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All animals…

What book would you pick to read and reread if you were going to an uninhabited island? Well, as we have been under the spell of the worldwide covid-19 pandemic for some time, seemingly in splendid isolation, I have had the chance come forward with three titles. Although all three reflect on animals, it would be difficult to find any three books that describe animals from such extremely different perspectives, than *Animal farm* (George Orwell 1945), *Variability in mammals* (Alexej Yablokov 1966) and *The song of the dodo* (David Quammen 1996). The differences in size, style, and scope are striking.

Animal farm, published in English and already by 1947 printed in Russian [Ukrainian] is well known among Dutch scholars as a lean, one hundred page, book, often prominently featured on secondary school English literature lists. *Animal farm*, is a story about farm animals -mainly mammals and poultry who revolted against their owner and tried to create a new society. It is a thinly disguised metaphor of the changes that occurred in the Soviet Union in the decades after the Revolution of 1917. Many intellectuals at the time (Orwell included) had great hopes for the Revolution, which descended into pogroms and a reign of terror. The new society in Orwell's book was based on seven commandments of which the last one was: *All animals are equal*. At the end of the tale the pigs, the self-announced leaders, deleted the original commandments. Only the seventh remained, but with a salient addition: *All animals are equal, but some animals are more equal than others*. In the past, this last, slightly changed commandment was an oft-cited passage, brought up during discussions on political and sociological topics. There are obvious differences between the species/animals living on *Animal Farm*. There was Boxer, the ever-trustworthy carthorse who looked forward to his retirement, so he could dedicate the rest of his life to learning the alphabet beyond the letter 'd'. By contrast there were the pigs, who as the real politicians, could totally change the meaning even of commandments, simply by adding words. At the end it is obvious that this bunch of animals are far from equal, whether socially or physically. The pigs discriminated against the other species. Boxer, one of the Equidae is just a simple carthorse, while another one, Benjamin is a cynical donkey, the oldest of all the animals. All those animals/species turn out to be different, completely different.

Variability in mammals, written in Russian, became available world-wide in 1974 when an English version was produced. It is a medium sized textbook, containing 271 pages (excluding the appendix) and it ends by illustrating the differences (in populations) of mammals, using some 100 tables, 67 figures and some 670 references. In *Variability of mammals*, Yablokov describes phenotypic variation, the

Figure 1. Harp seals (*Phoca/Pagophilus groenlandicus*) on an ice-floe off the coast of Svalbard. *Photo: Kees Mostert.*

raw material for natural selection and Darwin's basic theme and the intraspecific variability of mammals: the differences between mammals of the same species. Yablokov presents coefficients of variation (the standard deviation divided by the mean) in standard body measurements (length of body, tail, feet, ear and body weight) and the regular skull measurements of mammal species in different orders (mainly Rodentia) that you can find from studies of mammals from all over the world. More peculiarly, he also describes the seemingly unimportant variability of the integumentary -skin- system (as he describes it): the number of vibrissae in sequential lines on the upper lips of harp seals (*Phoca/Pagophilus groenlandicus*), ringed seals (*P. hispida*), hooded seal (*Cystophora cristata*) and other Phocidae.

Besides measurements Yablokov also presents some non-metric variations such as the six basic patterns on the back of the harp seal (figure 1): a. horseshoe. b. open-p. c. open-q. d. horseshoe with point. e. loop and f. scattered (figure 2). There are significant differences in the presence of these basic patterns between the breeding populations in the White Sea, the Greenland sea ice (north of Jan Mayen) and the Newfoundland region.

Kükenthal (1890) had already described the splitting of the fourth digit in beluga (*Delphinapterus leucas*) specimens from the Barents Sea and the Kara Sea. However, Yablokov (1974) observed that this splitting occurred on the fifth digit among belugas from the Okhotsk Sea. After reading *Variability of mammals* one must conclude that there are significant intra species differences within mammals although sometimes these need detailed observing and measuring.

The song of the dodo is a page turner of more than 638 pages -beware of getting repetitive strain injury, excluding an extended glossary and more than nine hundred references. It is highly informative and a great primer for courses in population biology, genetics and more. A good friend recommended this book to me a long time ago. Being a full-blooded mammalogist I hesitated to read it, as the title seems to suggest it is about a bird (and an extinct species at that!). However from the

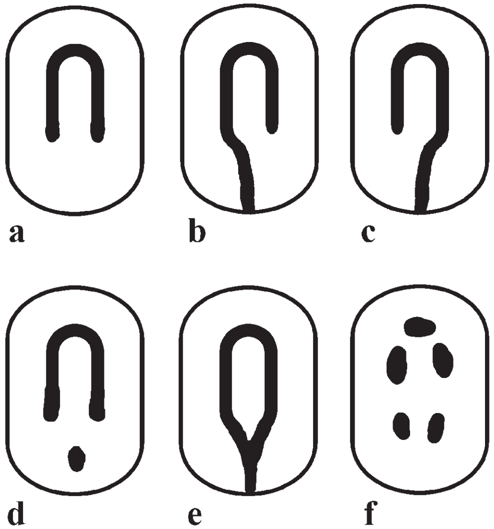

Figure 2. Scheme of different back patterns of adult males of harp seals (*Phoca groenlandicus*). Explanation: a. horseshoe. b. open-p. c. open-q. d. horseshoe with point. e. loop and f. scattered (simplified after an image by Yablokov 1974).

