Genstat (Genstat 5 Committee 1993, Genstat 5 Committee 1995). REML is a standard feature of the programme, IRREML is available as a procedure (Keen 1996).

For the analysis of this bat data (sound recorded per 5 minutes), IRREML seemed the most appropriate approach. No analysis of number of feeding buzzes was undertaken, as there seemed to be too little information in the values (mostly 0s or 1s). Given the scheme above the specification of the random terms was easy. 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 can 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}):

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

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 analysis of the transformed data is a relatively standard approach for this type of data, so large differences between the results from the two 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 any major misspecification within the model.

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

$$\ln \{ E(t_{sound})/[300-E(t_{sound})] \} = \mu + \alpha_i + \beta_{ij} + \gamma_{ik} + \delta x_{ijk}$$

$$\text{var}\,(t_{sound}) = \sigma^2\, 300\, E(t_{sound})\, \{300-E(t_{sound})\}$$

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 needs to be estimated from the data.