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The shoulders of giants

"If I have seen further it is by standing on the shoulders of giants", Isaac Newton once wrote. The findings and observations of our colleagues and predecessors can inspire us, spark a new idea, or form the basis for new theories or hypotheses. Using the work of others to design new methods or integrate previous findings to reach new conclusions has always been, and still is, common practice in science. For example, Brugge's article on mustelid diets in the Netherlands, published in Lutra 19 in 1977, helped other scientists understand the differences in PCB loads between different mustelid species (Leonards et al. 1998) and thereby comprehend how mustelids coexist (Powell & Zielinksi 1983). In the current issue, Oerlemans and Koene review earlier studies on raccoon dogs from the US, Japan and European countries to identify potential issues of concern for nature conservation and public health in the Netherlands. Earlier articles using photography and stereo photogrammetry to determine the heights at which trawling bats fly inspired Van De Sijpe to develop a method to estimate the flight heights of pond bat and Daubenton's bat using the bats' calls and their echoes from the water surface.

Other papers in this issue of Lutra draw on papers in earlier volumes. With their paper on strandings of caetaceans in the Netherlands between 1998 and 2007, Camphuysen, Smeenk, Addink, van Grouw and Jansen carry on a tradition of reporting Dutch strandings through Lutra that was started by van Deinse in 1931 and carried on between the 1970s and 1990s by others, including van Bree and Smeenk The most recent article not only reports on strandings of two new species for the Netherlands, the humpback whale (*Megaptera novaeangliae*) and Blainville's beaked whale (*Mesoplodon densirostris*), but by using previous reports, constructs the numbers of larger whales stranded on Dutch shores from the 1300s to the present, and the number of harbour porpoise from 1970 to the present. The number of stranded porpoises is still rising, probably as a result of changes in their distribution. About 58% of stranded harbour porpoises were by-catches. The authors propose initiating discussions with the fishing industry to explore, develop and implement mitigation measures.

The badger is a good example of how populations can be protected by opening a dialogue between conservationists, scientists and other stakeholders. In recent years a number of badger conservation measures have been implemented; establishing fences and tunnels to mitigate the effect of roads and railways and compensating farmers for damage that badgers cause to crops. The paper by Vink, van Apeldoorn and Bekker, on the expansion of the badger population in Eindegooi cite the national badger censuses previously published in Lutra (volumes 29, 35 and 48) to illustrate the increase in distribution and numbers of badgers that has occurred in recent decades as a result of these changes.

To ensure optimal use of the papers that are published in Lutra, the Society for Study and Conservation of Mammals has, since issue 48-1 (in 2005) published all the papers from Lutra online, which are accessible free of charge. It turns out that many readers find their way to the online Lutra: some papers have been downloaded by more than 2000 people! Lutra online is read by many people in European countries, but also by those farther afield including the US and Japan.

However, the availability of issues of Lutra dating from before 2005 is still limited: they are available in some libraries, and in the Society's archive, but cannot easily be accessed, browsed or searched. To break down this barrier and increase the accessibility and use of all Lutra publications, the editorial board has made all the issues of Lutra available on DVD. Thanks to a subsidy from the 'Stichting Publicatiefonds Lutra', we have been able to scan all of the first 50 volumes of Lutra and convert them into fully searchable digital documents. The DVD will be available in early January 2009 from the VZZ office at a cost of € 10,00. For ordering details, see www.vzz.nl.

The DVD will contain true pearls, such as the first documented case of American mink in the Netherlands (Mededelingenblad 17, Volume 1, 1958: 177-178), the national mammal survey by van Wijngaarden, van Laar and Trommel (Volume 13, 1971), and the special issue on changes in the numbers and distribution of hibernating bats in the Netherlands between the 1940s and 1980s (Volume 22, 1980).

We hope that by making the first 50 volumes of Lutra widely available, the work of our predecessors will continue to inspire present and future mammologists.

Meanwhile we are happy to announce that Johan Thissen has joined the editorial board. Johan is one of the authors of The Atlas of European Mammals (Mitchell-Jones et al. 1999). In this full scale project, one of his tasks was the co-ordination of the data and the editing of the distribution maps. Over the years, Johan has gained much experience in the practice of policy development and decision making for nature conservation, including mammals. He was involved in producing the Second Red List of Mammals for The Netherlands, which is to be published in 2009. Lutra will certainly benefit from Johan's extensive knowledge of various aspects of European mammals.

Leonards, P.E.G. , S. Broekhuizen, P. de Voogt, N.M. Van Straalen, U.A.Th. Brinkman, W.P. Cofino & B. van Hattum 1998. Studies of bioaccumulation and biotransformation of PCBs in mustelids based on concentration and congener patterns in predators and preys. Archives of Environmental Contamination and Toxicology 35: 654–665.

Mitchell-Jones, A.J., G. Amori, W. Bogdanowicz, B. Kryštufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Vohralík & J. Zima. The atlas of European mammals. Academic Press, London, UK.

Powell, R.A. & W.J. Zielinski 1983. Competition and coexistence in mustelid communities. Acta Zoologica Fennica 174: 223-227.

Flight height of trawling pond bats and Daubenton's bats

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Abstract: This article presents an indirect way to estimate the flight height of trawling bats by measuring the small time intervals between pulses and echoes from the water surface. A particular study site, the historical Vauban ramparts around the town of Ieper, Belgium, allowed for time expansion recordings made from trawling pond bats (*Myotis dasycneme*) and Daubenton's bats (*M. daubentonii*) when they were skimming the water surface close to the wall. The surface echoes were used to estimate the flight height. This method was confirmed by a detailed analysis of a feeding buzz performed by a pond bat close to the wall, where the bat finally broke the water surface, which was revealed by expanding waves in the water. The pulse-echo time interval gradually decreased from search to buzz phase, corresponding with a gradually decreasing flight height from circa 53 to circa 6 cm. Sound analysis of bat passes of Daubenton's bats and pond bats in the search phase revealed the pond bat to have higher flight heights (median: 43 cm) than Daubenton's bat (median: 24 cm).

Keywords: pond bat, Daubenton's bat, *Myotis dasycneme*, *Myotis daubentonii*, flight height, trawling.

Introduction

The trawling technique, sometimes referred to as gaffing or water gleaning, is used by specialised chiropterans, which probably evolved from ancestral aerial hawking forms through morphological adaptations (Fenton & Bogdanowicz 2002). These bats catch insects from the water surface and/or fish and crustaceans just below the surface, by using their enlarged hind feet, which are equipped with long claws (Jones & Rayner 1988, Kalko & Schnitzler 1988, Jones & Rayner 1991, Britton et al. 1997). They also take flying insects in the air just above the water surface by using the tail membrane, a hunting strategy commonly referred to as aerial hawking (Jones & Rayner 1988, Todd & Waters 2007). Trawling bats emerged all over the world and appeared in different chiropteran families by convergent evolution (Fenton & Bogdanowicz 2002). Various opportunities may have triggered the emergence of trawling. Food resources close to, and on the water surface, are often abundant and largely unavailable to non-trawling species. Aldridge (1988) and Jones and Rayner (1991) suggest that flying close to the ground reduces the energy that bats expend (25 to 30% in Daubenton's bat (*Myotis daubentonii*) and *Myotis adversus*). However these savings rapidly decrease with increasing height, as shown by Britton et al. (1997) who found lower savings (9%) in commuting pond bats (*Myotis dasycneme*) flying at an average height of 26 cm. Furthermore, prey is more conspicuous over smooth surfaces than textured ones, since a smooth surface will reflect much of the sound energy away from a bat, if the latter flies sufficiently low so that the emitted sound beam hits the surface at a narrow angle (Boonman et al. 1998, Rydell et al. 1999, Siemers et al. 2001). These low background echo levels make smooth surfaces favourable hunting grounds for echolocating bats. Siemers et al. (2005) found that prey protruding sufficiently above a smooth surface provide greater

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echo amplitudes compared to the same prey in mid-air because of a mirror effect, by which indirect echo reflections from the immediate surface add to the direct echo from the insect. Hence, trawling bats can detect similar sized prey at greater distances than hawking bats in mid-air. In spite of these advantages there is no evidence of obligate trawling forms having evolved. Even the most specialised ones, i.e. the piscivorous and insectivorous greater bulldog bat (*Noctilio leporinus*), have maintained the ability to hawk insects in mid-air and for at least part of the season extensively hunt airborne insects (Schnitzler et al. 1994). For some reason, non-trawling bats are unable or unwilling to continuously fly as low over a water surface as trawling bats and aerially hawking species that extensively hunt over water, e.g. gray bats (*Myotis grisescens*), fly and catch insects at higher heights (2-5 m) (Brack & Laval 2006).

The common search phase of trawling bats most often consists of a flight at 10 to 60 cm over the water surface with the body axis and feet positioned horizontally (Baagøe 1987). Only the most specialised species (*Noctilio leporinus*) are capable of making prolonged flights of at least 10 m, raking through the water surface (random rake technique, Schnitzler et al. 1994). They use their long calcars to turn their tail membrane forwards and keep it out of the water. During capture attempts trawling insectivorous bats perform pointed dips, during which the bat first descends to the surface, lowers its feet to a more vertical position until the claws rake the surface and turns the tail membrane backwards so that minimum interference with the water occurs. Finally the insect is scooped from the surface either with the feet or tail membrane. The bat brings head and foot together to transfer the prey item to the mouth and then regains height to continue its search flight at 10-60 cm (Jones & Rayner 1988,

Figure 1. View of the ramparts, stone walls and moats of Vauban's historical fortifications around the town of Ieper, Flanders, Belgium. The combination of tall vegetation, large open water surfaces, and sheltered microhabitats with a favourable climate, offers an insect-rich habitat and attracts many species of bats, including in spring when the bats awake from hibernating in several underground sites in and around this fortification.

Kalko & Schnitzler 1988, Jones & Rayner 1991, Britton et al. 1997).

There is still little available information about the flight heights of trawling bats. In Denmark, Baagøe (1987) established flight heights of 10 to 20 cm for trawling Daubenton's bats, and 10 to 60 cm for trawling pond bats. Based on photographs, hunting Daubenton's bats were found to fly at an average height of 15.8 ± 6.7 cm (min-max 8-28 cm) over tributaries of the river Rhine in Germany (Kalko & Schnitzler 1988). Pond bats commuting over a canal near a summer roost in Friesland (the Netherlands), flew at a height of 26 ± 2 cm, as recorded by stereo photogrammetry (Britton et al. 1997). Schnitzler et al. (1994) reported flight heights as low as 4 to 10 cm during low search phase flight of *Noctilio leporinus* in Neotropical Costa Rica.

This paper describes an indirect way of estimating flight height in trawling bats by means of time expansion recordings. Daubenton's bats and pond bats were hunting on the same spring nights over the same large water surface and used a similar flight style and at a similar distance to a rampart wall bordering the water surface. This was a good opportunity to test whether the two species used different flight heights in the same field conditions.

Methods

Study site

Observations of hunting Daubenton's bats and pond bats were made in Ieper (French/English name: Ypres), a town with 30,000 inhabitants in the western lowlands of Flanders (Belgium) at 25 m above sea level. The historical town centre is partly surrounded by rampart walls and large moats, remains of the fortifications built by the French architect Vauban in the 17th century (figure 1). The recordings and observations were made north of the Menin Gate Bridge. At this point the moat is about 200 m long and has an an average width of 50 m and a water depth of 1.5-2 m. The inner side of the moat is bordered by an 8 m high stone wall, the top of which is overgrown by tall trees, bushes and scrub. The outer side is bordered by a 2 m high grass covered talus, a small grass stretch with trees, a road, and houses.

Visual observations

A monocular image intensifier, the ITT Night Mariner 150 (ITT Industries, Roanoke, Virginia, USA), was used for visual observations. The monocular does not magnify and has a view angle of 40 degrees. A circuit of 49 GaAs infrared leds with a wavelength of 880 nm (Vision Nachtzicht Techniek, Born, the Netherlands) was mounted on the Night Mariner to improve the image contrast. When the lights were on, the scene viewed through the image intensifier was that of a dark green water surface with bright green bat silhouettes flying above it (figure 2). The observations were made from the top of the 8 m high stone wall, looking down on the trawling bats below. The image intensifier was used to estimate the distance between the bats and the wall (see below).

Sound recordings

A Pettersson D240 ultrasound detector with heterodyne and time expansion systems (Pettersson Elektronik AB, Uppsala, Sweden), with a memory storage time of 1.7 s, was used for acoustic observations, instant species identification in the field and sound recordings in the time expansion mode.

Recordings were made with the detector held on top of the wall taking care that it didn't protrude (so as to avoid reflections from the wall to the microphone). Sounds were recorded from bats in their search phase, flying in a straight line parallel to the wall and of bats performing feeding buzzes, circular manoeuvres with a diameter of about 1 m. The stages between the search phase and the final buzz were evaluated by analysing the pulse lengths and intervals, following Kalko and Schnitzler (1998). Combined heterodyne and time expansion recordings were stored on a stereo Minidisc Walkman MZ-R35 at a sampling rate of 44 kHz.

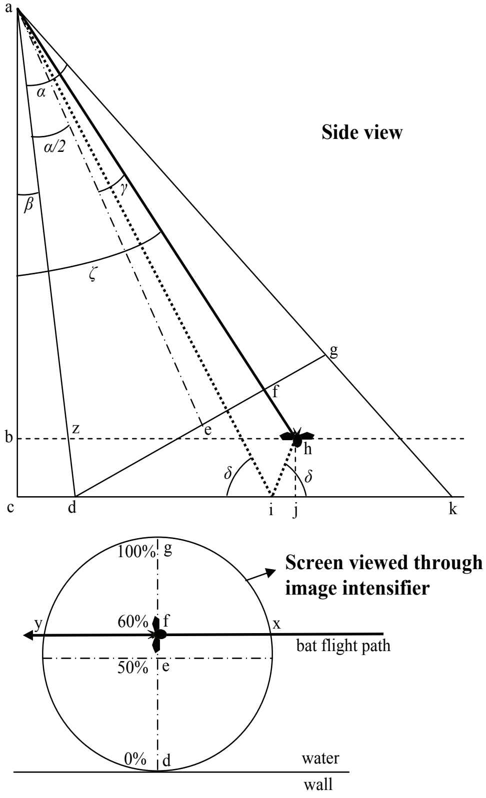

Figure 2. Schematic representation of visual observations made from the top of a rampart wall, of trawling bats hunting low over the water surface close to the wall. Side view of the scene (top) and field of view seen through an image intensifier (bottom) show the method of estimating bat flight height (*hj*) and the distance of the bat to the wall (*hz*). *a*: observation point (visual and acoustic), *h*: position of bat at moment when it crosses the perpendicular of the image intensifier screen, held in such a position that the bottom of the screen rakes the border line of the wall and –water. The full bold line in the side view represents the pathway of the pulse from the mouth of the bat to the microphone in *a*, the bold dotted lines show the pathways of the echo reflected by the water surface in *i*.

Sound analysis

The BatSound programme (Pettersson Elektronik AB) was used to analyse the time expansion recordings. Pulse-echo time interval (*dt*), pulse length and pulse interval were measured in spectrograms made from Fast Fourier Transforms, Hanning window, FFT size: 256 samples, FFT-overlap: -1. The pulse interval (PI) was defined as the time between the start of one pulse and the start of the next. Since pulses and surface echoes overlap in time, the oscillogram could not be used to measure *dt*.

Analysis of time expansion recordings of bats flying below the wall revealed that every pulse was followed by an almost exact copy with a delay of a maximum of 3.1 ms (figure 3). The second pulse is a strong reflection of a point (*i*) on the smooth water surface between the bat and the microphone where the angles of reflection (δ) are the same (figure 2). Siemers et al. (2001) described a similar ground echo in recordings made from an artificial bat positioned 12 cm above a smooth screen in laboratory conditions. The time delay they measured (0.73 ms) corresponded exactly to the height of 12 cm. The field recordings from this study only yielded these strong pulse-echo pairs from recordings made from above the bats; they were not so clearly observed in recordings made from ground level. In recordings made from ground level the reflection point on the surface may be too far away from the bat, so the energy of the sound beam when it hits the surface may be too weak to give a noticeable echo, due to atmospheric attenuation and spherical spreading. In recordings from (nearly) above the bat, the reflection point will be very close to the bat. While trawling bats in horizontal flight emit sound in a directional fashion (and not primarily directed downwards), the surface echoes are still strong enough to be picked up by a microphone at a distance of about 9 m.

Species identification

Trawling bats were identified in the field, by listening to the sounds in the heterodyne mode, with the detector being adjusted to 38 kHz. Dauben-

Variables and equations	**Definition**	**Example**
a	top of the wall where visual observations (image intensifier) and time expansion recordings (ultrasound detector) were done.	
d	bottom of the wall, this is the point where the water surface of the moat touches the wall.	
dk	water surface of the moat	
h	position of the bat at the moment when it crosses the perpendicular of the image intensifier screen at a certain percent of the screen diameter (image intensifier held so that the bottom of the screen raked the border line between wall and water surface).	
hj	bat flight height (cm)	55 cm
ad	length of the inclined side of the wall, measured using a chord (cm).	802 cm
α	field of view of the image intensifier (Deg)	40 Deg
β	angle of the wall inclination, measured using a water level and a protractor (Deg).	9.7 Deg
$ac = ad.\cos\beta$		791 cm
$ab = ac - hj$		736 cm
$bz = ab.\sin\beta$		124 cm
$cd = ad.\sin\beta$		135 cm
$ae = ad.\cos\left(\frac{\alpha}{2}\right)$		754 cm
$de = ad.\sin\left(\frac{\alpha}{2}\right)$		274 cm
$percentSD$	estimated intersection of the bat's flight path with the diameter of the screen of the image intensifier (perpendicular to the wall) expressed as percent of the full screen diameter (%).	60%
$df = 2.de.\frac{percentSD}{100}$		329 cm
$ef = df - de$		54.8 cm
$\gamma = \arctan\left(\frac{ef}{ae}\right)$		4.16 Deg
$\zeta = \beta + \frac{\alpha}{2} + \gamma$		33.8 Deg
$ah = \frac{ab}{\cos\zeta}$	pathway of direct pulse from mouth of bat to microphone (cm)	886 cm
$cj = bh = ab.\tan\zeta$		494 cm
$hz = cj - bz$	horizontal distance bat to wall edge (cm)	397 cm
$ai = \sqrt{ac^2 + \left(\frac{ac.cj}{ac + hj}\right)^2}$	pathway of echo from water surface to microphone (cm)	915 cm
$\delta = \arcsin\left(\frac{ac}{ai}\right)$	angle of sound reflection on the water surface (Deg)	59.7 Deg
$ci = ai.\cos\delta$		461 cm
$di = ci - cd$	distance reflection point water surface to wall edge (cm)	326 cm
$hi = \frac{hj}{\sin\delta}$	pathway of pulse from mouth of bat to reflection point on water surface (cm)	63.7 cm
$xy = 2.de.\cos\left[\arcsin\left(\frac{ef}{de}\right)\right]$	length of the bat's flight path between entry point (x) and exit point (y) of the image intensifier screen (cm)	538 cm
w	flight speed of the bat (supposed) (m/s)	4 m/s
t	time required by bat to cross the screen of the image intensifier (from x to y) at the supposed bat flight speed w (s)	1.3 s
v	speed of sound (cm/ms) at air temperature (°C)	33.1 cm/ms (at 5°C)
$dt = \frac{1}{v}(ai + hi - ah)$	pulse-echo time difference (ms)	2.8 ms

Table 1. Equations used to calculate the pulse-echo time interval *dt* from a known flight height *hj*. Right column: example of a calculation for a flight height of 55 cm and a bat-to-wall distance corresponding to an estimated 60% of the diameter of the screen (as observed through an image intensifier positioned so that the bottom of the screen was set to where the wall and water met (see figure 2).

ton's bats produce dry clicks at this frequency and pond bats relatively loud, wet, smacking sounds of a slightly higher pitch, since the detector was tuned a few kHz above the pond bat's QCF-frequency (33-35 kHz) (Limpens & Roschen 1995, Limpens 2001). Each identification was checked by analysing the corresponding time expansion recordings. The pulse series of pond bats included at least some characteristic FM-QCF-FM signals with the QCF part at 33-35 kHz. Daubenton's bats don't use QCF parts in their signals. Visual observations confirmed the acoustic identification. When passing close to the wall, the silhouettes of pond bats seen through the image intensifier were clearly larger than those of Daubenton's bats, and the difference in head-body size was particularly obvious. Pond bats also flew faster than Daubenton's bats, although no speed measurements were done.

In July 2000 samples of both species were caught in Japanese nets positioned under a low bridge over these moats and identification was confirmed by examination of the bat and measuring the forearm length (following Schober & Grimmberger 1998). In August 2000 a small pond bat maternity roost (20-30 individuals) was found about 5 km from the recording site, by radio tracking a juvenile pond bat that was caught in the Japanese net (Van De Sijpe 2001, Van De Sijpe 2003).

Flight height calculation method

The pulse-echo time interval *dt* can be calculated from a known flight height *hj* by applying the equations and relations shown in table 1 and figure 2. This calculation requires the following input data: the length of the inclined wall (*ad*) ,the view angle of the image intensifier (α*),* the angle of wall inclination (β)*,* and the distance of the bat to the wall (*hz*). The length *ad* and the angle β were measured in the field, the angle α was taken from the image intensifier specifications and *hz* was derived by estimating the position of the bat in the screen of the image intensifier, expressed as percent of the full

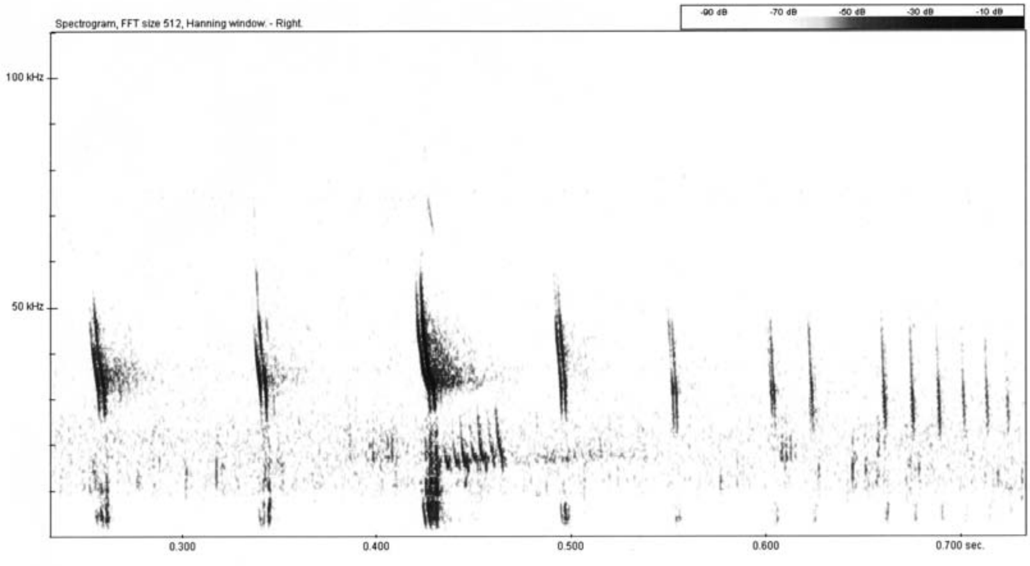

Figure 3. Spectrogram of a trawling pond bat in approach phase prior to a feeding buzz. The recording was made from the top of a high stone wall with the bat flying below over the water surface close to the wall. All the original pulses were followed by surface echoes, exact copies of the original pulse. As the bat approached the water surface to capture a prey item, the time interval of the pulse-echo pairs gradually shortens.

screen diameter (*percentSD*) at which the bat intersects the perpendicular (figure 2).

An iteration of the above calculation was done based on a measured pulse-echo time interval (*dt)* to find the unknown flight height *hj.* In the first step a flight height *hj* was assumed and *dt* was calculated and compared with the measured *dt*. The calculation was repeated until the calculated *dt* became equal to the measured *dt.*

Error estimates

Errors due to inaccurate estimation of the percent of the screen diameter
Assuming *dt* = 2.8 ms, and with the percent screen diameter estimated at 60%: the calculated flight height would be 55 cm. If the percent screen diameter was 70% the flight height would be 57.5 cm (4.5% error). At 80%, 90% and 100% screen diameter the error would increase to 10%, 16% and 24% respectively. For 50% screen diameter an error of 3.6% was found. Although the percent screen diameter is an estimate, the accuracy obtained in the field is estimated to be within ± 10%.

Errors due to incorrect timing of recording
Assuming *dt* = 2.8 ms, and with the percent screen diameter estimated at 60%: the calculated flight height would be 55 cm for a bat emitting a pulse precisely at the intersection with the perpendicular (*hz* = 369 cm). Incorrect timing of recording will cause a deviation from the perpendicular (figure 4). Assume that the recording is stopped when the bat emitted a pulse at *h*' (the exit point of the screen) instead of *h*. The distance *hh*' would be 269 cm, and the correct bat to wall distance would be 457 cm instead of 369 cm. This would give a flight height of 58 cm instead of 55 cm for the given dt of 2.8 ms, hence a 5.5% error. Bats flying at a speed of 4 m/s stay within the field of vision for a period of about 1.3 s, and will take circa 0.6 s to travel from *h* to *h*'. The time required by the bat to cross the entire screen is long enough for the observer to react in a more or less timely manner. In reality the error induced by incorrect timing of recording is estimated to be less than in the example above.

Errors due to discontinuous sound emission
Assume *dt* = 2.8 ms, and the percent screen diameter is estimated at 60%: the calculated flight height would be 55 cm for a bat emitting a pulse exactly at the intersection with the perpendicular. Bats flying at a speed of 4 m/s using a pulse repetition rate of 10 Hz (average pulse interval 100 ms) will travel a distance of 40 cm between two pulse emissions. Assume the recording was stopped exactly at the intersection with the perpendicular, but the bat emitted the last pulse 40 cm before the intersection, when at point u (figure 4). The flight height would be 55.1 cm (0.2% error).

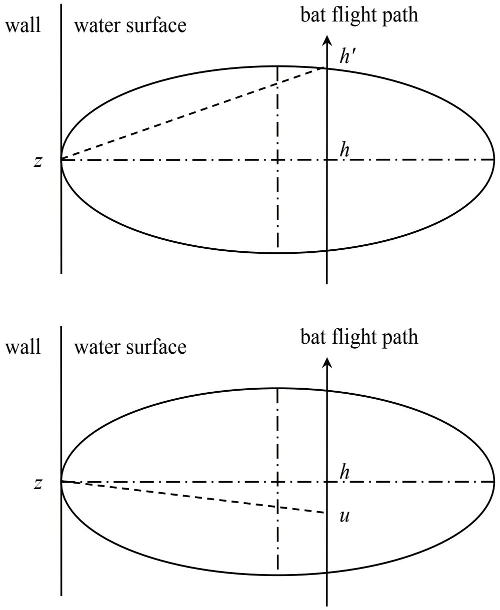

Figure 4. Examples used for error estimations due to incorrect timing of recording (above) and discontinuous nature of sonar emissions (below). The cross section of the horizontal plane through *z* and *h* (the flight height of the bat) with the conical space projected on the screen of the image intensifier is elliptical.

Data collection and statistical analysis

Sound recordings of pond bats and Daubenton's bats were made on the 29th of March 2004 and the 9th and 10th of April 2004. On these nights between 1-5 pond bats and 1-2 Daubenton's bats hunted over the water surface north of the Menin Gate Bridge. One time expansion sequence was analysed of a pond bat capture buzz close to the wall at circa 50% of the screen diameter and one bat pass of a pond bat in the search phase flying parallel to the wall was made at circa 60% of screen diameter. These sequences were used to estimate the change of flight height during the bat pass or manoeuvre. Additionally the flight height of bats in the search phase of hunting, when passing in front of the observer at circa 60% screen diameter was calculated for 30 bat passes of Daubenton's bats and 25 bat passes of pond bats. In parallel search phase flights pond bats did not fly closer to the wall than the estimated 60%, but during capture attempts they came closer (circa 50%). Daubenton's bats flew closer and both species flew also further away (>60%) but these recordings were not retained for analysis. To obtain an accurate value of flight height, it was necessary to find and record the pulse corresponding to the position of the bat as closely as possible to the intersection point with the perpendicular. The instant that the bat crossed the screen of the image intensifier in the centre, the time expansion button on the back of the detector was pushed and the contents of the detector's memory were transferred to the recorder. The pulse emitted by the bat when it passed the perpendicular of the screen then corresponded to the last pulse of the recorded time expansion sequence. Deviations that occurred have been discussed above.

Data sets of pulse-echo time interval*,* flight height, pulse length and pulse interval of pond bats and Daubenton's bats were statistically compared using Mann-Whitney non-parametrical tests with the Analyse-it programme running in Microsoft Excel (Analyse-it Software Ltd, Leeds, UK).

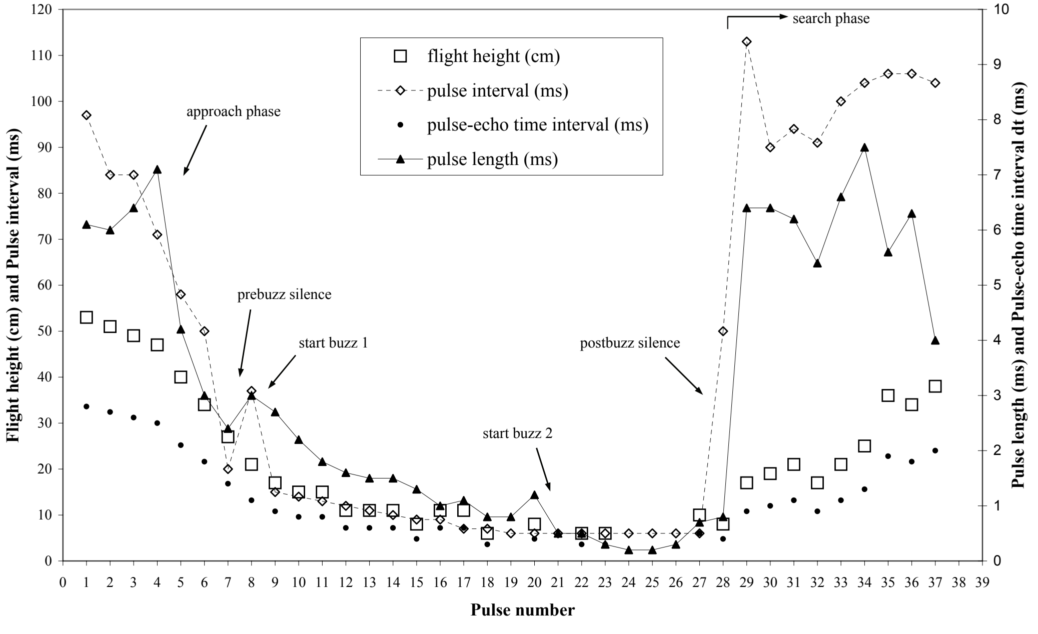

Figure 5. Change of pulse-echo time intervals, flight height, pulse length and pulse interval during a capture attempt by a trawling pond bat (39 consecutive pulses analysed). The various stages of the capture attempt were evaluated by pulse length and pulse interval changes, as per Kalko and Schnitzler (1998).

