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Panta rhei

Panta rhei is the ancient Greek expression for 'everything flows.' It is a valuable aphorism for all aspects of life. The famous Greek philosopher Heraclitus (who lived around 600 B.C.) is said to have remarked: "Only change itself is a real, constant and eternal flux, like the continuous flow of the river which always renews itself." He argued that people never cross the same river twice, as both the river and the person are constantly changing. Heraclitus was one of the first Greek philosophers who made the transition from natural philosophy (defined by Wikipedia as 'the analysis and synthesis of common experience and argumentation to explain or describe nature') to a more empirical way of thinking. In this respect he may be considered as one of the founding fathers of modern natural sciences, including biology, physics and chemistry.

In nature, *panta rhei* can be used to characterise the cycle of plants and animals; that are born, grow older and eventually die but will be superseded by their descendants. In science, *panta rhei* can characterise the experiments of scientists who can only report their results to each other because they are standing on the shoulders of giants: their predecessors. Scientists are constantly using the results of others in order to generate improvements in mankind's knowledge.

Panta rhei can also aptly describe the continuously changing needs of the readers of scientific journals. It would not be good if Lutra stayed the same and didn't change. It is the task of the editorial board to see how the journal can best be adapted to current needs. In the words of our previous editor, Edgar van der Grift (Lutra 53-1: Editorial): 'Lutra is an instrument to present valuable research results or interesting observations on mammals to the scientific world'. We have recently implemented major changes: introducing double-blind peer review procedures and deciding to publish solely in English. These changes were made in order to improve the quality of submitted papers and raise the profile of Lutra among mammalogists around the globe. Currently, we are in the process of obtaining an impact factor, which will further help us to increase our visibility among (more or less) similar journals in the field. Full internet access to the content of previous issues is also important and offers new opportunities for existing readers of the journal and others. The editorial board thinks that such changes will contribute positively to the vitality and standing of Lutra in the future.

And finally, the phrase *panta rhei* also can be applied to the editorial board and its members. It was September 2009 when I joined the board of Lutra and, a little later, became its secretary. Since then there have been considerable changes in my life (a new job, political work) that require a lot of my attention. This has had many effects on the amount of time that I can

attribute to the journal. Lutra needs a secretary who can dedicate sufficient time to maintaining and further improving the quality of the journal and to face future challenges. Although I could continue to make a contribution to these goals, I feel it would not be enough. Lutra deserves better, so I have decided to step down from the editorial board.

Jasja Dekker is also leaving our board, after nine years. Besides being an editor, Jasja was Lutra's secretary from 2003 to 2008. In addition, he made some much appreciated initiatives, such as the compilation and production of the '50 Volumes of Lutra' DVD in 2008. We thank Jasja for being a great colleague over the years and wish him all the best in his career at the Dutch Mammal Society.

2011 is the United Nations' Year of the Bat (or, preferably, 'Bats'; cf. our last issue's editorial). Therefore, this issue is largely devoted to this highly successful group of mammals. Martijn Boonman's paper on the use of culverts by bats presents information that is highly pertinent when planning (new or wider) roads or railways, that may cause habitat fragmentation. Marc Van De Sijpe provides us with some new insights into the echolocation of the trawling bats of Europe, employing an extremely sensitive type of ultrasound microphone. Furthermore, we also have papers on the population trends of the harbour porpoise and the occurrence of the bicoloured white-toothed shrew in Zeeuws-Vlaanderen and its current status in the Netherlands.

Lutra has an interesting future ahead. I wish my colleagues on the editorial board all the best in realising its potential.

In this edition of Lutra a new general layout has been adopted which features the Dutch Mammal Society's new logo: a more modern design of our traditional symbol of the long, whiskered otter. The old logo has embellished this journal and many other documents for many years. But *panta rhei* also applies to the image of the Dutch Mammal Society. And, while we have maintained *Lutra lutra* as the symbol of our society and its scientific journal, we have opted for a more modern representation of it.

Bastiaan Meerburg

Factors determining the use of culverts underneath highways and railway tracks by bats in lowland areas

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Abstract: In urbanising environments the construction of suitable underpasses for bats under highways and railway tracks is becoming increasingly important to avoid habitat fragmentation. Culverts provide valuable and low cost underpasses as they are already an intrinsic part of highway design and many bat species associated with water are likely to follow the streams or canals that flow through them. Bat detectors were employed to study the use of 54 culverts by bats in the Netherlands. The aim of the study was to define the factors that determine bats' use of culverts. Bats were observed in the vast majority of the culverts that were studied, thereby underlining the importance of culverts in habitat de-fragmentation. Species adapted to hunting in open habitats, such as the noctule (*Nyctalus noctula*) and the serotine (*Eptesicus serotinus*), were often recorded in front of the entrance but rarely inside culverts. For the three species that were regularly recorded inside culverts, Daubenton's bat (*Myotis daubentonii*), the pond bat (*Myotis dasycneme*) and the common pipistrelle (*Pipistrellus pipistrellus*), cross sectional area was the most important factor that determined their use of culverts. Height was the most important component of cross sectional area for bats. Length proved a non-significant factor, suggesting that bat underpasses are not affected by the widening of the above-lying infrastructure. Additional guidance by treelines along the banks did not increase the use of culverts by the three species. The implication of the different preferences for cross sectional area on the design of infrastructure is discussed.

Keywords: connectivity, anthropogenic barriers, highways, underpasses, bats.

Introduction

In densely populated areas anthropogenic barriers such as highways and railway tracks can pose a number of problems for flora and fauna. They can lead to habitat fragmentation and when there is a small remnant population this can increase the risk of inbreeding and lead to a loss of genetic variability (Hedrick 2000, Keller & Largiadèr 2003). At the same time the chance of local extinctions increases, by destroying effective meta-population structures (Gonzales et al. 1998). For flying animals such as bats, highways do not constitute complete barriers and it seems unlikely that these two processes play a major role. It has been demonstrated, however, that highways do provide barriers to bat movements (Kerth & Melber 2009). Slow and/or low flying bat species such as the lesser horseshoe bat (*Rhinolophus hipposideros*) and the brown long-eared bat (*Plecotus auritus*) seem reluctant to cross highways at high altitude and their mortality caused by collision with vehicles seems to be higher than among fast hawking, aerial insectivorous bats (Russell et al. 2009, Lesinski et al. 2010). Geoffroy's bats (*Myotis emarginatus*) and Bechstein's bats (*Myotis bechsteinii*) make detours to reach suitable underpasses to cross a highway (Krull et al. 1991, Kerth & Melber 2009), thereby increasing the length of their commuting flight. As most vespertilionid bats make use of the peak in food availability at the onset of the night (Kunz 1973, Swift 1980), a longer commuting flight time can significantly reduce foraging efficiency.

The construction of overpasses and under-

passes improves the connectivity of habitats adjacent to highways and is therefore likely to reduce these negative effects. Underpasses are readily accepted and used frequently by slow/low flying bat species (e.g. Bach et al. 2004), in many cases more frequently than green bridges (Bach & Müller-Stieß 2005). Culverts provide valuable underpasses because they generally do not have the illumination or traffic that is present in most tunnels and because many bat species associated with water are likely to follow the streams or canals that lead through them. Because culverts are an intrinsic part of a highway design, the cost of making a suitable culvert underpass is much lower than creating a fauna tunnel.

However, there is limited available data about the appropriate dimensions or other factors that determine the use of bat underpasses. Several studies provide dimensions based on known bat underpasses and expert judgements (Brinkmann 2003, Bach et al. 2004, Limpens et al. 2004, National Roads Authority 2006, Brinkmann 2008). To date no quantitative analysis has been done that relates the characteristics of underpasses with bat usage. Many highways are currently being widened to add traffic lanes to accommodate the increasing number of vehicles. This will increase the length of the underlying tunnels and culverts. It is unclear what the effect of these measures will be on existing bat commuting flight routes. This study was undertaken to define the orthogonal factors that determine the use of culverts underneath highways and railway tracks by bats.

Methods

Study area

Fifty-four culverts underneath highways (24), provincial/secondary roads (11), railway tracks (5) and local roads (14) were studied. All the culverts are located in the Netherlands, the majority in the centre or mid-western part of the country (figure 1). The area is flat, mostly consisting of intensively cattle-grazed meadows interrupted by urban environments and patches of deciduous forest. All the culverts are for canals, streams or ditches with stagnant or slow flowing water. The water surface level of these locations is just below (<1.5 m) the surrounding area, as is typical in lowland areas. Underpasses that contain larger water bodies (canals, small rivers) are usually called bridges but in this study the term culverts is consistently used to avoid confusion.

Figure 1. Map of the Netherlands indicating the locations of the studied culverts.

The culverts were selected in order to obtain a sample containing different dimensions (height, width and length; table 1. photos 1-3). Culvert length is defined as the distance between the two entrances. Culvert height is defined as the distance from the water level to the ceiling of the culvert (photo 4). As larger

Table 1. Dimensions (m) of the studied culverts (n=54).

	Average	Minimum	Maximum
Length	36	3.6	132
Width	8.1	1.4	37
Height	2.1	0.3	6.1

Photos 1-3. Three of the culverts studied, showing dimensional differences. *Photographs: M. Boonman.*

culverts tend to be both wide and tall, culverts with unusual shapes (e.g. narrow and tall underpasses for boats) were included to maintain parameter independence. Culvert dimensions were measured with a Bosch digital range finder. Culverts longer than 80 m were measured by using Google Earth. None of the culverts contained illumination, traffic or physical barriers such as fences or grills.

Measuring bat activity

Bat activity was simultaneously measured in the middle of the culverts as well as in front of one entrance by using Anabat SD II bat detectors (Titley Electronics, Ballina, Australia). The Anabat inside the culvert was placed on a small raft that was secured by two anchors with the microphone directed at a 45 degrees angle between the entrance and the middle of the culvert (photo 5). In culverts with an existing platform for terrestrial animals, the Anabat was placed on top of that platform. All the Anabats were operated at sensitivity 4. This prevented repeated recordings of traffic noise, although it may mean that bat species that emit very low intensity echolocation calls (such as brown long-eared bats) may occasionally have been missed. Bat activity

Photo 4. Length (L), height (h) and width (b) of a culvert. *Photograph: M. Boonman*

was recorded at each culvert for a full night between the 15th of May and the beginning of September 2010 during good weather conditions (no data was collected during nights with heavy rain). Echolocation calls were identified by using Analook software (Titley Electronics, Ballina, Australia) and reference sonogram databases. The shape (frequency modulated (FM) or quasi-constant frequency (QCF)) as well as minimum frequency and the number of pulses per second of recorded bat echolocation calls were used for species identification. The slope and end frequency of echolocation calls can reliably be used for species identification (Britzke et al. 2002, Obrist 2004, Redgwell et al. 2009).

The number of bat echolocation passes, defined as a series of echolocation pulses, was tallied for each Anabat night, resulting in an index of bat activity (Thomas 1988, Broders 2003). The time of sunset and sunrise were used as the beginning and end of each night.

In very short culverts it is possible that bats flying outside will be recorded by the Anabat located inside the culverts. Bats adapt their echolocation calls according to the environment they fly in. For example pulse duration is shortened in confined environments to avoid pulse echo overlap (Kalko & Schnitzler 1989). Figure 2 shows the difference between calls from common pipistrelles (*Pipistrellus pipistrellus*) flying inside the culvert and those of bats flying outside. The echolocation calls of bats flying outside that were accidentally recorded inside the short culverts could be discarded by paying attention to this difference.

A.-J. Haarsma provided data from 21 of the 54 culverts. She counted the number of bat passes hour^{-1} with a Pettersson D240 bat detector (Pettersson Electronics, Uppsala, Sweden) during similar weather conditions in the same time of the year. While present at the entrance, she determined both visually and acoustically whether bats were flying inside or outside culverts. By listening to the amplitude of the bat pulses and alternating the direction of the microphone of the detector between the middle of the culvert and towards the area outside, it was determined whether or not bats were flying inside the culverts. Visual observations in the early evening provided additional information on the bats' flight paths. The number of bat passes was thus quantified both inside and outside the culverts. Tests were performed to see if the two different methods to measure bat activity (Anabat versus Pettersson D240) revealed different results.

Photo 5. An Anabat detector, placed on a small raft. *Photograph: M. Boonman*

Definition of use

Culverts where no bats were recorded either inside or in front of the entrance were not used in the analysis because it was unclear why bats were not using these culverts. The bats may have been absent on that particular night or the location could have been outside their geographical range. Only when bats were present (which was clear when they are recorded in front of the entrance) was there a possibility that they might use the culvert.

Culverts where bats were recorded in front of the entrance, but not inside, were defined as 'unused'. Culverts where bats were recorded inside but the number of bat passes was lower than 0.55 hour^{-1} were defined as 'incidentally used'. Many bat species such as Daubenton's bats (*Myotis daubentonii*) use well-defined commuting routes between the roost site and foraging area that many individuals traditionally use (Rieger et al. 1990). Even though these vital commuting routes are protected under European law (The Habitats and Species Directive 92/43/EEC), there is no definition separating them from random flight routes of a single individual. For the purpose of this study I defined a regularly used commuting route as a route that at least two individuals used to fly from their roost site to their foraging area and back. If a culvert is part of such a route than it would have at least four bat flights through it per night. During the shortest night (June 21) this results in 0.55 bat passes hour^{-1}. The use of this value is speculative as 1. the duration of the night varies through the year and 2. the number of recorded bat passes is a relative measure of bat activity that does not necessarily correspond to the number of bats that pass. However, in the absence of a better definition, this value is useful for differentiating between well used and incidentally used commuting routes and is at least better than an arbitrarily chosen value.

Culverts where the number of recorded bat passes exceeded 0.55 hour^{-1} were thus defined as 'used'.

Statistical analysis

The use of culverts by bats was related to the following parameters: method used to

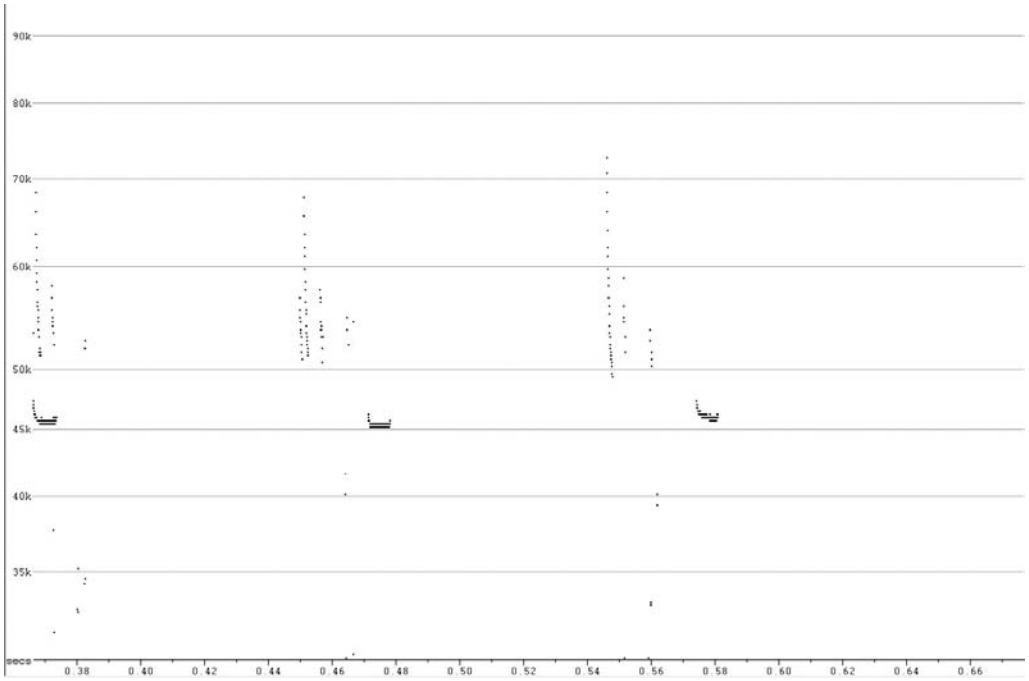

Figure 2. Sonogram of two common pipistrelles recorded by an Anabat detector. One is flying through a culvert (three vertical pulses above) and the other is flying outside (three pulses below).

measure bat activity (Anabat versus Pettersson D240), length (distance between both entrances), width, height, cross sectional area and additional guidance. Culverts for a water body with tall vegetation (>2 m) along the banks were defined as culverts with additional guidance. The guidance is called additional because the water body itself is a guiding structure that bats tend to follow (Lookingbill et al. 2010). Because cross sectional area (width x height in rectangular culverts) is strongly related to width and height, it was only used in the analyses as an alternative to both parameters (to avoid multi-collinearity). Other factors such as the position of the culvert relative to the surface were excluded from the analysis as this varied little between the studied locations.

It was not possible to use multiple linear regression in a consistent way to identify the factors that determine the use of culverts by all species. Each species required its own set of transformations to avoid violations of the required conditions of multiple linear regression. A plausible definition of culvert usage was used to transform the number of bat passes into a dichotomous variable. Logistic regression was subsequently used to obtain a comparable result for each bat species and to avoid the overrepresentation of locations with a large number of bat passes. The response variable is binary in logistic regression. Unused and incidentally used culverts (see definition of use) were included in the analysis as 0, while used culverts were defined as 1.

Other analysis techniques were used to provide further information on how bat activity is related to the significant parameters (as revealed by the logistic regression analysis). Multiple linear regression was used when the number of bat passes did not violate the required conditions. Otherwise negative binomial regression was used.

The minimum dimensions of culverts used by bats were determined in two ways. First, they were determined directly by using the

Table 2. Results of the logistic regression analysis. For each species the significance level of all parameters is given. Width and height were only analysed as a substitute for cross sectional area. ns= not significant.

	Parameter	Wald χ^2	Significance level (*P*)
Daubenton's bat	method	2.0	0.15 ns
(*n*=45)	additional guidance	0.52	0.47 ns
	length	0.77	0.38 ns
	cross sectional area	6.1	0.014
	width	2.6	0.11 ns
	height	5.2	0.023
Pond bat	method	1.9	0.17 ns
(*n*=25)	additional guidance	0.042	0.84 ns
	length	0.022	0.88 ns
	cross sectional area	4.0	0.047
	width	2.1	0.15 ns
	height	0.083	0.77 ns
Common pipistrelle	method	0.88	0.35 ns
(*n*=52)	additional guidance	0.29	0.59 ns
	length	0.67	0.41 ns
	cross sectional area	10.4	0.001
	width	4.5	0.034
	height	6.9	0.009

Table 3. Lowest height (m) and cross sectional area (m^2) of culverts that bats used (>0.55 bat passes $hour^{-1}$) and incidentally used (0-0.55 bat passes $hour^{-1}$).

Lowest height (m)	Incidentally used culverts	Used culverts
Daubenton's bat	0.4	0.9
Pond bat	0.4	1.0
Common pipistrelle	1.5	1.5
Lowest cross sectional area (m^2)		
Daubenton's bat	1.2	2.2
Pond bat	1.2	6.4
Common pipistrelle	8.0*	7.5

*Incidental use of culverts was not frequently observed in common pipistrelles. One of the used culverts had a smaller cross sectional area than the smallest incidentally used culvert.

minimal height and cross sectional area of the culverts used (and incidentally used) by bats. However, these minimal values can represent coincidental outliers that are not representative for the species. The minimal dimensions were therefore also calculated by using the best fitting logistic regression model containing the factor 'cross sectional area'. The probability of Y=1 (culvert is used by bats) was calculated by using the logistic function (Agresti 2007).

The statistical analysis was done by using SPSS (PASW statistics 18.0; SPSS Inc., Chicago, IL, USA).

Results

Forty-six (85%) of the 54 culverts studied were used by bats. In the other eight culverts, bats were registered in front of the entrance but not inside. Culverts were used as a part of the bats' commuting route but also as a foraging

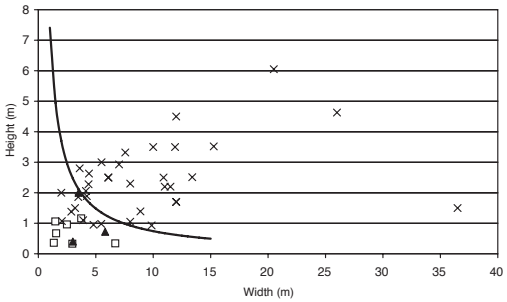

Figure 3. The use of culverts by Daubenton's bats in relation to height and width. Open square = unused, solid triangle = incidentally used, cross = used. The line indicates the cross sectional area with a 95% probability of usage. Height =7.4 / width; *n*=45.

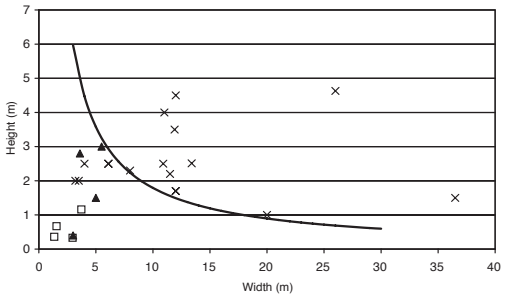

Figure 4. The use of culverts by pond bats in relation to height and width. Open square = unused, solid triangle = incidentally used, cross = used. The line indicates the cross sectional area with a 95% probability of usage. Height =18 / width; *n*=25.

