L U T R A

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LUTRA

LUTRA

Lutra is a scientific journal published by the Society for the Study and Conservation of Mammals (VZZ). The society is dedicated to the study and protection of native mammals in Europe. Lutra publishes peer -reviewed scientific papers on mammals across all disciplines, but tends to focus on ecology, biogeography, behaviour and morphology. Although exceptions are made in some cases, Lutra generally publishes articles on mammal species native to Europe, including marine mammals. Lutra publishes full articles as well as short notes which may include novel research methods or remarkable observations of mammals. In addition Lutra publishes book reviews, and compilations of recent literature on mammals. Lutra publishes in British English as well as Dutch. Lutra publishes two issues per year and Lutra is indexed in 'Biological Abstracts' and 'Zoological Record' and 'Artik'.

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4. Use up to ten different key words or short phrases that best identify the manuscript.
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Clarke, G.P., P.C.L. White & S. Harris 1998. Effects of roads on badger Meles meles populations in south-west England. Biological Conservation 86: 117-124.
Clevenger, A.P. 1998. Permeability of the Trans-Canada Highway to wildlife in Banff National Park: importance of crossing structures and factors influencing their effectiveness. In: G.L. Evink, P. Garrett, D. Zeigler & J. Berry (eds.). Proceedings of the international conference on wildlife ecology and transportation: 109-119. FL-ER-69-98. Florida Department of Transportation, Tallahassee, USA.
Shkedy, Y. & B. Shalmon 1997. Evaluating open land scapes in the Negev Desert, and the implications on military activity. Nature Reserves Authority, Jerusalem, Israel. (In Hebrew with English summary).

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Looking to the next 50 Volumes

The production of a peer-reviewed scientific journal is a considerable undertaking, particularly for a small organisation, largely reliant on voluntary contributions. The route from a submitted draft to a published paper is a time-consuming trajectory that requires considerable work from authors, editors and referees. The result can be very satisfactory, and the feeling of seeing your own paper in print is almost indescribable.

The difference between a peer-reviewed and other "journals" is the review process: submitted drafts are not simply edited and sent to print, but are anonymously scrutinised first by external experts, revised by the authors to include suggestions made by the referees and finally accepted or rejected by the editor. Not everyone is prepared to accept rejections or even a critical review, and find that it's a bridge too far to get a paper published in a peer-reviewed journal. That is a great pity, for these people may certainly have interesting material to present and stories to tell.

With the number of journals and other communication channels continuing to grow it can become increasingly difficult for smaller journals to attract authors and to produce timely publications with sufficient content: even when there is an enthusiastic and hard working editorial board. Fortunately, the number of manuscripts submitted to *Lutra*, albeit still quite small, continues to increase every year. There are numerous parallels to be drawn between *Lutra* and ornithological journals like *Ardea* or the more popular *Limosa*

(both published by the Netherlands Ornithologists' Union, NOU). There are so many active biologists, amateurs as well as professionals, in the Netherlands that it is quite remarkable that these journals receive so few submissions.

We should be proud that we are able to keep journals like these going in a small country: high quality journals, published by non-profit organisations that are available at very low cost. The obligation to contribute to these journals should be felt by all those who are active in field biology in our country, amateurs and professionals alike. After all, your observations and measurements are of no value (other than your personal pleasure) while the data have not been published. For a proper recognition of changes in population or significant ecological findings, publication is a must! Where would one go to for information if our own journal were to be discontinued?

One important question may be: why should we produce a (high quality) journal in the first place? In the recent past, journals and meetings were the most important means of communication. Whenever one found something special or recorded something interesting, one had to wait for a society meeting to be organised or the journal to be published before a wider audience could be informed. We are lucky to have those journals stocked in our libraries, so that we can read back in time. We can compare our own data with published material and see how the world has changed and what is really new. The meet-

ings however interesting become just memories for the participants after a while, except when the minutes or proceedings were formally published.

It is important to realise that both methods of communication, presentations at meetings and published accounts, trigger debate. "Did you see that right? Did I find that also? Was the method of measuring appropriate?" People respond by publishing their own views and findings, by debating and discussing material at society meetings, and informing each other about what is to be seen in the world around us. Together this contributes to an exchange of ideas and an increase in knowledge.

Recently, there have been dramatic changes in our ways of communication. We speak to each other continuously, we promptly post our recent findings on the internet, or we alert co-workers instantly by phone, skype, e-mail, sms, msn or whatever means are currently available. The journals are generally considered very late when they do "finally publish" the material. Few realise that all the rapid data exchange is not particularly long-lasting. Will your personal web-log be available for consultation in 2034?

Papers published in journals generally have a higher quality than those in any other publication, simply because there is an editor in charge (and a peer review), that guarantees a minimum quality standard. Papers in journals can be found with little effort while reports of projects get easily lost, or may simply be impossible to track down because the publisher has long gone out of business.

Professional biologists are encouraged to publish their work in peer-reviewed journals, probably even more so today than ever in the past. They are also under pressure to publish in so-called *high-ranking* journals (with a high citation index), such as *Nature* or *Science*. Such publications are the fruits of their labour and are often the main criteria for evaluating academic performance. So what is the position of a peer-reviewed journal such as *Lutra* in this ball game? *Lutra* is not a prestigious journal, it is not particularly high-ranking, but it is taken seriously enough to attract some of the more interesting spin-offs of professional biologists. Perhaps we don't attract the most significant or spectacular new findings, material that stands a fair chance of being published in the 'upper class' journals, but by increasing the quality of the journal (helped by the recent change from the Dutch to English language!), the journal will be noted and become acknowledged in international fora. The contribution by Kuijper et al. in the present issue is a fine example of the type of papers that professionals can produce and publish in a journal like *Lutra*. We hope that, over time, *Lutra* will become more and more attractive as a recognised publication platform for Dutch and for foreign professionals. We think that the availability of *Lutra*-papers on the internet, for free, will help to spread these papers in the Netherlands and Belgium and far over their borders.

Amateur biologists are not under any pressure to publish. They enjoy their field work, engage in projects of their own free will, and may at best feel a moral obligation to try and get their work published. For many of them, publishing in *Lutra* is a challenge, something that is relatively hard to achieve. Other journals are easier, perhaps better known among their friends or relatives, and being published in these may be nice enough. Yet, a lot of their work is highly interesting and worthy of publication for future consultation. One example within the present issue is the contribution by Boshamer and Bekker on the occurrence of bats on offshore platforms in the Dutch sector of the North Sea. We are very keen to encourage amateur biologists to summarise their findings or work in a format suitable for publication in *Lutra*. The effective conservation of mammals is aided by knowledge, much of which exists only within our extensive community of amateur biologists. That information needs to be shared to be of any use. Only too often do we hear people responding to papers with expressions

like "I knew that twenty years ago", or "Didn't they know that….", but when you kindly ask: "Did you actually publish that expert knowledge anywhere?" a prolonged silence follows. How could we have known?

A journal such as *Lutra* relies heavily on membership (in our case to the Society for the Study and Conservation of Mammals) and subscriptions. Again there are parallels with our ornithological counterparts and societies which similarly have to work hard to maintain their membership. A journal cannot be produced if membership sinks below a certain threshold level. The editors of some journals have observed a decline in subscriptions and have responded by changing their style to a glossier, full colour format with less detailed texts. We feel strongly that this is not the way forward for *Lutra*. Internet publications are glossy, full colour and less complicated (though often lacking in content or credibility), and a serious journal will loose that battle. To enhance our knowledge of mammals in the Netherlands and the rest of Europe, we need a high quality publication platform like a peer-reviewed journal. Commercial journals (the high-ranking ones) have subscription rates that are up to fifty times higher than a journal like *Lutra*. Yet they also have a general scope and are not specifically focused on scientific mammalian research. To offer a publication platform for our acknowledged community of biologists – professional and amateur – and a constant source of information for that community, now and in the future, journals like *Lutra* should be treasured and supported by all possible means.

The use of the 'Woeste Hoeve' wildlife overpass by mammals

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Abstract: The Woeste Hoeve is a wildlife overpass in the Netherlands, built in 1988, to reconnect parts of the Veluwe nature reserve, which were separated by the A50 motorway. Wildlife overpasses cost a substantial amount of money, but apart from an evaluation one year after its construction, the use of the Woeste Hoeve has not been investigated. This study was performed to quantify the use of the Woeste Hoeve by large mammals. The fieldwork used track counts to record the number of passages across the Woeste Hoeve and compare these to passage rates on pathways in the adjacent nature area. To quantify the movement of animals across the wildlife overpass, the direction of the tracks and the distance to the edge of the overpass were recorded. In addition to these observations, pathway densities on the Woeste Hoeve and in the neighbouring nature area were recorded and compared. The Woeste Hoeve wildlife overpass is frequently used by wild boar (*Sus scrofa*), red deer (*Cervus elaphus*) and red fox (*Vulpes vulpes*), and to a lesser extent by roe deer (*Capreolus capreolus*), badger (*Meles meles*) and domestic cat (*Felis catus*). The overpass is used by species to the same degree as found in the first survey by Litjens (1991) in 1989, with the exception of fallow deer (*Dama dama*), which were not recorded in the present study. No preference for the middle section of the wildlife passage was detected. Red deer and wild boar have a significant preference for using pathways to cross the wildlife overpass. The density of pathways is higher on the Woeste Hoeve compared to the surrounding areas. This research confirms that a width of 50 m seems adequate for a wildlife overpass to be used by large herbivores on a regular basis.

Keywords: wildlife overpass, track counts, passages, pathways, badger, red fox, red deer, roe deer, wild boar, Veluwe.

Introduction

Many wildlife overpasses have been built in order to mitigate the consequences that wildlife suffers from manmade structures, particularly road networks (van Wieren & Worm 2001, Bissonette 2002, Woess et al. 2002). Apart from the direct effect of road kills, there are indirect effects of habitat loss, fragmentation and the reduced quality and connectivity of habitats. These latter effects have been significantly underestimated (Bekker 1989, Bissonette 2002). As large wildlife overpasses are expensive to construct, their effectiveness is a point of debate. Although many studies have been conducted on the use of wildlife overpasses, only a few studies address the effectiveness of these measures in reducing the barrier effect of motorways (Forman 2003).

According to Pfister et al. (1997) there are several advantages of wildlife overpasses. First, they reduce animal mortality from traffic. Second, the opportunity for individuals to migrate from one area to another facilitates genetic exchange between populations, increasing their viability. Third, wildlife overpasses enlarge habitats by linking fragmented areas. The linkage of these fragments facilitates (seasonal) migratory movements and enhances the (re)colonisation of areas by animals.

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The use of a wildlife overpass is determined by several factors including its location, dimensions and nearby alternatives for crossing the highway (Pfister et al. 1997, Forman 2003). Pfister et al. (1997) conducted a study on the effectiveness of green bridges in Europe. Sixteen wildlife overpasses with different dimensions, located in France, Germany, Switzerland and the Netherlands, were investigated by means of track counts and video monitoring. The narrow overpasses of less than 20 m in width were used significantly less than the wider structures. Moreover, animals cross these narrow structures at a higher speed (Pfister et al. 1997). However a standard required width can not be given, since this depends on the function and the target species of the wildlife overpass. It is important that the wildlife overpass meets the species-specific habitat requirements of large mammals. Pfister et al. (1997) suggested that at a minimum width of 50 m these requirements are fulfilled for all mammal species covered in his surveys.

During the study conducted by Pfister et al. (1997) it was observed that animals avoid using the outer sections of the wildlife overpass. Red fox (*Vulpes vulpes*), badger (*Meles meles*), and hare (*Lepus europeus*) all mainly made use of the middle section. Roe deer (*Capreolus capreolus*) also preferred the middle sections, although to a lesser extent than other species (Pfister et al. 1997). This behaviour was also observed in a study carried out by Mathiasen & Madsen (2000) at a fauna underpass located in Denmark. During this research, involving infrared video-monitoring of mammals crossing a 13 m wide underpass, it was observed that roe deer always kept a distance of 3.5 m from the wall. No explanation for this behaviour was given in either of the two studies.

In the Netherlands the Woeste Hoeve and Terlet wildlife overpasses, both 50 m wide, have been built across the A50 motorway. This motorway intersects the Veluwe, a large forested area in the eastern parts of the Netherlands. Since the end of 1988 these two overpasses have been the only possibilities for mammals to cross the A50 motorway (Litjens 1991). They were mainly built to serve as a corridor for red deer (*Cervus elaphus*) and were constructed on traditional migration paths, and therefore referred to as 'Cerviducts'.

The use of the Woeste Hoeve and Terlet overpasses by larger mammals was studied by Litjens (1991) in 1989, shortly after the completion of their construction. The study involved counting tracks on a track plot, a strip of bare soil that was raked after each count. Litjens found that both wildlife overpasses were used by roe deer, red deer, wild boar (*Sus scrofa*) and red fox. In addition the Woeste Hoeve was used by fallow deer (*Dama dama*) and badgers, and rabbits (*Oryctolagus cuniculus*) were observed on Terlet (Litjens 1991). Litjens observed roe deer and fallow deer residing on the Woeste Hoeve. Animals residing on an overpass might block it for other animals. In view of this, Litjens recommended considering changing the management of the area surrounding the Woeste Hoeve to make the wildlife overpass less attractive as a foraging area, thereby enhancing the crossing of animals. Litjens also observed that more animals passed from west to east than in the opposite direction. No explanation was given for this finding.

This study focuses on the use of the Woeste Hoeve by wildlife, using techniques similar to those of Litjens (1991). The study was designed to quantify the use of the overpass by different medium-sized to large mammal species, to compare the pathway (the number of pathways crossing a line of a fixed length) and track densities (the number of tracks per unit area on a track plot) on the overpass and in the surrounding area and to test whether animals crossing the overpass had a preference for the middle section while crossing. Use of the areas surrounding the Woeste Hoeve was taken as a baseline reference, enabling a comparison to be made between frequency of use of the overpass and the nearby habitats of these species.

Study area

The study was performed in the southern part of the Veluwe in the Netherlands, which covers an area of 23,500 ha, and where forest and

heath lands are the main vegetation types. Larger mammals within the reserve include badger, fallow deer, muntjac (*Muntiacus reevesi*), rabbit, raccoon dog (*Nyctereutes procyonoides*), red deer, red fox, roe deer*,* Scottish highland cattle, and wild boar. Not all these species are present in the direct vicinity of Woeste Hoeve. At the time of our study (winter 2004/2005) the estimated densities of red deer, roe deer and wild boar were 2.4, 4.6 and 6.9 animals/100 ha respectively (figures estimated from spring counts of red and roe deer and a total autumn count of wild boar - G.J. Spek, unpublished data).

The Woeste Hoeve wildlife overpass (52.07 ° N, 5.57 ° E) has a minimum width of 50 m and a length of 140 m. The wildlife overpass is level with the surrounding nature area and slightly concave in shape. The vegetation on the wildlife overpass mainly consists of grasses, common rush (*Juncus effusus*), dwarfed pedunculate oak (*Quercus robur*) as a result of browsing, and Scotch pine (*Pinus sylvestris*). The visual disturbance of the traffic is reduced by 1.5 m high earth walls along both sides of the overpass. The overpass and the surrounding area are not accessible to the public. Some people do visit the area, but this does not seem to influence the use of the wildlife overpass by mammals (Litjens 1991). Two small ponds that function as watering places for animals were constructed in the surrounding area. One is located 500 m northwest of the wildlife overpass, the other 500 m northeast. The forest surrounding the Woeste Hoeve has patches of pine forest, areas with deciduous trees and some mixed forest. In addition to the closed forest there are patches of open forest and heather.

Materials and methods

Track observations on Woeste Hoeve wildlife overpass

From November 2004 to January 2005 tracks were measured, photographed, and the species identified using Diepenbeek (2003). A 3 m wide strip of sand was created in the middle section of the wildlife overpass, covering the whole width of the overpass (figure 1 and photo 1). The small, relatively steep earth walls (width ~0.7 m) on both sides of the overpass, without any visible sign of tracks or pathways, were excluded from the track plot. The sand strip was raked every day before crossings were recorded. From Tuesday till Friday, when weather conditions allowed, the tracks of animals that had crossed the sand strip were measured. The direction of each group of tracks belonging to a single animal was noted, the distance from the northern side of the wildlife overpass and the distance from the nearest wildlife pathway crossing the overpass were measured. It was assumed that if an animal uses a pathway to cross the wildlife overpass, its tracks will continue on the sand strip. Passages were assigned to the nearest pathway (<1 m distance) to obtain data on the number of passages per pathway. After the measurements, the strip was raked to erase old tracks.

Track observations on track plots in the surroundings of the overpass

The wildlife overpass is covered by numerous wildlife pathways. To check if there was a difference between the number of tracks per pathway on the wildlife overpass and in the adjacent nature area, track plots were also made in the adjacent nature areas on both sides of the wildlife overpass (figure 1). At each side 25 randomly placed plots were made on existing pathways, by removing the vegetation and the upper soil layer, and loosening the soil along a 1 m length of the pathway. The width of the plots varied, ranging from 40 cm on very narrow pathways to up to 1 m on broader pathways. The distance between these track plots and the wildlife overpass ranged from 123 to 726 m (median: 296 m). The number and direction of crossing animals were noted on the same days as on the Woeste Hoeve.