Results

Observations of hunting activity

Bat hunting activity over the Ieper town moats usually resumes every year by the middle or the end of March, following the winter months of inactivity. The often low temperatures in early spring, means that activity over the moats at this time is generally limited to four more or less cold-tolerant species: Daubenton's bat, pond bat, common pipistrelle (*Pipistrellus pipistrellus*) and Nathusius' pipistrelle (*Pipistrellus nathusii*). Both Pipistrelle species were active shortly after dusk but often disappeared after one to two hours, when the temperature dropped and the numbers of flying insects became too low. Both trawling bats continued their hunting activities for longer periods, even when the air temperature became as low as two to three degrees Celcius. Apparently there was still enough insect activity on the water surface or in the air just above it. Air temperature can be several degrees higher a few cm over water surfaces than a few metres higher (A.-J. Haarsma, personal communication).

During cold spring nights both Daubenton's bats and pond bats regularly flew close and parallel to the inner stone wall. The search flight was now and then interrupted by a manoeuvre (a tight circle when seen from above), which coincided with a feeding buzz (as heard through a bat detector) and visual observations revealed expanding circular waves in the water, indicating that the bat broke the surface. Later in the season, when temperatures increased the bats did not forage so close to the inner walls. The early spring bat activity was related to the mass emergence of non biting midges (Chironomidae) as revealed by visual observations with a torch. These midges and the emerging pupae also attracted many small surface dwelling fish, that were observed feeding on them. The moats are well protected against western winds by the high wall and tall trees on the rampart talus, and the shallow water is exposed to the morning and

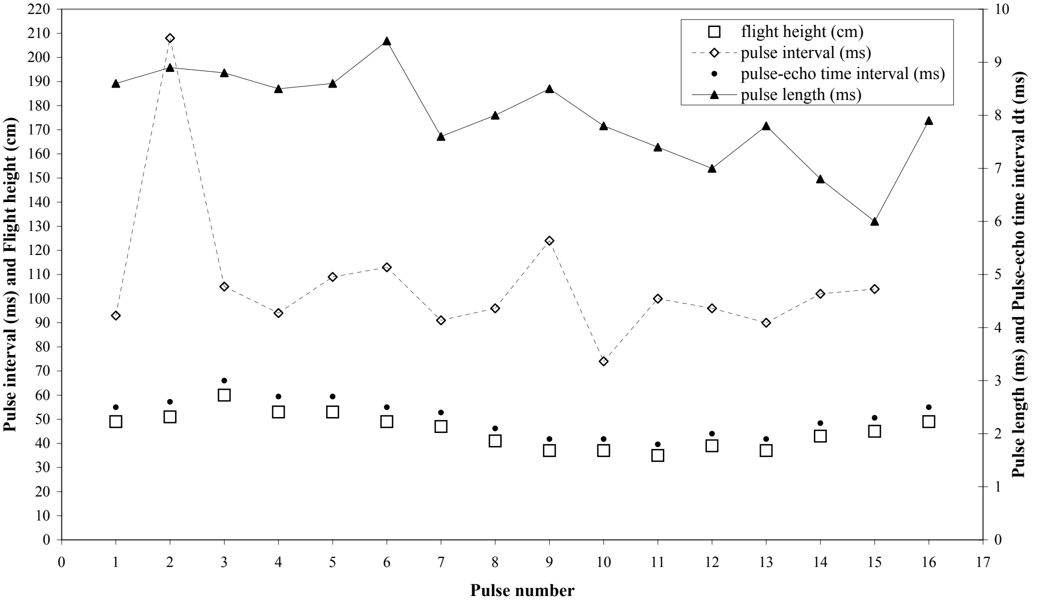

Figure 6. Change of pulse-echo time interval, flight height, pulse length and pulse interval during a bat pass of a trawling pond bat in the search phase of hunting.

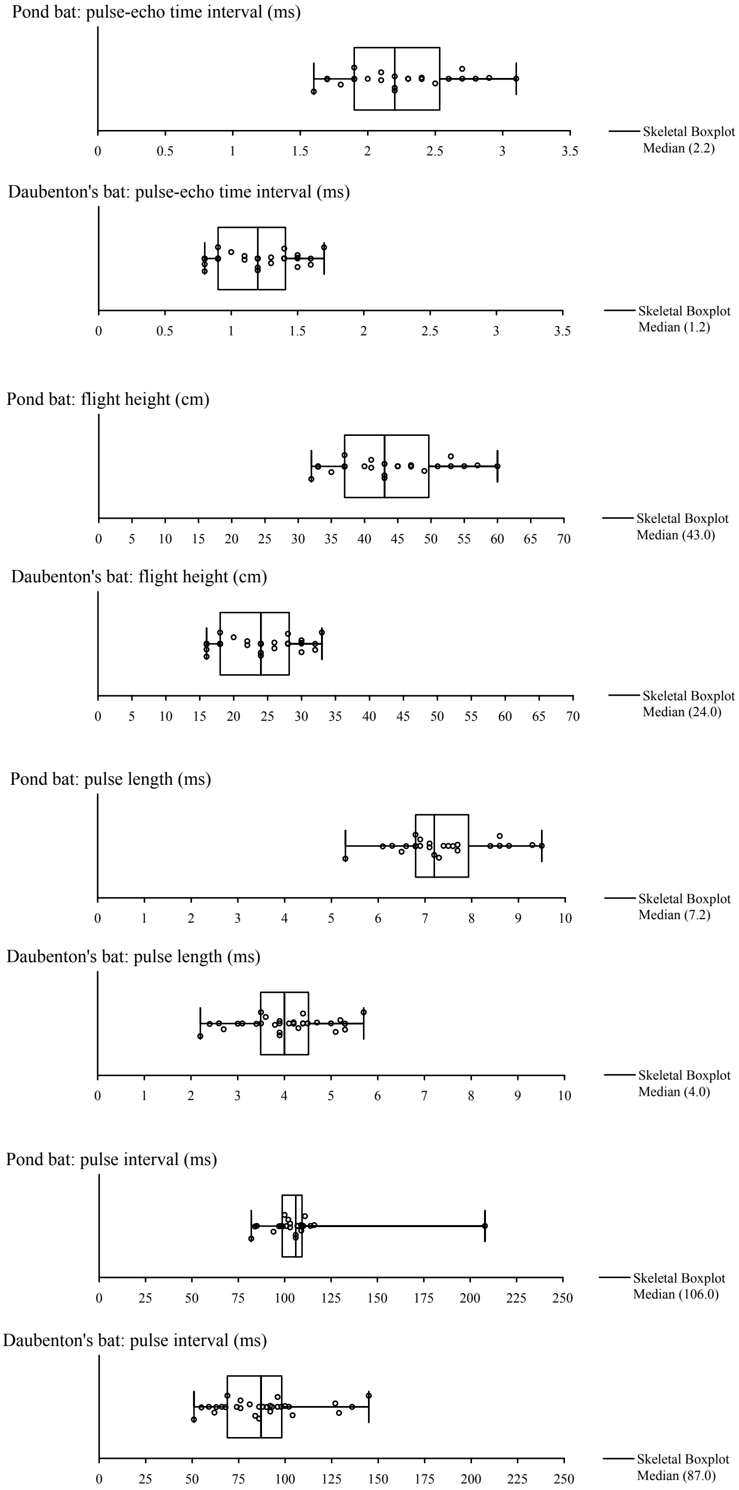

Figure 7. Dot and box plots of pulse-echo time interval, (ms) flight height (cm), pulse length (ms) and pulse interval (ms) including 25 recordings of pond bats and 30 recordings of Daubenton’s bats in linear search flights parallel to a rampart wall at a distance of circa 4 m from the wall. Dots represent individual data, the box defines first quartile, median and third quartile, the traits define minimum and maximum values

midday sunshine. In early spring shallow water warms up quicker than deep water, and so insect activity starts earlier in shallow waters. The presence of several bat hibernacula in the immediate vicinity of the moats also influences the intense early season bat activity.

Changes of flight height during a pond bat capture buzz

Figure 5 shows the change of pulse-echo interval, flight height, pulse length and pulse interval of a series of consecutive pulses from a time expansion recording of a pond bat manoeuvring in a tight circle at a distance of circa 3 m from the wall (estimated 50% of screen diameter) whilst trying to catch an insect. The capture attempt was observed visually by using the image intensifier and expanding waves were observed in the water indicating that the bat briefly touched the water surface during the attempt. The time interval between pulse and surface echo gradually decreased from 2.8 ms in the initial search phase to values as low as 0.3 ms during buzz 1 and buzz 2 and increased again after the post-buzz silence towards 2 ms at the 9th search phase pulse following the post-buzz silence. This corresponds to a flight height change from 53 cm in the search phase to about 6 cm during the final stages of the capture buzz, and back to 38 cm at the ninth pulse following the post-buzz silence (figure 5). These results confirm that the method for estimating flight height appears to be quite accurate because trawling bats are known to gradually descend to the water surface (pointed dips) in order to pick up an insect sitting on the water surface. At the moment of capture the hind feet just rake the water surface, the mouth of the bat then is at a height above the water of slightly less than the head-body length (5.5–6.7 cm for the pond bat, according to Schober & Grimmberger 1998). Other recordings made of capture buzzes of both pond bats and Daubenton's bats showed a similar pattern of gradually decreasing flight height from search to final buzz phase.

Changes of flight height during the linear search phase flight of a pond bat

Figure 6 shows the flight heights of a pond bat in a linear search phase flight, while passing parallel to the wall at an estimated distance of about 4 m (60 percent screen diameter). During 16 consecutive pulses the calculated flight height varied between 60 and 35 cm.

Flight heights of pond bats and Daubenton's bats in the search phase

Figure 7 shows dot and box plots for pulse-echo time interval, flight height, pulse length and pulse interval for 25 recordings of pond bats and 30 recordings of Daubenton's bats in the linear search phase. Pulse-echo time intervals were significantly greater in pond bats than in Daubenton's bat (pond bat median 2.2 ms, Daubenton's bat median 1.2 ms, $P<0.0001$) and so were the calculated flight heights (pond bat median 43 cm, Daubenton's bat median 24 cm, $P<0.0001$). Pond bats used significantly longer pulses (pond bat median 7.2 ms; Daubenton's bat median 4.0 ms; $P<0.0001$) and longer pulse intervals (pond bat median 106 ms; Daubenton's bat median 87 ms; $P=0.0003$) than Daubenton's bats.

Discussion

Comparison with literature data

The pond bat flight heights recorded in this study (6-60 cm) accord well with previous data (10-60 cm) published by Baagøe (1987). The median of 43 cm is also close to the height of circa 50 cm found by Siemers et al. (2005) who used videogrammetry in the artificial conditions of a flight room where pond bats searched for mealworms on a linoleum screen. However, the heights of hunting bats in the search phase (median 43 cm) were markedly higher than the ones of commuting bats obtained using photogrammetry by Britton et al. (1997) (26 ± 2 cm). This said, the data in this study are restricted to hunting activities and limited to a couple of nights in early season and at the same location. More data will be required to evaluate potential flight height differences due to behaviour (commuting vs. hunting), habitat type and/or season.

The flight height found for hunting Daubenton's bats (median 24 cm, min-max: 16-33 cm) is higher than the value reported by Kalko and Schnitzler (1988) by a photographic method (15.8 ± 6.7 cm, max 28 cm) and Baagøe (1987) (10-20 cm) but falls within the range of heights reported by Siemers et al. (2001) of Daubenton's bats flying over an artificial smooth surface (5-30 cm) in laboratory conditions.

Possible relations between height and flight behaviour in trawling bats

Bats fly by alternating upstrokes and downstrokes of their wing membrane. In order to avoid collisions with the water surface trawling bats have to fly as horizontally as possible especially when they fly very low over the surface and need to reduce the amplitude of their wing beats to avoid contact with the water. Piscivorous bats raking through the water with their claws for prolonged distances and flying as low as 4 cm above the surface (i.e. *Noctilio leporinus*) are the most extreme example. Insectivorous trawling bats catching prey from the surface by using pointed dips fall somewhere between the highly specialised piscivores and fully aerial hawking bats operating at heights of a few metres. Because of its lower flight height Daubenton's bat seems to be a more specialised trawling species than the pond bat.

The pond bat (17 g) has a higher wing loading (10.4 N/m²) compared to Daubenton's bats (7 g; 7.0 N/m²) and therefore is less manoeuvrable and tends to fly faster (Norberg & Rayner 1987, Schober & Grimmberger 1998). Britton et al. (1997) found flight speeds of 3.21 ± 1.92 m/s in hunting pond bats and 7.35 ± 1.26 m/s and 9.13 ± 0.41 m/s in commuting pond bats, depending on the location. Compared to Daubenton's bats the wing tips of pond bats are longer (wing tip length ratio pond bat: 1.43, Daubenton's bat: 1.22) and more pointed (wing tip index pond bat: 1.20; Daubenton's bat: 2.05) (Norberg & Rayner 1987). The wing tip values of pond bats are quite close to those of fast hawkers that operate at high altitude (*Nyctalus*, *Vespertilio*). High wing loading, long and pointed wingtips are adaptations to fast and agile flight at the expense of manoeuvrability. Pond bats prefer large open water bodies where speed and agility can be advantageous and manoeuvrability less important.

Daubenton's bat is a lightweight version of trawling bat with lower wing loading and shorter and more rounded wing tips, thus having a slower and more manoeuvrable flight (Norberg & Rayner 1987). Baagøe (1987), Kalko and Schnitzler (1988) and Jones and Rayner (1988) have reported flight speeds of 4.1 m/s, 3.4 ± 0.6 m/s and 3.87 ± 0.84 m/s respectively. Daubenton's bats are probably more efficient in trawling close to obstacles such as the edges of reedbeds and among the narrow spaces of riverine habitats thanks to their better manoeuvrability.

Daubenton's bat's lower flight height may provide it with greater energy savings thanks to the ground effect (Norberg & Rayner 1987, Britton et al. 1997) although the potential benefit of the ground effect on trawling bats should be studied more in detail.

Possible relations between height and echolocation behaviour in trawling bats

Pond bats and Daubenton's bats also differ in their echolocation behaviour (Ahlén 1990, Limpens & Roschen 1995). Pond bats use longer pulses with a smaller bandwidth, hence their distance of focus will be greater (Holderied et al. 2006, Boonman 2007, personal observations). They also use a lower peak frequency (pond bat: 33-38 kHz, Daubenton's bat: 38-45 kHz) and often a QCF part, both features that enlarge the detection distance (Schnitzler et al. 2003). In combination with the higher flight speed, these longer detection ranges may allow pond bats to scan larger areas of open water surface or larger volumes of air per unit of time than Daubenton's bats. As such pond bats may specialise on larger sized insects available in quite low densities. Higher flight heights may still provide small angles of incidence at the (larger) distance of focus, so pond bats may still also take advantage of the low background noise of smooth water surfaces, as stated by Siemers et al. (2001). In this study trawling pond bats performed several feeding buzzes in which the bat touched the water surface. The search phase heights found in this study (median 43 cm, min-max 32-60 cm) are apparently still low enough to detect small sized aquatic insects on the water surface. In summer pond bats sometimes use yet faster hunting flights while foraging low over open water for big insects (i.e. moths). In spite of the low flight heights in the search phase this strategy seems to be more a kind of fast aerial hawking than trawling, as the bats often catch the insects above their own search phase height (Van De Sijpe & Holsbeek 2007).

Daubenton's bats use a range of shorter pulse lengths of a higher peak frequency without QCF but with higher starting frequencies and larger bandwidths than pond bats (Boonman 2007). Although the shorter pulses probably limit the detection distance to a smaller volume of air in front of the bat, the shorter pulses and greater bandwidths yield more precise acoustic images at short range and a shorter distance of focus (Schnitzler et al. 2003, Holderied et al. 2006). This will be advantageous close to the bank side or near to floating aquatic vegetation where background echoes might interfere with prey echoes.

Potential niche differentiation between trawling bats

The two sympatric trawling insectivorous bats of the Northwestern Palaeartic, Daubenton's bat and the pond bat, differ in many aspects such as body size and weight, jaw and teeth row size, flight morphology, flight height, echolocation, roosting ecology and habitat preferences (Baagøe 1987, Norberg & Rayner 1987, Kapteyn 1995, Mostert 1997, Schober & Grimmberger 1998, Limpens et al. 1999, Krapp 2001, Dietz & von Helversen 2004). Although they are potential competitors since both hunt for prey exposed on the water surface and flying in the air just above it, niche differentiation seems to exist and might explain the large overlap of their distribution ranges and the fact that they sometimes hunt together in the same habitat.

Daubenton's bat is an efficient and successful trawling bat, given its large distribution area, high population density and the diversity of aquatic habitats it uses. Its range spans nearly the entire arboreal zone of the Palaearctic from the British Isles to the Far East, and also enters the Mediterranean zone in the south (Horáček et al. 2000) where Daubenton's bat competes with the Mediterranean trawling insectivorous and piscivorous long-fingered bat *Myotis capaccinii* (Aihartza et al. 2003, Levin et al. 2006, Biscardi et al. 2007). Based on DNA studies, Stadelmann et al. (2004) found that the lineage leading to the recent Daubenton's bat separated probably as late as the early Pliocene from a common ancestor shared with the forest-dwelling *Myotis bechsteinii*. The lineage leading to the recent pond bat apparently separated from an ancestral form in the earliest stages of the *Myotis* radiation, most likely some 10 million years ago in late Miocene (Stadelmann et al. 2004). Today the pond bat occupies a limited distribution area within the temperate humid and boreal zones of the western Palaeartic and is a rare species in large parts of its range (Horáček & Hanák 1989, Limpens et al. 1999, Horáček et al. 2000, Ciechanowski et al. 2007). This bat seems to only build large populations in areas with abundant large water surfaces and the core centres of its population are dispersed as islands in lowlands of northerly latitudes.

Further studies

Further work is recommended to study flight heights, speeds and flight mechanisms of trawling bats in more detail in order to better understand differences in behaviour and niche differentiation as well as to find answers to questions such as how trawling bats maintain the right height. The method described in this paper can be used in various locations where a microphone can be positioned above the bat. These would include high quay walls in villages, ramparts with wet moats bordered by walls, bridges over canals and rivers etc. If recordings can be made perpendicularly above the bats the equation for solving flight height will be much simpler than in this study, which involved oblique viewing. Other more accurate techniques such as flight path tracking by laser scans, stereo videogrammetry, or sound recording by multiple microphone arrays, as suggested by Jones and Holderied (2007) can also be recommended. The use of microphone arrays low over water may however be difficult since various reflections might result in ambiguous bat positions.

Conclusion

When foraging together over the Ieper town moats in March and April, both pond bats and Daubenton's bats used the trawling foraging tactic to feed extensively on emerging early season non-biting midges. By measuring the minute time intervals between pulses and echoes reflected by the water surface, the flight height of the bats at moments when the bats passed close to the stone wall could be estimated. This method confirmed literature data asserting that the medium-sized pond bat usually hunts higher over the water surface than the smaller Daubenton's bat. Whilst flying in a similar way in a same habitat and at a similar distance to the nearest clutter producing background (i.e. a stone wall), pond bats used longer pulses and longer pulse intervals than Daubenton's bats. Gradually decreasing time intervals during pond bat capture buzzes revealed that the bats descended to the water surface to catch insect prey and visual observations of circular waves in the water, seen from above, confirmed that the bat broke the water in the final stages of the capture buzz.

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References

Aihartza, J.R., U. Goiti, D. Almenar & I. Garin 2003. Evidences of piscivory by *Myotis capaccinii* (Bonaparte, 1837) in Southern Iberian Peninsula. Acta Chiropterologica 5 (2): 193-198.

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

Aldridge, H.D.J.N. 1988. Flight kinematics and energetics in the little brown bat, *Myotis lucifugus* (Chiroptera:Vespertilionidae), with reference to the influence of ground effect. Journal of Zoology, London 216: 205-217.

Baagøe, H. 1987. The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. In: M.B. Fenton, P.A. Racey & J.M.V. Rayner (eds). Recent advances in the study of bats: 57-73. Cambridge University Press, Cambridge, UK.

Biscardi, S., D. Russo, V. Casciani, M. Mei & L. Boitani. 2007. Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. Journal of Zoology, London 273: 372-381.

Boonman, A.M. 2007. Echolocatiepulsen. Zoogmail 2007-07.

Boonman, A.M., M. Boonman, F. Bretschneider & W. van de Grind 1998. Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in Daubenton's bat, *Myotis daubentonii*. Behavioral Ecology and Sociobiology 44: 99-107.

Brack, V. Jr. & R.K. La Val 2006. Diet of the gray myotis (*Myotis grisescens*): variability and consistency, opportunism and selectivity. Journal of Mammalogy 87 (1): 7-18.

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

Ciechanowski, M., K. Sachanowicz & T. Kokurewicz

2007. Rare or underestimated? – The distribution and abundance of the pond bat (*Myotis dasycneme*) in Poland. Lutra 50 (2): 107-134.

Dietz, C & O. von Helversen 2004. Illustrated key to the bats of Europe. Electronic publication – version 1.0., Tübingen and Erlangen, Germany. URL: http://www.unituebingen.de/uni/bzt/Kontakt/mitarbeiter_seiten/Dietz_von%20Helversen%202004ID%20key_1.pdf; viewed 29 October 2008

Fenton, M.B. & W. Bogdanowicz 2002. Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. Canadian Journal of Zoology 80: 1004-1013.

Holderied, M.W., G. Jones & O. von Helversen 2006. Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design, Doppler tolerance and evidence for 'acoustic focussing'. Journal of Experimental Biology 209: 1816-1826.

Horáček, I. & V. Hanák 1989. Distributional status of *Myotis dasycneme*. In: V. Hanák, I. Horáček & J. Gaisler (eds.). European Bat Research Symposium 1987: 565-590. Charles University Press, Prague, Czech Republic.

Horáček, I., V. Hanák & J. Gaisler 2000. Bats of the Palearctic Region: a taxonomic and biogeographic review. In: B.W. Woloszyn (ed.). Proceedings of the VIIIth European Bat Research Symposium 1: 11-157. CIC ISEZ PAN, Krakow, Poland.

Jones, G. & J.M.V. Rayner 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). Journal of Zoology, London 215: 113-132.

Jones, G. & J.M.V. Rayner 1991. Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae). Journal of Zoology, London 225: 393-412.

Jones, G. & M.W. Holderied 2007. Bat echolocation calls: adaptation and convergent evolution. Proceedings of the Royal Society of London, B 274: 905-912.

Kalko, E.K.V. & H.-U. Schnitzler 1988. The echolocation and hunting behaviour of Daubenton's bat, *Myotis daubentonii*. Behavioral Ecology and Sociobiology 24: 225-238.

Kalko, E.K.V. & H.-U. Schnitzler 1998. How echolocating bats approach and acquire food. In: T. H. Kunz & P. A. Racey (eds.). Bat biology and conservation: 197-204. Smithsonian Institution Press, Washington D.C., USA.

Kapteyn, K. 1995. Vleermuizen in het landschap. Over hun ecologie, gedrag en verspreiding. Schuyt and Co, Haarlem, the Netherlands.

Krapp, F. 2001. Handbuch der Säugetiere Europas. Fledertiere I. Aula Verlag, Wiebelsheim, Germany.

Mostert, K. 1997. Meervleermuis *Myotis dasycneme* (Boie, 1825). In: H.J.G.A. Limpens, K. Mostert and W. Bongers (eds.). Atlas van de Nederlandse vleermuizen: 124-150. K.N.N.V. Uitgeverij, Utrecht, the Netherlands.

Levin, E., A Barnea, Y. Yovel & Y. Yom-Tov 2006. Have introduced fish initiated piscivory among the long-fingered bat? Mammalian Biology 71 (3): 193-143.

Limpens, H.J.G.A. 2001. Assessing the European distribution of the pond bat (*Myotis dasycneme*) using bat detectors and other survey methods. Nietoperze II, 2: 169-178.

Limpens, H.J.G.A. & A. Roschen 1995. Bestimmung der mitteleuropäischen Fledermausarten anhand ihrer Rufe: Lern- und Ubungskassette mit Begleitheft. – BAG Fledermausschutz im Naturschutzbund Deutschland and NABU Projectgruppe Fledermauserfassung Niedersachsen. Bremervörde, Germany.

Limpens, H.J.G.A., P.H.C. Lina & A.M. Hutson 1999. Revised action plan for the conservation of the pond bat (*Myotis dasycneme*) in Europe (Mammalia: Chiroptera). Report to the Council of Europe, Strassbourg, France.

Norberg, U.M. & J.M.V. Rayner 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B. 316: 335-427.

Rydell, J., L.A. Miller & M. Jensen 1999. Echolocation constraints of Daubenton's Bat foraging over water. Functional Ecology 13: 247-255.

Schnitzler, H.-U., E.K.V. Kalko, I. Kaipf & A.D. Grinnell 1994. Fishing and echolocation behavior of the greater bulldog bat *Noctilio leporinus*, in the field. Behavioral Ecology and Sociobiology 35: 327-345.

Schnitzler, H.-U., C.F. Moss, I. Kaipf & A. Denzinger 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution 18: 386-394.

Schober, W. & E. Grimmberger 1998. Die Fledermäuse Europas. Kosmos, Stuttgart, Germany.

Siemers, B. M., P. Stilz and H.-U. Schnitzler 2001. The acoustic advantage of hunting at low heights over water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*. Journal of Experimental Biology 204: 3843-3854.

Siemers, B. M., E. Baur & H.-U. Schnitzler 2005. Acoustic mirror effect increases prey detection distance in trawling bats. Naturwissenschaften 92: 272-276.

Stadelmann, B., D.S. Jacobs, C. Schoeman & M. Ruedi 2004. Phylogeny of African *Myotis* bats (Chiroptera:Vespertilionidae) inferred from cytochrome b sequences. Acta Chiropterologica 6 (2): 177-192.

Todd, V.L.G. & D.A. Waters 2007. Strategy switching in the gaffing bat. Journal of Zoology, London 273: 106-113.

Van De Sijpe, M. 2001. De vondst van een kraamkolonie van de meervleermuis (*Myotis dasycneme*) te Boezinge en verdere gegevens over deze soort in de regio Ieper. Referatenmap Vierde Belgische Vleermuizenstudiedag. 17 November 2001. Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium.

Van De Sijpe, M. 2003. Meervleermuis (pond bat). In: S. Verkem, J. De Maeseneer, B. Vandendriessche, G. Verbeylen & S. Yskout (eds.). Zoogdieren in Vlaanderen (Mammals in Flanders): 111-117. Natuurpunt Studie & JNM Zoogdierenwerkgroep, Mechelen & Gent, Belgium.

Van De Sijpe, M. & L. Holsbeek 2007. Hunting strategy and tympanate moth predation by the pond bat (*Myotis dasycneme*). Lutra 50 (2): 91-106.

Samenvatting

Vlieghoogte bij harkende meervleermuizen en watervleermuizen

Dit artikel beschrijft een indirecte manier om de vlieghoogte van harkende vleermuizen te schatten aan de hand van zeer kleine tijdsintervallen tussen de pulsen en echo's van het wateroppervlak. De bijzondere locatie van de Vauban-vestingen rond de stad Ieper, maakte het mogelijk om tijdexpansie opnamen te maken van harkende vleermuizen schuin boven de vleermuizen. De opnamen werden gemaakt op de top van een hoge muur die een brede vestinggracht begrenst aan de binnenzijde, terwijl watervleermuizen (*Myotis daubentonii*) en meervleermuizen (*Myotis dasycneme*) over het wateroppervlak jaagden en daarbij parallel en vrij dicht langs de muur vlogen. De sterke echo's waren bruikbaar om de vlieghoogte vrij nauwkeurig te schatten, zo bleek uit een gedetailleerde analyse van een vangstmoment van een meervleermuis dicht langs de muur, waarbij in de finale fase de vleermuis de waterspiegel doorbrak en uitdijende golfjes in het water zichtbaar werden. De tijdsintervallen tussen puls en echo verminderden gradueel van zoekfase tot de finale buzz fase. Deze stemden overeen met een geleidelijke vermindering van de vlieghoogte van circa 53 cm in de zoekfase naar circa 6 cm in de buzz fase. Geluidsanalyses van jagende water- en meervleermuizen bracht aan het licht dat meervleermuizen hoger boven de waterspiegel vlogen (mediaan 43 cm) dan watervleermuizen (mediaan 24 cm) tijdens de zoekfase van de jachtvlucht.

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Defragmentation measures and the increase of a local European badger (*Meles meles*) population at Eindegooi, the Netherlands

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Abstract: Twenty four years' data on European badger (*Meles meles*) and sett numbers have been collected by direct observation of a local population at Eindegooi, which straddles the Dutch provinces of Utrecht and Noord-Holland. The population has shown periods of both slow and exponential growth and spatial dynamics show colonization of the entire study area. Analysis of how population dynamics respond to defragmentation measures involving roads has been undertaken. This suggests that tunnels and other measures make a positive contribution. At low densities and during periods of slow growth these measures can increase the lifetime of reproducing individuals and help badgers to safely disperse and colonize new habitat patches. Their positive effect on the population is illustrated by the fact that an individual's mortality risk from traffic has remained more or less constant, despite the increasing number of cars on motorways and provincial roads that dissect the study area.

Keywords: badger, *Meles meles*, population growth, badger friendly measures, traffic, roads.