very first page I discovered that I was completely wrong: this is a wonderful book, written in exquisite English, and containing solid summaries of key theories (e.g. the island theory, genetic drift or impeding extinctions) as well as mini interviews with influential scientists and personal observations by the author himself. One of these observations is of the golden bamboo lemur (*Hapalemur aureus*), an elusive species which the author, accompanied by a very competent Malagasy guide, was searching for. After two hours climbing uphill over a ridge and pushing through thick groves of bamboo, they came to a spot where they found two golden bamboo lemurs, as he describes it: "… a pair of fuzzballs no bigger than house cats". The observers sat down and for more than an hour they watched the lemurs in a constant, drumming rain. When several leeches started creeping their way up over his legs, searching for blood, the author realised it was time to go. The intestinal revenge of the bamboo groves' hardships came, back in the basecamp, that night… *The song of the dodo* hides an important message: finding the origins of differences between mammals and other animals, can be a demanding task. Sometimes the differences turn out to be decisive in different ecological circumstances, sometimes the significance stays concealed until the species is challenged by a new situation.

The prominent element shared among these three books is the existence of intraspecific differences in mammal species or between individuals of closely related species. The recognisable elements point all three in the same direction and are in line with each other. These lines in the three books are: Orwell comes to the conclusion that all animals are different, Yablokov presents a wide variety of examples of differences (all concerning mammals), while Quammen basically describes the causes leading to those differences. Now it is time to perceive differences between (populations of) mammal species and to address their origins. This is even possible on an (almost) uninhabited island.

In this issue of *Lutra* a longstanding tradition is continued with the publication of the new list of stranded cetaceans: Keijl et al.'s list (2016) has now been updated to cover the period 2015-2019 (Keijl et al). A rather successful story comes from 'De Onlanden' in the northern part of the Netherlands where van Boekel reports on a study of otters (*Lutra lutra*) based on pictures from camera traps. In contrast to the prospering of otters, Vink & Schröder describe a drastic decline of occupied badger setts in the Veluwe region. Van der Veken et al. describe the diet of the first wolves (*Canis lupus*) to settle in Flanders, confirming these large predators are now part of the ecosystem in this part of Belgium.

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Jan Piet Bekker

Decline of the number of occupied badger (*Meles meles*) setts in the Veluwe region (the Netherlands) and its possible causes

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Abstract: Comparison of surveys shows that the number of occupied badger (*Meles meles*) setts has declined by 42% in the past 25 years in the Central Veluwe (192 setts less) and by 15% in the Peripheral Veluwe (33 setts less). Probably this had a proportionally negative effect on the number of badgers. Concomitantly, the number of occupied 1 km^2 squares (km squares) has declined by 33% in the Central Veluwe (112 km squares less) and by 6% (11 km squares less) in the Peripheral Veluwe. The share of occupied km squares supporting more than one occupied sett dropped from, on average, 22 to 12%. These declines may result from diminishing supplies of food and accessibility of food for badgers. Some of the factors determining these supplies and their accessibility apply as much to the Central Veluwe as to the Peripheral Veluwe. However, long dry spells during summer, potential food competition with wild boar (*Sus scrofa*), the diminishing area of accessible manured grassland and local recreation pressure, probably have had a greater negative impact in the Central Veluwe than in the Peripheral Veluwe. The present paper proposes several measures to preserve and restore the badger population of the Veluwe.

Keywords: badger, *Meles meles*, sett, earthworms, grassland, drought, food accessibility, food competition.

Introduction

The population size of badgers (*Meles meles*) in the Netherlands hit an all-time low of around 1,500 animals in the beginning of the 1980s (Wiertz & Vink 1983). After that period their numbers started to increase as a result of re-introductions and better protection, including mitigation of traffic mortality (van Moll 2005, Dekker & Bekker 2010, La Haye & Vink 2016). The nationwide population in 2015 has been estimated at 5,000-6,000 animals, occupying around 2,000 setts (La Haye et al. 2015). Badgers have been present in the Province of Gelderland for many centuries, particularly in the Veluwe region (Vink 1985). This is confirmed by a listing of badger setts near Wageningen, Ede, Bennekom and Renkum (Ritzema Bos 1879). Moreover, there is a bounty administration In the Royal House Archives indicating the number of badgers killed in 1844 on the Royal Estate Kroondomeinen near Apeldoorn.[1]

Applicable legislation demands that the conservation status of animal species is seriously taken into account when deciding on changes in land use or land management. The Province of Gelderland recently assessed the conservation status of the badger from that

[1] Koninklijke Verzamelingen, Den Haag, Archief: Intendance van het Koninklijk Paleis en Domein Het Loo, inventarisnummer E09c-448.

perspective (Logemann 2018). His report qualifies the status of the species as 'favourable' and still considers the Veluwe a stronghold and a source from where badgers disperse. However, the report also expresses doubts about the future prospects of the badger population within the Veluwe region. This concern was also raised by badger specialists and pertains to the central part of the Veluwe in particular (Hollander & La Haye 2013, La Haye et al. 2015, van den Bosch 2015). The present paper intends to underpin this concern numerically by comparison of a recent survey of the number of occupied main setts and a similar survey that was executed 25 years ago. In this comparison a distinction was made between the central part (Central Veluwe) and the borders of the Veluwe (Peripheral Veluwe) as these two areas differ in land use and hydrology.

