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The bat, the weevil and other ‘species’

The International Year of Biodiversity, as declared by the United Nations, is coming to an end. Worldwide, there have been many biodiversity conferences, lectures, celebrations, competitions, even ‘bioweeks’, all meant to increase understanding about biodiversity issues. Ever since scientists first drew attention to the pressure on the world’s biodiversity caused by human activities, public awareness of the significance of biodiversity has gradually increased, as has recognition of the need to maintain it. This implies a corresponding increase in public knowledge of the diversity of the natural world. After all, why should people be worried about the extinction of a species if they have no idea that it even exists? People only care about what they know.

Yet, despite media attention to biodiversity, there is evidence that knowledge about nature is deteriorating. A British survey revealed that primary school children were better at recognising Pokémon characters than at identifying common native plants and animals (Balmford et al. 2002): the children were able to recognise 32% of (a selection of) common British wildlife at the age of four, and 52% at the age of eight; the eight year olds could, however, correctly identify 80% of a sample of Pokémon characters. According to the Cambridge zoologists that performed the study, this study contained some good news: that children apparently have an enormous capacity to learn differ-

ent characters, whether from natural or man-made ‘species’.

Another conclusion to be drawn from this study is that the creators of Pokémon are doing a better job than conservationists and school teachers, in stimulating children to learn about their subjects. More recent studies from Germany and the UK confirm these results and show a decline of knowledge of and interest in nature that parallels the increased abundance and availability of electronic devices in children’s everyday lives.

So how important is it for people to have at least some idea about the diversity of life forms around them? When IUCN scientists tell us that at least 21% of the earth’s mammals are endangered, how many people are aware that the number of known mammal species currently exceeds 5,400? And how important is it if they don’t know this? Or for instance, if they don’t know the difference between a field vole and a root vole, or even between a hare and a rabbit? Maybe it’s not at all important, as long as people care about their natural environment and are willing to protect it. On the other hand, a certain awareness of the diversity of species, and the ecosystems which we are part of, may be a prerequisite for fully appreciating nature.

People can acquire knowledge about the diversity of the natural world in many different

ways, but whether people will retain that information, depends greatly on their interest in storing it. Yet, information provided by the media can often be confusing. For example, the twenty or so different bat species in the Netherlands are frequently lumped together as 'the bat'. To (over)simplify things for readers and listeners, the media frequently reports that "the bat is protected" or that "the bat is an endangered species". It is not that we should expect everyone to know all the different species of bat, but a little more information on the magnitude of such diverse taxa would certainly help keep things in perspective. And in case of a species that is thought to cause damage, it might also help to keep their many harmless relatives from being persecuted.

As an example of the latter, last summer's media fuss about the introduced species of weevils (Coleoptera: Curculionoidea) destroying gardens created much confusion among both journalists and the public. Photographs of non-beetle insect taxa (such as Heteroptera in my own - well-esteemed - newspaper) appeared alongside articles about these specific weevils. News messages persistently spoke about 'the weevil'. But of course there is no single 'weevil': there are about 60,000 known species of weevil worldwide (including some 500 in the Netherlands), belonging to a number of families. While most weevils are completely harmless or will never enter a garden, there is now the possibility of a general suspicion of all weevils.

Fortunately, for anyone interested, the richness of species of our natural world is very well-documented in books. This certainly applies to

the Netherlands. Most taxa of Dutch flora and fauna are nowadays represented in a wealth of ecological atlases and field guides. One of these that might be of special interest to the readers of *Lutra* is a long awaited, recently issued guide to the mammals of Europe, which is reviewed in this issue. It is written in Dutch, as is the review by Vincent van Laar. This review will be the last Dutch language contribution to *Lutra*. As mentioned in previous editorials, from 2011 on *Lutra* will only publish contributions in English. Coincidentally, van Laar also wrote the first research paper ever published in *Lutra*, on the remains of mammals in pellets of the barn owl - more than fifty years ago (van Laar, July 1959, *Lutra* 1 (20): 209). Van Laar, by the way, used to offer his manuscripts to *Lutra* in handwritten form, but this time the 'manuscript' was typewritten (although still not submitted through e-mail): strong evidence for the times that are at changing.

There is one announcement to make. After ten years, Edgar van de Grift has left our board. As an editor, managing editor and secretary, Edgar has left a strong mark on our journal. He was one of those 'angry young editors' of *Lutra* around the year 2000 who inspired his fellow editors by bringing up many interesting ideas, and who initiated a change of style of *Lutra*. We thank Edgar for being an inspiring colleague over the years, and for helping *Lutra* to become an even better journal!

Balmford, A., L. Clegg, T. Coulson & J. Taylor 2002. Why conservationists should heed Pokémon. *Science* 295: 2367.

Ben Verboom

A comparison of the hibernation patterns of seven bat species in Estonia

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Abstract: We investigated whether bat species with a more northerly border of distribution would hibernate in colder conditions and use fewer crevices and clusters for hibernation than species with a more southerly northern border of distribution. To this end, we measured the temperature and water vapour pressure (as an absolute measure of humidity) of hibernation locations, crevice occupation and clustering among seven sedentary bat species in Estonia. The pond bat (*Myotis dasycneme*), Daubenton's bat (*Myotis daubentonii*) and Brandt's bat/whiskered bat (*Myotis brandtii/mystacinus*) hibernated at higher temperatures and humidity whereas the northern bat (*Eptesicus nilssonii*), the brown long-eared bat (*Plecotus auritus*) and Natterer's bat (*Myotis nattereri*) hibernated at lower temperatures and humidity. The majority of northern bats, Daubenton's bats, brown long-eared bats and Natterer's bats hibernated solitarily whereas Brandt's bats/whiskered bats and pond bats tended to hibernate in clusters. All Natterer's bats hibernated in crevices whereas the six other species hibernated both in crevices and hanging freely on the wall/ceiling. Northern bats inhabiting regions further north than the other six species typically hibernated alone on the wall/ceiling, whereas pond bats, whose distribution border lies further south than those of the other six species, hibernated in warmer and more humid conditions, and often in clusters. However, Natterer's bats inhabiting regions further north than those of pond bats, but whose northern border of distribution lies further south than those of the remaining five species preferred lower temperatures and humidity than the other five species. The results suggest that during the hibernation season in the north of Europe, pond bats focus on saving energy during arousals and subsequent periods of euthermia, whereas Natterer's bats focus on saving energy during hibernation.

Keywords: clustering, crevice occupation, *Eptesicus*, hibernation, humidity, *Myotis*, *Plecotus*, temperature, winter roosts.

Introduction

Hibernation is an energy-saving mechanism for insectivorous bats to survive the cold winter months when food is scarce. In autumn, bats accumulate body fat, which serves as their energy source during winter. During hibernation, their body temperature falls to within 1-2°C of ambient temperature and their metabolic processes slow down, which reduces energy requirements (e.g. Thomas et

al. 1990, Geiser 2004). The temperatures at which bats hibernate are species specific (e.g. Siivonen & Wermundsen 2008a). In addition, intraspecific variations exist (e.g. Nagel & Nagel 1991, Webb et al. 1996) because individuals select locations based on their energy reserves (Boyles et al. 2007). Individuals with high energy reserves are less vulnerable to potential negative ecological and physiological effects of hibernation, such as detection by predators, the likelihood of freezing, decreased immune response, motor function and protein synthesis and sleep deprivation (Clawson et al. 1980, Choi et al. 1998, Fre-

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richs 1998, van Breukelen & Martin 2002, Humphries et al. 2003, Kokurewicz 2004, Luis & Hudson 2006). They actively select relatively warm locations and spend less time in hibernation (shorter hibernation bouts; Wojciechowski et al. 2007). Individuals with low energy reserves choose longer hibernation bouts by actively selecting colder temperatures which will minimise their energy expenditure (Wojciechowski et al. 2007). Hibernation is not continuous; bats periodically and spontaneously arouse from torpor (e.g. Krzanowski 1959, Willis 1982). Arousals and subsequent periods of euthermia increase their energy expenditure and account for over 80% of fat depletion during hibernation (Thomas et al. 1990, Speakman et al. 1991, Thomas 1995).

Webb et al. (1996) reviewed the hibernal temperatures of 34 bat species and found large inter and intra species variations in the temperatures at which bats hibernate. They suggested that species with a more northerly distribution are able to hibernate in colder conditions than species with a more southerly distribution. Some authors have reported intra-specific differences in hibernal temperatures between geographic regions (Strelkov 1958, Gaisler 1970, McNab 1974, Masing 1982, Kokurewicz & Kováts 1989). Humidity is another important microclimatic factor for hibernating bats, especially in arid regions (Thomas & Cloutier 1992, Lausen & Barclay 2006). Bats have no special mechanism for controlling water loss during hibernation, so many species hibernate in very humid locations.

Some bat species prefer thermally stable areas, whereas others hibernate in thermally more variable areas (Brack 2007). By hibernating in crevices and by clustering, bats can decrease their exposure to airflow and fluctuating air temperatures and thereby reduce heat and water loss (e.g. Hock 1951, Kokurewicz 2004). Typically these actions reduce heat and water loss by reducing an individual's exposed surface area. However, when

body temperature approaches the ambient temperature, heat loss and the potential for saving energy is low. During arousals, bats raise their body temperature to euthermic levels; which is when the benefit of reduced heat loss through hibernation in clusters is highest (Clawson et al. 1980, Arnold 1990, Boyles et al. 2008). Clustering behaviour is also species specific (e.g., Twente 1955, McNab 1974, Clawson et al. 1980, Brack 2007, Siivonen & Wermundsen 2008a). Among the seven bat species that hibernate in Estonia, Daubenton's bat (*Myotis daubentonii*) is reported to hibernate in large groups of up to 140 individuals in Central Europe (Bogdanowicz 1994), Brandt's bat (*Myotis brandtii*) and whiskered bat (*Myotis mystacinus*) hibernate in clusters of up to 13 individuals in Finland (Siivonen & Wermundsen 2008a) and the pond bat (*Myotis dasycneme*) is reported to hibernate in small groups of 2 to 10 bats (Limpens et al. 2000).

To date, no studies on the hibernation ecology of bats in Estonia have systematically compared the use that species make of microclimates (temperature, water vapour pressure), crevices and clusters (for a review of publications, see Masing & Lutsar 2007). Previous studies in Europe have typically used relative humidity as a measure of the humidity of hibernacula. Relative humidity provides information on water vapour pressure in saturated air at a given ambient temperature (Louw 1993). So to compare humidity at different temperatures, water vapour pressure is a better measure of humidity and is the one used in this study.

Higher latitudes (distance from the equator) bring shorter winter days and colder and longer winters. In this study, we tested the theory that species with a more northerly northern border of their range hibernate in colder conditions than species with a more southerly northern border of their range. As hibernating in crevices and clusters means that bats can save energy, we further hypothesised that species with a more southerly northern border of their range would hibernate more often in

clusters and/or in crevices than species with more northerly northern border of their range. Among the seven bat species that hibernate in Estonia, the northern distribution border of the pond bat clearly lies further south (at 60°N; Siivonen & Wermundsen 2003, IUCN 2010) than those of the other six species, whereas that of the northern bat (*Eptesicus nilssonii*) lies further north than those of the other six species. The northern distribution borders of Natterer's bat (*Myotis nattereri*) lies north of 63°N, and that of the brown long-eared bat (*Plecotus auritus*) lies north of 64°N (IUCN 2010, Siivonen & Wermundsen 2008b, respectively): one brown long-eared bat has been found north of 67°N in Russia (Siivonen & Sulkava 1999). The northern edge of the distribution areas for Daubenton's bat and Brandt's bat/whiskered bat lie north of 66°N (Siivonen & Wermundsen 2008b).

Materials and Methods

Study area

We conducted this study in Estonia (24°00'–25°00'E and 58°30'–59°30'N), a country lying within the northern part of the mixed forest sub-zone of the temperate forest zone (Estonica 2007). Seven bat species hibernate in the Estonian study area (Masing 1983, Masing & Lutsar 2007): Daubenton's bat, the pond bat, Brandt's bat, the whiskered bat, Natterer's bat, the northern bat and the brown long-eared bat. In Estonia, bats hibernate from October to April (Masing 1984).

The climate of Estonia contains a mixture of maritime and continental influences. Special characteristics of the Estonian weather include high variability, occasionally strong winds, high precipitation and abrupt fluctuations in temperature. The average annual temperature is between 4.3 and 6.5°C and annual average precipitation ranges from 550 to 800 mm (Estonica 2007). In Estonia, winter lasts from November until April and the cold-

est month is February (Estonica 2007). The average winter temperature between 1971 and 2000 was -3.6°C (Eesti Meteoroloogia ja Hüdroloogia Instituut 2010).

Data collection

We measured the use of temperature, humidity, crevices, and clusters by hibernating bats in Estonia in March 2005 (three days) and January 2006 (three days). The Estonian Ministry of the Environment issued permission Nr 16-4/2003/T32/8912 for these observations. To minimise disturbance, we identified bat species and took all measurements without handling the bats. Brandt's bat and the whiskered bat closely resemble each other, and can only be definitely identified by examining their teeth or penis. As this was not possible within this study, we present these two species together as Brandt's bat/whiskered bat.

To identify species, we used a Sony DSC-F828 digital camera, a SnakeEye video inspection system, Swarovski EL 10x32 binoculars, a dentist's mirror, and a two-sided make-up mirror (one side being a normal mirror and the other a magnifying mirror) with a 1.5 m handle which allows the mirror to be moved to permit us to inspect crevices from different angles. This equipment enabled us to thoroughly investigate most of the crevices in the hibernacula. The clusters were relatively small, so we could determine the exact number of bats in a cluster.

Overall we measured the use of microhabitat variables by 1214 hibernating bats (table 1). In 2005, we measured the use of hibernation locations by 414 bats in seven underground sites: the Ülgase abandoned mine, four abandoned limestone cellars (three in Järvikandi and one in Haimre); and two military constructions, one with walls of natural stone (in Väänäposti) and another one with concrete walls (in Viti). In 2006, we measured the use of hibernation locations by 800 bats in the same sites and one other, a military construc-

Table 1. Environmental measurements, clustering, and location of bats in Estonian hibernacula in March 2005 and January 2006. Temperature: the temperature at which a bat hibernated; water vapour pressure: the humidity at which a bat hibernated; clustering index: the average size of a cluster that a bat used for hibernation; solitary hibernation: the percentage of bats that hibernated solitarily; crevice occupation: the percentage of bats that hibernated in crevices; clustering of crevice bats: the percentage of bats that hibernated in crevices and were clustered.

	Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Brown long-eared bat	Natterer's bat	Pond bat
<i>N</i>						
2005	116	88	65	48	23	74
2006	195	100	252	69	34	150
Temperature (°C) ± sd						
2005	4.1 ± 1.5	5.9 ± 0.8	4.8 ± 1.6	3.8 ± 1.7	2.7 ± 0.5	6.8 ± 0.9
2006	4.3 ± 2.0	6.0 ± 1.1	6.5 ± 1.7	4.6 ± 1.7	3.4 ± 0.8	7.1 ± 1.2
Water vapour pressure (Pa) ± sd						
2005	749 ± 105	870 ± 59	799 ± 104	723 ± 126	653 ± 41	935 ± 89
2006	751 ± 16	876 ± 82	923 ± 131	783 ± 112	737 ± 49	960 ± 97
Clustering index ± sd						
2005	1.1 ± 0.4	1.6 ± 0.7	1.1 ± 0.3	1.1 ± 0.2	1.2 ± 0.4	3.6 ± 2.9
2006	1.4 ± 0.9	2.2 ± 1.2	1.2 ± 0.5	1.0 ± 0.0	1.3 ± 0.6	6.6 ± 8.6
Solitary hibernation (%)						
2005	90	49	89	94	83	36
2006	74	38	86	100	79	43
Crevice occupation (%)						
2005	35	74	49	58	100	69
2006	39	71	45	68	100	44
Clustering of crevice bats (%)						
2005	10	55	19	11	17	74
2006	26	59	14	0	21	48

tion, with walls of natural stone (in Humala). The mine and military constructions had back sections (rear wings) with stable conditions and a higher temperature, whereas in the front sections, the temperature was lower and more variable, fluctuating according to the climatic conditions outside. The cellars had no back parts with more stable conditions and their temperature fluctuated according to the climatic conditions outside.

We recorded whether bats hibernated solitarily or in clusters, the size of cluster and whether the bats hibernated on the wall/ceiling or in crevices. We classified bats that were in body contact with each other as clustered. We measured the temperature and rel-

ative humidity within 5 cm of the bat(s) by using two portable humidity and temperature meters: a VAISALA HM 34 and a VAISALA HMI 41 with an HMP 44L probe (2.7 m). These digital meters provide quick (approximately 10 s) yet accurate spot checks of relative humidity and temperature, thus avoiding any influence from human presence. The measurement range is 0-100% (0-90% ± 2%, 90-100% ± 3%) for humidity and -20-60°C (± 0.3°C) for temperature. Water vapour pressure difference determines the direction and rate of water vapour movement and this was calculated from the relative humidity and temperature (e.g. Louw 1993).

Table 2. Intraspecific comparison of temperature, water vapour pressure, clustering index, solitary hibernation, crevice occupation, and clustering in crevices between March 2005 and January 2006. Temperature: the temperature at which a bat hibernated; water vapour pressure: the humidity at which a bat hibernated; clustering index: the size of a cluster that a bat used for hibernation; solitary hibernation: the proportion of bats that hibernated solitary; crevice occupation: the proportion of bats that hibernated in crevices; clustering of crevice bats: the proportion of bats that hibernated in crevices in clusters.

		Northern bat	Brandt's bat/ whiskered bat	Dauben- ton's bat	Brown long- eared bat	Natterer's bat	Pond bat
<i>N</i>	2005	116	88	65	48	23	74
	2006	195	100	252	69	34	150
Temperature							
Mann-Whitney U-test	<i>z</i>	-2.132	-1.156	-6.929	-2.198	-3.588	-3.342
	<i>P</i>	0.033	0.248	0.000	0.028	0.000	0.001
Water vapour pressure							
Mann-Whitney U-test	<i>z</i>	-0.140	-0.946	-6.651	-1.984	-5.157	-2.338
	<i>P</i>	0.889	0.344	0.000	0.047	0.000	0.019
Clustering index							
Mann-Whitney U-test	<i>z</i>	-3.487	-3.181	-0.799	-2.095	-0.438	-0.500
	<i>P</i>	0.000	0.001	0.425	0.036	0.661	0.617
Solitary hibernation							
Chi-Square test	Pearson's χ^2	12.044	2.253	0.545	4.426	0.090	0.960
	df	1	1	1	1	1	1
	<i>P</i>	0.001	0.133	0.460	0.035	0.764	0.327
Crevice occupation							
Chi-Square test	Pearson's χ^2	0.408	0.192	0.332	1.177	-	12.333
	df	1	1	1	1	-	1
	<i>P</i>	0.523	0.661	0.565	0.278	-	0.000
Clustering in crevices							
Chi-Square test	Pearson's χ^2	4.479	0.197	0.434	-	0.090	8.107
	df	1.000	1	1	-	1	1
	<i>P</i>	0.034	0.657	0.510	-	0.764	0.004

Data analysis

We used SPSS 16.0 for Windows (SPSS Inc. 1989–2005) to analyse the data. We first compared the data from March 2005 and January 2006 within species (tables 1 and 2) by using the Mann-Whitney U-test (temperatures, water vapour pressure and clustering index) and the Chi-square test (solitary hibernation, crevice occupation and use of clusters in crevices). We compared temperatures, water vapour pressure and the clustering index among species using the

Kruskal-Wallis test, because the data were not normally distributed. We performed post hoc comparisons of the groups using Dunn's test. We compared crevice occupation, solitary hibernation and clustering in crevices using the Chi-square test, with the binomial test as a post hoc test. We also compared temperatures used by solitary bats in crevices and bats in clusters outside crevices within species using the Mann-Whitney U-test. We considered a *P* value of <0.05 significant. Means appear with standard deviations (\pm sd).