Density of pathways

In addition to differences in the number of tracks recorded on each pathway, there could also be

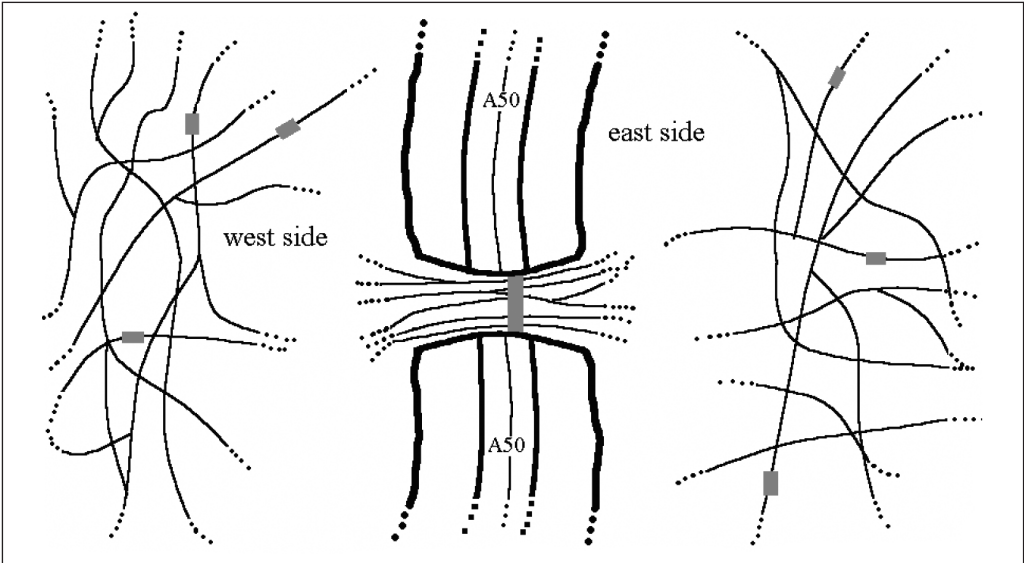Photo 1. Woeste Hoeve with track plot, seen from the southern side. *Photograph: M. Renard.*

Figure 1. Schematic drawing of the positions of the track plots on the pathways on the west and east side of the wildlife overpass together with the track plot on the Woeste Hoeve wildlife overpass. Track plots are shown as grey fields. Dots indicate that only a part of the pathway and road structure is shown.

a possible difference in the density of the pathways over the wildlife overpass and in the surrounding area. To compare pathway densities, transects were made on the Woeste Hoeve and in the adjacent nature areas. Ten parallel transects crossing the entire width of the wildlife overpass were walked to record the location of the pathways. Similarly ten randomly placed transects of 50 m were walked on both the east and west sides of the wildlife overpass. The pathway density was determined by the ratio between number of recorded pathways crossing the transects and the transect length. The pathway density and the number of passages per pathway were combined to calculate the number of passages per metre, on the assumption that all the passages were recorded in the track plots.

Statistical analysis

Statistical tests were performed in SPSS 12.0 for Windows. The track data did not follow a normal distribution, and we therefore report on the 5th and 95th percentiles to illustrate the range of data distribution. Non-parametric tests were used to test for differences between the three areas (the overpass and the areas west and east of the overpass). A Mann Whitney-U and a Kruskal Wallis test were applied to test for differences in the number of passages per pathway. In case of a significant difference between groups a non-parametric multiple comparison test for unequal sample sizes was performed (Zar 1984). The density of the tracks per metre followed a normal distribution and could be analysed with an ANOVA, followed by a Tukey multiple comparison test.

To test if the animals had a preference for the middle section of the wildlife overpass, the observed distances of their tracks from the northern side of the overpass were compared with computer-generated random distances from the northern side. These distances ranged between 0 and 48.5 m, the length of the sand strip. To test if animals follow pathways while passing the wildlife overpass, the observed distances from the nearest pathway were compared with distances from the pathway derived from computer generated random passages.

Results

Recording of tracks occurred on 33 days. In total 547 passages were registered. A large variation in number of passages per day was observed, but there were no days without passages (figure 2). The number of passages of red deer and wild boar were tested for changes over time; and no significant trends over time were detected (Kruskal Wallis test; figure 3).

The use of the Woeste Hoeve in 1989 and in the present study is given in table 1 which shows the mean number of passages per species per day. The total number of passages per day appeared to be larger in 2004-2005, but this could not be confirmed statistically. The larger number of passages in 2004-2005 was mainly caused by more passages per day by wild boar and red fox. Fallow deer were not observed during the present study.

There was a significant difference between the number of passages per pathway in the three test areas (Mann Whitney U test, P=0.002, n=335, 411 and 672 respectively). The number of passages per pathway was significantly higher ($P<0.05$) on the east side (5th and 95th percentiles: 0-1.4 passages per pathway), compared to both the west side (0-0.9) and the wildlife overpass (0-0.9). There was no significant difference between the number of passages per pathway on the west side and on the wildlife overpass. These data are highly skewed, due to the large number of zero counts.

However, the relatively low number of tracks per pathway on the wildlife overpass compared to the east side could, in theory, be compensated by the higher pathway density on the overpass. The pathway density averaged 0.67 pathways/m on the Woeste Hoeve (95% confidence intervals: 0.63-0.70), but only 0.30 (0.24-0.33) and 0.34 (0.25-0.39) pathways/m in the nature areas on the west and east sides respectively. This gives a significant higher number of passages per metre on the Woeste Hoeve (ANOVA $F_{2,31}$=75.607,
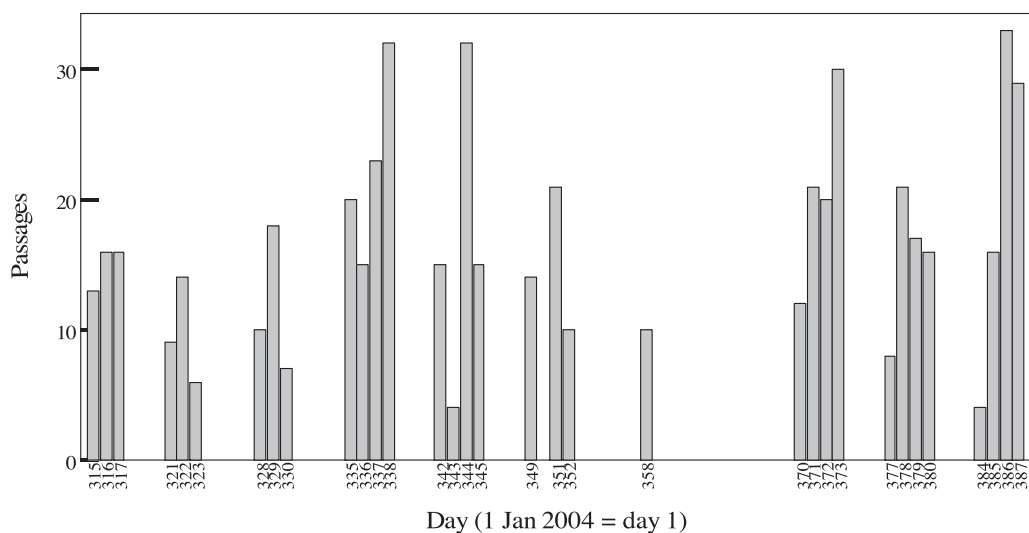
Figure 2. Overview of the use of the Woeste Hoeve wildlife overpass. Bars represent the total number of passages per observation day. Day numbers start at 1 January 2004 and continue to 2005; 1 January 2005 = day 367.

Week (46-52: Nov-Dec '04; 1-3: Jan '05)
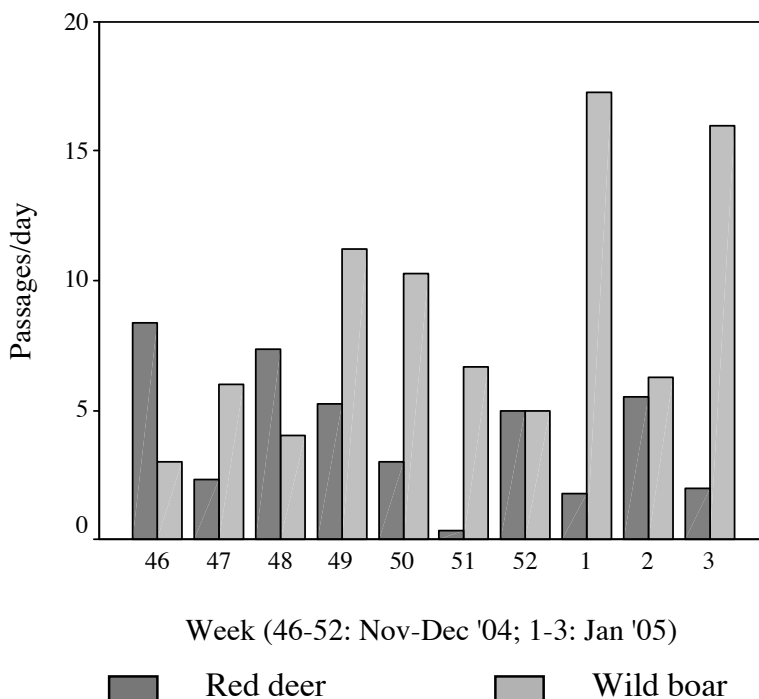
Red deer   Wild boar

Figure 3. Mean daily passages of red deer and wild boar over the Woeste Hoeve wildlife overpass. Observations were performed in the period between November 2004 (weeks 46-52) and January 2005 (weeks 1-3).

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Table 1. Mean number of passages per day in 1989 (Litjens 1991) and 2004-2005 and total number of observed passages in 2004-2005 on the Woeste Hoeve wildlife overpass. Observations in January, November and December 1989 and the period November 2004 - January 2005.

Woeste Hoeve	Total	Red deer	Wild boar	Roe deer	Fallow deer	Red fox	Badger
Passages/day 1989	12.6	4.1	6.0	0.7	1.7	0.1	0
Passages/day 2004/2005	16.6	3.9	9.3	0.5	0	1.91	0.5
Total 2004-2005	547	130	308	15	0	63	15

$P<0.001$) compared to the west and east sides (Tukey multiple comparison test $P<0.05$). No significant differences were found between the east side of the nature area and the Woeste Hoeve in terms of the number of passages per metre. Furthermore, there was no significant difference between the number of passages per pathway on the Woeste Hoeve and those in the combined nature areas.

Observed passages were divided into three groups, according to their distance from the north side of the overpass (north, middle and south; figure 4). For all species, the observed distances between the passages and the north side of the overpass were compared with randomly generated distances from the north side (Kruskal Wallis test). No significant difference was found for the track locations of red deer, with the observed distance being similar to the randomly generated distances. For wild boar however, there was a difference between the observed data and the randomised track locations ($P<0.001$, $n=303$); wild boar used the north side of the wildlife overpass significantly less than they used the middle and the south sides. No significant differences between the groups were demonstrated for roe deer, red fox, badger, or domestic cat.

Of the total number of 547 tracks observed on the Woeste Hoeve, 254 tracks were of animals passing the wildlife overpass in a west to east direction, and 290 were passages in the opposite direction.

On the overpass the distances of observed passages from the nearest pathway were more clustered around zero (the midpoint of the nearest pathway) than the random distances ($P<0.001$, $n=534$). The observed distances from the nearest pathway were significantly lower than the random distances for both wild boar and red deer ($P<0.001$, $n=303$ and $P=0.033$, $n=122$ respectively), indicating that these two species preferred walking on pathways while crossing the overpass, in stead of using the areas next to pathways. The low number of roe deer, red fox and badger tracks meant that this test could not be performed for these species.

Discussion

Use of the Woeste Hoeve

During this survey the Woeste Hoeve wildlife overpass was frequently used by wild boar, red deer and red fox, and to a lesser extend by roe deer, badger and domestic cat. Litjens (1991) found that fallow deer used the Woeste Hoeve in 1989. However, during this study, no tracks of fallow deer were recorded, presumably because fallow deer have disappeared from this part of the Veluwe (J. Heikens, personal communication).

No tracks of smaller mammal species were found on the Woeste Hoeve track plot, nor on the plots in the adjacent nature area. This could imply that the sand that was used for the track plots was not suitable for detecting smaller tracks. It may also be the result of a low density of small

mammals in the area, or because they cross the overpass using the fence or along the relatively steep earth walls on either sides of the overpass (Litjens 1991), which were not included in our track plot. The species composition in this survey was identical to that found by Litjens in 1989, with the exception of fallow deer and domestic cat.

Quantitative use of the Woeste Hoeve

The results show that the Woeste Hoeve was used at least as much as the surrounding areas. The number of crossings per pathway was slightly lower on the wildlife overpass, but the pathway density per metre was higher. The number of crossings per metre was higher on the overpass than on the west side and similar to that on the east side. However, this calculation is based on the multiplication of the mean number of passag-

es per pathway and the density of the pathways per metre. The passages per pathway did not follow a normal distribution, and had a skewed distribution with many zero counts, so the error margins of these estimates are large. However use of the Woeste Hoeve seems at least comparable with that of nearby habitats. We did not measure the density of wildlife passages outside pathways in the two nature areas. We therefore recommend also carrying out track counts away from pathways in nature areas in future studies.

Another issue to consider is that we do not know how far the disturbance effect of the road extends, and whether this affects the density of wildlife, even at distances greater than those between the overpass and our track plots in the two nature areas. For instance Ward et al. (2004) showed that roe deer densities are lower near roads, although the ranges at which roads influence deer densities are still unknown. It would
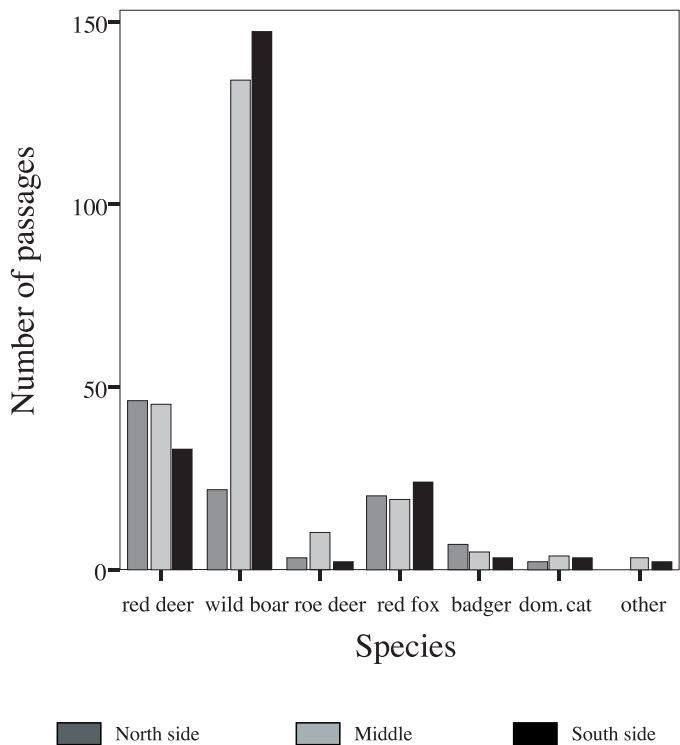

Figure 4. The total number of passages per species observed in the period November 2004 - January 2005 on the north (0-16 m), middle (16-32 m) and south sides (32-48 m) of the Woeste Hoeve wildlife overpass.

therefore be useful to include track plots at varying distances from the road to detect whether it causes a gradient in wildlife density.

Animals residing on the Woeste Hoeve

With the exception of a domestic cat, the researchers saw no animals on the Woeste Hoeve. This strongly indicates that no animals currently reside on the wildlife overpass. Furthermore, roe deer, one of the species that Litjens observed residing on the overpass in 1989, only passed over the sand strip on the overpass 15 times during the present study. This indicates that roe deer do not permanently inhabit the overpass. However, the browsed vegetation on the Woeste Hoeve clearly shows that some animals do forage on the Woeste Hoeve. Video monitoring of the behaviour of the animals using the overpass could provide information on the behaviour of the animals while crossing the overpass.

Direction of passages

There was no significant difference between the number of passages from west to east and the number of passages in the opposite direction. While seasonal variations in the direction of passages could occur, this could not be demonstrated within a period of 3 months. A year-round study should be performed in order to evaluate the difference in direction of animal passages between different seasons. The factors that influence the direction of the movements of animals should also be studied and should include a study of the difference in forage availability between the west and east sides.

Spatial preference for crossing the wildlife overpass

Pathways were evenly distributed across the wildlife overpass. This indicates that the whole width of the wildlife overpass is being used. The measurements of the distance of pathways from the northern side show that species differed in their preference for the sides of the area while crossing the wildlife overpass. For red deer no difference

was found between the observed distance of pathways from the north side and the randomised distances from the north side. For wild boar though, a significant difference was found, as it mainly used the south and middle section of the overpass and avoided the north side. No explanation can be given for this although it could be speculated that this is influenced by the patterns of vegetation growth on the wildlife overpass. This is supported by a study carried out by Clevenger & Waltho (2005) on attributes of highway crossing structures that facilitate movement of large mammals. They found that distance from cover was the most important landscape attribute determining the passage of several large mammal species, with increased cover providing greater protection and security for animals approaching the overpass (Clevenger & Waltho 2005). The south side of the Woeste Hoeve has more shrubby vegetation, which could explain the preference of wild boar for this side.

Preference for pathways

The distances from the observed passages on the track plots to the nearest pathway were less than the distance from randomly generated pathways. These differences were significant for observed and random distances from the pathways of wild boar and red deer and imply that these species prefer following pathways while crossing. This supports the observation by Litjens (1991) that large mammals mainly used fixed pathways while crossing the wildlife overpass.

Differences between species

Red deer and wild boar frequently used the wildlife overpass. Roe deer only sporadically passed over the Woeste Hoeve. This can not be explained by differences in population numbers, since the population density of roe deer is higher than that of red deer. It may be due to a smaller home range or lower dispersal distances of roe deer, compared to those of red deer and wild boar, or the time of year the survey was carried out. Roe deer have a more solitary lifestyle compared to red deer and show territorial behav-

iour throughout some parts of the year (S.E. van Wieren, personal observation). In a forest environment Roe deer have home ranges varying from 60-200 ha (Raesfeld et al. 1986), while the home ranges of red deer range from less than 40 ha up to 500 ha (Bützler 1986).

The difference between red deer and wild boar, although less striking, can partly be explained by differences in the population densities of these species. As mentioned before, species-related seasonal differences may influence the number of passages. The rutting season for red deer occurs in September and October, and in November and December for wild boar, so the current study does not demonstrate the effects of rutting behaviour.

In order to determine the factors that affect the inter-species differences in the use of wildlife overpass, behavioural observations are recommended, preferably through video monitoring.

The width of the wildlife overpass

None of the wildlife species studied here avoided the margins of the passage and showed a preference for the middle section. The number of pathways can have an important influence on the total number of animals crossing the wildlife overpass, as most animals used pathways while crossing. Since more pathways can be accommodated on a wider overpass, the width of an overpass could influence its use. However, this also depends on the intensity of use of these pathways, and more importantly, whether the total number of crossings would increase, and whether animals from a larger source area would cross a wider overpass. This can only be solved through an experimental approach, or a good meta-analysis, that includes passages of different widths.

The width of the Woeste Hoeve overpass appears to be adequate, given that all the large mammal species that reside in the area around it make use of it. In addition the track density and pathway density estimates indicate that use of the overpass is similar to use of the nearby nature area, although wildlife densities might be higher further away from the road. The density of the tracks on the overpass showed a funnelling effect, with a far higher pathway density than on the areas west or east of the overpass. While the track density per passage was no higher on the overpass than in the surrounding areas, the number of passages per metre was higher on the overpass than in the surrounding area due to the higher pathway density. Pfister et al. (1997) recommend a width that is sufficient for larger mammals to pass the overpass in a stress-free manner, so that they will use it not solely for emergencies, but on a regular basis. They also recommend that overpasses contain an environment that is comparable with the natural habitat of the mammals that will use it (Pfister et al. 1997). Our results show a substantial use of the Woeste Hoeve, and this indicates that, according to Pfister's conclusions, it meets the requirements of large mammals.