Introduction

The Dutch European badger (*Meles meles*) population is recovering after a strong decline in the second half of the last century (Wiertz & Vink 1986, Wiertz 1992, Moll 2002, Moll 2005). The decline of the species in the 1960s and 1970s seems to be strongly related to the growing density of roads at all spatial levels (motorways, provincial and local roads) and the more intensive use of the road network (van der Zee et al. 1992). In the 1970s this decrease in badger numbers was the main reason for carrying out the first badger friendly measures, which were spread across the entire country and mainly consisted of tunnels under roads and motorways and badger guiding fences. These measures focused mainly on reducing fatal traffic accidents, but also on defragmenting isolated badger populations. Initially organized at the local level, a national defragmentation policy was initiated, which is still ongoing (Ministerie van Landbouw, Natuurbeheer en Visserij 1990, Bekker & Canters 1997, Ministerie van Verkeer en Waterstaat et al. 2004). Since 1990 such measures have become an integrated part of motorway building and renovation projects. Special programmes have been formulated for existing roads that aim to mitigate the threat to local badger populations. Since these measures have been implemented, the Dutch badger population has shown an increase in numbers. The contribution of these measures to the population increase has never been analyzed, but can be hypothesized to be positive for a species that suffers from traffic, as illustrated by modelling work based on traffic casualty data (Seiler 2003) and on the survival of European badger meta-populations (Lankester et al. 1991).

Lutra articles also on the internet: http://www.vzz.nl

Several studies in the Netherlands and other countries show that defragmentation measures such as tunnels and ecoducts are used by badgers and other mammal species (e.g. Nieuwenhuizen & van Apeldoorn 1995, Smit et al. 1996, Pfister et al. 1997, Clevenger & Waltho 1999). Furthermore, it has been shown that fences help to reduce the number of traffic victims but only if they are used in combination with passages that meet recommended standards for criteria such as size and accessibility (Clevenger et al. 2001, Iuell et al. 2003, Jaeger & Fahrig 2004). However, it is much more difficult to prove that these measures have caused the population increase in the Netherlands.

During a 24 year study of a local badger population in an area in the provinces of Noord-Holland and Utrecht, data was collected on the changes in badger numbers and their setts and their spatial distribution (Vink & van Apeldoorn 1995, Apeldoorn et al. 2006). A first analysis of data from 1983-2001 suggested the availability of good feeding areas as being the main cause for the increase of the local population and its spreading out over a larger area.

The study by Apeldoorn et al. (2006) does not analyze in detail the possible role of the badger friendly measures in the area and this study seeks to address this question, using the available badger population data up until 2006.

Material and methods

The study area

The area where badgers and badger activity have been studied lies near Eindegooi, between the cities of Hilversum and Baarn in the north, Soest and De Bilt in the east, Utrecht in the south and lake Loosdrechtse Plassen in

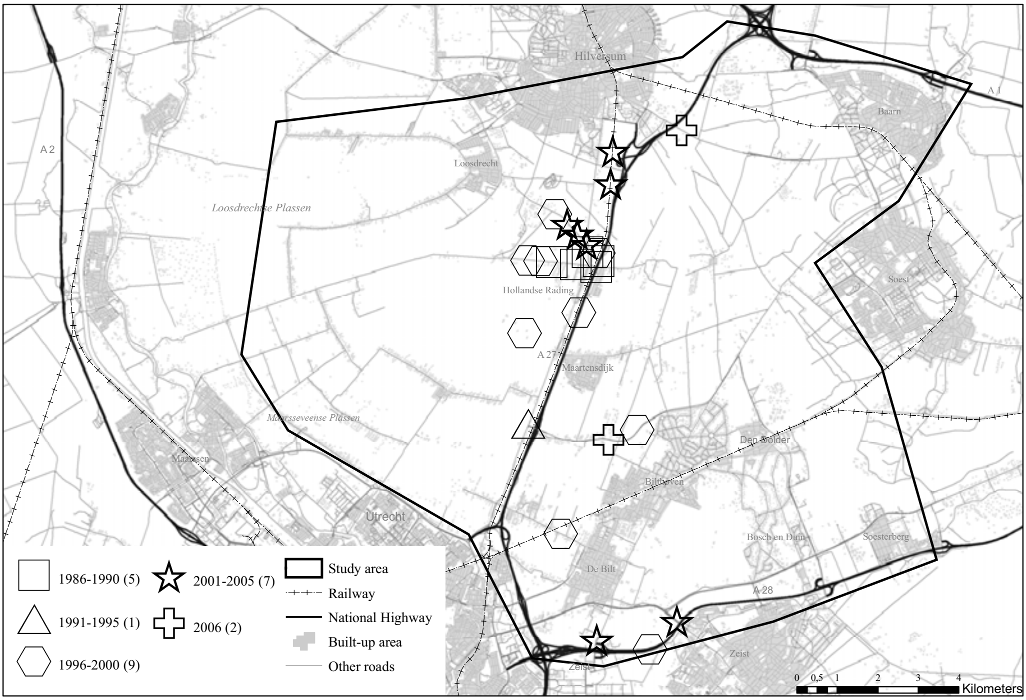

Figure 1. Badger tunnels in the study area and their use over five periods.

the west. The area is dissected by railways and motorways (A27, A1 and A28) and several provincial and local roads. Between Utrecht and Hilversum the A27 motorway, a secondary road and the railway line all run very close to each other (figure 1). Other secondary roads (provincial and local) cross the area, connecting small villages such as Bilthoven, Maartensdijk, and Nieuw Loosdrecht. The A28 motorway is situated to the south of this area and the A1 motorway to the north. These motorways constitute strong dispersal barriers in the north, south and east of the study area and contribute to the isolation of the population. The area is situated on a soil gradient, with a sandy wooded bank above sea level in the east (the Utrechtse Heuvelrug) and a peaty area that lies below sea level around lake Loosdrechtse Plassen in the west, where a mixture of pastures, marshland and open water can be found. Urban areas, pastures and woodland are the most important habitat types. An increasing amount of farmland is used for growing maize for cattle feed. More detailed information on the habitat types in the area and how they are used by badgers can be found in Apeldoorn et al. (2006).

The badgers in the study area are considered to be more or less isolated because of the long distance (about 30 km) across open landscape to the nearest other area permanently inhabited by badgers. However a few badger setts have been found in the southern part of the wooded Utrechtse Heuvelrug, about 15 km from the edge of this study area. This area is densely populated, contains many small villages and is crossed by crowded secondary roads and separated from the study area by the A28 motorway. To date, no dead badgers have been found on this motorway.

Counting badgers and setts

Apeldoorn et al. (2006) give a detailed description of the methods they used for counting badgers (adults and juveniles) and setts. Badgers were counted several times each year between May and July. A yearly an area-wide search for setts was carried out. Setts were searched for in the whole area and were visited at least five times a year. Victims of traffic accidents were also counted. All the data collection involved the help of many volunteers.
The mean number of badgers counted in the period May-July was taken as an estimate of the number of badgers present in the study area (minimum numbers alive). The number of all cubs observed above ground at different setts was taken as an estimate of the reproduction.

Permanently inhabited setts (main setts) in which cubs were born or regularly observed were classified as main ‘breeding’ setts. Setts only used by badgers during a short period were identified as ‘outliers’. The number of social groups was estimated according to the number of main setts and by using qualitative field data (latrines). The use of tunnels was observed using barbed wire and footprint beds. Data on traffic victims were collected monthly and the search area was enlarged following the badger expansion.

Results

Use of roads

Traffic data for motorways and other types of roads was collected in 1995, 2000 and 2005 by the Rijkswaterstaat (Centre for Transport and Navigation) and by Utrecht Province (Verkeersinformatie Systeem Puvis). These figures show a clear increase in the number of cars on most motorways and provincial roads during the study period (table 1). The traffic levels in 1985 and 1990 are assumed to be lower than the numbers mentioned here (Rijkswaterstaat Adviesdienst Verkeer en Vervoer 2003). Along the motorways traffic flow occurs at all hours of the day and night. Traffic flows are lowest during the night and the early hours of the morning, when badgers are most active. Traffic volumes at weekends are lower and fluctuate more during the day than on weekdays.

Table 1. Use of different types of roads by number of cars; (1) average of three working days in February, May and October; (2) average use per day.

	1995	2000	2005
Motorways (1)			
A27 S=>N	33620	42812	46310
A27 N=>S	32779	42012	44478
A28 W=>E	43044	50156	52641
A28 E=>W	44179	51958	55468
Provincial roads (2)			
234	12400	14700	15000
237	18400	17600	18100
238	8900	10300	11700
413	9200	8600	12500
415	8900	9500	9500
417	11400	12200	12500

Badger friendly measures on and around roads

Since the mid 1980s, a range of badger friendly measures has been undertaken across the area. This was partly stimulated by estimates that, in 1987, two-thirds of the local badger population were dying in traffic accidents (Vink, personal communication). Badgers almost immediately started to use these facilities. In each study period, badgers used more than 50% of the tunnels (figure 1). By 2006, more than 14.2 km of fences and 27 tunnels had been constructed, alongside and under motorways, provincial and local roads. Six existing civil engineering structures, bridges, viaducts and tunnels for crossing local and provincial roads, were adapted so they could also be used by animals, including badgers. Sound walls along the motorways were also found to function as badger fences, guiding individuals during their daily movements.

Numbers of badgers, setts and social groups

Regular observations and counting of badgers and setts started in 1984, under the lead of the first author, with the help of many volunteers. Over 22 years the population increased from six animals (1984) to 91 in 2006 (figure 2). During the first five years the increase was very slow. Between 1988 and 1997 the numbers of badgers fluctuated and then began to increase again. Overall the population shows an exponential growth ($y=4.3\exp^{(0.13x)}$, $R^2=0.92$; figure 2), while the regression curve shows a yearly growth of 13%. We have indications that in 2007 and 2008, the population continues to grow (J. Vink, unpublished data).

Until 1996 reproduction was low in most years (fewer than six juveniles) but between 1996 and 2006 the number of juveniles increased, with the most (twenty-four) cubs being born in 2003 (figure 2). Probably no cubs were born in 1989, 1990 and 1994. The occurrence of more than one litter at main breeding setts was only observed in a few years. In 1999 two litters were found at an old main sett at the Eindegooi estate, with a third litter found at a former main sett 30 m away (J. Vink, unpublished data). In 2003 three cubs were born at an artificial sett very close to an existing main sett in the north of the area near Loosdrecht. The numbers of cubs per main breeding sett (BR; see figure 2) was usually between two to three, although in five years (1991, 1998, 1999, 2002 and 2003) more than three cubs per main breeding sett were born.

In addition to the increases in the numbers of adults and juveniles (figure 2), there was also an increase in the number of social groups and setts (breeding and non-breeding) over time. Before 1998 the number of social groups never increased by more than one per year. Since 1998 the annual increase has generally been by more than one group. The increase in number of social groups coincides with an increase in the number of permanently inhabited setts (figure 3; main BR and NBR setts) and their distribution (figure 4), and illustrates the growth of the local population and its expansion all over the area.

The occupation of the area

Badgers have shown a strong expansion across the study area, starting from the Eindegooi estate in Hollandsche Rading, where badgers were present when observations began (figure 4). After an initial increase of the population at this location, the first new main sett was built to the north in the vicinity of Loosdrecht. This was followed by new inhabited setts on the eastern side of the A27 motorway and to the southeast of the Eindegooi estate between 1986 and 1995. Between 1996 and 2000 there was a further expansion, mostly to the eastern side of the motorway in a small-scale landscape with good grasslands. From 2001 onwards, inhabited setts could be found spread across the area enclosed by the mires in the west and the cities of Utrecht and Zeist in the south, Soest and Baarn in the east and Hilversum in the north (figure 4). Between 2001 and 2005 setts were also built in the western part of

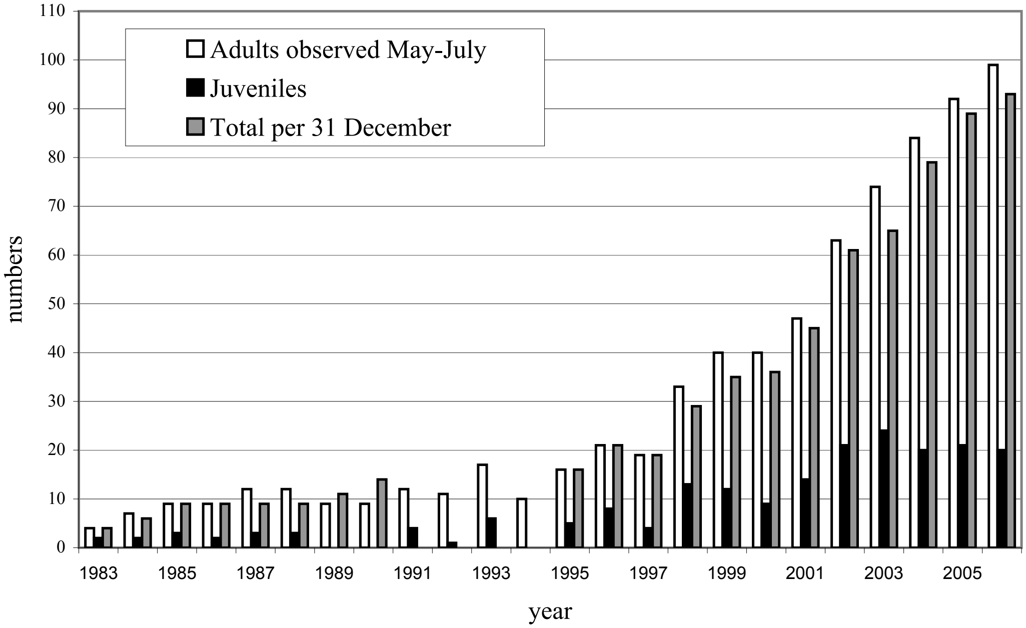

Figure 2. Number of badgers (adults and juveniles) observed during the period 1984-2006 and assumed end-of-year survival rate

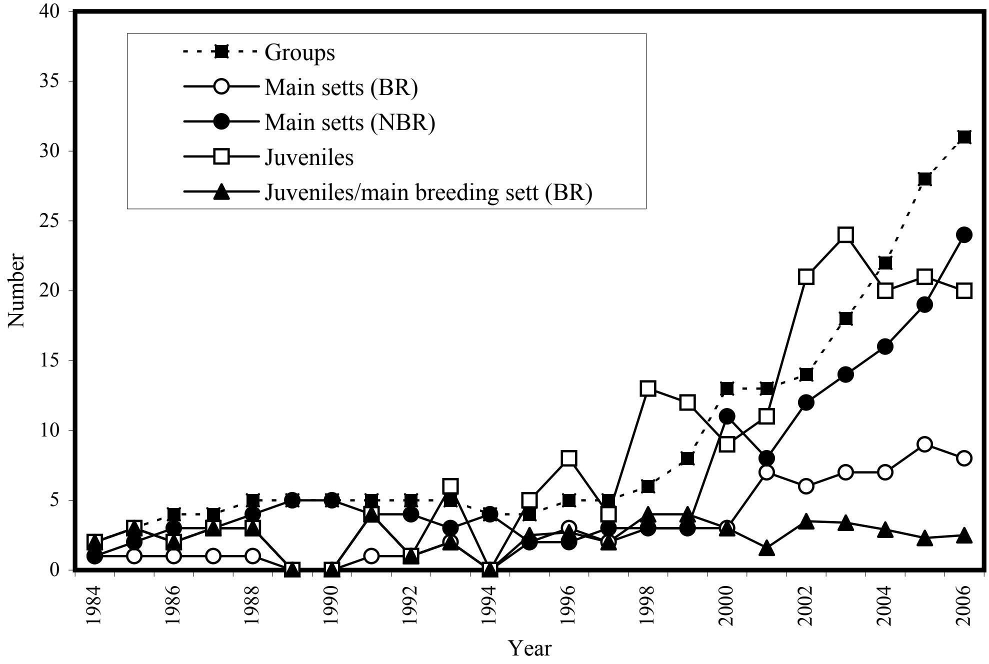

Figure 3. Number of social groups, main setts with and without breeding (BR, NBR), juveniles and juveniles per main breeding sett (as an index of reproduction).

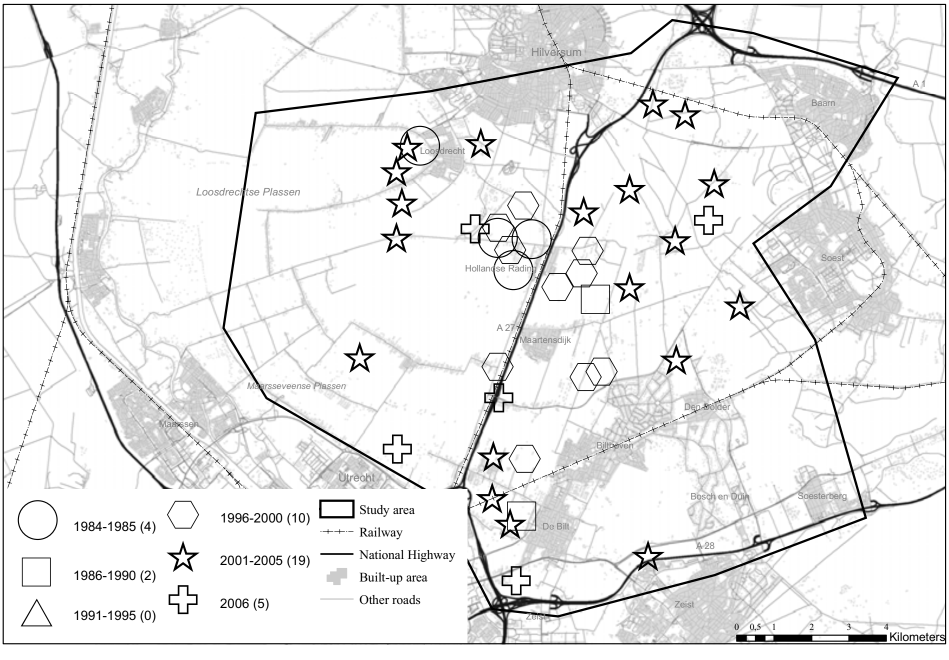

Figure 4. Inhabited badger setts during six periods.

the area, where the predominant habitat is wet peaty grasslands, and in the east, with relatively monoculture coniferous forest (Apeldoorn et al. 2006). Although all the good habitat patches seemed to be already in use, five new setts were discovered in 2006. A more detailed description of the occupation process can be found in Apeldoorn et al. (2006).

Mortality

Of the 98 badgers found dead in the area between 1984 and 2006, 28 were found along motorways, 3 on the railway, 19 on provincial roads and 48 on local roads (figure 5). The number of traffic victims remained quite low till 1998 (six or fewer) but, following the rapid population increase since then, the number of traffic victims increased, although it has not exceeded 14 (in 2000) and 11 (in 2006).

By comparing the number of traffic victims with the total number alive each year, one can calculate the risk to individual badgers of being killed by a car. While this has varied over time, it has not increased significantly (figure 6; P=0.557).

Until 1995, most traffic victims were concentrated around the Eindegooi estate, although a few dead badgers were found further away (figure 7). Since 1995 the distribution of road kills, which are now found all over the area, illustrates the expansion of the population (figure 2). Several victims were found alongside the A28 and A1 motorways, although all were within the area that these motorways enclose.

It is noticeable that dead badgers are no longer (or less frequently) found at several locations where measures have been taken to reduce badger/traffic conflicts. One of the roads crossing the area (Graaf Florisweg) yielded six victims before four badger tunnels and badger-proof fences were built, but only two since this time, despite badger numbers in this area increasing strongly. At another road (Noodweg) there were nine traffic victims before one km of badger-proof fences were installed, but only two since then. On a third road (Groenekanse weg) two badgers were killed before a badger tunnel was built, but none since.

Until 1988 all except one of the victims along the A27 were found close to Eindegooi. After fences were built there in 1988, the victims were found further to the south (between 1988–1995). After the fence was extended in this direction in 1995, the victims were again found further to the south. Over recent years the victims are found along the unfenced sections of the motorway. A similar shift in the location of fatal accidents has been found along the Noodweg and the Graaf Florisweg.

In 1999 twelve tattooed badgers were translocated from elsewhere into the study area. Due to concerns about the genetic background of these animals, three of them were recaptured and replaced by four new ones. In the same year a high number of traffic victims (eleven) was registered; five of which were identified as introduced badgers. For a combination of reasons, the other dead badgers can also be assumed to be released badgers (Apeldoorn et al. 2006).

Discussion

Growth

Before 1940, the European badger was assumed to be commonly found on the wooded sandy soils in the eastern part of the study area, but was thought to have become extinct there during the 1960s (van Wijngaarden et al. 1971). In 1983, four badgers and a permanently occupied sett were observed in a woodlot close to the Eindegooi estate (figure 2). The population grew slowly in the first years of observation, but in more recent years numbers have grown exponentially. The initial increase in groups and numbers does not seem to result from an increase in mean litter size. Given an assumption of no immigration, the population growth can be explained by a reduction in mortality resulting in a higher individual survival that will increase the reproduction rate. The

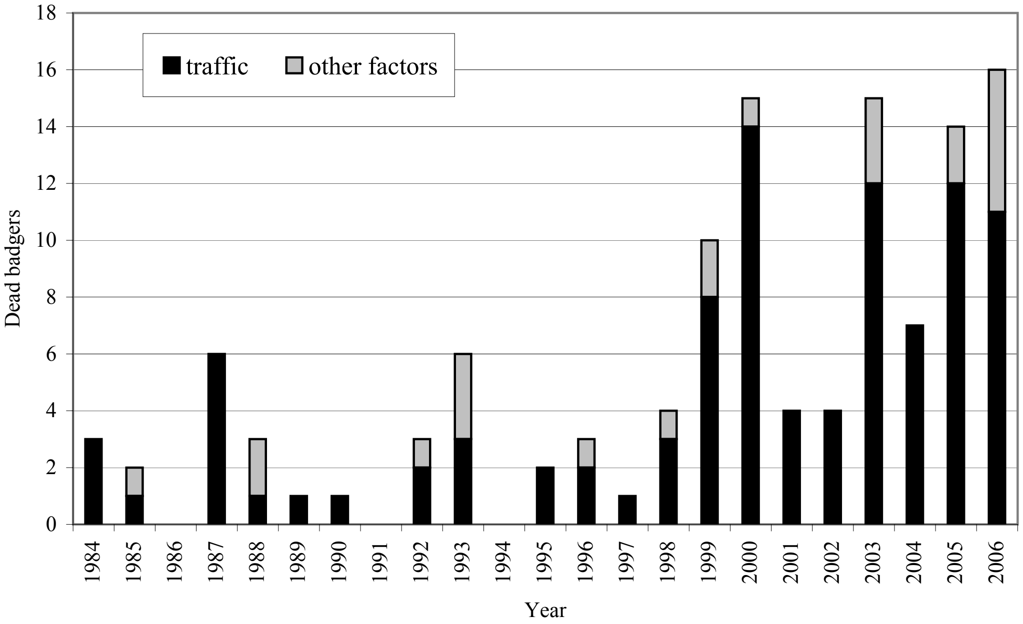

Figure 5. Mortality due to traffic and other factors.

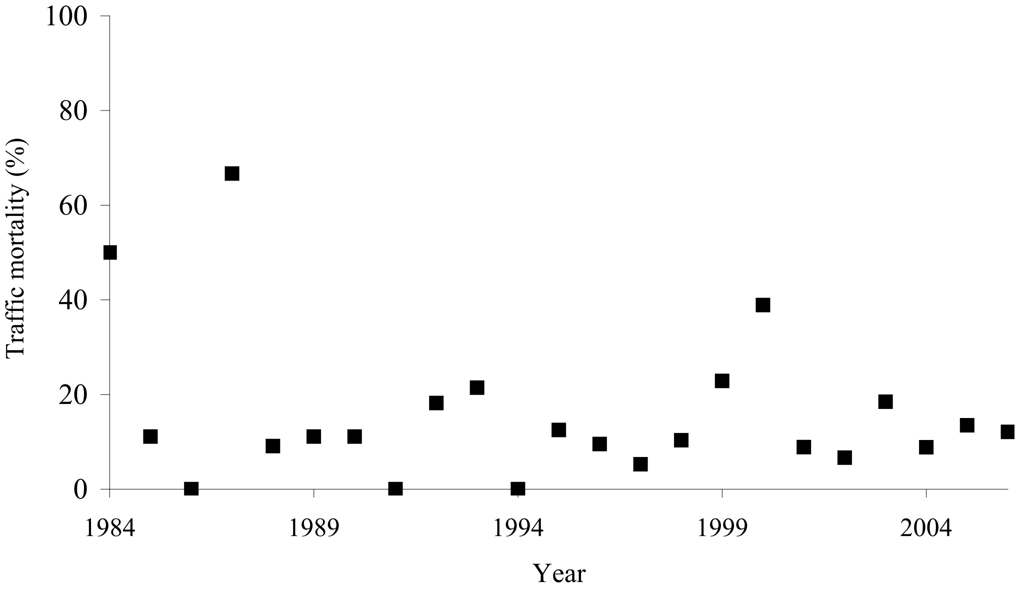

Figure 6. Traffic mortality (% of badgers killed by cars annually).

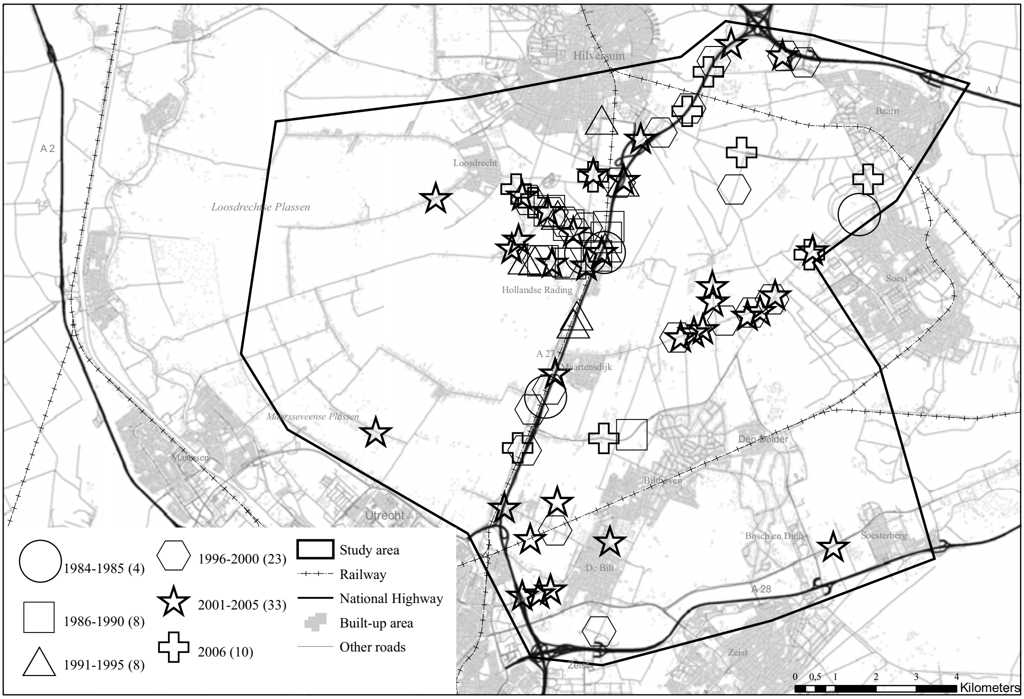

Figure 7. Locations of traffic victims in four periods.

initial slow population growth occurred before tunnels were constructed and fences were erected. Although tunnels were put in place and were being used between 1988 and 1995, there was little increase in badger numbers, suggesting the tunnels did not directly affect population growth. However, these measures may have indirectly stimulated population growth, by making it easier for badgers to safely cross their home ranges in their search for food, causing individuals to live longer and to take part in reproduction longer. This is especially important in populations with low densities. At the same time, the measures have also helped badgers to disperse safely over the busy motorways and secondary roads and thereby enabled a rapid colonization of parts of the study area that provide good habitat. The exponential growth of the population is described by Apeldoorn et al. (2006) who also discuss the possible causes. They analyzed the population growth up till 2001 and concluded that better habitat quality is the main cause of the exponential population growth. This exponential growth suggests that badger numbers are not regulated by internal population factors (Begon et al. 2006). This interpretation of density independence is supported by the increased productivity of younger sows, which correlates with the observations of more than one litter at main setts and with breeding at an artificial sett that can be interpreted as breeding at an annex sett (Cresswell et al. 1992). The authors also concluded that the population still had not reached its population ceiling; this was confirmed by the subsequent increase in badger numbers since 2001.

Mortality

Our data clearly shows that traffic is the most important cause of badger mortality in the study area (figure 5). With three motorways and a number of very crowded secondary roads in the study area, one would expect traffic mortality to increase because of increases both in traffic volumes and in the number and density of badgers. Since 1999, levels of fatalities were higher in two years, but this is most likely due to the high number of badgers that were introduced into the area in 1999. Introduced animals can influence the social structure of badgers and can cause dispersal of resident badgers, thereby influencing mortality rates (Rogers et al. 2000).

Throughout the period there was no increase in an individual badger's risk of dying in a traffic accident (figure 4). This can be explained by the expansion of the species throughout the area during the period of growth which offset an increase in population density. At the same time the number of cars on all types of roads in the area also increased, but this did not result in higher traffic mortality, indirectly showing the positive effect of the protection measures that were taken. This is also illustrated by the fact that dead badgers were no longer found at locations where measures had been taken.

So far, no new setts or signs of badger activity have been found outside the area enclosed by the A28 and A1 motorways, the cities and villages. These features seem to function as absolute barriers. However, the colonization of parts of the study area by badgers after measures were taken on the A27 motorway and smaller roads indicate that measures are effective in decreasing this barrier effect.

The increased badger abundance in the study area has coincided with an increase of the species in the Netherlands from 1990-2000 (Moll 2002). It is not known whether the local and national increase have the same causes, although factors relating to improvements in habitat quality seem to play a dominant role at both the local and national scale (Apeldoorn et al. 2006).

Conclusions and recommendations

Based on the existing data it is hard to prove that badger friendly measures caused the increase of the local badger population. Habitat quality alone may be more important (Apeldoorn et al. 2006). However, it can be concluded that measures have made a positive contribution to the increase, as demonstrated by the reduction in mortality at places where fences and badger tunnels are installed. The colonization of the study area by badgers that followed the weakening of the barrier effect of roads illustrates the effectiveness of such measures in creating ecological corridors that enhance the movement and dispersal of badgers into unoccupied habitats.

The five new setts found in 2006 and the increase in numbers and occupied setts in 2007 indicate that the carrying capacity of the area still has not been reached and higher densities of badgers and setts might be expected. At present the badger population is still expanding and dispersing badgers may potentially colonize adjacent (uninhabited) areas.