Table 3. Comparison of environmental measurements and clustering among seven bat species in Estonian hibernacula in March 2005 and January 2006. Temperature: the temperature at which a bat hibernated; water vapour pressure: the humidity at which a bat hibernated; clustering index: the size of a cluster in which a bat hibernated.

		Temperature		Water vapour pressure		Clustering index	
		2005	2006	2005	2006	2005	2006
Kruskal-Wallis test	<i>K</i>	218.013	304.234	199.223	304.750	122.853	191.978
	<i>df</i>	5	5	5	5	5	5
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Dunn's test							
Northern bat vs. Brandt's bat/whiskered bat	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Northern bat vs. Daubenton's bat	<i>P</i>	0.000	0.000	0.017	0.000	<1.000	0.027
Northern bat vs. brown long-eared bat	<i>P</i>	<1.000	<1.000	<1.000	<1.000	<1.000	0.000
Northern bat vs. Natterer's bat	<i>P</i>	0.000	0.000	0.000	0.705	<1.000	<1.000
Northern bat vs. pond bat	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Brandt's bat/whiskered bat vs. Daubenton's bat	<i>P</i>	0.000	0.001	0.000	0.002	0.000	0.000
Brandt's bat/whiskered bat vs. brown long-eared bat	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Brandt's bat/whiskered bat vs. Natterer's bat	<i>P</i>	0.000	0.000	0.000	0.000	0.045	0.000
Brandt's bat/whiskered bat vs. pond bat	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.330
Daubenton's bat vs. brown long-eared bat	<i>P</i>	0.000	0.000	0.029	0.000	<1.000	0.013
Daubenton's bat vs. Natterer's bat	<i>P</i>	0.000	0.000	0.000	0.000	<1.000	<1.000
Daubenton's bat vs. pond bat	<i>P</i>	0.000	0.000	0.000	0.176	0.000	0.000
Brown long-eared bat vs. Natterer's bat	<i>P</i>	0.043	0.001	<1.000	0.465	<1.000	0.002
Brown long-eared bat vs. pond bat	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Natterer's bat vs. pond bat	<i>P</i>	0.000	0.000	0.000	0.000	0.001	0.000

Results

Comparison of March 2005 and January 2006

As the data between 2005 and 2006 differed for between two and five variables per species (tables 1 and 2), we treated the two years separately when making comparisons among species. All species except Brandt's bat/whiskered bat hibernated in higher temperatures in 2006 than in 2005. All species except the northern bat and Brandt's bat/whiskered bat hibernated in higher humidity conditions in 2006 than in 2005. More northern bats hibernated in clusters in 2006 than in 2005 and the clustering index was higher in 2006 than in 2005. In contrast, no brown long-eared bats hibernated in clusters in 2006, and 16% in

2005. More pond bats hibernated in crevices in 2005 than in 2006. More of the pond bats and brown long-eared bats hibernating in crevices were clustered in 2005 than in 2006. In contrast, more northern bats hibernated in clusters in crevices in 2006 than in 2005. In both years, Natterer's bats were found to hibernate only in limestone cellars, whereas pond bats never hibernated there.

Use of microclimates

Hibernation temperatures and humidity (water vapour pressure) differed among species (tables 1 and 3). Pond bats, Daubenton's bats and Brandt's bats/whiskered bats hibernated in higher temperatures and humidity levels than northern bats, brown long-eared bats and Nat-

Table 4. Comparison of solitary hibernation, crevice occupation and clustering of crevice bats among seven bat species in Estonian hibernacula in March 2005 and January 2006. Solitary hibernation: the proportion of bats that hibernated solitarily; crevice occupation: the proportion of bats that hibernated in crevices; clustering in crevices: the proportion of bats that hibernated clustered in crevices.

		Solitary hibernation		Crevice occupation		Clustering in crevices	
		2005	2006	2005	2006	2005	2006
Chi-square test	Pearson's χ^2	110.9	123.4	37.681	40.225	69.161	51.997
	df	5	4	4	4	5	4
	<i>P</i>	0.000	0.000	0.000	0.000	0.000	0.000
Binomial test	<i>P</i> (northern bat)	0.000	0.000	0.002	0.003	0.000	0.000
	<i>P</i> (Brandt's bat/whiskered bat)	0.915	0.021	0.000	0.000	0.457	0.154
	<i>P</i> (Daubenton's bat)	0.000	0.000	1.000	0.147	0.001	0.000
	<i>P</i> (brown long-eared bat)	0.000	–	0.312	0.004	0.000	–
	<i>P</i> (Natterer's bat)	0.003	0.001	–	–	0.003	0.001
	<i>P</i> (pond bat)	0.027	0.121	0.002	0.165	0.902	0.902

Table 5. Cluster sizes of seven bat species in Estonian hibernacula in March 2005 and January 2006. Clusters formed by one species are included.

	2005			2006		
	<i>N</i>	$\bar{x} \pm \text{sd}$	Max	<i>N</i>	$\bar{x} \pm \text{sd}$	Max
Northern bat	4	2.2 ± 0.5	3	20	2.4 ± 0.8	5
Brandt's bat/whiskered bat	19	2.2 ± 0.4	3	20	2.8 ± 0.9	5
Daubenton's bat	3	2.0 ± 0.0	2	15	2.2 ± 0.6	4
Brown long-eared bat	1	2.0 ± 0.0	2	0	–	–
Natterer's bat	1	2.0 ± 0.0	2	3	2.3 ± 0.6	3
Pond bat	11	3.9 ± 2.5	9	13	5.6 ± 6.3	25

terer's bats. Natterer's bats hibernated in lower temperatures and humidity than other species, and pond bats hibernated in higher temperatures and humidity than other species. Northern bats and brown long-eared bats used similar temperatures and humidity. Brown long-eared bats and Natterer's bats hibernated in similar humidity conditions in 2005 and 2006. Daubenton's bats, pond bats, northern bats and Natterer's bats all hibernated in similar humidity conditions in 2006.

Use of clusters and crevices

Northern bats, Daubenton's bats, brown long-eared bats and Natterer's bats typically hiber-

nated solitarily whereas pond bats hibernated in clusters (tables 1, 3 and 4).

The size of the clusters varied from 2 to 25, and clusters typically contained only one species (table 5). On 15 occasions, we found clusters with two species: pond bat & Brandt's bat/whiskered bat ($n=7$), northern bat & Daubenton's bat ($n=2$), Daubenton's bat & pond bat ($n=2$), northern bat & Daubenton's bat ($n=1$), Daubenton's bat & Brandt's bat/whiskered bat ($n=1$), northern bat & Natterer's bat ($n=1$), brown long-eared bat & Natterer's bat ($n=1$). Most of these multispecies aggregations were formed by only two individual bats. We found one multispecies aggregation with three bats, and one with four bats.

The clustering index differed among spe-

Table 6. Comparison of temperatures used by bats in clusters outside crevices and solitary bats in crevices in four species of bats in Estonia in 2006. In 2005 very few bats (<10) in all species hibernated in clusters outside crevices, so comparisons could not be made. In 2006 all brown long-eared bats hibernated solitarily and all Natterer's bats in crevices, so comparisons could not be made.

		Northern bat	Brandt's bat/ whiskered bat	Daubenton's bat	Pond bat
Year		2006	2006	2006	2006
<i>N</i>	Clustered	30	20	20	53
	In crevice	58	29	98	34
Temperature	Clustered	5.4 ± 0.9	6.7 ± 0.8	7.6 ± 0.9	7.8 ± 0.7
	In crevice	3.3 ± 2.3	5.8 ± 1.1	5.7 ± 2.0	6.5 ± 1.4
Mann-Whitney U-test	<i>z</i>	-4.300	-2.520	-4.157	-5.113
	<i>P</i>	0.000	0.012	0.000	0.000

cies (tables 1 and 3). Brown long-eared bats, northern bats, Daubenton's bats and Natterer's bats hibernated in smaller clusters while pond bats and Brandt's bats/whiskered bats hibernated in larger clusters.

All the individuals of Natterer's bats hibernated in crevices, so this species could not be included in the Chi-Square test. Crevice occupation differed among the other species (tables 1 and 4). Northern bats typically hibernated on the ceiling/wall, whereas Brandt's bats/whiskered bats and brown long-eared bats favoured crevices. The northern bats, Daubenton's bats, the brown long-eared bats and Natterer's bats hibernating in crevices were typically solitary. Brandt's bats/whiskered bats typically hibernated in clusters in crevices. More than 50% of pond bats hibernated in clusters in crevices in 2005, but less than 50% in 2006.

Temperatures used by solitary bats in crevices were lower than those used by bats in clusters outside crevices in the northern bat, Brandt's bat/whiskered bat, Daubenton's bat and the pond bat (table 6).

Discussion

As predicted, the species with the more southerly northern border of distribution, the pond bat, used warmer locations for hibernation

than the other six species. This species also hibernated in conditions with the highest humidity and tended to hibernate in clusters. Hibernating in warmer temperatures raises the body temperature and induces shorter hibernation bouts (Wojciechowski et al. 2007). This means that the pond bat has more frequent periods of euthermia than bats that hibernate in colder places. In this study, these bats hibernated in clusters at higher temperatures and in crevices at lower temperatures. The greatest benefit of clustering is reduced heat loss during arousals and subsequent periods of euthermia (Boyles et al. 2008), so the pond bat focuses on saving energy during active periods of the hibernation season. Evaporative water loss is greater at higher body temperatures (Thomas & Cloutier 1992, Thomas 1995), so by hibernating in high humidity conditions, the pond bat reduces evaporation and, consequently, energy loss (Louw 1993).

Natterer's bat inhabits regions further north than those of the pond bat, but its northern border of distribution is further south than those of the remaining five species. In Finland, Natterer's bats inhabit regions below 62°N although in Sweden, it ranges up to 63°N (IUCN 2010). Contrary to our predictions, Natterer's bat hibernated in the coldest conditions used by the bats we encountered, and our results indicate that this species tends to minimise its energy expenditure in all possible ways. Nat-

terer's bats hibernated at temperatures closest to 2°C, and all of them hibernated in crevices. Water loss due to evaporation is lowest at 2°C and increases at both higher and lower ambient temperatures (Thomas & Geiser 1997). Evaporation increases energy loss (Thomas & Cloutier 1992, Thomas 1995) and airflow increases evaporation rates by transporting water vapour away from the evaporating surface (Louw 1993) which may trigger arousals (Thomas & Geiser 1997). All Natterer's bats hibernated in crevices, which shelter bats from airflow, which decreases evaporation. Natterer's bats hibernated in the driest locations, yet tended to minimise evaporation. Unlike pond bats, Natterer's bats focused on saving energy during periods of hibernation. Natterer's bats typically hibernated solitarily. Longer hibernation bouts lead fewer active periods during hibernation. Thus Natterer's bats do not require to cluster as much as pond bats which saves their energy during euthermic periods.

The northern bat inhabits regions further north than those of the other six species. As predicted, the northern bat typically hibernated alone on the wall/ceiling (using no additional energy-saving methods) in cold and dry places, confirming that it is a hardy species, well adapted to the harsh conditions of the north (e.g. Siivonen & Wermundsen 2008a). The fact that it hibernates in cold places suggests that it tends to save energy (long hibernation bouts) rather than to minimise the cost of hibernation (short hibernation bouts). Brandt's bat/whiskered bat, Daubenton's bat and the brown long-eared bat inhabit regions further north than those of the pond bat and Natterer's bat, but further south than those of the northern bat. Brandt's bats/whiskered bats hibernated in warmer locations than the other two species, suggesting that they tend to minimise the cost of hibernation rather than to save energy. Brandt's bats/whiskered bats used both available energy-saving methods (clusters and crevices) for hibernation, as in Finland (Siivonen & Wermundsen 2008a), and

also clustered in crevices, as did the pond bat. Brown long-eared bats tended to save energy during hibernation (choosing cold locations, leading to long hibernation bouts) as did Natterer's bats, which used crevices, although to a lesser extent than Natterer's bats. Daubenton's bats have recently been found to inhabit regions north of the Arctic Circle in summer (Siivonen & Wermundsen 2008b). This species used additional energy-saving methods (clusters and crevices) to a lesser extent (as Kokurewicz 2004 and Siivonen & Wermundsen 2008a have shown) and this suggests that they may tolerate harsh conditions, despite hibernating in relatively warm and humid conditions, especially in 2006.

Previous studies have compared the hibernation conditions of these species in Europe, but none of them have compared all seven of these species. Among the four *Myotis* species in Holland, Natterer's bats hibernated in the coldest conditions (mean = 6.1°C), Brandt's bats (mean = 7.2°C) and Daubenton's bats (mean = 7.3°C) hibernated in more moderate conditions, and pond bats in the warmest conditions (mean = 7.6°C; Daan & Wichers 1968). These findings were in line with those of this study. Masing (1982) reports that among three *Myotis* species in Estonia, pond bats hibernated in the warmest locations (mean = 5.5°C), followed by Daubenton's bats (mean = 5.4°C) and Brandt's bats/whiskered bats (mean = 5.1°C). In Germany, a study of four species found that brown long-eared bats (mean = 4.0°C) hibernated in the coldest conditions, then Brandt's bats/whiskered bats (mean = 4.6°C), with Natterer's bats (mean = 4.9°C) choosing the warmest conditions (Nagel & Nagel 1991) - a result that does not match our own. Bogdanowicz (1983) studied the temperatures at which brown long-eared bats, Daubenton's bats and Natterer's bats hibernated and their use of crevices in Poland. Brown long-eared bats preferred temperatures ranging from 0.5 to 4.0°C, Daubenton's bats from 1.5 to 6.0°C and Natterer's bats from 2.0 to 6.5°C. Crevice occupation was 82.1% for the

brown long-eared bat, 71.4% for Daubenton's bat, and 84.9% for Natterer's bat. Bogdanowicz & Urbańczyk (1983) compared brown long-eared bats, Daubenton's bats and Natterer's bats in Poland and found that the mean hibernation temperature was lowest among brown long-eared bats, followed by Daubenton's bats and Natterer's bats, although Natterer's bats hibernated in the widest range of temperatures. The Polish study found that the mean hibernation humidity was lowest among the brown long-eared bat followed by Daubenton's bat, and highest among Natterer's bat. In Poland, 89% of Natterer's bats, 85% of brown long-eared bats, and 74% of Daubenton's bats hibernated totally or partly in crevices (Bogdanowicz & Urbańczyk 1983). The fact that, further south, Natterer's bat hibernates in warmer condition than other species suggests that it employs a different hibernation strategy near the northern border of its distribution.

In an earlier study in southern Finland, comparing five species, we found that the northern bat ($2.0 \pm 0.1^\circ\text{C}$) and the brown long-eared bat ($2.7 \pm 0.2^\circ\text{C}$) hibernated in colder and drier locations whereas Daubenton's bat ($4.4 \pm 0.1^\circ\text{C}$) and Brandt's bat/whiskered bat ($4.0 \pm 0.1^\circ\text{C}$) hibernated in warmer and more humid locations (Siivonen & Wermundsen 2008a). This is also in line with the present study. Multispecies clusters were also uncommon in the Finnish study, which also found no examples of brown long-eared bats clustered with Daubenton's bats. Bogdanowicz (1983) suggests that the formation of multispecies clusters depends on the similarity of the ecological requirements of species. The present study found that pond bats and Natterer's bats never used the same hibernaculum, which may also indicate differences in ecological requirements of these two species.

Hibernacula are typically at their coldest in mid-hibernation season (e.g. Webb et al. 1996, Wermundsen & Siivonen 2009). Bats can move between hibernation bouts, adapting themselves to changes in temperature and humidity (e.g. Wermundsen & Siivonen 2009).

This feature should not affect the results of this study however, as the moment of measurement is independent of species. In addition, species-specific patterns of hibernation behaviour remain consistent throughout the hibernation season (Wermundsen & Siivonen 2009).

Further studies

Further studies are recommended to gather data during the entire hibernation season and to determine the availability of temperatures, humidity and crevices. Such work will help improve understanding about differences in hibernation strategies among the seven species. One interesting question is why pond bats and Natterer's bats are much rarer in southern Finland than in Estonia. Is this because Finnish and Estonian bedrock differs? Finnish bedrock conducts heat better, which means that frost penetrates deeper and faster, suggesting that underground conditions are perhaps more unstable in Finland than in Estonia. According to Webb et al. (1996), bats' susceptibility to mortality at subzero temperatures during hibernation may limit the northerly spread of some species. Individual Natterer's bats are sometimes found frozen in Estonia (Masing & Lutsar 2007). Pond bats hibernate at warmer locations which may be difficult to find in Finland in mid and late hibernation season (Wermundsen & Siivonen 2009).

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References

- Arnold, W. 1990. The evolution of marmot sociality: II. Cost and benefits of joint hibernation. *Behavioural Ecology and Sociobiology* 27: 239-246.
- Bogdanowicz, W. 1983. Community structure and interspecific interactions in bats hibernating in Poznań. *Acta Theriologica* 28: 357-370.