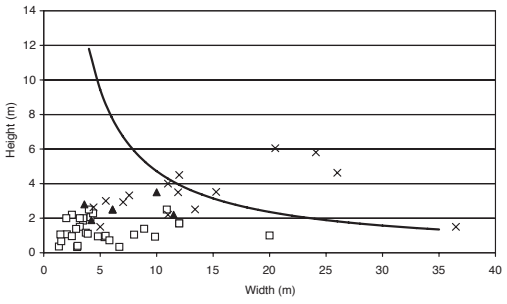

Figure 5. The use of culverts by common pipistrelles in relation to height and width. Open square = unused, solid triangle = incidentally used, cross = used. The line indicates the cross sectional area with a 95% probability of usage. Height =47 / width; *n*=52.

Table 4. Cross sectional area (m^2) of culverts that have an 80, 90 and 95% probability of being used. Values were calculated using the best fitting logistic regression model with the parameter cross sectional area.

	80%	90%	95%
Daubenton's bat	5.4	6.5	7.4
Pond bat	12	15	18
Common pipistrelle	36	42	47

area, as shown by frequently recorded feeding buzzes. The distinction between commuting and foraging bats was not made as commuting bats also occasionally catch prey items (Britton et al. 1997). In one culvert a day roost of Daubenton's bats was present.

The following species were recorded in front of the entrance of the culverts: whiskered/Brandt's bat (*Myotis mystacinus/brandtii*), Daubenton's bat, pond bat (*Myotis dasycneme*), common pipistrelle, soprano pipistrelle (*Pipistrellus pygmaeus*), Nathusius' pipistrelle (*Pipistrellus nathusii*), noctule, serotine and brown/grey long-eared bat (*Plecotus auritus/austriacus*).

Of these nine species only Daubenton's bat, pond bat, common pipistrelle, noctule and serotine were recorded regularly. The number of recorded bat passes varied from less than 0.1 to 312 $hour^{-1}$. The highest number of bat passes was recorded at the leeward side in front of the entrance of a culvert where a large group of common pipistrelles was foraging.

Species that ignore culverts

Of the five species that were recorded regularly in front of the entrance, noctules and serotines were never or rarely recorded inside the culverts. Noctules were recorded at 21 locations but never inside the culverts. Serotines were registered at 31 locations but were only recorded inside three culverts. These three culverts were exceptionally spacious (cross sectional area 120, 124 and 140 m^2).

Species that use culverts

Daubenton's bats, pond bats and common pipistrelles were recorded regularly inside the culverts. The logistic regression analyses showed that the variable 'method' was not a significant factor for any of the three species (table 2), i.e. the two methods used to determine bat activity (Anabat and Pettersson D240) revealed similar results. Culvert length and additional guidance were not significant in explaining the use of culverts by any of the three species. Cross sectional area was a significant factor for all three species. In separate analyses cross sectional area was replaced by width and height. Height was a significant factor for Daubenton's bat and common pipistrelle. Width was only significant for common pipistrelle, but with a lower significance level than height. Height was thus the most important component of the cross sectional area for Daubenton's bat and common pipistrelle (table 2).

For pond bats and common pipistrelles the number of passes inside the culvert was positively correlated to the cross sectional area (pond bat: linear regression, F=17.3, df=24, P<0.05; common pipistrelle: negative binomial regression, likelihood ratio χ^2=35.2, df=50, P<0.01). For Daubenton's bat this correlation was not significant for all culverts (linear regression, F=0.037, df=44, P>0.05) but was significant after root transformation of the number of bat passes in culverts with a cross sectional area of less than 30 m^2 (linear regression, F=5.9, df=36, P<0.05). Culverts where no bats were registered almost invariably had a small cross sectional area and in spacious culverts many bat passes were recorded.

The smallest culverts used by bats

The minimal height and cross sectional area of the culverts that were used (and incidentally used) by bats are shown in table 3. These were also calculated by using the best fitting logistic regression model containing the factor "cross sectional area". These models were significant for all species (table 2). Table 4 shows the cross sectional area corresponding to the probability that a culvert is used by each bat species (when the bats are recorded in front of the entrance). There was a clear difference between the three species. Daubenton's bats used culverts with the smallest cross sectional area, while common pipistrelles only used the more spacious culverts. Figures 3-5 show the minimal height and width of a culvert suitable for bats. The line corresponds to a probability of 95% of a culvert being used. The line divides the used culverts (crosses) from the incidentally used (triangles) and unused culverts (squares).

Discussion

In this study, the vast majority of the culverts were used by bats. Bats were recorded in all culverts, except the smallest ones (cross sectional area <4 m^2). The culverts that were studied were not a random sample. Small culverts and those with odd shapes were overrepresented in the study, compared to their occurrence in 'the field'. Therefore the actual percentage of the culverts used by bats might even be higher than our results suggest. This underlines the importance of culverts in countering habitat fragmentation.

Species that ignore underpasses

Fast hawking, aerial insectivorous bats are less likely to use underpasses such as culverts. They are adapted to flying in open areas by their wing morphology (high aspect ratio, pointed wing tips) and echolocation (narrowband QCF pulses of a long duration; Norberg & Rayner 1987, Fenton 1989). These species are able to cross highways above traffic height, but might not do so when there is no guiding, tall vegetation. Northwest European bat spe-

cies belonging to this category are: noctule, parti-coloured bat (*Vespertilio murinus*) and serotine (Limpens et al. 2004). The results of this study are consistent with these findings. Noctule bats were never observed inside culverts and serotines only in the most spacious ones. In Germany serotines have regularly been observed in tall underpasses (L. Bach, unpublished data). Although it seems unnecessary to take these three species into account when constructing underpasses in lowland areas, this could be different in areas with taller underpasses, such as highland areas.

Species that typically use underpasses

Bat species that use underpasses relatively often and seem hesitant to cross highways at high altitude are those species that are adapted to dense environments (particularly foliage-gleaning bats), and also trawling bats (Norberg & Rayner 1987, Bach et al. 2004). In Northwest Europe species belonging to this category are the vespertilionid species of the genus *Myotis* and *Plecotus* and rhinolophid species. Their wing morphology (low aspect ratio, low wing loading) allows manoeuvrable flight which is necessary for flying in confined spaces, such as culverts. Their echolocation (broad-band FM pulses of short duration in vespertilionids) is clutter-resistant, enabling the bats to detect small obstacles within confined areas. The bats' behaviour also seems to play a role. Pond bats are not very well adapted (by wing morphology and echolocation) to confined habitats (Norberg & Rayner 1987, Britton et al. 1997) but nonetheless they frequently use underpasses because of their habit of flying close to the water surface. In this study, two species that belong to this category, Daubenton's bat and pond bat, were frequently observed inside culverts. It is important to consider the requirements of these species when designing new underpasses or changing existing ones.

Factors determining the use of the culverts

For all species there was a substantial variation in the number of recorded bat passes within and in front of culverts. Wind, distance to the nearest roost site and the amount of foraging exhibited by bats in culverts are probably among the most important factors contributing to this.

In this study, the cross sectional area was the most important factor determining the use of underpasses by bats. Among all species the number of bat passes increased with increasing cross sectional area. Height was the most important component of the cross sectional area in this study. This is not surprising since culverts are generally not constructed for very narrow (<1 m), slow flowing or stagnant water bodies. In lowland areas, where this study took place, culverts are almost invariably wider than they are tall. It is likely that width may be more critical for bats in upland areas where many culverts for seasonally fast-running streams are narrow and tall.

It has been noted that, in order to be used by large terrestrial mammals, underpasses need to be more spacious when the length is increased (van Nierop 1988, Ministerie van Verkeer en Waterstaat 2005). Because of their echolocation system, bats are distinctly different in this aspect. Bats are less hesitant to travel through extremely long tunnels, as shown by hibernating bats which can use (artificial) caves with a length of several kilometres. Length was not a significant factor in determining the use of culverts in this study. Thus, there is no reason to assume that longer underpasses (up to 130 m length) are used less frequently by bats than short ones. This result is significant, now that many highways are being widened to add traffic lanes to accommodate more vehicles.

Additional guidance (tree lines) was also not significant in determining the use of culverts by Daubenton's bats, pond bats and common pipistrelles. Guiding structures could

nonetheless be an important factor as the water body itself is a guiding element that bats tend to follow (Lookingbill et al. 2010). Guiding structures have been reported to be important factors explaining the use of green bridges by bats (Bach & Müller-Stieß 2005).

The smallest culverts used by bats and the implications of this

This study shows that knowledge about the appropriate cross sectional area is of critical importance when constructing suitable bat underpasses. A larger cross sectional area leads to an increase in usage, although there is probably a certain saturation level. This saturation level is of minor importance because it probably represents a large number of foraging bats. The aim of constructing bat underpasses is to maintain vital commuting routes, rather than to create foraging habitats. It is therefore more useful to determine the smallest cross sectional area of underpasses that are used more than incidentally, as done in this study.

This cross sectional area differs per species, it is 7 m^2 for Daubenton's bats, 18 m^2 for pond bats and 47 m^2 for common pipistrelles (based on a probability of 95% that a culvert is used). This interspecific difference is in accordance with Schaub & Schnitzler (2007) who found that commuting common pipistrelles flew at higher altitude and maintained a larger distance from vertical background structures than commuting Daubenton's bats. The minimal required cross sectional area of suitable bat underpasses has also been reported by Brinkmann (2003), Bach et al. (2004), Limpens et al. (2004) and Brinkmann (2008), based on known bat underpasses and expert judgement. Their values are substantially lower (2-3 m^2 for Daubenton's bat and 16 m^2 for common pipistrelle) than those calculated by this study. Their reported values are likely to represent the smallest underpasses where bats were observed, and could reflect coincidental outliers that are not representative for the species. A few locations were found during this study where Daubenton's bat and common pipistrelle frequently use very small culverts (2 and 8 m^2 respectively; table 3). But taking this minimal value ignores the fact that there are many underpasses with the same dimensions where bats are present but not using them. It is therefore important to construct bat underpasses that are larger than the reported minimal values.

If bats prefer to maintain a certain distance to both horizontal and vertical obstacles (Schaub & Schnitzler 2007), an underpass with a width/height ratio of one would be preferable to a wide and low underpass with the same cross sectional area. Most of the studies mentioned above are based on findings from upland areas where the width/height ratio of culverts is closer to one (lower) than in lowland areas. Therefore the cross sectional area of suitable bat underpasses might be lower in upland areas.

The width of a water body can only be slightly adapted and is thus a more or less fixed value that road constructors have to work with. The minimal height of a culvert that is suitable for bats can be determined by using this width and the cross sectional areas from table 4 or figures 3-5. This minimal height should not be less than the minimal height of culverts in which bats were observed (table 3) to stay within each species' recorded range. In lowland areas the construction of large underpasses can be expensive as large amounts of soil are required for the ramp to attain an elevated height. Increasing the width by incorporating the banks of the water body into the underpass can reduce these costs. Common pipistrelles only used very spacious culverts. In practise it may often not be affordable to construct underpasses with suitable dimensions for this species. Compared to Daubenton's and pond bat we can expect this species to use overpasses, such as green bridges, more easily (Bach & Müller-Stieß 2005). The construction of hop-overs to create an overpass for bats is generally recommended (Limpens

et al. 2004), but their use has never been systematically determined.

Every highway reconstruction provides an opportunity to create suitable or better bat underpasses. Most environmental impact assessments discuss baseline survey data extensively and only briefly deal with the most important part: mitigation measures. In the U.K., it is standard procedure to monitor the effectiveness of mitigation measures, but this is not the case in the Netherlands. It is therefore usually not known whether these mitigation measures are effective. A major step forward will be to set aside a budget within highway (re) construction projects, to improve knowledge about the effectiveness of mitigation measures.

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Samenvatting

Welke factoren bepalen het gebruik van duikers onder wegen en spoorlijnen door vleermuizen?

De aanleg van geschikte voorzieningen voor vleermuizen onder wegen en spoorlijnen wordt steeds belangrijker om versnippering van leefgebieden te voorkomen. Duikers vormen waardevolle voorzieningen omdat veel vleermuizensoorten die gebonden zijn aan water geneigd zijn de watergangen te volgen die door de voorzieningen stromen. Daarnaast zijn duikers goedkoop omdat ze een intrinsiek onderdeel van een weg vormen. Het gebruik van 54 duikers door vleermuizen werd onderzocht met bat detectors. Deze studie had tot doel om de factoren te bepalen die het gebruik van duikers door vleermuizen verklaren. Vleermuizen werden in het merendeel van de duikers vastgesteld, waarmee het belang van duikers in de ontsnippering van infrastructuur werd onderstreept. Soorten die aangepast zijn aan een open omgeving zoals de rosse vleermuis en de laatvlieger werden vaak voor de ingang van duikers geregistreerd, maar zelden of nooit in duikers. Van de drie soorten die regelmatig in duikers werden vastgesteld, de watervleermuis (*Myotis daubentonii*), de meervleermuis (*M. dasycneme*) en de gewone dwergvleermuis (*Pipistrellus pipistrellus*), was de dwarsdoorsnede de meest belangrijke factor waarmee het gebruik van duikers verklaard kon wor-

den. 'Hoogte' was de meest belangrijke component van de dwarsdoorsnede voor vleermuizen. De lengte bleek geen significante factor. Dit suggereert dat vliegroutes van vleermuizen onder wegen geen effect ondervinden van wegverbreding. Additionele geleiding in de vorm van opgaande begroeiing langs de oevers had geen effect op het gebruik van de duikers door de drie soorten. De geschikte dwarsdoorsnede verschilde per soort. Watervleermuizen gebruikten de duikers met de kleinste dwarsdoorsnede, gevolgd door de meervleermuis en de gewone dwergvleermuis. Deze resultaten kunnen gebruikt worden bij de aanleg of reconstructie van infrastructuur.

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Differentiating the echolocation calls of Daubenton's bats, pond bats and long-fingered bats in natural flight conditions

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Abstract: Echolocation calls of the three European species of trawling bats were studied in their natural habitats, during hunting, commuting and swarming activities. Daubenton's bats (*Myotis daubentonii*) used pulse durations below 8 ms in most cases, however on rare occasions they used some longer search phase calls up to 13 ms. Pond bats (*Myotis dasycneme*) used a wide variety of pulse durations of up to 26 ms, with signals of >15 ms regularly recorded. The longest pulse durations recorded from the long-fingered (*Myotis capaccinii*) bat were 8 ms. The three species usually emitted starting frequencies below 100 kHz, however some recordings made at very close range revealed starting frequencies up to circa 120 kHz in Daubenton's bat and the long-fingered bat and circa 110 kHz in the pond bat. Although the peak frequencies were variable in all species, the pond bat generally used lower peak frequencies (median 41 kHz for durations of 1-4 ms and median 35 kHz for durations of >14 ms) compared to Daubenton's bat (median 49 kHz for durations of 1-4 ms and median 37 kHz for durations of 8-14 ms) and the long-fingered bat (median 45 kHz for durations of 1-4 kHz). End frequencies were significantly higher in the long-fingered bat (median 32 kHz, for durations of 1-4 ms) than in the other two species (pond bat median 25 kHz, Daubenton's bat median 26 kHz, for durations of 1-4 ms). Quasi-constant frequency parts in the middle of the signal were only found in the pond bat. Long-fingered bats sometimes used pulse series with alternating end frequencies.

Keywords: Daubenton's bat, pond bat, long-fingered bat, *Myotis daubentonii*, *Myotis dasycneme*, *Myotis capaccinii*, echolocation, trawling.

Introduction

Myotis is the largest bat genus with more than 100 species globally and 17 of the 51 currently known European species belong to this genus (Eurobats 2004). They occupy territories all over the world, with the exception of areas where climates are too extreme (such as Antarctica). The extensive spread of the genus is thought to have happened during the late Miocene, when the global climate cooled. Fossil records prove that during this time the original bat fauna disappeared from large land masses at medium latitudes where climates changed from tropical and non-seasonal to temperate and seasonal (Horáček et al. 2000). In Europe, where other Vespertilionid genera (*Pipistrellus*, *Nyctalus*, *Vespertilio, Eptesicus*) hunt prey in open or semi open environments, many *Myotis* species are well adapted for efficient hunting in confined spaces. In order to navigate and detect prey in environments with large amounts of echo-producing obstacles, they use brief frequency modulated echolocation calls with a large bandwidth (Schnitzler & Kalko 2001, Schnitzler et al. 2003). Because of ecological conditions often being similar and the large number of species that have evolved in this genus, identification of *Myotis* species by their echolocation calls is generally considered to be

tricky (Ahlén 1990, Barataud 1996). This issue has challenged bat researchers across Europe. In a review of echolocation calls of wild bats communicated via the Dutch mailing list Zoogmail, Boonman (2007) pointed out that there are differences in pulse shapes, starting and end frequencies among European *Myotis*. In France, Barataud (2004) developed a system of identification of *Myotis* species based on subtle differences in audible sounds of 1/10 time expanded echolocation calls, allowing identification of species that are considered 'very difficult to identify'. Recent advances in portable and lightweight bat detector technology, (i.e. 16 bit analogue-to-digital resolution and better ultrasonic microphones) increase the capability of detecting the very high frequencies that some *Myotis* species use (L. Pettersson & Y. Tupinier, personal communication). This manuscript describes the echolocation calls of the three trawling species of Europe, Daubenton's bat (*Myotis daubentonii*), the pond bat (*Myotis dasycneme*) and the long-fingered bat (*Myotis capaccinii*) that were recorded with a 16 bit detector.

Trawling behaviour, i.e. gleaning the water surface and capturing either floating or submerged prey, is thought to be a derived hunting behaviour in the genus *Myotis*, and aerial hawking probably represents the ancestral state (Fenton & Bogdanowicz 2002). Trawling has appeared through convergent evolution in many parts of the world. Some of the most specialised forms are found in the Neotropical genus *Noctilio* (Hood & Jones 1984, Schnitzler et al. 1994, Kalko et al. 1998) although trawling behaviour has been reported to mainly occur in the genus *Myotis* (Jones & Rayner 1988, Kalko & Schnitzler 1988, Britton et al. 1997, Blood & Clark 1998, Jones & Rayner 1991, Fenton & Bogdanowicz 2002). Trawling bats share a number of key morphological adaptations, such as enlarged hind feet, enlarged claws, modifications to the calcar and a specific wing morphology (long and often broad wings) to allow for slow, manoeuvrable and economical flight, low over water surfaces (Norberg & Rayner 1987, Schober & Grimmberger 1998). Daubenton's bat occupies large parts of the Palaearctic territory, ranging from the boreal to the Mediterranean zone. The two other species have a more restricted distribution area, and are either limited to the temperate humid and boreal zones (pond bat) or the Mediterranean (long-fingered bat) (Horáček & Hanák 1989, Mitchell-Jones et al. 1999).

The abundance of insect prey over freshwater bodies probably triggered the evolution of trawling insectivores. Several insect families have aquatic larval and terrestrial adult stages, including those within Diptera, Ephemeroptera, Trichoptera and Plecoptera. Larvae, pupae and adults of these taxa are commonly found in the diet of bats hunting over water (Brack & Laval 2006, Todd & Waters 2007). Dietary studies confirmed that the three European trawling bats consume a lot of Chironomidae, which are abundant in a wide variety of freshwater habitats (Britton et al. 1997, Sommer & Sommer 1997, Flavin et al. 2001, Levin et al. 2006, Almenar et al. 2007, Biscardi et al. 2007, Krüger et al. 2010). Terrestrial insects and spiders can accidentally fall into the water or are drawn to the water surface by blustery winds and are commonly found in the stomachs of surface dwelling fish, such as trout, as well as in the faeces of Daubenton's bat (Flavin et al. 2001). Large terrestrial insects can also be preyed upon by trawling bats in the air above still water surfaces or around the riparian vegetation. Terrestrial insects can be rewarding prey for trawling bats, not only because they are often larger in size, but terrestrial taxa are also more nutritional per unit of dry weight compared to insects with aquatic subadult stages (Brack & Laval 2006).

Daubenton's bats can spend more than 90% of their nightly foraging time over water surfaces (Encarnação et al. 2004, Encarnação et al. 2005, Dietz & Kalko 2006). In the open habitats of the Netherlands, where large water surfaces are abundant, pond bats spent 75% of

their time hunting over water, 20% over meadows (often in the vicinity of canals) and 5% in other habitats (Haarsma et al. 2006). Hunting behaviour over land, in villages, along linear vegetation and at the edge of small woodlands has been reported by Kapteyn (1995) and Limpens et al. (1997). Long-fingered bats spend the night almost exclusively flying over water, sometimes up to 100% of their foraging activity (Almenar et al. 2006). Observations of individuals hunting over land are rare (Biscardi et al. 2007, Davy et al. 2007, Némoz & Brisorgueil 2008).