Materials and methods

Study area

The Veluwe region finds itself in the province of Gelderland, the Netherlands. The central part, from here on referred to as Central Veluwe, measures 1150 km^2 and is dominated by a mosaic of forests and heathlands (43%), locally larded by grassland and maize land (43%) on deeply drained dry sandy soils low in organic matter, and a relatively small amount of built-up areas (14%) (CBS Statline 2021a). Land use within the area devoted to agriculture has hardly changed between 2000 and 2015 (CBS Statline 2021b) and comprised 78% grassland, 16% silage maize and 6% arable crops. The Central Veluwe is known for its rich wildlife, among which red deer (*Cervus elaphus*) and wild boars (*Sus scrofa*), and appreciated by tourists. The Central Veluwe is defined as the area delineated by the motorways and roads A28 (Harderwijk-Hattemerbroek), A50 (Hattemerbroek-Hattem), N794 (Hattem-Apeldoorn), N786 (Apeldoorn-Dieren), A348 (Dieren-Arnhem), the northern bank of the Neder-Rijn river along the N225 (Arnhem-Wageningen), N781 (Wageningen-Ede), Ede-Lunteren-Otterlo, N310 (Otterlo-Stroe), Stroe-Veenhuizerveld and N303 (Veenhuizerveld-Harderwijk). Within the Central Veluwe two sub-regions are discerned (figure 1): the so-called Enclave westward from the village of Elspeet (denoted by a red line) which is almost entirely devoted to agriculture and the Southwest Veluwe (denoted by a brown line) finding itself between the motorway A12 (Ede-Arnhem) and the Neder-Rijn river. From both sub-regions wild boars are completely banned by fences and road grids. The Central Veluwe is adjoined by valleys in the west and east of which the total area amounts to 1040 km^2. These valleys are from here on referred to as Peripheral Veluwe. They are confined by the Veluwe Border Lakes in the northwest, the border with the Province of Utrecht in the southwest and the river IJssel in the east. Within the Peripheral Veluwe three sub-regions are discerned (figure 1): the Northwest Veluwe and the Gelderse Valley in the west and the IJssel Valley in the east. The soil type of the first two sub-regions is also mainly sandy but loamy here and there, more fertile and less prone to droughts. This applies also to the loamy and clay soils of the IJssel Valley. The Peripheral Veluwe is predominantly used for grassland and the production of silage maize amidst many villages and several cities. In our analysis we make a distinction between population trends in the (sub-regions of the) Central Veluwe and the (sub-regions of the) Peripheral Veluwe because of the differences in hydrology and land use.

Surveying method

We took the badger sett survey of van Moll (1999) executed between 1995 and 1996 as a reference for the present survey of 2019-2020. The reference survey was based on the then available locations of main setts compiled by Das & Boom (Dutch society for the protection