This leads us to recommend the construction of more fences and badger tunnels (following the technical descriptions of Kruidering et al. 2005). According to the Long Term De-Fragmentation Programme, the Ministry for Transport, Public Works and Water Management is currently planning to install several more badger friendly measures along the A27 and A28 motorways between 2009 and 2011 (Ministerie van Verkeer & Waterstaat et al. 2004). An ecoduct will be built over the A27 motorway and the adjacent provincial road and railway line. Another ecoduct will be built over the A28 motorway, between Zeist and Soesterberg, and a third will be constructed over the A1 motorway, just outside our study area to the west of the junction of the A1 and A27 motorways. In addition the Province of Utrecht is planning to build some ecoducts and other badger friendly measures inside the study area.

In addition to these measures we also recommend the building of fences and tunnels at several other specific locations. These are:

- local roads that produce relatively high numbers of traffic victims (the road between Maartensdijk and Pijnenburg, the remaining part of the Noodweg, the Biltse Rading, the

provincial road between Bilthoven and Soest and the road linking Hilversum with Baarn);
- Across the A1 motorway, between km 30 and km 40 as there is good feeding habitat to the north of this motorway;
- Across the A27 motorway (north of km 82), where many victims are found;
- Across the A28 motorway, because there is good badger habitat south of this motorway.

Such measures are likely to continue to support the continued growth in badger numbers in this area and their dispersal to adjoining attractive habitats, although with an expanding badger population in this crowded part of the Netherlands, traffic victims are inevitable.

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References

Apeldoorn, R.C. van, J. Vink & T. Matyáštík 2006. Dynamics of a local badger (*Meles meles*) population in the Netherlands over the years 1983–2001. Mammalian Biology 71: 25-38.

Begon, M., C.R. Townsend & J.L. Harper 2006. Ecology. From individuals to ecosystems. Fourth edition. Blackwell Publishing, Oxford, UK.

Bekker, G.J. & K. J. Canters 1997. The continuing story of badgers and their tunnels. In: K. Canters, A. Piepers & D. Hendriks-Heersma (eds.). Proceedings of the international conference: Habitat fragmentation, infrastructure and the role of ecological engineering: 344-353. 17-21 September 1995, Maastricht/Den Haag, the Netherlands. DWW publication P-DWW-97-046, Delft, the Netherlands.

Clevenger, A.P. & N. Waltho 1999. Dry drainage culverts use and design considerations for small- and medium sized mammal movement across a major transportation corridor. In: Proceedings of the Third International Conference on Wildlife Ecology and Transportation: 263-277. September 13-16, Missoula, Montana, USA.

Clevenger, A.P, B. Chruszcz & K. Gunson 2001. Drainage culverts as habitat linkages and factors affecting passage by mammals. Journal of Applied Ecology 38: 1340-1349.

Cresswell, W.J., S. Harris, C.L. Cheeseman & P.J. Mallinson 1992. To breed or not to breed: an analysis of the social and density-dependent constraints on the fecundity of female badgers (*Meles meles*). Philosophical Transactions of the Royal Society of London 338: 393-407.

Iuell, B., G.J. Bekker, R. Cuperus, J. Dufek, G. Fry, C. Hicks, V. Hlavac, V. Keller, C. Rosell, T. Sangwine, N. Torslov & B. Le Maire Wandall 2003. Wildlife and Traffic: A European Handbook for Identifying Conflicts and Designing Solutions. KNNV Publishers, Utrecht, the Netherlands.

Jaeger, J.A.G. & L. Fahrig 2004. Effects of road fencing on population persistence. Conservation Biology 18 (6): 1651-1657.

Kruidering, A.M., G. Veenbaas, R. Kleiberg, G. Koot, Y. Rosloot & E. van Jaarsveld 2005. Leidraad Faunavoorzieningen bij wegen. Rijkswaterstaat, Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.

Lankester, K., R. van Apeldoorn, E. Meelis & J. Verboom 1991. Management perspectives for populations of the eurasian badger (*Meles meles*) in a fragmented landscape. Journal of Applied Ecology 28: 561- 573.

Ministerie van Landbouw, Natuurbeheer en Visserij 1990. Natuurbeleidsplan. SDU, Den Haag, the Netherlands.

Ministerie van Verkeer en Waterstaat, Ministerie van Landbouw, Natuur en Voedselkwaliteit & Ministerie van Volkshuisvesting, Ruimtelijke Ordening en Milieu 2004. Meerjarenprogramma Ontsnippering. SDU, Den Haag, the Netherlands.

Moll, C.M. 2002. Verspreiding van de Das in Nederland 1995-2000. Rapport 2000/150. Expertisecentrum LNV, Wageningen, the Netherlands.

Moll, C.M. 2005. Distribution of the badger (*Meles meles* L.) in the Netherlands, changes between 1995 and 2001. Lutra 48 (1): 3-34.

Nieuwenhuizen, W. & R.C. van Apeldoorn 1995. Het gebruik van faunapassages door zoogdieren bij rijksweg A1 ter hoogte van Oldenzaal. Project Versnippering, deel 20. Dienst Weg- en Waterbouwkunde, Delft, the Netherlands.

Pfister, H.P., V. Keller, H. Reck & B. Georgii 1997. Bio-ökologische Wirksamkeit von Grünbrücken über Verkehrswege. Forschung, Strassenbau und Verkehrstechnik 756. Bundesministerium für Verkehr, Bonn, Germany.

Rijkswaterstaat Adviesdienst Verkeer en Vervoer, 2003. Prestaties Nederlands Wegennet; de ontwikkeling van het wegverkeer, de wegcapaciteit en congestie in verleden en toekomst. Rotterdam, the Netherlands.

Rogers L.M., R.J. Delahay, T.D. Hounsome & C.L. Cheeseman 2000. Changes in badger, *Meles meles*, social organisation in response to increasing population density at Woodchester Park, south-west England. In: H.I. Griffiths (ed.). Mustelids in a Modern World: 267-279. Backhuys Publishers, Leiden, the Netherlands.

Seiler, A., J-O Helldin & T. Eckersten 2003. Road mortality in Swedish badgers (*Meles meles*): Effect on population. In: A. Seiler. The toll of the automobile: wildlife and roads in Sweden. PhD thesis. Swedish University of Agriculture Sciences, Uppsala, Sweden.

Smit, G.F.J., G. Veenbaas & J. Brandjes 1996. Het gebruik van faunapassages bij Rijkswegen. Overzicht en onderzoeksplan. Report W-DWW-96-116. DWW Ontsnipperingsreeks deel 29. Delft, the Netherlands.

van der Zee, F.F., J. Wiertz, C.J.F. ter Braak, R.C. van Apeldoorn & J. Vink 1992. Landscape change as a possible cause of the badger *Meles meles* L. decline in the Netherlands. Biological Conservation 61: 17-22.

van Wijngaarden A. & J. van den Peppel 1964. De das, *Meles meles* (L.) in Nederland. RIVON, Zeist, the Netherlands.

van Wijngaarden, A., V. van Laar & M.D.M. Trommel 1971. De verspreiding van de Nederlandse zoogdieren. Lutra 13 (1-3): 1-41.

Vink, J. & R.C. van Apeldoorn 1995. De Das *Meles meles* in Keent, Noord-Brabant: de geschiedenis van een locale dassenpopulatie. Lutra 38 (2): 105-119.

Wiertz, J. 1992. De Nederlandse dassenpopulatie anno 1990. Lutra 35 (2): 75-89.

Wiertz, J. & J. Vink 1986. The present status of the badger *Meles meles* (L., 1758) in the Netherlands. Lutra 29 (1): 21-53.

Samenvatting

Ontsnipperingsmaatregelen en de groei van de lokale dassenpopulatie (*Meles meles*) op Eindegooi

Vanaf 1984 zijn gegevens verzameld over aantallen dassen (*Meles meles*) en burchten op het landgoed Eindegooi en omgeving. De gegevens tot 2006 laten zien dat de populatie eerst langzaam en vanaf midden jaren ’90 exponentieel groeide. Daarbij koloniseerde de das nieuwe terreinen. In dezelfde periode zijn vele ontsnipperende maatregelen bij wegen getroffen, waaronder een groot aantal tunnels en rasters. Deze maatregelen lijken een positieve bijdrage aan de groei van de populatie te leveren. Dit zou blijken uit de kans dat individuele dassen slachtoffer worden van het verkeer. Deze kans bleef min of meer constant gedurende de waarnemingsperiode, ondanks het toegenomen autoverkeer op de snelwegen en provinciale wegen die het gebied omgeven en doorkruisen. Bij lage dichtheden en een langzame populatiegroei kunnen de maatregelen de gemiddelde leeftijd van dieren verhogen waarbij ze indirect de overlevingskans van de populatie positief beïnvloeden. Daarnaast kunnen ze de (lokale) sterfte van dassen verlagen gedurende bewegingen binnen hun leefgebied en tijdens dispersie.

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Cetaceans stranded in the Netherlands from 1998 to 2007

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Abstract: Between 1998 and 2007, 2063 cetaceans were found stranded in the Netherlands, representing at least 14 species. Two species, humpback whale (*Megaptera novaeangliae)* and Blainville's beaked whale (*Mesoplodon densirostris)*, are additions to the Dutch list. Apart from the first humpback whales, relatively many balaenopterid whales were found in comparison with previous decades. Range extension of recovering populations may explain part of this trend. However, the decline in strandings frequency in sperm whales (*Physeter macrocephalus)*, another species with a slowly recovering Atlantic population but with a distinct peak in strandings in the 1990s, suggests that the factors underlying these changes are complex. During the 20th century, the strandings frequency of some dolphin species regularly occurring in the North Sea has changed markedly. Bottlenose dolphins (*Tursiops truncatus)* disappeared in the 1960s, common dolphins (*Delphinus delphis)* were fairly numerous during some decades in the mid-20th century, and white-beaked dolphins (*Lagenorhynchus albirostris)* became abundant and virtually replaced bottlenose dolphins in the strandings records since the 1970s. Numbers of stranded harbour porpoises (*Phocoena phocoena)* continued to increase over the years. All individual cases other than harbour porpoises are listed in this paper, reporting species, date, locality, reporter, sex, total length (TL), collected remains, and remarks. A total of 1968 reports of stranded harbour porpoises were received, ranging from 59 in 1998 to 539 in 2006. It is estimated that along the North Sea coast at least 19% more porpoises were washed ashore than were actually recorded. On the Wadden Sea islands, this discrepancy is estimated as at least 30%. The mean length of porpoises declined gradually with time and the sex ratio was male-biased in all subregions. From measurements (TL) it is concluded that circa 72% were juveniles, with small proportions of adults (15.5%; unsexed and ♂♂ animals of TL>150 cm, ♀♀ animals of TL>145 cm) and neonates or stillborns (12.4%; all porpoises of TL<90 cm). The predominance of males is evident only in juveniles (62.8%), whereas the sex ratio in adults and neonates is not significantly skewed. 20.2% of the females and 12.1% of the males are large enough to be regarded as sexually mature. The overall strandings pattern of the harbour porpoise is bimodal, with peaks in strandings in March-April and August. Presumed adults were proportionally numerous in winter (December-January) and in June, whereas about a quarter of all porpoises found in July, August and September were neonates or stillborn. At least ten porpoises were very large (TL estimated or measured >170 cm) and a minimum of 14 females were either pregnant or had recently given birth. It should be noted, however, that only a small proportion of the porpoises was checked for reproductive status. Foetuses ranged in length from 22 cm (December 2006) to 75 cm (May 2004). Many porpoises were decomposed when found and these were buried or removed and destroyed. At least 38 cases were reported with evident external signs of by-catches, another 17 carcasses had been heavily mutilated with knives. A combination of histopathology and gross pathology of 255 harbour porpoises found in the period 1990-2000 and in 2006 and 2007 suggested that between 50 and 60% of the animals showed signs of definite or probable by-catch in fishing gear. Many of the stranded porpoises found had come into conflict with fisheries and had died, as several of the larger (baleen) whales did. A dialogue with fisheries organisations is proposed to explore the issue further and to try and mitigate the problem.

Keywords: cetaceans, strandings, the Netherlands, North Sea, Wadden Sea, fin whale, sei whale, minke whale, humpback whale, sperm whale, Sowerby's beaked whale, Blainville's beaked whale, long-finned pilot whale, bottlenose dolphin, striped dolphin, common dolphin, white-beaked dolphin, white-sided dolphin, harbour porpoise.

Introduction

Stranded cetaceans found on the Dutch coast have received considerable attention, in particular since the early 20th century when A.B. van Deinse published his thesis on recent and fossil cetaceans in the Netherlands (van Deinse 1931). Following some earlier papers, his thesis and his review of cetaceans stranded from 1931 to 1944 (van Deinse 1946b), he produced annual reports until his death, reporting strandings from 1942 through 1964 (van Deinse 1943-1966). The regular publication of reviews, first in the format of biennial, later triennial reports, was resumed in the early 1970s, covering 1970 and later years (van Utrecht & Husson 1968, Husson & van Bree 1972, van Bree & Husson 1974, Husson & van Bree 1976, van Bree & Smeenk 1978, van Bree & Smeenk 1982, Smeenk 1986, Smeenk 1989, Smeenk 1992, Smeenk 1995, Smeenk 2003). The most recent paper (Smeenk 2003) covered five years of data (1993-1997) and was the last comprehensive review so far. As in the previous decades, during the past ten years stranded cetaceans have been documented by the staff of the National Museum of Natural History (*Naturalis*) in Leiden. Several spectacular strandings have occurred, including two species not earlier recorded from the Dutch coast: the humpback whale (*Megaptera novaeangliae*) (Smeenk et al. 2003) and Blainville's beaked whale (*Mesoplodon densirostris*). Perhaps even more significant, however, was a drastic increase in the frequency of harbour porpoise (*Phocoena phocoena*) strandings, from 26.3 ± 2.0 (mean ± SE) porpoises annum^{-1} from 1971 to 1997 to as many as 194.2 ± 23.2 annum^{-1} from 1998 to 2007. These events were noticed (cf. Camphuysen 2004) and, in response to an urgent demand for updated strandings data, C.J. Camphuysen digitised published and unpublished data and made an effort to update the resulting database with new strandings. The database was transferred to and is currently managed by Hein van Grouw at *Naturalis*. The database is frequently updated and made available on the internet (www.walvisstrandingen.nl).

Chris Smeenk, author or co-author of seven of the previous reviews reporting strandings of cetaceans in the Netherlands (covering 1976-1997), retired in 2005. With his retirement, and in the absence of a full-time successor at *Naturalis*, there was a risk that the series of carefully documented reviews would come to an end. Some may consider the online database a sufficiently accurate replacement of these publications. However, the authors feel that a printed review providing the possibility of re-assessing reported strandings is a valuable and much needed step in the process of documentation of stranded cetaceans. Strandings data add considerably to our knowledge and understanding of these animals and their occurrence in the (southern) North Sea. Remarkable changes in abundance have occurred over the last century, many of which are touched upon in this review. The possible correlation of these changes with environmental conditions including climate change, make a careful documentation urgent. Some of the data reported here have been included in other recent publications evaluating the status of cetaceans in the Dutch sector of the North Sea (Camphuysen & Peet 2006, van der Meij & Camphuysen 2006). Concerning the validation of the strandings data, the conclusions given in the present paper and in the earlier reviews should be followed.

Methods

Following conventions in previous reviews of stranded cetaceans, details are listed for each individual found ashore, dead or alive, including species, date, locality, total length (TL, cm), sex (♂, ♀ or unknown), reporter, registration numbers of any remains in museum collections, and interesting facts such as the proximate cause of death, physical condition or other circumstances. Indications of the status of cetaceans in the Netherlands in the headlines of the species accounts follow the proposals formulated by van der Meij and Camphuysen (2006). A complete listing was impossible for the harbour porpoise, with nearly 2000 documented strandings between 1998 and

2007. For some of the analyses in that species, the data were grouped for 15 subregions, including: the North Sea shoreline of the Wadden Sea islands: Rottum, Schiermonnikoog, Ameland, Terschelling, Vlieland, and Texel (1-6); four stretches of mainland coast: Noord-Holland N (north), Noord-Holland M (central), Noord-Holland Z (south), and Zuid-Holland (7-10), the Voordelta, including the North Sea beaches of Voorne-Maasvlakte (11), and the former Delta islands Goeree, Schouwen, Walcheren, as well as Zeeuws-Vlaanderen (12-15; figure 3). A more simple subdivision used in this paper comprises only five subregions, separating the North Sea shoreline from more inland sites: all sandy beaches and dikes bordering the North Sea of the Wadden Sea islands, the mainland coast of Noord- and Zuid-Holland and the Voordelta as three separate areas, to be distinguished from the inner Delta and Wadden Sea area (including the Wadden Sea sides of the islands). The latter are mainly estuarine areas, consisting of a mixture of beaches, dikes, dams, sluice-complexes, salt marshes, flood plains and river mouths, and none of these are directly exposed to the North Sea.

Some of the frequent contributors to the strandings database are associated with institutes or organisations, which are indicated by abbreviations. The following were used: EHBZ (Eerste Hulp bij Zeezoogdieren: rescue organisation for stranded marine wildlife, co-ordinated by seal rescue centre Zeehondencreche Pieterburen), KNRM (Koninklijke Nederlandse Redding Maatschappij: life-boat organisation), and NZG/NSO (Nederlands Stookolieslachtoffer-Onderzoek (NSO): national beached bird survey, organised by the Nederlandse Zeevogelgroep (NZG), or Dutch Seabird Group). *Ecomare* is an educational centre based on Texel (with natural history exhibitions and a seal rescue centre). Dolfinarium Harderwijk is the cetacean rescue centre, currently named SOS Dolfijn. The seal rescue centre Zeehondencreche Pieterburen, as frequently referred to in this paper, has recently been renamed “Zeehondencreche Lenie ‘t Hart”. Two natural history museums were regularly in-

Photo 1. Fin whale, 24 August 2004, Noordwijk aan Zee. *Photograph: L. van Duijn*.

Table 1. Stranded whales and dolphins on the Dutch coast, 1998-2007.

		1998	99	00	01	02	03	04	05	06	07	Totals
unidentified whale or dolphin					1							1
fin whale	*Balaenoptera physalus*	1			1			2		1		5
sei whale	*Balaenoptera borealis*								1			1
minke whale	*Balaenoptera acutorostrata*	2		1	1				2			6
humpback whale	*Megaptera novaeangliae*						2	1				3
sperm whale	*Physeter macrocephalus*							4				4
Sowerby's beaked whale	*Mesoplodon bidens*					1						1
Blainville's beaked whale	*Mesoplodon densirostris*								1			1
long-finned pilot whale	*Globicephala melas*						1			1		2
bottlenose dolphin	*Tursiops truncatus*										1	1
striped dolphin	*Stenella coeruleoalba*		1					1		1		3
common dolphin	*Delphinus delphis*						1			1		2
white-beaked dolphin	*Lagenorhynchus albirostris*	4	3	11	7	5	4	6	6	3		49
white-sided dolphin	*Leucopleurus acutus*		1	1						1	1	4
harbour porpoise	*Phocoena phocoena*	59	89	69	115	107	148	196	306	539	340	1968
unidentified dolphin		1		3			1	1	1		1	8
unidentified small cetacean						1			1		2	4
		67	94	85	125	114	157	211	318	547	345	2063

volved: the National Museum of Natural History *Naturalis* in Leiden, with RMNH as collection number (from the former name: Rijksmuseum van Natuurlijke Historie), and the Natural History Museum Rotterdam, with collection numbers abbreviated as NHMR. The Royal Netherlands Institute for Sea Research (NIOZ) and Wageningen IMARES based on Texel jointly conducted mass autopsies on harbour porpoises and on some dolphins in 2006 and 2007. Work referring to these autopsies is abbreviated NIOZ/IMARES.

E.J.O. Kompanje compiled lists of accepted and unaccepted historical identifications (distinguishing between records with and without physical or other unambiguous evidence such as photographs or recognisable drawings) of bottlenose dolphins (*Tursiops truncatus*) (Kompanje 2001, 2005a), killer whales (*Orcinus orca*) (Kompanje 1995a) and common dolphins (*Delphinus delphis*) and striped dolphins (*Stenella coeruleoalba*) (Kompanje 2005b). In those publications, which include some of the cases reported in the present paper, both categories were numbered case by case. For bottlenose dolphin and common dolphin hitherto unknown cases were unearthed later by C.J. Camphuysen while checking logbooks of the Zoological Station in Den Helder (1931-1950) and diaries of F. Niesen (1930-1971), an amateur ornithologist who was based in Haarlem. These are included in some of the long-term reviews of strandings provided in the present paper and explain some of the differences in numbers between this and earlier publications on cetacean strandings in the Netherlands.

O.E. Jansen scrutinised and corrected the lists of white-beaked dolphin (*Lagenorhynchus albirostris*) strandings and combined autopsy reports with strandings data. In anticipation of a complete historical review, including a corrected list of strandings of white-beaked dolphins in the Netherlands, we have used the updated information for 1998-2007, but refrained from listing corrections and additions to earlier publications.

Goodness-of-fit tests were carried out using

Photo 2. Fin whale afloat, 21 August 2004, off Goeree (Z). *Photograph: J. Rooks*.

Table 2. Known strandings of large whales in the Netherlands, per century (1200-1900) and per decade (1900-2007). The bottom line gives the number of large whales stranded in the period 1998-2007 (overlapping two decades).

	fin whale	sei whale	minke whale	humpback whale	sperm whale
1200-1299					2
1300-1399					1
1400-1499					1
1500-1599	1				11
1600-1699	1				12
1700-1799	1				12
1800-1899	8	1	4		
1900-1909	1				
1910-1919	7		2		
1920-1929			3		
1930-1939			2		2
1940-1949	1		6		
1950-1959	1		1		1
1960-1969					
1970-1979		1	1		2
1980-1989		1	1		
1990-1999	1		4		10
2000-2007	4	1	4	3	4
(1998-2007)	5	1	6	3	4

the *G*-test. For two-cell comparisons the value of G was adjusted using Williams' correction to avoid Type I statistical errors (Sokal & Rohlf 1981). The student's *t*-test was used to test the null hypothesis that the means of two (normally distributed) groups of means were equal.

Strandings between 1998 and 2007

Reported strandings in the Netherlands comprise 2063 individual whales and dolphins representing at least 14 species, found between 1998 and 2007 (table 1). Twelve species had been recorded before; two species, humpback whale and Blainville's beaked whale, were new for the Dutch list.

Fin whale (*Balaenoptera physalus*) gewone vinvis
Irregular visitor; 1900-1997: 10 strandings; 1998-2007: 5 strandings

Fin whales normally occur in deeper waters in the North Atlantic region. Sightings within the North Sea are rare, even in deeper parts further to the north. Five strandings or near-strandings were reported between 1998 and 2007, which is rather more than could be anticipated from numbers recorded in the rest of the 20th century (table 2). The strandings coincided with three recent sightings of apparently healthy fin whales off the Dutch coast in August and September 1998 and in April 2000 (Camphuysen & Peet 2006, van der Meij & Camphuysen 2006). Tall vertical blows produced by large, probably balaenopterid whales were observed from the Dutch coast in

Photo 3. Sei whale, 1 August 2005, Texel. *Photograph: C.J. Camphuysen*.

March and December 2000. Of the strandings listed below, one involved a fin whale that died after having entered the Sloehaven (Vlissingen harbour, Walcheren) in January 2001. The recent sightings and this live-stranding confirm that fin whales enter the southern North Sea and are often capable of leaving the area again. The carcass of an individual found at the bulge of a Stena Line freighter was not fresh, and the same holds true for the other strandings in 1998, 2004 and 2006. These carcasses may have drifted over considerable distances before being washed ashore on the Dutch coast.

4 Aug 1998, afloat off Egmond (NH), ♂, TL circa 1800 (estimated), dragged ashore for examination, badly decomposed, skeleton in Fort Kijkduin (Den Helder). Publications: Kompanje 1998, Trouw 6 Aug 1998 erroneously reported a length of 23m.

14 Jan 2001, alive in Sloehaven, Vlissingen (Walcheren), reported by J. van der Hiele (EHBZ Zeeland), ♀, TL 1254, 10.500 kg. Entered the harbour earlier on the day, but drowned when it got stuck behind wooden mooring poles at the quayside. Autopsy, by M. García Hartmann, revealed infections in the inner ear, many bones broken during life; various infections and internal bleedings. Skull and incomplete skeleton collection *Naturalis*, RMNH 41217, many photographs available at *Naturalis*. Publications: Provinciale Zeeuwse Courant 15 Jan 2001, 16 Jan 2001, Meininger et al. 2003.

5 Jun 2004, southern North Sea (52°1.5'N, 2°08'E), off Hoek van Holland (ZH), reported by Stena Line, ♂, TL unknown, found at the bulb of the Stena Line freighter *Discovery* while still at sea. Carcass discovered by the pilot and mate when the ship seemingly lost power. The carcass was again reported 7 June 2004 by the crew of *Nordsea Trader* near Noordhinder. Several slides made during both encounters revealed the sex of the animal and facilitated identification.

25 Aug 2004, Noordwijk aan Zee (ZH), ♀, TL 1735, reported by L. van Duijn (EHBZ Katwijk), badly decomposed but complete carcass (photo 1), reported and photographed 21 Aug while still afloat and more intact at sea off Goeree (several slides; photo 2). Several internet publications.

13 Nov 2006, Maasvlakte, Westplaat (ZH), sex unknown, flukes and tail-stock missing, TL>1000 (estimated), reported by KNRM and RWS, corpse badly decomposed. Skull, vertebrae and scapula collection *Naturalis*, RMNH 41465, EHBZ 159/06. Possibly related to a corpse seen at the bulb of SS *California Luna*, off Cherbourg (F) in October 2006.

Sei whale (*Balaenoptera borealis*) noordse vinvis
Vagrant; 1900-1997: 2 strandings; 1998-2007: 1 stranding

Not many observers are familiar with the identification characters of the sei whale and possibly as a result, little is known of its status in the North Sea. There is no evidence, however, to suggest that this species is anything but rare. The stranding reported here is only the third sei whale reliably documented for the Netherlands in the past 100 years and the first since November 1986. The carcass was incomplete and not fresh and may thus have drifted over a fairly long distance.

1 Aug 2005, Texel p24, ♀, TL circa 1000 (estimated), reported by C.J. Camphuysen, incomplete carcass, head and flippers (partly) missing, remaining parts less than 9 m total length. Incomplete skeleton, including scapula and vertebrae collection *Naturalis*, RMNH 41459 (photo 3).

Minke whale (*Balaenoptera acutorostrata*) dwergvinvis
Irregular visitor; 1900-1997: 18 strandings; 1998-2007: 6 strandings

Minke whales, largely piscivorous baleen whales, are common in the northern half of the North Sea. Several recent sightings indicate that minke

Photo 4. Minke whale, 7 January 2005, Ameland. *Photograph: J. Krol / Natuurmuseum Ameland.*

whales at least incidentally use foraging areas to the south of the Dogger Bank, such as the Klaverbank and at the Frisian Front (Camphuysen & Peet 2006, C.J. Camphuysen & M.F. Leopold, unpublished data). Over the past 100 years, however, only 24 strandings have been documented, six of which within the period 1998-2007 (table 2). Two recent cases concerned live-strandings, the other animals were washed ashore in various states of decomposition and these may have drifted over some distance. Only three minke whales were recorded between 1950 and 1990, against at least 13 between 1910 and 1950. Even if some of these strandings were related to war activities, this higher frequency could point to a more regular occurrence closer to the Netherlands in the early 20th century. The total of eight stranded minke whales found since 1990 could indicate a return or range extension of a nearby stock, which would be concurrent with a recent increase in sightings south of the Dogger Bank (Camphuysen & Peet 2006, van der Meij & Camphuysen 2006).

20 Mar 1998, Terschelling p17, sex unknown, TL 450, reported by R. Hofland (Brandaris). Live-stranding, pushed back into the sea. No further reports.

23 Jun 1998, Texel p16, sex and TL unknown, reported by C. Ellen, badly decomposed and incomplete carcass.

30 Jul 2000, Vliehors (Vlieland), sex and TL unknown, reported by C.J. Camphuysen and C. Zuhorn. Identification based on vertebrae by C. Smeenk, *Naturalis*, found again in Aug 2000 (NZG/NSO 200288). Not collected.

15 Apr 2001, Noordwijk aan Zee (ZH), ♂, TL 429, reported by KNRM and C. Kooimans (EHBZ Noordwijk). Live-stranding, rescue attempts failed, euthanized and autopsied by N. van Elk. Extensive middle ear infection on one side.

7 Jan 2005, Ameland, sex unknown, TL 405, reported by J. Krol (Natuurcentrum Ameland), badly decomposed, skeleton in Natuurcentrum Ameland (photo 4).

20 Aug 2005, Katwijk aan Zee p86.5 (ZH), ♀, TL 460, reported by L. van Duijn (EHBZ Katwijk). Skull, scapula and other skeletal parts collection *Naturalis*, RMNH 41460. Flukes cut off, probably by-catch.

Humpback whale (*Megaptera novaeangliae*) bultrug
Vagrant; 1900-1997: not recorded; 1998-2007: 3 strandings (new species)

Since 1751, when a baleen whale was found near Blankenberge in Belgium, identified 255 years later as a humpback whale on the basis of an old painting (Camphuysen & Peet 2006), there had been no record of this species anywhere near the Dutch or Belgian coast. An exception was a fairly recent find of an apparently fresh (dripping with whale oil) scapula of a young humpback whale in February 1995 on the sea-floor near the Klaverbank (53°40’ N, 3°50’ E) by the Dutch beam-trawler UK43 from Urk (Kompanje 1995b, 1996). The stranding of a fairly fresh carcass in October 2003 was surprising (Smeenk et al. 2003), and even more so were several further sightings and strandings in the Netherlands (5x) and Belgium (1x) in 2003 and in 2004. Unfortunately, all strandings were the result of an unnatural death. A humpback whale calf died off Katwijk in December 2003 under suspect circumstances. Since flukes and one flipper had been cut off, this animal probably had drowned in fishing gear, with the carcass subsequently removed. This stranding occurred after an adult with calf had been seen foraging off the coast up to the previous day, so the damage to the calf must have been inflicted overnight. A lonely adult was seen feeding in that same area for up to a few months after the stranding (Camphuysen & Peet 2006). A young whale found at the Vliehors in 2004 had a rope around its body behind the head, which had inflicted deep wounds and apparently had strangled the animal to death. Finally, a whale stranded in nearby Nieuwpoort (Belgium), 5 March 2006, had died from loss of blood, probably resulting from a collision with a ship’s propeller (Haelters et al. 2006). Several humpback whales have visited the southern North Sea and even successfully foraged off the Dutch coast for some time. The most recent event so far was a sighting of a young humpback whale foraging in the Marsdiep area near Den Helder in May 2007, subsequently reported off SW Ireland in September 2007 and back again near IJmuiden in November 2007 (Camphuysen 2007, Strietman 2008). The sightings and strandings follow an increase in sighting frequency in the North Sea as a whole since 1992, which may be due to a general increase in stocks in the Atlantic Ocean, and an extension of range.