Conclusions

The Woeste Hoeve wildlife overpass is well-used. All large mammal species that occur in the area around the Woeste Hoeve use the overpass to a certain extent. The number of passages recorded on the Woeste Hoeve was in the same order of magnitude as in the adjacent habitat. There was not a significant difference in the direction of recorded passages.

In contrast to the observations made by Pfister et al. (1997), there was no preference for the middle section of the wildlife overpass. Only wild boar showed a preference for some sections, preferring the south and middle sections to the northern section.

Red deer and wild boar preferred to follow pathways while crossing the overpass, as calculated from a comparison of observed and random passages.

Although it is difficult to make a solid statement about the quantitative use of wildlife overpasses they increase the possibility for genetic exchange between populations and connect different habitats, thereby enhancing the foraging and migratory movements.

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Samenvatting

### Gebruik van wildviaduct 'Woeste Hoeve' door zoogdieren

Hoewel de kosten voor de constructie van een wildviaduct hoog zijn, is er tot op heden betrekkelijk weinig onderzoek gedaan naar de effectiviteit van wildviaducten. Dit onderzoek concentreerde zich op het gebruik van wildviaduct Woeste Hoeve door middelgrote tot grote zoogdieren op de Veluwe. Er is gekeken of er een toename in gebruik was te zien in vergelijking met de laatste evaluatie in 1989. Daarnaast is er onderzocht of dieren op het wildviaduct gebruik maken van de totale beschikbare breedte. Voor het kwantificeren van het gebruik van het wildviaduct is het gebruik van wissels in het omringende natuurgebied vergeleken met het gebruik van de wissels op Woeste Hoeve. Het veldwerk vond plaats tussen november 2004 en februari 2005. Met behulp van een zandbed zijn de dagelijkse passages van dieren op de Woeste Hoeve geteld. De positie van de sporen op het wildviaduct is ingemeten om het bewegingspatroon van dieren op Woeste Hoeve te analyseren. In het omringende natuurgebied zijn 50 plots aangelegd op bestaande wissels om daar het aantal passages per dag te kunnen tellen. De Woeste Hoeve wordt frequent gebruikt door wild zwijn (*Sus scrofa*), edelhert (*Cervus elaphus*) en vos (*Vulpes vulpes*), en in mindere mate door ree (*Capreolus capreolus*), das (*Meles meles*) en (verwilderde) huiskat (*Felis catus*). In tegenstelling tot het onderzoek van 1989 zijn er geen sporen van damherten (*Dama dama*) gevonden. Edelhert en wild zwijn maken gebruik van wissels als ze het wildviaduct passeren. Er is geen voorkeur gevonden voor het passeren van het wildviaduct over het middelste gedeelte dus de dieren vermijden de zijkanten van het wildviaduct niet. De wissels op de Woeste Hoeve worden in dezelfde mate gebruikt als de wissels in het natuurgebied aan de westkant en minder dan de wissels aan de oostkant. Doordat

de wisseldichtheid op de Woeste Hoeve hoger is, is het aantal passages per meter op de Woeste Hoeve gelijk aan het aantal passages per meter in het omringende natuurgebied. De Woeste Hoeve wordt op een regelmatige basis gebruikt door grote zoogdieren. De mate van gebruik is gelijk aan die van het omringende natuurgebied. Hieruit kan geconcludeerd worden dat de Woeste Hoeve met een breedte van 50 meter voldoet voor een regelmatig gebruik door middelgrote tot grote zoogdieren en hiermee succesvol twee gebieden van de Veluwe met elkaar verbindt.
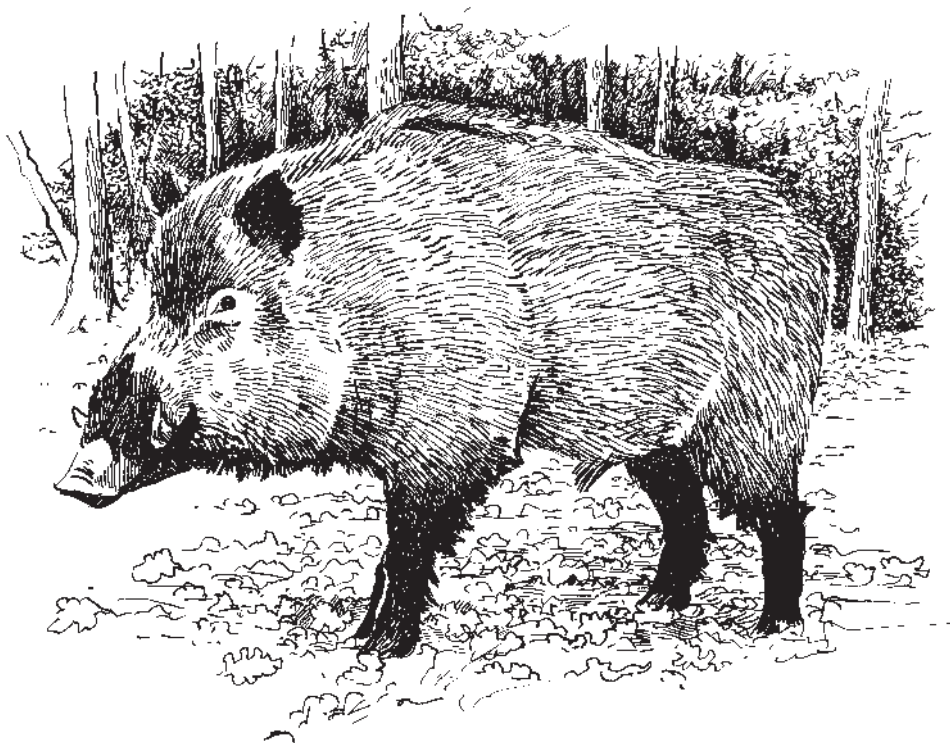
Nathusius' pipistrelles (*Pipistrellus nathusii*) and other species of bats on offshore platforms in the Dutch sector of the North Sea

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Abstract: Between 1988 and 2007, 34 reports of bats were received from offshore platforms in the Dutch sector of the North Sea. These reports involved Nathusius' pipistrelle (*Pipistrellus nathusii*) (26x), noctule (*Nyctalus noctula*) (2x), northern bat (*Eptesicus nilssonii*) (2x), serotine (*Eptesicus serotinus*) (1x) and parti-coloured bat (*Vespertilio murinus*) (3x). Their distribution over the 65 offshore platforms in the Dutch sector of the North Sea is described. A population of Nathusius' pipistrelle on the mainland, monitored in bat boxes located in the north of North Holland Province was used to compare sex ratio, age composition, body condition and biometrics with the bats found on offshore platforms. Since the first report of a bat on a platform in the Dutch sector of the North Sea in 1988, there has been an increase in the number of bats reported from offshore platforms over five yearly periods, with the maximum number (15) occurring between 1998-2002. The records of Nathusius' pipistrelle and most other bat species (with the exception of the noctule) on offshore platforms show no demonstrable bias towards platforms closer to the shore (most were recorded as distances of 60-80 km from the shore). Eighteen adult Nathusius' pipistrelles have been recorded on offshore platforms in the Dutch sector of the North Sea, and 6 in their first calendar year. Half of the males (50%) were juveniles, while 87% of the females were adults. The sex ratio of Nathusius' pipistrelles was biased to males during the autumn migration, whereas in spring most bats were females. No significant correlation was found in the numbers of reported Nathusius' pipistrelles in autumn or spring and wind speed or prevailing wind directions, suggesting the bats were not blown off course. The body mass of both male and female Nathusius' pipistrelles from offshore platforms was on average lower than for those from bat boxes in mainland North Holland.

Keywords: bats, oil platform, oil rig, offshore platform, Nathusius' pipistrelle, noctule, northern bat, parti-coloured bat, serotine, The Netherlands, North Sea, distribution, migration.

Introduction

Since the mid 1980s, there have been reports of the presence of various bat species from offshore platforms in the Dutch sector of the North Sea. These reports included recoveries of Nathusius' pipistrelle (*Pipistrellus nathusii*), noctule (*Nyctalus noctula*), northern bat (*Eptesicus nilssonii*), serotine (*Eptesicus serotinus*) and parti-coloured bat (*Vespertilio murinus*) (Boshamer 1993 & 1998). With the exception of the *Eptesicus* genus, these are all migratory species; the serotine is known to be a non-migrant species, while the northern bat is capable of long distance flights that could be interpreted as migration (Dietz et al. 2007).

The discovery of a bat on a platform usually starts with visual observations of the bat flying around the structure. When the bat's hiding place is found it can normally readily captured, in contrast to bats found in hides on the mainland.

There are very few published accounts of bats on offshore installations in the North Sea. In this paper, we report on the frequency of occurrence of bats on offshore platforms in the Dutch sector of the North Sea and describe the spatial pattern of their offshore distribution in

terms of the distances (km) from the coast. We examined the prevailing weather conditions when the bats were recorded, evaluating wind directions and speeds to investigate the hypothesis that the bats may have been blown off course during their natural migration and ended up seeking refuge at offshore platforms (Swift 1998). In addition, we address other questions, particularly with regard to the Nathusius' pipistrelle, about any possible differences in the sex ratio, age composition, body condition, or biometrics of bats found on offshore platforms and on the adjacent mainland. These issues are relevant in revealing the origin of the bats involved (i.e. whether they are an identifiable subpopulation of this species), or to see if a particular type of bat is more prone to drift into the open sea. For example, individuals with longer forearms may have a greater flight capacity (Bogdanowicz 1999). A population of Nathusius' pipistrelles, monitored in bat boxes in the north of the province of North Holland, was used to compare the results.

We provide a description of the migration patterns of the Nathusius' pipistrelle and other bats (as far as these are currently understood) to aid the interpretation of the offshore results. We also studied data collected from the Dutch Wadden Islands and other islands in the North Sea to get an idea of any further species of bats that are likely to be encountered on offshore platforms in the Dutch sector of the North Sea.

The Nathusius' pipistrelle and other bats are listed under the Convention on the Conservation of Migratory Species of Wild Animals (Bonn 1997; Agreement on the Conservation of Bats in Europe). This status, and the duty to take care of individual animals, should stimulate efforts to protect and rescue these animals when they have landed on offshore platforms. Requests were made to the oil-producing companies to capture and report bats and to organise proper care prior to rehabilitation attempts and release on land. Bat conservation organisations could help in this by drafting a protocol for staff on offshore platforms, describing how to handle and keep bats while they remain on board and how the animals should be transported to the coast.

Material and methods

Study area

This paper lists the bats recorded and captured at offshore platforms in the Dutch sector of the North Sea (the prime study area), situated at 51°-56°N latitude and 2°-7° E longitude. Since 1975 there has been a gradual increase in number of oil and gas producing platforms in the North Sea. In 2006 there were approximately 270 platforms and 15 light vessels or semi submersible crane vessels in the North Sea at large (figure 1). In interpreting the results we do not make any difference in this paper between platform type: oil platforms, gas platforms, and other semi submersible crane vessels are all referred to as 'offshore platforms' or 'offshore installations'. Within the study area, there were approximately 61 offshore installations in 2006, in the Zuidwal, Ameland, De Ruyter and Hanze oil fields, located in quadrants E, F, K, L, P and Q. The geographical positions of these offshore platforms were taken from a nautical chart of the North Sea (Charts and Publication 2001, with supplements up to 2006) and were measured with a chart compass (degrees and minutes N latitude and W longitude / E longitude). Some of these offshore platforms have subsequently been moved for maintenance or exploration.

Material

Between 1988 and the end of 2007 all bats reported on offshore platforms in the Dutch sector of the North Sea were captured by hand and directly transported to Den Helder Airport by helicopter. The first named author has been responsible for receiving the animals and taking them into care. After care (water and meal-worms), the animals were identified using Schober and Grimmberger (1987, 2001). Standard data has been collected about the species, date of capture, sex, forearm length, body mass and overall condition of all these captured bats. Age categories were determined according to the pattern of closure of the cartilaginous epiphyseal growth plates in long
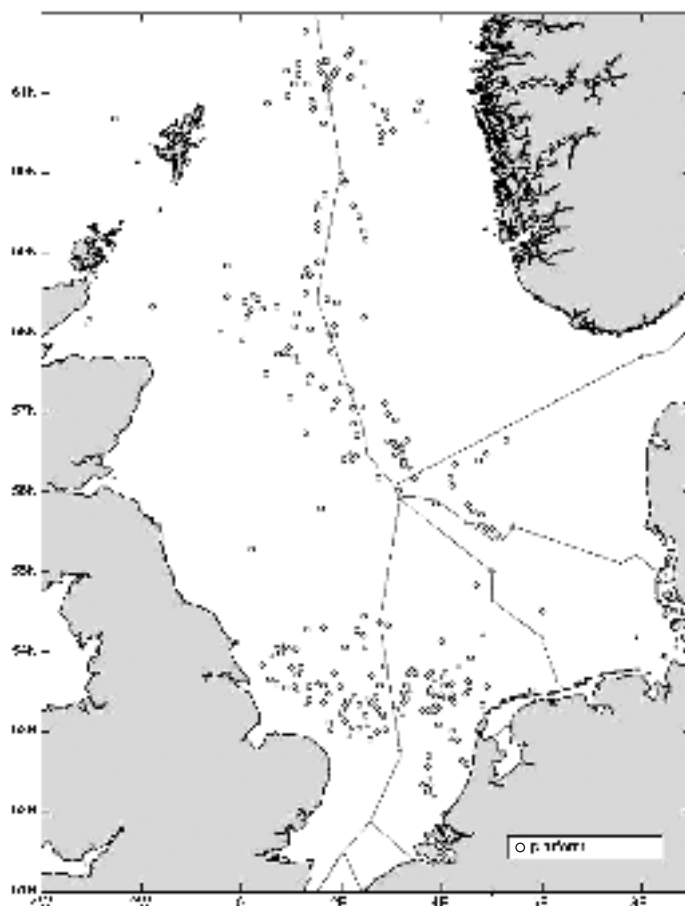
Figure 1. Positions of offshore platforms in the North Sea, with territorial borders of the Netherlands, the UK, Norway, Denmark and Germany.

bones, the shape of the finger joints and dental wear. The body mass of all animals was determined with a Pesola 20 grams (eventually 100 grams) steelyard and the length of the forearm was measured with vernier callipers (accuracy 0.05 mm). The names and geographical positions of the offshore platforms where the bats came from were provided by the Airport Authority. From 1991 through to 2006, all Nathusius' pipistrelle bats were ringed and set free in Julianadorp (52° 53'N 4°44'E). The distances (km) between the offshore platform and the nearest shore have been determined using Google Earth.

Since 1987 a population of mainly Nathusius' pipistrelles (*n*=1431) has been monitored in bat boxes in the north of North -Holland Province (photo 1). In the summer of 1990, 175 bat boxes were set out over six areas of forest. Since 1991, the sex, age, and some biometrics of the bats in these boxes have been recorded, including body mass and right forearm length. All these bats were banded (with the Bat ring developed by the Natural History Museum, Bonn, Federal Republic of Germany). Currently, there are six areas with 180 bat boxes that are checked every month (and more often during the autumn migration period). The locations are Robbenoordbos (State Forestry Service; 52°54'N 5°02' E, 30 bat boxes), Eendenkooi 't Zand (Landschap Noord-Holland; 52°49' N 4°47' E, 25 bat boxes), Noorderhaven

(Foundation 's Heerenloo; 52º53' N 4º46' E, 50 bat boxes), Eendenkooi Callantsoog (State Forestry Service; 52º50' N 4º42' E, 25 bat-boxes), 't Wildrijk (Landschap Noord-Holland; 52º47' N 4º41' E, 40 bat boxes), and Het Paardenweitje (State Forestry Service/Forestry Schoorl; 52º41' N 4º40' E, 10 bat boxes) (Boshamer 2005). The data gathered during this study formed the background material to interpret data collected from Nathusius' pipistrelles from offshore platforms. Body mass and forearm length of other bats have been compared with the measurements as described in Dietz et al. (2007).

Completeness of material

Since 1998 the first author has kept records of the numbers and species of bats reported on offshore installations within the Dutch sector of the North Sea. Figure 1 shows that the offshore platforms are unevenly distributed over the North Sea and this spatial pattern may have influenced the number of reported animals form different parts of the study area. Relatively more reports

have been received from the L10 grouping of offshore platforms (Gaz de France) where several staff members seem to have a genuine interest in birds and bats. This could skew the results since interested people are more likely to send in specimens than those who are indifferent. To stimulate wider interest, some articles were published in the offshore industry newsletters, highlighting recent sightings and attempts to rescue bats found on board offshore installations. The sightings should be considered as incidental ones since it is not possible to make any observer-effort correction for any of the trends and patterns described in this paper.

Analyses

Vierhaus (2004) mentions migratory routes of Nathusius' pipistrelles along coasts, following linear landscape elements and roosting by day in groves. They mostly travel from the northeast to the southwest in autumn (and in the opposite direction in spring), mostly following an assumed path along the North Sea coast, with a highest

Photo 1. Nathusius' pipistrelle (*Pipistrellus nathusii*) from a bat box in Noorderhaven, August 2003. *Photograph: Rollin Verlinde*.

density near the shoreline. Dietz et al. (2007) mentioned travelling distances of 29-48 (up to 80) km night[-1] for Nathusius' pipistrelles during migration. Nathusius' pipistrelles, as other bats, prefer to migrate at night, but sometimes do so by day, at periods of low wind-speed flying at 3-20 m altitude over the water. Our own observations during migration in autumn confirm this behaviour. Experienced birdwatchers know that many migrating passerines (Deelder 1949) and other flying migratory species, such as beetles and butterflies (Heydemann 1968) prefer to travel during periods of low wind-speeds, or with (strong) tailwinds. When flying into headwinds migrants fly closer to the surface, while tailwinds let them fly higher (Krüger & Garthe 2001). Migrants may drift into the North Sea during strong sidewinds.

Hence, strong southeast winds may blow migratory Nathusius' pipistrelles, travelling along the coast, off course and leading them to seek refuge at offshore installations. Bats tend to seek refuge during strong winds (>6B). Ahlén (2006) observed that foraging activity of bats around offshore windmills (3-10 km from the shore) ceased at 5 Beaufort or more, with peak activities recorded at 3 Beaufort.