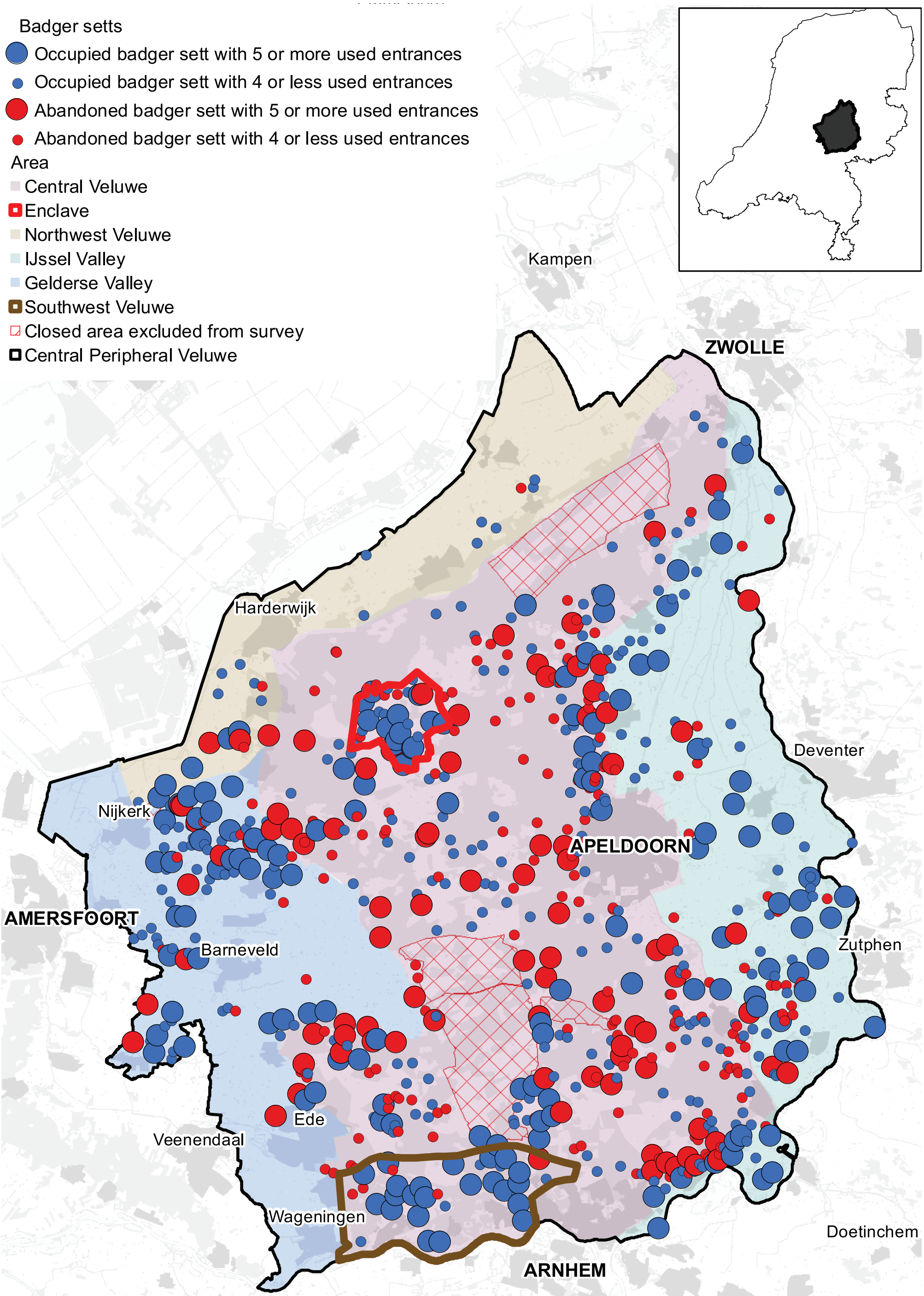

Figure 1. Occupation and abandonment of main setts of badgers (*Meles meles*), either once occupied in 1994-1996 or newly discovered between 1997 and 2020, as observed in 2019-2020 (Veluwe region, Province of Gelderland, the Netherlands.

of badgers) since 1981. Details of this survey were presented in van Moll (2005). His data set was supplemented with data based on a parallel survey of the Instituut voor Bos- en Natuuronderzoek (IBN) carried out between 1994 and 1996 (van Apeldoorn et al. 1997). For the purpose of this paper we took the number of occupied main setts as a proxy for the population size. An occupied main sett was defined as in Roper (2010), i.e. a regularly if not permanently inhabited multi-entrance sett with fresh signs of digging, traces of bedding material, foot prints, well-used tracks or latrines. Better ways to determine the exact size of a badger population are cumbersome, not in the least because of the nocturnal activity of the species. We excluded so-called subsidiary setts and outliers because of their notoriously variable state of occupation, as opposed to main setts including annexes (Roper 2010). The combined data sets of van Moll (1999) and van Apeldoorn et al. (1997) comprised 665 occupied main setts for the period 1994-1996 next to several abandoned main setts. Of these abandoned setts only three were found re-occupied in the 2019-2020 survey. Between 1997 and 2020, 46 new main setts were discovered, added to the database and included in the analysis. As opposed to the initial surveys, the present survey also recorded the size of a main sett by counting the number of open entrances, regardless whether they were in use or not. The relationship between the number of entrances and the number of inhabitants is quite weak (Roper 2010) but it may give at least an impression of possible differences between regions and be of use for future comparisons over time. We distinguished two classes of entrance numbers: main setts with at least five used entrances and main setts with at most four entrances. As in other surveys (e.g. van Moll 2005) we also expressed our findings in terms of the number and share of km squares (1 km^2) containing one or more occupied main setts. The significance of observed differences between the 1994-1996 and the 2019-2020 surveys was determined with chi-quadrat tests per region and for the Veluwe region as a whole. Significances were denoted with $_*$ and $_{***}$ for, respectively, P<0.10 and P<0.01.

Table 1. Precipitation and average daily temperature (meteorological station De Bilt) during the autumn-winter season (September-February) and the spring-summer season (March-August) during years in which the surveys were conducted.

Winter, summer	Precipitation (mm)		Temperature (°C)	
	Winter	Summer	Winter	Summer
1993-1994, 1994	n.a.[a]	447	n.a.	13.7
1994-1995, 1995	650	337	8.2	13.7
1995-1996, 1996	252	207	5.6	12.1
2018-2019, 2019	n.a.	423	n.a.	14.3
2019-2020, 2020	585	308	8.6	14.3
Normal winter, normal summer[b]	445	391	7.0	13.3

[a]not applicable
[b]1981-2010

Unfortunately we did not get permission to visit and check setts in the National Park Hoge Veluwe (Central Veluwe, 55 km squares), the military training grounds of 't Harde (Central Veluwe, 20 km squares) and De Harskamp (Central Veluwe, 14 km squares), the private Deelerwoud (Repelaer) Estate (Central Veluwe, 6 km squares) and the Salentein Estate (Peripheral Veluwe, 2 km squares). These omitted km squares represented 8% of the Central Veluwe and less than 0.2% of the Peripheral Veluwe.

Due to their laboriousness, region-wide surveys can only be carried out periodically. Therefore, collected data are based on snap shots and can be affected by weather-induced factors, bearing in mind that even a main sett might be temporarily left during dry and hot summers. For this reason the checking of badger setts has been carried out entirely outside the summer-season. Therefore, the combination of high temperatures and droughts as, for instance, in the summer of 2020 (table

Table 2. Number of main setts of badgers in the Veluwe region occupied in 1994-1996 (van Apeldoorn et al. 1997, van Moll 1999), newly discovered and re-occupied in 1997-2020, occupied in 2019-2020 and abandoned between 1994-1996 and 2019-2020.

Region	Sub-region[a]		Old surveys 1994-1996	Newly discovered and re-occupied 1997-2020	Present survey 2019-2020	
	Name	Total km²	Occupied setts	Occupied setts	Occupied setts	Abandoned setts
Central Veluwe	Enclave	39	31	0	24	7
	Southwest Veluwe	104	24	6	27	3
	Remainder Central Veluwe	1003	397	5	209	193
	Sub-total	1146	452	11	260 ***	203
Peripheral Veluwe	Gelderse Valley	351	107	13	83	37
	Northwest Veluwe	238	22	2	22	2
	IJssel Valley	449	84	23	75	32
	Sub-total	1038	213	38	180 *	71
TOTAL		2184	665	49	440 ***	274

[a]see figure 1 for exact locations

1) will not have affected our findings.