The echolocation and flight behaviour of European bats has been studied quite intensively since the 1980s, following pioneer work by Ingemar Ahlén in Sweden (Ahlén 1990). Since the requirements for trawling are not much different than those of hawking in the air, the trawling insectivorous bats navigate and detect prey using intense frequency modulated (FM) calls of a short duration (a few milliseconds) and large bandwidth, similar to aerial hawking bats close to vegetation (Thompson & Fenton, 1982, Kalko & Schnitzler 1988, Britton et al. 1997, Jones et al. 1988, Jones et al 1991, Kalko & Schnitzler 1998). The behaviour of trawling insectivores in the buzz phase is remarkably similar to that of aerial hawking bats and all trawling insectivores are also capable of catching flying insects in air. The fine details and the advantages of echolocating over smooth water surfaces have been illustrated in experiments in flight tents (Siemers et al. 2001, Siemers et al. 2005) and in field studies (Boonman et al. 1998). The smooth surface does not act as an echo producing background for trawling bats flying at low height. The pond bat is the only one out of the three European trawling bats known to use echolocation calls of long duration with a quasi-constant fequency (QCF) part (Ahlén 1990, Kapteyn 1995, Limpens et al. 1995, Limpens et al. 1997). Over water they often hunt in a very similar way to Daubenton's bats, focussing on the large numbers of small prey items that can be found in freshwater habitats. In these flight conditions they use either short FM calls or mixed FM-QCF calls of medium duration. When using high intensity long duration FM-QCF-FM signals (ca 20 ms), pond bats either commute or hunt over large waterways, often chasing large insects in the air above the water surface up to a few metres, and over the adjacent reeds and willows (Ahlén 1990, Kapteyn 1995, Limpens et al. 1997, Van De Sijpe & Holsbeek 2007). A recent study of the diet of long-fingered bats revealed a relatively large amount of terrestrial Lepidoptera, which may have been caught in the air above water surfaces (Almenar et al. 2008).

Compared to insectivorous trawling bats, piscivorous species have larger feet, longer claws and tend to have a larger body size (Fenton & Bogdanowicz 2002). Although Daubenton's bat is able to catch small fish in laboratory conditions (Siemers et al. 2001) piscivorous behaviour in the natural conditions in Europe has only been reported for the long-fingered bat (Levin et al. 2006, Aihartza et al. 2003, Biscardi et al. 2007). *Myotis capaccini* is probably mainly insectivorous, and its piscivorous behaviour seems to be opportunistic, unevenly distributed in space and time. In some diet studies no fish remains at all were found (Almenar et al. 2008), but in others a high occurrence of fish remains (up to 100%) and high volume percentages (up to 82%) were detected (Almenar et al. 2003). In a flight tent the bats used a technique of random dips to catch fish, but only did so only if fish were present in high density (Aihartza et al. 2008). During search flight the bats emitted short FM types and did not use complete buzz phases while dipping in the water, suggesting that they don't rely on echolocation to track individual fish. Short broadband FM calls have also been reported in other (occasional) piscivores, including *Myotis adversus* in the Oceanic zone, *Myotis ricketti* in China and *Myotis vivesi* in Central America (Robson 1984, Blood & Clark 1998, Ma et al. 2003). Whereas *Myotis* species use FM signals (or

sometimes FM-QCF-FM types), *Noctilio* species emit CF-FM calls of medium duration (ca 10 ms) when trawling over water surfaces (Hook & Jones 1984, Schnitzler et al. 1994, Kalko et al. 1998). *Noctilio leporinus,* maybe the most specialised fisher among bat species, uses various techniques to catch fish. Directed pointed dips have been observed, in which the bats use the CF part in the signal to detect and track movements of individual fish on the surface. An alternative random rake technique has also been described, during which the bats can fly up to 10 metres with their claws continuously submerged in the water (Schnitzler et al. 1994).

Methods

Recording sites

Daubenton's bat

Field recordings of Daubenton's bats in natural flight conditions were made in various locations in Belgium (Province of West-Vlaanderen; table 1). Daubenton's bats and pond bats are the only two trawling bat species known to occur in Belgium and the Netherlands. Hunting bats were recorded over water (a rampart moat and a number of small ponds) and over land (in a forest near a roost tree). Commuting bats were recorded over a forest path, in a tunnel and at the edge of a large pond. Swarming bats were recorded in a forest and a castle park where roost sites are known. The forest roosts of Daubenton's bats had been known for about ten years and the bats were identified either by following commuting bats to nearby water surfaces, where they start to hunt in the typical trawling manner, or by sighting the bats in the roost using a Sandpiper tree camera (B. Vandendriessche & F. Verhaeghe, personal communication). One recording of a bat released from captivity was made in a marlow pit (Zichen, Province of Limburg) This bat was identified in the hand prior to release. Commuting activity was identified if a large number of individuals were observed passing by for a brief period of time, with all bats flying in the same direction and not returning. Hunting activity was identified if a bat was found to fly around for a long period of time in a small space, regularly emitting feeding buzzes (Limpens et al. 1997).

Pond bat

Pond bats are rare in Belgium. The only known roost, in a brewery in the Province of West-Vlaanderen, disappeared sometime ago, although since then recordings have been made of pond bats hunting over water (a large canal) south of Mechelen (Muizen, Province of Antwerpen; table 1). The presence of the pond bat around Mechelen was discovered about 10 years ago (S. Verkem, personal communication). Additional recordings of hunting behaviour over water, as well as commuting, swarming and hunting over land were recorded in the Friesian village of Tjerkwerd (the Netherlands; table 1) where a large roost has been known to exist for many years.

Long-fingered bat

A limited number of recordings of this species was made on three consecutive April nights, during a visit to Spain (Province of Valéncia; table 1). The bats were recorded in the vicinity of a known large maternity roost where the main hunting areas were found by radio telemetry (Almenar et al. 2006). The recordings of long-fingered bats were limited to hunting behaviour over smooth river surfaces by trawling. No recordings were made of commuting and swarming behaviour.

Visual observations

Visual observations of the bats' flight behaviour and size were made at dusk, against the bright evening sky, or where light sources in the vicinity provided sufficient illumination to see the bats. In situations too dark for the unaided eye, a monocular image intensifier

Table 1. Details of recording situations of Daubenton's bat (A1-A14), pond bat (B1-B15) and long-fingered bat (C1-C7). SP = search phase, AP = approach phase.

Recording number	Date and time	Location	Habitat		Flight activity over		Flight height	Hunting style
A1	12/08/2007 22:47	Kemmel, BE	small pond	Hunting	water	SP	< 0.5 m	Trawling (*)
A2	25/08/2007 00:11	Loppem, BE	castle pond	Hunting	water	SP	< 0.5 m	Trawling (*)
A3	12/08/2007 22:59	Kemmel, BE	small pond	Hunting	water	SP	< 0.5 m	Trawling (*)
A4	17/07/2010 01:36	Ieper, BE	rampart moat 50 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
A5	17/07/2010 01:07	Ieper, BE	rampart moat 50 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
A6	04/04/2008 22:30	Ieper, BE	rampart moat 50 m wide	Hunting	water	AP	< 0.5 m	Trawling (*)
A7	12/07/2010 22:46	Zillebeke, BE	in the forest	Hunting	land	SP	ca 3 m	Hawking
A8	12/07/2010 22:47	Zillebeke, BE	in the forest	Around roost	land	AP	ca 3 m	-
A9	08/09/2007 22:10	Loppem, BE	tunnel under motorway	Commuting	land	SP	ca 2 m	-
A10	08/09/2007 22:12	Loppem, BE	tunnel under motorway	Commuting	land	SP	ca 2 m	-
A11	27/06/2007 22:21	Zillebeke, BE	edge of large pond	Commuting	land	SP	ca 2 m	-
A12	12/05/2008 22:11	Zedelgem, BE	forest path	Commuting	land	SP	ca 3 m	-
A13	25/04/2008 05:53	Woumen, BE	castle park	Swarming	land	-	ca 3 m	-
A14	29/09/2007 00:09	Zichen, BE	marlow pit	Released	land	-	ca 2 m	-
B1	30/07/2009 23:50	Muizen, BE	canal 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (*)
B2	10/06/2008 23:27	Tjerkwerd, NL	canal 13 m wide	Hunting	water	SP	< 0.5 m	Trawling (*)
B3	30/07/2009 23:56	Muizen, BE	canal 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
B4	03/07/2010 23:59	Muizen, BE	canal 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
B5	24/07/2009 00:35	Muizen, BE	canal 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
B6	25/07/2009 23:45	Muizen, BE	canal 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
B7	30/07/2009 00:06	Muizen, BE	canal 30 m wide	Hunting	water	AP	< 0.5 m	Trawling (*)
B8	03/08/2009 22:41	Muizen, BE	over a field of bulrush	Hunting	water	SP	ca 3 m	Hawking
B9	13/07/2007 23:23	Tjerkwerd, NL	church square	Hunting	land	SP	ca 3 m	Hawking
B10	13/07/2007 22:50	Tjerkwerd, NL	village road	Commuting	land	SP	< 0.5 m	-
B11	10/06/2008 23:00	Tjerkwerd, NL	church square	Commuting	land	SP	ca 3 m	-
B12	10/06/2008 23:01	Tjerkwerd, NL	church square	Commuting	land	SP	ca 3 m	-
B13	10/06/2008 23:27	Tjerkwerd, NL	church square	Commuting	land	SP	ca 3 m	-
B14	10/06/2008 23:23	Tjerkwerd, NL	canal 13 m wide	Commuting	water	SP	< 0.5 m	-
B15	11/06/2008 04:21	Tjerkwerd, NL	church square	Swarming	land	-	-	-
C1	29/04/2010 22:55	Prov. Valéncia, ES	river ca 15 m wide	Hunting	water	SP	< 0.5 m	Trawling (*)
C2	29/04/2010 22:48	Prov. Valéncia, ES	river ca 15 m wide	Hunting	water	SP	< 0.5 m	Trawling (*)
C3	28/04/2010 23:04	Prov. Valéncia, ES	river ca 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
C4	28/04/2010 22:53:	Prov. Valéncia, ES	river ca 30 m wide	Hunting	water	SP	< 0.5 m	Trawling (**)
C5	27/04/2010 22:04	Prov. Valéncia, ES	small pool in a river	Hunting	water	SP	< 0.5 m	Trawling (*)
C6	29/04/2010 22:31	Prov. Valéncia, ES	river ca 15 m wide	Hunting	water	SP	< 0.5 m	Trawling (*)
C7	28/04/2010 23:13	Prov. Valéncia, ES	river ca 30 m wide	Hunting	water	SP	ca 2 m	Hawking

* Flight height during recording was <0.5 m over the water surface. During this night the bats were flying continuously low over the water surface and did not make any excursions higher in the air. The bats only attacked prey items floating on the water surface or flying in the lower air <0.5 m.

** Flight height during recording was <0.5 m over the water surface. During this hunting behaviour the low search flights were now and then interrupted by sudden rises whereby the bat chased a prey item after an excursion higher up in the air.

was used (ITT Night Mariner 150, ITT Industries, Roanoke, Virginia, USA). A circuit of 49 GaAs infrared leds with a wavelength of 880 nm (Vision Nachtzicht techniek, Born, the Netherlands) was mounted on the Night Mariner to improve the contrast of the images. When observed flying at close range, pond bats are visibly larger in body size than Daubenton's bats.

Sound recordings

Recordings were made between 2007 and 2010, with a Pettersson D1000X detector (Pettersson Elektronik AB, Uppsala, Sweden), in the direct ultrasonic recording mode, using a sampling rate of 500 kHz (aliasing-free up to 200 kHz; Pettersson Elektronik AB 2005-2007). Input gain was adjusted close to minimum, to avoid clipping when the bats are flying very close to the microphone. The detector has an ADC resolution of 16 bit and the microphone has a flat frequency response between 5 and 170 kHz. Ultrasonic recordings were stored directly on a Compact Flash card for later analysis.

Definitions of the parameters used for sound analysis

The analysis in this paper includes the basic parameters that describe echolocation calls: pulse duration, interpulse interval, starting frequency, end frequency, peak frequency (frequency corresponding to the maximum amplitude) and QCF frequency (see definition below). Pulse duration was defined as the time between the start and the end of the echolocation call, the interpulse interval (IPI) as the time between the start of the call (n) and the start of the next call (n+1). The starting and end frequencies were taken from the fundamental (or first harmonic), excluding higher harmonics. In this paper the QCF part of a signal was defined as the signal part with a minimum duration of 1 ms and a maximum modulation rate of 1 kHz/ms.

Sound analysis methods

The BatSound 4.03 programme (Pettersson Elektronik AB, Uppsala, Sweden) was used for sound analysis. Time related parameters (pulse duration and IPI) were measured using the combined oscillogram-spectrogram. Time measurements are more accurate when measured in the oscillogram, however errors can occur if the signals have a very weak start or end, or are followed by strong echoes. The combined oscillogram-spectrogram allows one to use the spectrogram window to check if a signal has a weak high frequency start and/or echoes are masking the signal end.

Frequency related parameters were measured in the spectrogram. Starting and end frequencies were measured using the highest visible value in the spectrogram (FFT size 1024, Hanning window). Peak frequency was computed automatically using the Pulse Characteristics Analysis function in BatSound. This algorithm automatically searches for the frequency with the maximum amplitude (in the spectrum, not the oscillogram). In a linear signal, typical of *Myotis* bats in highly cluttered conditions, there is not really a discernable 'peak frequency'. When the power spectrum is examined in detail, the amplitude appears quite constant over a wide range of frequencies. Although the algorithm will still find one 'peak frequency' where the energy is a bit higher than elsewhere, the amplitude will be little less at many other frequencies. The longer the signal becomes, the more likely there will be a distinct zone somewhere in the middle where the slope becomes less steep and where the energy is concentrated. In those signals, typical of *Myotis* bats flying in semi-open or open spaces, the peak frequency will most often be located somewhere in the zone of the smallest slope. The modulation rate was checked for signal parts with small

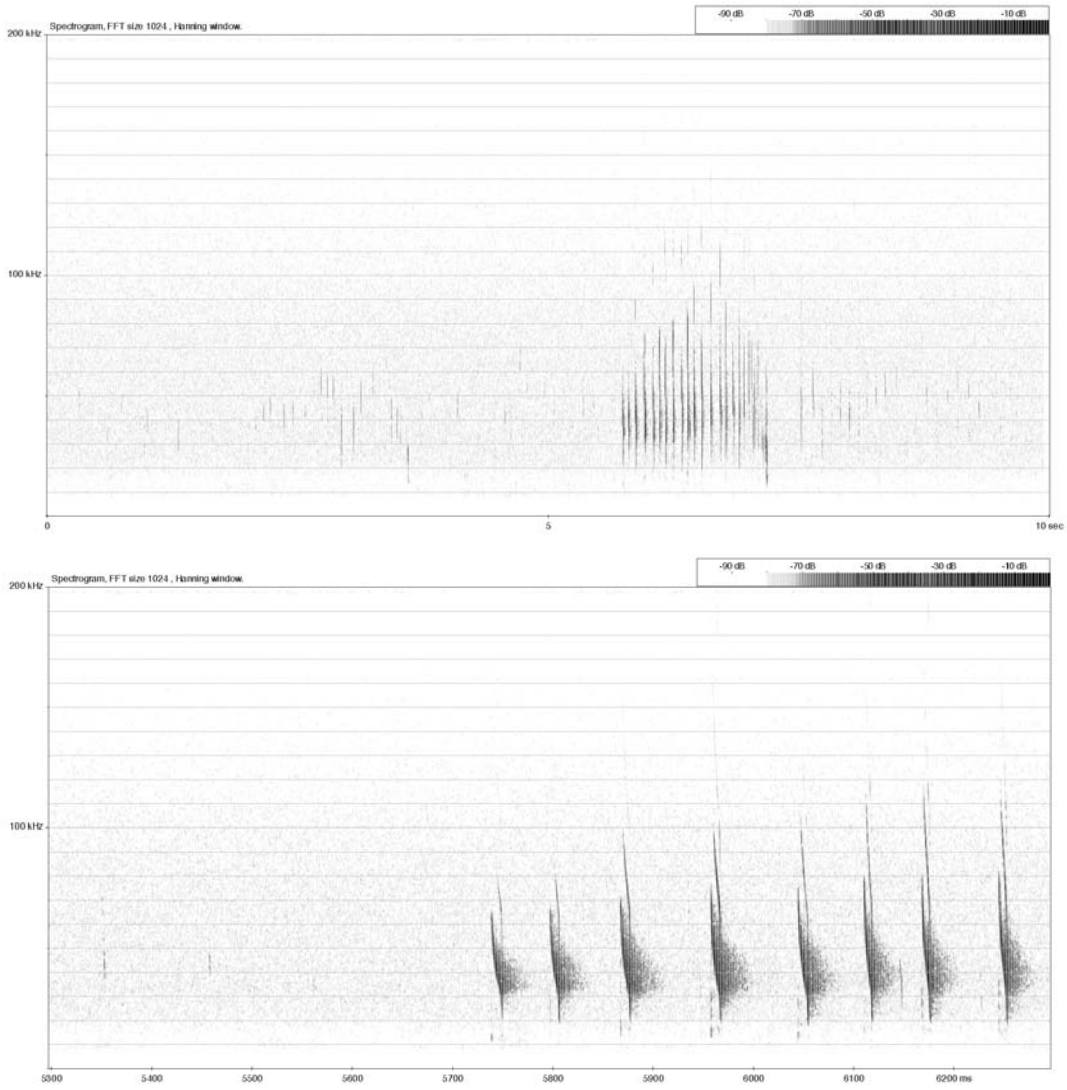

Figure 1. Daubenton's bat hunting low over water, while using an unusual discontinuous echolocation pattern. Flying parallel to and at a distance of approximately 3 m from the bank, the bat was first observed passing by closely while emitting only very weak signals. All of a sudden the bat started to emit a series of very loud echolocation calls (starting at 5730 ms in the spectrogram). Above: 10 s interval. Below: detail of the start of a series of loud calls after a period of weak calls.

slopes. If the frequency modulation rate was less than 1 kHz/ms, the QCF frequency was measured using a power spectrum of a time interval of 1 ms preceding the steep final FM part. In the pond bat the QCF part always precedes the final FM. The other trawling *Myotis* do not use QCF.

Selection criteria

Analysis of echolocation calls was limited to search and approach phase calls. The very short calls of final buzz phases were not included. When selecting the best recordings for analysis, preference was given to those

Table 2. Median (in brackets: minimum - maximum) values of pulse interval, starting, end and peak frequency of echolocation calls of Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined.

		Mdau	Mdas	Mcap
Pulse durations 1-4 ms	Pulse interval (ms)	46.7 (11.6 - 72.5)	67.1 (29.8 - 110.0)	13.5 (9.0 - 95.8)
	Starting frequency (kHz)	101 (86 - 118)	87 (79 - 94)	93 (70 - 117)
	End frequency (kHz)	26 (22 - 38)	25 (24 - 28)	32 (24 - 40)
	Peak frequency (kHz)	49 (42 - 63)	41 (39 - 46)	45 (42 - 59)
Pulse durations 4-8 ms	Pulse interval (ms)	67.0 (41.5 - 161.2)	71.5 (15.6 - 116.6)	64.8 (12.6 - 129.3)
	Starting frequency (kHz)	99 (66 - 114)	95 (62 - 110)	95 (72 - 123)
	End frequency (kHz)	26 (18 - 32)	26 (23 -31)	30 (24 -39)
	Peak frequency (kHz)	46 (38 - 62)	39 (35 - 49)	47 (40 - 57)
Pulse durations 8-14 ms	Pulse interval (ms)	81.5 (57.9 - 191.9)	111.4 (62.2 - 211.4)	-
	Starting frequency (kHz)	72 (61 - 87)	84 (52 - 100)	-
	End frequency (kHz)	20 (18 - 25)	28 (23 - 33)	-
	Peak frequency (kHz)	37 (33 - 40)	37 (35 - 41)	-
Pulse durations >14 ms	Pulse interval (ms)	-	131.3 (111.2 - 227.3)	-
	Starting frequency (kHz)	-	46 (40 - 56)	-
	End frequency (kHz)	-	28 (24 - 30)	-
	Peak frequency (kHz)	-	35 (33 - 38)	-

recordings with the best signal-to-noise ratios, when the bat was flying close to the microphone (<2 m if possible). This made it possible to pick up the high frequencies at the start of the signal. The direction of the bats in relation to the microphone varied, some recordings include bats heading towards the microphone and emitting the sound beam directly towards it (see below). Small bat-to-microphone distances were not always possible due to technical limitations (hand held detector), especially when bats were flying over open water far from the banks or higher in the air. Some signal parameters, especially starting frequency and duration, might be biased in recordings with lower signal-to-noise ratios.

Statistics

Because the starting, end and peak frequencies of pulses within a species may strongly vary with pulse duration, it is advisable to compare echolocation calls of similar durations. For this purpose the respective data sets were split into three sub-sets, based on pulse durations: 1-4 ms (short duration), 4-8 ms (medium duration) and 8-14 ms (long duration). Only the pond bat used very long durations (>14 ms). In several data sets these subsets were normally distributed. In others they were not (Shapiro-Wilk W-tests, $P<0.05$), even after removing the outliers. Non-parametric Mann-Whitney tests were used to analyse the data (Analyse-it Software Ltd, Leeds, UK).