- Bogdanowicz, W. 1994. *Myotis daubentonii*. Mammalian Species 475: 1-9.
- Bogdanowicz, W. & Z. Urbańczyk 1983. Some ecological aspects of bats hibernating in city of Poznań. Acta Theriologica 28: 371-385.
- Boyles, J.G., M.B. Dunbar, J.J. Storm & V. Jr. Brack 2007. Energy availability influences microclimate selection of hibernating bats. Journal of Experimental Biology 210: 4345-4350.
- Boyles, J.G., J.J. Storm & V. Jr. Brack 2008. Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. Functional Ecology 22: 632-636.
- Brack, V. Jr. 2007. Temperatures and Locations Used by Hibernating Bats, Including *Myotis sodalis* (Indiana Bat), in a Limestone Mine: Implications for Conservation and Management. Environmental Management 40: 739-746.
- Choi, I.-H., Y. Cho, Y.K. Oh, N.-P. Jung & H.-C. 1998. Shin Behavior and muscle performance in heterothermic bats. Physiological and Biochemical Zoology 71: 257-266.
- Clawson, R.L., R.K. Laval, M.L. Laval & W. Caire 1980. Clustering behavior of hibernating *Myotis sodalis* in Missouri. Journal of Mammalogy 61: 245-253.
- Daan, S. & H.J. Wichers 1968. Habitat selection of bats hibernating in a limestone cave. Zeitschrift für Säugetierkunde 33: 262-287.
- Eesti Meteoroloogia ja Hüdroloogia Instituut 2010. URL: <http://www.emhi.ee>; viewed 20 November 2010.
- Estonica 2007. Climate. Estonica, Tallinn, Estonia. URL: <http://www.estonica.org>; viewed 20 November 2010.
- Frerichs, K.U., C.B. Smith, M. Brenner, D.J. DeGargia, G.S. Krause, L. Marrone, T.E. Dever & J.M. Hallenbeck 1998. Suppression of protein synthesis in brain during hibernation involves inhibition of protein initiation and elongation. Proceedings of the National Academy of Sciences of the United States of America 95: 14511-14516.
- Gaisler, J. 1970. Remarks on the thermopreferendum of Palearctic bats in their natural habitats. Bijdragen tot de Dierkunde 40: 33-36.
- Geiser, F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annual Review of Physiology 66: 239-274.
- Hock, R.J. 1951. The metabolic rates and body temperature of bats. Biological Bulletin 101: 289-299.
- Humphries, M.M., D.W. Thomas & D. Kramer 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. Physiological and Biochemical Zoology 76: 165-179.
- IUCN 2010. IUCN Red List of Threatened Species. Version 2010.1. URL: www.iucnredlist.org; viewed 20 November 2010.
- Kokurewicz, T. 2004. Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) hibernating in natural conditions. Acta Chiropterologica 6: 121-144.
- Kokurewicz, T. & N. Kováts 1989. Interpopulation differences in thermopreferendum of the lesser horseshoe bat, *Rhinolophus hipposideros* Bechstein, 1800 (Chiroptera: Rhinolophidae) in selected areas of Poland and Hungary. Myotis 27: 131-137.
- Krzanowski, A. 1959. Some major aspects of population turnover in wintering bats in the cave at Pulawy (Poland). Acta Theriologica 3: 27-43.
- Lausen C.L. & R.M.R. Barclay 2006. Winter bat activity in the Canadian prairies. Canadian Journal of Zoology 84: 1079-1086.
- Limpens, H.J.G.A., P.H.C. Lina & A.M. Hutson 2000. Action plan for the conservation of the pond bat in Europe (*Myotis dasycneme*). Nature and environment 108. Council of Europe Publishing, Strassbourg, France.
- Luis A.D. & O.J. Hudson 2006. Hibernation patterns in mammals: a role for bacterial growth? Functional Ecology 20: 471-477.
- Louw, G.N. 1993. Physiological Animal Ecology. Longman Scientific and Technical, Essex, UK.
- Masing, M. 1982. Öhuterapeutuurist nahkhiirte talvituspaikades Eesti ulukid. Eesti Terioloogia Selts, Tartu, Estonia.
- Masing, M. 1983. On the hibernation of bats in Estonia. Myotis 20: 5-10.
- Masing, M. 1984. Lendlased. Pääsuke, Tallinn, Estonia.
- Masing, M. & L. Lutsar 2007. Hibernation temperatures in seven species of sedentary bats (Chiroptera) in northeastern Europe. Acta Zoologica Lituanica 17: 47-55.
- McNab, B.K. 1974. The behaviour of temperate cave bats in a subtropical environment. Ecology 55: 943-958.
- Nagel A. & R. Nagel 1991. How do bats choose optimal temperatures for hibernation? Comparative Biochemistry and Physiology Part A: Physiology 99: 323-326.
- Siivonen, L. & S. Sulkava 1999. Pohjolan nisäkkäät. Otava, Helsinki, Finland.
- Siivonen, Y. & T. Wermundsen 2003. First records of *Myotis dasycneme* and *Pipistrellus pipistrellus* in Finland. Vespertilio 7: 177-179.
- Siivonen, Y. & T. Wermundsen 2008a. Characteris-

- tics of winter roosts of bat species in southern Finland. *Mammalia* 72: 50-56.
- Siivonen, Y. & T. Wermundsen 2008b. Distribution and foraging habitats of bats in northern Finland: *Myotis daubentonii* occurs above the Arctic Circle. *Vespertilio* 12: 41-48.
- Speakman, J.R., P.I. Webb & P.A. Racey 1991. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology* 28: 1087-1104.
- SPSS Inc. 1989-2005. SPSS for Windows, version 14.0 for Windows. SPSS Inc., Chicago, USA.
- Strelkov, P.P. 1958. Materials on the winter quarters of bats in the European part of the Soviet Union. Works of the Zoological Institute of the Academy of Sciences of the USSR 25: 255-303 [In Russian].
- Thomas, D.W. 1995. The physiological ecology of hibernation in vespertilionid bats. *Symposia of the Zoological Society of London* 67: 233-244.
- Thomas, D.W. & D. Cloutier 1992. Evaporative water loss by hibernating little brown bats, *Myotis lucifugus*. *Physiological Zoology* 65: 443-456.
- Thomas, D.W., M. Dorais & J. Bergeron 1990. Winter energy budgets and costs of arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* 71: 475-479.
- Thomas D.W. & F. Geiser 1997. Periodic arousals in hibernating mammals: is evaporative water loss involved? *Functional Ecology* 11: 585-591.
- Twente, J.W. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology* 36: 706-732.
- van Breukelen, F. & S.L. Martin 2002. Reversible depression of transcription during hibernation. *Journal of Comparative Physiology. B* 172: 355-361.
- Webb, P.I., J.R. Speakman & P.A. Racey 1996. How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology* 74: 761-765.
- Wermundsen, T. & Y. Siivonen 2009. Seasonal variation in use of winter roosts by five bat species in south-east Finland. *Central European Journal of Biology* 5: 262-273.
- Willis, J.S. 1982. The mystery of the periodic arousals. In: C.P. Lyman, J.S. Willis, A. Malan & L.C.W. Wang (eds.). *Hibernation and torpor in mammals and birds*: 92-103. Academic Press, New York, USA.
- Wojciechowski, M.S., M. Jefimow & E. Tęgowska 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). *Comparative Biochemistry and Physiology* 147A: 828-840.

Samenvatting

Een vergelijking van overwinteringsstrategieën van zeven soorten vleermuizen in Estland

We onderzochten of vleermuizensoorten met een noordelijker verspreidingsgebied in een winterverblijf op koudere plekken overwinteren, minder in spleten overwinteren en minder in clusters overwinteren dan soorten met een zuidelijker verspreidingsgebied. Hiertoe bepaalden we de temperatuur en luchtvochtigheid van hangplekken van dieren in overwinteringslocaties, alsmede de mate van bezetting van spleten en de mate van clustering van zeven inheemse vleermuizensoorten in acht hibernacula in Estland. De meervleermuis (*Myotis dasycneme*), de watervleermuis, (*Myotis daubentonii*) en Brandt's vleermuis/ baardvleermuis (*Myotis brandtii/mystacinus*) overwinterden op plekken met een met hogere temperatuur en luchtvochtigheid dan de noordse vleermuis (*Eptesicus nilssonii*), de bruine grootovleermuis (*Plecotus auritus*) en de franjestaart (*Myotis nattereri*). Het merendeel van de noordse vleermuizen, watervleermuizen, bruine grootovleermuizen en franjestaarten overwinterden solitair, terwijl Brandt's vleermuizen/baardvleermuizen en meervleermuizen meer in clusters overwinterden. De franjestaart overwinterde uitsluitend in spleten, terwijl de andere zes soorten zowel in spleten als vrij hangend overwinterden. Noordse vleermuizen hebben een noordelijker verspreidingsgebied dan de andere zes soorten en overwinterden alleen op de wanden of aan de plafonds, in koude en droge omstandigheden, terwijl meervleermuizen, die een relatief zuidelijk verspreidingsgebied hebben, een voorkeur hadden voor warmere en vochtigere omstandigheden. De resultaten suggereren dat de strategie van de meervleermuis gericht is op het sparen van energie tijdens het periodieke ontwakken en de daarop volgende perioden van euthermie, terwijl die van de franjestaart zich richt op het besparen van energie tijdens de overwintering zelf.

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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 leeward side of landscape

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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 = Grijskerke.

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 Grijskerke.

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 Grijskerke (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 hour¹. 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 hand-net, 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 Grijskerke.

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.

	number of fixed observation points	feeding 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 leeward side, and when bats were restricted to the leeward side.

	sound recorded (s)	feeding buzzes	wind speed (m/s)	wind incidence angle (°)
road (+ leeward)				
mean \pm s.d.	16.1 \pm 25.5	0.5 \pm 1.1	2.5 \pm 2.6	33.6 \pm 28.9
<i>n</i>	61	61	62	43
leeward 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
<i>n</i>	10	10	10	10
<i>P</i> (<i>t</i> -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 over-dispersed (parameter: number of observations per 1000 m, dispersion parameter = 1.85, $\chi^2 = 92.59$, *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 leeward side, 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 leeward 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 (\pm standard errors) of marginal effects on bat activity. Insect densities were skewedly 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 \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 (m/s)	-0.10 (0.23)	0.22 \pm 0.19	0.5	0.0	0.7	3.0
incidence angle (degrees)	0.001 (0.008)	0.009 \pm 0.009	0.4	0.5	0.9	2.7

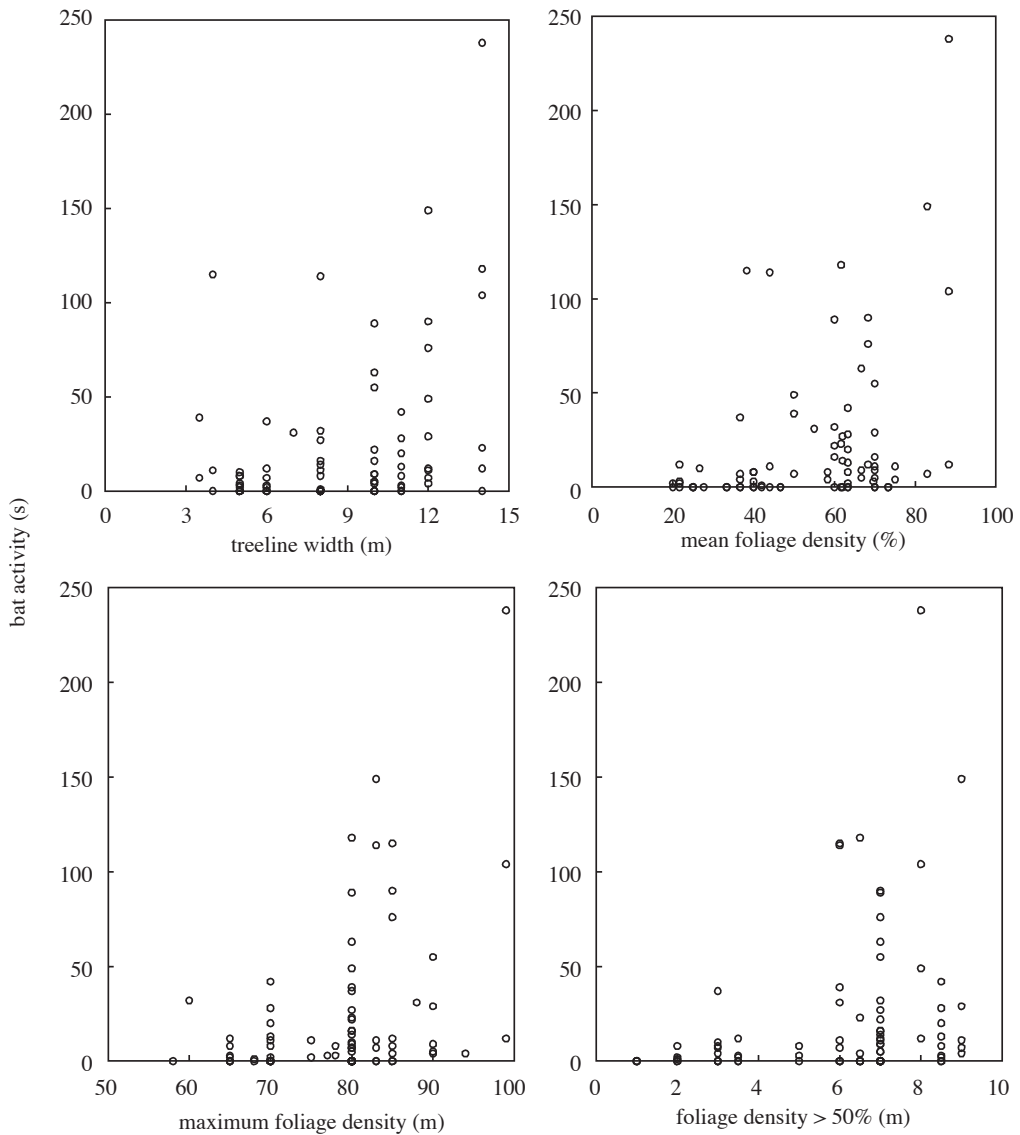


Figure 3. Bat activity on fixed observation points against four treeline parameters.

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 \pm 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 \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 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	overall mean (min-max)	transect M1		transects G1/G2		
		single obser- vations (min-max) ($n=24$)	feeding obser- vation points (min-max) ($n=22$)	overall mean (min-max)	single obser- vations (min-max) ($n=26$)	feeding obser- vation points (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)
maximum foliage den- sity (%)	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. Simultaneous evening counts of pipistrelle bats commuting over roads leading away from Grijpskerke. For route numbers see figure 2; mv = missing value.

date (d/m/yr)	wind direction and 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	
24/06/1994	SE 3	12 (10)	31(25)	19 (15)	24 (19)	30 (24)	10 (8)	126
		80/20/0	87/13/0	mv	85/15/0	100/0/0	100/0/0	145
21/06/1996	NNW 5	39 (31)	43 (34)	18 (14)	10 (8)	12 (9)	5 (4)	127
		0/100/0	100/0/0	100/0/0	58/42/0	100/0/0	100/0/0	108
18/07/1996	N 3	27 (23)	31 (27)	12 (10)	12 (10)	17 (15)	17 (15)	116
		24/76/0	97/3/0	100/0/0	57/36/7	mv	71/29/0	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 perme-

able (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 deter-

mine 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. Pennycuik 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 (Pennycuik 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 (Pennycuik 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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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, Sweden.
- Bell, G.P. 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology* 58: 1876-1883.
- Blake, D., A.M. Hutson, P.A. Racey, J. Rydell & J.R. Speakman 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoology* (London) 34: 453-462.
- Charnov, E.L. 1976. Optimal foraging: The marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- de Jong, J. 1994. Distribution patterns and habitat use by bats in relation to landscape heterogeneity, and consequences for conservation. PhD thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Downs, N.C. & P.A. Racey 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterologica* 8 (1): 169-185.
- Ekman, M. & J. De Jong 1996. Local patterns of distribution and resource utilization of four bat species (*Myotis brandtii*, *Eptesicus nilssoni*, *Plecotus auritus* and *Pipistrellus pipistrellus*) in patchy and continuous environments. *Journal of Zoology* (London) 238: 571-580.
- Engel, B. 1997. Extending generalized linear models with random effects and components of dispersion. PhD thesis, Wageningen Agricultural University, Wageningen, the Netherlands.
- Engel, B. & A. Keen 1994. A simple approach for the analysis of generalized linear mixed models. *Statistica Neerlandica* 48: 1-22.
- Fenton, M.B. & M.B. Griffin 1997. High-altitude pursuit of insects by echolocating bats. *Journal of Mammalogy* 78 (1): 247-250.
- Furlonger, C.L., H.J. Dewar & M.B. Fenton 1987. Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology* 65: 284-288.
- Genstat 5 Committee 1993. Genstat 5 Release 3 Reference Manual. Clarendon Press, Oxford, UK.
- Genstat 5 Committee 1995. Genstat 5 Release 3.2 Reference Manual Supplement. Numerical Algorithms Group, Oxford, UK.
- Haffner, M. & H.P. Stutz 1985-1986. Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at streetlamps. *Myotis* 23/24: 167-172.
- Hoare, L.R. 1991. The diet of *Pipistrellus pipistrellus* during the prehibernal period. *Journal of Zoology* (London) 225: 665-670.
- Jones, G. & J.M.V. Rayner 1989. Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus*. In: V. Hanak, I. Horacek & J. Gaisler (eds.). *European Bat Research 1987*: 247-253. Charles University Press, Praha, Tsjechoslovakia.
- Keen, A. 1996. Procedure IRREML. In: P.W. Goedhart & J.T.N.M. Thissen (eds.). Genstat 5 GLW-DLO Procedure Library Manual Release 3.2. Report LWA-96-05, DLO Agricultural Mathematics Group, Wageningen, the Netherlands.
- Kronwitter, F. 1988. Population structure, habitat use and activity patterns of the Noctule bat, *Nyctalus noctula* Schreber 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis* 26: 23-85.
- Lewis, T. 1969a. The distribution of flying insects near a low hedgerow. *Journal of Applied Ecology* 6: 443-452.
- Lewis, T. 1969b. The diversity of the insect fauna in

- a hedgerow and neighbouring fields. *Journal of Applied Ecology* 6: 453-458.
- Lewis, T. 1970. Patterns of distribution of insects near a windbreak of tall trees. *Annals of Applied Biology* 65: 213-220.
- Lewis, T. & G.C. Dibley 1970: Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. *Annals of Applied Biology* 66: 477-484.
- Lewis, T. & J.W. Stephenson 1966. The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. *Annals of Applied Biology* 58: 355-363.
- Limpens, H.J.G.A. & K. Kapteyn 1991. Bats, their behaviour and linear landscape elements. *Myotis* 29: 63-71.
- Limpens, H., K. Mostert & W. Bongers (eds.) 1997. *Atlas van de Nederlandse vleermuizen*. KNNV-uitgeverij, Utrecht, the Netherlands.
- McCullagh, P. & J.A. Nelder 1989. *Generalized linear models*. Chapman & Hall, London, UK.
- Norberg, U.M. 1990. Vertebrate flight. Mechanics, physiology, morphology, ecology and evolution. Springer, Berlin, Germany.
- Norberg, U.M. & 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.
- Patterson, H.D. & R. Thompson 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58: 545-554.
- Pennycuik C.J. 1969. The mechanics of bird migration. *Ibis* 111: 525-556.
- Racey, P.A. & S.M. Swift 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *Journal of Animal Ecology* 54: 205-215.
- Rieger, I., D. Walzthöny & H. Alder 1990. Wasserfledermäuse, *Myotis daubentonii*, benutzen Flugstrassen. *Mitteilungen der Naturforschungs-gesellschaft Schaffhausen* 35: 37-68.
- Rydell, J. 1992. Exploitation of insects around street-lamps by bats in Sweden. *Functional Ecology* 6: 744-750.
- Rydell, J., A. Entwistle & P.A. Racey 1996. Timing and foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 76: 243-252.
- Schnitzler, H.-U. 1971. Fledermäuse im Windkanal. *Zeitschrift für Vergleichende Physiologie* 73: 209-221.
- Schofield, H.W. 1996. The ecology and conservation biology of *Rhinolophus hipposideros*, the lesser horseshoe bat. PhD thesis. University of Aberdeen, Aberdeen, Scotland.
- Rydell, J., A. Bushby, C.C. Cosgrove & P.A. Racey 1994. Habitat use by bats along rivers in north-east Scotland. *Folia Zoologica* 43: 417-424.
- Simon, M., S. Hüttenbügel & J. Smit-Viergutz 2004. Ecology and conservation of bats in villages and towns. *Schriftenreihe für Landschaftspflege und Naturschutz*, Heft 77. Bundesamt für Naturschutz, Bonn – Bad Godesberg, Germany.
- Speakman, J.R. 1991. The impact of predation by birds on bat populations in the British Isles. *Mammal Review* 21 (3): 123-142.
- Sullivan, C.M., C.B. Shiel, C.M. McAney & J.S. Fairley 1993. Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentonii* and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *Journal of Zoology (London)* 231: 656-663.
- Swift, S.M. 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology (London)* 190: 285-295.
- Swift, S.M., P.A. Racey & M.I. Avery 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *Journal of Animal Ecology* 54: 217-225.
- Verboom, B. & H. Huitema 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12 (2): 117-125.
- Verboom, B. & K. Spoelstra 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Canadian Journal of Zoology* 77 (9): 1393-1401.
- Verboom, B., A.M. Boonman & H.J.G.A. Limpens 1999. Acoustic perception of landscape elements by the pond bat *Myotis dasycneme*. *Journal of Zoology (London)* 248: 59-66.
- Voûte, A.M. 1972. *Bijdrage tot de oecologie van de meervleermuis, Myotis dasycneme* (Boie, 1825). PhD thesis. University of Utrecht, Utrecht, the Netherlands.
- Walsh, A.L. & S. Harris 1996. Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology* 33: 508-518.
- Wilkinson, G.S. 1992. Information transfer at evening bat colonies. *Animal Behavior* 44: 501-518.
- Williams, T.C., L.C. Ireland & J.M. Williams 1973. High altitude flights of the free-tailed bat, *Tadarida brasiliensis*, observed with radar. *Journal of Mammalogy* 54: 807-821.