We had access to a subset of nine main setts situated around the village of Buurlo in the Central Veluwe, that has been surveyed annually between 1980 and 2020 in a similar way. This subset was used to test whether the observed changes could have been coincidental or reflecting a consistent trend. Regression analysis was used to assess the significance of observed changes around Buurlo.

Results

A map showing the checked setts (figure 1) indicates that the occupation status has changed considerably. Particularly in the Central Veluwe many of the once occupied main setts were abandoned in 2019-2020, but less so in the subregions Enclave and Southwest Veluwe. The decline of occupied setts also occurred in the Peripheral Veluwe, however. Of the 665 setts that qualified as occupied main setts in 1994-1996 a total of 274 appeared to be abandoned in 2019-2020. This loss was compensated by in total 49 main setts that were either re-occupied (3) or discovered (46). The latter occurred particularly in the IJssel Valley (table 2). The relative net loss amounted to 42% in the Central Veluwe and 15% in the Peripheral Veluwe. An annual survey of 9 setts around Buurlo (Central Veluwe) shows a consistent downward trend ($P<0.05$) over time (figure 2) and suggests that the observed decline in the Veluwe region as a whole is not just determined by two arbitrary points in time as implied by figure 1. The reduction of the number of setts was accompanied by a reduction of the number of occupied km squares, absolute losses being greatest and significant ($P<0.01$) in the Central Veluwe (table 3). Relative losses amounted to 33% in the Central Veluwe and 6% in the Peripheral Veluwe. Nevertheless, the share of occupied km squares remained slightly higher in the Central Veluwe than

Table 3. Number of km squares with main setts of badgers in the Veluwe region occupied in 1994-1996 (van Apeldoorn et al. 1997, van Moll 1999), newly occupied and re-occupied in 1997-2020, occupied in 2019-2020 and abandoned between 1994-1996 and 2019-2020.

Region	Sub-region[a]		Old surveys 1994-1996	Newly discovered and re-occupied 1997-2020	Present survey 2019-2020	
	Name	Total km^2	Occupied km squares	Occupied km squares	Occupied km squares	Abandoned km squares
Central Veluwe	Enclave	39	22	0	18	4
	Southwest Veluwe	104	23	6	26	3
	Remainder Central Veluwe	1003	296	3	185	114
	Sub-total	1146	341	9	229 ***	121
Peripheral Veluwe	Gelderse Valley	351	82	11	72	21
	Northwest Veluwe	238	18	2	16	4
	IJssel Valley	449	70	22	71	21
	Sub-total	1038	170	35	159 *	46
TOTAL		2184	511	44	388 ***	167

[a]see Figure 1 for exact locations

in the Peripheral Veluwe. Within the Central Veluwe region the Enclave and Southwest Veluwe were least affected (table 4). The share of occupied km squares containing just one main sett increased from 78% to 88% (table 5). Most setts had four used entrances or less. Small setts seemed, on average, as often abandoned as the larger setts (table 6).

Discussion

General

Comparison of the 2019-2020 survey and the 1994-1996 survey indicates that the number of occupied main setts, the number of occupied setts per occupied km square, and the number of occupied km squares has declined drastically during the last 25 years, particularly in the Central Veluwe. The risk of becoming abandoned appeared as great for setts with many open entrances as for setts with fewer entrances, considering the comparable shares of large setts among both occupied and abandoned setts in the 2019-2020 survey. However, entrances of abandoned setts may partly have collapsed in the course of years and the number of entrances can thus initially have been greater. That could mean that the true share of large setts has been greater among abandoned setts than among setts that are still occupied, implying that it is not the marginal sett that is particularly at risk of becoming lost. The fraction of km squares with at least one occupied main sett in the Veluwe region as a whole dropped from, on average, 0.23 in 1994-1996 to 0.18 in 2019-2020. Note that this is much lower than the 0.40 reported by van Moll (1999) for 1995-1996. However, van Moll expressed the occupation of km squares as a fraction of the cells with habitat that he considered suitable, whereas we expressed it as a fraction of the total area. Our analysis shows that the number of occupied main setts has decreased slightly more than the number of km squares with an occupied main sett. The vast majority of occupied km squares con-