Results

Description of the recording conditions

Details of the selected recordings of Daubenton's bats (A), pond bats (B) and long-fingered bats (C) are shown in table 1. The spectrum of recording conditions is more complete for Daubenton's bat and the pond bat than for the long-fingered bat.

Daubenton's bat

Recordings of Daubenton's bat include hunting flight low over water (A1 to A6), hunting flight over land (A7), commuting flight

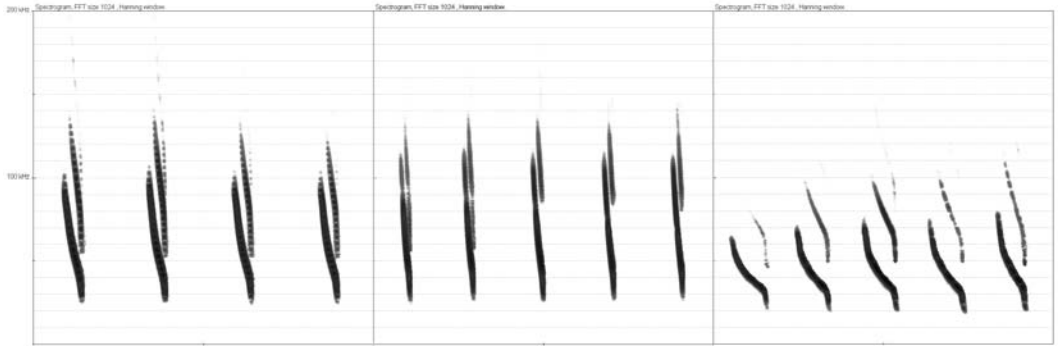

Figure 2. Echolocation calls of Daubenton's bats. Left: bat hunting over a small pond (recording A1). Middle: bat hunting in the forest near the roost (recording A7). Right: bat hunting over a large water surface close to the bank (recording A4).

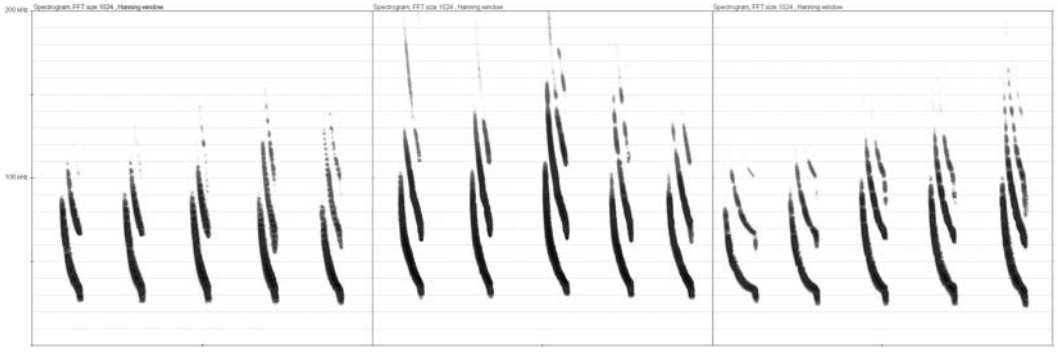

Figure 3. Echolocation calls of pond bats. Left: bat hunting over a large canal close and parallel to the reed margin (recording B1). Middle: bat swarming around a church roof (recording B15). Right: bat commuting low over a small canal (recording B14).

Figure 4. Echolocation calls of pond bats. Left: bat hunting over a large canal, approaching the canal bank (recording B7). Middle: bat hunting over a large canal far from the banks, change from search to approach phase (recording B3). Right: bat hunting over a large canal far from the banks, search phase (recording B6).

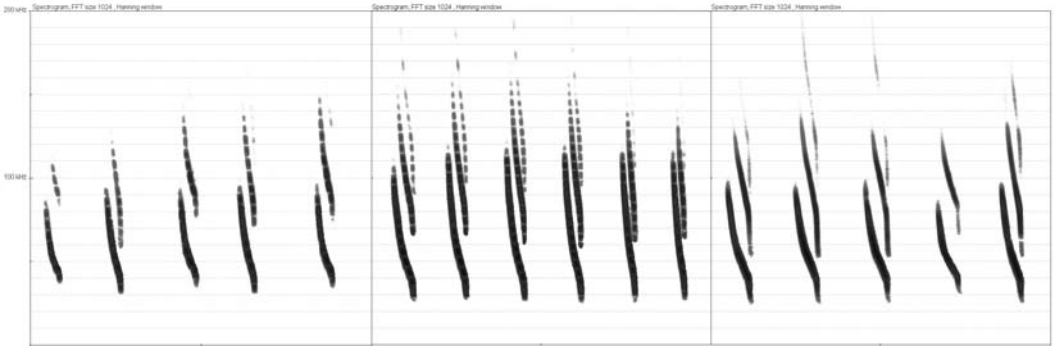

Figure 5. Echolocation calls of long-fingered bats. Left: bat hunting over a small meandering river (recording C1). Middle: bat hunting over a zone of tranquil water in a small river (recording C5). Right: bat hunting over a large river upstream of a waterfall (recording C7).

over land (A9 to A12), swarming flight (A13) and flight after release from captivity (A14). Recording A1 was made shortly after dusk when a few Daubenton's bats arrived at a small pond. A lot of feeding buzzes occurred, indicative of active hunting and an abundance of prey. These pulse durations were fairly short. Recording A3 was made a bit later over the same pond when all the bats except one had disappeared and pulse durations were longer. Recordings A4-A5 represent a rare hunting behaviour for Daubenton's bat. This behaviour took place during a few midsummer nights when the bats were patrolling at a distance of two to three metres from the banks of a large moat. Visual observations, using an image intensifier and infrared illumination, of bats passing at very close range revealed that these were Daubenton's bats (small body size) rather than pond bats. Their flight was linear and a bit faster than usual. A single bat alternated groups of loud pulses with periods of weak pulses, the longest durations were emitted immediately after each silence period (figure 1). Sometimes the bats would suddenly rise and chase an insect in the air. This behaviour resembles a particular hunting mode associated more with the pond bat, although in the latter, the pulse durations and flight speed are considerably larger (Van De Sijpe & Holsbeek 2007). Recording A6 includes an approach phase of a Daubenton's bat, passing very close to the microphone (<1 m), held on the tip of a fisherman's quay protruding over the moat. In A7 a Daubenton's bat was hunting in the forest shortly after emerging from a nearby roost tree. The bat returned to the roost tree (recording A8), maybe to feed its young. A9 and A10 were made in a tunnel under a motorway, used by Daubenton's bats at dusk, as they were travelling from roost to their hunting site. In A13 a group of Daubenton's bats were swarming in front of their tree roost in a park, just before dawn. The bat recorded in A14 was identified in the hand after capture at the entrance of a marlow pit in the late summer swarming season. It was then placed onto a wall in a dead end gallery inside the marlow pit. After a short period of resting it took off spontaneously and flew through the gallery towards the exit where the recording was made. At the exit the bat was flying steadily and the echolocation pattern resembled that of a natural flight condition, though the pulse durations were very short (short distances between the bat and the walls and ceiling).

Pond bat

The selection of pond bat recordings includes hunting flight low over water (B1 to B7), hunting flight over land (B9), commuting flight over water (B14), commuting flight over land (B10 to B13) and swarming flight (B15). In recording B1 a pond bat was flying parallel and close to a reed

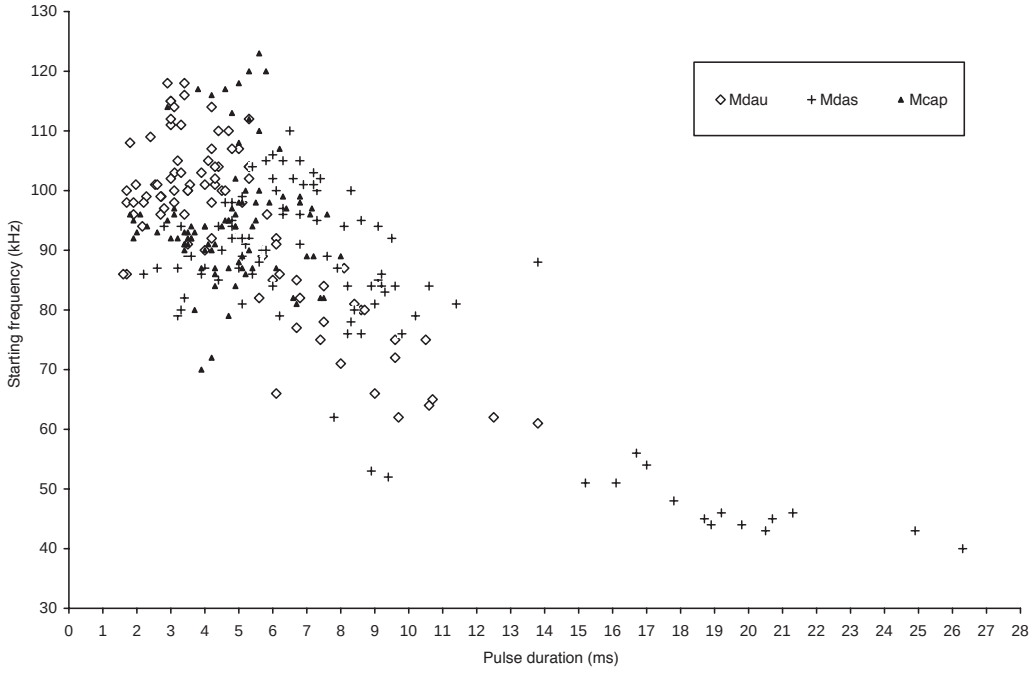

Figure 6. Scatter plot of starting frequencies vs. pulse durations in Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined.

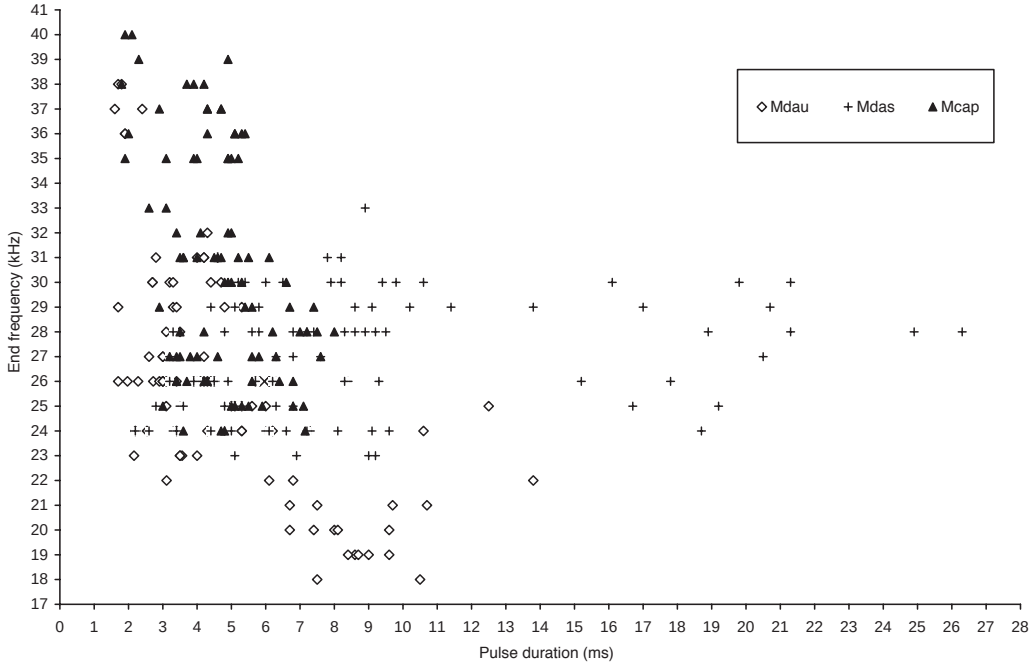

Figure 7. Scatter plot of end frequencies vs. pulse durations in Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined.

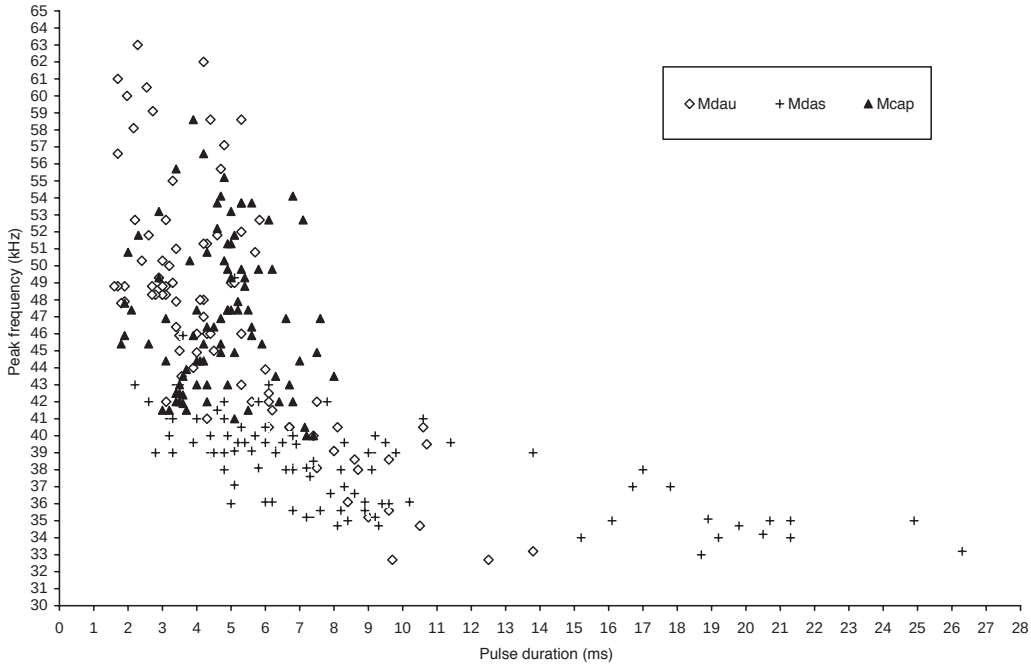

Figure 8. Scatter plot of peak frequencies vs. pulse durations in Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined.

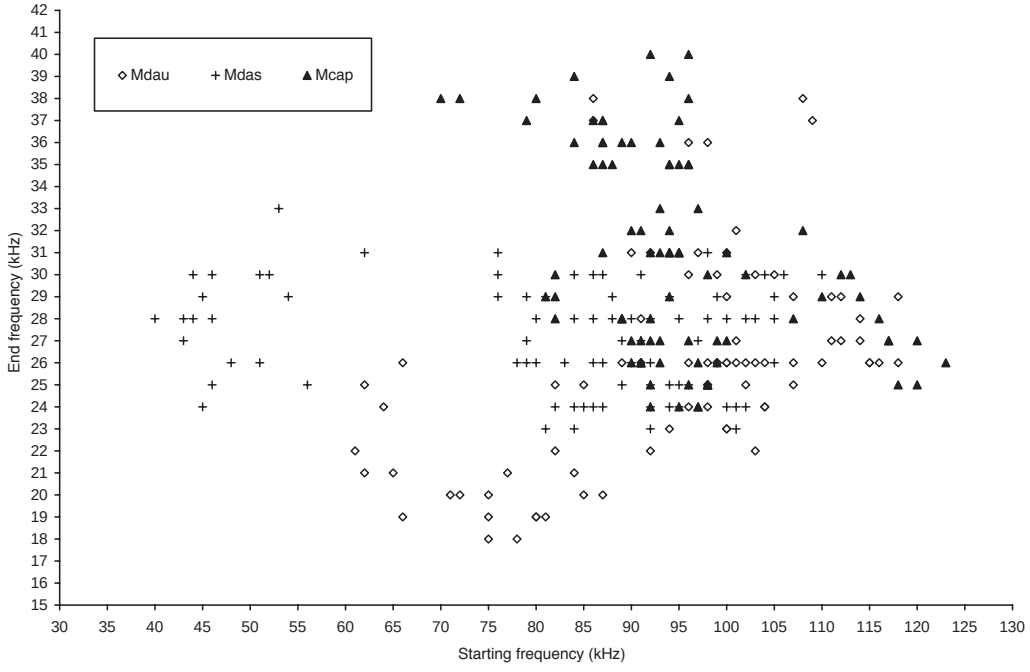

Figure 9. Scatter plot of end frequencies vs. starting frequencies in Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined.

margin (distance to the reeds ca 1 m) where it used FM signals of short duration, before flying more in the middle of the canal where the calls changed to the species-specific long duration FM-QCF-FM types. B2 was made over a rather small canal and includes pulses of medium duration with QCF. B3 to B6 were made during a couple of midsummer nights where pond bats were hunting over a large canal, using fast, linear search flights at a low height along the midline. They often made excursions higher up in the air (ca. 3 m) to chase large insects. In B7 a pond bat was first flying fast along the midline, then suddenly changed flight direction (almost 90°) and flew towards the bank, where it caught an insect on the water surface (ca 2 m from the bank). Recording B8 included short search phase calls of a pond bat flying just above the tops of bulrush (*Typha latifolia*), after an attack on a large insect higher in the air (2 to 3 m). In B9 a pond bat was hunting for a few minutes over a church square after emergence at dusk. The bat continued flying in large circles at a height of approximately 3 m. Several feeding buzzes revealed that this pond bat was hunting by means of aerial hawking. B10 is a recording made from a pond bat commuting very low over a village road (<0.5 m). The durations of B11 to B13 are longer. Here the bats were flying higher over a church square. In B14 a pond bat was flying low over a canal, and passed close to the microphone on the bank (ca. 2 m). These signals have high signal to noise ratios, a QCF part and the durations are of medium size.

Long-fingered bat

Recordings of long-fingered bats were limited to hunting behaviour low over water (C1 to C6) and higher in the air (C7). Recordings C1, C2 and C6 were made at the banks of a small meandering river with alternating zones of smooth and turbulent water surfaces. C5 was made of a bat trawling over a small sized river pool, surrounded by zones with rippling water, steep rocks and reed formations. The long-fingered bat continued to hunt over the pool and passed the bank and microphone at a distance of one metre, just before capturing a prey item. C3, C4 and C7 were made at a larger river (30 m) upstream of a waterfall where the surface was smooth. In the beginning of the night a large group of bats were hunting together. Later on, when the number of hunting bats decreased, one of the remaining individuals changed behaviour and started to make long linear flights low over the surface at a higher speed. Every now and then the bat soared upwards to ca 2 m to attack an insect. C7 was recorded when this bat was flying higher in the air. The recording includes search and approach phase calls preceding a feeding buzz.

Sound analysis data and spectrogram representations

A summary of sound analysis data can be found in table 2. Echolocation calls are presented in spectrograms (frequency versus time plot) in figure 2 (Daubenton's bat), figures 3 and 4 (pond bat) and figure 5 (long-fingered bats). The intervals are partially cut away to show more signals in the same window. Echoes and background noise were removed from the spectrograms for aesthetic reasons.

The ranges of pulse durations

Pulse durations varied between 1.6 and 13.8 ms in Daubenton's bat, between 2.2 and 26.3 ms in the pond bat and between 1.8 and 8.0 ms in the long-fingered bat. Daubenton's bats flying over water usually had durations of below 8 ms, except in recordings A4 (durations up to 10.7 ms) and A5 (durations up to 13.8 ms). The longest duration recorded over land was 6.2 ms (commuting over a broad forest path). Pond bats regularly used signals of a long duration both over water (up to 26.3 ms) and over land (up to 10.2 ms). As the surroundings become more and more confined, the durations decreased. In confined spaces

Table 3. Statistical comparison of datasets of echolocation call parameters between Daubenton's bat (Mdau), pond bat (Mdas) and long-fingered bat (Mcap), all behaviours combined. Significant results ($P<0.01$) in bold.

		Mdau vs. Mdas	Mdau vs. Mcap	Mdas vs. Mcap
Pulse durations 1-4 ms	Pulse interval (ms)	$P=0.0117$	**$P<0.0001$**	**$P=0.0004$**
	Highest frequency (kHz)	**$P<0.0001$**	**$P<0.0001$**	**$P=0.0025$**
	Lowest frequency (kHz)	$P=0.0360$	**$P=0.0017$ ***	**$P=0.0001$**
	Peak frequency (kHz)	**$P<0.0001$**	**$P=0.0002$**	**$P=0.0017$**
Pulse durations 4-8 ms	Pulse interval (ms)	$P=0.7908$	$P=0.1309$	$P=0.4206$
	Highest frequency (kHz)	$P=0.4239$	$P=0.5021$	$P=0.8422$
	Lowest frequency (kHz)	$P=0.1721$	**$P<0.0001$**	**$P<0.0001$**
	Peak frequency (kHz)	**$P=0.0001$**	$P=0.3822$	**$P<0.0001$**
Pulse durations 8-14 ms	Pulse interval (ms)	$P=0.0426$	-	-
	Highest frequency (kHz)	**$P=0.0013$**	-	-
	Lowest frequency (kHz)	**$P<0.0001$**	-	-
	Peak frequency (kHz)	$P=0.5145$	-	-

* $P<0.0001$ if data A8 removed

they used very brief FM signals (2 to 3 ms). Long-fingered bats did not use durations above 8 ms, however the number of surveys was limited to only three nights in the same period of the season.