7 Oct 2003, Maasvlakte (ZH), ♀, TL 850, first discovered 29 Sep 2003 when afloat in the Nieuwe Waterweg, dragged into open sea after misidentification as minke whale, seen afloat offshore and finally washed ashore in bad condition at the Maasvlakte. Skull and incomplete skeleton collection *Naturalis*, RMNH 41367.

20 Dec 2003, Katwijk aan Zee (ZH), ♂, TL circa 950 (estimated), seen alive the previous day, accompanied by adult whale, found freshly dead with part of flipper and flukes cut off. Skeleton collection *Naturalis*, RMNH 41368; many photographs available at *Naturalis*.

22 Jun 2004, Vliehors (Vlieland), ♂, TL 800, reported by M. Nijman and C. Zuhorn, fresh and intact carcass, buried at first, retrieved the next day by *Ecomare* (Texel) (photo 5). Skeleton with baleens in *Ecomare*, Texel. Skin samples for DNA. Animal had been strangled by a rope around the head which had inflicted deep cuts into blubber, flesh and organs.

Of all stranded humpback whales, ectoparasites (barnacles and whale lice) were sampled and are preserved in museum collections (*Naturalis*, NHMR, *Ecomare*).

Sperm whale (*Physeter macrocephalus*) potvis
Irregular visitor; 1900-1997: 15 strandings (individuals); 1998-2007: 4 strandings (individuals)

The sperm whale occurs worldwide in deep oceans and seas. Males of the populations in the North Atlantic Ocean migrate north in summer,

Photo 5. Humpback whale, 22 June 2004, Vlieland. *Photograph: D. Bruin*.

as far as Iceland and northern Norway. Occasionally, sperm whales stray into the North Sea, where strandings occur mainly in the period November-February. There is a long history of documented sperm whale strandings around the North Sea, with evidence of 'influxes' followed by prolonged periods with none or very few strandings and sightings (Sliggers & Wertheim 1992, Smeenk 1997); for a discussion of this aspect, see Pierce et al. (2007). One such peak in strandings occurred in the 1990s (table 2), leading to several mass (live-) strandings in Britain, Denmark, Germany, the Netherlands and Belgium (Smeenk 1997). The frequency appears to have declined again, with only four animals recorded stranded or washed ashore in the Netherlands and few elsewhere around the North Sea over the past ten years. All recent strandings on the Dutch coast occurred in 2004; the live-stranding of two individuals at the Richel (near Vlieland) in November 2004 is remarkable, because the animals were pushed off the sandbank and not seen again (photographs in Camphuysen & Peet 2006).

5 Jun 2004, Noordpolderzijl (G), ♂, TL unknown, reported by Zeehondencreche Pieterburen, incomplete carcass, lower jaw removed by Zeehondencreche Pieterburen. Remains were left on the scene and were reported several times, up to Jan 2005 (NZG/NSO 204181, 205005).

24 Jun 2004, Vlieland dam 22, ♂, TL 1500, reported by W. Stel, decomposed carcass. Skeleton in collection Vlieland's Natuurmuseum.

2 Nov 2004, Richel (Vlieland), two ♂♂, TL unknown, reported by Doeksen ferry *Oost-Vlieland*, live-stranding, both animals pushed back into the sea (H. Wiegman and KNRM) (photo 6). No further reports since rescue operation.

Sowerby's beaked whale (*Mesoplodon bidens*) gewone spitssnuitdolfijn
Irregular visitor; 1900-1997: 13 strandings; 1998-2007: 1 stranding

All beaked whales (Ziphiidae) are deep-diving species. Sowerby's beaked whale occurs in the North

Photo 6. Sperm whale, 2 November 2004, live-stranding, Richel (Vlieland). *Photograph: D. Bruin*.

Atlantic Ocean, where it is commonly found along the shelf-break in the Bay of Biscay and off the British Isles. It is the only species that regularly enters the North Sea (Evans 2008). Several (live-) strandings in the Netherlands and Belgium were of pregnant females or females with calves. Most strandings have occurred in July-September (Smeenk et al. 1993).

31 Aug 2002, Schiermonnikoog, ♀, TL 354, reported by Dolfinarium Harderwijk, found alive by birdwatchers, but dead when the rescue team arrived on the scene. Autopsy by N. van Elk (Dolfinarium Harderwijk) and T. Jauniaux (University of Liège) revealed a severe bacterial infection (*Aeromonas salmonicida*). Skeleton collection *Naturalis,* RMNH 41153.

Blainville's beaked whale (*Mesoplodon densirostris*) spitssnuitdolfijn van De Blainville
Vagrant; 1900-1997: not recorded; 1998-2007: 1 stranding (new species)

Blainville's beaked whale is new to the Dutch list. The species occurs worldwide in tropical and subtropical, deep oceanic waters, in the Atlantic Ocean occasionally as far north as the Bay of Biscay. Extra-limital strandings have occurred in Wales in July 1993 (Herman et al. 1994) and in Iceland (MacLeod 2000). The stranding in the Netherlands constitutes the first record for the North Sea.

12 Apr 2005, Ameland p11, ♀, TL 435, reported by J. Krol (Natuurcentrum Ameland), pregnant female, estimated mass 1000 kg, TL foetus 118. Autopsy on the beach by T. Kuiken (Erasmus University, Rotterdam). CT-scan and MRI-scan made of the head of the adult animal at Erasmus University. No significant diagnosis could be made. Skeleton and foetus collection *Naturalis* RMNH 41458; many photographs available at *Naturalis* (photos 7 and 8).

Long-finned pilot whale (*Globicephala melas*) griend
Irregular visitor; 1900-1997: 12 strandings; 1998-2007: 2 strandings

Photo 7. Blainville's beaked whale, 12 April 2005, Ameland. *Photograph: J. Krol / Natuurmuseum Ameland.*

Photo 8. Blainville's beaked whale (head), 12 April 2005, Ameland. *Photograph: J. Krol / Natuurmuseum Ameland.*

Long-finned pilot whales are rare in the southern North Sea, even though rather large pods may be encountered in the English Channel and around Shetland and Orkney. Given the small number of sightings and strandings in the Netherlands (Camphuysen & Peet 2006), there appears to be no regular passage from north to south or vice versa. There are two historical accounts of mass strandings in the Delta area: near St Annaland in April 1825 (38 animals) and near Ouddorp in April 1856 (61 animals stranded, 300-400 escaped; van Deinse 1931). Recent sightings of up to 175 pilot whales off the Belgian coast (Van Gompel 1991) suggest that such strandings would still be possible, but even confirmed sightings of individual pilot whales in Dutch waters are very rare (van der Meij & Camphuysen 2006).

24 May 2003, Hondsbossche Zeewering (NH), ♀, TL 222, reported by A. Gronert. Skeleton collection *Naturalis*, RMNH 41369. Publication: De Windbreker, maart 2004: 14.

23 May 2006, Schiermonnikoog, ♀, TL 465, fresh carcass, numerous photographs (photo 9). Autopsy Pieterburen. Skeleton collection *Naturalis*, RMNH 41463. Publication: Leeuwarder Courant 24 May 2006.

Bottlenose dolphin (*Tursiops truncatus*) tuimelaar
Irregular visitor (until recently common resident), 1900-1997: 387 strandings; 1998-2007: 1 stranding

Van der Meij and Camphuysen (2006) listed the bottlenose dolphin as a regular visitor in the southern North Sea, based on strandings and sightings in the past 35 years (being represented in 23 of these years). Earlier in the 20th century, the bottlenose dolphin was a common resident in Dutch waters. However, with only a single stranding of an animal that stayed in the Oosterschelde for some time, and only few well-documented sightings in recent years, the qualification 'regular visitor' as in van der Meij and Camphuysen (2006) is currently unjustified. One or more large herds were seen entering the Wadden Sea in August and September 2004. Otherwise, only solitary dolphins were encountered, most of them with a rather 'dubious' history (individually recognisable, nick-named, stray dolphins from the Channel population, showing aberrant behaviour and making frequent contact with humans).

12 Sep 2007, Lodijksche Gat (Oosterschelde), ♀, TL 262, reported by J. van der Hiele (EHBZ Zeeland), known to have stayed for some weeks in the Oosterschelde basin. Autopsy by T. Jauniaux (NIOZ/IMARES autopsies 2007): 221 kg, fresh corpse, rake-marks on skin and possible rope- or line-marks on flukes, not emaciated, trauma and infections. Skeleton collection *Naturalis*, RMNH 41469.

Striped dolphin (*Stenella coeruleoalba*) gestreepte dolfijn
Irregular visitor; 1900-1997: 5 strandings; 1998-2007: 3 strandings

Photo 10. Striped dolphin, 14 November 2004, live-stranding, Brouwersdam. *Photograph: L. Provoost*.

Striped dolphins occur worldwide in tropical and warm-temperate waters. The species is abundant in the western Mediterranean, off NW Africa and west and northwest of the Iberian Peninsula as far as the Bay of Biscay. In the North Sea and English Channel, striped dolphins are rare, with most records from the Southwest Approaches to the Channel and off southern Ireland, occasionally as far north as Shetland. Any status changes cannot readily be assessed through lack of quantitative data, but records of striped dolphins have become more frequent in Britain during the 1990s, suggesting a recent northward extension of range (Evans 2008). The few, relatively recent strandings in the Netherlands (table 3) and recent records from Denmark, Norway, the Faeroes and Iceland, seem to fit that picture. There are no sightings in Dutch waters, but the three stranding records below were probably all of live animals.

5 Nov 1999, Ter Heijde (ZH), ♂, TL 180, live-stranding. Animal was transported to Dolfinarium Harderwijk and named “Sten”, where it died the next day. Kompanje (2005b): case #6.

14 Nov 2004, Brouwersdam (Schouwen-Goeree), ♂, TL 168, live-stranding, reported by J. van der Hiele and M. Geerse (EHBZ Zeeland) (photo 10). Animal was transported to Dolfinarium Harderwijk and named “Indra”, died later. Kompanje (2005b): case #7. Skull collection *Naturalis*, RMNH 41479.

Photo 9. Long-finned pilot whale, 23 May 2006, Schiermonnikoog. *Photographer: unknown*.

Table 3. Documented strandings of dolphins in the Netherlands, per century (1800-1900) and per decade (1900-2007). The bottom line gives the number of dolphins stranded in 1998-2007 (overlapping two decades). For bottlenose dolphin and white-beaked dolphin, the lists include records that were recently recovered from diaries and old data files (C.J. Camphuysen, O.E. Jansen & C. Smeenk, unpublished data).

	bottlenose dolphin	striped dolphin	common dolphin	white-beaked dolphin	white-sided dolphin
1800-1899	11		1	2	1
1900-1909	1		1	1	
1910-1919	12		2	1	
1920-1929	35		5	1	
1930-1939	88		16	1	
1940-1949	75		36	3	
1950-1959	80		17	4	
1960-1969	75	1	2	16	1
1970-1979	12			17	1
1980-1989	8	1	3	54	4
1990-1999	1	4	1	69	1
2000-2007	1	2	2	44	4
(1998-2007)	1	3	2	49	4

2 Mar 2006, Posthuiskwelder (Vlieland), ♀, TL 144, 36.5 kg, reported by V. Kikstra, very fresh with marks in the sediment indicating a live-stranding. Skeleton collection *Naturalis*, RMNH 41462.

Common dolphin (*Delphinus delphis*) gewone dolfijn
Irregular visitor; 1900-1997: 83 strandings; 1998-2007: 2 strandings

For some decades in the first half of the 20th century, common dolphins were fairly common in the North Sea and strandings occurred regularly in the Netherlands (Camphuysen & Peet 2006, table 3). Offshore sightings of these dolphins, which would be easily recognised during the frequent ship-based and aerial surveys of the area, are now rare, as are strandings. Some recent sightings were of common dolphins that took up residency: in the Westerschelde, in Scheveningen harbour and in the Marsdiep area. These dolphins showed aberrant behaviour and were often closely associated with buoys marking shipping lanes. The Westerschelde individual, a pseudo-hermaphrodite, was one of only two documented strandings in the study period.

8 Apr 2003, Verdronken Land van Saeftinge (Zeeuws-Vlaanderen), known to have been resident from Nov 2001 to at least Feb 2003 in Westerschelde (Camphuysen & Peet 2006). Autopsy by *Naturalis*: genetically ♂, but with female characteristics ('pseudo-hermaphrodite'), TL 154. Skeleton collection *Naturalis*, RMNH 41214, urogenital organs preserved in formalin. Kompanje (2005b): case #50.

15 May 2006, Brouwersdam (Schouwen-Goeree), ♀, TL 120, reported by M. Geerse (EHBZ Zeeland), fresh corpse of young animal. Skeleton collection *Naturalis*, RMNH 41478.

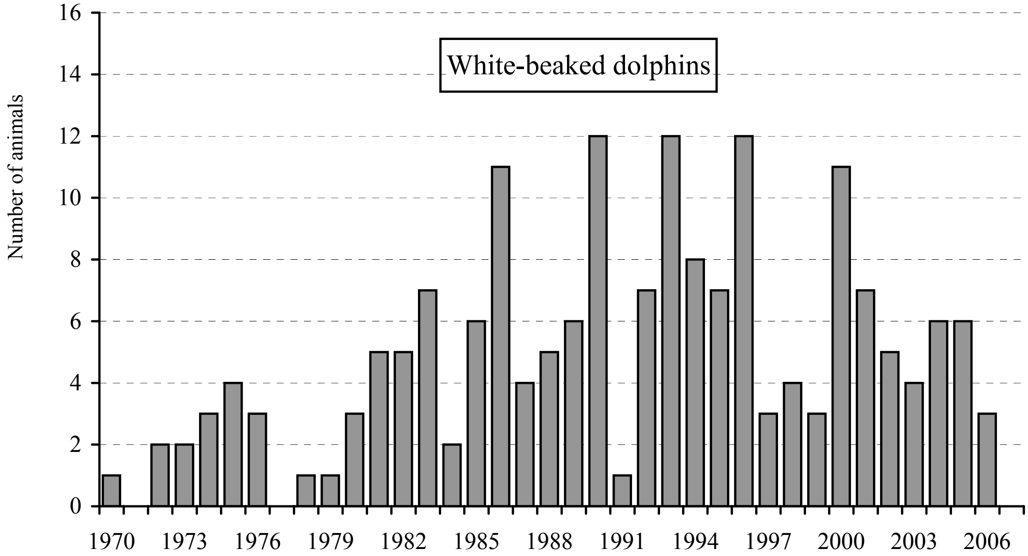


Figure 1. Documented strandings of white-beaked dolphins in the Netherlands in 1970-2007, including records that were recently recovered from diaries and old data files (O.E. Jansen & C. Smeenk, unpublished data).

White-beaked dolphin (*Lagenorhynchus albirostris*) witsnuitdolfijn
Resident or annual visitor; 1900-1997: 160 strandings; 1998-2007: 49 strandings

The white-beaked dolphin is a cold-water species, endemic to the North Atlantic Ocean; it is abundant in the northern and central North Sea. Since 1970, stranded white-beaked dolphins have been found nearly every year, with a maximum of twelve individuals per year (figure 1, table 3). White-beaked dolphins do not normally enter shallow coastal waters and therefore seldom approach the Dutch sandy shorelines. Most sightings are made at least 10 km from the coast. Occasionally, large pods are seen, mostly in winter (Camphuysen & Peet 2006). A total of 49 white-beaked dolphins were found from 1998 to 2007, and all cases are listed below.

27 Jan 1998, Scheveningen (ZH), ♂, TL 173, reported by E.J.O. Kompanje. Autopsy *Naturalis*, La980127: by-caught in set net. Skeleton Natural History Museum Rotterdam, NHMR 193.

3 Aug 1998, Razende Bol (Texel), ♀, TL 256, reported by Fort Kijkduin. Autopsy *Naturalis*, La980805. Skeleton in Fort Kijkduin (Den Helder). Publications: Algemeen Dagblad 4 Aug 1998, Kompanje 1998.

15 Sep 1998, Texel p14, sex unknown, TL circa 300 (estimated), reported by A. Oosterbaan (*Ecomare*), badly decomposed, not collected.

1 Oct 1998, Braakmanhaven (Zeeuws-Vlaanderen), ♀, TL 258, reported by Zeeland police. Skeleton collection Natural History Museum Rotterdam, NHMR 197.

9 Nov 1999, Texel p28, sex unknown, TL circa 250 (estimated), reported by Rijkswaterstaat, ropes around head, flippers and tail, badly decomposed, not collected.

23 Dec 1999, Het Kuitje, Balgzand (NH), ♀, TL 251, reported by C. de Greeuw, live-stranding, lactating female that had recently given birth. Autopsy *Naturalis*, La991224, blubber layer 19 mm, cysts in thyroid gland, pneumonia, partly calcified abdominal blood vessels. Skull and part of skeleton collection *Naturalis*, RMNH 41213, rest of skeleton (the last thoracic and first three

Photo 11. White-beaked dolphin, 4 March 2006, Noordwijk aan Zee. *Photograph: P. Thomas and J. Wierda*.

lumbar vertebrae, longitudinally divided) with Schmorl's nodes (in formalin) collection Natural History Museum Rotterdam, NHMR 475. Publications: De Windbreker Jan 2000, Kompanje 2000, Kompanje & García Hartmann 2001.

Insufficient details are known of a possible third stranding: 6 Jan 1999. Locality, sex and TL unknown. Skeleton collected by E.J.O. Kompanje for Natural History Museum Rotterdam, apparently reported by Zeehondencreche Pieterburen (needs confirmation).

4 Jan 2000, Schoorl aan Zee (NH), ♂, TL 172, reported by C. de Greeuw, live-stranding, transported to Dolfinarium Harderwijk, died the same day. Autopsy Harderwijk, LalSh 014. Severely emaciated (blubber layer 1 cm, plastic in first stomach, bleedings and worm-infested second stomach, estimated age 1-1.5 yrs).

6 Jan 2000, Noordpolderzijl (G), two animals, sex and TL unknown, reported by J. de Boer, live-stranding, successfully released into the Wadden Sea (observed swimming, no strandings reported soon thereafter; but see 30 Jan 2000).

30 Jan 2000, Noordpolderzijl (G), ♂, TL 235, reported by Zeehondencreche Pieterburen. Autopsy by T. Kuiken, La010200, body mass circa 200 kg, blubber layer 20 cm, tip of fluke missing, heamorrage in lower jaw, full stomach but ulcerated, worm-infested, and containing part of beer-tin; lung oedema.

30 Jan 2000, Texel p23, ♂, TL 210, reported by M. Brugge (*Ecomare*), head badly damaged and lower jaw missing. Skull and partial skeleton collection Natural History Museum Rotterdam, NHMR 1337.

14 Feb 2000, Kornwerderzand (Afsluitdijk, F), ♀, TL 256, reported by Zeehondencreche Pieterburen, badly decomposed. Skeleton probably in collection Natura Docet, Denekamp.

6 Jun 2000, Texel p15, sex unknown, TL>300 (estimated), reported by R. van der Zwaag

(*Ecomare*), badly decomposed and buried on the spot, identification not verified.

19 Jun 2000, Bloemendaal/Velzen (NH), ♂, TL>200 (estimated; 180 without head), reported by Gemeente Bloemendaal. Skull collection Naturalis.

13 Jul 2000, Julianadorp (NH), sex unknown, TL circa 200 (estimated), reported by M. Roeper (tourists had reported a living seal on the beach), badly decomposed, not collected.

Dec 2000, Camperduin p26 (NH), sex and TL unknown, old skeleton uncovered at old tideline, no flesh remaining. Note that a decomposed carcass of a white-beaked dolphin had been reported on the same locality, 25 Feb 1990 (reported by C.J. Camphuysen, NZG/NSO 90045, TL 230, several slides available), listed as 'probably washed away' in Smeenk (1995). It is likely that the skeleton in 2000 was of the same animal.

14 Dec 2000, Groote Keeten p9 (NH), ♀, TL 242, reported by R. Roos, very fresh corpse. Autopsy by N. van Elk and T. Jauniaux, *Naturalis,* La001216, lung oedema. Skeleton/skull collection *Naturalis*, RMNH, also NZG/NSO 114121.

29 May 2001, Texel p19, ♀, TL 180, reported by M. Zijm (Rijkswaterstaat), badly decomposed, flippers and dorsal fin decayed or absent, not collected.

9 Sep 2001, Texel p22-23, ♂, TL 290, reported by K. Uitgeest, no further details known. Publication: Texelse Courant 15 sep 2001 (the total length is provided there).

30 Sep 2001, Hoek (Zeeuws-Vlaanderen), ♀, TL 280, reported by M. Geerse (EHBZ Zeeland), badly decomposed, destroyed.

5 Nov 2001, afloat off Vlissingen, Westerschelde (Walcheren), ♀, TL 239, reported by J. van der Hiele (EHBZ Zeeland). Autopsy *Naturalis*, La011106, haematomes. Skeleton collection Natural History Museum Rotterdam, NHMR 1336.

9 Nov 2001, Nieuw Haemstede (Schouwen), ♀, TL 241, reported by S. Hart (later reported by J. van der Hiele, 12 Nov 2001, EHBZ 053/01). Lower jaws sent to *Naturalis* for identification.

23 Nov 2001, Langevelderslag (ZH), ♀, TL 228, reported by KNRM Zandvoort. Autopsy *Naturalis*, La011126, pregnant, female foetus TL 28. Skeleton collection *Naturalis*, RMNH 34670.

27 Dec 2001, Wassenaarseslag (ZH), sex and TL unknown, reported by Dierenambulance Den Haag, badly decomposed, not collected.

9 Feb 2002, Texel p22, ♂, TL 290, reported by M. de Jong and E. Wieman, carcass not fresh, not collected (NZG/NSO NSO 122624). Publication: Texelse Courant 12 Feb 2002.

7 Apr 2002, Renesse (Schouwen), ♀, TL 282, reported by J. van der Hiele (EHBZ Zeeland). Autopsy *Naturalis*, La020420. Skeleton collection *Naturalis*, RMNH 41152.

6 Jul 2002, Zandvoort (NH), ♂, TL unknown, reported by Dierenambulance Zandvoort, badly decomposed. Skeleton collection *Naturalis*, RMNH 41151.

18 Sep 2002, Texel p20, sex unknown, TL circa 160 (estimated), reported by A. Oosterbaan (*Ecomare*), badly decomposed, destroyed.

27 Nov 2002, IJmuiden (NH), ♀, TL 160, reported by IJmuider Courant, very fresh corpse, body mass 49.5 kg, several dozens of whale lice (*Scutocyamus parvus*) (collection *Naturalis*). Autopsy *Naturalis*, La011201, severely emaciated.

9 May 2003, Texel p12, sex unknown, TL circa 200 (estimated), reported by H. Brugge (*Ecomare*), rope around tail, no head, destroyed.

9 Jun 2003, Vliehors p36 (Vlieland), sex unknown, TL 270, reported by W. Stel, buried on the spot, slides provided by C. Zuhorn (Staatsbosbeheer) used for identification.

21 Sep 2003, Texel p12, sex and TL unknown, reported by S. de Wolf (*Ecomare*), a very decomposed white mass, identification based on teeth, destroyed.

23 Oct 2003, Kwade Hoek (Goeree), ♀, TL 178, reported by K. Margry, fresh carcass, total mass 55 kg. Autopsy by T. Jauniaux (University of Liège); emaciated, anemia, pneumonia.

3 Mar 2004, Griend, sex unknown, TL circa 200 (estimated), reported by A. Liebrand, photographs of skeleton used for identification.

11 May 2004, Balgzanddijk (NH), sex unknown, TL<200 (estimated), reported by H. Kleef, photographs of rather fresh carcass used for identification.

13 May 2004, Brouwersdam (Schouwen-Goeree), ♂, TL 274, reported by J. van der Hiele (EHBZ Zeeland). Autopsy *Naturalis*. Skull collection *Naturalis*, RMNH 41471.

22 Oct 2004, Texel p28, ♀, TL 247, reported by A. Oosterbaan (*Ecomare*), fresh corpse. Autopsy *Naturalis*, La041022, worn teeth, not pregnant.

18 Nov 2004, Ouddorp (Goeree), ♀, TL 248, reported by J. van der Hiele (EHBZ Zeeland), live-stranding, died on the beach. Autopsy *Naturalis*, La041118, worn teeth. Skull collection *Naturalis*, RMNH 41474.

22 Nov 2004, Verklikkerstrand, Nieuw-Haemstede (Schouwen), ♀, TL 245, reported by J. van der Hiele (EHBZ Zeeland), not fresh. Autopsy *Naturalis*, La041124. Skeleton collection *Naturalis*, RMNH 41472.

4 Jan 2005, Renesse (Schouwen), ♀, TL 187, reported by M. Geerse (EHBZ Zeeland), very fresh corpse. Autopsy *Naturalis*.

23 Feb 2005, Nieuw Haemstede (Schouwen), ♀, TL 170, reported by J. van der Hiele (EHBZ Zeeland), badly decomposed, destroyed.

22 May 2005, Westenschouwen (Schouwen), ♂, TL 240, reported by J. van der Hiele (EHBZ Zeeland), first seen afloat some 15 m offshore, dragged ashore, total mass 250 kg, rake-marks of conspecifics on skin. Autopsy *Naturalis*, La050523, large lung abcess. Skeleton collection *Naturalis*, RMNH 41475.

22 Aug 2005, Marrum (F), sex unknown, TL circa 250 (estimated), reported by P.W. van Leeuwen (IMARES), old corpse, skeleton with remains of skin and some flesh, identification based on slides.

19 Dec 2005, Oostvoornsemeer (Oostvoorne), ♂, TL 278, reported by M. Lievaart and R. Pronk, and J. van der Hiele (EHBZ Zeeland), very fresh carcass, numerous photographs. Autopsy *Naturalis*. Skeleton collection *Naturalis*, RMNH 41125.

30 Dec 2005, Noordwijk aan Zee (ZH), ♂, TL 175, reported by L. van Duijn (EHBZ Katwijk), very fresh carcass. Autopsy *Naturalis*, La060407-2. Skeleton collection *Naturalis*, RMNH 41470.

4 Mar 2006, Noordwijk aan Zee p74.7 (ZH), ♂, TL 185, reported by P. Thomas and J. Wierda, very fresh carcass, transported to *Naturalis* by C. Kooimans (EHBZ Noordwijk aan Zee) (photo 11). Autopsy *Naturalis*, La0600407-1. Skeleton collection *Naturalis*, RMNH 41477.

18 May 2006, Blauwe Slenk (Griend), ♀, TL 250, reported by A. Hazekamp (Zeehondencreche Pieterburen) and Brandaris. Autopsy Zeehondencreche Pieterburen. Skeleton collection *Naturalis*, RMNH 41476.

10 Dec 2006, De Hors p6 (Texel), ♀, TL 240, reported by S. de Wolf (*Ecomare*). Autopsy T. Jauniaux (NIOZ/IMARES autopsies 2007): not fresh, rake-marks of various size but consistent with conspecifics, 214 kg, moderately emaciated, blubber 13-16 mm, cause of death unclear. Skeleton collection *Naturalis*, RMNH 41467.

No strandings reported in 2007.

White-sided dolphin (*Leucopleurus acutus*)
witflankdolfijn
Irregular visitor; 1900-1997: 6 strandings; 1998-2007: 4 strandings

The white-sided dolphin is another cold-water species that is endemic to the North Atlantic Ocean. In the (southern) North Sea it is much less common than the white-beaked dolphin. Generally, the species occurs in deeper waters, with frequent sightings, often in larger groups, in the north-central North Sea and west of the British Isles (Evans 1980). Several live-strandings have been documented. The four animals listed below too, were either still alive or were only just dead when found, and all animals were found on the Wadden

Photo 12. White-sided dolphin, 10 April 2007, Schiermonnikoog, just prior to autopsy. *Photograph: C.J. Camphuysen*.

Sea islands. As with the striped and white-beaked dolphins, most strandings on the Dutch coast have occurred in the last 25 years (table 3).

23 Jan 1999, Ameland p2, ♂, TL 241, reported by Rijkswaterstaat, live-stranding, died the same day. Autopsy Dolfinarium Harderwijk, LaSh 002, 134 kg. Skeleton collection *Fries Natuurmuseum*, Leeuwarden.

11 Dec 2000, Terschelling, ♀, TL 216, reported by Dolfinarium Harderwijk, live-stranding, "Wieke", died next day. Autopsy Dolfinarium Harderwijk, LaSh 004: pregnant female, foetus 25 cm.

8 Mar 2006, Balg, Schiermonnikoog, ♀, TL 222, reported by T. Talsma, transported to *Naturalis* via Zeehondencreche Pieterburen. Autopsy *Naturalis,* Lac060407: had recently given birth, uterus still very large; *Crassicauda* in milk-duct. Skeleton collection *Naturalis*, RMNH 41473.

10 Apr 2007, Schiermonnikoog p7, ♂, TL 256, reported by T. Talsma, very fresh, transported to *Naturalis* via Zeehondencreche Pieterburen. Autopsy T. Jauniaux (NIOZ/IMARES autopsies 2007): 156 kg, lamprey marks and rake-marks of conspecifics, severely emaciated, probable by- catch, lung oedema (photo 12). Skeleton collection *Naturalis*, RMNH 41468.