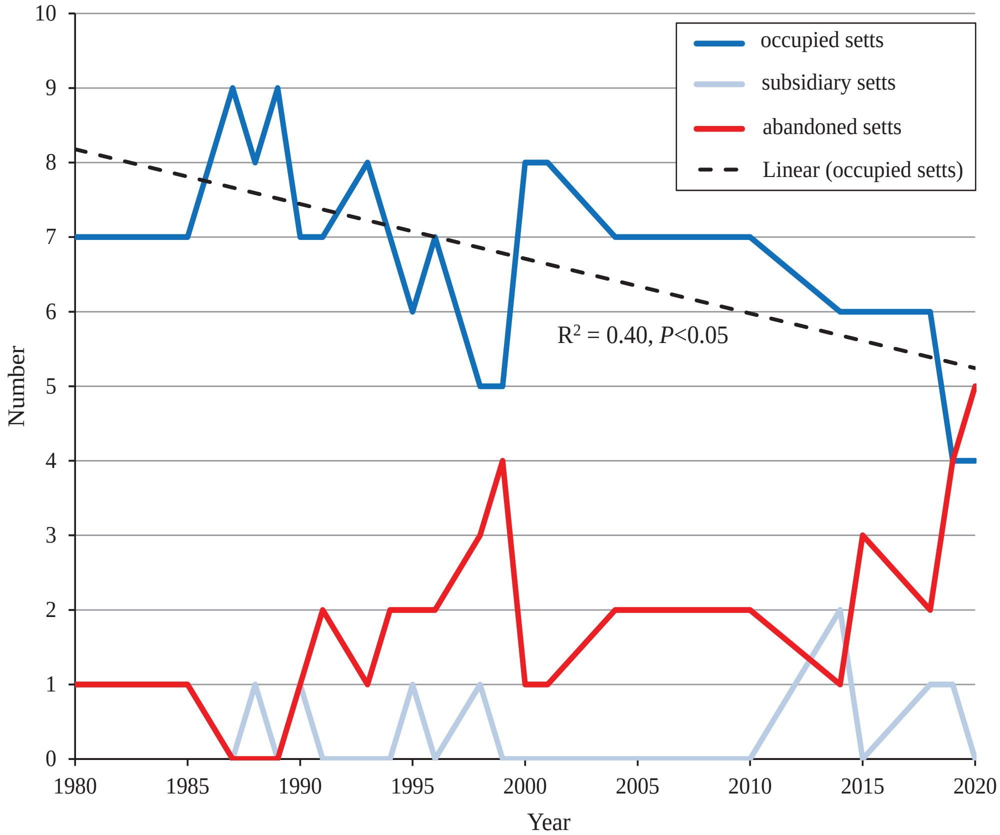

Figure 2. Long-term monitoring of the typology of nine setts around Buurlo, Central Veluwe.

tained only one occupied main sett nowadays as was the case 25 years ago, suggesting that the size of a badger territory in the Veluwe region was and still is generally at least 100 hectares and often more. That confirms what Mulder et al. (2015) consider typical for drier environments. Abandonment of initially occupied setts was slightly compensated by the discovery of setts that were not known before. Theoretically, these newly discovered setts might have been already existing 25 years ago. In that case the relative declines are even greater. Surely there must have been some main setts in 1994-1996 that have not been discovered until the present day, implying that the true relative declines are smaller rather than greater. However, this error is probably very small, bearing in mind the dense network of dedicated observers in the Veluwe region who all submit their findings to the database of Das & Boom.

The observed changes call for a closer look at possible explanations and measures to stop the decline. As for explanations, the availability of food, the accessibility of food sources, disturbance and non-natural mortality seem potential factors. The following sections explain why some of these factors may have had a greater negative impact in the Central Veluwe than in the Peripheral Veluwe. As for the measures, it must be emphasised that interventions favouring one aspect, in this case the wellbeing of badgers, are not necessarily in favour of other biota or welcomed by other land users (e.g. Schröder et al. 2020). Decisions on measures are, as such, nothing but a matter of political preferences.

Table 4. Fraction of km squares containing one or more occupied badger setts in 1994-1996 (van Apeldoorn et al. 1997, van Moll 1999) and in 2019-2020, and the relative change (%) over time.

Region	Sub-region[a]		Fraction of occupied km squares in:		Relative change over time (%)
	Name	Total km^2	1994-1996	2019-2020	
Central Veluwe	Enclave	39	0.56	0.46	-18
	Southwest Veluwe	104	0.22	0.25	-14
	Remainder Central Veluwe	1003	0.30	0.18	-40
	Sub-total	1146	0.30	0.20	-33
Peripheral Veluwe	Gelderse Valley	351	0.23	0.21	-9
	Northwest Veluwe	238	0.08	0.07	-13
	IJssel Valley	449	0.16	0.16	0
	Sub-total	1038	0.16	0.15	-6
TOTAL		2184	0.23	0.18	-22

[a]see Figure 1 for exact locations

Availability of food

Analysis of the content of stomachs and excrements reveals that the diet of badgers in the Netherlands consists for at least one third of earthworms, surface dwelling *Lumbricus* spp. in particular (Wansink et al. 1995, Mos et al. 2014, van Bommel et al. 2015). Because of this preference for earthworms, badgers tend to live close to agricultural land (Kruuk 1989). One hectare of grassland may contain around 700 kilograms of earthworms. The supply in arable land is often 80% less (Mos et al. 2014, van Eekeren et al. 2014). In forests the relative presence may even be 90% less, whereas earthworms are virtually absent under heather. The dependence on earthworms puts the forested Central Veluwe hence *a priori* in a disadvantaged position. Awaiting the results of an ongoing survey in various kinds of habitats across the Netherlands (Rutgers et al. 2009), it is yet unclear whether and where earthworm densities have declined over the past few decades. Such a decline cannot be fully ruled out as earthworms are sensitive for drought, heavy metals, organic micro-pollutants, veterinary medicine residues, acidification and a low base saturation of the soil adsorption complex (Butter 1990, Ma 1990, Kerkhofs et al. 1993, Klok et al. 1998, Klok 2004, Rutgers et al. 2008, van Eekeren et al. 2008, Usmani & Kumar 2015, Lahr et al. 2017, De Vries et al. 2019). As for the incidence of droughts it must be noted that the precipitation deficit between April and September has increased by, on average, 86 mm from 2000 to 2019 but not yet statistically significant due to considerable differences between separate years (KNMI 2020). In dry soils earthworms withdraw to deeper layers and may thus have become less available for badgers, particularly where soils tend to dry out easily as when soils are sandy.