Starting, end and peak frequencies

General trends

Scatter plots of starting, end and peak frequency are plotted against pulse duration in figures 6, 7 and 8 respectively.

Starting frequencies were highest in signals of about 2 to 5 ms, they gradually decrease with increasing pulse duration (>5 ms) (figure 6). In the range of 2 to 5 ms durations, there is substantial overlap in the starting frequencies between the three species (figure 6). The lowest starting frequencies were found in the longest signals of the pond bat (figures 6 and 9). The end frequencies of pond bats do not change much between short to long duration calls (figure 7). The end frequency of the calls of Daubenton's bat decreases with increasing duration (figure 7). The lowest end frequencies of the three species were found in the longer signals of Daubenton's bat (figures 7 and 9). Long-fingered bats used high end frequencies (30 to 40 kHz) and medium end frequencies (25 to 30 kHz) (figure 7). In the long-fingered bat, end frequencies were lower in longer signals (25 to 30 kHz, durations 7 to 8 ms), nevertheless they are still higher than in signals of a similar duration of Daubenton's bat (17 to 22 kHz) (figures 7 and 9). Long-fingered bats sometimes used a regular alternation of two types of FM signals with a different end frequency (35 versus 30 kHz, e.g. recording C1, figure 5 left), a feature that was not found among Daubenton's bat or the pond bat.

Peak frequencies generally decreased with increasing pulse duration (figure 8). The pond bat generally used the lowest peak frequencies, those of Daubenton's bat and long-fingered bat largely overlapped (figure 8).

Specific patterns in the short duration pulse range (1 to 4 ms)

In this range of durations, the starting frequencies of Daubenton's bats were higher than those of the other two species (tables 2 and 3) and long-fingered bats used higher starting frequencies than pond bats (figure 6). These differences were statistically significant. End frequencies did not differ significantly between Daubenton's bats and pond bats ($P>0.01$) but were significantly higher in long-

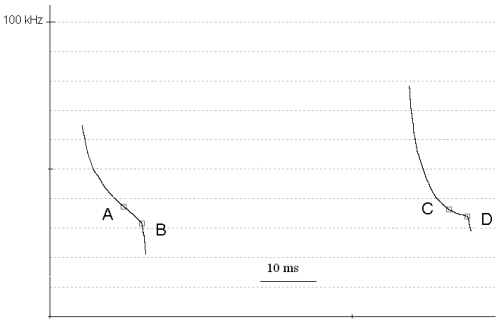

Figure 10. Difference in modulation rates in the last two milliseconds before the final FM part. Left: a 10.5 ms long signal of a Daubenton's bat, modulation rate between A and B: 2.5 kHz/ms. Right: a 10.3 ms long signal of a pond bat, modulation rate between C and D: 0.7 kHz/ms.

fingered bats (tables 2 and 3, figure 7). When recording A8 (Daubenton's bat approaching tree roost and using exceptionally high end frequencies) was excluded from the data set, the difference in end frequencies between Daubenton's bat and long-fingered bat became even more pronounced (P<0.0001). Peak frequencies were highest in Daubenton's bats and lowest in pond bats (figure 8).

Specific patterns in the medium duration pulse range (4 to 8 ms)

In the range of medium durations there were not any differences in the starting frequencies of the three trawling species (tables 2 and 3, figure 6). For end frequencies there was a significant difference between the long-fingered bat and the other two species (tables 2 and 3), with the long-fingered bats' being higher (see figure 7). For peak frequencies, the pond bats' had a significantly lower frequency than the other two species (table 3 and figure 8).

Specific patterns in the long duration pulse range (8 to 14 ms)

Starting frequency and end frequency in the long duration pulse range differed significantly between pond bat and Daubenton's bat (tables 2 and 3, figures 6 and 7), although their peak frequencies were not significantly different (table 3, figure 8). Above 8 ms almost all pond bat signals have a QCF part before the final downward FM sweep, Daubenton's bats did not use QCF.

The QCF part

Pond bats start to introduce a QCF part in the middle of the signal as soon as its duration exceeds ca 8 ms. The QCF frequency varies between 31 and 37 kHz (most often 33-35 kHz). The longest pond bat signal without QCF was 9.5 ms, the shortest signal with QCF 7.6 ms. Daubenton's bat do not use QCF, not even in their longest signals (13.8 ms). Instead of introducing a QCF part in the zone just before the final FM, Daubenton's bats gradually decrease the modulation rate of a much wider range of frequencies in the middle of the signal (60 to 30 kHz). Figure 10 shows the difference in modulation rate in the zone of 2 ms just before the final FM between signals of similar duration (around 10 ms) of a Daubenton's bat and a pond bat. In heterodyne, the pulse series of Daubenton's bat, including 10 to 13 ms durations, can be perceived as slightly 'wet' sounds, however when scanning along the frequency band there is no detectable null frequency. When pond bats use signals of 10 ms there is a well marked null frequency (often between 33 and 35 kHz) where the pitch of the wet sound becomes very low.

Discussion

Daubenton's bat

Daubenton's bats only used FM calls, which is in accordance with the literature (Kalko & Schnitzler 1988, Rydell et al. 1999, Siemers et al. 2001, Skiba 2003, Papadatou et al. 2008, Arthur & Lemaire 2009). Most sources mention maximum pulse durations of 7 or 8 ms in Daubenton's bat (Skiba 2003, Arthur & Lemaire 2009). During this study some surprisingly long duration signals in Daubenton's bat

were recorded, including durations between 8 and 13 ms. The peak frequency of these pulses (33-40 kHz) is similar to the pond bat calls of a similar duration, however the pulse shapes are different. The long calls of Daubenton's bat do not have QCF, whereas a QCF-part was always present in signals >10 ms in the pond bat. The flight and echolocation patterns associated with Daubenton's bats emitting long pulses were similar to patterns observed in the pond bat (discontinuous sounds, bats passing at close range without loud sonar emissions, sudden bursts of loud calls, Van De Sijpe & Holsbeek 2007). Some hawking bats are known to skip several consecutive calls in order to wait for the arrival of echoes from distant objects (Holderied & von Helversen 2003). However the periods without high intensity calls that precede periods of loud calls are longer than just a few skipped calls. Therefore this may be a strategy to avoid sonar jamming with nearby conspecifics, as described by Chiu et al. (2008) or maybe a stealth strategy.

When small aquatic insects are abundant on or over the water surface, Daubenton's bats usually emit short FM calls with durations of 4-5 ms. The short durations indicate that the bats are focussing on 'short' distances (Schnitzler & Kalko 2001, Schnitzler et al. 2003). In good hunting conditions there is probably no need for a Daubenton's bat to focus on more distant points. In less favourable conditions, e.g. when the density of small insects is low (i.e. on cool spring nights) one more often hears longer signals, with durations in the range of 6-8 ms. This is also observed in aerial hawking bats, e.g. in pipistrelles (Barataud 1996). By using these longer durations Daubenton's bats are probably trying to increase the detection distance to improve the chances of detecting the few small sized insects available. The small size of the prey probably sets a maximum to the durations that Daubenton's bats can use, because when duration increases the forward masking zone increases in direct proportion (Schnitzler et al. 2003). The smaller the size of the prey, the smaller its 'target strength' and the smaller the detection distance (Waters et al. 1995). The longest signals (8-13 ms) were used during rare behaviour on warm summer nights, when bats also made excursions higher in the air, and suggest that the bats were focussed on larger sized prey items occasionally crossing the air above the water body. Larger prey items have stronger target strengths and allow for larger forward masking zones and hence larger pulse durations (Waters et al. 1995). On warm summer nights many larger insects are on the wing (e.g. Lepidoptera) flying over bodies of water at heights below 3 to 5 m, where they can be detected by trawling bats. Because of the low density of larger insects in the air over open water, long range echolocation will certainly be more appropriate than short range echolocation for efficiently hunting this type of prey.

Although the vast majority of starting frequencies in this study were below or around 100 kHz, in a number of cases they appeared to be higher, up to 118 kHz. Some individuals within a given species have been observed to use exceptionally high frequencies (Markmann & Ronkel 2010). This may be the explanation for the higher frequencies recorded in this study (using a D1000X detector). Most recordings made from Daubenton's bats at very close distance, either with a D1000X detector (own data) or with a high quality Bruel & Kjaer microphone (anonymous referee, personal communication) reveal starting frequencies up to 100 kHz.

The end frequencies recorded match with data in the literature. Kalko and Schnitzler (1998) suggest that each individual may have a preferred end frequency when trawling over the water surface (in their study some individuals used end frequencies of 30 kHz, others of 25 kHz). Similar intra-specific differences between end frequencies were also found here (e.g. recordings A1 versus A2).

In the usual range of durations (1-8 ms) the peak frequencies of Daubenton's bats are between 38 and 50 kHz, generally higher than pond bats. However in the rare long pulses (>8

ms) the peak frequency decreases to between 35 and 40 kHz, creating an overlap of peak frequencies with pond bats. The absence of QCF in Daubenton's bat, even in calls of medium duration, can still be used to separate Daubenton's bats and pond bats in these conditions.

Pond bat

Pond bat echolocation has been studied in detail in the Netherlands, not surprisingly since a large part of the European population of this rare species is concentrated in the country's low-altitude provinces. The signal types (FM and FM-QCF-FM), pulse durations, end frequencies, peak frequencies and QCF frequencies described here are in accordance with the available literature data (Kapteyn 1993, Britton et al. 1997, Limpens et al. 1997, Verboom et al. 1999, Siemers & Schnitzler 2001, Skiba 2003).

Whereas most literature sources mention maximum starting frequencies of 80 to 90 kHz, some starting frequencies in this study exceeded 100 kHz (with a maximum of 110 kHz). Starting frequencies above 100 kHz were found in short duration echolocation signals recorded from pond bats flying close to the microphone, as well as some signals of longer duration (8 ms). However, frequencies above 100 kHz were quite rare and a lot of short signals recorded at close range had starting frequencies around or below 100 kHz. It is not easy to obtain field recordings from this species very close to the microphone, because of its preference for hunting over large open expanses of water, where it is technically difficult to get close to the bat without influencing the flight and echolocation behaviour.

Long-fingered bat

Even though the field surveys of long-fingered bats were limited in this study, they did produce a wide range of pulse durations (1.8 to 8.0 ms). This range corresponds well with data in published literature (Skiba 2003, Arthur & Lemaire 2009). Almenar et al. (2008) found that long-fingered bats not only preyed upon aquatic insect taxa, such as Nematocera and Trichoptera, but also consume terrestrial taxa including Lepidoptera. The authors suggest that long-fingered bats may be able to take Lepidopterans higher in the air. Sudden excursions in the air over water bodies were observed in the long-fingered bat in this study, and are also reported in Daubenton's bat (e.g. in this paper) and in the pond bat (Ahlén 1990, Kapteyn 1995, Van De Sijpe & Holsbeek 2007). Long-fingered bats might possibly use echolocation calls longer than 8 ms when they are focussing on large prey in the air above water surfaces. It can take a lot of time and survey effort, before one comes across rare hunting behaviours that involve echolocation patterns that substantially differ from the 'normal' behaviour (e.g. the observation of Daubenton's bats in this study).

On most occasions the starting frequencies were around or below 100 kHz, although in some recordings substantially higher starting frequencies were detected. Exceptionally high signal-to-noise ratios were recorded from a long-fingered bat that passed very close to the microphone on the bank of a river. The starting frequencies of his recording exceeded 120 kHz. Skiba (2003) previously listed maximum starting frequencies of 90 kHz. Papadatou et al. (2008) and Boonman et al. (2009) mention 100 kHz as a maximum. The few high starting frequencies detected in long-fingered bats suggest these are quite rare situations and may originate from a few individuals in a population who use exceptionally high frequencies. The majority of starting frequencies (even short signals with high signal to noise ratios from short distances) are not higher than 100 kHz, which is in accordance with the literature sources.

The end frequencies correspond well with data listed in Skiba (2003), Papadatou et al. (2008) and Arthur and Lemaire (2009). In Greece, Papadatou et al. (2008) found that the

end frequencies of long-fingered bats (ca 35 kHz) were significantly higher than Daubenton's bats (ca 30 kHz). In France, Arthur and Lemaire (2009) also found that long-fingered bats use higher end frequencies than Daubenton's bat.

Echolocation and flight behaviour

The three European trawling bats use a wide variety of echolocation signals, reflecting their variable flight and hunting behaviours both low over water (their specialised and preferred foraging niche) and over land (where they can exploit habitats in an opportunistic way). All the species can use FM calls of short duration and large bandwidth. This signal type provides the bat with accurate information about distances and angles to objects within their flight path at short ranges. However, the trawling bats appear not to use the very high starting frequencies and bandwidths that are observed in a number of other *Myotis* species, including Natterer's bats (*Myotis nattereri*) and Geoffroy's bats (*Myotis emarginatus*) (Siemers & Schnitzler 2004). The latter are specialised in hunting for prey in confined terrestrial habitats. Increased bandwidths and modulation rates increase the ability to spatially distinguish between two nearby objects (Schnitzler & Kalko 2001, Schnitzler et al. 2003). When occasionally hunting over land, Daubenton's bats and pond bats prefer edge habitats rather than very confined spaces.

The small size of aquatic insects in combination with the large numbers in which they occur explains the short broadband FM calls of high intensity that are typical for trawling insectivorous bats (Rydell et al. 1999). Longer calls would make these prey virtually inaudible, since the forward masking zone created by the long signals is likely to overlap with the small detection range provided by the small target strength of a tiny insect. Long calls are sometimes used in an alternative hunting mode, where the bats focus on larger insects present on the water surface or in the air above the water body. The piscivorous *Myotis* species also use short broadband FM when hunting for fish over water surfaces. They may rely on other sensory systems to detect prey or use random dipping techniques at sites with a high density of fish (Aihartza et al. 2008).

Conclusions

This study of echolocation calls of trawling *Myotis* species in natural flight conditions using a 16 bit detector revealed that some individuals can use higher starting frequencies than currently described in most literature sources. However the majority of starting frequencies did not exceed 100 kHz. High starting frequencies in *Myotis* signals can more easily be recorded using a D1000X detector than other detectors, because of the flat frequency response up to very high frequencies (170 kHz at least), the high sensitivity of the ultrasonic microphone and the large dynamic range inherent to the 16 bit resolution. However even with this detector a lot of short FM calls recorded at very close range did not start at frequencies higher than 100 kHz. The highest frequencies were found only in those sequences captured from the bats flying very close to the microphone and/or pointing the sound beam towards it. Although there is considerable overlap in some of the basic signal parameters, it does seem to be possible to identify the three trawling *Myotis* species in good recording conditions. Pond bats generally use lower peak frequencies and insert a QCF part in signals of medium and long duration, which makes confusion impossible. Daubenton's bats use higher peak frequencies than pond bats and lower end frequencies than long-fingered bats. Pond bats and Daubenton's bats flying over land in confined spaces can emit rather similar short broadband FM calls. In such conditions it can be tricky to identify these species. In short FM signals, the peak frequency

of the pond bat will increase to 40 kHz or even higher. The repertoire of echolocation calls of long-fingered bats presented in this study may be incomplete, although some interesting patterns were found, including sequences in which the bat regularly alternates between two types of FM signals with different end frequency. Finally some sequences of Daubenton's bat revealed medium durations, around 10 ms or even a bit longer.

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Samenvatting

Echolocatiegeluiden van watervleermuizen, meervleermuizen en Capaccini's vleermuizen in natuurlijke omstandigheden

Een studie van echolocatiegeluiden van de drie Europese harkende *Myotis*-soorten met de hulp van een 16 bit bat detector leverde iets hogere startfrequenties op dan doorgaans vermeld in de literatuur. De hoogste frequenties zijn wellicht afkomstig van een beperkt aantal individuen die exceptioneel hoge frequenties gebruikten. De meerderheid van de dieren hadden startfrequenties die beperkt waren tot 100 kHz of lager, zoals ook in de literatuur beschreven. De hoogste frequenties werden enkel gevonden in pulsreeksen van vleermuizen die erg dicht bij de microfoon vlogen en/of die hun sonarbundel naar de microfoon richtten. Alhoewel er veel overlap bestaat in start-, eind- en piekfrequenties lijkt identificatie van de drie

harkende *Myotis*-soorten haalbaar in een aantal omstandigheden. Meervleermuizen (*Myotis dasycneme*) gebruikten in het algemeen lagere piekfrequenties en hebben een QCF-gedeelte in signalen van middellange en lange pulsduur. Dit laatste sluit verwarring uit met de andere twee harkende soorten. Watervleermuizen (*M. daubentonii*) gebruikten doorgaans hogere piekfrequenties dan meervleermuizen en lagere eindfrequenties dan Capaccini's vleermuizen (*M. capaccinii*). Startfrequenties zijn erg variabel, wellicht deels omwille van verschillende afstanden van de vleermuis tot de microfoon tijdens de diverse opnamen (atmosferische uitdoving van hoge frequenties). De drie soorten kunnen vrij hoge startfrequenties gebruiken met maxima tot 110 à 120 kHz wanneer ze dicht bij de microfoon vliegen. Meervleermuizen en watervleermuizen die in gesloten habitat over land vliegen gebruiken korte breedbandige FM-signalen. Onderscheid tussen deze twee soorten wordt dan moeilijk. Bij korte signalen van meervleermuizen kunnen de piekfrequenties rond 40 kHz liggen. Het scala echolocatiegeluiden van de Capaccini's vleermuis is allicht nog onvolledig wegens het beperkt aantal veldexcursies waarbij deze soort bestudeerd werd. Desalniettemin kon interessant materiaal verzameld worden, waaronder pulsreeksen met alternerende eindfrequenties, een echolocatiegedrag dat niet bij water- en meervleermuizen werd waargenomen. Tenslotte werden ook pulsreeksen met middellange echolocatiesignalen opgenomen bij watervleermuizen, waarbij de pulsduur soms meer dan 10 ms bedraagt, maar dergelijke lange pulsen zijn wel heel uitzonderlijk.

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Recent trends and spatial patterns in nearshore sightings of harbour porpoises (*Phocoena phocoena*) in the Netherlands (Southern Bight, North Sea), 1990-2010

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Abstract: The harbour porpoise (*Phocoena phocoena*) returned in Dutch waters in the late 20th century after a near-absence of three decades. Gradually increasing numbers of sightings in the early 1990s were followed by a proportional rate of increase of 41% per annum over a period of 15 years until 2003. More data have been collected since and this paper reports on the most recent trends, changes in seasonality and spatial patterns in nearshore sightings between 1990 and 2010. The results show that the rapid increase came to a halt, but current sightings frequencies are on a higher level than before 2005. The highest numbers are now recorded in the northern half of Noord-Holland, whereas sightings rates in Zuid-Holland have declined. Sightings were made almost year-round, but with very low frequencies in May and June. During July-November a gradual increase was found, followed by some stabilisation in numbers during December-January and a marked further increase in February-March. The frequency in sightings crashed every year in early April. Additional (ecological) research is needed to enhance our understanding of the observed patterns and to link the nearshore sightings data with offshore population assessments during aerial surveys.

Keywords: Cetacea, *Phocoena phocoena,* sightings, seasonality, trends, Netherlands.

Introduction

The harbour porpoise (*Phocoena phocoena*) returned as an abundant, indigenous species in Dutch waters in the late 20th century, after a virtual absence of three decades (1960-1990; Camphuysen 2004, Camphuysen & Peet 2006). The causes of this decline in the 1950s and 1960s in the Southern Bight (North Sea south of 54°N) are not well understood and also the return in recent years remains largely unexplained (Smeenk 1987, Addink & Smeenk 1999, Camphuysen & Peet 2006). Results of two synoptic surveys of harbour porpoises in the North Sea (Hammond et al. 2002, SCANS II 2008) suggest that a distributional shift from more northerly areas to the south has been underlying the recent increase in Dutch waters. A decline in prey resources in the north, whether or not influenced by climate change, could have been responsible for this shift, but the factual evidence is slender (Camphuysen 2004, MacLeod et al. 2007, Thompson et al. 2007).

Camphuysen (2004) has documented the return of the harbour porpoise in Dutch nearshore waters, based on an analysis of sightings obtained from systematic, effort-corrected seawatches from headlands and vantage points along the coast (1972-2003). A small, but gradually increasing number of sightings

Table 1. Hours of observation at each of the observatories along the Dutch coast (*n*= 73,332 hours) and the proportion of time spent observing during periods of peak abundance of harbour porpoises in Dutch nearshore waters (February-March; mean ± SD = 10. ± 4.8 percent of time).