Harbour porpoise (*Phocoena phocoena*) bruinvis
Resident or annual visitor; 1900-1997: >2000 strandings (incomplete count); 1998-2007: 1968 strandings

The harbour porpoise is in fact the only indigenous species in the Netherlands that can often be seen from land and is commonly found on beaches throughout the year in varying numbers. The decline in abundance in the 1950s and 1960s as well as the recent increase, particularly since the mid 1990s, has been documented in considerable detail and is not again dealt with here (see Kinze et al. 1987, Smeenk 1987, Addink & Smeenk 1999, Camphuysen 2004, Camphuysen & Peet 2006). It is important to remember that harbour porpoises were so numerous in the first half of the 20th century, that systematically recording corpses was not feasible with the limited strandings network of those days. Van Deinse (1931) indicated the number of porpoises found stranded with the symbol ∞ (infinite) and only listed individuals he considered noteworthy for various reasons such as pregnant females, sharp-pointed snout, abnormalities of flippers and flukes, and so forth. Somewhere in the 1950s, when he received repeated comments suggesting a decline in abundance, van Deinse called for strandings data, and from 1951 onwards started listing stranded harbour porpoises (van Deinse 1952). It is unlikely that his figures have ever been anywhere close to representative, and the

Photo 13. Harbour porpoise, neonate (TL 79), 3 June 2006, Noordwijk aan Zee. *Photograph: Arie van Dijk*.

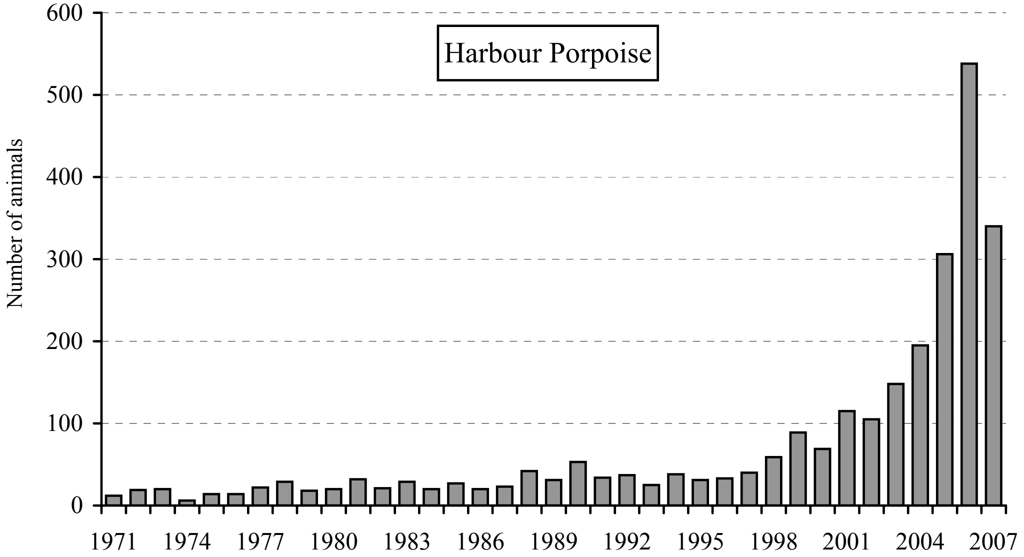


Figure 2. Strandings of harbour porpoises reported in the Netherlands since 1970 (*n*=2697).

decline and near-extinction occurred almost immediately after this initiative.

Harbour porpoises are currently widespread in the southern North Sea and fairly common off the Netherlands, Belgium and northern France. In near-shore waters in the Netherlands, peak numbers are found in winter and spring (December-April) and very low numbers are observed in June (Camphuysen 2004, Camphuysen & Peet 2006). Following a steep increase in sightings, strandings reports have increased in frequency, particularly during the last decade (figure 2), to the extent that it is now impossible to list individual cases in this review.

We received 1968 reports of stranded harbour porpoises, with a minimum of 59 in 1998 and a maximum of 539 in 2006. This means that the number of porpoises reported each year within this period is higher than in any other year since 1970 (max 53 in 1990). The increase in strandings is evident in all subregions of the Dutch coast (figure 3), but it should be emphasised that some recorded patterns are influenced by regional differences in observer effort (i.e. the presence of sufficient observers and the willingness to report strandings to *Naturalis*). This bias in observer effort may lead to wrong conclusions regarding any regional differences in stranding frequencies. Assuming that spatial patterns in the frequency of strandings, or densities (number of animals per km coastline per unit time) of stranded porpoises along the Dutch sandy North Sea shoreline would be gradual rather than abrupt, the data suggest that strandings may be underreported in at least four of these subregions (Rottum, Schiermonnikoog, Voorne-Maasvlakte, and Zeeuws-Vlaanderen; figure 3B-C). Each of these areas could qualify as relatively 'remote', with limited or sometimes even strictly seasonal access, or are simply off range for many regular contributors to the *Naturalis* database. We therefore may assume that the lower densities found in these subregions are indeed artefacts (bias in observer effort) rather than a representation of true spatial patterns.

Similarly, given the densities on the other Wadden Sea islands, it is clear that the number of porpoises recorded on Terschelling was also too low from 1998 to 2005, but normal in the last two years (figure 3). Densities in the central part of the mainland coast (Noord-Holland M) are slightly on the low side. Both trends agree with

Table 4. North Sea beach length (km), number of documented strandings of harbour porpoises, regional densities (*n* km^{-1}), adjusted densities (adjusted *n* km^{-1}), and estimated total numbers of stranded harbour porpoises per subregion in the Netherlands, North Sea beach areas only, 1998-2007 (*n*=1733). Adjusted densities marked with ● are adjusted to regional levels (for Wadden Sea islands, mainland coast and Delta area, see text).

	km	totals reported	*n* km^{-1}	adjusted *n* km^{-1}		totals estimated
Rottum	9	9	1.00	6.43	●	58
Schiermonnikoog	19	29	1.53	6.43	●	122
Ameland	27	163	6.04	6.04		163
Terschelling	27	103	3.81	6.43	●	174
Vlieland	29	195	6.72	6.72		195
Texel	32	208	6.50	6.50		208
Noord-Holland N	31	147	4.74	4.74		147
Noord-Holland M	29	121	4.17	4.17		121
Noord-Holland Z	26	149	5.73	5.73		149
Zuid-Holland	36	187	5.19	5.19		187
Voorne-Maasvlakte	25	43	1.72	4.62	●	115
Goeree	16	55	3.44	3.44		55
Schouwen	24	95	3.96	3.96		95
Walcheren	37	206	5.57	5.57		206
Zeeuws-Vlaanderen	14	23	1.64	4.62	●	65
		1733				2060

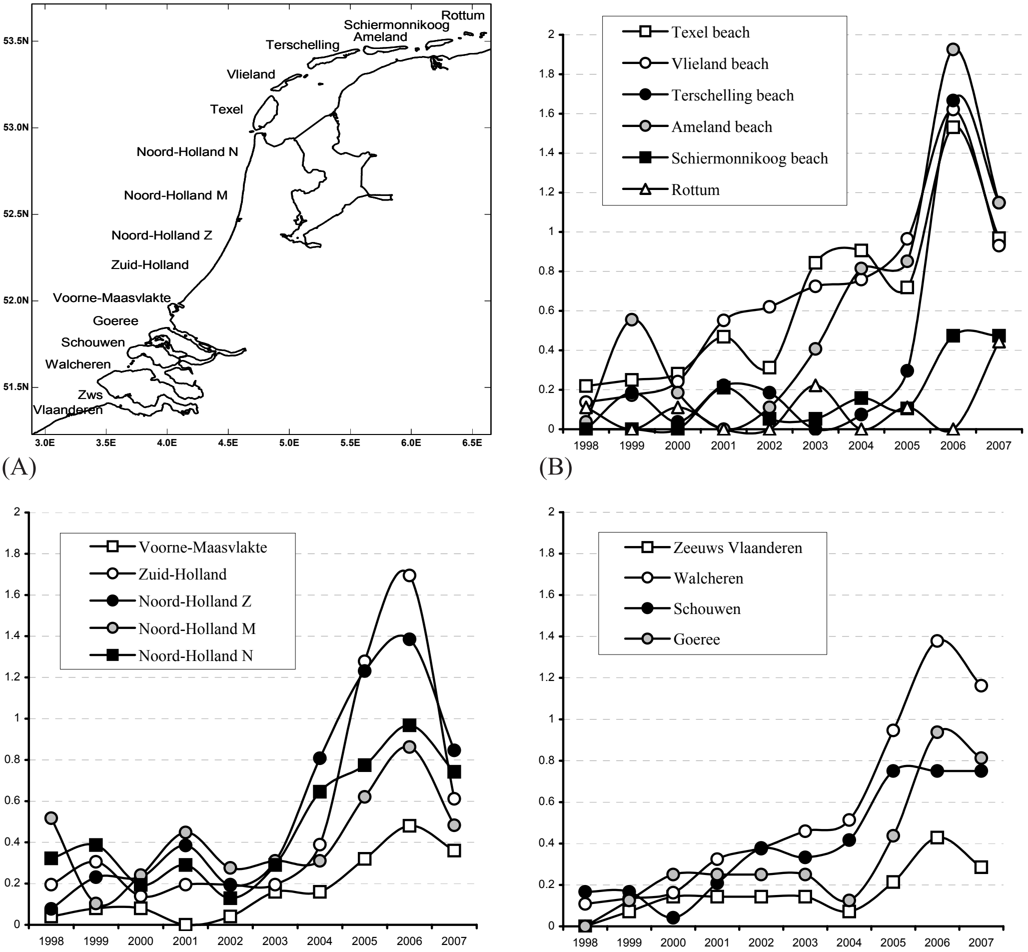
the fact that reporting tendencies in these subregions have been inconsistent over the years. If we correct these outlying low densities with values based on surrounding areas (table 4), we could estimate that at least 19% more porpoises may have washed ashore along the North Sea shoreline than were actually reported (2060 rather than 1733 individuals). The difference between reported and expected strandings is particularly substantial in the Wadden Sea area (a 30% correction).

Such calculations are impossible for strandings within the inner Delta and Wadden Sea areas, given the heterogeneity in exposure and geography, with all sorts of local effects on the likelihood of strandings and recordings. Moreover, harbour porpoises live predominantly offshore and are uncommon in inshore waters. Within the Wadden Sea itself, along a meandering shoreline of circa 300 km in length with estuaries, dikes, salt-marshes, and floodplains, 158 harbour porpoises were retrieved (0.53 km^{-1}). In the Delta area (again excluding the North Sea beaches), with approximately 430 km of inlets, salt-marshes, salt or brackish lakes, creeks, sluices, barriers, dams, and dikes, a total of 73 porpoises were found (0.17 km^{-1}). It is highly likely that individuals may have been overlooked in these areas, but we cannot estimate how many.

Of 1968 reported harbour porpoises, 1092 were sexed (55.6%) and 59.0% of these were males. Males predominated in all major subregions, and there is no significant difference in the sex ratio between any of these (table 5). The mean total length (TL) of 1353 individuals for which this was measured or estimated, was 117.4 ± 23.0 cm (mean ± SD, range TL 42-183). Note that the smallest individual reported was a stillborn (a foetus), carefully measured, of 42 cm in length. The data suggest a slight decline in mean length over the past decade, from 120.9 ± 25.8 (range TL 60-183, *n*=354) between 1998 and 2002, to 116.2 ± 21.8 (range TL 42-180,

n=998) between 2003 and 2007. The difference in mean total length of porpoises found stranded in these two periods is statistically significant (t_{1350}=3.35, $P<0.001$, two-tailed t-test), but the decline is in fact gradual, and with some ups and downs. The TL for males (116.9 ± 20.1, range 42-178, n=569) was significantly smaller than for females (121.6 ± 24.2, range 71-183, n=392; t_{959}=3.28, $P<0.005$). Plotting the mean length for either sex in time, we see a rather erratic pattern, with a distinct dip in mean length in 2006 (figure 4), when overall numbers washing ashore were higher than ever (figure 2).

Ageing cetaceans is a more delicate matter, but total length was used here as a proxy for age, to be able to include as many individuals as possible. Harbour porpoises with a TL of ≤90 cm were classified as neonates (or stillborns) (photo 13). Males with TL ≥145 cm and females with TL ≥150 cm were classified as adults, and animals of intermediate size as juveniles. Because not all measured individuals could be sexed, we have



(A)

(B)

(C)

(D)

Figure 3. Annual densities (n per km) of documented strandings of harbour porpoises per subregion in the Netherlands (North Sea beach areas only), 1998-2007 (n=1733). The figures show an outline map (A) and regional trends in strandings on the Wadden Sea islands (B), along the mainland coast (C) and in the Delta area (D) (all graphs the same scale).

Table 5. Sex ratio of harbour porpoises stranded from 1998 to 2007 per subregion in the Netherlands. G-tests were applied for subsequent regions (all *P*>0.05).

	female	male	unknown	% male	sample	G_{adj}	
Voordelta	128	188	106	59.5	316		
Delta	22	38	13	63.3	60	0.31	n.s.
Mainland	167	204	233	54.9	371	1.47	n.s.
Wadden Sea Isles	109	175	423	61.6	284	2.90	n.s.
Wadden Sea	22	39	97	63.9	61	0.11	n.s.
	448	644	872	59	1092		

Table 6. Age composition based on total length (TL) of harbour porpoises stranded from 1998 to 2007 per subregion in the Netherlands (neonates TL ≤90 cm, juveniles TL>90, <145 (♂) or <150 (♀), adults ≥145 (♂) or ≥150 (♀ and unsexed)).

	adult	juvenile	neonate	unknown	% adult	% neonate	sample
Voordelta	49	256	44	73	14.0	12.6	349
Delta	9	46	6	12	14.8	9.8	61
Mainland	72	300	38	194	17.6	9.3	410
Wadden S Isles	74	317	73	243	15.9	15.7	464
Wadden Sea	6	55	7	90	8.8	10.3	68
	210	974	168	612	15.5	12.4	1352

Table 7. Age composition based on total length (TL) with sex of harbour porpoises stranded from 1998 to 2007 in the Netherlands. See table 6 for conventions.

	female	male	unknown	% male	sample
adult	80	69	61	46.3	149
juvenile	267	450	257	62.8	717
neonate	46	50	72	52.1	96
unknown	55	75	482	57.7	130
totals	448	644	872	59.0	1092
% adult	20.4	12.1	15.6		
% neonate	11.7	8.8	18.5		
sample	393	569	390		

classified unsexed individuals as adults when TL ≥150 cm, thereby providing a conservative estimate of the fraction of adult, potentially sexually active individuals.

Following this classification, it appeared that the proportion of adults was lower in the Wadden Sea (8.8%), but fairly consistent around 15% in other subregions (table 6). The proportion of neonates (including stillborns) found, 12.4% overall, varied from 9.3% along the mainland coast to 15.7% on the Wadden Sea islands. When combining the data on sex and expected age (table 7), it appears that the sex ratio in juveniles was strongly biased towards males (62.8% ♂♂, G_{adj} 23.8, *P*<0.001). The sex ratio of adults and neonates was not significantly different from even. As a re-

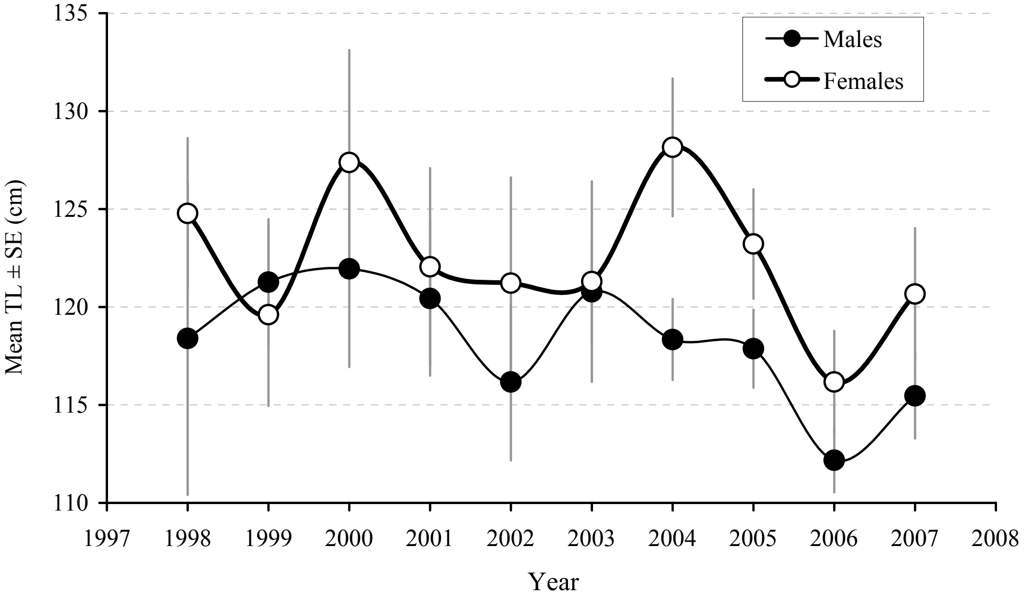


Figure 4. Mean length (± SE) of sexed harbour porpoises, 1998-2007 (*n*=960 individuals measured and sexed).

sult, the sex ratio in juveniles was significantly different from that in adults (G_{adj} 13.6, $P<0.01$) and neonates (G_{adj} 3.97, $P<0.05$). Overall, 20.4% of the female porpoises were adults, against only 12.1% of the males.

The monthly pattern in strandings was bimodal, with distinct peaks in March-April (23.0% of all animals found, *n*=1968) and August (12.6%). The relative abundance of animals identified as sexually mature was also bimodal, but with distinct peaks in June (27.0%, *n*=89 aged individuals) and December through January (25.8%, *n*=178; figure 5), indicating that the proportion of adults was highest when frequencies were relatively low. About one quarter of all porpoises in late summer (July-September) were classified as neonates (23.6%, *n*=433), but small individuals were found in low frequencies (<10%) throughout the year (figure 5). The majority of the stranded porpoises were classified as juveniles, throughout the year, with a weak bimodal pattern showing peaks in March (89.2%, *n*=157) and October (79.5%, *n*=73) and relatively low numbers in July (59.2%, *n*=120).

Harbour porpoises are known to reach a maximum length in the order of about 180 cm, but such large animals are uncommon in Dutch waters. Between 1998 and 2007, ten individuals were reported with a TL>170 cm (0.7%, *n*=1352), but unfortunately, the length of most of these animals was estimated rather than carefully measured. Four large animals were measured, and three of these were females:

17 Jun 1998, Julianadorp (NH), adult ♂, TL 178, reported by Gemeente Den Helder.

14 Dec 2000, Petten p19 (NH), adult ♀, TL 183, reported by A. Gronert, NSO 114084, carcass sent to *Naturalis*.

14 Aug 2001, Dishoek (Walcheren), ♀, TL 171, reported by J. van der Hiele (EHBZ Zeeland). Autopsy *Naturalis*, Pp020531-1: large uterus, stomach collected.

7 Mar 2007, Ameland p14.4, ♀, TL 171, reported by J. Krol (Natuurcentrum Ameland). Autopsy Zeehondencreche Pieterburen: mass 65.2 kg, pregnant, foetus 50 cm.

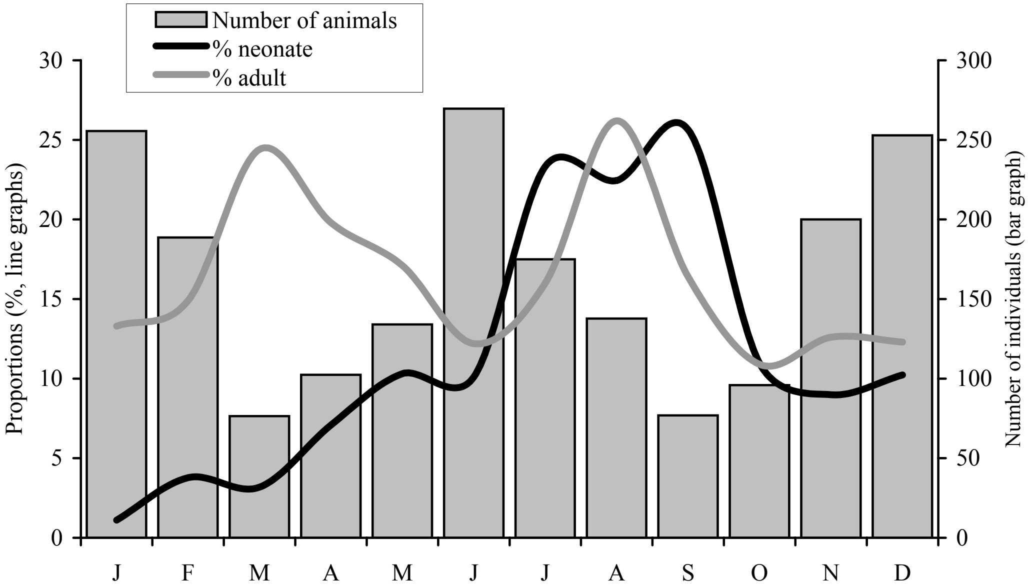


Figure 5. Monthly proportions (%) of harbour porpoises classified as adults and neonates (including stillborns), 1998-2007 (*n*=1349 individuals aged on the basis of total length; see text), relative to the monthly total reported number of stranded harbour porpoises (*n*=1968 individuals, bar-graph).

These three large females were either pregnant or had recently given birth. Since only a small fraction of the porpoises found was dissected, we have little idea about the reproductive status of harbour porpoises in the southern North Sea. Including animals dissected at *Naturalis* and during mass-necropsies conducted by NIOZ/IMARES in 2006 and 2007, at least thirteen more females appeared to be pregnant, and these were at least 142 cm in total length. Foetuses ranged in length from 23 cm (Nov 1998, ♀ TL 150, Texel) to 75 cm (May 2004, ♀ TL 149, Vrouwenpolder, Z). One porpoise was found with a calf half-way down the vagina (tail protruding; May 2006, ♀ TL 152, Schoorl aan Zee). The adult had the flukes cut off, suggesting it was a by-catch, released from the net after the flukes had been removed.

Live-strandings were frequent. At least 83 of the reported porpoises were live-stranded (4.2%, *n*=1964), but this is an underestimate given that many more individuals showed signs of having been stranded alive, but were dead when found. Of the known live-strandings, 55 animals were transported to Harderwijk (66.2%) for treatment and care. Several of these were successfully released after treatment.

Necropsies often revealed signs that the animals found were actually by-catches in fishing gear, drowned in and removed from nets, with or without showing clear external damage (García Hartmann et al. 2004, Leopold & Camphuysen 2006). Many porpoises were decomposed when found and were buried or otherwise disposed of, but even with fresh material, the cause of death can rarely be determined in the absence of a proper necropsy. At least 38 casualties were reported with evident external signs of by-catch. Signs of by-catches included clear net-marks on the body, hooks and nylon line sticking out of the mouth, cut-off flippers and flukes, long, linear knife-cuts from anus to throat, or pieces of fishing net still attached to the animal. Another 17 porpoises were heavily mutilated with knives. We suspect that these were by-catches used for other purposes (flesh and/or blubber taken for consumption or as bait), or deliberately damaged to make the carcass sink more rapidly. Mutilated individuals were often fresh, with blubber or skin, and sometimes the 'best meat' carefully cut away (suggesting consumption by humans or dogs), or the animal was simply destroyed and parts were found scattered over some distance along the shoreline. Possible ship's propeller's marks were reported only twice, suggesting that this may be a rather insignificant threat. Emaciation was reported very frequently, as were reports of all kinds of skin lesions and occasional (shark?) bites in the bodies of the stranded animals. Scavenging pressure is so high, however, with abundant gulls Laridae, crows Corvidae and red foxes (*Vulpes vulpes*) roaming the Dutch shores, that external damage is often caused well after death, confusing the strandings reporter.

One individual was described as having a colour pattern remarkably lighter than normal (12 November 2001, Bergen aan Zee, photographs *Naturalis*), but otherwise, no anomalies were reported.

Discussion and conclusions

During the ten-year period discussed here, 14 species of cetaceans were found stranded on the Dutch coast. In anyone year since recording began, between three and five species were reported; only in two years, 1935 and 2006, as many as seven species were found. The average number and diversity of baleen whales found stranded (and observed alive; van der Meij & Camphuysen 2006) was higher than in previous years, with the appearance of the humpback whale as an addition to the Dutch fauna. The frequency of humpback and minke whale, and perhaps also of fin whale, may be signs that populations from more northerly waters are extending their range into the southern North Sea. The increase in sightings and strandings of humpback whales in the southern North Sea may be related to a population increase of this species in the Atlantic Ocean, which could have led to a range extension into new habitats (Camphuysen 2007). Repeated sightings of the same individual humpback whale in the Netherlands and SW Ireland suggest that at least some whales reach Dutch waters via the English Channel (Camphuysen 2007, Strietman 2008).

The pattern of sperm whale strandings seen in the last decades indicates that population recovery and a possible associated range extension alone may not explain all trends. After a peak in strandings in the 1980s and 1990s in the countries around the North Sea and the adjacent NE Atlantic (Christensen 1990, Berrow et al. 1993, Smeenk 1997), the frequency has declined again. Even though the North Atlantic sperm whale stock has been slowly recovering from centuries of over-exploitation, factors leading to strandings in the North Sea are clearly more complex than just stock size. One or more comparable peaks in strandings occurred in the past, particularly in the last decades of the 18th century, before the onset of sperm whale hunting. Climatic vicissitudes, possibly associated with the distribution and availability of food, may play a part (discussion in Pierce et al. 2007).

Annual or biennial strandings reports give no more than a state of affairs, but overseeing a long series of data reveals interesting trends. Even though the quality and coverage of a strandings network shows considerable variations with time (the early 20th century was a build-up phase for A.B. van Deinse and during the first decades, strandings were not systematically recorded), the comparison of strandings frequencies of some dolphin species, particularly as expressed in the relative numbers in the strandings, points to important changes in the biodiversity of the area. Killer whales, irregular visitors to the southern North Sea during much of the 20th century, have not been found or seen since the early 1960s (Kompanje 1995, Camphuysen & Peet 2006, van der Meij & Camphuysen 2006). Bottlenose, white-beaked and common dolphins show striking changes in strandings frequency over the past century (figure 6). A high frequency of strandings of bottlenose dolphins was record-

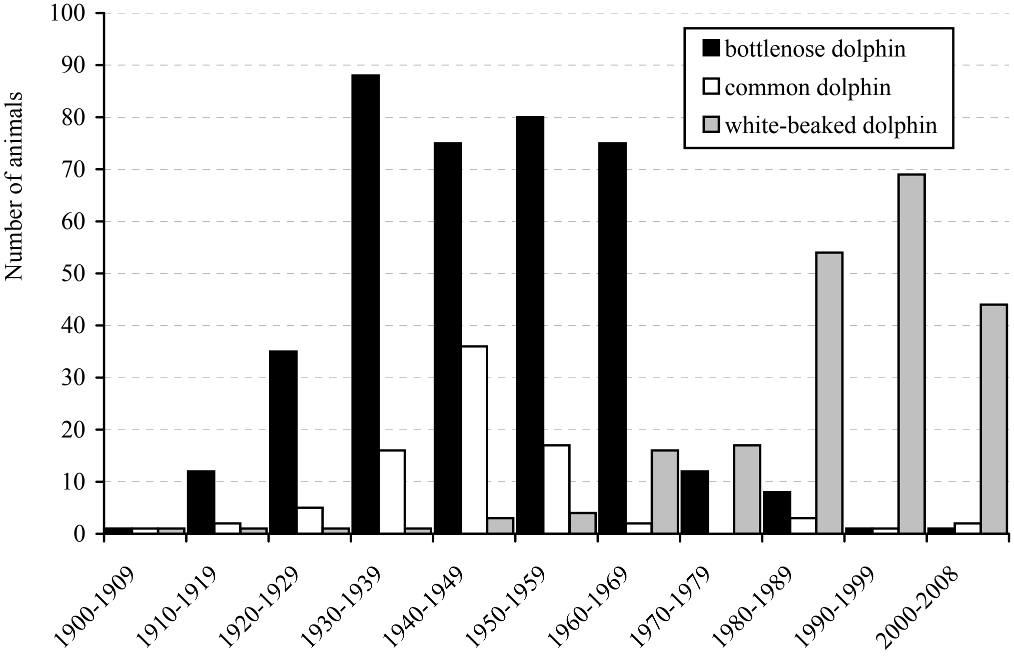


Figure 6. Documented strandings of bottlenose, common and white-beaked dolphins in the Netherlands, 1900-2008, including unpublished records that were recently recovered from diaries and old data files (C.J. Camphuysen, O.E. Jansen & C. Smeenk, unpublished data).

ed up to the 1960s (the first two decades of the 20th century are almost certainly under-reported and therefore unclear for any species), whereas white-beaked dolphins increased in frequency only after the 1950s (Kinze et al. 1997). In the strandings records, this species is now the most numerous dolphin on the Dutch coast, though its numbers have never reached the levels formerly shown by the coastal bottlenose dolphin. Both habitat choice and foraging ecology of bottlenose dolphins and white-beaked dolphins within the North Sea, for as far as currently understood, are rather different. Therefore, the disappearance of the bottlenose dolphin may not have been directly related to the appearance of white-beaked dolphins in the strandings records. The common dolphin, nowadays a rarity, was fairly common in the strandings during the 1930s-1950s. The common dolphin is an oceanic species and it is interesting to note that other oceanic species such as bluefin tuna (*Thunnus thynnus*) and several oceanic seabirds (van Blerkom et al. 1936, van der Heide 1938, Gullick 1949) were unusually common in the North Sea in those years, at least in comparison with present abundance estimates. A tuna fishery developed, flourished and subsequently collapsed in these years (Tiews 1978). This co-occurrence could be just coincidental, but a possible link between the abundance of common dolphins and bluefin tuna (these dolphins are known to associate with hunting tuna in the Atlantic Ocean), is at least intriguing. However, these observed trends in strandings can only be explained satisfactorily when we know more about the spatial and temporal patterns in distribution and abundance of each species in the North Sea at large and the underlying ecological conditions. Unfortunately, high-quality sightings data for the North Sea only exist for the past three to four decades. For the earlier period, we only have the strandings records, however imperfect these may be. The intriguing changes recorded over the past century clearly illustrate that a careful recording of strandings data is very valuable for our understanding of the cetacean fauna of the North Sea, and the possible impact of changing ecological conditions. It is beyond the scope if this paper to explore these issues further.