Samenvatting

Effecten van windbeschutting op het land- schapsgebruik door gewone dwergvleer- muizen (*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 dwergvleermui-

zen. De hoogte, breedte en vegetatiedichtheid (permeabiliteit) 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.

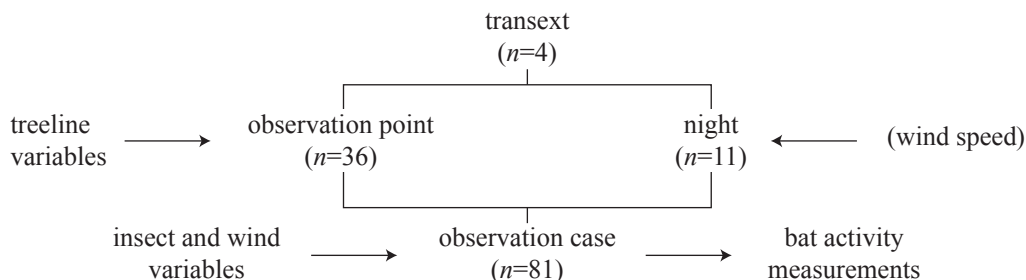
The direction of the arrows indicates ways in which the survey was structured so as to model bat activity as a function of the other variables.

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 these 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 obser-

vations 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}):

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

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 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:

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

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

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.

Badger (*Meles meles*) road mortality in the Netherlands: the characteristics of victims and the effects of mitigation measures

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Abstract: Of the badger (*Meles meles*) population in the Netherlands of the 1980s, a high percentage (locally up to 25%) of the population was killed yearly by road traffic. This led the Dutch authorities to instigate mitigation measures such as fauna tunnels and fences. Between 1990 and 2006 data has been gathered on badger victims in the Netherlands which can be used to test if these mitigation measures have been effective. We present here data on the total number, age and sex of the victims, their distribution over the Netherlands, and over national, provincial and municipal roads and test whether mitigating measures results in a decrease in traffic victims. The badger victim dataset shows a clear peak in victims in March, and relatively low numbers in December, January and February. Most fatalities occurred within the distribution range of the badger. Nationally, the sex-ratio of victims did not differ from 1:1, but in 1990, more of the fatalities outside the badger's distribution range were female. In absolute terms, most victims were reported from municipal roads. However, relative to the total length of roads within the range of the badger, most victims occurred on provincial roads. The number of traffic victims is significantly lower when mitigation measures have been in place for a while. The challenge for conservation lies in minimising victim numbers at provincial and municipal roads. As badger victims occur over a huge length of municipal roads mitigation along these routes will be difficult. Still, a number of measures are recommended, including for example placing fauna passages at well-known badger tracks, decreasing speed limits, relocating badger setts or closing roads for through traffic.

Keywords: traffic victims, fauna tunnels, road fences, eco-ducts, wildlife passages, road ecology, *Meles meles*, badger.

Introduction

In the 1900s, the badger (*Meles meles*) population in the Netherlands was estimated to number between 2500 and 3000 setts, containing over 4000 individuals (van Moll 2005). By the 1960s this number had declined drastically (van Wijngaarden & van de Peppel 1964) and it stayed low until the mid 1980s (van Wijngaarden et al. 1971, Wiertz & Vink 1986), with about 400 setts in the whole of the Netherlands.

A number of causes for this decline have been suggested (van Wijngaarden & van de Peppel

1964, Wiertz & Vink 1986, van Apeldoorn et al. 1995). These included hunting and poaching, the disturbance and destruction of setts, habitat loss, pollution, isolation of metapopulations, hampered migration and road traffic. By the 1980s, it was clear that the number of badger traffic victims was continuing to rise (Wiertz & Vink 1986; figure 1) and that a high percentage of the population, in some areas up to 25%, was being killed by road traffic: (Broekhuizen et al. 1994, van Apeldoorn et al. 1995, Bekker & Canters 1997). In 1984 the Dutch Ministry of Agriculture, Nature and Fisheries launched a badger protection policy to address the decline in badger numbers (Beheersoverleg Dassen 1983, Sneepe 1986).

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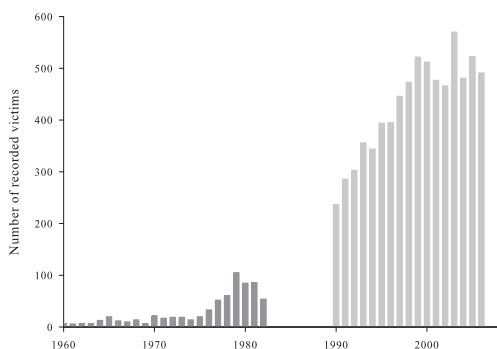


Figure 1. The number of recorded badger traffic victims in the period 1960-1982 (Wiertz & Vink 1986) and 1990-2006 (this study); in the period in between there was no registration.

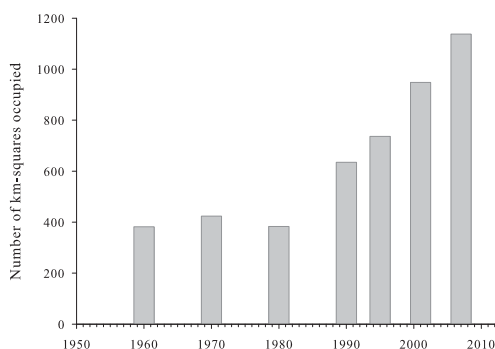


Figure 2. Number of 1x1 km squares in the Netherlands, occupied by the badger. Sources: van Wijngaarden & van de Peppel (1964), van Wijngaarden et al. (1971), Wiertz & Vink (1986), Wiertz (1991), van Moll (2005), Witte et al. (2008).

The proposed measures included habitat improvement and de-fragmentation, reintroductions, refunding farmers for crop damage and educating hunters and landowners (Sneep 1986). In 1990 national policies for nature and transport (the Nature Policy Plan and the Second Transport Structure Plan (Ministerie van Landbouw, Natuurbeheer en Visserij 1990, Ministerie van Verkeer en Waterstaat 1990 respectively) underlined the necessity of halting further habitat and population fragmentation by roads and to counter the existing level of fragmentation. These policies paved the way for de-fragmentation programmes (Bekker & Canters 1997). The Nature Policy Plan introduced the National Ecological Network (NEN) and the Second Transport Structure Plan stated that no further fragmentation of nature and landscape by motorways would be allowed and that the existing level of fragmentation must be decreased. These policies, updated in 2000 (Ministerie van Landbouw, Natuur en Voedselkwaliteit 2000) and in 2005 (Ministerie van Verkeer en Waterstaat 2005) are the basis of current policy, described in the Long Term De-fragmentation Programme (Ministerie van Verkeer en Waterstaat et al. 2004). This programme has identified 208 bottlenecks between national infrastructure (roads, rail roads and canals) and the National

Ecological Network (NEN) and has set a target of eliminating these bottlenecks by 2018.

In the 1990s and 2000s, the distribution and population size of the badger increased strongly (Wiertz 1992, van Moll 2005, Witte et al. 2008) (figure 2). This increase may be attributed to addressing most of the assumed causes of decline, such as compensation for damage to crops (Faunafonds 2006), establishing management scheme agreements with farmers that have setts on their land (Faunafonds 2006), a decrease in PCBs and heavy metals (except in floodplains, van den Brink & Ma 1998), the raising and translocation of orphaned or threatened badgers (van Moll 2005), the countering of habitat loss and implementing mitigation measures at problem sites on the national road network. Here we focus on the efficacy of the latter.

The most frequently implemented mitigation measures to help badgers safely across roads are small round tunnels (with a diameter of 40-50 cm), constructed from concrete or steel, combined with fencing (Kruidering et al. 2004). These tunnels are known to be used by badgers (Maaskamp 1983, Derckx 1986, van Dinther 1994, Bekker & Canters 1997, Brandjes et al. 2002). Apart from tunnels there have also been adaptations to existing infrastructures, such as bridges and viaducts,

to make them suitable for co-use by badgers (Kruidering et al. 2004).

There is no current data on the proportion of the national badger population (also in terms of age and sex) that is killed by traffic, whether there is any difference between road types, and whether establishing tunnels contributes to a decrease mortality. This knowledge can help to optimise conservation and mitigation measures, by aiming them at certain road types or certain parts of the badger range and can also be used as a model for other terrestrial mammals.

In this paper, we present and analyse data on badger traffic victims gathered by the Das & Boom Society and Rijkswaterstaat between 1990 and 2006. As a first step we present the age and sex of the victims and the temporal and spatial patterns in victim numbers. In an expanding population, females are the agents of population spread. For this reason, we pay extra attention to the sex-ratio of victims found outside the known distribution range of badgers, and compare these results with an earlier study. As a second step, we determine the distribution of victims along national, provincial and municipal roads. Finally, as a third step, we test whether taking mitigating measures results in a decrease in traffic victims.

Methods

Collecting badger traffic victim data

The datasets of badger traffic victims and of mitigation measures were not specifically gathered for this study. Traffic victim data were gathered by the Das & Boom Society and Rijkswaterstaat. Badger victims were generally found by the public, by inspectors of Rijkswaterstaat and a network of volunteers. Until 2000, volunteers of the Das & Boom Society went to the majority of reported sites to determine the age (sub-adult, adult) and sex of traffic victims. After 2000, the age and sex were no longer determined in the field by these

volunteers, but were sometimes given by the person reporting the badger victim. The location of accidents is available, with in coordinates precise to within ten metres, as well as the road name, type and responsible authority and date. The dataset covers the period from 1 January 1990 to 31 December 2006.

Estimating badger range and population size

The changes in badger range and population size in the last 40 years have been well documented through national badger censuses: systematic surveys in which all suitable badger habitats were checked for inhabited setts. Badger censuses were carried out in 1960 (van Wijngaarden & van de Peppel 1964), 1970 (van Wijngaarden et al. 1971), 1980 (Wiertz & Vink 1986), 1990 (Wiertz 1992), 1995 (van Moll 2005), 2001 (van Moll 2005) and 2007 (Witte et al. 2008) (figure 2). A badger census involves conducting a survey of the potential habitats of badgers, with each square km of potential habitat being checked for badger presence, setts or tracks. The exact methodology is described in the reports of each census. We assume that the 2007 census is a good representation of the range and population in 2006 and use this data to compare the traffic victims of 2006 with the badger range.

Roads and road mitigation

Rijkswaterstaat provided us with spatial data about the Dutch national road network. Data on fauna tunnels and eco-ducts at motorways came from the WEGENSNIP database (Rijkswaterstaat 2007). Additional data about fauna tunnels along provincial and municipal roads were provided by the Das & Boom Society. These datasets detailed the type of wildlife crossing, structure, location, road type and year of construction. Our analysis only looked at wildlife crossing structures

that were accompanied with wildlife fences to guide the animals to the structure and keep them off the road. Roads with wildlife fences but without wildlife crossing structures were not considered as sites with mitigation measures for the purpose of this analyses.

Demographic analyses and distribution of victims

First, we report the descriptive statistics from the traffic victim database: the number of victims each year and the total number of victims each month, with an age and sex class breakdown. We separately analyse victims were reported outside the known range, for the years when a badger census was carried out. Badgers are considered to be outside their known range when they are reported from a location more than two kilometres from the known distribution range of badgers in that year (two kilometres is the maximum distance that resident badgers move away from their setts in the Netherlands (van Wijngaarden & van de Peppel 1964, Wansink 1995) and elsewhere in western Europe (Neal & Cheeseman 1996, Palphramand et al. 2007)). We use a Chi-square test to test for the sex-ratios within the total victim population over the whole year, in the mating period only, and among fatalities outside of the known badger range. We compare these data with data reported by Müskens & Broekhuizen (1993) whose study of badger victims in the 1980s, found that badgers killed by traffic further than three kilometres from known setts were more often females.

Next, to correct for the effects of population growth and wider distribution on victim numbers, we express the number of recorded victims as a percentage of the population for the years in which a census was done (dividing the number of victims by population size in the census years). Following Wiertz & Vink (1986) we assume that there is usually one sett per km², and that setts are inhabited by 3.2 badgers. We divide the number of badger

victims by the number of populated km² x 3.2 badgers km⁻² x 100% in order to calculate the percentage of the population that were recorded as traffic victims.

Badger victims by road type

In the analysis we distinguish three road types: national roads, provincial roads and municipal roads. These road types have different speed limits (respectively 120 or 100 km hour⁻¹, 100 or 80 km hour⁻¹ and 50 to 30 km hour⁻¹), and different traffic densities.

We then enter traffic victims and road maps into a GIS, with the location of each fatality also being coded in terms of road type. Next, we calculate the absolute number of traffic victims by road type. As there are far more municipal roads than provincial or national roads, it is likely these roads will claim more victims. To take this into account we also calculated the number of victims per kilometre of each type of road within the known range of badgers, for each of the census years.

The effect of mitigation measures

We tested the effect of mitigation measures on badger mortality by comparing the number of victims around each road mitigation site, before and after the construction of the wildlife crossing structure. We used two kilometres of road length on each side of the mitigation site, as this is the maximum range a non-dispersing badger will move from its sett in the Netherlands (van Wijngaarden & van de Peppel 1964). We assumed that the number of badger fatalities more than two km from the mitigation measure would be unaffected by the measure.

An increase in numbers and/or the expansion of the range of badgers over the study period are potentially confounding factors when testing the effect of mitigation measures: a road may show more victims after the

implementation of a mitigation measure if badgers were absent in the area in the years preceding the implementation and moved into the area afterwards. To avoid such problems, we only selected mitigation sites ($n=126$) situated within the 1990 badger range, locations which could potentially have had badger victims over the whole period. To further correct for population change, we weighted the number of victims at each location in a given year by dividing this figure by the number of victims that occurred nationally in that year.

We tested the effect of mitigation measures on the number of victims using a Generalised Linear Model approach, modelling the number of victims in each year at these locations, divided by the number occurring nationally in this year as a function of the number of years that each mitigation measure has existed. So, for a location with a measure implemented in 1998, this number would be -8 in 1990 and +2 in the year 2000. Location is included in the model as a factor. Because

the pattern of victims follows a Poisson-distribution, with many zero counts, we used a quasi-Poisson error term, with a log link function. We evaluated the model by using Nagelkerke's R^2 (McCullagh & Nelder 1983). All statistical analyses were done in statistical package R (R Development Core Team 2008).

Results

Demography, phenology and distribution of victims

There was a steady rise in the number of badgers recorded as victims of traffic between 1990 and 2000, which then seemed to stabilise at around 500 victims per year between 2000 and 2006 (figure 1). Of course, these numbers may underestimate the true figure: not all animals that are found are reported, and not all animals hit by cars are found.

Of the 7,279 badger victims reported between

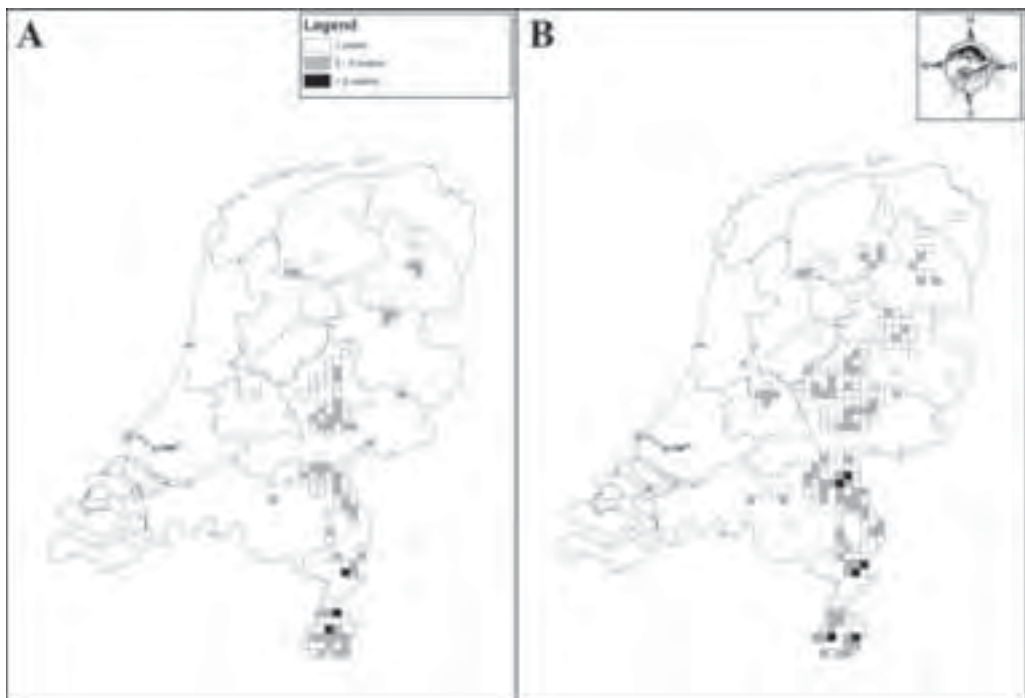


Figure 3. Distribution of victims in 1990 (A) and 2006 (B).

Table 1. Number of badger traffic victims (with sex and sex ratio) for the period 1990-2006; for the mating period (March) in the period 1990-2006, and found outside known badger range in the 1980s and badger census years (1990, 1995, 2001 and 2006). * $P < 0.05$ ** $P < 0.01$.

¹ Data from Müskens & Broekhuizen (1993).

		Male victims	Female victims	Sex ratio	χ^2
1990-2006	all victims	2539	2447	1.04	1.700
1990-2006	victims in March	325	296	1.10	1.354
1980s ¹	all victims	277	249	1.1	1.491
	outside range	5	20	0.3	9.000**
1990	all victims	78	89	0.9	0.725
	outside range	3	16	0.2	8.895**
1995	all victims	171	156	1.1	0.688
	outside range	27	15	1.8	3.429
2001	all victims	122	100	1.2	2.180
	outside range	5	7	0.7	0.333
2006	all victims	105	135	0.8	3.750*
	outside range	10	9	1.1	0.053

1990 and 2006, 142 animals were killed by trains. Another 140 victims in the dataset were badgers that had drowned in canals. The distribution of victims generally follows the range of badgers, although some victims do occur far outside the known range (figure 3).

There is no difference in the number of male and female badgers that were killed by traffic in the whole set (table 1) or in the mating season, March ($\chi^2_{1,621} = 1.35$, $P = 0.24$). In 1990 there

was a difference in the number of males and females killed outside the badger distribution range, but not in 1995, 2001 and 2006 (table 1). The number of victims is lower in the winter months (November to January) than in other months (figure 4), whilst in March there is a peak in numbers of victims. Sub-adult victims are seen first in April, but are only numerous in June, July and August. They constitute more than 10% of the victims in those months.

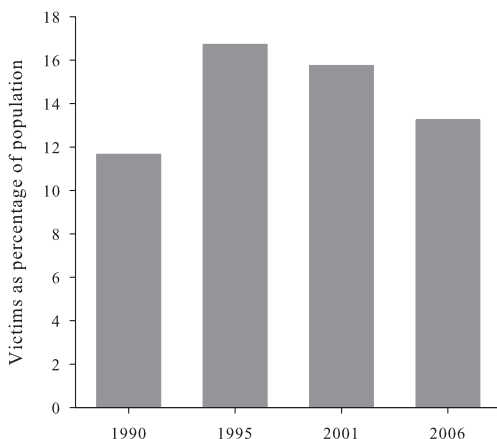


Figure 4. Number of traffic victims per month per age class in the period 1990-2006.