Observatory	Vlieland	Texel	Huisduinen	Camperduin	Egmond	Bloemendaal	Noordwijk	Katwijk	Scheveningen	Maasvlakte	Westkapelle
Latitude	53.28°N	53.06°N	52.95°N	52.73°N	52.62°N	52.4°N	52.25°N	52.18°N	52.1°N	51.99°N	51.53°N
Longitude	04.98°E	04.72°E	04.72°E	04.64°E	04.62°E	04.54°E	04.42°E	04.36°E	04.25°E	04.01°E	03.45°E
Region	W-Wadden Sea area		Noord- Holland				Zuid-Holland			Delta area	
1990	15	23	40	816	428	361	126	2	1274	0	0
1991	2	18	24	792	534	327	152	7	1334	10	0
1992	10	47	29	1091	356	294	137	0	721	143	18
1993	30	37	32	1220	419	341	60	109	989	93	15
1994	48	53	42	1287	247	224	66	136	1288	102	164
1995	144	29	49	1256	119	232	89	21	1595	20	120
1996	80	34	386	1090	31	143	146	27	2449	52	212
1997	8	13	584	925	54	91	75	25	1686	56	102
1998	19	11	718	320	25	111	92	10	1503	57	42
1999	5	0	707	434	19	188	64	102	1005	76	11
2000	8	9	770	530	6	270	58	15	828	90	30
2001	0	15	894	464	27	288	84	12	1302	68	156
2002	11	25	918	543	37	267	161	25	1070	60	281
2003	21	31	986	550	20	344	221	102	940	36	459
2004	0	0	1046	516	14	241	372	134	863	76	633
2005	9	15	1019	489	180	231	496	189	1034	80	502
2006	3	0	1068	560	234	74	454	203	887	94	273
2007	1	18	1070	538	231	201	461	245	961	109	377
2008	39	37	907	565	263	132	428	183	926	107	326
2009	31	28	805	703	391	53	479	223	557	120	137
2010	28	11	641	556	273	117	418	237	458	79	246
Totals	512	454	12735	15245	3908	4530	4639	2007	23670	1528	4104
% peak	2.1	5.9	13.2	13.9	14.1	15.2	13.2	10.9	13.8	5.9	3.4

in the mid-1980s to early 1990s was followed by a proportional rate of increase of 41% per annum over a period of 15 years. With its return in waters under Dutch jurisdiction, the harbour porpoise also returned on the animal conservation agenda. Its status was re-evaluated and has been described as "*vulnerable*" (VZZ 2007). Reasons for concern were the unexplained recent shift in harbour porpoise distribution within the North Sea at large, and the age structure (many immatures, few adults), reproductive condition (low number of calves, infrequent birth rates), and incidental by-catches in fishing gear of porpoises in Dutch waters (VZZ 2007, Jak et al. 2009).

Two factors triggered the analysis presented in this contribution. Firstly, the concerns regarding the conservation status of these elusive cetaceans, which simply called for more data on current abundance and trends. Secondly, a recent merge between two large, non-overlapping datasets (the seawatching data mentioned earlier and similar, but more recent data stored online at www.trektellen.nl [see methods]) facilitated a more comprehensive analysis and an update of recent trends in abundance in nearshore waters. Three main issues are addressed in this paper: 1. did nearshore numbers continue to increase in recent years, 2. did the tendency of an increase in

sightings throughout the year continue, or are we still dealing with peak abundances in late winter and early spring, and 3. is there any evidence of spatial patterns through the year in the frequency of sightings along the Dutch coast?

Methods

Harbour porpoise abundance was analysed by extracting sightings from the seawatching databases of the Dutch Seabird Group (Nederlandse Zeevogelgroep NZG/CVZ database; 1972-2005) and www.trektellen.nl (2006-present). The analysis is based on material collected during seawatches at: 1. Westkapelle and Maasvlakte ("Delta area"), 2. Scheveningen, Katwijk, Noordwijk and Bloemendaal (mainland coast "Zuid-Holland"), 3. Egmond, Camperduin and Huisduinen (mainland coast "Noord-Holland"), and 4. Texel and Vlieland ("Wadden Sea islands").
over a period of 21 years (1990-2010). The counts are basically conducted year-round, but with slightly increased intensity during periods of (waterbird) migration: spring (March-May) and autumn (August-October). The results from sites in the Delta and Wadden Sea areas must be treated with some caution, because relatively few hours of observation were conducted in February-March, the period of prime abundance of porpoises in Dutch nearshore areas (table 1).

Observations are from vantage points (dune-tops, piers, dikes), with observatories normally at a height of 5-15 m a.s.l., to provide excellent views over at least the nearshore strip (up to 5-10 km distance) of coastal sea (Camphuysen 1985). Porpoises were normally detected only within 2 km from the observers. Observers recorded date, duration of the observation (start- and end-time),

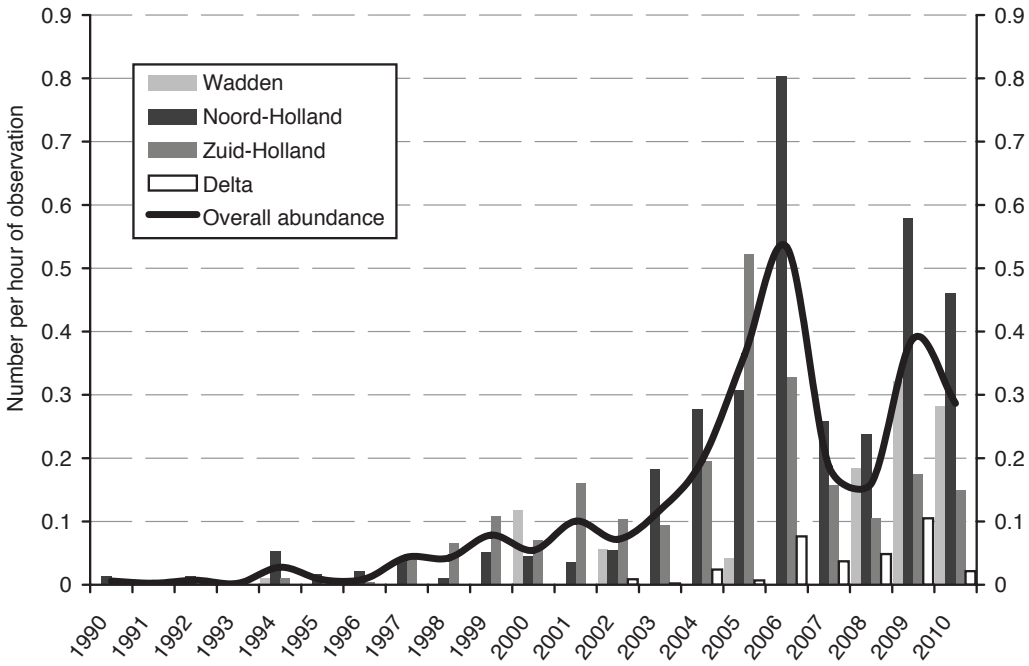

Figure 1. Numbers of harbour porpoises per hour of observation per year in the W-Wadden Sea area (Vlieland and Texel), in the north of Noord-Holland (Egmond, Camperduin, Huisduinen), in Zuid-Holland (Noordwijk, Katwijk, Scheveningen plus Bloemendaal in the south of Noord-Holland) and in the Delta area (Maasvlakte and Westkapelle), 1990-2010.

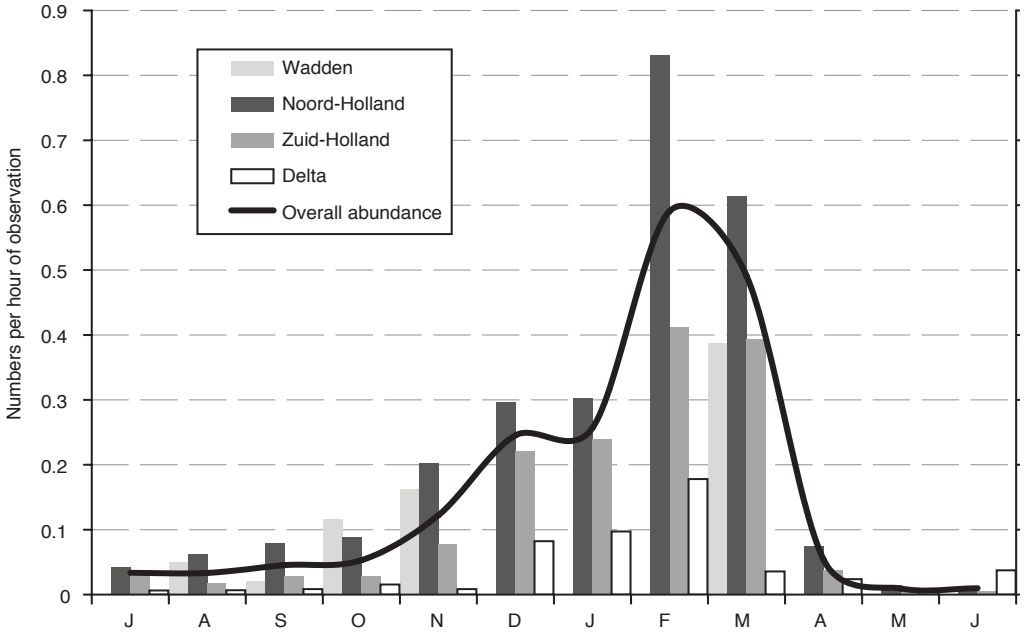

Figure 2. Seasonality in sightings of harbour porpoises per hour of observation per year in the W-Wadden Sea area, in the north of Noord-Holland, in Zuid-Holland and in the Delta area, 1990-2010. See figure 1 for conventions.

and weather characteristics and logged their sightings usually per hour of observation. The observers are well-trained and sufficiently experienced in cetacean identification. The data are expressed as "number per hour of observation" (n h^{-1}) unless otherwise indicated. The database is currently not sufficiently geared up to correct for differences in wind and weather.

Results

The frequency in sightings per annum increased until 2006, followed by two years with relatively modest numbers and rather high numbers again in 2009 and 2010 (figure 1). Sightings were almost year-round, but with very low frequencies in May and June (figure 2). During late summer and autumn (July-November) a gradual increase was found, followed by some stabilization in numbers in mid-winter (December-January) and a marked further increase in sightings in February-March. The frequency in sightings crashed early April, followed by the annual low abundance in early summer. Over the years, the seasonal pattern of harbour porpoise sightings has been fairly consistent. Notably in the southern half of the mainland, however, relatively high numbers of porpoises could be observed as early as in December. A December peak was also prominent in much of the material collected in the most recent years in the north of Noord-Holland (2008-2010), and this has contributed to the 'hump' (or first peak) in overall abundance in figure 2 for the mid-winter period. Extreme peak-abundances for February and March occurred in 2005-07, but the frequency of sightings in these months was much less extreme in comparison with the rest of the winter in later years. Typical in *every* year, however, were the rapidly dwindling numbers in April, leading to the summer dip with extremely low frequencies of sightings in nearshore waters.

During the period of nearshore peak-abundance in February-March, the highest fre-

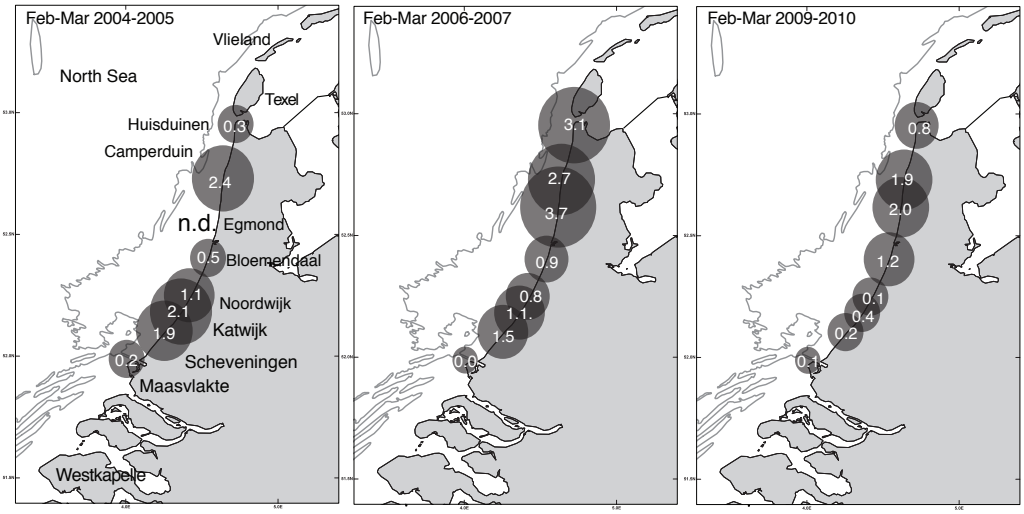

Figure 3. Relative abundance of harbour porpoises (number per hour of observation) at eight observatories along the mainland coast during peak appearances in February-March in 2004-2005, 2006-2007, and 2009-2010.

quencies of sightings in Zuid-Holland were recorded in Scheveningen and Katwijk; clearly lower numbers were recorded in Bloemendaal (except 2009-2010), Noordwijk and the nearby Maasvlakte (Delta area; figure 3). Further north along the mainland coast, Egmond tended to produce slightly higher numbers than the nearby site Camperduin and the frequency at Huisduinen varied markedly, but was very high in 2006-2007. It is clear that the peak abundances in 2006 were caused largely by a very high number of sightings at the northernmost observatories. Just prior to 2006, Zuid-Holland produced the higher sightings frequencies (figures 1 and 3). Now that the numbers are apparently stabilising (>2006), sightings frequencies are significantly higher in the northern part of the mainland and in fact fairly low in Zuid-Holland. Yet, mean abundances of 3-4 porpoises per hour of observation at any of the observatories, as in 2006, are currently rather rare, even during the late winter months.

Discussion

The sightings from vantage points along the coast could be indicative of the overall abundance of harbour porpoises in the Southern Bight. The fact that nearshore sightings and strandings are so strongly, positively correlated (annual sightings frequency from this study and annual number of harbour porpoise strandings from www.walvisstrandingen.nl, 1990-2010; Spearman test, r_S=0.95, n=21, P<0.001) would support that suggestion. As such, the return of porpoises in the southern North Sea has already been documented by the very long time-series that seawatching data provide (1972-today; cf. Camphuysen 2004). Yet, the seasonal pattern in strandings (Camphuysen et al. 2008) does not fit the picture described here from nearshore sightings: summer strandings are common, and a late winter peak in strandings frequency does not occur. In nearshore waters, harbour porpoises are still mostly winter visitors, whereas strandings records point at a year-round occurrence of animals.

Several of the most recent, dedicated aerial surveys for harbour porpoises have been conducted in the period of peak-abundance in nearshore sightings. The results have been staggering, in a sense that while only half of the Dutch sector of the North Sea has been surveyed (between 3 February and 3 April 2009),

37,000 harbour porpoises (95% C.I. 19,000-68,100) were estimated to be present (Scheidat & Verdaat 2009). In March 2010, when the exercise was repeated, but while covering ≈80% of the Dutch sector, an estimated 66,250 animals (95% C.I. 34,250–134,750) were found (Scheidat et al. 2011). An earlier survey in May in roughly the same study area produced a considerably more modest estimate of 6300 (95% C.I. 1300-15,000) porpoises (Scheidat 2008). In the adjacent waters of Belgium, combined data derived from aerial surveys, passive acoustic monitoring and strandings revealed a clear seasonal pattern, with porpoises being typically abundant in late winter and early spring, whereas lower numbers tended to stay in more offshore and northerly waters from late spring to autumn (Haelters et al. 2010). This pattern certainly did fit the picture derived from Dutch nearshore observations. Also, the substantial lower numbers recorded offshore during aerial surveys in May (2008) in comparison with surveys in March/April (2009-2010) seem to confirm a similar seasonal trend. Rather different results were reported by Arts (2010), who found the highest densities of porpoises during aerial seabird surveys in a not precisely defined part of the Dutch sector of the North Sea in April/May, and rather lower densities in February/March. More work is needed to complete the picture and to allow us to sketch the seasonality in overall abundance in the Southern Bight, which would help interpret the nearshore sightings reported in this and previous studies (Camphuysen & Leopold 1993, Camphuysen 2004).

The seawatching results point to some stabilisation in recent years: the period of rapid increase is over. Current sightings frequencies are on a considerably higher level than before 2005 and rather higher numbers are nowadays recorded by the northernmost observatories (Bloemendaal and further to the north). Within the Wadden Sea area, accidental sightings are frequent, notably in the period of peak abundance (late winter), but constant effort sites such as along the mainland coast are non-existent. Our understanding of the ecology of harbour porpoises is running behind, unfortunately, and new studies to try and help understand the current trends and processes are urgently required. Are the animals in later winter attracted to nearshore waters by some rich but as yet unidentified food source? Is the sudden disappearance in spring simply a contraction away from the coast, or an overall movement north towards open (deeper) sea for the calving period? Are the animals generally doing rather well in Dutch waters, or are we in fact looking at 'refugees', driven away from their original wintering areas as a result of food shortages further north (MacLeod et al. 2007, VZZ 2007)? These and other questions should trigger more directed studies of an animal that can be regarded once more as a common and much appreciated indigenous species of Dutch waters (cf. van Deinse 1925, Verwey 1975).

Acknowledgements: The material described here was collected by hundreds of observers over a 21-year period. Gerard Troost (www.trektellen.nl) and Erik van Winden (SOVON) were instrumental during the data merge of the NZG/CvZ database and the online database of www.trektellen.nl, in a project that was funded by the Ministry of Transport and Public Works under co-ordination of Marc van Roomen. Chris Smeenk and Kees Canters kindly commented on a draft version of this article.

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Samenvatting

Recente veranderingen, seizoenpatroon en ruimtelijke verdeling van waarnemingen van bruinvissen (*Phocoena phocoena*) langs de Nederlandse Noordzeekust, 1990-2010

De bruinvis (*Phocoena phocoena*) is aan het einde van de 20e eeuw teruggekeerd als een talrijke, inheemse soort in de Nederlandse Noordzee na een schijnbare afwezigheid van minstens 30 jaar waarin zo goed als geen enkel levend dier in onze omgeving werd gezien. Zowel de redenen voor de afname in de loop van de jaren vijftig en zestig van de vorige eeuw als voor de toename of terugkeer in de loop van de jaren negentig zijn onbekend. Tijdens twee uitgebreide tellingen van bruinvissen in de Noordzee, de eerste in de zomer van 1994, de tweede in de zomer van 2004, werd geconstateerd dat er een verschuiving in voorkomen van noord naar zuid was opgetreden. Waren bruinvissen in 1994 zo goed als afwezig in de Zuidelijke Bocht (de zuidelijkste punt van de Noordzee), tijdens de tellingen van 2004 werden hier heel wat dieren gezien, vooral langs de Engelse oostkust. Doordat zeetrekwaarnemers (tellers van zeevogelbewegingen langs de Nederlandse kust) al een enorme toename in het aantal bruin-

Harbour porpoises near Texel, March 2011. *Photograph: G. Aarts.*

vissen hadden geconstateerd, kwam deze verschuiving in ons land niet als een verrassing. Vooral in het begin van deze eeuw namen de aantallen snel toe. Om de ontwikkelingen te blijven volgen is een nieuwe analyse van de gegevens van de zeetrekwaarnemers uitgevoerd. De redenen daarvoor waren: 1. de terugkeer van de bruinvis op de agenda van de soortbescherming in Nederland (er waren nu immers weer dieren in ons gebied), en 2. het samenvoegen van twee grote gegevensbestanden: de zeetrektellingen van de Club van Zeetrekwaarnemers (Nederlandse Zeevogelgroep, vooral 1972-2005) en de trektellingen die online werden verzameld door Stichting Trektellen (www.trektellen.nl, vooral 2006-2010). Dankzij deze samenvoeging ontstond een continue reeks van waarnemingen, die nu gecorrigeerd kunnen worden voor variatie in waarnemingsinspanning, aangezien de tellers precies bijhouden wanneer en waar zij gegevens verzamelen. Voor de belangrijkste kustposten, waar sinds 1990 gedurende ongeveer 73.000 uren werd waargenomen, worden de gegevens hier gepresenteerd. Het blijkt dat de eerder al gerapporteerde, snelle toename in aantallen langs de kust na 2006 niet verder heeft doorgezet. Na twee relatief magere jaren (2007-2008) volgde weer een opleving (2009-2010), maar de aantallen waren niet zo groot als in het topjaar 2006. De bruinvis wordt nu gedurende bijna het gehele jaar gezien, maar is dicht onder de kust vrij zeldzaam in mei en juni, neemt dan geleidelijk in aantal toe tot in december, piekt in februari/maart en verdwijnt in de loop van april uit beeld. Deze snelle afname houdt vermoedelijk met een vertrek uit de directe kustzone, maar waarnemingen op zee (vooral gerichte tellingen van bruinvissen vanuit de lucht zijn geschikt om de aantallen nauwkeurig vast te stellen) ontbreken nog om het seizoenspatroon goed te begrijpen. Uit recente tellingen op zee is gebleken dat in de piekperiode langs de kust (maart 2009-2010) in de zuidelijke helft van het Nederlandse Continentale Plat ongeveer 40.000-50.000 bruinvissen voorkomen. Tellingen in mei (2008) leverden een schatting op van bijna 7000 dieren.