Nathusius' pipistrelles, as well as other migrating bats, migrate along the coast in autumn and in spring. Prevailing wind direction and speed are clearly the only weather conditions that can act as a vector (wind-drift). Therefore we made the assumption that prevailing wind conditions, during the three full days prior to a bat's discovery on an offshore platform, may have influenced its whereabouts. If wind-drift were responsible for most of the offshore encounters, we would expect that many of the bats would have been found after periods of prevailing (strong) southeast (≥90° and ≤180°) winds and high daily wind-speeds (in m/s). Meteorological data were obtained from De Kooy weather station in Den Helder (KNMI 2007).

Apart from the wind direction and wind-speed, precipitation has also been taken into account. We have assumed that bats cannot fly during prolonged and heavy rain, that they only travel to sea when the weather is sufficiently dry or that they are more likely to seek refuge onboard offshore installations in rainy weather.

Autumn and spring migration periods of the Nathusius' pipistrelle movements have been defined as running between from 15 August to 1 November and from 15 March to 1 July.

Differences in the means of the continuous variables were tested by using the Student's t-test (two-tailed). χ^2 statistics were used to test differences in categorical data (Wijvekate 1976). Spearman's rank correlation test was used to test for correlation between a sequence of pairs of values (Boon 1979), with the upper and lower limits of the coëfficients retrieved from tables compiled by Diem & Lentner (1968). For all tests, the significance level was set at $P<0.05$.

Results

Between 1988 and 2007, 34 bats were received from offshore platforms in the Dutch sector of the North Sea (table 1). Most of the reports involved Nathusius' pipistrelle (26x); with some reports of noctules (2x), northern bats (2x), serotine (1x) and parti-coloured bats (3x).

Of these bats 14 were brought in during the spring migration and 18 during the autumn. Two bats were brought in outside of the prime migration seasons: a serotine on 28 July 1995 and a parti-coloured bat on 10 January 2006. Three Nathusius' pipistrelles were dead on arrival (2 and 4 October 2000, 10 October 2002) and a parti-coloured bat, received on 7 May 2006 had a fracture in the right forearm and was euthanized.

Since the first report of a bat on a platform in the Dutch sector of the North Sea in 1988 there has been an increase in the number of bats reported from offshore platforms in each five year period, with the most recorded between 1998 and 2002 (figure 2).

The mean distances between all offshore platforms in the Dutch sector of the North Sea and the Dutch coast is 66.2 km (min 5.3 km; max 168.5 km). Recordings of Nathusius' pipistrelle

Table 1. Reports of bats from offshore platforms in the Dutch part of the North Sea: 1988-2006.

| Date	Species	Sex	Age category	Name of platform
16-9-1988	Nathusius' pipistrelle	M	adult	Dan Earl
17-9-1993	Nathusius' pipistrelle	F	adult	Dan Earl
25-9-1993	northern bat	M	adult	K 12 B
1-10-1993	Nathusius' pipistrelle	F	adult	Meetpost Noordwijk
6-10-1993	Nathusius' pipistrelle	F	adult	J 6 A Markham AWG 1 Ameland
5-9-1994	noctule	F	adult	Westgat
10-9-1996	noctule	F	adult	L15 A
13-6-1997	Nathusius' pipistrelle	F	adult	Ensco 72
30-4-1998	Nathusius' pipistrelle	F	adult	Hoorn platform
10-6-1998	northern bat	F	adult	Unocal Horizon
19-4-2000	Nathusius' pipistrelle	F	adult	P 15 E Amoco
27-4-2000	Nathusius' pipistrelle	F	adult	L 10 F
20-5-2000	Nathusius' pipistrelle	M	adult	K 12 BP
22-9-2000	Nathusius' pipistrelle	M	1st year	K 12 E
2-10-2000	Nathusius' pipistrelle	M	1st year	P 6 Clyde
4-10-2000	Nathusius' pipistrelle	F	adult	L 7 Q Petroland
9-5-2001	Nathusius' pipistrelle	F	adult	F 3 B
5-6-2001	Nathusius' pipistrelle	F	adult	L 7 Q Petroland
31-3-2002	Nathusius' pipistrelle	F	adult	L 10 AD
18-5-2002	Nathusius' pipistrelle	M	adult	L 7 B Total Fina Elf
6-9-2002	Nathusius' pipistrelle	M	1st year	F 2 Hanse
11-9-2002	Nathusius' pipistrelle	M	1st year	L 8 P 4 Wintershall
10-10-2002	Nathusius' pipistrelle	M	adult	K 12 Bravo
6-10-2003	Nathusius' pipistrelle	M	adult	L 8 P 4 Wintershall
9-6-2004	Nathusius' pipistrelle	F	adult	D 15 A
23-8-2004	parti-coloured bat	M	adult	K 12 B
4-10-2004	Nathusius' pipistrelle	M	1st year	L 10 B
28-7-2005	serotine	F	1st year	K 15 B
2-9-2005	Nathusius' pipistrelle	F	1st year	K 15 B
10-1-2006	parti-coloured bat	F	adult	L 10 Alpha
3-5-2006	Nathusius' pipistrelle	F	1st year	L 10 Alpha
7-5-2006	parti-coloured bat	F	adult	K 4 B E
10-5-2006	Nathusius' pipistrelle	F	adult	L 10 Alpha
27-10-2006	Nathusius' pipistrelle	F	1st year	De Ruyter-rig
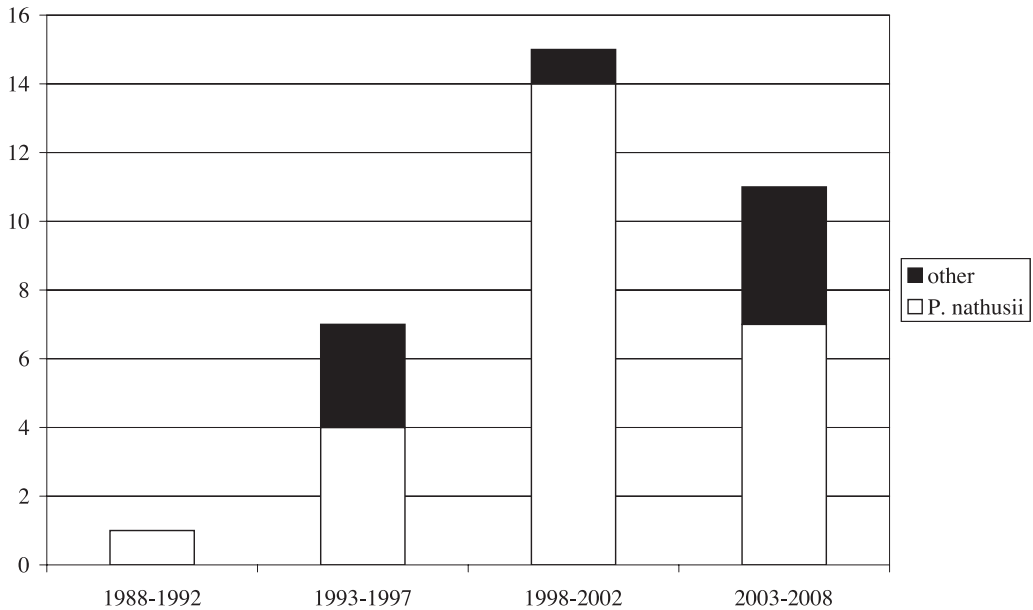
Figure 2. Numbers of reports of bats from offshore platforms in the Dutch sector of the North Sea.

Table 2. Mean distances in kilometres between offshore platforms in the Dutch Sector of the North Sea and the Dutch coast for Nathusius' pipistrelles and other species of bats; number (*n*) and probability of differences of mean distances between all offshore platforms and offshore platforms with species of bats in last column (Student's T-test; *P*<0.01).

	mean distance	*n*	*P*
All offshore platforms	66.20	61	1.00
Nathusius' pipistrelle males in autumn	55.80	8	1.00
Nathusius' pipistrelle females in autumn	67.13	5	0.12
Nathusius' pipistrelle males in spring	61.72	2	0.97
Nathusius' pipistrelle females in spring	65.39	11	0.96
Noctule	6.51	2	<0.01**
Northern bat	59.54	2	0.28
Serotine	61.44	1	-
Parti-coloured bat	83.34	3	0.49

and most other bat species show no obvious bias towards those offshore platforms closest to the shore. The exception to this was the noctule, which was more frequently reported from platforms closer to the Dutch coast (mean distance 8.1 km; n=2, Student's t-test: 10.02; P<0.01) (table 2).

Nathusius' pipistrelle

Most Nathusius' pipistrelles were received from offshore platforms situated between 60 and 80 km from Den Helder (figure 3). Of the 26 reported Nathusius' pipistrelles, 12 were collected during the spring migration and 14 during autumn (see table 1, figure 4).

Eighteen Nathusius' pipistrelles were adults and 6 animals were in their first calendar year. Males (n=10) and females (n=16) were found in spring and in autumn, but most females were captured earlier (April) and later (October) in the year than males, with male captures peaking in September. Half of the males (50%) were juveniles, while 87% of the females were adults (table 3). The sex ratio of Nathusius' pipistrelles

Figure 3. Distribution of reported Nathusius' bat (*Pipistrellus nathusii*) from offshore platforms in the Dutch sector of the North Sea.

was biased towards males during the autumn migration, whereas in spring most bats were females (table 4).

Correlation between body mass and distance of the offshore platform to the Dutch shore was compared using Spearman's rank correlation test. No positive nor negative correlations were found for the whole sample of Nathusius' pipistrelles (n=23, R=2684, 0.1<P<0.9), for males (n=8, R=88, 0.1<P<0.9), females (n=15, R=704,5, 0.1<P<0.9), or for specimens found in autumn (n=9, R=181.5, 0.1<P<0.9) or spring (n=14, R=526, 0.1<P<0.9).

The autumn migration periods (15 August and 1 November) between 1988 and 2007 contain a total of 1,519 days. On 309 of those days the prevailing winds were from the south-east and on 1,210 of those days the winds were non-south-easterly. 14 Nathusius' pipistrelles were found on offshore platforms in autumn, so the reports of prevailing wind directions were checked for 42 days (=14*3). The expected prevailing wind directions were 2.85 (=14*309*1,519^{-1}) from the south-east and 11.15 (=14*1,210*1,519^{-1}) from non-south-east directions. The observed prevailing wind directions were 5.67 (17*3^{-1}) from the south-east and 8.33 (25*3^{-1}) from non-south-east directions. Applying Chi-square test, there was no significant difference in the numbers of reported bats in autumn and the prevailing wind directions (south-east and non-south-east - χ^2=2.01, df=1, P=0.07).

The daily mean wind-speed for the 14 Nathusius' pipistrelles in autumn on offshore platforms was on average lower, but not significantly so, than for the rest of the days (5.03 m/s, n=42 respectively 5.45 m/s, n=1519; Student's t-test: 1.53, P=0.13). However, selected for prevailing wind directions from the south-east (n=17 respectively n=309 days) the average daily mean wind-speed was (almost significantly) higher than for other days (5.10 and 4.49 m/s respectively; Student's t-test: 1.89, P=0.07).

Migration periods in spring between 15 March and 1 July, total 2,124 days. On 246 days the prevailing winds were from the south-east: non-south-east wind directions accounted for the other 1,875 days. The 12 Nathusius' pipistrelles
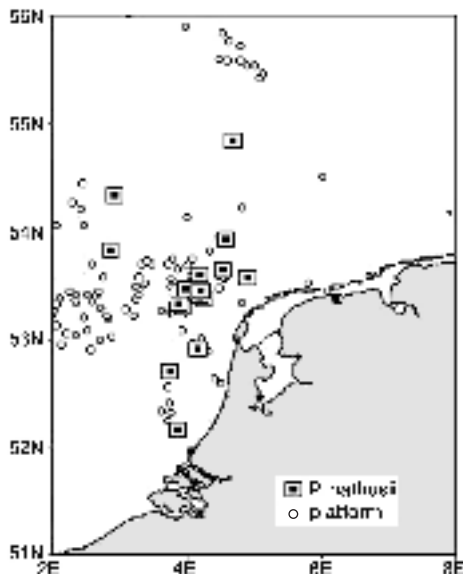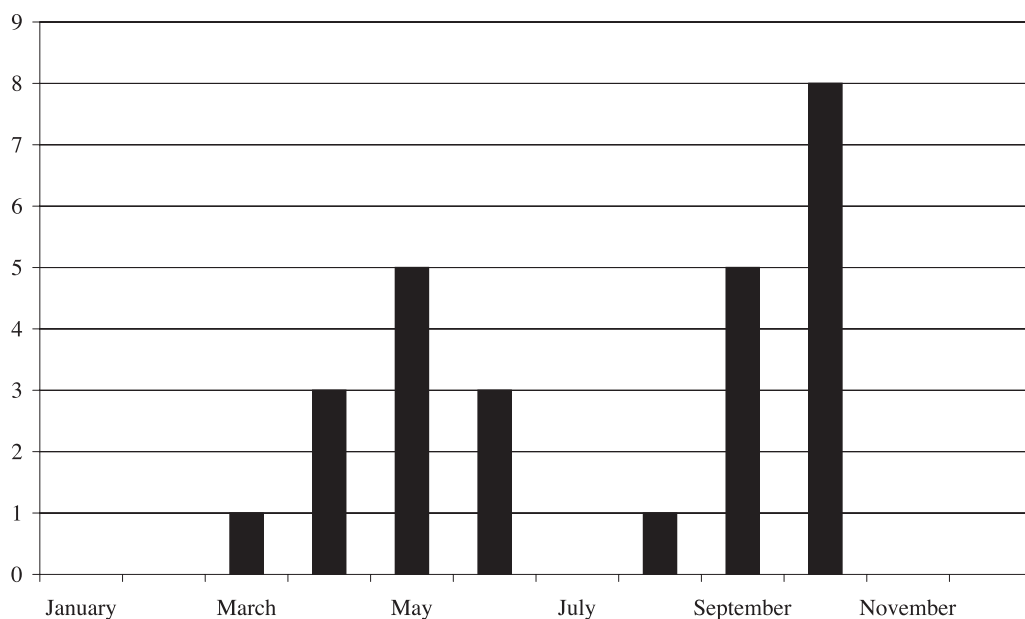
Figure 4. Monthly distribution of reported Nathusius' bat (*Pipistrellus nathusii*) from offshore platforms in the Dutch sector of the North Sea.

on offshore platforms in spring resulted in 36 (=12*3) prevailing wind direction reports. The number of expected prevailing wind directions were 1.39 (=12*246*2,124^{-1}) from the south-east and 10.61 (=12*1878*2,124^{-1}) from non-south-east directions. The numbers of observed prevailing wind directions were 3.00 (9*3^{-1}) from the south-east and 9.00 (27*3^{-1}) from non-south-east directions: the difference in the numbers of reported bats in spring between prevailing wind directions from the south-east and non-south-east was not significant (χ^2=2.01, df=1, *P*=0.16).

The daily mean wind-speed at the time that the 12 Nathusius' pipistrelles were recoded on offshore platforms in spring was on average equal to that on other days (5.42 m/s, *n*=36 respectively 5.44 m/s, *n*=2,124; Student's t-test: 0.06, *P*=0.95). Selected for prevailing wind directions from the south-east (*n*=9 respectively *n*=246 days) the average daily mean wind-speed was higher than for the other days, however, the difference was not significant (4.93 and 4.77 m/s respectively; Student's t-test: 0.35, *P*=0.74).

The body mass of male Nathusius' pipistrelles from offshore platforms (excluding specimens dead when received) was on average lower than for males from bat boxes in mainland North Holland (5.46 g, *n*=8 and 7.90, *n*=699 respectively; Student's t-test: 10.95, *P*<0.01). For female Nathusius' pipistrelles the average body mass was also lower among those from offshore platforms than from bat boxes (6.04 g, *n*=15 and 9.17 g, *n*=738 respectively; Student's t-test: 13.19, *P*<0.01). Figures 5a and 5b illustrate the monthly percentiles in body mass of Nathusius' pipstrelles from bat boxes in North Holland with those from offshore platforms. Both box plots indicate that the Nathusius' pipistrelles from offshore platforms in all months had, on average, lower body masses compared to the animals found in bat boxes. Between April and October, six of the eight live males were under the 5th percentile and two were between the 5th and 25th percentile of animals found in bat boxes. Four of the fifteen live females brought from offshore platforms between March and October were be-

Table 3. Reported Nathusius' pipistrelles (*Pipistrellus nathusii*) from offshore platforms; showing differences in the age categories and sex (χ^2=4.06, df=1, *P*=0.04*).

Age category	Male	Female	Total
Adult	5	13	18
1st year	5	3	8
Total	10	16	26

Table 4. Reported Nathusius' pipistrelles (*Pipistrellus nathusii*) from offshore platforms; showing differences between seasonal distribution and sex (χ^2=5.61, df=1, *P*=0.02).

Season	Male	Female	Total
Spring	2	10	12
Autumn	8	6	14
Total	10	16	26

low the 5th percentile and ten between the 5th and 25th percentile. The female with a body mass that was close to the median of animals found in bat boxes, was reported from Meetpunt Noordwijk, 10 km offshore.

The average length of the forearm of Nathusius' pipistrelles from the offshore platforms was on 33.61 mm and 34.17 mm, for males and females respectively, both within the ranges of male and female length of forearm (32.6-34.5 and 33.0-35.5 respectively) in Nathusius' pipistrelles from the mainland study area.

Noctule

One noctule (body mass 23 g, 11 km from the shore, wind: NW 3-4B, rainy weather) was received from platform L 15 A, another (body mass 20.5 g, 5 km from the shore, wind: NE 2B, dry weather; figure 6) from a survey station north of Ameland.

Northern bat

On 25 September 1993 an adult male northern bat (body mass 8 g, 69 km from the shore, wind: NE 2-3B, some showers) was found at platform K 12 Bravo. The bat was lean, but otherwise in good condition and this was the first documented case of this species in the Dutch sector of the North Sea (Boshamer 1993). In June 1998, an adult female (body mass 7.6 g, 50 km from the shore, wind: SW 4-6B, rainy weather; figure 6) was found at the Unocal Horizon Platform.

Serotine

On 28 July 2005 a first calendar year female serotine (body mass unknown) was collected from platform K 15B (61 km from the Dutch coast, wind: E→NW→W gentle breeze 2-3B, some rain; figure 6). This is the first documented case of this species in the Dutch sector of the North Sea. .