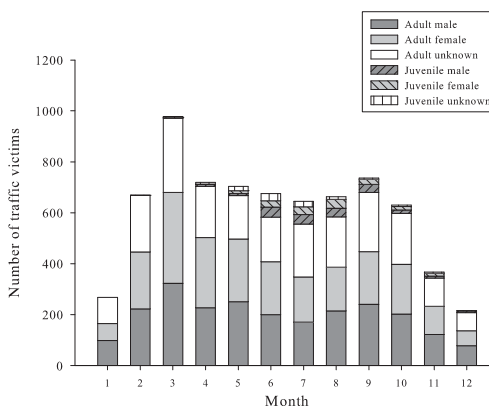


Figure 5. Estimate of the percentage of the Dutch badger population that is killed by traffic for census years.

On the basis of these calculations we estimate that in 1990, recorded badger traffic victims accounted for 12% of the (estimated) Dutch badger population. In 1995, this percentage rose to 18%. In the 2000s, it declined again: an estimated 17% of the population was killed by traffic in 2001, and 13% in 2006 (figure 5).

Road types

In absolute terms, most badgers are killed on municipal roads and the fewest on national roads (figure 6A). When corrected for the length of each road type within the range of badgers, a different pattern emerges: the lowest number of victims per kilometre of road occurs on municipal roads, and the most on provincial roads (figure 6B).

The effect of mitigation measures

There is no clear pattern in the relative number of victims before, during and after a mitigation measure is taken (figure 7), and there are large standard deviations within the data. However the generalised linear mixed model shows that the number of traffic victims is significantly lower the longer mitigation measures have been in place ($P < 0.04$, Nagelkerke's $R^2 = 0.41$).

Discussion

The demography and distribution of victims

In line with earlier studies (Berendsen 1986, Davies et al. 1987) the majority of the animals killed were adults. The figures suggest that between 12% and 18% of the Dutch badger population was killed by traffic each year. However these percentages are almost certainly an underestimate, because not all victims that are found are reported and animals that are hit by cars but not killed immediately

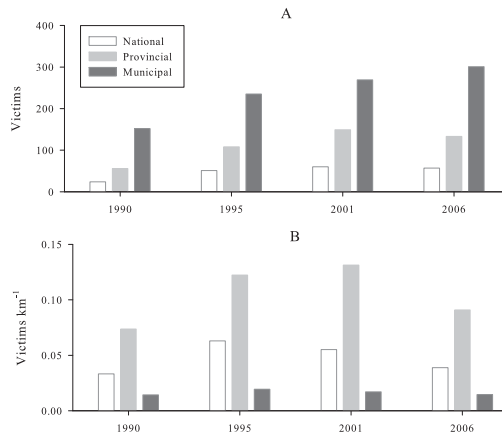


Figure 6. Absolute (A) and mean (B) numbers of victims on national roads, provincial roads and municipal roads.

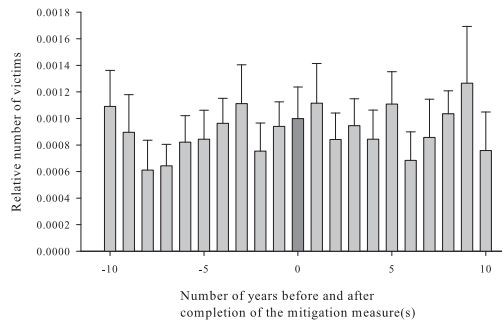


Figure 7. Average (+ s.d.) number of victims relative to the national number of victims and the number of years a mitigation measure is in place. Year '0' is the year the mitigation measure was implemented, 'year -8' is eight years before construction, year 8 is eight years after construction.

will move themselves away from the roadside and will not be found. Our estimates also do not include the number litters or juveniles that became orphans and subsequently died, Broekhuizen et al. (1994) estimated that at least 10% of all litters were lost because lactating females were killed at roads.

Overall, between 1990 and 2006, similar numbers of male and female badgers were killed by traffic, corroborating earlier studies (Davies et al. 1987, Müskens & Broekhuizen 1993, Broekhuizen et al. 1994). This is in con-

trast to other mustelids such as pine marten (*Martes martes*) (Muskens & Broekhuizen 2000), where more males than females die in traffic. We attribute this to the difference in the social structure of badger families. Badgers live and mate within social groups, which occupy a fixed home range, whilst other mustelid species live solitarily and mate promiscuously. For this reason, other male mustelids have larger home ranges than females (Johnson et al. 2000), resulting in higher mobility, increasing the frequency of road crossing, and thus increasing the chance of becoming a traffic victim.

There were relatively few victims in the period between November and January. Badger activities are lower in winter (Neal & Cheeseman 1996) and home ranges are smaller than in other seasons (Palphramand et al. 2007). Less mobility means there will be a smaller chance of being killed by traffic. Our results are supported by several other studies: road fatalities are lower in the winter months for badgers in the UK (Davies et al. 1987), in the Netherlands (Muskens & Broekhuizen 1993) and for other mustelid species (Muskens & Broekhuizen 2000).

There is a peak in victim numbers in March, with no difference in the number of male and female victims. As dispersal of badgers is not an event, but a slow and gradual process (Roper et al. 2003), we rule out the dispersal of young adult males and females as the main cause of the peak in victims in our dataset in March. Badgers show a peak in mating activity in early spring, which coincides with increased mobility due to marking of territory boundaries and looking for mates (Woodroffe et al. 1993). This increased mobility will increase the chance of getting killed by traffic. An earlier study found a bimodal pattern in victim numbers, with a peak in March, similar to our findings, and a second, smaller peak in August-September, which was attributed to a second peak in sexual activity (Davies et al. 1987). Such a late summer peak is not present in our

data. However, Davies et al. (1987) analysed data from one year only, and report this year to be a particularly dry one. Drought can increase traffic mortality because of difficulties in finding food (Neal 1977), so the second peak reported by Davies et al. 1987 may well be an anomaly. We found no significant differences in the sex-ratio of traffic victims found outside known badger range in 1995, 2001 and 2006, although more females were killed in 1990. Muskens & Broekhuizen (1993), in their study of badger victims in the 1980s, found that badgers killed by traffic further than three kilometres from known setts were more often female. Possibly, the expanding population during our study period increased the number and proportion of dispersing males, resulting in increased mortality among them.

Road type

Most victims occurred on municipal roads (figure 6A). This is hardly surprising: this type of road makes up for the majority of the road network of the Netherlands. Yet these are also the hardest type of road on which to decrease traffic victims as the fatalities are widely dispersed. The number of victims per km of road is highest on provincial roads (figure 6b) and this number increased over the study period. We hypothesise that the difference in mortality between road types is caused by the greater ease of access for wildlife on provincial roads, as opposed to national roads. In the Netherlands, national roads must have a ten metre obstacle free zone on either side (Dienst Verkeerskunde 1992, Adviesdienst Verkeer en Vervoer 2006), which makes traffic more visible to wildlife and vice versa. Higher traffic speeds on provincial roads may also increase the risk of wildlife being hit. Badgers may also avoid wider, noisier and busier national roads more than the quieter provincial and municipal roads. In the south of the UK, most victims

also occur on smaller roads and far fewer on motorways (Clarke et al. 1998). And, during the study period (and especially in the first half) many more mitigation measures were implemented on national roads than on provincial and municipal roads.

Policy-wise, measures to lower the number of badger traffic victims should be primarily be taken along municipal and especially on provincial roads, as the relative number of victims per km on these roads is higher. The number of victims on the provincial roads and municipal roads could be lowered with management measures such as implementation and maintenance of fauna tunnels (Kruidering et al. 2005), fauna passages at well-known badger tracks, lowering of speed limits, or by closing off certain stretches of road (Jaarsma et al. 2007) during the night and/or in periods when collision probabilities are high. To be most effective, measures should be planned along sections with many recorded mortalities, making use of relevant landscape elements (ditches, tree lines, etc) and following a landscape-oriented approach (Kruidering et al. 2005).

The effect of mitigation measures

At many locations mitigation measures show an effect in reducing victim numbers and our analyses show fewer victims in the years following mitigation measures being taken. In these analyses there were confounding factors. The effects of implementing mitigation measures may have been obscured by the growth and expansion of the badger population in the Netherlands during the study period, despite our efforts to correct for this. An analysis of well studied local situations, as performed by van Apeldoorn et al. (2006) and Vink et al. (2008), or a measure-by-measure analysis, taking also into account factors such as roadside habitat and municipal population size, give additional insights in the effects of these measures on badger mortality.

Conclusion

We calculate that around 10-20% of the total badger population in the Netherlands is killed by road traffic annually, although this is probably an underestimate. March is the most common month for badger road mortalities, with figures being much lower in the winter months. In absolute terms, most badger mortalities are on municipal roads, but when expressed per kilometre of road, most mortalities occur on provincial roads. Mitigation measures reduce the number of victims. As there are several factors that could have affected the Dutch badger population it is hard to establish the extent to which road management has contributed to the recent increase of badgers in the Netherlands. However it is clear that mitigation measures have decreased mortality among Dutch badgers. For this reason it is important that these mitigation measures remain operational (Janssen et al. 1997, Vereniging Das & Boom 2002, Ouden & Piepers 2006).

In absolute terms most traffic victims are reported from municipal roads, but in relative terms most occur on provincial roads. In the case of municipal roads, the mortalities occur over a huge length of roads, making it difficult to take appropriate mitigation measures that will reduce these numbers. Still, some measures are feasible. These include fauna passages along well known badger routes or at locations where fatalities occur, decreasing speed limits or closing roads for through traffic (Jaarsma et al. 2007), closing them at night, or closing them during the peak fatality season.

Victim numbers are highest in March and lowest in the winter months, implying that major maintenance of tunnels and other mitigating measures is best undertaken between November and January. This way badgers, and other mustelids, will find the measures functioning and ready to use when they become more active in spring. However, frequent inspections and maintenance remain

important throughout the year. Specific mitigation measures, such as fences or tunnels, are more effective when backed up by knowledge of the local badger population and its spatial behaviour.

Mathematical models indicate that an increase of life expectancy of badgers will result in more females in the age of highest reproductive success, and therefore in a relatively big increase in the population (Seiler et al. 2003). However, this proposed mechanism has not been tested in the field. The challenge now lies in testing the extent to which the decrease in mortality brought about by mitigation measures, together with the decrease in habitat fragmentation, will translate into a growth in the badger population as a whole.

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References

- Adviesdienst Verkeer en Vervoer (ed.) 2006. Nieuwe Ontwerprichtlijn Autosnelwegen (NOA). Adviesdienst Verkeer en Vervoer, Rijkswaterstaat, Rotterdam, the Netherlands.
- Beheersoverleg Dassen 1983. Beleidsaanbevelingen inzake het behoud en herstel van de dassenpopulatie in Nederland. Beleidsnota voor de Minister van Landbouw, Natuur en Visserij. Ministerie van LNV, the Hague, the Netherlands.
- Bekker G.J. & K.J. Canters 1997. The continuing story of badgers and their tunnels. In: K.J. Canters, A. Piepers & D. Hendriks-Heersma (eds.). Proceedings of the international conference: Habitat fragmentation, infrastructure and the role of ecological engineering. Maastricht/Den Haag, the Netherlands; 17-20 September 1995: 344-353. DWW publication P-DWW-97-046. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.
- Berendsen, G. 1986. De Das (*Meles meles* L.) als verkeersslachtoffer. Rijksinstituut voor Natuurbeheer, Arnhem, the Netherlands.
- Brandjes, G.J., R. van Eekelen, K. Krijgsveld, K. & G.F.J. Smit 2002. Het gebruik van faunabuizen onder rijkswegen; resultaten van literatuur- en veldonderzoek. DWW-Ontsnipperijsreeks deel 43. Report DWW-2002-123. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.
- Broekhuizen, S., G.J.D.M. Müskens & J. Sandifort. 1994. Invloed van sterfte door verkeer op de voortplanting bij dassen. Report 055. Instituut voor Bos- en Natuuronderzoek, Wageningen, the Netherlands.
- Clarke, G.P., P.C.L. White & S. Harris 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biological Conservation 86: 117-124.
- Davies, J.M., T.J. Roper & D.J. Shepherdson 1987. Seasonal distribution of road kills in the European badger (*Meles meles*). Journal of Zoology 211 (3): 525-529.
- Derckx, H. 1986. Ervaringen met dassenvoorzieningen bij Rijksweg 73, tracé Teersdijk-Maasbrug. Lutra 29 (1): 67-75.
- Dienst Verkeerskunde (ed.) 1992. Richtlijnen voor het ontwerp van autosnelwegen (ROA). Dienst Verkeerskunde, Rijkswaterstaat, Rotterdam, the Netherlands.
- Faunafonds 2006. Jaarverslag Faunafonds 2006. Faunafonds, Dordrecht, the Netherlands.
- Jaarsma, C.F., F. van Langevelde, J.M. Baveco, M. van Eupen & J. Arisz 2007. Model for rural transportation planning considering simulating mobility and traffic kills in the badger *Meles meles*. Ecological Informatics 2: 73-82.
- Janssen, A.A.W., H.J.R. Lenders & S.E.W. Leuven 1997. Technical state and maintenance of underpasses for badgers in the Netherlands. In: K.J. Canters, A. Piepers & D. Hendriks-Heersma (eds.). Proceedings of the international conference: Habitat fragmentation, infrastructure and the role of ecological engineering. Maastricht / Den Haag, the Netherlands; 17-21 September 1995: 362-366. DWW publication P-DWW-97-046. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.
- Johnson, D.D.P., D.W. Macdonald & A.J. Dickman 2000. An analysis and review of models of the sociobiology of the Mustelidae. Mammal Review 30 (3-4): 171-196.
- Kruidering, A.M., G. Veenbaas, R. Kleijberg, G. Koot, Y. Rosloot & E. van Jaarsveld 2005. Leidraad Faunavoorzieningen bij Wegen. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.

- Maaskamp, F. 1983. Het gebruik van een duiker door dassen als onderdoorgang van een weg. *Huid en Haar* 2: 163-165.
- McCullagh, P. & J.A. Nelder 1983. Generalized linear models. Chapman and Hall, London, UK.
- Ministerie van Landbouw, Natuurbeheer en Visserij 1990. Natuurbeleidsplan. Tweede Kamer der Staten-Generaal, the Hague, the Netherlands.
- Ministerie van Landbouw, Natuur en Voedselkwaliteit 2000. Natuur voor mensen, mensen voor natuur. Nota natuur, bos en landschap in de 21e eeuw. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag, the Netherlands.
- Ministerie van Verkeer en Waterstaat 1990. Tweede Structuurschema Verkeer en Vervoer (Second Transport Structure Plan). Deel d: regeringsbeslissing. SDU, The Hague, the Netherlands.
- Ministerie van Verkeer en Waterstaat 2005. Nota Mobiliteit, Deel d: Regeringsbeslissing. SDU, The Hague, the Netherlands.
- Ministerie van Verkeer en Waterstaat, Ministerie van Landbouw, Natuur en Voedselkwaliteit & Ministerie van Volkshuisvesting, Ruimtelijke Ordening en Milieu 2004. Meerjarenprogramma Ontsnippering. Beleidsnota. The Hague, the Netherlands.
- Muskens, G.J.D.M. & S. Broekhuizen 1993. Migratie bij Nederlandse dassen *Meles meles* (L., 1758). Report 3. Instituut voor Bos- en Natuuronderzoek, Wageningen, the Netherlands.
- Muskens, G.J.D.M. & S. Broekhuizen 2000. De boomarter *Martes martes* als verkeersslachtoffer. *Lutra* 43 (2): 229-235.
- Neal, E.G. 1977. Badgers. Blandford Press, Poole, UK.
- Neal, E. & C. Cheeseman 1996. Badgers. T & AD Poyser Natural History, London, UK.
- Ouden, J.B. & A.A.G. Piepers 2006. Richtlijnen voor inspectie en onderhoud van faunavoorzieningen bij wegen. Nieuwland, Wageningen, the Netherlands / Dienst Weg- en Waterbouwkunde, Rijkswaterstaat, Delft, the Netherlands.
- Palphramand, K.L., G. Newton-Cross & P.C.L. White 2007. Spatial organization and behaviour of badgers (*Meles meles*) in a moderate-density population. *Behavioural Ecology and Sociobiology* 61: 401-413.
- R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [also available at: <http://www.R-project.org>]
- Roper, T.J., J.R. Ostler & L. Conradt 2003. The process of dispersal in badgers *Meles meles*. *Mammal Review* 33 (3-4): 314-318.
- Seiler, A., J.O. Helldin & T. Eckersten 2003. Road mortality in Swedish Badgers. Effect on population. In: A. Seiler. The toll of the automobile: Wildlife and roads in Sweden. Appendix 2: 1-20. PhD thesis. Silvestria 295. Department of Conservation Biology, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Sneep, J.W. 1986. Het overheidsbeleid inzake het dassenbeheer in Nederland. *Lutra* 29 (1): 76-80.
- Rijkswaterstaat 2007. Database Wegensnip. Rijkswaterstaat, Ministerie voor Verkeer en Waterstaat, Delft, the Netherlands.
- van Apeldoorn, R.C., H. Houweling & G. Veenbaas 1995. Mitigerende maatregelen voor de das; een methode voor probleemdetectie en evaluatie van voorzieningen. *Landschap* 12 (5): 5-12.
- van Apeldoorn, R.C., J. Vink & T. Matyáščík 2006. Dynamics of a local badger (*Meles meles*) population in the Netherlands over the years 1983-2001. *Mammalian Biology* 71: 25-38.
- van den Brink, N.W. & W.-C. Ma 1998. Spatial and temporal trends in levels of trace metals and PCBs in the European badger *Meles meles* L., 1758 in The Netherlands: Implications for reproduction. *The Science of the Total Environment* 222: 107-118.
- van Dinther, B. 1994. Gebruik van dassentunnels door dassen en andere dieren. Report 324. Werkgroep Dieroecologie, Katholieke Universiteit Nijmegen, Nijmegen, the Netherlands.
- van Moll, G. 2005. Distribution of the badger (*Meles meles* L.) in the Netherlands; changes between 1995 and 2001. *Lutra* 48 (1): 3-34.
- van Wijngaarden, A. & J. van de Peppel 1964. The badger, *Meles meles* (L.) in the Netherlands. *Lutra* 6 (1-2): 1-60.
- van Wijngaarden, A., V. van Laar & M.D.M. Trommel 1971. De verspreiding van de Nederlandse zoogdieren. *Lutra* 13 (1-3): 1-41.
- Vereniging Das & Boom 2002. Landelijk onderzoek naar de kwaliteit van de dassenvoorzieningen. Vereniging Das & Boom, Beek-Ubbergen, the Netherlands.
- Vink, J., R.C. van Apeldoorn & G.J. Bekker 2008. Defragmentation measures and the increase of a local European badger (*Meles meles*) population at Eidegoot, the Netherlands. *Lutra* 51 (2): 75-86.
- Wansink, D. 1995. Kansen voor de Gooise Das. Een onderzoek naar populatieontwikkeling, het habitatgebruik en het dieet van een dassenpopulatie bij Hollandse Rading. Report P-UB-95-08. Wetenschapswinkel Biologie, Utrecht, the Netherlands.
- Wiertz, J. & H. Vink 1986. The present status of the

- badger *Meles meles* (L, 1758) in The Netherlands. *Lutra* 29 (1): 21-53.
- Wiertz, J. 1992. De Nederlandse dassenpopulatie anno 1990. *Lutra* 35 (2): 75-89.
- Witte, R.H., D. Bekker, J.J.A. Dekker, C. Achterberg & M. Moonen 2008. Inhaalslag Verspreidingsonderzoek Nederlandse Zoogdieren (VONZ) 2007. Report 2008.01. Zoogdiervereeniging VZZ, Arnhem, the Netherlands.
- Woodroffe, R., D.W. Macdonald, & J. da Silva 1993. Dispersal and philopatry in the European badger, *Meles meles*. *Journal of Zoology* 237: 227-239.