Tegenwoordig worden langs de kust de meeste bruinvissen in de kop van Noord-Holland gezien. In Zuid-Holland, waar de soort al een jaar eerder piekte (2005), lijken tegenwoordig iets kleinere aantallen voor te komen. Het wordt nu tijd om gericht ecologisch onderzoek aan bruinvissen op te zetten, zodat we kunnen begrijpen wat de dieren (vooral) in de late winter en het vroege voorjaar zo dicht naar de kust lokt en waarom ze in april daar weer zo plotseling vertrekken. Voortzetting van de tellingen langs de kust is belangrijk om ook in de toekomst een vinger aan de pols te houden.

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The distribution and relative numbers in barn owl pellets of the bicoloured white-toothed shrew (*Crocidura leucodon*) in Zeeuws-Vlaanderen; a meta-analysis

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Abstract: Changes in the distribution of the bicoloured white-toothed shrew (*Crocidura leucodon*) in Zeeuws-Vlaanderen (Province of Zeeland, the Netherlands) are described, going back to the first catch of a specimen in 1937. An analysis is made of the relative numbers of this species found in the pellets of barn owls (*Tyto alba*) since 1943. Two white-toothed shrew species, the bicoloured and the greater white-toothed shrew (*Crocidura russula*) are present in this region. The distribution of both species is evaluated with special reference to their simultaneous presence in trap localities and in barn-owl pellets. In four periods (before 1950, 1950-1969, 1970-1988 and 1989-2008) the number of occupied 5x5 km grid cells of bicoloured white-toothed shrew has increased from 2 (first period) to 36 (last period). The increase in their occurrence in 1x1 km blocks (to 78 in the last period) has been almost exponential. Between 1989 and 2008 trappings have been made of bicoloured white-toothed shrew in the area between the Kanaal van Gent naar Terneuzen and the Braakman, where the species has not previously been observed. The percentage of remains of the species found in barn owl pellets between 1943 and 2008 has also shown an increase. Until 1990 this proportion remained far below 2%; after 1995, the percentages were well above 2%, except for 1998 and 2004. Almost all the separate lots of pellets contained both bicoloured and greater white-toothed shrew, meaning that both species are present within the home range of hunting barn owls. The trapping results varied from 0 to more then 2 percent. At the 65 locations where *Crocidura* species were captured, 32 contained only bicoloured white-toothed shrew and 31 contained only greater white-toothed shrew. At two locations both species appeared to be present. The data from Zeeuws-Vlaanderen for 1964-1970 and 1987-2002 is compared to similar data from the bordering provinces in Belgian Vlaanderen. According to the criteria of Red List definitions, the change in the status of bicoloured white-toothed shrew in the Netherlands towards 'least concern' has been justified by the findings presented in this study.

Keywords: bicoloured white-toothed shrew, *Crocidura leucodon*, greater white-toothed shrew, *Crocidura russula*, barn owl pellets, interspecific competition, Zeeuws-Vlaanderen, the Netherlands.

Introduction

The improved status of the bicoloured white-toothed shrew (*Crocidura leucodon*) on the Red List of Mammals in the Netherlands from 'susceptible' in 1994 to 'low risk' (Zoogdiervereniging VZZ 2007) was expected by some insiders. But it surprised many members of the Dutch Mammal Society. One of the few ways to assess the presence of small mammals, such as the bicoloured white-toothed shrew, in a certain area and evaluating its rarity is by analysing barn owl (*Tyto alba*) pellets. Live-trapping is another method, but it is much more laborious to get enough specimens. Evaluating the first year of the Owl Pellet Monitoring Project, La Haye (1998) con-

cluded that it is feasible to track the trend of small mammals through the analysis of skull fragments in the pellets of barn owls, but some years later there still are statistical, methodological and biological flaws in this method (van Engeldorp Gastelaars 2001). In the case of the bicoloured white-toothed shrew, a lack of continuity in the availability of barn owl pellets has made it impossible to make a proper analysis of population trend developments in western and eastern Zeeuws-Vlaanderen and the interconnected north-eastern Overijssel and south-eastern Drenthe regions, the two regions in the Netherlands where the species is known to occur. Moreover, the sensitivity of this method appeared to be low (van Engeldorp Gastelaars 2001). Another problem is the interdependency of prey species: an increase in the ratios of specific prey species in barn owl pellets automatically induces a decrease in one or more other prey species and vice versa. This relation is evident for prey species that can be regarded as staple food, e.g. comparing years with cyclic high and low densities of common vole (*Microtus arvalis*) and greater white-toothed shrew (*Crocidura russula*). However, this effect could not be demonstrated for species with low densities (van Engeldorp Gastelaars 2001).

The population of bicoloured white-toothed shrew in the northwest of Europe extends from Belgium into Zeeuws-Vlaanderen, with a (sub-)population in north-eastern Overijssel and south-eastern Drenthe and adjacent areas in Germany. This group is isolated from the main distribution area in Europe by a distance of more than 150 km (Krapp 1999). Snaak (1999) has extensively described barn owl pellet analysis and trapping results for bicoloured white-toothed shrew in Drenthe and Overijssel. He also included the neighbouring German county of Bentheim in his analyses. He extended his study from 1999 to 2007 (Snaak 2008) and during this period identified 53 5x5 km grid cells with evidence of bicoloured white-toothed shrew presence. The Red List evaluation of the species for the Netherlands needs to take into account the status of these two geographically separate populations. The available population descriptions for Zeeuws-Vlaanderen are also compared with those from the adjacent part of Belgium.

Kruseman (1937) caught the first bicoloured white-toothed shrew found in Zeeuws-Vlaanderen in 1937, near Terneuzen. In 1943, Schreuder (1945) identified the species among 85 mammal preys found in one lot of barn owl pellets collected in Axel, Zeeuws-Vlaanderen. Mulder (1969) mentions three locations where bicoloured white-toothed shrew was found in barn owl pellets: Hoofdplaat (1 specimen), Ossenisse (2 specimens), and Kloosterzande (1 specimen); besides these identified bicoloured white-toothed shrew some *Crocidura* spec. were established: Zaamslag (4 specimens), Ossenisse (17 specimens) and Kloosterzande (14 specimens). In 1965 there was an (unconfirmed) capture of three specimens near the Zevenaarhaven at Terneuzen and Buise & Sponselee (1978) report the capture in 1972 of a female bicoloured white-toothed shrew near Terhole. Van Netten (1976) mentions two locations where bicoloured white-toothed shrew was found in barn owl pellets: Koewacht (1 specimen) and Terneuzen (13 specimens), and from Koewacht also 6 *Crocidura* spec. More inventories and captures have been described by 't Hart & Straetmans (1984) (7 specimens, 7 locations), Kapteyn (1988) (15 specimens, 5 locations) and Keijl (1995) (3 specimens, 2 locations). Buise (1984) mapped the locations (in five 5x5 km grid cells) of the 23 specimens found in barn owl pellets in the eastern part of Zeeuws-Vlaanderen. Hoekstra (1992), describing the distribution of the bicoloured white-toothed shrew in the Netherlands, mapped 20 occupied grid cells in Zeeuws-Vlaanderen; seven of these based on identification by finding or capture. Recently, four new 1x1 km blocks, and two new grid cells were added, based on finding specimens in barn owl pellet material collected in 1984 an 1985 in new locations (J.P. Bekker, unpub-

lished data). In addition, Luciën Boerjan (personal communication) has, with the help of members of the local natural history organisation *'t Duumpje*, analysed barn owl pellets, containing 43 lots with remains of bicoloured white-toothed shrew (excluding two *Crocidura* spec.) in the west of Zeeuws-Vlaanderen. These recent survey results suggest that the gaps in the distribution for the species in Zeeuws-Vlaanderen, as described by Dijkstra (1997) and also mentioned by van Engeldorp Gastelaars (2001), have been filled (Bekker 2007).

Population estimates, in general, are difficult to obtain. This is especially true for small mammals in low densities. Even so, data on the long term population trends of bicoloured white-toothed shrew are limited. Buise's analysis on terrestrial mammals in eastern Zeeuws-Vlaanderen (1984) mentions that about 0.5% of mammal remains found in barn owl pellet lots were those of bicoloured white-toothed shrew.

Schreuder (1945) mentions the result of analyses of barn owl pellets, collected in 1943 in Damme, in the Belgian Province of West-Vlaanderen: besides ten greater white-toothed shrews, no other *Crocidura* species were found among the remains of 26 small mammals. Between 1964 and 1970, Asselberg (1971) analysed barn owl pellets collected in Belgium, including the two provinces bordering Zeeuws-Vlaanderen, West-Vlaanderen and Oost-Vlaanderen. The proportion of bicoloured white-toothed shrew for these two provinces amounted 0.38% (15 specimens out of 3,940 vertebrates) and 0.61% (21 specimens out of 3,460 vertebrates) respectively of the mammal species found. Almost two decades later, Verkem (2003) revealed 201 specimens of the bicoloured white-toothed shrew from 1987 to 2002, in the five provinces of Vlaanderen; half of the data came from barn owl pellets and a considerable number from live trappings.

Crocidura species seem to be parapatric as a result of interspecific competition (Meylan 1967). In Westfalen (Germany), the bicoloured white-toothed shrew seems to live in cultivated areas without connections with human settlements (Vierhaus 1984). Frank (1984) captured this species near Oldenburg in human settlements before the greater white-toothed shrew entered the area. Recently (Kraft 2000) noticed a shift in the distribution of greater white-toothed shrew at the expense of the lesser white-toothed shrew (*Crocidura suaveolens*) in Bayern, Germany. Vogel et al. (2002), investigating range expansion of the greater white-toothed shrew in the lower part of the Rhone valley in Switzerland, found the bicoloured white-toothed shrew to be locally extinct along both banks over 18 (south) and 35 (north) km respectively.

Because both the bicoloured white-toothed shrew and greater white-toothed shrew are present in Zeeuws-Vlaanderen, the distribution of the latter is evaluated with special reference to its simultaneous presence in trap localities and in barn-owl pellet lots. Therefore the ratio of bicoloured white-toothed shrew / total *Crocidura* found in pellets is important. Buise (1984) already mentioned almost all pellet lots contain remnants of both species, which means that both are present within the home range of hunting barn owls. As the size of these home ranges are no more than ca. 925 ha (Bond et al. 2004), we can calculate that the (sub)populations of the white-toothed shrew species live, at maximum, within ca. 2 km of each other. A change in the ratio of bicoloured white-toothed shrew / total *Crocidura* in barn owl pellets will reflect the outcome of interspecific concurrence between the two white-toothed shrew species. On the other hand, the rate of co-occurrence of both species at one trapline locality will reflect the degree of parapatry at a lower level.

This paper presents the changes in the distribution of bicoloured white-toothed shrew in Zeeuws-Vlaanderen over four periods. The ratios of the two species in the pellets of the barn owl since 1989 shows an undulating pattern in the population of the bicoloured white-toothed shrew in Zeeuws-Vlaanderen

(Bekker 2010a) with no definitive indication of a long-term decline or incline. The changes in the relative numbers of this species in this region are described from 1943, the first year when lots of barn owls pellets were collected.

Material and methods

Geography

The study area, Zeeuws-Vlaanderen (Province of Zeeland, the Netherlands), stretches over 61 km from west to east and a maximum distance of 20 km from north to south. It lies south of the Westerschelde. Its southern border area with Belgium partly consists of sandy pleistocene soils, with relatively small-scale plots. The large clay polders, next to the Westerschelde, are relatively new and intersected by numerous creek-rests. Along the Westerschelde new dykes provide a solid demarcation between land and water. Older dykes separate the polders from each other. These dykes, made of clay or sandy soils, form the ecological backbone of this area. Many dykes are planted with poplar (mostly *Populus canadensis*), elm (*Ulmus x hollandica*) or willow (*Salix* spec.) and they are usually managed by extensive grazing (Jacobusse 2010).

Over the long west-eastern axis there are three main barriers that restrict the movement of small terrestrial mammals. To the west, the Braakman, formerly a creek running into, but now blocked off from, the Westerschelde, runs south to the Belgian border via the Isabellakanaal. In the centre, the Kanaal van Gent naar Terneuzen completely splits Zeeuws-Vlaanderen, with four bridges providing crossing points. To the east the Otheense Kreek forms a smaller barrier, stretching almost five kilometres inland from the Westerschelde. Zeeuws-Vlaanderen shares 97 km frontier with the Belgian province of Oost-Vlaanderen and the most western tip of Zeeuws-Vlaanderen shares a 13 km frontier with the province of West-Vlaanderen.

Barn owl pellets

Barn owl and tawny owl (*Strix aluco*) regularly take shrews, as shown by pellet-analysis. However, the tawny owl is rare in Zeeuws-Vlaanderen and pellets from this species have never been collected in this region. Although little owl (*Athene noctua*) sometimes takes shrews, the numbers involved are small. The other owl species found living in the area, long-eared owl (*Asio otus*) and short-eared owl (*Asio flammeus*) almost never take shrews (Mostert 1993). Up to now, in Zeeuws-Vlaanderen there have been no reports of remnants of bicoloured white-toothed shrews found in pellets other than barn owls. Barn owl pellets seem the best option for analysing the distribution and numbers of bicoloured white-toothed shrew. Barn owls often breed in barns in Zeeuws-Vlaanderen and have regularly been enticed to breed in human made nestboxes. This makes it relatively easy to collect their pellets. During the severe winter of 1962/63, the number of breeding barn owls in the Netherlands almost completely collapsed (Texeira 1979). Since then a slow recovery has been reported, both in the Netherlands and in Zeeuws-Vlaanderen. When close monitoring started in this region in 1985 there were four breeding pairs – which has risen gradually to a maximum of 74 in 2007 (M. Buise, personal communication).

The gathered lots of barn owl pellets over Zeeuws-Vlaanderen are unevenly distributed. There are also gaps in the continuity of lots collected from one locality. The density of the distribution, as well as the number of serial lots, is higher in the eastern part of Zeeuws-Vlaanderen.

Period categorisation

For the analysis the history of biogeography of bicoloured white-toothed shrew in Zeeuws-Vlaanderen has been divided into four periods: before 1950 (period 1), 1950-1969 (period 2), 1970-1988 (period 3) and 1989-2008

(period 4). These four periods are closely related to investigation activities and key publications: van Wijngaarden et al. (1971) covered the period to 1969 and Hoekstra (1992) described period 3. Although the periods are not exactly equal (- , 20 years, 18 years and 20 years), the time span is long enough to avoid misleading results arising from annual fluctuations in field vole years.

Based on the information described by the literature cited in the introduction, the catches have been related to the trapping effort and presented as ratio of used traps per night. The presence of bicoloured white-toothed shrew, measured for captures, finds and remains in owl pellets together, has been scored for each period in 1x1 km blocks (also visible in grid cells of 5x5 km). The number of occupied 5x5 km grid cells forms the basis for assessing trends in population at the national level. The number of occupied 1x1 km blocks gives a more detailed picture, often used for regional purposes.

Red List criteria

The IUCN does not provide quantitative criteria for the categories 'susceptible' or 'near threatened'. As a result the Dutch Mammal Society adopted criteria for the Netherlands, based on the Basisrapport voor de Rode Lijst Vogels (Zoogdiervereniging VZZ 2007). These adopted criteria for the categorie 'near threatened' are: 1. a decline in the population: a 20-30% reduction in the last ten years or last three generations; 2. area of occupancy fragmented: <2,000 km^2 and ≤10 locations or a continuing decline; 3. area of occupancy fragmented: <4,000 km^2 and ≤10 locations and a continuing decline; 4. population: <15,000 individuals and a decline of at least 10% in the last ten years or last three generations; 5. very small or restricted population: 1,000-1,500 individuals. We do not have any data on absolute numbers for the bicoloured white toothed shrew, but only have data on the (relative) population size and on the area of occupancy.

Statistical analysis

Spearman's rank correlation test was used to test for correlation of pairs of values (Boon 1979), with the upper and lower limits of the coefficients retrieved from tables compiled by Diem & Lentner (1968). χ^2 statistics were used to test differences in categorical data. For all tests, the significance level was set at $P<0.05$.

Results

Analysis of barn owl pellets

Table 1 summarises an account of all the barn owl pellet lots analysed by individuals, organisations or cited from literature references over the four periods. The figures from the first two periods are mainly based on the literature, and show 85 and 3,253 mammal preys respectively. In the third period the total number of analysed lots increased to 107, and the mammal prey items amount to 14,927. For this period the results consist of compiled information kept mainly by Luciën Boerjan (personal communication) for the western part of Zeeuws-Vlaanderen, by Marc Buise (personal communication) for the eastern part and partly by others. Several preserved lots from this period were analysed in the second half of the 1990s, by Kees Mostert and/or the author. The analysis of barn owl pellet lots for this last period is presented here for the first time. The total number of analysed lots in this period almost tripled to 293, while the total number of mammal prey items doubled to 29,791.

Distribution

Since the first period the distribution of bicoloured white-toothed shrew in Zeeland was restricted to south of the Westerschelde (figure 1). In the four periods (figure 1a-1d), the number of occupied 5x5 km grid cells increased from 2 (in the first period), to

Table 1. Account of the numbers of analysed barn owl pellet lots and the total mammal prey items in Zeeuws-Vlaanderen provided by individuals, organisations or published references; *: see reference list; **: referred to as the analyser of pellets in a special edition of *De Bosmuis 1969 7 (5): 1-20*, ***: referred to as the analyser of pellets in a special edition of *De Bosmuis 1976 14 (1): 1-20 and I-XVI*; #: Owl pellet analysing group of *'t Duumpje* consisting of core volunteers LB and AdZ together with HB, GvD, JJ, PS and HvdV (see 'Acknowledgements' for abbreviations); ##: VWG & ZWZ: members of the Field Study Group of the Dutch Mammal Society and members of the Zoogdierwerkgroep Zeeland, see 'Acknowledgements'. Period 1: before 1950; Period 2: 1950-1969; Period 3: 1970-1988; Period 4: 1989-2008.

Individual, organisation or published reference	Lots	Number of prey animals
Period 1		
* A. Schreuder 1945	1	85
Period 2		
** Arie Bijl	7	1,725
*** Jack Groefsema	1	232
** Mieke de Haan & Gerhard Glas	1	554
* W. Krommenhoek 1967	1	47
** Jaap Mulder & Mieke de Haan	1	378
** Eduard Osieck & Jaap de Vlas	1	174
** Jaap de Vlas	1	143
Period 3		
Jan Piet Bekker	5	1,146
Lucien Boerjan	14	2,466
*** Flip Bossenbroek	2	107
Marc Buise	15	3,529
*** Rob Bijlsma	1	288
Henk Castelijns & M. Ploegaart	1	129
*** Rudy van Diggelen	1	88
H. van Iwaarden	1	41
*** Reyer Kommer	1	7
J. Molenaar	8	1,021
Kees Mostert	20	2,861
Kees Mostert & Jan Piet Bekker	2	357
Luud Persijn	18	1,072
Arthur Schotman	8	547
Arthur Schotman & Lucien Boerjan	1	131
Wies Vonck	7	452
Rob van Westrienen	2	685
Period 4		
Jan Piet Bekker	250	26,292
Lucien Calle	2	21
Pepijn Calle	1	53
Arnoud van der Meulen	4	177
Kees Mostert	2	255
# Barn owl pellet analysing group of *'t Duumpje*	29	2,558
## VWG & ZWZ	5	435

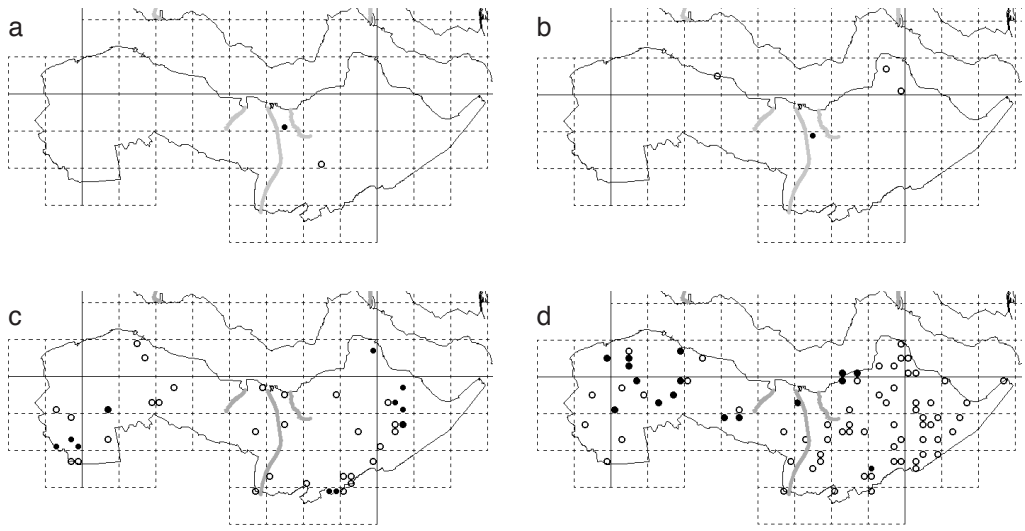

Figure 1. Distribution of bicoloured white-toothed shrew (*Crocidura leucodon*) in Zeeuws-Vlaanderen, the Netherlands. a: to 1950, b: 1951-1969, c: 1970-1988, d: 1989-2008; solid dots = catches, open circles = remains in barn owl pellets.