Parti-coloured bat

In August 2004 a male was brought in to Den Helder Airport from K 12 Bravo (69 km from the shore, wind: SW→N 2B, some rain). Eighteen months later a healthy female was reported from L 10 Alpha on 10 January 2006 (48 km from the shore, wind: E→SE 3B, -1 C°, no rain; photo 2). The last report from an offshore platform (figure 6) was from 7 May 2006 when an adult female was reported from K4BE (124 km from the shore,
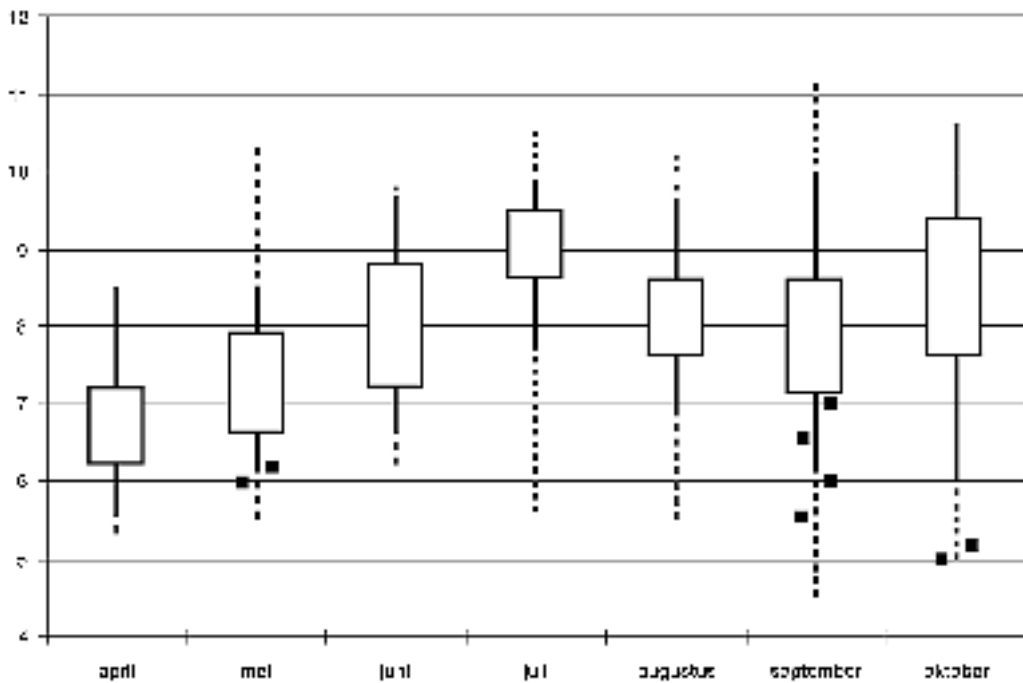
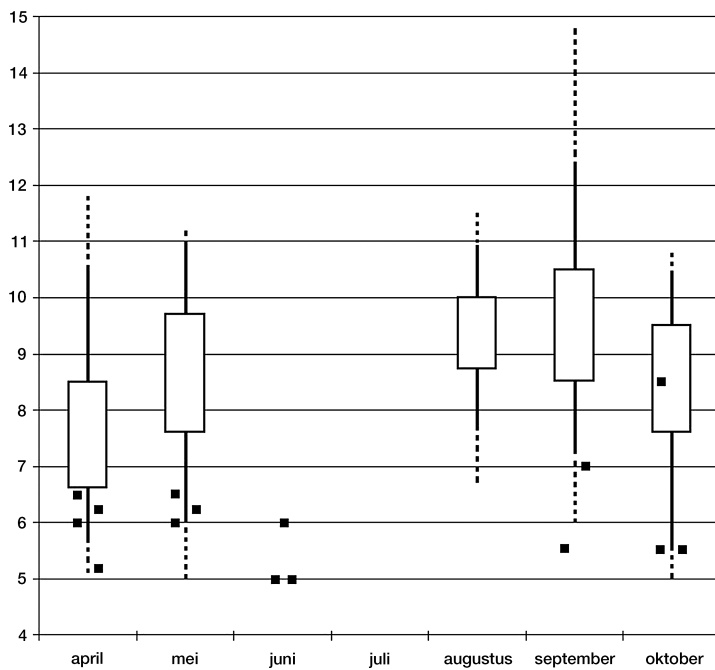**A**

Figure 5. Box plots of the body mass of males (a) and females (b) Nathusius' pipistrelle (*Pipistrellus nathusii*) from on shore bat boxes (100%-95%-75%-25%-5%-0%) and from offshore platforms (black squares).
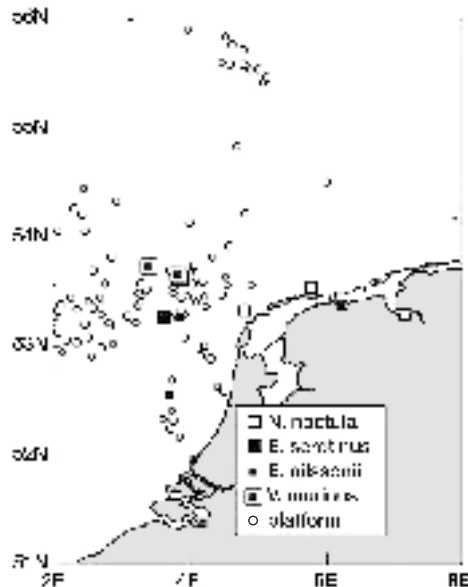
B

Figure 6. Distribution of noctule (*Nyctalus noctula*), northern bat (*Eptesicus nilssonii*), serotine (*Eptesicus serotinus*) and parti-coloured bat (*Vespertilio murinus*) reported from offshore platforms in the Dutch sector of the North Sea.

wind: E 3-4B, no rain). The body mass of the first two specimens was 11.5 and 12 g respectively, while that of the last one was not measured (normal range 10-15 g; Dietz et al. 2007). The oil offshore platforms where these recording were made were on average 83.3 km from the coast (*n*=3, sd=5.07).

Discussion

Bat spectrum

The species composition of bats found offshore differs greatly from those found in the adjacent coastal mainland area. Nathusius' pipistrelles and noctules are common species along the coast, but only the former was recorded in some numbers offshore. Records of northern bat represent new sightings within the Dutch sector of the North Sea (Boshamer 1993, Boshamer 1998). Common pipistrelles (*Pipistrellus pipistrellus*) common as a species on land, were not found on offshore installations.

Because of their position, and their orientation, which forms an extension of the Northern Dutch

coastline The Wadden Islands are of particular interest for bats migrating along the coast. Table 5 compares all the species of bats (and their respective numbers) found on offshore platforms in the Dutch sector of the North Sea with the species of bats found on the Wadden Islands and the mainland of North Holland (numbers in km^2). The most common bats on the Wadden Islands are serotine and Nathusius' pipistrelle. Common pipistrelle and Daubenton's bat (*Myotis daubentonii*) occur in small numbers. Noctule and pond bat (*Myotis dasycneme*) are rare on the Wadden Islands. Daubenton's bats migrate over short distances at best, so it is understandable that this species, restricted to small, fresh waters, does not naturally occur over the sea. Pond bats are observed over large open water areas (such as the fresh-water IJsselmeer and the salt-water Wadden Sea) their migration to wintering areas up to 330 km away from their breeding grounds could lead to some individuals going astray in unfamiliar areas. Although by far the most numerous bat on the mainland, the common pipistrelle occurs only in low numbers on the Wadden Islands.

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Photo 2. Parti-coloured bat (*Vespertilio murinus*) ♀, from platform L 10 A, 53º24'N, 04º12'E, 10 January 2006. *Photograph: Bert Pijs.*

Observations by other bat workers illustrate the diversity of bat species found along the Northern European coastlines. Ahlén (2006) recorded 104 foraging Nathusius' pipistrelles near offshore windmills, using automatic recording bat detector devices at Kalmarsund, a 15 km wide strip within the Baltic Sea, and at Öresund, a 3 km wide sea strait between Denmark and Sweden. He also recorded the ultrasonic signals of noctule (287x), northern bat (29x), serotine (34x), parti-coloured bat (44x) and other species (323x). Skiba (2007) used bat detectors to record bats on the island of Helgoland (Germany) (36 days between 2000 and 2006) and on the island of Borkum (8 days in 2006) during autumn migration (from one hour after sunset until 01.00 h). On Helgoland this resulted in recordings of Nathusius' pipistrelle (84x), noctule (12x), Leisler's bat (*Nyctalus leisleri*) (1x) and common pipistrelle (8x). In Borkum the recordings were of Nathusius' pipistrelle (37x), pond bat (3x), Daubenton's bat (2x), common pipistrelle (9x), northern bat (29x), serotine (1x) and parti-coloured bat (1x). It would be interesting to replicate these experiments and set up an automated system recording ultrasonic echolocation signals from offshore platforms

all over the (Dutch part of the) North Sea. Such devices would not only produce considerably more 'sightings' of bats at sea, but also provide data that can be corrected for spatial and temporal patterns in observer effort.

Leisler's bat is another migratory species (Dietz et al. 2007), but there have been no reports from offshore platforms in the Dutch sector of the North Sea. On 5 September 1979 a dead adult female was reported on the Isle of Texel (53º 05' N, 4º 45' E; Boshamer 1991). In October 1990, the first named author obtained an adult female captured in Nieuw Den Helder (52º 56' N, 4º 44' E). Further south, an observation was made of a Leisler's bat on 28 September 1992 near the lighthouse on the Maasvlakte (Mostert & Wondergem 1993). This species is occasionally observed in the Netherlands in the eastern parts of Gelderland and Limburg provinces, but it is common in Britain. The Leisler's bats on the Wadden Islands and the Maasvlakte were far from their usual distribution range and their presence can be directly related to migration above and along the North Sea coast.

Walter et al. (2007) referred to a Leisler's bat found at the Uisge Gorm floating production and

Table 5. Species of bats in square kilometres on offshore platforms in the Dutch sector of the North Sea, the Wadden Islands and Noord-Holland. "Other species" of bats include whiskered bat (Myotis mystacinus), Natterer's bat (Myotis nattereri), greater mouse-eared bat (Myotis myotis) and greater noctule (Nyctalus lasiopterus) (after Kapteyn 1995, Vos 2007 and Kees Verschoor, personal communication).

	Offshore platforms	Wadden Islands	North Holland
Nathusius' pipistrelle	17	20	755
Noctule	2	7	237
Northern bat	2	0	0
Serotine	1	66	1032
Parti-coloured bat	3	0	4
Pond bat	0	5	546
Daubenton's bat	0	3	286
Common pipistrelle	0	10	1075
Leisler's bat	0	1	1
Brown long-eared bat	0	4	88
Other species	0	0	40

storage vessel in spring 2002. Skiba (2007) described a dead Leisler's bat from Memmert (East Frisian Isles - Germany) discovered on 11 June 1961. Corbet (1970) mentions this species being spotted at Nissetter, Shetland, on 24 July 1968. Baagøe and Bloch (1994) report an adult male observed on the landing strip of Mykines on the Far Oer (Denmark) on 28 June 1984. As this species has been reported on offshore platforms and islands in the North Sea (non Dutch sectors), it might be well possible that it will be found in the future on offshore platforms in the Dutch sector of the North Sea.

There have been incidental reports in British literature of brown long-eared bats (*Plecotus auritus*) being found far from the coast. Corbet (1970) mentions a group of brown long-eared bats 70 km off the coast of Yorkshire in November 1948 and a dead animal on a light ship (50 km east of Norfolk in October 1968). Hutson (1996) reports a brown long-eared bat on an offshore platform in the North Sea, 150 km off the coast in September 1996. Further afield, Barrett-Hamilton (1910-1911) reported two autumn records of brown long-eared bats on offshore lighthouses in Ireland. These observations suggest that this species might also be expected to be found on offshore platforms in the Dutch sector of the North Sea.

A grey long-eared bat (*Plecotus austriacus*) was found 18 km south of Bognor Regis (Sussex) in 1969 (Corbet 1971) in the British sector of the Channel. However, based on the distribution of this species in the Netherlands (where it is only found in the southern provinces of Zeeland, North Brabant and Limburg) its occurrence on offshore platforms in the Dutch sector seems unlikely.

Nathusius' pipistrelle

In this study the presence of Nathusius' pipistrelles on offshore platforms during migration cannot be explained as a result of the influence of prevailing south-easterly wind directions, nor of the daily mean wind speed. In autumn the daily mean wind speed during the relevant days on which the 14 Nathusius' pipistrelles were found was on average lower (though not significantly so) than on other days. However when selected for prevailing south easterly wind directions, the daily mean wind-speed was on average higher (almost, but not quite significant).

In our study strong winds (>5 and 6 Beaufort) occurred only occasionally in autumn and spring, on 12% and 28% respectively of the rest of the days when bats arrived at platforms, suggesting that wind-speed was not a major limiting factor for migration over sea. Vierhaus (2004)

mentions autumn migration peaks during periods with light to moderate breeze from a southerly or easterly direction. Nathusius' pipistrelles will seek refuge during periods of strong winds (Walter et al. 2007): offshore platforms or vessels are the only available options at sea.

In addition to records from offshore platforms, there are several records of bats visiting vessels travelling across the North Sea (all these instances concerned Nathusius' pipistrelles). In 1978 the first named author obtained a Nathusius' pipistrelle found onboard the hydrographical survey vessel Hr. Ms. Blommendal. On 14 September 2006, a Nathusius' pipistrelle flew in broad daylight towards a ship with bird observers and landed on board where it was caught, 22 km northwest of Den Helder (K. Mostert, personal communication). A male Nathusius' pipistrelle flew towards a beamtrawler (TX1), 60 km northwest of Den Helder (location 53˚ 07' N, 03˚ 05' E) in broad daylight on 13 October 2006. One week later, a Nathusius' pipistrelle landed on board beamtrawler TX 48, also in broad daylight (P. Bonnet, personal communication). Vauk (1974) recalls an incident with this species being captured onboard a vessel steaming between Amrum and Helgoland on 3 September 1927.

In November 1940, a male Nathusius' pipistrelle was found on Whalsay (Shetland Isles), the first ever sighting in Britain (Herman 1992). Until 1984 there had been only three documented observations in the British Isles (Stebbings 1988), but given recent reports of 'songflighting' males, copulating pairs and the presence of maternity colonies of Nathusius' pipistrelle, the species now must be regarded as a resident breeding species in this country (Russ et al. 2001).

Since 1984, several Nathusius' pipistrelles have been found on ships or offshore platforms in the British section of the North Sea (>10; Russ et al. 2001) and on remote British islands, particularly the Shetlands (more than twelve before 2000). There seems to be an increase in the number of Nathusius' pipistrelles observed in the British sector of the North Sea, which is consistent with developments in the Dutch sector. However, it has not been possible to make a correction for observer effort to confirm this trend.

More dispersed sitings of Nathusius' pipistrelles include records from 1971 (male) and 1985 (female) from the south west of Iceland (Petersen 1994) and one individual on a platform off from Brønnøysund, about 250 km north of Trondheim, Norway in September 2006 (van der Kooij, in prep.). The two specimens from Iceland were probably ship-assisted transports (Petersen 1994), but Van der Kooij (in prep.) assumes that the animal off Brønnøysund was a genuine migrant.

The increase of records of Nathusius' pipistrelle in Britain has been interpreted as an expansion of the range of this species (Stebbings 1988). Given the frequent occurrence of migratory Nathusius' pipistrelles along northern European coasts, it is not surprising that some individuals are found on offshore platforms or vessels at sea near the coast. The number of animals reported from offshore platforms is probably only a fraction of the actual number of animals that migrate over the North Sea.

The average body mass of male and female Nathusius' pipistrelles from the offshore platforms was substantially lower than that of bats from the mainland reference population. However, their structural size (forearm length), was similar, suggesting that the offshore animals must have been in a relatively poor condition. Despite the absence of a negative correlation between the body mass of the Nathusius' pipistrelles and the distance from the shore of the offshore platforms from where bats were recovered from this does not support the supposition that stranded Nathusius' pipistrelles used too much energy (and body mass) during this part of their migration.

Russ et al. (2001) concluded that "the occurrence of *P. nathusii* in May on North Sea platforms is consistent with migration in a north-easterly direction". The finding of two females half way between the UK and the Dutch coast during spring migration is in line with this view (Russ et al. 2001). However, not all Nathusius' pipistrelles migrate in spring. Russ et al. (1998) suggested that in Britain, where the winters are relatively mild, Nathusius' pipistrelle might relinquish its migratory behaviour in favour of a

more sedentary lifestyle, demonstrated by their forming nursery colonies. It is remarkable that two females were found at offshore platforms during the breeding period (June) since female Nathusius' pipistrelles usually migrate to breeding areas in northeastern Europe and only occasionally stay in the Netherlands, (reproduction has been verified on one occasion in Jisp, North Holland by Kapteyn & Lina 1994).

The results suggest that Nathusius' pipistrelles (as well as other bats) seek refuge on offshore platforms only after they became exhausted. They then need to stay in the vicinity of the platform and try and replenish their fat reserves to be able to leave again.

Noctule

Noctules were observed on offshore platforms during periods of onshore winds, so wind-drift is an unlikely factor in explaining their presence at sea. Racey (1990) reported a noctule from Fulmar Alpha (56º 30' N, 2º 10' E). This species is known on two of the Wadden Islands (Boonman et al. 1997) with incidental occurrences reported from the Shetlands and Orkneys (Racey 1977) and Helgoland in Germany (Mohr 1931, Vauk 1974). Because of the relative abundance of noctules during the migration periods along coastlines of northwestern Europe, we would expect this species more often than it was reported on offshore platforms.

Serotine

This paper documents the first case of this species in the Dutch sector of the North Sea. The serotine was found after a period of gentle, initial easterly, later westerly breezes, with showers. This animal could have been blown off course. Vauk (1974) recalled an old report of a serotine from Helgoland (Germany). Hutson (1991) reported the discovery of a serotine on the Shetlands which Baagøe and Bloch (1994) describe as a vagrant or a ship-assisted transport. The few other reports in the literature suggest that any future recordings from offshore platforms for this, generally numerous, species of bat in northwestern continental Europe will be quite rare.

Northern bat

The northern bats recorded from offshore platforms were seen in conditions that did not support the wind-drift theory (a slight north-easterly breeze preceding the first case, strong south-westerly winds prior to the second report). Baagøe (1981) reported a northern bat on a platform off of Aberdeen and Baagøe and Bloch (1994) found several specimens on the Faroe Islands. A possible migrant relation with the record of this species from Betchworth, Surrey (UK) (Gerell & Rydell 2001) remains open. The island reports and those of Greenway and Hill (1987) of the northern bat from the British Isles support the supposed vagrant status.