Samenvatting

Verkeersmortaliteit onder dassen (*Meles meles*): eigenschappen van slachtoffers en effectiviteit van mitigerende maatregelen

In de jaren '80 werd jaarlijks een groot deel (op sommige locaties 25%) van de in Nederland aanwezige dassenpopulatie (*Meles meles*) door het verkeer gedood. Dit gegeven was de aanleiding voor de Nederlandse overheden om een groot aantal uiteenlopende mitigerende maatregelen te realiseren, zoals de aanleg van faunatunnels en de plaatsing van rasters. Om de effectiviteit van deze maatregelen te kunnen nagaan werden vervolgens in de periode 1990-2006 gegevens over het voorkomen van dassenslachtoffers verzameld. We presenteren hier de verkregen dataset, tonen de verdeling van slachtoffers over wegtypen

en toetsen of mitigerende maatregelen een afname van slachtoffers tot gevolg had. Het verloop op jaarbasis van de gevonden aantallen dode dassen vertoont een duidelijke piek in april. Er vallen daarentegen relatief weinig slachtoffers in de maanden december, januari en februari. De meeste slachtoffers vallen binnen het verspreidingsgebied van de das, maar ook daarbuiten werden slachtoffers gevonden. De sex-ratio onder de slachtoffers was 1:1, met uitzondering van 1990 toen er buiten het verspreidingsgebied van de das meer vrouwelijke dan mannelijke slachtoffers werden gevonden. In absolute aantallen vielen de meeste slachtoffers op gemeentewegen; gewogen naar lengte van elk wegtype vielen de meeste slachtoffers op provinciale wegen. Het aantal verkeerslachtoffers onder dassen was significant lager nadat er mitigerende maatregelen waren gerealiseerd. De uitdaging voor wegbeheerders ligt nu vooral in het minimaliseren van slachtoffers op gemeentewegen. Aangezien het aantal kilometers van dit wegtype in het verspreidingsgebied van das enorm groot is, is dit geen geringe opgave. Er zijn echter goed implementeerbare methoden zoals aanleg van tunnels en rasters bij bekende dassenwissels, het verlagen van de maximumsnelheid of het verkeersluw maken van bepaalde wegen in kerngebieden van de das.

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The first historic record of a humpback whale (*Megaptera novaeangliae*) from the Low Countries (Southern Bight of the North Sea)

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Abstract: In 1751 the corpse of a large whale was found floating at sea near Blankenberge (currently Belgium). The case was illustrated at the time by a water-colour of the whale and of an associated barnacle. In earlier publications, this whale has been regarded as a northern right whale (*Eubalaena glacialis*). However, morphological characteristics depicted in the original water-colour, published here for the first time, and in a copy of the original, point towards a humpback whale (*Megaptera novaeangliae*). Also, the illustrated barnacle can only represent *Coronula diadema*, a species typically associated with humpback whales. Thus, the case of a right whale in the southern North Sea in 1751, often cited because of the rarity of that species in this area by then, has to be deleted from the records. In this article also the size of the animal, the circumstances and the date are corrected with regard to the previous description of this record, and more information is given about the various artists to whom the water-colours can be attributed.

Keywords: *Megaptera novaeangliae*, humpback whale, southern North Sea, Belgium, Cirripedia, whale barnacles, *Coronula diadema*.

Introduction: a whale at Blankenberge in 1751

In 1962 Mol described the painting of a whale stranded at Blankenberge, currently Belgium, in 1751. He identified the animal depicted as a baleen whale “*Balaena spec.*”, in the French summary of the article translated as “*une baleine vraie*”, or a right whale (*Eubalaena glacialis*). De Smet (1974), in his overview of historic records of cetaceans in Flanders and the Scheldt estuary, agrees with Mol (1962), indicating that this surely is the illustration of a right whale, given the form of the mouth, the callosities on the dorsal side, and the depicted associated barnacle. We inspected the water-colour closer, and tried to elucidate the identity of both whale and painter, in relation to the

comparison of recent and historic strandings of large cetaceans in Belgian and Dutch waters.

Description of the water-colour

While preparing a book on whales (Camphuysen & Peet 2006), Gerard Peet succeeded in tracking down the current location of the water-colour of the whale at Blankenberge in 1751, described by Mol (1962): the New Bedford Whaling Museum, USA. The illustration, 57 cm high, 46 cm wide, water-colour on paper with manuscript additions in ink, is not signed (figure 1). Mol (1962), who did not publish the text below the water-colour, attributed it to Pierre Ledoulx (1730-1807), an artist who lived in Bruges, currently Belgium, on the basis of the title of the album in which it figures together with other illustrations. The name of another artist, Jan Karel



Figure 1. Detail of the water-colour (copy) by Jan Karel Verbrugghe of the painting of the whale on a beach at Blankenberge, currently Belgium, in 1751 (© courtesy of the New Bedford Whaling Museum). The text below the painting, in French, reads: “A. C’est la Baleine proprement dite, qui sert pour les corps de jupes; B. Place ou il se trouvaient des porreaux qui furent remplis des petits poissons semblables aux sardines; C. La langue; D. La queue; E. L’œil; F. La Nageoire; G. Le nez; H. Un endroit troué; I. Un porreau dans sa grandeur”, or translated: A. This is the baleen itself, which serves for the fabrication of the core of skirts; B. Place where warts were located, filled with small sardine-like fish; C. The tongue; D. The tail; E. The eye; F. The pectoral fin; G. The nose; H. An area with holes; I. A wart in its entirety.

Verbrugghe, appeared to have been added afterwards in this title. Mol (1962) dates the album as collated in (around) 1755. However, the text below the illustration is very interesting, in that it indicates that it concerns a copy of an earlier illustration of the whale that was thrown onto the beach of Blankenberge on 30 December 1751:

“Copie d’une Baleine jetée sur les sables devant la ville et port de Blankenberge le 30 Decembre 1751”,

and further down, that details were presented in the Inbona manuscript, which had been sold by Pierre Ledoulx to Jacques Goethals Vercruysse at Kortrijk (a town located in current Belgium, 50 km from Bruges):

“Le Manuscrit d’Inbona, que Mr P Le doulx a vendu a Mr Jacques Goethals Vercruysse a Courtray en donne le détail”

The handwriting below the illustration matches exactly the one on two other illustrations in the album at the New Bedford Whaling Museum (NBWM) which were signed by Jan Karel Verbrugghe (maritime curator NBWM, personal communication), and the handwriting on drawings by Verbrugghe present in the collection of the Steinmetzkabinet, Bruges, Belgium. As Verbrugghe was born in 1756 (he died in 1831), we can conclude that the water-colour of the whale was made not earlier than the last quarter of the 18th century by Jan Karel Verbrugghe, after an original.

Another correction of Mol (1962) and De Smet (1974) that needs to be made, concerns the reported length of the animal. The text below the water-colour mentions 40 feet (approximately 12 m), and not 28 feet, or 8.4 m as in Mol (1962), copied by De Smet (1974); 28 feet is mentioned as the “épaisseur” (thickness).



Figure 2. Original contemporary water-colour of the whale, by Jan Gareminj (© courtesy of the Public Library of Kortrijk, Fonds Jacques Goethals-Vercruysse). The text additions are similar to those in the copy, but are in the local Dutch dialect. We noted the following differences: H is located differently, and reads “het holeken”, or the anus, and the text under the detail of the barnacle reads: “*nota benee dater in dese puste kleene wiskern bestendig waere bij na gelyck aen schardin*”, i.e. translated: note that in the warts small whiskers were present, almost like sardines.

In search of the original illustration

Jacques (Jacob) Goethals-Vercruysse (1759-1838) was a wealthy industrial, collector and historian who lived in the city of Kortrijk. After his death, he left his extensive collection of books (12,000) and manuscripts (600) to the city of Kortrijk, where it remains until today as the *Goethals Vercruyssefonds*, managed by the city library. It is strange that the Inbona manuscript (public library of Kortrijk, Fonds Jacques Goethals-Vercruysse, GV. Cod. 175 fol. 29), by the hand of Jacques Inbona, and containing chronological accounts of noteworthy events in the city of Bruges between 1645 and 1684, would mention something that happened in 1751. However, when consulting the manuscript, it becomes clear that it has been completed with yearly events, until 1781, by Pierre Ledoulx. His elegant handwriting

is much easier to read than the notes made by Inbona. By looking through the pages, it becomes obvious that Ledoulx only started to complete the manuscript years after 1751. For 1751, only two events were noted: the first one about some infrastructure works in Bruges, ending with the fact that they were completed in 1752, and the second one about the whale at Blankenberghe:

“op den 30. september wiert tot blankenberghe eenen walvisch op het strange gesmeten”.

More interestingly, with the accounts of 1751, the original water-colour of the whale is inserted; it measures 32 cm by 20.5 cm, and is more basic than the copy, but otherwise nearly identical (figure 2). However, it also contains a drawing of a baleen plate. At the back of the

water-colour, Ledoulx wrote the following:

“Dit is de origineele teeckeninge vanden walvisch geteeckent tot blanckenberge ten jaere 1751 door Joannes garemijn, konstschilder van brugge”,

stating that this was the original illustration made at Blankenberge in 1751 by Jan Antoon Garemijn, a well-known artist who lived in Bruges from 1712 to 1799, and who was a teacher of Pierre Ledoulx. The date of 1751 seems to have been corrected from 1761 at the back of the illustration, which might further confirm that the additions to the Inbona manuscript by Ledoulx were made only years later. This could also explain why Ledoulx made a mistake in dating the event.

Considering the dates, De Smet (1974) mentions two possible dates for the stranding: 30 December 1751, as in the text below the copy of the water-colour made by Jan Karel Verbrughe, and 30 September 1751, as mentioned by Bowens (1792). Bowens (1792) gives the same date as Ledoulx in the Inbona manuscript, and uses exactly the same wording, suggesting that Ledoulx copied his accounts in the Inbona manuscript from the publication by Bowens (1792), printed in Bruges. However, neither of these dates is correct. A contemporary description of the event can be found in the 3 December 1751 edition of the newspaper *Gazette van Gendt*, which mentions a floating whale at sea on 30 November 1751, and local fishermen towing the whale to the beach off the town of Blankenberge (Anonymus 1751a):

“Blanckenberge den 1. December. Gisteren waerender dry onze Schuyten in Zee, welker visschers verre van hun eenen grooten Walvisch zagen drijven, die zig aenstonds met hunne Schuyten naer toewenden, die dezen Monstreuzen Visch met tauwen aan hunne Schuyten vast hechtende, met groot gevaer van te vergaen, dezen Walvisch alhier op het strange hebben gesleept.”

Also in the next edition of this newspaper, three days later (Anonymus 1751b), the whale is still mentioned:

“Dezer dagen is door die van Blanckenberge in Zee gevischt en aldaer opgebracht een Walvisch van redelycke lengde.”

Identity of the whale

Mol (1962) and De Smet (1974) state that the painting (of which we now know it is a copy) depicts a northern right whale. This species used to occur in the north-eastern Atlantic Ocean and the North Sea, and was intensively hunted there from the early Middle Ages onwards (Slijper 1958, De Smet 1974, Smeenk in Holthuis et al. 1998). It was undoubtedly already scarce in the North Sea during the Middle Ages (Kompanje & Smeenk 1996), and according to Van Beneden (1886) was only very rarely observed in European coastal waters in general during the middle of the 18th century. Still, in the early 20th century circa 140 right whales were captured by whalers in the north-eastern Atlantic, especially around the Hebrides (Brown 1986). The species is nearly extinct now, with little more than 300 animals remaining in the north-western Atlantic. Observations in the eastern part of the North Atlantic are extremely rare (Kompanje & Smeenk 1996, Reid et al. 2003), but include one animal photographed in 2005 off the coast of Zeeland (the Netherlands; Camphuysen & Peet 2006).

The illustrated barnacle

For the identity of the barnacle, a number of which are depicted on the dorsal side of the whale, with one being presented in detail below the whale, in theory three possibilities exist: *Coronula diadema*, *Coronula reginae* en *Cetopirus complanatus* (figure 3). Clearly, the barnacle cannot be other than

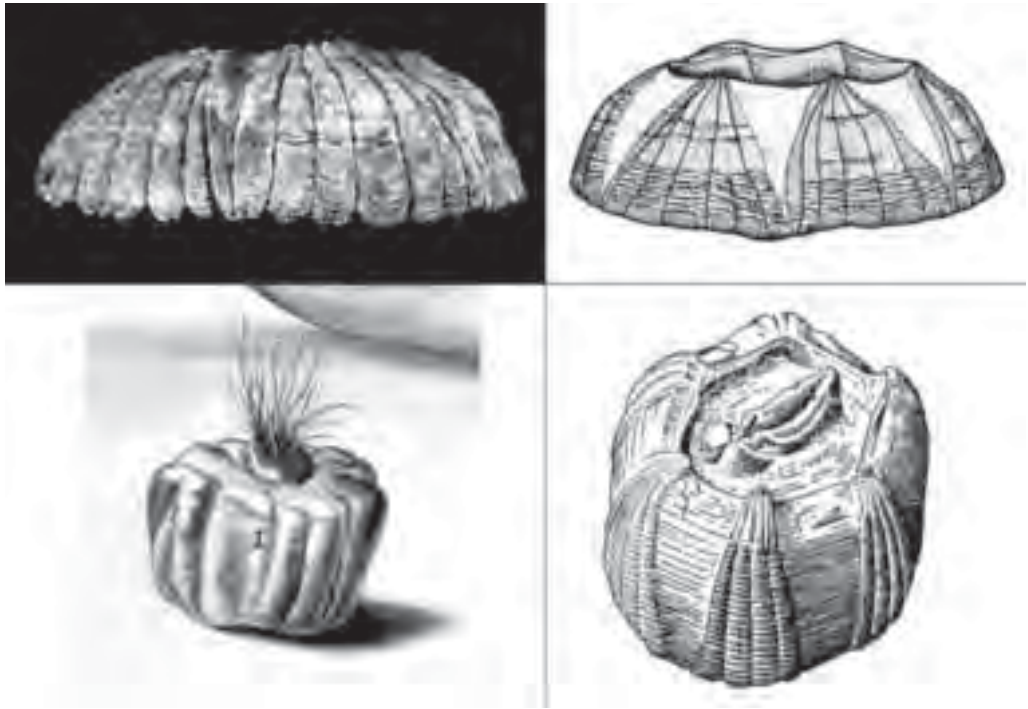


Figure 3. Top left: *Cetopirus complanatus* (from Holthuis et al. 1998); top right: *Coronula reginae* (from Zullo 1979); bottom left: the barnacle depicted in the original water-colour of the whale at Blankenberge in 1751 (courtesy of the Public Library of Kortrijk, Fonds Jacques Goethals-Vercruysse); bottom right: *Coronula diadema* (from Tarasov & Zevina 1957).

Coronula diadema. This is, together with *Coronula reginae*, the most typical barnacle on humpback whales (*Megaptera novaeangliae*), occurring on almost every individual, and often in large numbers. This species has also been reported, though less commonly, from fin whales (*Balaenoptera* spp.) and sperm whales (*Physeter macrocephalus*) (Zullo 1979, Scarff 1986). *Coronula* sp. was observed on a living right whale (in the Pacific Ocean), but it proved impossible to take samples (Scarff 1986). Besides this, some old, but very doubtful records exist of *Coronula* sp. on right whales. Scarff (1986) did not find recent indications, except his own observation, of the presence of *Coronula* sp. on right whales, and no barnacles were found on more than 30 right whales stranded during the last decades on the shores of the western North Atlantic (S. Kraus, New England Aquarium, Boston, per-

sonal communication in 2006).

The barnacle *Cetopirus complanatus* is enigmatic. Apparently it can be easily confused with *Coronula reginae*, and it has not been reliably recorded since the 19th century (Holthuis et al. 1998). Also, it is, or was, typical for whales of the genus *Eubalaena*, but rather for the southern than the northern hemisphere (Darwin 1854). In the Netherlands *Cetopirus complanatus* was found, near right whale remains, in an archaeological site from the 10th century (Holthuis et al. 1998), a period in which the right whale was hunted in the North Sea and English Channel. Very few remains of *Cetopirus complanatus* exist in natural history collections (Holthuis et al. 1998). Scarff (1986) concluded that the populations of *Coronula* sp. and *Cetopirus complanatus* have virtually disappeared from right whale populations due to the near-

extinction of their host species. Whereas currently all, or the vast majority of right whales do not host *Coronula* sp. or *Cetopirius complanatus*, it cannot be stated that this was the case in the middle of the 18th century.

Anatomical features depicted

We thoroughly investigated the anatomical features in the water-colours of the whale, and these too made us conclude that this animal was a humpback whale rather than a right whale. The only characteristics that could plea for a right whale, but are surprisingly not mentioned by De Smet (1974), are the lack of ventral grooves and a dorsal fin (the latter being very small in many humpback whales). However, the water-colours display several features typical for a humpback whale, not occurring in right whales. These are: 1. the irregular shape of the posterior margin of the tail flukes, 2. the irregular margin of the flipper, 3. the elongated form of the flipper, and 4. the partially white, irregular pigmentation of the tail flukes and the flipper. Furthermore, there is no trace of the extensive callosities in distinct places on right whales. Moreover, the original of the illustration shows a baleen plate that could not possibly originate from a right whale. It is short and triangular, typical for humpback whales.

The humpback whale is indigenous in all oceans, from tropical to polar areas. Whereas it is regularly observed in the western part of the English Channel (Reid et al. 2003), it was, until recently, very rare in the southern North Sea. When in February 1995 a fresh scapula of a humpback whale was found in Dutch waters (Kompanje 1996), this then represented the only known record of this species for the Netherlands. In the early 21st century the situation changed: between 2003 and 2010 five individuals were washed ashore in the Netherlands (Smeenk et al. 2003, Camphuysen et al. 2008; www.walvisstrandingen.nl, viewed 25 November 2010) and one in Belgium (Hael-

ters et al. 2006). Given the size of humpback whales, it is unlikely that other strandings of this species would have gone unnoticed or unrecorded in Belgium or the Netherlands in historical days. In addition to, or in association with these strandings, at least five different individuals were observed along the coast in these years and a further two animals were recorded nearby, off the coast of northern France (Camphuysen & Peet 2006, Camphuysen 2007, Strietman 2009). Confirmed sightings within the area are lacking prior to 2003 (van der Meij & Camphuysen 2006).

Conclusions

Although the water-colours of the whale of 1751 are crude and hence unclear, it appears beyond doubt that a humpback whale is depicted rather than a northern right whale, given anatomical details and the illustration of the associated barnacle. This concerns the first documented case of a humpback whale in the Low Countries (Belgium and the Netherlands). As a consequence, the only documented and probable case of a right whale in what is currently Belgium dates back to 1178, when a carcass washed ashore in Oostende (De Smet 1974). The original water-colour of the whale, held at the public library of Kortrijk, Belgium, is by Jan Antoon Garemijn, whereas the copy, produced not before the last quarter of the 18th century, and currently in the New Bedford Whaling Museum, is by the hand of Jan Karel Verbrugghe.

It is remarkable that for centuries the humpback whale of 1751 remained the only one recorded in the Low Countries, whereas for unknown reasons the situation changed dramatically in the 21st century, with six animals washing ashore in this area between 2003 and 2009.