The number of harbour porpoises found in this period, particularly since the turn of the century, was very large in comparison with the 1970s, 1980s and early 1990s. Unfortunately, we will never know how many porpoises were washed ashore annually earlier in the 20th century. The increase is mainly caused by larger numbers of juveniles, mostly males, travelling into the southern North Sea from areas further north. DNA studies which included samples of stranded Dutch porpoises, suggest that males may disperse further than females (Walton 1997). Also, Dutch samples were genetically heterogeneous and likely comprised a mixture of individuals of diverse origin, many of them probably migrants from the British and Danish North Sea (Andersen et al. 2001). Although the DNA material used in the above studies was collected in the 1990s, before the recent large increase in Dutch strandings, it may help explain the significantly higher numbers of especially juvenile males.

Relatively few adults were found, but pregnant females and numerous neonates illustrate the fact that porpoises currently reproduce successfully in the southern North Sea. The smallest of pregnant females (TL 142 and 149) indicate that an arbitrary minimum length set at TL 150 for adult females, as used in this analysis, is a somewhat conservative estimate of the proportion of mature animals. We have only a limited understanding of the reproductive status of harbour porpoises in the southern North Sea. Pierce et al. (2008) conclude that recent studies mainly suggest that the pregnancy rate in North Sea porpoises is lower than in the western Atlantic and in Icelandic waters and, coupled with evidence of high PCB levels in North Sea animals, they consider this a cause for concern. Also, in view of the present distributional changes of harbour porpoises in the North Sea, an estimate of the overall pregnancy rate for the North Sea as a whole would seem more realistic, rather than an attempt to provide details of small samples. Finally, a possible bias in our samples is that there may well be differences in pregnancy rate as calculated from samples of by-caught and non-by-caught animals, respectively.

The most recent trends in sightings and strandings of harbour porpoises in the Netherlands (since 2006) seem to point to a decline (Camphuysen 2008a), and the need for continuation of an effective strandings network covering the whole Dutch shoreline is urgent. The network is currently maintained by researchers who have other duties and hence priorities. We therefore express here our hope that in the near future some dedicated person or group of persons will rise to safeguard a permanent nation-wide strandings network, as this provides a rich source of valuable data, complementary to sightings records. In view of the rapidly changing marine environment, only such a network can provide reliable data and other material for future monitoring cetacean populations in our waters, in close cooperation with *Naturalis* and other institutes.

The effect of fisheries

Over the period 1990-2000, 130 stranded porpoises were intensively dissected under the responsibility of the National Museum of Natural History (*Naturalis*) in Leiden. Of these, at least 58.5% consisted of by-catches in fishery operations, washed ashore after death (García Hartmann et al. 2004). For that study, gross post-mortem autopsy was combined with further histological examination. Based on histopathological criteria, 43.0% of the porpoises examined were diagnosed as by-catch, against 46.1% based on gross pathology alone, whereas 15.3% were diagnosed as ‘definitely not by-catch’, against 24.6% by gross pathology. The category ‘equivocal by-catch’ increased from 19.2% by gross pathology to 29.2% by histopathology. By gross pathology and histopathology combined, 10.1% and 12.5%, respectively, could not be evaluated with certainty, due to constraints in the interpretation of tissue or other data. By combining both techniques, 58.5% of the animals were definitely identified as 'by-catch', 27.7% as 'not by-catch', 7.7% as 'equivocal', and 3% as either 'not classifiable' or 'absolute discrepancy'. About half of the porpoises examined were found in the period reported in the present paper, the other half had been collected before 1998.

It took some years before a similar set of data could be collected, during mass necropsies concerning animals stranded in 2006 (Leopold & Camphuysen 2006) and 2007 (NIOZ/IMARES, unpublished data), respectively. Using largely the same techniques, a combination of gross pathology and histopathology, autopsies were carried out according to the 'Kuiken protocols' (Kuiken & García Hartmann 1992, 1993, Kuiken 1994), under the responsibility of T. Jauniaux (University of Liège, Belgium) in 2006 and 2007, supervised by A. Gröne (Utrecht University) in 2007. In 2006, 64 harbour porpoises (24 females and 40 males, of which 7 neonates, 45 juveniles and 12 adults) were examined and sampled following the standard necropsy procedure. Frequent observations included net-marks on the skin, sub-cutaneous and muscular bruises, emaciation, pulmonary and gastric parasites, acute pneumonia, pulmonary congestion and oedema. In 26 cases, the animals were too putrefied to identify lesions. In the remaining porpoises, two causes of death were significant: by-caught in fishing gear and infectious disease. By-catch in fishing gear (64%) was mostly observed in animals stranded in March and April, whereas infectious disease (30%; mainly acute pneumonia) occurred throughout the year. External evidence of by-catch (net-marks, incisions penetrating into the body cavity) was observed in 57% of the porpoises diagnosed as by-caught. In addition, 43% of the by-caught animals were healthy, others showed evidence of slight to severe emaciation, acute pneumonia or mild to severe parasitosis. At least eleven animals had still food remains in the digestive tract. The study confirmed that the diagnosis of by-catch in many cases cannot be based solely on external observations, and that not all by-caught porpoises are healthy individuals. Preliminary results over 2007 suggest that slightly less than half of the porpoises were either definite or probable/possible by-catch, but a further histopathological study should confirm and refine this preliminary outcome (NIOZ/IMARES, unpublished data).

All studies indicate that, generally spoken, cetaceans and fisheries are often in conflict. Set nets and anglers (sports fishermen included) seem to cause most problems for cetaceans, but proof is difficult to obtain. It should be realised, however, that the recent increase in strandings of harbour porpoises cannot be attributed to by-catch. Almost certainly, changes in distribution have caused an increase in sightings, first in the NW of the Netherlands, later in the Delta area (Camphuysen & Heijboer 2008), and still later in Belgium and the north of France (Kiszka et al. 2004). Strandings increased in frequency when the numbers of porpoises observed in the southern North Sea increased. The use of set nets, which is among the potentially most dangerous fishing gear for porpoises, has increased in recent years, due to soaring prices of gasoline. But those fisheries were already operational when the influx of porpoises arrived. Lack of appropriate action (by acknowledging and mitigating the problem) has caused so many animals to drown in nets, or to get hooked by anglers. We hope that by emphasizing the problem once more, immediate measures will be taken to reduce by-catch. Such measures can only be effective and satisfactory in co-operation with the fisheries themselves.

Evidence of conflicts with fisheries was not restricted to harbour porpoises. At least two humpback whales were killed directly as a result of fisheries interactions. The humpback whale found on Vlieland, however, was not the victim of a local incident, but must have become entangled long before the stranding, when a loop of a rope got stuck around its head. Several of the recently found minke whales too, including animals recently found in Belgium (Jan Haelters, personal communication), had drowned in fishing gear, or had their flukes or flippers cut off, evidence that someone must have released the animal or the corpse from entanglement. All these problems are fairly new, but with an apparent increase in abundance of porpoises and other cetaceans nearer to the Dutch coast, our responsibility to try and solve the problem has become more urgent. Providing reliable information is the first step toward solving the problem, to be followed by acknowledging the issue, and to trying to identify the exact circumstances and other details of the by-catch. Only then will we be able to formulate measures to mitigate the problem.

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References

Addink, M.J. & C. Smeenk 1999. The harbour porpoise *Phocoena phocoena* in Dutch coastal waters: analysis of stranding records for the period 1920-1994. Lutra 41: 55-80.

Andersen, L.W., D.E. Ruzzante, M. Walton, P. Berggren, A. Bjørge & C. Lockyer 2001. Conservation genetics of harbour porpoises, *Phocoena phocoena*, in eastern and central North Atlantic. Conservation Genetics 2: 309-324.

Berrow, S.D., P.G.H. Evans & M.L. Sheldrick 1993. An analysis of sperm whale *Physeter macrocephalus* stranding and sighting records, from Britain and Ireland. Journal of Zoology, London. 230: 333-337.

Camphuysen, C.J. 2004. The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. Lutra 47: 113-122.

Camphuysen, C.J. 2007. Foraging humpback whale (*Megaptera novaeangliae*) in the Marsdiep area (Wadden Sea), May 2007 and a review of sightings and strandings in the southern North Sea, 2003-2007. Lutra 50: 31-42.

Camphuysen, C.J. 2008. Bruinvis *Phocoena phocoena* op zijn retour in de Zuidelijke Noordzee. Sula 21 (1): 39-43.

Camphuysen, C.J. & K. Heijboer 2008. Bruinvis *Phocoena phocoena* in het Grevelingenmeer: een bijzonder geval met afwijkend gedrag. Sula 21 (2): 74-85.

Camphuysen, C.J. & G. Peet 2006. Walvissen en dolfijnen in de Noordzee. Fontaine Uitgevers, Kortenhoef, The Netherlands.

Christensen, I. 1990. A note on recent strandings of sperm whales (*Physeter macrocephalus*) and other Cetaceans in Norwegian waters. Reports of the International Whaling Commission 40: 513-515.

Evans, P.G.H. (ed.) 2008. Whales, porpoises and dolphins. Order Cetacea. In: S. Harris & D.W. Yalden (eds.). Mammals of the British Isles. Handbook, 4th edition: 654-779. The Mammal Society, Southampton, UK.

García Hartmann, M., C. Smeenk, L. Fichtel & M. Addink 2004. The diagnosis of by-catch: Examining harbour porpoises *Phocoena phocoena* stranded on the Dutch coast from 1990 to 2000. Report National Museum of Natural History (*Naturalis*), Leiden, The Netherlands / Zoo Duisburg AG, Duisburg, Germany.

Gullick, T.M. 1949. Great Shearwaters in the Skagerrak in early June. British Birds 42: 250.

Haelters, J., T. Jauniaux & F. Kerckhof 2006. Bultrug op Belgisch strand. Zoogdier 17 (2): 3-5.

Herman, J.S., A.C. Kitchener, J.R. Baker & C. Lockyer 1994. The most northerly record of Blainville's beaked whale, *Mesoplodon densirostris*, from the eastern Atlantic. Mammalia 58: 657-661.

Husson, A.M. & P.J.H. van Bree 1972. Strandingen van Cetacea op de Nederlandse kust in 1970 en 1971. Lutra 14: 1-4.

Husson, A.M. & P.J.H. van Bree 1976. Strandingen van Cetacea op de Nederlandse kust in 1974 en 1975. Lutra 18: 25-32.

Kinze, C.C., M. Addink, C. Smeenk, M. García Hartmann, H.W. Richards, R.P. Sonntag & H. Benke 1997. The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas: Review of available information. Reports of the International Whaling Commision 47: 675-681.

Kinze, C.C., R.H.H. Kröger, C. Smeenk & P.G.H. Evans 1987. The decline of the Harbour Porpoise in the North Sea. Statement of Concern of the European Cetacean Society. European Cetacean Society, Copenhagen, Denmark.

Kiszka, J.J., J. Haelters & T. Jauniaux 2004. The harbour porpoise (*Phocoena phocoena*) in the southern North Sea: a come-back in northern French and Belgian waters? Document AC11 / Document 24(P/R). Paper presented 11th ASCOBANS Advisory Committee Meeting, 27 - 29 April 2004, Jastrzebia Góra, Poland.

Kompanje, E.J.O. 1995a. Strandings of killer whales *Orcinus orca* in the Netherlands between 1783 and 1995 with some remarks on skeletal and dental pathology (Mammalia: Cetacea, Odontoceti). Deinsea 2: 67-82.

Kompanje, E.J.O. 1995b. Vondst van een schouderblad van de bultrug *Megaptera novaeangliae*. Straatgras 7: 14.

Kompanje, E.J.O. 1996. Vondst van een schouderblad van de bultrug *Megaptera novaeangliae* in de Zuidelijke Noordzee. Lutra 38: 85-89.

Kompanje, E.J.O. 1998. Gewone vinvis en witsnuitdolfijn bij Den Helder in begin augustus 1998: een verslag. Straatgras 10: 61-63.

Kompanje, E.J.O. 2000. De laatste dolfijnensectie van de eeuw. Straatgras 12: 26-28.

Kompanje, E.J.O. 2001. Review of strandings and catches of *Tursiops truncatus* (Mammalia: Cetacea, Odontoceti) in the Netherlands between 1754 and 2000. Deinsea 8: 169-224.

Kompanje, E.J.O. 2005a. Additions to the 'Review of strandings and catches of *Tursiops truncatus* (Mammalia: Cetacea, Odontoceti) in the Netherlands between 1754 and 2000. Deinsea 11: 175-178.

Kompanje, E.J.O. 2005b. Review of strandings of *Delphinus delphis* and *Stenella coeruleoalba* (Mammalia: Cetacea, Delphinidae) in the Netherlands between 1850 and 2005. Deinsea 11: 179-205.

Kompanje, E.J.O. & M. García Hartmann 2001. Intraspongious disc herniation (Schmorl's node) in *Phocoena phocoena* and *Lagenorhynchus albirostris* (Mammalia: Cetacea, Odontoceti). Deinsea 8: 135-141.

Kuiken, T. 1994. Review of the criteria for the diagnosis of by-catch in cetaceans. European Cetacean Society Newsletter 26 (special issue): 38-43.

Kuiken, T. & M. García Hartmann 1992. Draft standard protocol for the basic post-mortem examination and tissue sampling of small cetaceans. Guidelines and records form resulting from the 1st ECS workshop on cetacean pathology. Dissection techniques and tissue sampling, Leiden, 13-14 Sep. 1991. European Cetacean Society Newsletter 14: appendix.

Kuiken, T. & M. García Hartmann 1993. Proceedings of the First European Cetacean Society Workshop on Cetacean Pathology: Dissection techniques and tissue sampling, Leiden, The Netherlands, 13-14 September 1991. European Cetacean Society Newsletter 17 (special issue): 1-39.

Leopold, M.F. & C.J. Camphuysen 2006. Bruinvisstrandingen in Nederland in 2006: Achtergronden, leeftijdsverdeling, sexratio, voedselkeuze en mogelijke oorzaken. IMARES Rapport C083/06 / NIOZ Report 2006-5. Wageningen IMARES, Texel, The Netherlands / Koninklijk Nederlands Instituut voor Onderzoek der Zee, Texel, The Netherlands.

MacLeod, C.D. 2000. Review of the distribution of *Mesoplodon* species (order Cetacea, family Ziphiidae) in the North Atlantic. Mammal Review 30: 1-8.

Meininger, P.L., R.H. Witte & J. Graveland 2003. Zeezoogdieren in de Westerschelde: knelpunten en kansen. Rapport RIKZ 2003.041. Rijksinstituut voor Kust en Zee, Middelburg, The Netherlands.

Pierce, G.J., M.B. Santos, S. Murphy, J.A. Learmonth, A.F. Zuur, E. Rogan, P. Bustamante, F. Caurant,

V. Lahaye, V. Ridoux, B.N. Zegers, A. Mets, M. Addink, C. Smeenk, T. Jauniaux, R.J.Law, W. Dabin, A. López, J.M. Alonso Farré, A.F González, A. Guerra, M. García Hartmann, R.J. Reid, C.F. Moffat, C. Lockyer & J.P. Boon 2008. Bioaccumulation of persistent organic pollutants in female common dolphins (*Delphinus delphis*) and harbour porpoises (*Phocoena phocoena*) from western European seas: Geographical trends, causal factors and effects on reproduction and mortality. Environmental Pollution 153: 401-415.

Pierce, G.J., M.B. Santos, C. Smeenk, A. Saveliev & A.F. Zuur 2007. Historical trends in the incidence of strandings of sperm whales (*Physeter macrocephalus*) on North Sea coasts: An association with positive temperature anomalies. Fisheries Research 87: 219-228.

Sliggers, B.C. & A.A. Wertheim (eds.) 1992. 'Op het strand gesmeten'. Vijf eeuwen potvisstrandingen aan de Nederlandse kust. Walburg Pers, Zutphen, The Netherlands.

Smeenk, C. 1986. Strandingen van Cetacea op de Nederlandse kust in 1981, 1982 en 1983. Lutra 29: 268-281.

Smeenk, C. 1987. The harbour porpoise *Phocoena phocoena* (L., 1758) in The Netherlands: stranding records and decline. Lutra 30: 77-90.

Smeenk, C. 1989. Strandingen van Cetacea op de Nederlandse kust in 1984, 1985 en 1986. Lutra 32: 164-180.

Smeenk, C. 1992. Strandingen van Cetacea op de Nederlandse kust in 1987, 1988 en 1989. Lutra 35: 51-66.

Smeenk, C. 1995. Strandingen van Cetacea op de Nederlandse kust in 1990, 1991 en 1992. Lutra 38: 90-104.

Smeenk, C. 1997. Strandings of sperm whales *Physeter macrocephalus* in the North Sea: history and patterns. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 67 (Supplement): 15-28.

Smeenk, C. 2003. Strandingen van Cetacea op de Nederlandse kust in 1993-1997. Lutra 46: 45-64.

Smeenk, C., M. Addink & K. Camphuysen. 2003. De eerste bultrug voor Nederland. Zoogdier 14 (4): 3-4.

Smeenk, C., M. Addink & M. García Hartmann 1993. Vreemde walvissen op onze kusten. Deel 1: spitssnuitdolfijnen. Zoogdier 4 (4): 20-26.

Sokal, R.R. & F. Rohlf 1981. Biometry. Freeman, New York, US.

Strietman, W.J. 2008. 'Hollandse' bultrug op reis. Zoogdier 19 (2): 26-27.

Tiews, K. 1978. On the disappearance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer 172: 301-309.

van Blerkom, J., R. Honcoop & G. de Vries 1936. Grote Pijlstormvogel. Amoeba 15: 161.

van Bree, P.J.H. (ed.) 1970. Jaaroverzichten strandingen Cetacea in 1942 t/m 1951. Bundeling publicaties Van Deinse uit Het Zeepaard. Report Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam, The Netherlands.

van Bree, P.J.H. & A.M. Husson 1974. Strandingen van Cetacea op de Nederlandse kust in 1972 en 1973. Lutra 16: 1-10.

van Bree, P.J.H. & C. Smeenk 1978. Strandingen van Cetacea op de Nederlandse kust in 1976 en 1977. Lutra 20: 13-18.

van Bree, P.J.H. & C. Smeenk 1982. Strandingen van Cetacea op de Nederlandse kust in 1978, 1979 en 1980. Lutra 25: 19-29.

van Deinse, A.B. 1931. De fossiele en recente Cetacea van Nederland. PhD Thesis, Universiteit Utrecht, H.J. Paris, Amsterdam, The Netherlands.

van Deinse, A.B. 1933. Aanspoelingen van Cetacea in Nederland in de jaren 1931 en 1932. Uitgave Vereeniging tot oprichting en instandhouding van een natuurhistorisch museum te Rotterdam: 7-20.

van Deinse, A.B. 1943. De Cetacea van 1942. Het Zeepaard 3 (1): 2-4 (also published in: van Bree 1970: 1-3).

van Deinse, A.B. 1944. De Nederlandse Cetacea van 1943. Het Zeepaard 4: 21-23 (also published in: van Bree: 3-5).

van Deinse, A.B. 1945. De in 1944 bekend geworden vondsten van Nederlandse Cetacea. Het Zeepaard 5: 4-6 (also published in: van Bree 1970: 6-8).

van Deinse, A.B. 1946a. De gestrande Nederlandsche Cetacea van 1945. Het Zeepaard 6: 18-20 (also published in: van Bree 1970: 8-10).

van Deinse, A.B. 1946b. De recente Cetacea van Nederland van 1931 tot en met 1944. Zoologische Mededeelingen 26: 139-210.

van Deinse, A.B. 1948a. De Nederlandse Cetacea van 1946. Het Zeepaard 8: 6-9 (also published in: van Bree 1970: 11-12).

van Deinse, A.B. 1948b. De Nederlandse Cetacea van 1947. Het Zeepaard 8: 23-24 (also published in: van Bree 1970: 13).

van Deinse, A.B. 1949. De Nederlandse Cetacea van 1948. Het Zeepaard 9: 32-35 (also published in: van Bree 1970: 14-16).

van Deinse, A.B. 1951a. Het walvissennieuws van 1949. Het Zeepaard 11: 23-30 (also published in: van Bree 1970: 17-23).

van Deinse, A.B. 1951b. Onze walvisachtige dieren van 1950. Het Zeepaard 11: 64-73.

van Deinse, A.B. 1952. De walvisachtige dieren in Nederland waargenomen in 1951, alsmede bijzonderheden omtrent onze oude en moderne walvisvaart. Het Zeepaard 12: 19-29 (also published in: van Bree 1970: 23-31).

van Deinse, A.B. 1953. De Nederlandse Cetacea van 1952. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 3: 21-22 (= Lutra 1).

van Deinse, A.B. 1954. De Nederlandse Cetacea van 1953. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 6: 48-50 (= Lutra 1).

van Deinse, A.B. 1955. De Nederlandse Cetacea van 1954. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 10: 103-105 (= Lutra 1).

van Deinse, A.B. 1956. Walvissennieuws over 1955. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 12: 127-131 (= Lutra 1).

van Deinse, A.B. 1957. Walvisnieuws 1956. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 15: 153-158 (= Lutra 1).

van Deinse, A.B. 1958. Walvisnieuws over 1957. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 18: 183-190 (= Lutra 1).

van Deinse, A.B. 1959. Walvisnieuws 1958. Mededelingenblad van de Vereniging voor Zoogdierkunde en Zoogdierbescherming 20: 205-208 (= Lutra 1).

van Deinse, A.B. 1960. Walvisnieuws over 1959. Lutra 2: 42-47.

van Deinse, A.B. 1961. Walvisnieuws over 1960. Lutra 3: 19-23.

van Deinse, A.B. 1962. Walvisnieuws over 1961. Lutra 4: 33-40.

van Deinse, A.B. 1963. Walvisnieuws over 1962. Lutra 5: 31-35.

van Deinse, A.B. 1964. Walvisnieuws over 1963. Lutra 6: 61-66.

van Deinse, A.B. 1966. Walvisnieuws over 1964. Lutra 8: 22-26.

van der Heide, G. 1938. Waarnemingen over het voorkomen van enkele zeevogels bij de Doggersbank in October 1936. Ardea 27: 256-258.

van der Meij, S.E.T. & C.J. Camphuysen 2006. Distribution and diversity of whales and dolphins (Cetacea) in the Southern North Sea: 1970-2005. Lutra 49: 3-28.

Van Gompel, J. 1991. Cetacea aan de Belgische kust, 1975-1989. Lutra 34: 27-36.

van Utrecht, W.L. & A.M. Husson 1968. Strandingen van Cetacea in het voorjaar van 1967 op de Nederlandse kusten. Lutra 10: 7-17.

Walton, M.J. 1997. Population structure of porpoises in the seas around the UK and adjacent waters. Proceedings of the Royal Society B 264: 89-94.

Samenvatting

Strandingen van Cetacea op de Nederlandse kust in 1998-2007

Tussen 1998 en 2007 zijn er van de Nederlandse kust 2060 gestrande of aangespoelde walvisachtigen gerapporteerd, behorend tot tenminste 14 soorten. Twee soorten, de bultrug (*Megaptera novaeangliae*) en de spitssnuitdolfijn van De Blainville (*Mesoplodon densirostris*), waren nieuw voor de Nederlandse lijst. In dit artikel worden per soort alle strandingen (behalve die van de bruinvis, *Phocoena phocoena*) vermeld, met gegevens over datum, vindplaats, geslacht, lengte (TL), vinder, collectienummers en eventuele nadere bijzonderheden. Deze lijsten worden voorafgegaan door een korte samenvatting van het voorkomen van de soorten in onze wateren.

In vergelijking met eerdere jaren spoelden er opvallend veel vinvissen aan, waaronder voor het eerst ook bultruggen. Waarschijnlijk staat dit in verband met het toenemen van de vinvispopulaties (*Balaenoptera physalus* en *Megaptera novaeangliae*) in de Atlantische Oceaan en noordelijke Noordzee. Strandingen van potvissen (*Physeter macrocephalus*) in de landen rondom de Noordzee bereikten een piek in de jaren ’80 en ’90; daarna namen de aantallen weer af. Waarschijnlijk speelden hierbij klimaatfactoren (mede) een rol. De strandingsreeksen van de drie algemeenste dolfijnen laten zien dat er zich in de loop van de 20ste eeuw belangwekkende veranderingen hebben voorgedaan. De tuimelaar (*Tursiops truncatus*) verdween in de jaren ’60-’70 van onze kust, terwijl de aantallen witsnuitdolfijnen (*Lagenorhynchus albirostris*) in de jaren ’70 en vooral ’90 sterk toenamen. De ge-

wone dolfijn (*Delphinus delphis*) werd opvallend vaak gevonden in de jaren '30-'50, een periode waarin ook enkele andere oceanische diersoorten talrijk voorkwamen in de Noordzee.

Het aantal aangespoelde bruinvissen nam in de studieperiode zo sterk toe, dat opgave van elk exemplaar ondoenlijk was. Hiervoor verwijzen wij naar de strandingslijsten op www.walvisstran-dingen.nl, waar alle bekende gevallen zijn te vinden en waar men ook nieuwe strandingen kan melden. In totaal werden er 1968 meldingen van bruinvissen ontvangen, uiteenlopend van 59 in 1998 tot maar liefst 539 in 2006. Voor een nadere analyse van deze strandingen is de Nederlandse kust verdeeld in 15 zones. Aangenomen dat de regionale verschillen in aantallen strandingen langs de Noordzeekust voor een belangrijk deel het gevolg zijn van verschillen in dichtheid en activiteit van waarnemers en rapporteurs, schatten wij dat er in werkelijkheid 19% meer bruinvissen zijn aangespoeld dan er werden gemeld, op de Waddeneilanden zelfs 30% meer. De gemiddelde lengte van de gevonden bruinvissen nam in de loop van de jaren geleidelijk af en in alle zones werden meer mannetjes dan wijfjes gevonden. Op grond van de opgegeven lengtematen (deels bevestigd tijdens sectie) bleek, dat het merendeel van de aangespoelde bruinvissen onvolwassen dieren waren, voor 15,5% volwassen (TL ♀♀ >150 cm, ♂♂ >145 cm, sexe onbekend >150 cm) en voor 12,4% pas geboren dieren (= alle bruinvissen TL<90 cm). Het overschot aan mannetjes was alleen significant onder de juveniele bruinvissen; bij de volwassen en pas geboren dieren was de geslachtsverhouding vrijwel gelijk. Ongeveer 20,2% van het totale aantal wijfjes en 12,1% van de mannetjes werd geclassificeerd als adult en geslachtsrijp.

Het jaarlijkse patroon van bruinvisstrandingen vertoonde twee seizoenspieken: in maart-april en in augustus. Adulte dieren waren naar verhouding talrijk in de winter (december-januari) en in juni; ongeveer een kwart van de bruinvissen uit de maanden juli-september werd op grond van de lengte als pas geboren (neonaat) of dood geboren (geaborteerd) geclassificeerd. Er werden tien bijzonder grote bruinvissen gemeld (TL>170), maar slechts vier daarvan werden nauwkeurig gemeten; deze zijn in de tekst genoemd. Tenminste 14 wijfjes waren drachtig of hadden kort tevoren geworpen. Dit aantal is echter een minimum, daar slechts een klein deel van de dieren op de snijtafel is onderzocht. De lengte van de foetussen varieerde van 22 cm (december 2006) tot 75 cm (mei 2004). Veel van de gevonden bruinvissen waren al in staat van ontbinding; deze werden begraven of afgevoerd ter destructie. Op grond van uitwendige kenmerken (littekens, verwondingen) werden 38 gevallen van bijvangst herkend; nog eens 17 dieren waren met messen bewerkt, ontspekt of opengesneden kort na of vlak voor de dood. Pathologisch onderzoek aan bruinvissen, gevonden in de jaren 1990-2000 (Naturalis) en in 2006 en 2007 (NIOZ/IMARES), waarbij inwendige, microscopische weefselkenmerken, gegevens over de algehele conditie en uitwendige kenmerken werden gecombineerd, wees uit dat zo'n 50-60% van de onderzochte dieren vermoedelijk in vistuig was omgekomen. Ook enkele baleinwalvissen waren het slachtoffer van verdrinking of verstikking in vistuig. Een goed begrip van de omstandigheden waaronder deze zeezoogdieren verdrinken, is van essentieel belang om deze sterfte terug te dringen.

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Possible implications of the presence of the raccoon dog (*Nyctereutes procyonoides*) in the Netherlands

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Abstract: The raccoon dog (*Nyctereutes procyonoides*) is not an indigenous species in Europe. Russians introduced the species into European parts of the former Soviet Union between 1929 and 1955 and the species has spread westward to other European countries ever since. Raccoon dogs are nowadays occasionally seen in the Netherlands. With this new species being present in the Netherlands, it is important to identify the consequent implications for ecosystem functioning in the Netherlands. In this paper, we make a first attempt to identify these implications. The raccoon dog is an opportunistic feeder, what makes this species rather insensitive to fluctuations in single food resources and reduces dietary overlap with fox and badger. As a vector of rabies and the fox tapeworm, the presence of raccoon dogs in the Netherlands might have consequences for wild and domestic animals, as well as for people. Additionally, *Trichinella* can be carried by raccoon dogs and this disease thus might reach the Netherlands. Mortality, starvation, hunting, disease and traffic accidents often include animal suffering and are thus animal welfare issues. Further investigations of ecological consequences of the presence of raccoon dogs in Dutch ecosystems will contribute to the management and conservation of natural areas in the Netherlands..

Keywords: raccoon dog, *Nyctereutes procyonoides,* alien species, exotic species, the Netherlands, nature conservation.

Introduction

The raccoon dog (*Nyctereutes procyonoides,* Gray 1834) is not an indigenous species in the Netherlands or Europe in general. However, after being introduced by Russians into European parts of the former Soviet Union, the species has spread westward (Kauhala 1999). Recently, raccoon dogs are present in western European countries, including the Netherlands; Dutch newspapers regularly report sightings and road kills of raccoon dogs (figure 1) (Kauhala 1999, Levie 2003, Anonymous 2007, Mulder & van der Giessen 2007, van den Akker & Nieuwenhuizen 2007). Although we need to be critical on these reports (Buys 2004, La Haye 2004), they led to discussions in the Dutch Parliament in July 2007 about the status of raccoon dogs in the Netherlands, as well as the need for research on this exotic species in the Netherlands. The last decade, progressively more interest is shown in exotic species, also in the Netherlands, for they possibly threaten indigenous species, as is the case in parts of Belgium (Van Den Berge 2008). This growing interest applies for example the common muskrat (*Ondatra zibethicus*) (e.g. Bos & Tuenter 2007, Gaaff et al. 2007) and the raccoon (*Procyon lotor*) (e.g. Lammertsma et al. 2008).