Table 5. Distribution (%) of the number of occupied setts per occupied km square in 1994-1996 (van Apeldoorn et al. 1997, van Moll 1999) and in 2019-2020.

	Number of occupied setts	Old surveys 1994-1996	Present survey 2019-2020
Km squares with	1	78	88
	2	17	11
	3	3	1
	4	2	0

Table 6. Share (%) of setts with five or more open entrances in the 2019-2020 survey.

Region	Sub-region[a]	Share (%) of setts with 5 or more entrances used	
		Occupied setts	Abandoned setts
Central Veluwe	Enclave	54	29
	Southwest Veluwe	78	50
	Remainder Central Veluwe	22	32
	Sub-total	30	32
Peripheral Veluwe	Gelderse Valley	43	47
	Northwest Veluwe	28	50
	IJssel Valley	47	19
	Sub-total	43	35
TOTAL		35	33

[a]see Figure 1 for exact locations

The acidification of soils in the Netherlands still goes on, be it slowly, despite the drop in acidifying atmospheric deposition (Compendium voor de Leefomgeving 2020).

The presence of earthworms is not only determined by the above factors but as much by the provision of organic matter through crop residues and manures (Blakemore 2018, Onrust & Piersma 2019, Ros et al. 2020). Earthworms need something to eat, after all. The application of manure on sandy soils in the Netherlands has dropped by 15% between 2000 and 2015 (CBS Statline 2020a, Schröder & Neeteson 2008, CDM 2017). The lower input of organic matter might have had a negative effect on the presence of earthworms in arable land in particular. The provision of organic matter is less of a limiting factor in grassland due to the inherently extensive turn-over of grass roots, but even there inputs of organic matter through manuring stimulate the presence of earthworms (Onrust et al. 2019). Other management factors of grassland may have an impact on the availability of earthworms for badgers as well. It is much easier for badgers to acquire surface dwelling earthworms in short swards, as is the case when grasslands are regularly grazed. The extent to which grasslands are grazed instead of cut, has decreased. Consequently, the amount of dung pats per hectare in Gelderland has also dropped by circa 60% in between 2000 and 2015 (CBS Statline 2020b). Dung pats are appreciated by badgers as a source of earthworms and insects (Roper 2010).

Less grazing means that a greater share of the excrements is collected indoors and mechanically applied as slurry. From the late 1990s this slurry must be applied by injection into the grassland sods or top soil. Research has indicated that injection is not more harmful to earthworms than the former surface application of slurry (Huijsmans et al. 2008, Thissen 2018, Ros et al. 2020). The type of manure, however, is quite decisive as the input of organic matter per unit plant nutrient is much greater in farmyard manures than in slurries (den Boer et al. 2012, Onrust & Piersma 2019, Ros et al. 2020). The almost full transition from farmyard manure-based systems to slurry-based systems was already completed in the 1970s, however, and this disqualifies the abandonment of farmyard manure as an explanation for the recent decline of the number of occupied badger setts in the Veluwe region.

Until the beginning of this century badgers will undoubtedly have benefited from feeding practices of gamekeepers in the Central Veluwe in support of red deer and wild boar. This complementary feeding has been legally banned now. The summer population of wild boar has nevertheless almost doubled between 1995 and 2019 and amounts to almost four times more than the official management target (Spek 2019). It cannot be ruled out that badgers living in forested areas such as the Central Veluwe have to compete with wild boars for the same sources of food (Massei et al. 1996, Payne et al. 2013, Groot Bruinderink 2016, La Haye & Vink 2016). It is noteworthy that the Southwest Veluwe, a region just as forested as the remainder of the Central Veluwe but where wild boars are banned, shows no decline in the number of badger setts. This observation may serve as circumstantial evidence for the negative impact that wild boars may have.

From the above observations several interventions can be inferred to improve the food supply for badgers. Liming of soils may improve the living conditions for earthworms and soil fauna in general (Springett & Syers 1984). Similar results were recently obtained with high dose applications of ground stone meal (de Vries et al. 2019). More attention is also needed for the addition of organic matter to arable land. This can increase the presence of earthworms as well, particularly in combination with reduced tillage (Briones & Schmidt 2017). The availability of food for badgers is also enhanced by substituting grazing for cutting and farmyard manure for slurry. Halting the conversion of manured grassland to completely unfertilised 'natural' grassland, a conversion advocated in favour of the botanical diversity, can understandably also have a positive effect on the food supply for badgers. Last but not least, it seems plausible that a more stringent control of the numbers of wild boar might also improve the carrying capacity of the Central Veluwe for badgers.

Accessible hectares

Total food supplies are not just determined by the food supply per hectare but also by the total number of hectares and, obviously, their

Figure 3. PVC tube, 0.3 m diameter, across a fence enabling badgers to visit their feeding grounds. *Photo: Hans Vink.*

accessibility. The area under agriculture in the Veluwe region decreased by 5% (42 km^2) between 1996 and 2015, mainly in favour of the area devoted to roads, buildings and recreation (CBS Statline 2021a). The return of the wolf (*Canis lupus*) to the Veluwe from 2018 (Lelieveld et al. 2021) and the official designation of most of the Central Veluwe as a wolf area may further limit the accessibility of the remaining grassland for badgers now that farmers install wolf-averting fences in addition to wild boar-averting fences. These measures are unnecessarily denying badgers access to feeding grounds unless fences near setts would from now on be perforated with 0.3 m wide tubes (figure 3) allowing only badgers to pass. Accessibility of additional food sources can of course also be improved by the provision and maintenance of sufficient cover by hedgerows and re-wilded field edges.