Parti-coloured bat

The first recorded parti-coloured bat was preceded by a wind direction that might have driven the animal off course, but given the low wind velocity and the excellent flying capacities of this species (Dietz et al. 2007) we are tempted to conclude that the animal should have been capable of withstanding the weather conditions. The second parti-coloured bat was found in winter, at quite a low temperature (-1.7°C) following moderate easterly winds (3 B). The weather conditions preceding observation of the last individual were characterised by a persistent easterly wind of 3-4 B. Given the wind directions, all the specimens that were obtained could have been blown off to sea. Since 1977, the parti-coloured bat has been found more regularly in the Netherlands up to 60 km from the coast. Between 1977 and 1995, nearly half (11 out of the 24) of the reports of this species in the Netherlands were obtained from coastal localities (Hollander & Limpens 1997). Stebbings (1977) mentions three records in mainland Britain, two of which date back to the early nineteenth century (Plymouth and Yarmouth) and one from 1927 (Whalsay, Shetlands).

In June 1965, a parti-coloured bat was reported from an oil platform in the British sector of the North Sea, 285 km east of Berwick (Stansfield 1966). Hill and Smith (1988) mention this spe-

cies in 1985, also reported from an oil platform. Racey (1990) records observations from the Shetlands (1981 and 1984). Baagøe and Bloch (1994) report a parti-coloured bat in Sandavágur on the Faroe Islands on 27 June 1988. The parti-coloured bat has reached the British Isles, and therefore has crossed the North Sea several times, however, up until now no breeding colonies in the UK have been reported. In northern Germany, Skiba (2007) recorded this species with a batdetector on Borkum.

The general direction of autumn migration of parti-coloured bats in Western Europe is from northeast to southwest. However, some populations are not migratory (Dietz et al. 2007). Migratory distances of up to 180 km night^{-1} have been documented (Strelkov 1969); thus the bats found on platforms in the Dutch sector of the North Sea may have come from further away than the Dutch coast. The specimens reported from offshore platforms on the (Dutch sector of the) North Sea, therefore have to be regarded as vagrants.

Insect availability over the sea

Even if most bats on platforms were underweight and probably in a relatively poor condition, it is worth investigating the possibility that bats voluntarily fly over the North Sea to feed. If so, what might attract them? Could, as Oddane (2001) inquires, the bats be attracted to forage on insects? Butterflies, moths, beetles and countless flying bugs are all known to travel across the North Sea, or to be blown over the sea by offshore winds (Hardy & Milne 1938). Heydemann (1967), investigating the spectrum of insects on the lightship in front of the Elbe in the North Sea, 30 km from the coast, found 90% of the catches, lured with coloured dishes, to be Diptera; Lepidoptera and Coleoptera were also present. He also found that more active flying insects were caught in low wind-speeds. With increasing winds, passively transported aeroplankton (such as drifting ballooning small spiders) were observed. Winter (1995), sailing in the Dogger Bank area, described the contents of pellets produced by a common gull (*Larus canus*) in which hoverflies

(e.g. *Episyrphus balteatus*) were numerous. Observations onboard confirmed that the hoverflies were overabundant and taken in mid-air. Hoogendoorn (1997) reported black-headed gulls (*Larus ridibundus*) taking advantage of small spiders ballooning at sea, north of the Wadden Sea Islands. In exploring the phenomenon of insect migration, Drake and Farrow (1988) point to the importance of reverse circulation with alternating sea breezes at day and land breezes at night. Nocturnal flights of e.g. moths, several microinsects and ballooning small spiders are favoured by this situation. Most of these airborne insects fly for less than an hour, but other species fly for several hours, occasionally even all night.

The aerial plankton consist mainly of small or light-bodied insects with limited powers of flight but with a relatively large wing surface compared with body mass (Drake & Farrow 1988). It is unclear if this aerial plankton would be a suitable food source for bats flying above the sea or foraging from offshore platforms, due to the unpredictability of their presence. The low body mass of all bats found on offshore platforms may suggest that an adequate food supply over sea is very rarely available.

Predation

Various observers have reported bats flying onto ships in daytime. Bats at sea are very vulnerable to predatory birds and they are readily attacked. Bekker and Mostert (1991) report herring gulls (*Larus argentatus*) chasing and killing a bat flying near the sea surface in broad daylight. A similar incident was observed on 5 May 2006 near Huisduinen. An unidentified bat was chased by five herring gulls and was captured and eaten within ten minutes by one of the gulls (C. van der Vliet, personal communication). For bats, flying in broad daylight across the North Sea must be a risky business.

Light

The presence of 270 offshore platforms in the entire North Sea is one of many anthropogenic factors that may influence the presence and behaviour of fauna in various ways. Because offshore

platforms are stationary objects at sea, they are brightly illuminated, and thus have a clear beacon effect at night, being much more brightly lit than moving vessels. Although it is known that bats generally avoid artificial lighting, this raises the question of whether the brightly lit offshore platforms attract bats flying above the sea in the dark. Is the strong lighting as attractive to bats as it is to migrating birds? Another question raised is, whether, and to what extent, the lights attract insects in the summer, thereby providing an attractive source of food for bats travelling these waters? Incidental observations from ships show that bats leave ships by themselves once these vessels arrive at a harbour.

Answering these questions, and exploring relations with other (sub) populations of Nathusius' pipistrelle, as proposed by Dietz et al. (2007), will require a joint effort from all the countries surrounding the North Sea in conducting further research that can individually identify migrating bats with rings so and establishing the relations between different populations by means of tissue DNA samples from the wing membrane.

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Samenvatting

Ruige dwergvleermuizen (*Pipistrellus nathusii*) en andere vleermuissoorten op offshore-platforms in het Nederlandse deel van de Noordzee

In deze bijdrage worden de waarnemingen tussen 1988 en 2007 beschreven van vleermuizen afkomstig van offshore-platforms van het Nederlandse deel van de Noordzee. Het betreft merendeels ruige dwergvleermuizen (*Pipistrellus nathusii*) (*n*=26), maar ook rosse vleermuizen (*Nyctalus noctula*) (*n*=2), een laatvlieger (*Eptesicus serotinus*) en tweekleurige vleermuizen (*Vespertilio murinus*) (*n*=3) werden gemeld. Een voor het Nederlandse faunagebied nieuwe soort was de noordse vleermuis (*Eptesicus nilssonii*) (*n*=2). Alle vleermuizen werden aangeleverd via Den Helder Airport. Na ontvangst werden de dieren gedetermineerd, gesekst, opgemeten en gewogen. Tevens werd een indicatie van de leeftijd gemaakt aan de hand van de verbening van de epifysen en tandslijtage. Er blijkt, over periodes van vijf jaar gemeten, een toename van de aantallen aangebrachte vleermuizen met een piek in de periode 1998-2002. Voor ruige dwergvleermuizen van offshore platforms werd een vergelijking gemaakt met soortgenoten die sinds 1991 in vleermuiskasten in de Kop van Noord-Holland werden aangetroffen. De verdeling van de leeftijden en de geslachten bij de ruige dwergvleermuis blijkt te verschillen: van de mannen waren even veel adulte als jonge dieren (5 respectievelijk 5) terwijl bij de vrouwen er meer oudere dieren waren (13 respectievelijk 3). De verdeling van de geslachten over de jaargetijden bij de ruige dwergvleermuis blijkt ook te verschillen: van de mannen werden er 2 in de lente en 8 in de herfst op offshore platforms aangetroffen; bij de vrouwen waren die aantallen respectievelijk 10 en 6. Zowel mannelijke als vrouwelijke dieren afkomstig van offshore platforms hadden een significant lager gewicht. Bij analyse van de weersomstandigheden tot drie dagen voor de vangst op de offshore platforms is het niet aannemelijk gemaakt dat er meer ruige dwergvleermuizen werden gevonden na perioden met wind uit het zuidoosten. Het lijkt niet aannemelijk te zijn dat vleermuizen door voedsel boven zee zijn geraakt. Gezien het nog steeds toenemende scheepvaartverkeer, de intensivering van de winning van olie en gas, en de plaatsing van windturbineparken voor de kust mag verondersteld worden dat er in de nabije toekomst nog veel meer vleermuizen zullen worden aangeleverd. Ook in de andere sectoren van de Noordzee zullen vaker vleermuizen offshore gemeld gaan worden. Het spectrum aan soorten die er boven het Nederlands deel van de Noordzee worden waargenomen zal wellicht nog vergroot worden met bosvleermuis en mogelijk meervleermuis. Het is belangrijk dat de gegevens ter beschikking komen van al diegenen die werken aan het vergroten van de kennis en bescherming van deze diergroep. Zeker voor migrerende vleermuizen is internationale samenwerking noodzakelijk voor deze ook internationaal beschermde diergroep (Convention of Migratory Species of Wild Animals (Bonn 1997); Agreement on the Conservation of Bats in Europe).

Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*)

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Abstract: A population of pond bats (*Myotis dasycneme*) inhabits a network of foraging areas and separate male, female-breeding and temporary colonies. These are interconnected by commuting routes which are also used for foraging. The functioning of these networks is crucially important for the conservation of the species. Observations and anecdotal evidence suggest that light may be an important source of disturbance along commuting routes and potentially affect the connectivity of the networks. The disturbing effects of light on pond bats were experimentally studied by placing a strong lamp (1000 W) along existing pond bat commuting routes. Each experimental site had specific characteristics which allowed us to explore the interacting effects of light disturbance and the environment. The number of passing bats, the percentage of feeding buzzes relative to total commuting calls and flight patterns were compared between dark control nights and experimentally illuminated nights. There were no clear effects of experimental light on the number of passing bats nor did more bats use an alternative commuting route when just one of two possible routes was lit. However, light did reduce the percentage of feeding buzzes by more than 60%, although the abundance of insect food tended to increase. It was observed that light disturbs the flight patterns of pond bats. When approaching the beam of light, between 28% and 42% of pond bats turned before continuing on their normal commuting route. Virtually all pond bats (96%) turned when the light was erected on an existing barrier and they had to fly straight into the beam of light. These disturbing effects also seemed to occur at low levels of light intensity. This study is the first known experimental evidence on the disturbing effects of light on pond bat behaviour along commuting routes and raises many questions, especially as to whether these disturbing effects will have fitness consequences.

Keywords: ecological connectivity, conservation, illumination, foraging, turning behaviour.

Introduction

The pond bat (*Myotis dasycneme*) is insectivorous. In the Netherlands, where an important part of the European population is located (Limpens et al. 1999), this species mainly forages in open landscapes, rich in water and particularly over fresh water lakes and marshy areas (Kapteyn 1995, Limpens et al. 1997). Colonies are typically found in buildings such as churches and houses, which can be up to 20 km away from their foraging areas (Kapteyn 1995, Haarsma 2003, Van de Sijpe et al. 2004). Colonies of males and females are typically separated during the breeding season (Voûte 1972, Limpens et al. 1997, Haarsma 2002). Colonies of reproductive females are used for different lengths of time; some for the entire summer, others for much shorter periods. In addition some temporary colonies are only used for a few days or weeks. The main foraging areas, male, female and temporary colonies are interconnected by fixed commuting routes. These are also used for foraging and can be seen as part of the bats' foraging areas. Commuting routes often follow watercourses (such as canals) and sometimes are partly over land along linear landscape

elements, such as rows of trees (Verboom et al. 1999, Van de Sijpe et al. 2004).

The connectivity of this network of colonies and foraging sites is essential for the survival of a pond bat population (Limpens et al. 1999). The connectivity is highly dependent on the existence of undisturbed commuting routes that connect the different elements of the network. In addition to barriers that may be created along these commuting routes, such as roads (Bach et al. 2004), a common threat may be the disturbing effects of light.

Only a few studies have addressed the possible disturbing effects of light on bat behaviour. As light attracts insects, there may be an interaction between the effects of increased food availability and the disturbing effects of light. Studies performed in Sweden and England showed that an increased insect abundance observed under street lights offers preferred feeding sites for just a restricted number of bat species (Rydell 1992, Blake et al. 1994). Only fast-flying bat species that use long-distance sonar, such as noctule bat (*Nyctalus noctula*), parti-coloured bat (*Vespertilio murinus*), northern bat (*Eptesicus nilssonii*) and occasionally common pipistrelle (*Pipistrellus pipistrellus*) were observed foraging under street lights. By contrast, slow-flying species such as *Myotis spp.* and brown long-eared bat (*Plecotus auritus*) were observed to avoid these lit areas. Species from this last group are thought to be more vulnerable to avian predators in lit areas, and therefore avoid such sites (Speakman 1991, Rydell et al. 1996). In addition to these species-specific responses to light at feeding sites, there are indications that the effects of light are dependent on the time of year (Rydell 1991), weather conditions (Blake et al. 1994) or that they may differ between foraging sites and commuting routes, as has been suggested for common pipistrelle (Verboom 1998). In addition, there are several field observations and anecdotal evidence that suggest that light has disturbing effects on a number of bat species (for example Alder 1993, Shirley et al. 2001). However, these studies did not establish any direct relation between light and the disturbing effects on bat behaviour, and

factors other than light could potentially explain the effects on bat behaviour.

Knowledge on the potentially disturbing effects of light on bat behaviour is highly relevant. Most bat species have a high status of legal protection in EU countries (in the framework of the Habitats Directive) and effects that negatively impact on bats may be illegal. Equally, the amount of artificial light has increased substantially during recent decades (Longcore & Rich 2004) and this may be undermining conservation efforts for several bat species.

In this study we experimentally manipulated light levels by placing a strong lamp along existing commuting routes of pond bats in the Netherlands and measured the effects on bat numbers and behaviour. This is the first study we are aware of that experimentally studies the disturbing effects of light on bats and constitutes an important first step in increasing knowledge in this field.

Methods

Experimental set-up

To study the effects of light on the number and behaviour of pond bats a series of experiments was carried out, in which sites along commuting routes were experimentally illuminated. Depending on the study site (see below), the lamp was placed perpendicular to, or against, the flight direction of commuting pond bats. Data was collected on the number of passing bats and flight direction and since the commuting routes of pond bats are also important as foraging sites, the number of feeding buzzes (foraging calls). To investigate the possible disturbing effects of light, these measurements were collected on experimentally illuminated nights and compared with dark control nights before and after the experimental lighting.

For experimentally lightning we used a 1000 W halogen lamp connected to a generator for power supply. This lamp produced a beam of light ranging between 1-30 Lux with a range of approximately 10 m (N. Goossens & H. Toorman, unpublished data; photo 1). For comparison, natural

Photo 1. Experimental lighting consisted of a 1000 W halogen lamp, producing a beam of light between 1-30 Lux, with a diameter of approximately 10 m which was placed along the waterside of a commuting route of pond bats. *Photograph: N. Goossens.*

values of light intensity during moonlit nights can reach up to 0.12 Lux (van der Vegte 2005). At 10 m distance from the lamp slightly elevated levels of light intensity were measured, whereas 15 m from the lamp the values returned to the normal background values.

The lamp was placed on the banks of canals known to be commuting routes for pond bats. The generator was always placed more than 30 m away, to prevent any noise disturbance. All experiments were carried out between the 11th July and the 12th August 2005, during the period when pond bats are reproducing, giving birth and lactating (Limpens et al. 1997, Krapp 2001).

Study sites

All the study sites were located in the province of Friesland in the Netherlands (figure 1). Since the number of pond bats using the commuting routes at each location is highly dependent on the size of the nearest colony, and as each experimental location had its specific characteristics, the results from these locations were initially analysed separately. Experimental illumination was carried out at four locations, near the villages of Tjerkwerd, Warga, Allingawier and Workum. At Tjerkwerd illumination was applied on four nights. At Warga, Allingawier and Workum illumination was applied on just one night. The experimental set-up differed between the sites. Three types of experiments were performed:

1) Experiment monitoring an alternative route: light perpendicular to the assumed flight path

This experiment was carried out in Tjerkwerd where there is a colony of more than 175 pond bats (based on counts of swarming bats in 2005)
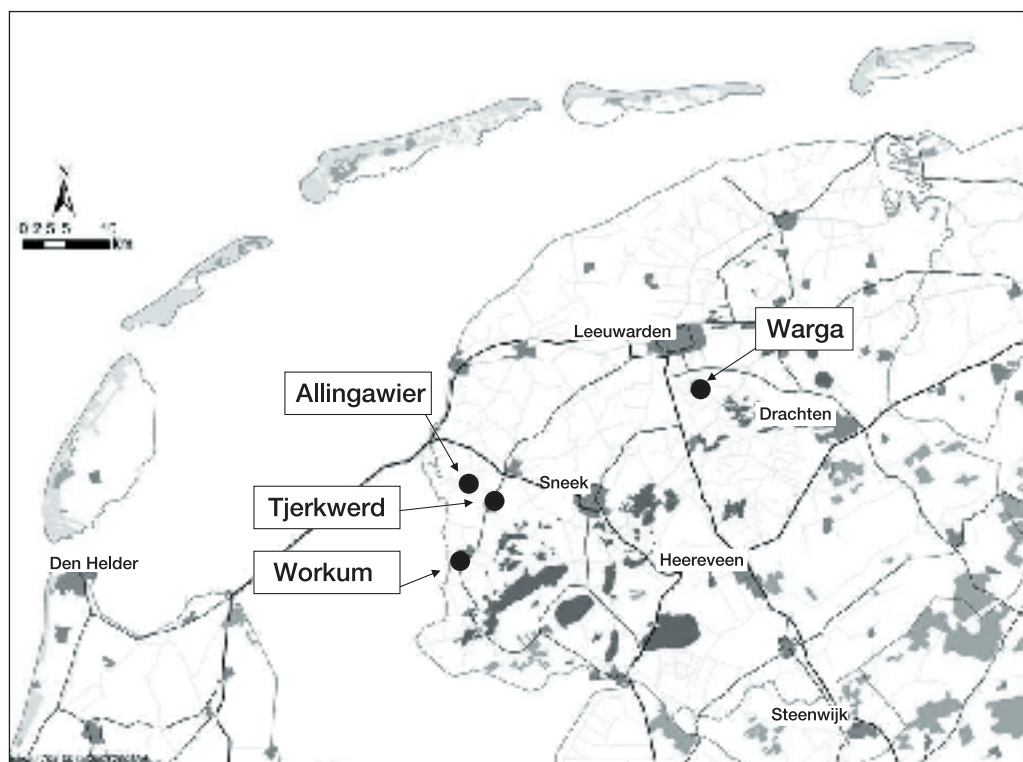
Figure 1. Locations of experiments.

located in the village church. The foraging areas of these bats are mainly situated along the Ijsselmeer Lake. Bats follow two alternative commuting routes to reach the foraging areas; via the 'Van Panhuys' and 'Workumertrekvaart' canals. Both are large canals approximately 15 m wide and the banks are mainly vegetated with common reed (*Phragmites australis*). The main experiment was carried out at this location. Experimental light was applied over four nights. It was placed on the waterside, perpendicular to the flight direction of the bats. Bat numbers and behaviour on the experimentally lit nights were compared to four dark control nights, immediately before and after the experimental nights. The experiment was carried out between the 11th and the 22nd July 2005 (period 1) and repeated between the 1st and the 12th of August 2005 (period 2). Light was applied to just one of the alternative commuting routes (the Wor-

kumertrekvaart). In this way we studied whether lighting one commuting route would increase the number of bats using the alternative, unlit, commuting route.