Although the raccoon dog is a well studied species outside central Europe, mainly in Finland and Japan, knowledge about its abundance level, biology and impact on ecosystems in central and western Europe remains scarce (Stier et al. 2003, Wittenberg et al. 2005). In Germany, for example, only until recently no specific data had been available on the species since it was first sighted in the 1960s (Stier et al. 2003). At this moment, the raccoon dog population is growing at an ex-

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tremely high rate (figure 2) (Goretzki & Sparing 2006, Zoller 2006), causing concerns for a strong negative influence on the indigenous fauna (Stier et al. 2003). During a five-year telemetry project in Vorpommern (Germany) many biological data of density, food, reproduction etc. are collected concerning their settlement as an exotic species in Germany (Stier 2006a, Stier 2006b).

Despite concerns in other countries regarding the implications of the presence of the raccoon dog for ecosystem functioning, the Dutch Minister of Agriculture, Nature and Food Quality states that no research on the raccoon dog's ecological impact will be initiated and the raccoon dog stays an unprotected species and hunting is allowed (Verburg 2007). For successful nature conservation, however, it is important to understand the potential influence of raccoon dogs on ecosystems that become, or already are, inhabited by raccoon dogs, as well as the consequent implications for management. In this paper, we therefore review literature on the biology and ecology of the raccoon dog and try to identify potential points of concern regarding the influ-

Figure 1. Regions where 90% of the raccoon dogs observed since 1990 in the Netherlands have been recorded. Altogether: 27 sightings ('not verified' included) and 31 found dead (after: Mulder & van der Giessen 2007).

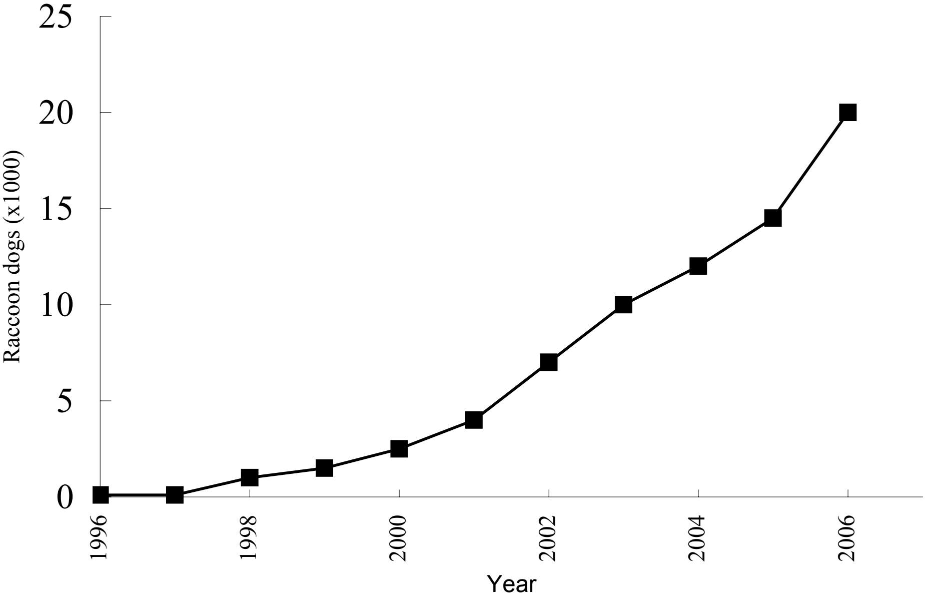

Figure 2. Growing number of raccoon dogs from 1992-2006 in Vorpommern, Germany (adapted from: Zoller 2006).

ence of raccoon dogs on ecosystem functioning in the Netherlands.

Geographical distribution

The raccoon dog originates from China, Korea, south-east Russia, north-east Indochina and Japan (Kauhala 1999). Russians introduced the subspecies *Nyctereutes procyonoides ussuriensis* (more than 9000 individuals) to the Ukraine, Belarus, Russia and Latvia between 1929 and 1955 (Kauhala 1999). The raccoon dog has subsequently spread to other European countries and is now also present in Moldova, Finland, Sweden, the Baltic States, Poland, Romania, Bosnia, Bulgaria, Hungary, Serbia, Germany, Norway, Denmark, France, Switzerland, Austria, Slovenia and the Netherlands (Helle & Kauhala 1991, Kauhala 1999).

The raccoon dog is a highly adaptable species and therefore lives in a variety of habitats. It inhabits both deciduous and coniferous forests, but prefers moist deciduous environments with some forest and thick vegetation and possible den sites in the near proximity of lakes and streams most (Novikov 1962, Corbet 1966, Kauhala 1999, Stier et al. 2003, Saeki & MacDonald 2004, Kauhala et al. 2006, Stier 2006a). The raccoon dog also lives near human settlements (Kauhala 1994, Stier et al. 2003), but avoids close human contact (Stier 2006a).

Social behaviour and reproduction

The raccoon dog is strictly monogamous, forming a pair for life (Corbet 1966, Helle & Kauhala 1993, Kauhala 1994, Stier et al. 2003, Kauhala et al. 2006, Stier 2006a). Male and female move together in their home range, mainly at night (Wittenberg et al. 2005), and share their winter den (Helle & Kauhala 1993). The home ranges of different pairs do not overlap and are stationary from year to year (Kauhala et al. 1993a, Holmala & Kauhala 2006). Latrines may act like landmarks (Ikeda 1984, Kauhala et al. 1998a).

In general, pregnancy lasts about two months and once a year the female gives birth to 5-8 cubs in June (Corbet 1966, Asikainen et al. 2002). The mean litter size in southern Finland and also in the original area in south east Asia is nine cubs (Helle & Kauhala 1995). Recent data from the North-East of Germany show an average of ten cubs per litter (Stier 2006a). Since energy requirements for nursing are high, the female usually forages, while the male stays in the den with the cubs, guarding and keeping them warm (Kauhala 1994, Kauhala et al. 1998b). The offspring leave the parental den by 4-5 months and attain sexual maturity at 9-11 months (Novikov 1962).

Reproduction in the raccoon dog is strongly affected by environmental factors, such as climate, length of the growing season and food availability, which affect body mass and fat reserves (Kauhala 1992, Kauhala 1994, Helle & Kauhala 1995). Especially in areas where the juveniles have enough time to gather fat reserves for hibernation, e.g. in temperate climate, a larger proportion of juveniles survives the winter and, when in a good condition, even breeds in the following spring, resulting in a rapid growth rate of the population (Helle & Kauhala 1991, Helle & Kauhala 1995, Thompson et al. 2006). In adult females, body condition mostly affects annual variation in litter size at birth; females with the largest amount of autumnal fat usually produce the most cubs (Helle & Kauhala 1995, Asikainen et al. 2002).

Diet composition

The raccoon dog is truly omnivorous (Kauhala et al. 1993b, Kauhala et al. 1998a) and its diet comprises a wide range of small rodents, ground-dwelling birds and bird eggs, carcasses, fish, insects (including members of *Hemiptera, Coleoptera, Diptera* and *Orthoptera*), earthworms, snails, plant material, berries, cereal grains, fruits, vegetables, hares, voles, shrews, frogs and lizards (Corbet 1966, Kauhala 1992).

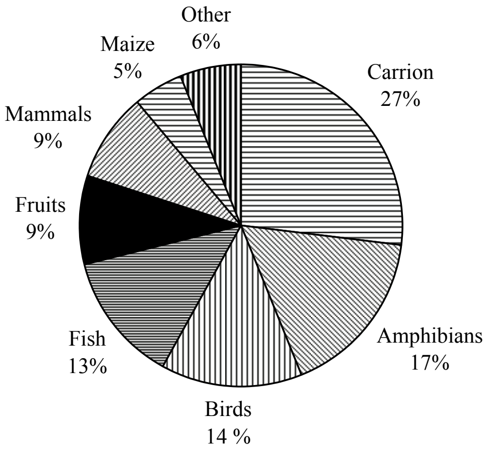

Figure 3. Biomass in 306 raccoon dog stomachs in north-east Germany (adapted from: Stier 2006a).

The diet composition of raccoon dogs differs geographically and temporarily (Kauhala 1992, Kauhala et al. 1993b). In Finland, small mammals are mainly eaten in spring and autumn when food is less abundant than in summer, while plants and birds are important food sources year-round (Kauhala et al. 1993b). Frogs and lizards are predominantly preyed on in late spring and early summer (Kauhala et al. 1993b, Stier 2006a).

Raccoon dogs are also capable of living near human settlements by utilizing man-made food resources, such as garbage cans (Kauhala 1994). This opportunistic and omnivorous foraging behaviour makes the species rather insensitive to fluctuations in single food resources, especially in areas near human settlements (Kauhala 1994). A recent record of the raccoon dog diet composition shows the variety and the importance of carrion, maize and amphibians (figure 3).

Food deprivation in winter

Seasonal changes in body weight are generally related to the availibilty of food. However, this cyclic pattern has also been observed in captive mammals with free access to food all year round (Le Magnen 1983). Farm raised raccoon dogs, having food freely available all year round, also lose their appetite in winter and body weight loss occur voluntary (Korhonen 1988).

Asikainen et al. (2002) studied the effects of food deprivation and hibernation and active winter feeding on the physiology and reproduction of farm-born raccoon dogs. Although food deprivation had no deleterious effects on the health of the study animals, food deprived females had more cubs compared to fed ones (Asikainen et al. 2002). Hence, Asikainen et al. (2002) postulate that the raccoon dog is finely adapted to a long period of food deprivation in winter.

Day length is the basic factor affecting the onset of winter lethargy in raccoon dogs (Kauhala et al. 2007). In Germany, raccoon dogs are known to be active throughout winter (Stier 2006a). Winters in Germany are milder compared to Finland and cold periods with snow are shorter and less frequent, probably shortening winter lethargy and interrupting hibernation (Kauhala et al. 2007).

Densities and competition

In north-east Poland the densities of the raccoon dogs, European badger (*Meles meles*) and the red fox (*Vulpes vulpes*) are 0.37, 0.36 and 0.27 per km², respectively (Goszczynski 1999). In southern Finland, red fox density was estimated to be 0.35 per km², but the density of the raccoon dog (0.76 km²) was higher (Holmala & Kauhala 2006). In Vorpommern (Germany) the density of raccoon dogs is 0.3-0.4 per km², in the preferred area up to 0.9 raccoon dogs per km² (Stier 2006a). Home ranges of red fox and raccoon dog show large overlap (Zoller 2006), although their habitat use is different. The red fox uses more the open areas, while the raccoon dog uses the covered and wet areas most (Zoller 2006). Based on a comparison of home ranges and densities of co-existing medium-sized carnivores, the raccoon dog density in Europe is generally in the same range and often higher than the badger and red fox density (Kauhala et al. 2006, van den Akker & Nieuwenhuizen 2007).

No severe competition for food has been observed between carnivores in Europe and the raccoon dog (Kauhala 1994). The diets of the red fox, European badger and the raccoon dog overlap to some extent, since all three species feed on small mammals, invertebrates, plants and carcasses, suggesting that competition may occur between them (Kauhala et al. 1998a). However, resource partitioning between these species reduces competition (Kauhala 1994, Zoller 2006), i.e. the badger consumes more invertebrates and the red fox more birds and vertebrates than the raccoon dog (Kauhala et al. 1998a) and the raccoon dog has more plants in its diet (Stier 2006a, Stier 2006b, Zoller 2006). Besides, in northern Europe, both the raccoon dog and European badger, with which the raccoon dog might compete most severely, hibernate, reducing competition for food in winter when food is most scarce (Kauhala 1994, Kauhala et al. 1998a, Kauhala 1999).

The red fox, badger and raccoon dog also compete for dens. The raccoon dog often uses old badger or fox dens (Stier 2006b), although both badger and fox tend to chase it away (Kauhala 1994). Raccoon dogs sometimes kill young red foxes and red foxes kill young raccoon dogs (Stier 2006b). Nonetheless, raccoon dogs are sometimes found in the same dens as badgers during the winter (Stier 2006b).

Predation

A study by Kauhala and Auniola (2001) on the diet of raccoon dogs on an island in the Finnish archipelago shows in what way raccoon dogs may affect sea-bird or other animal populations. Raccoon dogs frequently consume waterfowl, especially female eider. It seems improbable, however, that raccoon dogs affect eider populations, because they kill only a small proportion of the eider population (Kauhala & Auniola 2001). On the other hand, Kauhala and Auniola (2001) conclude that it is possible that raccoon dogs affect frog population in the archipelago, because few frogs are found on islands which have been inhabited by raccoon dogs for some years. The same preference for frogs and in general amphibians is found in Vorpommern, Germany (Stier 2006a). In general no severe effect of raccoon dogs on the prey populations are found in Germany, although more research is needed (Stier 2006b).

The colonisation of the raccoon dog in Finland started with a very rapid growth (Kauhala 1992). In the mid 1980s the population size reached its peak. Thereafter, the population size first declined slightly, stabilised afterwards and seems to vary in a density-dependent manner with food supply (Kauhala 1992). It is therefore plausible that the largest effect of the raccoon dog on indigenous fauna occurs in the colonisation-phase when the population size grows to its peak.

Diseases

The raccoon dog is a vector of the fox tapeworm (*Echinococcus multilocularis*), in a larval stage causing the potentially serious disease *Alveolar echinococcosis*, which exhibits a tumor-like growth, initially starting in the liver (Eckert & Deplazes 1999, Wittenberg et al. 2005, Kauhala et al. 2006, Romig et al. 2006, Thompson et al. 2006).

Together with the fox, the raccoon dog is one of the most important European wild animal hosts for classic rabies (Kauhala 1999, Bourhy et al. 1999, Finnegan et al. 2002, Johnson & Fooks 2005). Rabies has become more abundant in wildlife in the eastern and northern parts of Europe in the past few years and the proportion of raccoon dog infections has increased (WHO 2007). The spatial spread of rabies occurs through neighbour-to-neighbour infection and dispersal of infected animals (Holmala & Kauhala 2006). Especially juvenile raccoon dogs can disperse over long distances (Holmala & Kauhala 2006).

The raccoon dog also carries *Sarcoptic mange* (distributed by *Sarcoptes scabei*) and *Trichinella* (Oivanen et al. 2002), and therefore may be an important vector of these parasites (Kauhala

1999). *Trichinella* is found in many carnivorous and omnivorous species. The disease was found to be widespread in wildlife from all parts of Finland (Oivanen et al. 2002). Because the raccoon dog is still spreading westward in Europe, *Trichinellosis* is also thought to be spreading westwards (Oivanen et al. 2002).

Road kills and hunting

Raccoon dogs can be involved in traffic accidents in a density-dependent way. Thousands of road kills of raccoon dogs are reported from Japan with spring and autumn peaks and possibly early morning and evening peaks of mortality (Saeki & MacDonald 2004).

Hunting occurs for population control. Research in Finland by Helle & Kauhala (1991) indicates that mostly juveniles are killed during autumn, of which many will normally not survive the subsequent winter. To be efficient in population control, hunting should occur in late winter and spring and should focus on reproductive animals (Helle & Kauhala 1991). However, if hunting increases total mortality and the population is pressed below carrying capacity, this may lead to a compensating increase in litter size and thus increased productivity of the raccoon dog (Helle & Kauhala 1991, Helle & Kauhala 1995).

Since the raccoon dog is an alien species in the Netherlands, hunting is allowed to prevent the species from growing in number, avoiding fauna forging. Broekhuizen (2007) indicates that it is useless to authorise hunting to prevent the raccoon dog from settling in the Netherlands, especially when there are no indications that a control programme is needed.

Animal welfare

The invasion of an exotic species causes a large number of changes in the life, the environment and the survival of the exotic species itself (Saeki & MacDonald 2004). It is expected to have an impact on the lives and survival of competitors (badgers and foxes), survival of prey species and also on humans (road crossings may cause traffic accidents). Mortality, starvation, hunting, disease and traffic accidents often include animal suffering and are thus animal welfare issues (Sainsbury et al. 1995), of which the severity may be calculated in terms of the amount of harm to welfare caused, the duration and number of animals affected (Kirkwood et al. 1994). For the Netherlands no sufficiently data are yet available to make such calculations.

Discussion

It seems likely that the raccoon dog already is present in the Netherlands or will inhabit the Netherlands in the near future. The Netherlands has a similar or milder climate compared to north-eastern parts of Europe, where the raccoon dog is very abundant. From the history of its distribution in Germany, it can be learned that the population size of raccoon dogs can build up very rapidly after a slow start at low numbers (Stier et al. 2003, Zoller 2006).

A high reproduction rate of the raccoon dog can be expected because of the long growth season due to mild winters in the Netherlands, the monogamous breeding system of the raccoon dog, its omnivorous nature and a period of winter lethargy. Its omnivorous and opportunistic feeding behaviour makes the raccoon dog independent of any specific food items, especially in areas near human settlements. Winter lethargy makes the animal almost entirely independent of food availability during the most unproductive period of the year. These factors contribute to a good physical condition of females, both juveniles and adults, resulting in a high growth rate of the population (Helle & Kauhala 1995). Thompson et al. (2006) suggested that there will be a great opportunity for the racoon dog to increase in number and continue to extend its range in Europe, because of the effect of the European climate on the reproductive capacity of the raccoon dog.

When the raccoon dog is living in a milder climate, such as in the Netherlands, the population growth rate can be very high (Helle & Kauhala 1995) and the probable increase of movements during winter may accelerate the spread of rabies and other diseases and parasites (Kauhala et al. 2006). Moreover, because raccoon dog density will probably increase with rising temperatures (Helle & Kauhala 1995), there will be more raccoon dogs transmitting the parasite, even in winter (Kauhala et al. 2006). The fox tapeworm is present in the Netherlands; the presence of the raccoon dog as a new and important vector of this parasite might be a point of concern in the Netherlands. Although not yet present in the Netherlands, rabies also might be a point of possible concern in the next future.

Research on home ranges and densities of medium-sized carnivores shows that the raccoon dog density in Europe is in the same order of magnitude and often higher than the density of the badger and red fox (Kauhala et al. 2006). Expectations for the eventual population density of raccoon dogs in the Netherlands should take these data into account, along with the found association between raccoon dogs and badgers in home range and den use. Hunting may adversely influence population dynamics and development. Species population management by hunting should be considered very careful. Hunting may in fact even increase productivity of the raccoon dog (Helle & Kauhala 1991, Helle & Kauhala 1995).

Conclusion

In this paper, through reviewing literature and subsequently identifying possible issues of concern for nature management and conservation, we hope to have made a first step to a better understanding of the ecology and biology of the raccoon dog, as well as its probable role on ecosystem functioning in the Netherlands.

For successful nature conservation, we need to understand the biology of the raccoon dog and strive to avoid possible problems that might arise when raccoon dogs become abundant. Despite the recent statement of the Minister of Agriculture, Nature and Food Quality about the status of the raccoon dog in the Netherlands - “unprotected species and hunting allowed” -, further structural investigations of settlement, dispersal and ecological consequences of the presence of raccoon dogs in different Dutch ecosystems will greatly benefit nature conservation in the Netherlands, as already stated before by Broekhuizen (2007).

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References

Anonymous 2007. Wilde wasbeerhond rukt op. De Telegraaf 115 (18 juli): 7.

Asikainen, J., A.-M. Mustonen, P. Nieminen, S. Pasanen, H. Araja-Matilainen & H. Hyvarinen 2002. Reproduction of the raccoon dog (*Nyctereutes procyonoides*) after feeding or food deprivation in winter. Journal of Animal Physiology and Animal Nutrition 86: 367–375.

Bos, D. & T. Tuenter 2007. Muskusratten zonder bestrijding? Ontwerp van een onderzoek aan de gevolgen van tijdelijk niet bestrijden. A&W-rapport 1032. Altenburg & Wymenga, Veenwouden, the Netherlands.

Bourhy, H., B. Kissi, L. Audry, M. Smreczak, M. Sadkowska-Todys, K. Kulonen, N.I. Tordo, J.F. Zmudzinski & E.C. Holmes 1999. Ecology and evolution of rabies virus in Europe. Journal of General Virology 80: 2545–2557.

Broekhuizen, S. 2007. Wordt de wasbeerhond de nieuwe muskusrat? Zoogdier 18: 15-17.

Buys, J. 2004. Wees correct als je kritisch schrijft - ook als het om wasbeerhonden gaat. Zoogdier 15 (2): 28-29.

Corbet, G.B. 1966. The terrestrial mammals of western Europe. G.T. Foulis & Co, London, UK.

Eckert, J. & P. Deplazes 1999. Alveolar Echinococcosis in humans: the current situation in Central Europe and the need for countermeasures. Parasitology Today 15 (8): 315-319.

Finnegan, C.J., S.M. Brookes, N. Johnson, J. Smith, K.J. Mansfield, V.L. Keene, L.M. McElhinney & A.R. Fooks 2002. Rabies in North America and Europe. Journal of the Royal Society of Medicine 95: 9-13.

Goretzki, J. & H. Sparing 2006. Anstieg rasant und unbemerkt. Streckenentwicklung von Marderhund, Waschbär und Mink in Deutschland. In: R. Schneider (ed.). Neubürger auf dem Vormarsch: 8-11. Sonderheft von Unsere Jagd, Pirsch und Niedersächsischer Jäger. Deutscher Landwirtschaftsverlag, Berlin, Germany.

Goszczynski, J. 1999. Fox, raccoon dog and badger densities in North Eastern Poland. Acta Theriologica 44: 413-420.

Gaaff, A., R. de Graaff, R. Michels, S. Reinhard & H. Vrolijk 2007. Economische schade als gevolg van graverij en vraat door muskusratten. LEI-rapport 4.07.05. LEI, Den Haag, the Netherlands.

Helle, E. & K. Kauhala 1991. Distribution, history and present status of the raccoon dog in Finland. Holarctic Ecology 14: 278-286.

Helle, E. & K. Kauhala 1993. Age structure, mortality, and sex ratio of the raccoon dog in Finland. Journal of Mammalogy 74 (4): 936-942.

Helle, E. & K. Kauhala 1995. Reproduction in the raccoon dog in Finland. Journal of Mammalogy 76 (4): 1036-1046.

Holmala, K. & K. Kauhala 2006. Ecology of wildlife rabies in Europe. Mammal Review 36: 17-36.

Ikeda, H. 1984. Raccoon dog scent marking by scats and its significance in social behaviour. Journal of Ethology 2: 77-84.

Johnson, N. & A.R. Fooks 2005. Archival study of a Finnish isolate from the 1988/89 rabies outbreak. Archives of Virology 150: 1407–1414.

Kauhala, K. 1992. Ecological characteristics of the raccoon dog in Finland. PhD thesis. University of Helsinki, Helsinki, Finland.

Kauhala, K. 1994. The raccoon dog: a successful canid. Canid News 2: 37-40.

Kauhala, K. 1999. *Nyctereutes procyonoides* (Gray, 1834). In: A.J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Vohralík & J. Zima (eds.). The atlas of European mammals. Academic Press, London, UK.

Kauhala, K. & M. Auniola 2001. Diet of raccoon dogs in summer in the Finnish archipelago. Ecography 24: 151-156.

Kauhala, K., E. Helle & E. Taskinen 1993a. Home ranges of the raccoon dog (*Nyctereutes procyonoides*) in southern Finland. Journal of Zoology 231: 95-106.

Kauhala, K., M. Kaunisto & E. Helle 1993b. Diet of the raccoon dog, *Nyctereutes procyonoides*, in Finland. Zeitschrift für Säugetierkunde 58: 129-136.

Kauhala, K., E. Helle & H. Pietilä 1998b. Time allocation of male and female raccoon dogs to pup rearing at the den. Acta Theriologica 43 (3): 301-310.

Kauhala, K., P. Laukkanen & I. von Rége 1998a. Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. Ecography 21: 457–463.

Kauhala, K., K. Holmala, W. Lammers & J. Schregel 2006. Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. Acta Theriologica 51: 1-13.

Kauhala, K., K. Holmala & J. Schregel 2007. Seasonal activity patterns and movements of the raccoon dog, a vector of diseases and parasites, in southern Finland. Mammalian Biology 72 (6): 342-353.

Kirkwood, J.K., A.W. Sainsbury & P.M. Bennett 1994. The welfare of free-living wild animals: Methods of assessment. Animal Welfare 3: 257-273.

Korhonen, H. 1988. Voluntary regulation of energy balance in farmed raccoon dogs. Comparative Biochemistry and Physiology 89A (2): 219-222.

La Haye, M. 2004. Wees kritisch op de wasbeerhond! Zoogdier 15 (1): 6-8.

Lammertsma D.R., G.W.T.A. Groot Bruinderink & S. Broekhuizen 2008. Wasberen (*Procyon lotor* L. 1758) in Nederland. Verspreiding, ecologie en mogelijke gevolgen voor Nederland. Alterra-rapport 1741. Alterra, Wageningen, the Netherlands.

Levie, D. 2003. Steeds meer wasbeerhonden. De Stentor / Apeldoornse Courant 101 (36; 27 december; 2^e^ katern): 1.

Le Magnen, J. 1983. Body energy balance and food intake: a neuroendocrine regulatory mechanism. Physiological Reviews 63 (1): 314-386.

Mulder J. & J. van der Giessen 2007. Oproep: Dode wasbeerhonden bewaren en snel melden! Zoogdier 18 (2): 20.

Novikov, G.A. 1962. Carnivorous mammals of the fauna of USSR. Israel Program for Scientific Translations (translation), Jerusalem, Israel.

Oivanen, L., C.M.O. Kapel, E. Pozio, G. La-Rosa, T. Mikkonen & A. Sukura 2002. Associations between *Trichinella* species and host species in Finland. Journal of Parasitology 88: 84-88.

Romig, T., D. Thoma & A.K. Weible 2006. *Echinococcus multilocularis* - a zoonosis of anthropogenic environments? Journal of Helminthology 80: 207-212.

Saeki, M. & D.-W. MacDonald 2004. The effects of traffic on the raccoon dog (*Nyctereutes procyonoides viverrinus*) and other mammals in Japan. Biological Conservation 118: 559-571.

Sainsbury, A.W., P.M. Bennett & J.K. Kirkwood 1995. The welfare of free-living wild animals in Europe: Harm caused by human activities. Animal Welfare 4: 183-206.

Stier, N., F. Drygala & M. Roth 2003. Aktuelle Ergebnisse zur Marderhundforschung in Mecklenburg-Vorpommern. Angewandte Wissenschaft (= Schriftenreihe des Bundesministeriums für Verbraucherschutz, Ernährung und Landwirtschaft) 498 - "Bedrohung der biologischen Vielfalt durch invasive gebietsfremde Arten": 127-130.

Stier, N. 2006a. Ständig auf Beutezug: Biologie des Marderhundes. In: R. Schneider (ed.). Neubürger auf dem Vormarsch: 14-23. Sonderheft von Unsere Jagd, Pirsch und Niedersächsischer Jäger. Deutscher Landwirtschaftsverlag, Berlin, Germany.

Stier, N. 2006b. Rivale von Fuchs und Dachs? Marderhund: Ökologische Auswirkungen der Besiedlung. In: R. Schneider (ed.). Neubürger auf dem Vormarsch: 24-29. Sonderheft von Unsere Jagd, Pirsch und Niedersächsischer Jäger. Deutscher Landwirtschaftsverlag, Berlin, Germany.

Thompson, R.C.A., C.M.O. Kapel, R.P. Hobbs & P. Deplazes 2006. Comparative development of *Echinococcus multilocularis* in its definitive hosts. Parasitology 88: 84-88.

van den Akker, R. & A. Nieuwenhuizen 2007. Een wasbeerhond en een das samen aan de maaltijd. Zoogdier 18 (2): 21.

Van Den Berge, K. 2008. Carnivore exoten in Vlaanderen. Zoogdier 19 (2): 6-9.

Verburg, G. 2007. Kamervragen over de opkomst van de wilde wasbeerhond, 28-8-2007. Ministry of Agriculture, Nature and Food Quality, The Hague, the Netherlands.

WHO 2007 [World Health Organization = h.l. WHO Collaboration Centre for Rabies Surveillance and Research]. Available from the internet, accessed 15 November 2007. URL: http://www.who-rabies-bulletin.org.

Wittenberg, R., M. Kenis, T. Blick, A. Hänggi, A. Gassmann & E. Weber 2005. An inventory of alien species and their threat to biodiversity and economy in Switzerland. Report to the Swiss Agency for Environment, Forests and Landscape. CABI Bioscience Switzerland Centre, Delémont, Switzerland.

Zoller, H. 2006. Koexistenz zwischen Enok und Reineke. In: R. Schneider (ed.). Neubürger auf dem Vormarsch: 26. Sonderheft von Unsere Jagd, Pirsch und Niedersächsischer Jäger. Deutscher Landwirtschaftsverlag, Berlin, Germany.

Samenvatting

Mogelijke implicaties van de aanwezigheid van de wasbeerhond (*Nyctereutes procyonoides*) in Nederland

De wasbeerhond (*Nyctereutes procyonoides*) is geen inheemse diersoort in Europa. De soort is tussen 1929 en 1955 geïntroduceerd in Europese delen van de voormalige Sovjet Unie. Daarvandaan heeft de wasbeerhond zich verspreid naar andere Europese landen. Uit ons literatuuronderzoek blijkt dat de wasbeerhond sinds 1990 ook regelmatig in Nederland is waargenomen. Met deze nieuwe soort in Nederland is het van belang om mogelijke problemen in het functioneren van ecosystemen tijdig te signaleren. In dit artikel geven wij daartoe een eerste aanzet. De wasbeerhond staat bekend als een opportunist, waardoor voedselconcurrentie met de vos en de das nauwelijks is te verwachten. Als een vector voor rabiës en de vossenlintworm kan de aanwezigheid van de wasbeerhond in Nederland consequenties hebben voor wilde dieren, gedomesticeerde dieren en mensen. Ook is de wasbeerhond drager van de *Trichinella*-parasiet en door de uitbreiding van deze soort naar West-Europa zou deze parasiet in de toekomst ook Nederland kunnen bereiken. Bij een invasie van de wasbeerhond kunnen mortaliteit, honger, afschot, ziektes en verkeersongelukken het lijden van dieren veroorzaken. Daarom zal een invasie, maar ook een plotselinge exponentiële toename door natuurlijke aanwas, op de voet moeten worden gevolgd waarbij ook dierenwelzijnaspecten moeten worden betrokken. Verder onderzoek naar de invloed van de wasbeerhond op Nederlandse ecosystemen is van belang voor natuur, natuurbeheer en natuurbescherming.

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