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References

- Anonymus 1751a. Gazette van Gendt XCVII, 6 December 1751.
- Anonymus 1751b. Gazette van Gendt XCVIII, 9 December 1751.
- Bowens, J.J. 1792. Nauwkeurige beschrijving der oude en beroemde zee-stad Oostende gelegen in Oostenryksch Vlaenderen. Eerste deel. Joseph De Busscher, Brugge, Belgium.
- Brown, S.G. 1986. Twentieth-century records of right whales (*Eubalaena glacialis*) in the North-east Atlantic Ocean. Report of the International Whaling Commission, Special Issue 10: 121-127.
- Camphuysen, C.J. 2007. Foraging humpback whale (*Megaptera novaeangliae*) in the Marsdiep area (Wadden Sea), May 2007 and a review of sightings and strandings in the southern North Sea, 2003-2007. Lutra 50 (1): 31-42.
- Camphuysen, C.J. & G. Peet 2006. Walvissen en dolfinen in de Noordzee. Fontaine Uitgevers BV, Kortenhoef / Stichting De Noordzee, Utrecht, the Netherlands.
- Camphuysen, C.J., C. Smeenk, M. Addink, H. van Grouw & O.E. Jansen 2008. Cetaceans stranded in the Netherlands from 1998 to 2007. Lutra 51 (2): 87-122.
- Darwin, C. 1854. A monograph on the sub-class Cirripedia with figures of all the species. The Lepadidae; or, pediculated cirripedes. Ray Society, London, UK.
- De Smet, W.M.A. 1974. Inventaris van de walvisachtigen (Cetacea) van de Vlaamse kust en de Schelde. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 50 (1): 1-156, plates I-IV.
- Haelters, J., T. Jauniaux & F. Kerckhof 2006. Bultrug op Belgisch strand. Zoogdier 17 (2): 3-5.
- Holthuis, L.B., C. Smeenk & F.J. Laarman 1998. The find of a whale barnacle, *Cetopirus complanatus* (Mörch, 1853), in 10th century deposits in the Netherlands. Zoologische Verhandelingen Leiden 323: 349-363.
- Inbona, J., manuscript. Rare geschriften behelsende het gedenckweerdigste dat 'er is voorgevallen binnen de stadt van Brugghe, sedert het Jaer 1645. tot ende met het Jaer 1684. door Mr. Jacques Inbona met een vervolg ofte bijvoughsel van het geene sedert is voorgevallen binnen de stadt van Brugghe. Fonds Jacques Goethals-Vercruysse, GV. Cod. 175 fol. 29, Public Library Kortrijk, Belgium.
- Kompanje, E.J.O. 1996. Vondst van een schouderblad van de bultrug *Megaptera novaeangliae* in de zuidelijke Noordzee. Lutra 38 (2): 85-89.
- Kompanje, E.J.O. & C. Smeenk 1996. Recent bones of right whales *Eubalaena glacialis* from the southern North Sea. Lutra 39 (2): 66-75.
- Mol, T. 1962. Afbeeldingen van walvisachtigen (Cetacea) in een catalogus van een oud kabinet in Brugge. Lutra 4 (2): 21-22, plates II-III.
- Reid, J.B., P.G.H. Evans & S.P. Northridge 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough, UK.
- Scarff, J.E. 1986. Occurrence of the barnacles *Coronula diadema*, *C. reginae* and *Cetopirus complanatus* (Cirripedia) on right whales. The Scientific Reports of the Whales Research Institute 37: 129-153.
- Slijper, E.J. 1958. Walvissen. Uitgeversmaatschappij D.B. Centen, Amsterdam, the Netherlands.
- Smeenk, C., M. Addink & K. Camphuysen 2003. De eerste bultrug voor Nederland. Zoogdier 14 (4): 3-4.
- Strietman, W.J. 2009. Whale watching met een Texelse twist. Zoogdier 20 (1): 19-20.
- Tarasov, N.I. & G.B. Zevina 1957. Barnacles (Cirripedia Thoracica) of the seas of the USSR. Fauna of the USSR - Zoologicheskii Institut Akademii Nauk SSSR 69 [in Russian].
- van der Meij, S.E.T. & C.J. Camphuysen 2006. Distribution and diversity of whales and dolphins (Cetacea) in the Southern North Sea: 1970-2005. Lutra 49 (1): 3-28.
- Van Beneden, P.J. 1886. Histoire naturelle de la Baleine des Basques (*Balaena biscayensis*). Mémoires couronnés et autres mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique 38: 1-44.
- Zullo, V.A. 1979. Marine flora and fauna of the north-eastern United States. Arthropoda: Cirripedia. National Oceanic and Atmospheric Administration (NOAA), Technical Report National Marine Fisheries Service (NMFS) circular 425.

Samenvatting

De eerste historische waarneming van een bultrug (*Megaptera novaeangliae*) in de Lage Landen (zuidelijke Noordzee)

In 1751 werd een grote walvis op zee aange troffen nabij Blankenberge, nu in België, en naar het strand gesleept. Het dier werd afge beeld, samen met één van zijn geassocieerde zeepokken, op een aquarel. In eerdere publi caties werd de walvis beschouwd als een noordkaper (*Eubalaena glacialis*). Morfolo gische kenmerken op de originele aquarel, hier voor het eerst gepubliceerd, en een latere kopie, tonen echter aan dat de afgebeelde wal vis een bultrug (*Megaptera novaeangliae*) was. De afgebeelde zeepok, *Coronula dia dema*, is een soort die typisch op de bultrug

voorkomt. De stranding van een noordkaper in 1751, vaak vermeld omdat deze soort toen ook al zeer zeldzaam was in dit gebied, wordt daarom afgewezen. In het artikel worden ook correcties gemaakt met betrekking tot de omstandigheden van de vondst, de datum en de afmetingen van het dier. De aquarellen konden toegewezen worden aan twee Brugse schilders. Het is zeer merkwaardig dat eeu wen lang de bultrug van 1751 het enige geno teerde geval was van een bultrug in de Lage Landen, terwijl daarin door ongeken de oor zaken in de 21^e eeuw plots op een dramatische manier verandering kwam, met het stranden van niet minder dan 6 dieren tussen 2003 en 2009.

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A killer whale (*Orcinus orca*) in the castle: first find of the species in a Dutch archaeological context

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Bones and other non-skeletal remains of animals, such as antlers, shells, fish scales and remains of insects, are frequently found in archaeological sites (Bakels & Zeiler 2005). By studying these remains we can form an idea of the natural environment in the past and the use that people made of animals and animal products. The preservation of organic remains – both zoological and botanical – depends on the nature of the material and on the soil type: organic material decays rapidly in sandy soils above ground water level. Hence, most of the information from Dutch archaeozoological and botanical research originates from the lower lying parts of the Netherlands (including brook valleys from the Pleistocene areas), and other wet sites such as wells and cesspits in towns and villages. In this article we describe the find of two vertebrae of a whale during excavations at Brederode Castle (Noord-Holland).

The castle of Brederode, situated near the coast at Velsen, was built between the late 13th and early 14th centuries. In later centuries it was destroyed and rebuilt several times. Finally, in 1573, it was plundered and burnt down by Spanish troops. A few decades later (shortly after 1600), the remains of the castle were covered by sand from drifting dunes. During archaeological research in 1996, part

of the moat was excavated. The research was carried out by the local section of the Netherlands Archaeological Working Group (AWN). As the animal remains were collected both by hand and sieving, small birds and mammals are well represented in the faunal spectrum, as well as some fish, shellfish and amphibians. Fifteen species of mammals and 19 species of birds were found; both categories included domestic and wild forms. Five species of fish were found, both freshwater and marine (Zeiler 2007).

Some of the species discovered are rarely found in Dutch archaeological contexts. These include the fallow deer (*Dama dama*), short-eared owl (*Asio flammeus*) and (as far as Late Medieval sites are concerned) white-tailed eagle (*Haliaeetus albicilla*). The turtle dove (*Streptopelia turtur*) had never been found before.

Among the excavated bones were two vertebrae, a lumbar and a caudal vertebra, of an adult whale (figure 1). The vertebrae were compared with vertebrae of an adult female killer whale (NMR 9990-00002791) and adult male killer whale (NMR 9990-00002789) and with those of other medium sized whales: pilot whale (*Globicephala melas*), minke whale (*Balaenoptera acutorostrata*) and northern bottlenose whale (*Hyperoodon ampullatus*), all held in the collection of the Natural History Museum in Rotterdam. The round shape of the epiphyses and the shape

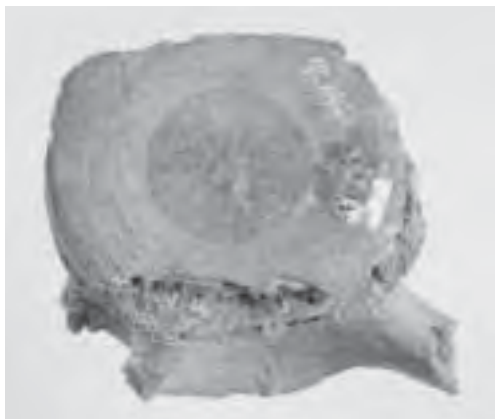


Figure 1. Lumbar (left) and caudal vertebra of a female killer whale (*Orcinus orca*) from the Late Medieval castle of Brederode. Photographs: J. Buist.

and dimensions of the vertebral bodies point to an adult female killer whale (*Orcinus orca*). The two vertebrae from Velsen are stored in the *Provinciaal Depot voor Bodemvondsten* at Wormer (collection numbers: 1531-1 and 1531-2).

This find represents the first record of this species from a Dutch archaeological site, and the earliest record of this species for the Netherlands. It also demonstrates the value of expertise in archaeozoological research. In an earlier study of the material (den Hartog 2005) the vertebrae were described as “whale species” and no further attempts were made to identify them to species level. Killer whales are nowadays very rare in the southern part of the North Sea (van de Mey & Camphuysen 2006, Camphuysen & Peet 2006) and it has probably been fairly uncommon as a species, even in historical times (Kompanje 1995). The oldest known record of a stranded killer whale dates back to December 1783 (a pregnant female of unknown total length at Walcheren, Zeeland), and a further 27 cases have been reported within the Netherlands, 20 of these during the first six decades of the 20th century.

The two excavated vertebrae are most probably from a killer whale that was found washed up on the shore. In view of its rarity and size, a carcass of a killer whale would have attracted

attention. In those days, everything of value that was found washed up on the shoreline belonged to the Count of Holland, who could pass on his rights to others (originally this was a royal right of the Frankish kings, instituted by Charlemagne). It is known that the Lord of Brederode was given this right in 1250 for the area between Zijpe and Huisduinen, about 40 kilometres to the north of Brederode Castle. In 1285 the Count of Holland decided to exercise the right himself, and from then on his annual accounts contain a list of everything that was found on the shore (and its yield). Sea mammals are regularly mentioned here, and they were clearly considered a delicacy (den Hartog 2005). Moreover, the consumption of their meat was permitted during Lent, as they were regarded as fish.

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References

- Bakels, C. & J. Zeiler 2005. De vruchten van het land. De neolithische voedselvoorziening. In: L.P. Louwe Kooijmans, P.W. van den Broeke, H. Fok-

- kens & A. van Gijn (eds.). Nederland in de prehistorie: 311-335. Bert Bakker, Amsterdam, the Netherlands.
- Camphuysen, C.J. & G. Peet 2006. Walvissen en dolfinen in de Noordzee. Fontaine Uitgevers, Kortenhoeve, the Netherlands.
- den Hartog, E. 2005. Dieren in en rond de kastelen Teylingen en Brederode, Haarlem, the Netherlands.
- Kompanje, E.J.O. 1995. Strandings of killer whales *Orcinus orca* in the Netherlands between 1783 and 1995 with some remarks on skeletal and dental pathology (Mammalia, Cetacea, Odontoceti). *Deinsea* 2: 67-82.
- van der Meij, S.E.T. & C.J. Camphuysen 2006. Distribution and diversity of whales and dolphins (Cetacea) in the Southern North Sea: 1970-2005. *Lutra* 49 (1): 3-28.
- Zeiler, J.T. 2007. Adellijk afval. Archeozoologisch onderzoek van de Laat- Middeleeuwse kastelen Egmond en Brederode. ArchaeoBone Report 61. ArchaeoBone, Leeuwarden, the Netherlands.

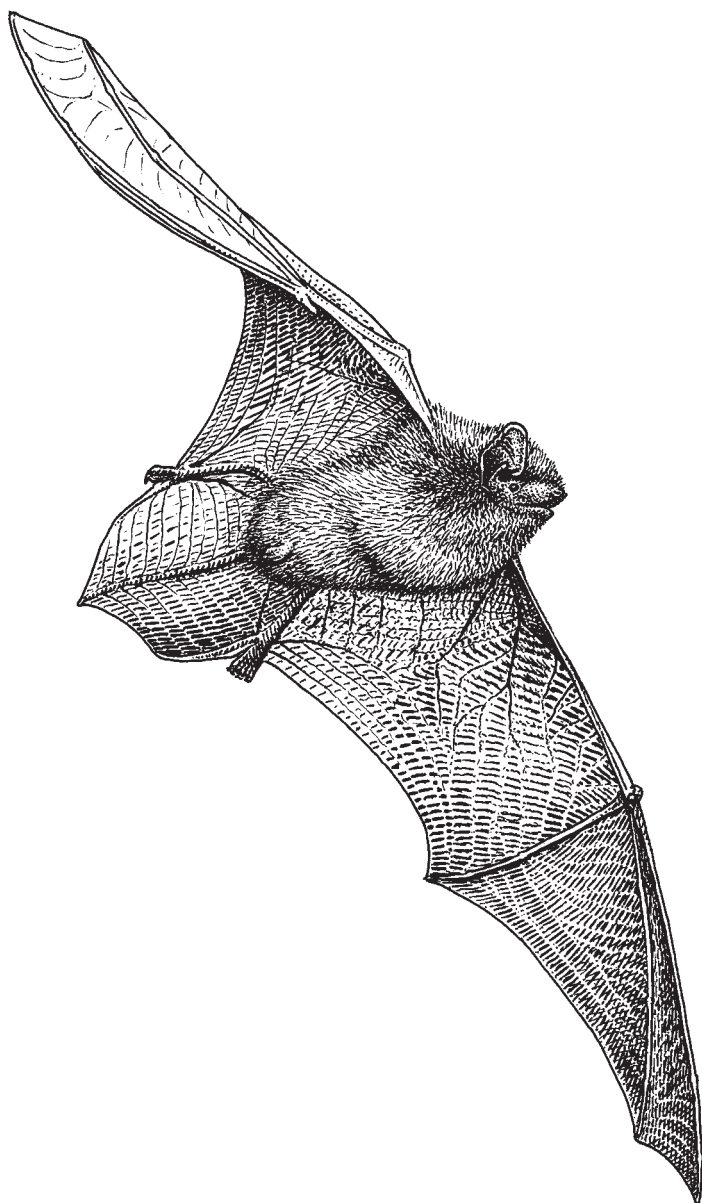
Samenvatting

Historisch bewijs voor de eerste orka (*Orcinus orca*) in Nederlandse wateren

In 1996 vond archeologisch onderzoek plaats op het terrein van het voormalige Laat-Middeleeuwse kasteel van Brederode te Velsen, waarbij een deel van de slotgracht werd opgegraven. De opgraving werd uitgevoerd door de afdeling Velsen van de Archeologische Werkgroep Nederland. Onder de circa 400 dierlijke resten waren twee wervels van een walvisachtige. Deze werden gedetermineerd als een volwassen orka (*Orcinus orca*). De wervels, hoogstwaarschijnlijk afkomstig van een gestrand exemplaar, vertegenwoordigen de eerste vondst van deze soort in een Nederlandse archeologische opgraving, en daarmee de vroegste documentatie van het voorkomen van de orka in Nederlandse wateren. Aangezien in de Middeleeuwen het vlees van zeezoogdieren als een delicatessen werd beschouwd en bovendien op vastendagen mocht worden gegeten, is het goed denkbaar dat we hier te maken hebben met resten van een bijzondere maaltijd.

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soprano pipistrelle

PT'10

First record of soprano pipistrelle (*Pipistrellus pygmaeus* Leach, 1825; Chiroptera: Vespertilionidae) in Wallonia (Belgium)

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The soprano pipistrelle, *Pipistrellus pygmaeus*, is a cryptic species that highly resembles the common pipistrelle, *Pipistrellus pipistrellus* (Barrett et al. 1997). Jones & Parijs (1993) show that standard measurements of the animal itself are of little use for distinguishing between both; the soprano pipistrelle is generally smaller than the common pipistrelle, but the overlap is too large to allow an unambiguous identification. Although the most useful method for determining the two species remains genetic analysis and the analysis of echolocation calls (Mayer & Helversen 2001), several authors mention reliable morphological characteristics to discriminate



Figure 1. Internarial ridge of the Wallonian soprano pipistrelle. Photograph: Johannes Regelink.

between the two species. The most important of these are the internarial ridge, the penial morphology and the wing membrane cell pattern (Häusler et al. 2000, Ziegler et al. 2001, Sendor et al. 2002, Dietz et al. 2007).

The soprano pipistrelle has a wide geographical distribution in Europe (Mayer & Helversen 2001). It lives in sympatry with its sibling species, the common pipistrelle, over most of its range. From Belgium there are only a few records of soprano pipistrelle, all of which are based on echolocation sound analyses (Kapfer et al. 2007). All observations come from Flanders (Provinces of West-Vlaanderen, Antwerp and Limburg) and Brussels, and they were mainly made in spring. In recent years, the species has been recorded annually in Brussels (Herr 2010).

On the 6th of August, 2009, between 9 pm and 2 am, bats were captured with mist nets

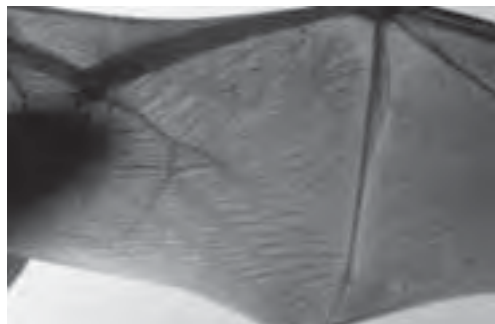


Figure 2. Wing cell membrane of the Wallonian soprano pipistrelle. Photograph: Johannes Regelink.

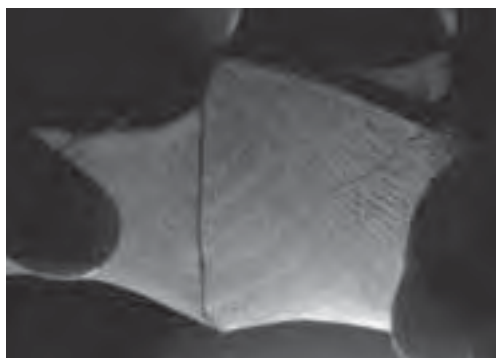


Figure 3. Wing cell membrane of the common pipistrelle (*Pipistrellus pipistrellus*). Photograph: Jeroen van der Kooij.



Figure 4. Soprano pipistrelle in the hand. Photograph: Daan Dekeukeleire.

at the northern entrance of an old railway tunnel (50°04'51" N 4°34'22" E) in Viroinval (Namur, Belgium). Various species were caught: the greater mouse-eared bat (*Myotis myotis*), Daubenton's bat (*M. daubentonii*), Bechstein's bat (*M. bechsteini*), and, with 42 individuals the most abundant species, the common pipistrelle. Of the latter species, swarming behaviour could be observed. The common pipistrelle also uses the aforementioned tunnel as a hibernaculum.

A small *Pipistrellus*, captured at 11.40 p.m., turned out to be a soprano pipistrelle. The animal showed the typical internarial ridge (figure 1) and the characteristic wing membrane cell pattern (figure 2) was present on both wings. Like in the common pipistrelle (figure 3), this soprano pipistrelle showed only one cell in the wing membrane between the first joint of the fifth finger and the elbow, but in contrast, the next cell above (closer to the wrist) was not divided, but connected the forearm and the fifth finger. The face (figure 4), moreover, was paler than that of common pipistrelle. The mass of the animal was 4.9 g and the forearm length was 30.9 mm. The epiphyses in the bones of the fingers were closed, and the nipple was entirely covered in fur, indicating that the bat was an adult and had not reproduced in the past season (Haarsma 2008). A second individual, an adult male, also showed the internarial

ridge and the wing membrane cell pattern, but was released before it could be measured.