2) Short experiment with light perpendicular to the flight path

This experiment was carried out in Warga, which has a colony of more than 118 pond bats (based on counts of swarming bats in 2005) located in a house inside the village. The main foraging areas are situated on open water in the 'Oude Venen' marsh land area. Bats follow the 'Meanewei', a small canal approximately 7 m wide, to these foraging areas. The banks along this canal are vegetated with common reed and bushes of willow (*Salix cinerea* and *Salix alba*). On this site during light was applied for just one night. Bat numbers and behaviour on the experimentally

lit night were compared to those in two dark control nights, immediately before and after the experimental night. The light was placed on the waterside perpendicular to the flight direction of the bats.

3) Short experiment with light pointing towards the flight path

This experiment was carried out in Allingawier and Workum. Pond bats observed in Allingawier most likely originate from the colony in the church at Tjerkwerd (over 175 individuals), approximately 4 km away from Allingawier. While following the Van Panhuys canal to foraging sites along the banks of Lake IJsselmeer they pass the village Allingawier. On this site light was applied on one night and the effects compared to two control dark nights immediately before and after the experimental night. The experimental light was placed under the bridge just north of Allingawier against the flight direction of the bats, with passing bats having to fly straight into the light.

Workum has a colony of more than 220 pond bats (based on counts of swarming bats in 2005) located in a house in the centre of the village. Bats reach their foraging areas on Lake IJsselmeer by following the 'It Soal' canal. A large sluice on the border of the village regulates the water level in this canal (approximately 7 m wide) and provides a barrier that bats have to cross on their route. Because of nearby houses, there is already much artificial light on this site. Here night light was applied on one night and compared to two control dark nights immediately before and after the experimental night. The light was placed on top of the sluice against the flight direction of the bats, with bats having to fly straight into the light.

Data collection

The number of passing bats was determined using D200 Petterson's heterodyne bat detectors. These detectors lower the frequency of bats' sonar so that it is within audible range for humans so they can observe and monitor bats (Limpens

1993). The bat detectors were connected to sound-controlled recorders which started recording the moment that bats passed. The detectors and recorders were placed inside waterproof PVC pipes placed on a Styrofoam disc and floated on the canals in front of the experimental light. After each night, the tapes with the recorded bat sounds were removed and then analysed in the lab.

Pond bats typically produce sounds ranging between 25 and 60(-80) kHz, with a clear peak at 35 kHz. While commuting from their colony to the foraging areas, pond bats produce commuting calls that can be characterized as steep FM-type (frequency modulating) pulses, sometimes alternating with long-range sonar (QCF type calls), the latter with a clear peak frequency at 35 kHz, a unique characteristic of the species (Limpens et al. 1997 & 1999). Foraging behaviour can acoustically be distinguished from these commuting calls. During foraging, the bats emit feeding buzzes, consisting of a series of short, quick pulses (Britton et al. 1997, Siemers et al. 2005). All the tapes recorded during the experimentally lit and dark control nights were analysed by experienced observers. The number of individual passing bats was determined by counting the commuting calls. The number of feeding buzzes relative to the number of commuting calls was used as an estimate of the amount of foraging behaviour. All the observations were carried out between 11:00 PM and 01:00 AM, the observed peak in commuting behaviour at these locations. The peak of commuting behaviour shifted during the experimental period, related to sun-set, although remained within this time range.

During the nights with experimental light, additional data were gathered on the behaviour of passing bats, always by the same two observers. These two observers, with D200 Petterson bat detectors stood, close to the experimental light. One observed the bats flying in the beam of light with high levels of light intensity (1-30 Lux), 10 m radius from the lamp. The second observed the bats approaching the beam of light at a distance of 15 m from the lamp, where the light intensity was slightly above natural levels (0.12-1 Lux, see 'Experimental set-up'). For each approaching bat

it was noted whether they turned away from, or flew straight on through, the beam of light.

In addition to data on the number of bats and their behaviour, data on insect abundance were collected to test for the possible effects of the experimental light in attracting insects. A strip of 'Yellow-sticky-traps' was attached to each floating PVC pipe, encircling it. These sticky-traps have an adhesive yellow surface of 10x30 cm traps insects landing on the surface. They are used as a method to determine insect abundance (see for example Heinz et al. 1992). After each night, the total number of insects per species per sticky trap was determined.

Statistical analyses

Differences in number of passing pond bats and the amount of foraging (percentage of feeding buzzes relative to total commuting calls) at the Workumertrekvaart and Van Panhuys canal during dark and light nights were tested using One-way ANOVA followed by Tukey multiple comparison tests for the two separate experimental periods. The overall effects of light for both experimental periods combined on the two canals were tested using univariate GLM using period and experimental manipulation as the fixed factors. The overall effects of light on the number and percentage foraging bats at the other three locations were tested in combination using One-way ANOVA followed by the Tukey-test.

Results

Experiment monitoring alternative routes with light perpendicular to flight path

During nights with experimental light, there was no observed reduction in the number of pond bats passing along the Workumertrekvaart canal (figure 2). While there was a tendency towards a lower number of passages during the illuminated nights in period 1 (the 11th to the 22nd July 2005), these differences were not significantly different ($F_{2,7}$=0.50, P=0.63). In period 2 (the 1st to the 12th of August 2005), a higher number of

pond bats was observed during the nights with experimental light, although this also did not differ significantly from the dark control nights ($F_{2,11}$=1.30, P=0.32). Combining both periods, the number of passing pond bats did not differ between dark control nights and experimentally illuminated nights ($F_{2,19}$=0.102, P=0.904). Experimental lighting along the Workumertrekvaart canal did not result in a higher number of pond bats using the alternative commuting route along the Van Panhuyskanaal in either period (period 1: $F_{2,6}$=1.70, P=0.30: period 2; $F_{2,11}$=0.72, P=0.51, see figure 2). The number of passing pond bats was either in the middle of the range (in period 1) or lower than those in the control nights (period 2). When both periods were combined, there was no overall effect of experimental lighting on the number of passing bats along the Van Panhuyskanaal. The detailed observations of flight behaviour during nights with experimental light showed that a high proportion (36-42%) of bats observed near the beam of light turned when they approached the lamp, before continuing along the same commuting route (table 1). Of these turning bats, the majority (54-89%) turned before the beam of light, compared to 11-47% that turned when in the beam of light. Bats that passed the light tried to evade the beam by flying around it at a large distance or flying partly overland.

Light, foraging behaviour and insect abundance

Foraging behaviour was significantly lower during the experimentally illuminated nights than during the dark control nights in period 1 ($F_{2,7}$=6.32, P=0.043, figure 3). This pattern was broadly repeated in period 2, but due to a high variation in the proportion of feeding buzzes recorded, there was no significant difference between the proportion of feeding buzzes on the lit and on the dark control nights ($F_{2,11}$=0.77, P=0.49). In the first period the amount of feeding buzzes was 69 to 84% lower during nights with experimental light than on dark control nights. This decrease in the proportion of feeding buzzes occurred despite an increase in the abundance of insect food. In both periods, more
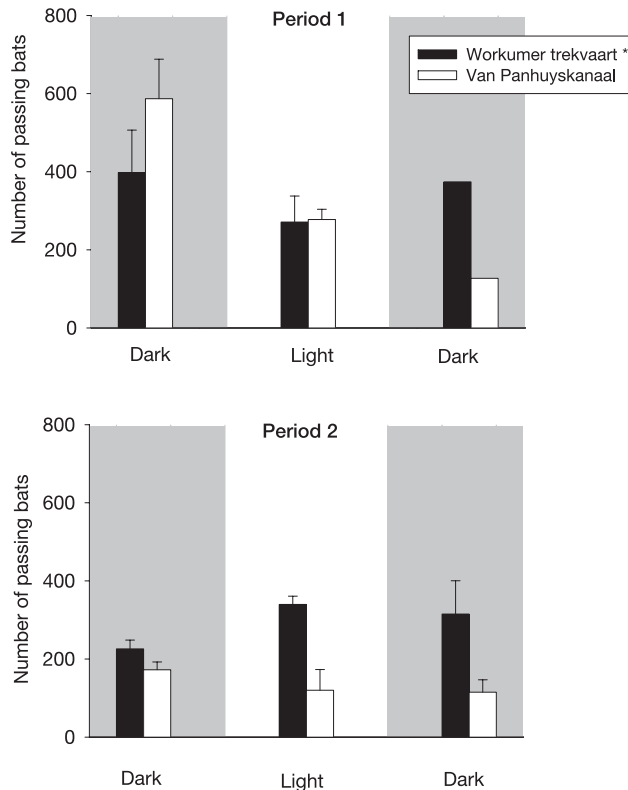
Figure 2. Number of passing pond bats on two alternative commuting routes during four nights with experimental light compared to four dark control nights before and after the experimental lighting. Experimental lighting was only carried out along the Workumertrekvaart canal (marked with an asterisk). Data were collected in two periods: from the 11th to the 22nd of July 2005 (period 1) and the 1st to the 12th of August 2005 (period 2).

Table 1. Percentage of turning pond bats in and before the light beam - based on the number of passing bats for which this could be observed. Turning bats were sub-divided into those that turned before the beam of light (15 m from the light source) and in the beam of light (less than 10 m from the light source). Numbers from the Workumertrekvaart canal refer to averages of four nights with experimental light, with standard errors in brackets.

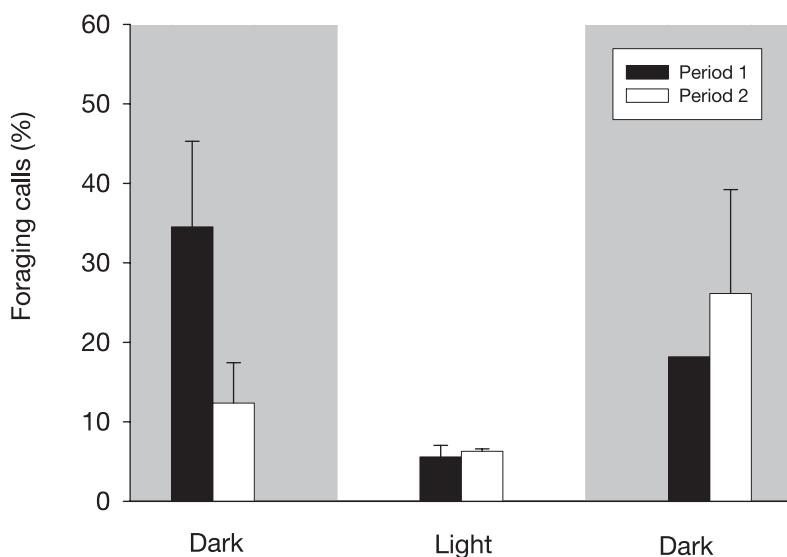| Location	Number of nights with light	Number of passing bats	% turning	% turning before light	% turning in light
Workumer-trekvaart					
Period 1	4	271 (67)	36 (8)	89 (26)	11 (26)
Period 2	4	340 (21)	42 (3)	54 (12)	47 (12)
Workum	1	170	96	57	43
Warga	1	177	28	86	14
Allingawier	1	-	-	-	-

Figure 3. Amount of foraging, expressed as the percentage of feeding buzzes relative to commuting calls, during four nights with experimental light compared to four dark control nights along the Workumertrekvaart canal before and after the experimental lighting. Periods as in figure 2.

insects, mainly of the order Diptera, were caught on the Yellow-sticky-trap during the nights with experimental light than on the dark control nights (table 2). However, due to a high variation in the number of insects caught per night, these differences were not significant, either for each period separately or for both periods combined ($F_{2,24}$=1.83, P=0.19).

Short experiments with light perpendicular to or pointing towards flight path

Experimental lighting during one night did not reduce the number of passing pond bats at the three selected different locations (figure 4). The number of passing bats during illuminated nights was higher than observed on the two dark control nights at Warga and Allingawier and approximately the same as on the control nights at Workum. Hence, there were no clear differences between the position of the lamp and the effect on the number of passing pond bats. Combining the results of all three locations, there was no overall significant effect of light on the number of passing pond bats ($F_{2,8}$=0.071, P=0.93).

Table 2. Average total number of insects recorded on Yellow-sticky-traps. Count taken during four dark control nights before experimental lighting, four nights with experimental lighting and four dark control nights after experimental lighting. Numbers refer to the averages of the four night periods, with standard errors in brackets.

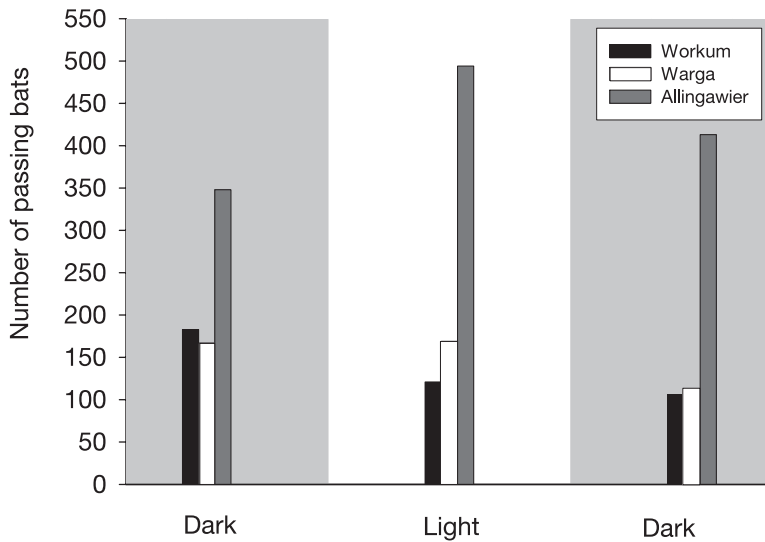| Location	Number of insects in dark	Number of insects in light	Number of insects in dark
Workumertrekvaart			
Period 1	2.3 (1.4)	23.3 (14.5)	3.8 (2.5)
Period 2	4.8 (4.4)	5.5 (4.2)	3.3 (1.8)

Figure 4. Number of passing pond bats during one night of experimental lighting and two dark control nights at three different locations. At Workum and Allingawier the light was pointing towards the flight direction: in Warga it was pointing perpendicular to the flight path.

However, more detailed observations of flight and foraging behaviour suggested that the position of the lamp did have an effect. Observation of flight behaviour during nights with experimental light showed that a high proportion of the bats turned when they approached the lamp (table 1). Virtually all (96%) the bats turned when they had to fly straight into the beam of light and over an existing barrier (Workum). Again, the majority of the turning bats at these sites, 57-86%, turned before entering the beam of light compared to 14-43% which turned when in the beam of light. At Allingawier no data on flight behaviour could be collected due to bad weather conditions preventing observation of animals during the lit night.

The proportion of feeding buzzes during the one night of experimental light was reduced by more than 39% (Warga) and 96% (Workum) compared to the dark control nights. Only at Allingawier there was no clear reduction in foraging behaviour, where the amount of feeding buzzes during the night with experimental light was somewhere between that on the two dark control nights. The largest reduction in foraging behaviour was observed when the light was

placed on an existing barrier in the flight direction of the pond bats (Workum).

Discussion

This study is the first we are aware of to demonstrate experimentally that light along the commuting routes of pond bats, which are also used as foraging areas, has disturbing effects on their behaviour. Although we did not find changes in the number of passing pond bats as a result of experimental illumination, the amount of foraging behaviour decreased (despite higher availability of insect food) and a high proportion of pond bats turned when approaching the light. These changes in behaviour are likely to result in negative effects on individuals by increasing their energy expenditure during the energy-demanding reproductive period.

Disturbing effects of light on bat behaviour

Commuting routes of pond bates are used for commuting between colonies and foraging areas,

but much foraging behaviour is also observed (Verboom 1998, Verboom et al. 1999). These routes therefore can be seen as part of the bats' foraging areas. Placing a light source along existing commuting routes clearly disturbed the behaviour of commuting pond bats. Foraging behaviour, expressed as the percentage of feeding buzzes, was reduced by 49-84% during the four nights along Workumertrekvaart with experimental light compared to nights without light. The illumination tended to increase insect abundance and hence food abundance, an effect also observed in several other studies (Rydell 1992, Blake et al. 1994). There was an increase in the number of insects of the order Diptera, especially mosquitoes, which constitute an important part of the diet of pond bats (Britton et al. 1997, Van de Sijpe et al. 2004). Despite increased food abundance, foraging behaviour did not increase, further illustrating the disturbing effects of light. It may be that pond bats do not profit from the increased food supply due to a higher risk of predation when foraging in illuminated conditions (Speakman 1991, Rydell et al. 1996). Commuting routes are an important part of pond bats' foraging areas, and illuminating them reduces the suitable foraging area for this species. This may have negative effects on individuals by decreasing their food intake. This may be especially harmful during their relatively short energy-demanding reproductive period (Duverge et al. 2000, O'Donell 2002). The present study demonstrated this effect by placing just one lamp along a commuting route. If we extrapolate these observed effects, placing a row of lamps along an existing commuting route may lead to a considerable reduction in foraging area of this species. In addition to less foraging behaviour close to the lamp, a high proportion (28-96%) of bats turned when approaching the beam of light. The position of the light seemed important, the highest proportion of bats (96%) turned when the light was placed on top of an existing barrier and they had to fly straight into the beam of light. The finding that most turning bats (54-89%) turned before reaching the beam of light suggests that these disturbing effects

operate at low levels of light intensity. The highest proportion of bats turned between 15 and 10 m distance from the light source at light levels of approximately 0.6-3.2 Lux. This indicates that light levels slightly above natural light values, (for example moon-lit nights can be 0.12 Lux - van der Vegte 2005), along commuting routes may have disturbing effects. As flight is energy-consuming for bats (Salcedo et al. 1995, Henry et al. 2002), a high amount of light-induced turning along a commuting route may increase their energy expenditure by increasing their flight distances. The combined effects of this and a lowered food intake (discussed above) may cause problems at periods of high energy demand, especially among lactating females, during their reproductive period. If these disturbing effects take place at a large scale, they may have negative effects on the fitness of individual bats.