3 (period 2), 23 (period 3) and 36 (period 4). The increase in 1x1 km blocks is even more impressive: from 2 (in the first period), to 4 (period 2), 39 (period 3) and 78 (period 4). This is an almost exponential growth.

Until 1969 there appeared to be a distribution gap for bicoloured white-toothed shrew between the Kanaal van Gent naar Terneuzen and the Braakman (figure 1a and 1b). This seems to have been filled in during the period 1970-1988 (figure 1c). However, the open circles are based on analysis of barn owl pellets (figure 1c). During the period 1989-2008 bicoloured white-toothed shrew has only been captured at one location between these ecological barriers (figure 1d).

Population

Table 2 presents data on the numbers of bicoloured white-toothed shrew and mammalian preys in barn owl pellets for the four periods. A significant difference exists between periods 2 and 3, 2 and 4, and 3 and 4 ($P<0.001$). Comparisons with period 1 could not be made, because there were less than five expected observations for bicoloured white-toothed shrew and this figure is too small to meet the criteria for a χ^2 test.

The presence of bicoloured white-toothed shrew as a percentage of all mammal preys in barn owl pellets for each year are shown in figure 2. These percentages increased between 1943 and 2008 (Spearman rho: 0.79, $P<0.001$). Until 1990 the percentages remain far below 2, except for in 1973 and 1986, when the figures were 2.0 and 2.3 respectively. After 1995 the situation is quite different: all the percentages, except in 1998 and 2004 (1.9 and 1.4 respectively) were well above 2, even rising to 4.9, 4.8 and 4.8 in 2000, 1997 and 2001 respectively (figure 2).

Competition

Almost all the separate lots of pellets contained both bicoloured and greater white-toothed shrew, meaning both species are present within the home range of hunting barn owls. The percentages of bicoloured white-

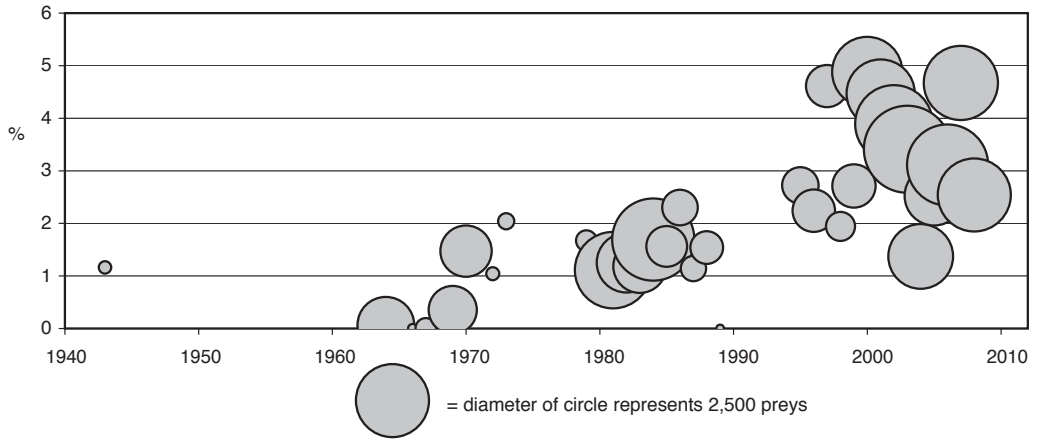

Figure 2. Percentages of bicoloured white-toothed shrew (*Crocidura leucodon*) found in all pellets of barn owl between 1943 and 2008 in Zeeuws-Vlaanderen; the diameter of the circles represents the total number of mammalian prey items in these pellets in each year.

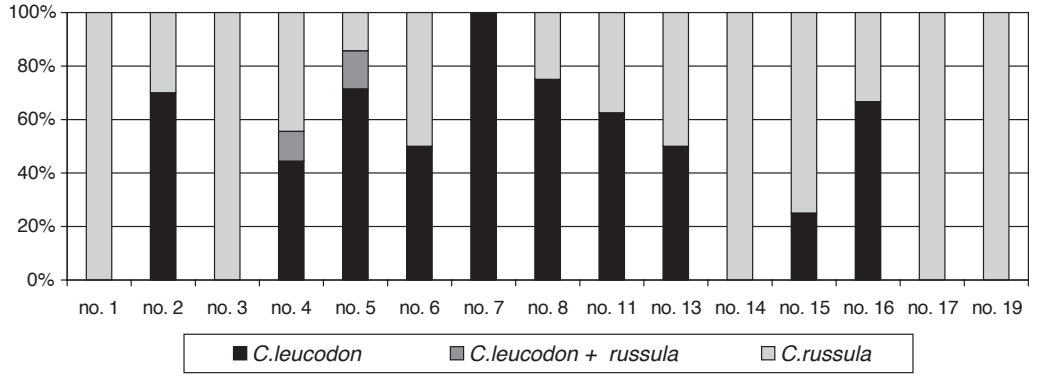

Figure 3. Studies describing trappings of *Crocidura* species: bicoloured white-toothed shrew (*Crocidura leucodon*) and / or greater white-toothed shrew (*Crocidura russula*) at the same spot (numbers on x-axis refer to table 4; studies without trapping *Crocidura* species have been omitted).

toothed shrew in barn owl pellets over the four periods vary from 0.24 to 14.29, while in greater white-toothed shrew these figures vary from 0.65 to 83.3 (table 3). The percentages of greater white-toothed shrew preys found in barn owl pellets increased from 1943 to 2008 (Spearman rho: 0.37, $P<0.001$), but at a lesser rate than bicoloured white-toothed shrew. This difference is also expressed in the ratio of bicoloured white-toothed shrew to all *Crocidura* between 1943 and 2008 (Spearman rho: 0.59).

The trapping result, as ratio of the number of successful trappings of bicoloured white-toothed shrew to trapping effort (number of traps per night), varies from 0 to more than 2 percent. The total number of trapped specimens was rather low (table 4). At the 65 locations where *Crocidura* have been caught, 32 exclusively contain bicoloured white-toothed shrew and 31 greater white-toothed shrew exclusively. Both species appeared to be present at two locations (figure 3). These species evidently show a parapatric occurence at the trap location sites ($P< 0.001$).

Table 2. Distribution of bicoloured white-toothed shrew (*Crocidura leucodon*) and mammal preys in barn owl pellets, by period; χ^2 test between periods: * $P<0.001$, # $P<0.001$, $ $P<0.001$ (definition of periods: see table 1).

	Crocidura leucodon in all lots	Mammal preys
Period 1	1	85
Period 2 (*, #)	5	3,253
Period 3 (*, $)	216	14,927
Period 4 (#, $)	1,056	29,791
Total	1,278	48,056

Comparison with the Belgian border area

This section adjusts some of the data and the periods from Zeeuws-Vlaanderen, in order to make a proper comparison possible with the two Belgium provinces, bordering Zeeuws-Vlaanderen, West-Vlaanderen and Oost-Vlaanderen.

In the period 1964-1970 4,242 vertebrata were collected from barn owl pellets in Zeeuws-Vlaanderen. They contained the remains of 13 (0.31%) specimens of bicoloured white-toothed shrew. An equivalent analysis over the same period for West-Vlaanderen and Oost-Vlaanderen gave results of 0.38% (15 specimens out of 3,940 vertebrates) and 0.61% (21 specimens out of a total number of 3,460 vertebrates) (Asselberg 1971).

Verkem (2003) compared the percentages of the number of grid cells where specimens of bicoloured white-toothed shrew were found in barn owl pellets between 1987 and 2002, using Asselberg's data from 1964-1970. This comparison revealed almost equal percentages over time in West-Vlaanderen (between 38% and 36%), but a decline in Oost-Vlaanderen (from 54% to 28%).

During the period 1964-1970 the number of analysed barn owl pellet lots in Zeeuws-Vlaanderen was low: in five of the ten grid cells (50%) with pellets, bicoloured white-toothed shrew was present. During the period 1987-2002 bicoloured white-toothed shrew was present in 22 of the 26 grid cells (85%) with barn owl pellet lots. Thus, there were more bicoloured white-toothed shrews occupying grid cells with barn owl pellets in Zeeuws-Vlaanderen in the periods 1964-1970 and 1987-2002, compared with the bordering provinces in Vlaanderen (Belgium).

Discussion

According to the percentages of bicoloured white-toothed shrew found in pellets of barn owls, this species has shown a remarkable increase during the four time periods: up to 1950, 1951-1969, 1970-1988 and 1989-2008. According to the species' presence in 1x1 km blocks the increase holds for all four consecutive periods; although the research effort has also increased in more recent periods. The number of 5x5 grid cells with bicoloured white-toothed shrew in the last period amounted 36. There has also been a notable increase over time in the ratio of bicoloured white-toothed shrew to the total number of *Crocidura*.

Table 3. Presence (% ranges) in barn owl pellets of bicoloured white-toothed shrew (*Crocidura leucodon*), greater white-toothed shrew (*Crocidura russula*) and all lots with range of number of prey animals; columns 2 and 3, in brackets: number of lots, only with percentages >0; for definition of periods: see table 1.

	% *Crocidura leucodon* (*n*)	% *Crocidura russula* (*n*)	All lots (range of prey numbers)
Period 1	1.18 (1)	17.65 (1)	1 (85)
Period 2	0.36-1.41 (3)	3.18 – 35.21 (12)	13 (47-553)
Period 3	0.24-7.69 (51)	1.37 – 66.67 (96)	107 (2-1560)
Period 4	0.46-14.29 (183)	0.65 – 83.33 (268)	293 (1-563)
Total	0.24 – 14.29 (227)	0.65 – 83.33 (341)	414 (1-1560)

Table 4. Details of trapping results (%) of bicoloured white-toothed shrew (*Crocidura leucodon*) in relation to trapping effort in Zeeuws-Vlaanderen for individuals, organisations or published references; *: see References; 'casual trappings' not included; (definition of periods: see table 1).

No.	Individual , organisation or published reference	Year	Trapped *Crocidura leucodon*	Traps per night	*Crocidura leucodon* / traps per night
	Period 2				
1	Erik Van der Straeten (personal communication)	1965-74	neg	291	Neg
	Period 3				
2	* 't Hart & Straatmans 1984	1980	7	1055	0.66
3	* Buise & Vonck 1985	1984	neg	2804	Neg
4	* Kapteyn 1988	1988	15	759	1.98
5	* Keijl 1995	1988	3	2083	0.14
	Period 4				
6	* Calle 1998	1992-98	1	244	0.41
7	Erasmus SBB (unpublished inventaries)	1999	1	345	0.29
8	Calle & Bekker (unpublished inventaries)	1999	6	276	2.17
9	Oranjedijk/Turkye (unpublished inventaries JPB)	1999	neg	63	Neg
10	Kriekeputten SBB (unpublished inventaries)	2000	neg	280	Neg
11	* Bekker & Honingh 2001	2000	7	1175	0.60
12	Sandra Dobbelaar (personal communication)	2002	neg	160	Neg
13	Akkerranden (unpublished inventaries JPB)	2002	1	800	0.13
14	Saeftinghe (unpublished inventaries JPB)	2002	neg	120	Neg
15	RWS N58 (unpublished inventaries JPB)	2004	3	600	0.50
16	* Bekker 2007	2006	5	580	0.86
17	Glacisweg (unpublished inventaries JPB)	2007	neg	250	Neg
18	Boschkreek (unpublished inventaries JPB)	2008	neg	224	Neg
19	* Bekker 2010b	2008	neg	620	Neg
Total			49	12729	0.38

To make changes to the status of species on Red Lists it is important to distinguish between changes in actual population trends and distributions and those that originate from an increase in research effort. Even taking this into account for the period 1999-2008, the last ten years of this study, there is evidence of 36 occupied grid cells in Zeeuws-Vlaanderen, together with a further 53 grid cells in north-eastern Overijssel and south-eastern Drenthe. Together these make up 2,225 km^2 of distribution, albeit fragmented between two regions. Snaak (2008) does not provide an analysis of the numbers of bicoloured white-toothed shrew found in barn owl pellets in the north-eastern part of the Netherlands; but his findings do not suggest a decrease of this northern population. The increase over years in the relative numbers of bicoloured white-toothed shrew found in barn owl pellets from Zeeuws-Vlaanderen, indicates an increase in the population.

According to the criteria of Red List definitions, the change in status of bicoloured white-toothed shrew to 'least concern' for the Netherlands is justified by the findings presented in this study. Yet the situation of this species in the Netherlands remains peculiar: it is almost completely restricted to a split distribution in the north- east of the country and one in the south-west. If the population in either part of Zeeuws-Vlaanderen experienced a sharp decline, the possibilities of a smooth recolonisation will be hampered by the almost total ecological barrier

posed by the Kanaal van Gent naar Terneuzen. At the same time a spontaneous recolonisation from Belgium is currently not obvious, given the decline of the population on the other side of the border. Therefore ongoing monitoring of bicoloured white-toothed shrew populations is highly recommended.

Although the results seem to show an increase in the population of bicoloured white-toothed shrew, there are some flaws in the data yielded by the barn owl pellet analysis that have to be considered. Several years of results are missing from the series of analyses of barn owl pellets (see figure 2), resulting in a lack of continuity. In addition the total number of analysed prey-items did not always reach 150, a desirable level for calculating trends of populations of small mammals (La Haye 1999).

Historically incorrect determinations of white-toothed shrews, at the cost of the proportion of bicoloured white-toothed shrew, could also have contributed to lower figures for the latter species being reported in the past (J.P. Bekker, unpublished data). Re-examination of the barn owl pellet remains of bicoloured white-toothed shrew is sometimes possible; however most of the time the remains of greater white-toothed shrew have been thrown away directly after analysis. In the following years Husson (1962) suggested to differentiate skulls of the two white-toothed shrews in the Netherlands with size differences between the 3rd praemolar and the front lobe of the 4th praemolar and the ante-orbital breadth; specimens that could not be assigned to the right category then were labeled '*Crocidura* spec.'. If all the specimens in the 1960s and early 1970s, then labeled '*Crocidura* spec', were assigned to bicoloured white-toothed shrew, the relative numbers found in barn owl pellets from Zeeuws-Vlaanderen for this species can be calculated as 3.1% in 1969, 1.5% in 1970, and 7.4% in 1972; these relative numbers will drop by approximately 50% if adjusted for the calculated misinterpretation based on measurements of the ante-orbital breadth (J.P. Bekker, unpublished data). After the results of the studies of Richter (1963, 1964) became widely available, this differentiation problem gradually faded away.

The scale, in which interspecific competition of white toothed shrews expresses itself, is well within the home range of a barn owl and the area of a trap line (ca. 700-1800 m^2). Although large parts of Zeeuws-Vlaanderen are probably occupied by populations of greater white-toothed shrew, there is also an intricate network of connections for populations of bicoloured white-toothed shrew which survives a range of threats. Detailed mapping of these connections and the threats can help ensure proper support and achieving nature conservation objectives. Large scaled plots, sandy soils near the Belgian border, inland dykes and differences in the densities of humans all seem to influence the unbalanced distribution of bicoloured white-toothed shrew over Zeeuws-Vlaanderen. Further research is needed to determine the contribution that these factors make.

Kraft (2000) and Vogel et al. (2002) both observed that the greater white-toothed shrew was dominant to both the lesser and bicoloured white-toothed shrew. Although the origin of the change in interspecific competition is not known, both authors suggest climatic change is responsible for the diminishing populations of lesser white-toothed shrew and bicoloured white-toothed shrew relative to greater white-toothed shrew, which has expanded its range. These observations and the explanation seem to be in conflict with the long term findings in Zeeuws-Vlaanderen. As white-toothed shrews originate from Africa, it is conceivable that bicoloured white-toothed shrew could benefit from climate change. An explanation for this conflict could be the change in outcome of interspecific competition, due to altitude differences, between greater white-toothed shrew and bicoloured white-toothed shrew, in favour of the latter, which could contribute to a higher population of bicoloured white-toothed shrew in Zeeuws-Vlaanderen during the last period. The effect of climate variables (if any exist) on the populations of bicoloured

and greater white-toothed shrew in Zeeuws-Vlaanderen still needs to be explored.

Conclusions

During four study periods (up to 1950, 1951-1969, 1970-1988 and 1989-2008), the percentage of bicoloured white-toothed shrew found in the pellets of barn owls in Zeeuws-Vlaanderen has shown an increase. Over the four study periods the number of grid cells occupied by bicoloured white-toothed shrew has risen from 2, to 3, 23 and 36 respectively. Their presence in 1x1 km blocks has shown a steady increase from two in the first period to 4 in the second, 39 in the third and 78 in the fourth. In addition an increase over time has been noted in the ratio of bicoloured white-toothed shrew to the total number of *Crocidura*. The continual increase in the ratio of bicoloured white-toothed shrew in barn owl pellets over time indicates an increase in the population in Zeeuws-Vlaanderen. According to the criteria for Red List definitions the downgrading of bicoloured white-toothed shrew towards the status of 'least concern' in the Netherlands is justified by the findings presented in this study.

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Samenvatting

De verspreiding en relatieve aantallen in kerkuilbraakballen van de veldspitsmuis (*Crocidura leucodon*) in Zeeuws-Vlaanderen; een meta-analyse

De veranderingen in de verspreiding van de veldspitsmuis (*Crocidura leucodon*) in Zeeuws-Vlaanderen gedurende de afgelopen 70 jaar worden beschreven. Daarnaast wordt voor deze soort met behulp van analyses van kerkuilbraakballen een aantalsontwikkeling geschetst. Het onderzochte tijdvak is opgedeeld in vier perioden: vóór 1950 (periode 1), 1950-1969 (periode 2), 1970-1988 (periode 3) en 1989-2008 (periode 4). Omdat van de *Crocidura*-soorten zowel de veldspitsmuis als de

huisspitsmuis (*Crocidura russula*) in Zeeuws-Vlaanderen voorkomen, wordt de ontwikkeling van de laatste soort ook geëvalueerd. Hiertoe wordt aandacht besteed aan de gelijktijdige aanwezigheid van de beide soorten in valraaien en in kerkuilbraakballen. In de vier perioden nam het aantal bezette uurhokken van veldspitsmuis toe van 2 tot 36. De toename in de vierkante kilometerhokken tot 78 in de laatste periode is bijna exponentieel; hierbij heeft ook de onderzoeksinspanning een rol gespeeld. Gedurende de periode 1989-2008 is het voorkomen van de veldspitsmuis tussen het Kanaal van Gent naar Terneuzen en de Braakman door vangsten aangetoond. De percentages veldspitsmuis in kerkuilbraakballen per jaar laten over de periode 1943 tot 2008 een stijging zien: tot 1990 blijven de percentages onder 2, na 1995 stijgen de percentages ruim boven 2, met uitzondering van 1998 en 2004. De percentages huisspitsmuis in braakballen over de periode 1943 tot 2008 laten ook een stijgend verloop zien, zij het minder uitgesproken dan die van de veldspitsmuis. Veel van de afzonderlijke braakbalpartijen bevatten veldspitsmuis en huisspitsmuis. Dit betekent dat beide soorten aanwezig zijn binnen de home-range van kerkuilen, maximaal ca. 2 km van elkaar. Het vangresultaat in de inloopvallen varieert van 0 tot meer dan 2 procent. Op de 65 locaties met *Crocidura*-soorten, werden op 32 uitsluitend veldspitsmuis en op 31 alleen huisspitsmuis gevangen; op slechts één locatie bleken beide soorten aanwezig te zijn. Binnen de perioden 1964-1970 en 1987-2002 vertoont de veldspitsmuis in Zeeuws-Vlaanderen een opmerkelijk hoog aantal bezette uurhokken op basis van de analyses van kerkuilbraakballen, vergeleken met de aangrenzende provincies in Vlaanderen (België). Volgens de criteria van de Rode Lijst is de opwaardering van veldspitsmuis naar 'thans niet bedreigd' voor Nederland gerechtvaardigd door de feiten en cijfers in deze studie. Toch is de situatie in Nederland merkwaardig doordat de soort nu letterlijk een marginaal voorkomen vertoont: in Drenthe en Overijssel, en in Zeeuws-Vlaanderen. Dit onderzoek vertoont een aantal gebreken. Zo zijn er in de serie analyses van kerkuilbraakballen enkele jaren zonder resultaten van braakbalanalyses, waardoor een gebrek aan continuïteit ontstaat. Ook wordt niet altijd het gewenste totale aantal van 150 geanalyseerde prooidieren bereikt. Onjuiste determinaties in het verleden van *Crocidura*-soorten ten koste van het aandeel van veldspitsmuis kan hebben bijgedragen tot lagere aantallen. De interspecifieke competitie tussen veldspitsmuizen en huisspitsmuizen speelt zich af tussen 0,7 en 925 ha. Of en hoe klimaatvariabelen van invloed zijn op de populaties van veldspitsmuis en huisspitsmuis in Zeeuws-Vlaanderen, zal nader moeten worden onderzocht.

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