The habitat surrounding the capture site, an old riparian woodland near the Viroin river, corresponds well with the typical habitat of the soprano pipistrelle as described by Davidson-Watts et al. (2006), Nicholls & Racey (2006) and Sattler et al. (2007).

In 2002, in the immediate surroundings of the capture site, two independent observations were made using bat detectors of a *Pipistrellus* bat with an end frequency of 55 kHz (B. Vandendriessche & B. Van der Wijden, personal communication). But as no recordings were made, and thus no additional sound analyses could be performed, these could not be confirmed as soprano pipistrelle.

Our finding represents the first confirmed record of the soprano pipistrelle in Wallonia, and the first identification based on morphological characteristics of this species in Belgium.

Acknowledgments: I would like to thank Johannes Regelink, Pierrette Nyssen and the participants of the JNM summer camp. Christian Dietz, René Janssen and Jeroen van der Kooij helped with the identification of the bat. Peter Lina and Marc Van De Sijpe provided literature. I also thank Pieter Blondé and Paul Van Daele, and two anonymous referees for their helpful comments on the manuscript.

References

- Barratt, E.M., R. Deaville, T.M. Burland, M.W. Bruford, G. Jones, P.A. Racey & R.K. Wayne 1997. DNA answers the call of pipistrelle bat species. *Nature* 387: 138-139.
- Davidson-Watts, I., S. Walls & G. Jones 2006. Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biological Conservation* 133: 118-127.
- Dietz, C., O. von Helversen & D. Nill 2007. Handbuch der Fledermäuse Europas und Nordwestafrikas – Biologie, Kennzeichen, Gefährdung. Kosmos, Stuttgart, Germany.
- Mayer, F. & O. von Helversen 2001. Sympatric distribution of two cryptic bat species across Europe. *Biological Journal of the Linnean Society* 74: 365-374.
- Haarsma, A.-J. 2008. Manual for assessment of reproductive status, age and health in European Vespertilionid bats. Version 1, Electronic publication. Hillegom, The Netherlands.
- Häusler, U., A. Nagel, M. Braun & A. Arnold 2000. External characters discriminating sibling species of European pipistrelles, *Pipistrellus pipistrellus* (Schreber, 1774) and *P. pygmaeus* (Leach, 1825). *Myotis* 37: 27-40.
- Herr, C. 2010. Retour sur le monitoring des étangs Bruxellois en 2009. *L'écho des Rhinos* 59 : 4-5.
- Jones, G. & S.M. van Parijs 1993. Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proceedings of the Royal Society B* 251: 119-125.
- Kapfer, G., M. Van de Sijpe, B. Van der Wijden, W. Willems, B. Vandendriessche & B. Mulkens 2007. First recordings of the soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) in Belgium. *Belgian Journal of Zoology* 137 (1): 111-113.
- Sattler, T., F. Bontadina, A.H. Hirzel & R. Arlettaz 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *Journal of Applied Ecology* 44: 1188-1199.
- Sendor, T., I. Roedenbeck, S. Hampl, M. Ferreri & M. Simon 2002. Revision of morphological identification of pipistrelle bat phonic types (*Pipistrellus pipistrellus* Schreber, 1774). *Myotis* 40: 11-17.
- Ziegler, T., A. Feiler & U. Zöphel 2001. New data on the genital morphology of the midge bat *Pipistrellus pygmaeus* (Leach, 1825) from Germany (Mammalia: Chiroptera: Vespertilionidae). *Zoologische Abhandlungen* 25: 435-444.

Samenvatting

Eerste waarneming van de kleine dwergvleermuis (*Pipistrellus pygmaeus*) in Wallonië

Tijdens een mistnetonderzoek in Viroinval (provincie Namen, België) werd op 6 augustus 2009 een kleine dwergvleermuis (*Pipistrellus pygmaeus*) gevangen. Het exemplaar, een adult vrouwtje, werd gedetermineerd op basis van morfologische kenmerken. Deze vangst is de eerste zekere waarneming voor Wallonië. Het is de eerste maal dat deze soort op morfologische kenmerken kon worden gedetermineerd in België.

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Zoogdieren in Europa

Veldgids Europese zoogdieren. P. Twisk, A. van Diepenbeek & J.P. Bekker 2010. KNNV Uitgeverij, Zeist, Nederland. 368 pp. ISBN 978 90 5011 260 4 [in Dutch].

Na de Zoogdierengids van Mr. F.H. van den Brink (1955), waarvan tussen 1955 en 1977 vier, steeds bijgewerkte drukken het licht zagen, zijn nog verscheidene zoogdiergidsen verschenen, die het concept volgen van Roger Petersons befaamde Vogelgids. Uitgangspunt hierbij is dat verwante soorten naast elkaar, meestal van opzij worden afgebeeld en dat de opvallendste verschillen, althans voor zover uitgegeven in de Petersons veldgidsenserie, met een pijltje of ander tekenetje worden aangegeven. Ook de nieuwe 'veldgids Europese zoogdieren' past in deze opzet, maar wijkt er in een aantal opzichten van af, onder andere doordat de determinatie in verschillende stappen wordt uitgevoerd. De eerste stap is een vergelijking van het waargenomen of gevangen zoogdier met een groep soorten van overeenkomstige grootte en / of vorm en wel tussen dwergspitsmuis en mol, tussen woelrat en haas, tussen steenmarter en ijsbeer en tussen muntjak en wisent. Dit is even wennen, omdat, ondanks het feit dat voor de schaal bij elke groep een mol is afgebeeld, het verwarrend kan werken dat hierdoor de wezel even groot lijkt als de steenmarter, voorts doordat het nogal wat voorstellingsvermogen vereist om in te schatten hoeveel mollen er in een eland gaan en tenslotte doordat op de pagina waar de mol zelf is afgebeeld deze groter lijkt dan de reusmuis, terwijl in werkelijkheid het omgekeerde het geval is. Ook is niet duidelijk waarom de hazelmuis en de eekhoorn met, zo te zien, een braam en een noot in de bek, maar de overige soorten met gesloten bek zijn afgebeeld. Wellicht een artistieke vrijheid van de tekenaar voortgekomen uit een heftige natuurbeleving.

Heeft men eenmaal zijn keus vastgesteld, dan wordt doorverwezen naar de familie of het genus waartoe de soort behoort. Deze tweede stap in de determinatie is met behulp van de naast elkaar staande illustraties goed uit te voeren doordat de kenmerken van de soorten binnen een familie of geslacht duidelijk en in vergelijkbare grootteverhoudingen worden weergegeven. Een bondige tekst naast de illustratie geeft aan op welke kenmerken in het bijzonder moet worden gelet. Soms echter komen illustratie en tekst in dit opzicht niet overeen. Zo worden in de tekst bij de dwergspitsmuis (*Sorex minutus*) en de kleine dwergspitsmuis (*Sorex minutissimus*) enkele verschillen in grootte en vachtkleur vermeld, terwijl de afbeeldingen van beide soorten identiek zijn. Daarnaast moet men er op bedacht zijn dat de illustraties en de ondersteunende teksten niet altijd uitsluitend geven welke soort men voor zich heeft omdat in zulke gevallen alleen anatomisch en / of DNA-onderzoek tot een zekere determinatie kunnen leiden. Dit is met name het geval bij enkele genera van de spitsmuizen, vleermuizen en knaagdieren.

Bij de meeste soorten wordt strak vastgehouden aan een laterale afbeelding. Hierdoor worden verschillen die zich bij sommige soorten in de kleur en tekening van de onderzijde van de vacht voordoen de ene keer wel (egels), de andere keer niet afgebeeld, terwijl die, zoals bij de bosmuissorten, in sommige streken van Europa aan een juiste determinatie kunnen bijdragen. Ook in de gevallen dat er binnen een soort grote variatie in tekening en kleur van de buikvacht kan optreden wordt dit niet altijd in een afbeelding tot uiting gebracht. Zo komt het bij de waterspitsmuis, die op wel haast traditionele wijze met een geheel witte onderzijde wordt weergegeven, toch zeer regelmatig voor dat er een donkerbruine en / of roestkleurige vlektekening aanwezig is in plaats van een hagelwitte

vacht. Wel worden naast de afbeeldingen soms kleurvarianten afgebeeld, maar deze zijn zo klein uitgevallen dat er maar weinig details in zijn te onderscheiden. Opmerkelijk is dat bij de mol, die toch bekend staat om het grote aantal verschillende kleurvarianten en waarnaar bovendien uitgebreid onderzoek is gedaan (Husson & van Heurn 1959), geen van deze varianten is afgebeeld (hoewel er in de tekst wel kort melding van wordt gemaakt). Daarnaast kunnen zoogdieren vaak herkend worden door de kleur en tekening die zij *en face* vertonen, bij voorbeeld winterslapende vleermuizen die in spleten zijn weggekropen, maar ook veel andere zoogdieren hebben van voren gezien een karakteristiekere gezichtsuitdrukking dan van opzij. Tenslotte verwijst de determinatietabel naar een beschrijving van de soort. Deze is meer of minder uitvoerig, al naar mate er veel of weinig over het uiterlijk, de habitat, de leefwijze, het voedsel, de verspreiding en de waarnemingsmethode(n) bekend is. Naast de beschrijving worden de meeste soorten opnieuw afgebeeld, vrijwel steeds met dezelfde tekening als die in de determinatielijsten is gebruikt, in enkele gevallen echter met een kleurenfoto. Deze foto's dragen soms wel, maar soms ook niet bij aan een betere herkenning van de soort, met name doordat de staart van het dier, zoals bij bosmuis, bruine rat, zwarte rat, woelrat, veldmuis, aardmuis en tuinslaapmuis (eikelmuis), niet is weergegeven. Het is een euvel dat men wel vaker bij foto's van zoogdieren tegenkomt. De geografische verspreiding in Europa wordt zoals gebruikelijk weergegeven op kaartjes. Voor de soorten met een aaneengesloten verspreidingsgebied zijn deze nog wel leesbaar, maar voor soorten met een versnipperd of beperkt verspreidingsgebied zijn ze wel erg klein uitgevallen en daardoor nauwelijks te raadplegen. Jammer dat hier het resultaat niet in overeenstemming is met de moeite en tijd die de auteurs in dit onderdeel zullen hebben gestoken. Daarnaast is de tekst gelardeerd met sfeervolle tekeningen van zoogdieren in hun natuurlijke omge-

ving en van in het veld opvallende sporen en bouwsels. Het is een punt waarop deze gids zich van de meeste andere zoogdiergidsen onderscheidt. Dat geldt ook voor de volledige behandeling van de schedelkenmerken van de soorten, wat bij het determineren van schedelresten, zoals die uit braakballen en dergelijke, van pas komt. Ook hier echter zijn de tekeningen (bij voorbeeld die van de vleermuizen) nogal klein uitgevallen of zeer fragmentarisch en men kan zich afvragen of zij zonder een oefening vooraf met behulp van vergelijkingsmateriaal tot een zekere determinatie zullen leiden.

Het aantal in het wild levende soorten dat wordt behandeld bedraagt (inclusief de robben en walrus maar exclusief de walvissen) 211, waaronder de hond en de (verwilderde) huiskat, die met de in het wild levende verwanten verwisseld kunnen worden; en verder een zestal grote grazers die men tegenwoordig in natuurgebieden kan tegenkomen. Dat zijn er zeer veel meer dan in eerder verschenen gidsen worden afgebeeld en besproken, hetgeen hoofdzakelijk zijn oorsprong vindt in het opsplitsen van soorten op grond van nauwkeuriger schedel- en DNA-onderzoek. Dit brengt ons op een punt dat in de gids onbesproken blijft: Hoe dienen dode zoogdieren behandeld te worden en voor nader onderzoek beschikbaar te blijven? Ook al wordt, in tegenstelling tot voorheen, veel veldonderzoek tegenwoordig met levend vangende vallen uitgevoerd, zodat de dieren na determinatie weer kunnen worden losgelaten, toch zijn ook hierbij geregeld slachtoffers te betreuren. Het zou dan ook aan te bevelen zijn dat deze, even als dood gevonden zoogdieren, hetzij droog het zij nat geconserveerd in een wetenschappelijke collectie bewaard zouden worden. Wat dit betreft had in de gids toch minstens een Nederlands en een Belgisch adres vermeld kunnen worden waarnaar men dode zoogdieren kan opsturen, alsmede een aanwijzing hoe dit dient te gebeuren en hoe men hiervoor een eventuele ontheffing van de Flora- en faunawet kan verkrijgen. Dit

bevreemdt des te meer als men bedenkt dat voor het vervaardigen van de illustraties in deze gids uitgebreid van geprepareerde huiden en schedels uit museumcollecties gebruik is gemaakt. Ook het bewaren van weefsels voor DNA-onderzoek blijft onbesproken, terwijl te verwachten is dat dergelijk materiaal in de nabije toekomst steeds gemakkelijker, ook door particulieren, geanalyseerd kan worden. Daarmee zal dan ook het onderscheiden van soorten die met deze gids niet definitief te determineren zijn, mogelijk worden. Aanwijzingen voor het conserveren van weefsel- en andere resten voor DNA-onderzoek zijn bijvoorbeeld wel te vinden in de onlangs verschenen determinatiegids voor de Zwitserse zoogdieren (Fumagalli 2008).

Tenslotte een opmerking over de literatuurlijst achter in het boek. Deze bevat de door de auteurs gebruikte en aanbevolen literatuur. Behalve voor de determinatie en algemene informatie onmisbare uitgaven, worden hierin ook (bundels van) artikelen vermeld die er voor de gebruiker minder toedoen. Wat de door Europa reizende veldbioloog in deze lijst zeker zal missen is een opgave van nationale determinatiewerken en verspreidingsatlassen. Met betrekking tot de laatste worden alleen die van Nederland en Vlaanderen vermeld, terwijl die van aangrenzende landen en streken, zoals Wallonië, de Duitse deelstaten en de Franse regio Nord-Pas-de-Calais voor de bewoners van de lage landen toch op z'n minst interessant genoemd mogen worden. Maar ook een in biogeografisch opzicht

nieuwe benadering van het samenstellen van verspreidingskaarten, zoals in het handboek van de Zwitserse zoogdieren (Hausser 1995), blijft hierdoor onvermeld.

Ondanks deze opmerkingen moet de aanschaf van deze gids zeker worden aanbevolen. Alleen al door de up-to-date presentatie van de in Europa voorkomende zoogdieren is hij zijn geld meer dan waard en het dwingt bewondering af dat het de auteurs en de illustrator gelukt is om van al deze soorten een kritische beschrijving en een afbeelding te geven.

Literatuur

- Fumagalli, L. 2008. Genetische Artbestimmung. In: P. Marchesi, M. Blant & S. Capt (eds.). Fauna Helvetica 22. Säugetiere der Schweiz. Bestimmungsschlüssel: 14-25. Centre suisse de cartographie de la faune / Schweizerische Gesellschaft für Wildbiologie, Neuchâtel, Switzerland.
- Hausser, J. (ed.) 1995. Säugetiere der Schweiz. Verbreitung - Biologie - Ökologie. Birkhauser Verlag, Basel, Switzerland.
- Husson, A.M. & W. C. van Heurn 1959. Kleurverschiedenheden van de mol, *Talpa europaea* L., in Nederland waargenomen. Zoölogische Bijdragen 4: 1-16.
- van den Brink, F.H. 1955. Zoogdierengids van Europa ten westen van 30° oosterlengte. Elsevier, Amsterdam, the Netherlands.

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Contents of Volume 53 (2010)

Research Papers

- Camphuysen, C.J., P. de Boer, W. Bouten, A. Gronert & J. Shamoun-Baranes. 5
Mammalian prey in Laridae: increased predation pressure on mammal populations expected.
- Dekker, J.J.A. & G.J. Bekker. Badger (*Meles meles*) road mortality in the Netherlands: the characteristics of victims and the effects of mitigation measures. 81
- Grol, B.P.F.E. & A.M. Voûte. Hibernating bats in the Schenkgroeve, an artificial limestone cave in south Limburg, the Netherlands. 29
- Haelters, J., F. Kerckhof & C. J. Camphuysen. The first historic record of a humpback whale (*Megaptera novaeangliae*) from the Low Countries (Southern Bight of the North Sea). 93
- MacPherson, J.L. & P.W. Bright. A preliminary investigation into whether grazing marsh is an effective refuge for water voles from predation. 21
- Verboom, B. & H.H. Huitema. The influence of treeline structure and wind protection on commuting and foraging common pipistrelles (*Pipistrellus pipistrellus*). 63
- Wermundsen, T. & Y. Siivonen. A comparison of the hibernation patterns of seven bat species in Estonia. 51

Short Notes

- Dekeukeleire, D. First record of soprano pipistrelle (*Pipistrellus pygmaeus* Leach, 1825; Chiroptera: Vespertilionidae) in Wallonia (Belgium). 105
- Zeiler, J.T. & E.J.O. Kompanje. A killer whale (*Orcinus orca*) in the castle: first find of the species in a Dutch archaeological context. 101

Book Reviews

- van Laar, V. Zoogdieren in Europa. 109

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- Barrett, G.W. & J.D. Peles (eds.) 1999. Landscape ecology of small mammals. Springer, New York, USA.
- Bergers, P.J.M. 1997. Versnippering door railinfrastructuur. Een verkennende studie. Report 262. Instituut voor Bos- en Natuuronderzoek, Wageningen, The Netherlands.
- Clarke, G.P., P.C.L. White & S. Harris 1998. Effects of roads on badger *Meles meles* populations in southwest England. *Biological Conservation* 86: 117-124.
- Clevenger, A.P. 1998. Permeability of the Trans-Canada Highway to wildlife in Banff National Park: importance of crossing structures and factors influencing their effectiveness. In: G.L. Evink, P. Garrett, D. Zeigler & J. Berry (eds.). *Proceedings of the international conference on wildlife ecology and transportation*: 109-119. FL-ER-69-98. Florida Department of Transportation, Tallahassee, USA.
- Shkedy, Y. & B. Shalmon 1997. Evaluating open landscapes in the Negev Desert, and the implications on military activity. *Nature Reserves Authority, Jerusalem, Israel*. (In Hebrew with English summary).
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Volume *Deel* 53 - Number *Nummer* 2 – December 2010

Contents *Inhoud*

Editorial / Redactioneel

- 49 **The bat, the weevil and other ‘species’**
Ben Verboom

Research Papers / Artikelen

- 51 **A comparison of the hibernation patterns of seven bat species in Estonia**
Terhi Wermundsen & Yrjö Siivonen
- 63 **The influence of treeline structure and wind protection on commuting and foraging common pipistrelles (*Pipistrellus pipistrellus*)**
Ben Verboom & Hans H. Huitema
- 81 **Badger (*Meles meles*) road mortality in the Netherlands: the characteristics of victims and the effects of mitigation measures**
Jasja J.A. Dekker & Hans (G.J.) Bekker
- 93 **The first historic record of a humpback whale (*Megaptera novaeangliae*) from the Low Countries (Southern Bight of the North Sea)**
Jan Haelters, Francis Kerckhof & Kees (C. J.) Camphuysen

Short Notes / Korte Berichten

- 101 **A killer whale (*Orcinus orca*) in the castle: first find of the species in a Dutch archaeological context**
Jørn T. Zeiler & Erwin J.O. Kompanje
- 105 **First record of soprano pipistrelle (*Pipistrellus pygmaeus* Leach, 1825; Chiroptera: Vespertilionidae) in Wallonia (Belgium)**
Daan Dekeukeleire

Book Reviews / Boekbesprekingen

- 109 **Zoogdieren in Europa**
Vincent van Laar

Index

- 112 **Contents of Volume 53 (2010)**

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