No effects of light on number of bats

Although this study clearly showed that light did disturb bat behaviour it did not find that lighting had any effect on the number of passing pond bats. There are several possible explanations for this not occurring, despite the clear disturbing effects of the light on bat behaviour. Firstly, the light source used, a lamp of 1000 W, may not be sufficiently disturbing to prevent bats from using the commuting route. This lamp provided light levels ranging between 1 and 30 Lux within a 10 m range of the lamp. These values close to the lamp are clearly above the maximum natural levels of light at night (see van der Vegte 2005). The lamp's range of 10 m fully illuminated the width of the smaller canals used in the experiment, but left several metres virtually unlit on the larger canals (approximately 15 m wide). Bats could have evaded the beam of light by flying on the unlit opposite site of the wider canals or by flying partly overland, behaviour that was observed during the experiments. Pond bats are already known to use commuting routes that are, partly, overland (Limpens et al. 1997, Haarsma 2003). Other studies indicate that bats evade light sources by flying at a distance around them (Alder 1993).

Another possible explanation is that the majority of the pond bats that turned in the proximity of the light turned again and flew straight through the light beam at a second attempt and so continued along the same commuting route. This would explain why the total number of passing bats during dark and illuminated nights was unaffected by the light. Pond bats are known to be habitual in their use of colony sites, commuting routes and foraging sites (Kapteyn 1995, Limpens et al. 1997) and hence are not likely to rapidly respond to changes which make a commuting route less attractive. As most experimental sites were located near colonies of reproducing females, the majority of passing bats most likely consisted of (lactating) females at the end of their reproductive season and with high energy demands (Duverge et al. 2000). For these individuals, the extra costs involved in choosing an alternative commuting route may not outweigh the negative effects of light applied during these experiments, so they continued along the known commuting route. Field observations of turning bats support this idea that a large number of bats did eventually pass the beam of light.

Focus of future research

This study clearly shows that light clearly does disturb the behaviour of pond bats and raises several questions for further study. As only one lamp, with one level of light intensity, was used in the present study it is not known what the effect of multiple light sources would be. It may be such that these effects are cumulative, and that the effect of several light sources along a commuting route would be much larger than the sum of individual light sources. In addition, the intensity or the colour of the light may have different effect on bats (see for example Rydell 1992 and Blake et al. 1994). A useful next step would be to establish a dose-effect relation between light level and type and the number of passing bats and their behaviour. The disturbing effects of light may also be lessened by habituation. In the present study, with short experimental periods of four nights of lighting, no habituation effect was discovered. However, it is unclear how long-term exposure of light along a commuting route will affect the behaviour of bats. It could lead to the use of an alternative commuting route (see for example Alder 1993) or to habituation to the new situation.

Another important question is whether and how these disturbing effects might affect the population level of pond bats. Several other studies have shown that disturbances that lead to an increase in energy expenditure can result in negative effects on a species' reproductive output. This has been demonstrated in detail for (among others) arctic breeding geese (Madsen 2001, Drent et al. 2003), where disturbing the geese at staging sites along their migration route eventually led to a decline in the population (Klaassen et al. 2006). To further quantify the disturbing effects on the fitness of individual bats and population size, further research into the energy cost of flying and detailed measurements on the reproductive output of individually marked females would be required.

In addition to these questions that are relate specifically to pond bats, the disturbing effects of light on other species of bats also warrant further study. While increased light levels may disturb the behaviour of some bat species, several species may benefit from increased lighting at their foraging areas (Rydell 1992, Blake et al. 1994). This may result in increased food competition for the light-sensitive species and could be an additional factor in the decline of some bat species (Arlettaz et al. 2000).

Despite the many questions that still need to be answered before we fully understand the effects of light on (pond) bats, this study is an important first step in this direction. Further development of our knowledge on the disturbing effects of light could play an essential role in contributing to the conservation of bats. As bats are often dependent on urban areas (at least for part of their life cycle), good spatial planning of light along commuting routes could prevent a growing conflict of interests and maintain suitable habitats for bats.

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Samenvatting

Experimenteel bewijs van lichtverstoring langs vliegroutes van meervleermuizen (*Myotis dasycneme*)

Een populatie van meervleermuizen (*Myotis dasycneme*) bestaat uit een netwerk van foerageergebieden, van elkaar gescheiden mannen-, vrouwen- en tijdelijke verblijven, onderling verbonden door vliegroutes. Een goed functionerend netwerk is essentieel voor het behoud van deze soort. Verschillende waarnemingen en anekdotisch bewijs suggereren dat licht een belangrijke verstoringsbron kan zijn langs bestaande vliegroutes. Verlichting die wordt ge-plaatst nabij vliegroutes kan de connectiviteit van een netwerk aantasten. De verstorende effecten van verlichting op meervleermuizen zijn in deze studie experimenteel onderzocht door het plaatsen van een sterke lichtbron (1000 W) langs bestaande vliegroutes. Elke experimentele plek had zijn eigen specifieke kenmerken waardoor we in staat waren om de interactie tussen licht-verstoring en de omgeving te exploreren. Het aantal passerende vleermuizen, het percentage 'vangstbuzzen' (foerageergeluiden) en het vliegpatroon werd vergeleken tussen donkere controle nachten en experimenteel verlichte nachten. In tegenstelling tot onze verwachting was er geen duidelijk effect van verlichting op het aantal passerende vleermuizen. Ook gebruikte geen groter aantal vleermuizen een alternatieve onverlichte route als twee mogelijke vliegroutes bestonden en langs slechts één vliegroute verlichting werd aangebracht. Echter, verlichting verminderde het percentage vangstbuzzen met meer dan 60% ten opzichte van controle nachten. Deze vermindering van foerageergedrag trad op ondanks dat het aanbod van insecten, geschikt als voedsel, de neiging had toe te nemen. Daarnaast werden verstorende effecten van verlichting op het vliegpatroon van vleermuizen waargenomen. Tussen 28 en 42% van de meervleermuizen keerde om bij het naderen van de lichtbundel alvorens door te vliegen op hun normale vliegroute. Vrijwel alle meervleermuizen (96%) keerden om als de verlichting was aangebracht op een bestaande barrière en de vleermuizen recht tegen het licht in moesten vliegen. Deze verstorende effecten traden al op bij lage waarden van lichtintensiteit die slechts iets boven natuurlijke waarden van lichtintensiteit 's nachts lagen. Dit suggereert dat meervleermuizen erg gevoelig zijn voor verhoogde waarden van lichtintensiteit. Hoewel nog veel vragen onbeantwoord zijn, vooral of deze verstorende effecten zullen leiden tot effecten op de fitness van individuen, demonstreert deze studie voor het eerst experimenteel de verstorende effecten van verlichting op het gedrag van meervleermuizen.

The history of urban foxes in Aarhus and Copenhagen, Denmark

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Abstract: Literature testifies to the presence of red foxes (*Vulpes vulpes*) in Copenhagen as early as the time of the Slesvig War in 1848-1850, and they became numerous from the middle of the 1960s onwards. In Aarhus red foxes have only become numerous within the last 15 years. In both cities foxes seem to have colonized the cities at times when the main cause of death around the city border was not hunting, but when there were protected green areas established close to the city border and/or during periods when persecution by man was low.

Keywords: urban ecology, red fox, colonization, city.

Introduction

Urban red foxes (*Vulpes vulpes*) are well-known in British cities (e.g. Macdonald & Newdick 1982, Harris & Rayner 1986) and have been present in London since the 1930s (Teagle 1967). Initially this was thought to be a uniquely British phenomenon (Harris 1977, Macdonald & Newdick 1982). However, during the past 25-30 years foxes have been reported in several European cities and suburbs e.g. Paris, France (Brosset 1975), Stockholm, Sweden (Page 1981), Oslo, Norway (Christensen 1985) and Stuttgart, Germany (Gloor et al. 2001). Since 1985 foxes have become widespread in the cities of Switzerland e.g. Zurich and Geneva (Gloor et al. 2001). In Denmark foxes have been observed in several cities, and they have been studied in Aarhus and Copenhagen (Nielsen 1989, Nielsen 1990, Simonsen et al. 2003).

The invasion times of foxes in different European cities are not synchronous. As a result, there are several theories and hypotheses about how, why and when foxes colonize urban areas. Gloor et al. (2001) propose two main hypothetical explanations for the presence of urban foxes: the population pressure hypothesis (PPH), and the urban island hypothesis (UIH). The PPH assumes these foxes to be intruders from adjacent rural areas, which invade human settlements because of high population density in rural areas. Hence the PPH assumes that the size of the urban fox population size is closely correlated to that of the fox population in adjacent rural areas, and as such does not expect any genetic isolation between the urban foxes and the population in the rural surroundings. Urban areas provide suboptimal habitats for foxes. The UIH postulates that urban foxes have adapted to specific urban conditions, such as a high density of human population, scavenging food items and finding special hiding places. It argues that foxes live in urban areas, not out of necessity due to lack of breeding space or food shortages in the surrounding areas, but because they find sufficient resources and conditions to breed and spread within human settlements. The UIH expects no correlation between fox populations in the urban and surrounding rural areas, and implies genetic isolation over time (Gloor. et al. 2001).

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This paper describes the history of foxes invading the cities of Copenhagen (1.8 million citizens) and Aarhus (293,000 citizens), and discuss this and its timing in relation to the two theories put forward by Gloor et al. (2001).

The history of urban foxes in Copenhagen

Literature testifies to the presence of foxes in Copenhagen already as early as the time of the Slesvig War in 1848-1850, where foxes denned in the embankments glacis of the ramparts of Copenhagen (Tauber 1878). According to Tauber (1878) the glacis were fertilized by refuses from the city and police and soldiers kept the ramparts under surveillance, both acts resulting in a rich mammal fauna. Foxes were also seen at the Marble Place in the centre of Copenhagen at that time (Tauber 1878). Tauber (1878) assumed that the men were then occupied with combat, and therefore had less time for hunting, so the fox population, together with other wildlife populations, increased noticeably both around and inside the city borders. After the war, when hunting was taken up again, the number of foxes outside the city decreased, but was maintained inside the ramparts (Tauber 1878). In 1860 foxes were so numerous in Frederiksberg Garden that they had almost undermined the Chinese Pavilion (Hvass 1940).

By the end of the 19th century foxes became rare within the city of Copenhagen, although they were still present (Tauber 1878). At the beginning of the 20th century foxes were present in the outskirts of Copenhagen, especially near waste deposits (Degerbøl 1930, Holten 1935, Hvass 1940). In two numbers of hunting magazines from 1953 foxes, seen in different residential areas of Copenhagen, are mentioned in short communications e.g. fox cubs playing at broad daylight by the road and foxes entering gardens to steel fowl in chicken runs (Anonymous 1953a, Anonymous 1953b). In the 1950s foxes are also known to have denned under a workmen's hut during the construction of the new Zoological Museum of Copenhagen and under the steps of the School of Dentistry (B. Jensen, personal communication, zoology student in Copenhagen in 1950).

In 1963 Hvass wrote that foxes had become numerous and he presented several records of fox sightings in built-up areas where the foxes showed little or no reaction to human activity (Hvass 1963). The presence of foxes in the suburbs of Copenhagen is also mentioned in literature from the 1970s (Jensen 1972). From 1980 onwards the foxes of Copenhagen received increasing media attention, with articles about fearless foxes entering gardens and houses.

In 2005 local authorities received more than 300 complaints about foxes being a nuisance to people in the built-up area of Copenhagen, according to the Danish Forest and Nature Agency, Ministry of Environment. A study, carried out between 1997 and 1999, found genetic and morphometrical differentiation between the foxes from Copenhagen and those from the rest of Zealand (Simonsen et al. 2003).

The rise of urban foxes in the city of Aarhus

There are no records about the presence of foxes in the city of Aarhus before 1986. The first survey of foxes in the city of Aarhus was carried out between 1986 and 1988 (Nielsen 1989). The investigation was advertized through announcements in three local newspapers and the radio. In addition, the Office of City Gardeners, around 250 taxi drivers, and the Animal Rescue Corps were asked to report foxes on seen or killed by car accidents in the built-up area of Aarhus. During the two years of investigation, 20 records of fox sightings within the built-up area were obtained; with one further observation recorded in the summer of 1989. Most sightings were glimpses of foxes close to green areas at the edge of the city. Apart from dens found in green areas and along railway lines, only two dens were found in built-up areas, in undisturbed gardens. The woods south of the city, partly surrounded by human

dwellings and partly by rural areas, was searched for dens. The frequency of occupied dens was about twice as high in the wood surrounded by human dwellings than it was in the wood outside the city, suggesting either a higher fox population in the former woods, or a higher intensity of human disturbance, causing foxes to move more frequently between dens (Nielsen 1989).

An investigation of eating habits of the foxes in the public woods of Aarhus showed that there was a significant higher frequency of feather remains of passerine birds in the fox scats from the woodland next to the suburban environment, than in the woods surrounded by rural areas (Nielsen 1990). As many passerine bird species are known to occur in higher densities in gardens and city parks than in intensively managed rural habitats, foxes from the woods near the city borders were assumed to forage in residential areas at night (Nielsen 1990). This was in agreement with the sightings of foxes in the residential areas edging the public woods.

From the middle of the 1990s and onwards more cases of fearless foxes in Aarhus appeared in the media. In July 2005 the Natural History Museum of Aarhus asked, via one of the free local newspapers, people who had seen foxes in the built-up area of Aarhus, to contact them. This enquiry resulted in 28 reports of fox sightings within 14 days of the request and one in December 2005. Most sightings were in residential neighbourhoods and allotments, 25 were from 2005, two fox sightings from 2004 and one from 2003, and one approximately 10 years old. There were numerous reports of foxes that had entered gardens or had passed by people at close hand, without showing signs of fear. This time the sightings were from all parts of the city and not only restricted to residential areas close to the public woods, as they were during the 1986-1989 survey.

Discussion

Considering the efforts made to obtain records of fox sightings during the investigation in 1986-

1989, and the relatively few sightings obtained at that time, the higher levels of sightings reported during the short public survey in 2005, suggest that foxes became more numerous in Aarhus between the two surveys. As previously observed in British cities by e.g. Harris and Rayner (1986) many fox sightings in this investigation were from owner-occupied housing. However, the arrival of foxes in Aarhus and Copenhagen cannot be related to the development of the suburbs. Foxes invaded Copenhagen long before, and Aarhus a long time after the main development of the suburbs, which in both cities was between the 1950s and the 1970s.

The PPH may explain the invasion of foxes in Copenhagen during the middle of the 19th century, when the number of foxes increased during the Slesvig War. On the other hand the genetic and morphometric differences found between the foxes in Copenhagen and the foxes from the rest of Zealand, suggests that the foxes in Copenhagen may be considered as an isolated population and that there is a limited gene flow between foxes in rural and urban areas (Simonsen et al. 2003), this supporting the UIH. Also the situation in Aarhus, where foxes have become numerous in the built-up areas during a 10 year period when the fox population has otherwise decreased by 50-60% as a result of an epidemic of sarcoptic mange (according to game bag records made by the National Environmental Research Institute of Denmark) supports the UIH.

There is also divergence in the results of other studies in relation to the two hypothetical explanations for the presence of foxes in urban areas. The fact that the smallest home range sizes and the highest fox population densities are found in urban areas (Harris 1981, Macdonald & Newdick 1982), suggests that foxes live in urban areas because they find sufficient resources and conditions to breed and spread within human settlements, which supports the UIH. By contrast, Gloor et al. (2001) found a significant correlation between the number of foxes in the canton of Zürich and the city of Zürich, and suggest that foxes invaded the city during high population density in the rural areas. Wandeler et al. (2003)

found genetic differentiation between rural and urban fox populations in Zürich, but assumed that these urban populations were founded by a small number of individuals from adjacent rural areas, resulting in genetic drift. They expect that the currently observed levels of migration between urban and rural populations of Zürich will erode genetic differentiation over time.

The PPH and the UIH may not be completely contradictory. As earlier described by Harris (1986) foxes seem to colonize cities in two steps. According to Harris (1986), foxes colonizing British cities first established themselves in the suburban fringes and from there spread into the city centres. Harris (1986) explains how fox populations during the inter-war years were enclosed in rural enclaves by the ribbon-like development of the suburbs. As a result foxes were isolated and forced to live in close contact with man. As these patches were later developed, the foxes had to move into the surrounding suburban areas (Harris 1986).

Foxes are known to spread over large distances (Jensen 1973), but dispersing rural foxes may avoid settling in areas with high human activity, due to centuries of persecution. Although at least some urban areas turn out to be rich habitats with plenty of anthropogenic food, sufficient to feed a much higher number of foxes than currently present (Contesse et al. 2004), rural foxes may not enter the city unless they have a period to become habituated to human activity. This may occur in the suburban fringes as suggested by Harris (1986), in protected green areas with little or no hunting activity or in periods when persecution is low. During the period when fox sightings became numerous in the build-up area of Aarhus, the public woods close to the city border were significantly extended (from 1,019 ha in 1989 to 1,897 ha in 2005). These public woods act as recreational areas for the citizens of Aarhus and during the last 20 years very few foxes have been shot in these woods (Svend Warming, forest ranger, personal communication). A change in the behaviour of foxes in the surrounding areas of the city, toward less fearfulness to humans, may lead more foxes to discover and explore the urban habitat. Once adapted to human activity foxes can settle and successfully spread in urban areas, independently of the fox population outside the city boundaries. Further investigations on this subject are needed.

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Samenvatting

De historie van stadsvossen in Aarhus en Kopenhagen, Denemarken

Het opduiken en voorkomen van de 'stadsvos' in de Deense steden Aarhus en Kopenhagen vertoont parallellen maar ook verschillen met andere Europese steden. Op basis van literatuur blijken vossen (*Vulpes vulpes*) reeds aanwezig in Kopenhagen ten tijde van de Slesvig oorlog in 1848-1850, en namen hun aantallen er toe vanaf het midden van de jaren 1960 tot op heden. In Aarhus werd de vos pas talrijk sinds de laatste 15 jaar. In beide gevallen lijken vossen de stad te zijn binnengedrongen in periodes dat de belangrijkste doodsoorzaak in de onmiddellijke omgeving van de stad niet de jacht was. Meer bepaald werden in die periodes rustige groene zones aangelegd aansluitend bij de stadsgrenzen, terwijl actieve vervolging door de mens gering was.