The accessibility of food might also have been deteriorated by a greater human disturbance. Recreation pressure in the Central Veluwe has increased considerably during the last 25 years (e.g. Bijlsma 2006, Provincie Gelderland 2017). This may have had a negative effect on the required peace and quietness near some of the setts and the routes of the badgers to their feeding grounds, especially at the borders of the Central Veluwe where recreational activities tend to concentrate and during summer when the time window for

Badger cubs. *Photo: Michiel Schaap*.

feeding in the dark is short. Awareness about it has recently lead to the intended decision to divert recreation from particular areas in the Veluwe region (Provincie Gelderland 2020b).

Disturbance and non-natural mortality

Traffic is still the major cause of mortality among badgers in the Netherlands (Dekker & Bekker 2010, Mulder et al. 2015). Traffic intensity increased by 13% in the province of Gelderland between 2000 and 2019 (Provincie Gelderland 2020a). Construction of new fauna passages and the maintenance of existing ones is therefore needed more than ever, as well as a decision to limit the permitted speed during nightly hours wherever relevant. Note that such measures become more urgent once food supplies diminish. Badgers have to increase their home range then and may have to cross more roads than before to take-in sufficient food.

The survival rate of badgers is of course also served by adequate control of illegal prosecution. There is a growing resentment among farmers that they have to adjust their management for the sake of nature conservation. Unfortunately, badgers and the damage they inflict to crops have become one of the symbols of this societal pressure in some regions (Thissen et al. 2020). This may particularly pertain to regions where farming and nature conservation are competing for space, such as in the Veluwe region.

Conclusion

The number of occupied badger setts in the Veluwe region has declined by 42% in the Central Veluwe during the last 25 years and by 15% in the Peripheral Veluwe. This development may result from a decrease of food supplies and accessibility of these supplies.

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Samenvatting

Afname van de dassenpopulatie op de Veluwe en de mogelijke oorzaken

Uit inventarisaties blijkt dat het aantal belopen dassenburchten op de Veluwe in de afgelopen 25 jaar met 42% is gedaald in de Centrale Veluwe (192 burchten minder) en met 15% aan de randen van de Veluwe (33 burchten minder). Dit gaat zo goed als zeker gepaard met een proportionele afname van het aantal dassen. Tegelijkertijd daalde het aantal bezette kilometerhokken met 33% (112 minder bezette hokken) in de Centrale Veluwe en met 6% (11 minder bezette hokken) aan de randen van de Veluwe. Deze afnames houden mogelijk verband met een afname van het voedselaanbod en de toegankelijkheid van voedselbronnen. Een aantal factoren die dit beïnvloeden, zijn zowel in de Centrale Veluwe als in de randen van de Veluwe aan de orde. Echter, periodieke droogte, mogelijke voedselcompetitie tussen dassen en zwijnen, de omvang en toegankelijkheid van bemeste graslanden en plaatselijke recreatiedruk, hebben waarschijnlijk een sterker negatief effect gehad in de Centrale Veluwe dan in de randen. Het artikel stelt maatregelen voor waarmee de daling van het aantal belopen burchten en hun bewoners kan worden gestopt.

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Cetaceans stranded in the Netherlands in 2015-2019

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Abstract: This report presents a validated list of stranded cetaceans in the Netherlands, as well as some cetaceans accidentally brought in on ship bulbs, between 2015-2019. During this period 2701 cetaceans representing eleven species were reported. The list also includes a few bones and skulls, among others of killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*), species not reported otherwise during this period. The most common species was harbour porpoise (*Phocoena phocoena*), with 2651 individuals. The average number of porpoises per year was 530, lower than the preceding seven-year average, but numbers fluctuated largely between years and there has been no particular trend after the strong increase in the early 2000s. The monthly pattern of strandings as recorded during the previous periods, with peaks in March and July-September, remained the same. The number of stranded porpoise is equally spread along the entire coastline. The density, expressed as the number of stranded porpoise per kilometre per year, is 0.6 for the entire coastline, or 1.2 if the extensive and less well surveyed areas of Western Scheldt, Eastern Scheldt and Wadden Sea proper are omitted. Sex ratio remained stable over the years and is in line with results from before 2015, with a preponderance of males. On the basis of length, over half were immature and 8.7% neonate. Among neonates and immatures there was a preponderance of males as well, but not in adults. In the Wadden Sea area more neonates and adults were found than in the other two subareas. The major cause of death was infectious disease, followed by predation by grey seal (*Halichoerus grypus*). Accidental by-catch was identified as the cause of death of 11% of the stranded animals. Of particular interest was the stranding of six sperm whales (*Physeter macrocephalus*) in January 2016, the largest stranding event of this species in the Netherlands. It was part of a stranding event spread out over the Central and southern North Sea, involving thirty individuals. During 2015-2019 four dead fin whales (*Balaenoptera physalus*) and eight minke whales (*B. acutorostrata*) were reported, several of which were hit by ships. There seems to be a slight increase in the strandings of fin whale and Sowerby's beaked whale (*Mesoplodon bidens*) since 2000, while white-beaked dolphin (*Lagenorhynchus albirostris*) shows a decrease. There is no temporal trend for any of the other species since 2000.

Keywords: Cetacea, harbour porpoise, *Phocoena phocoena*, sex bias, mortality, ship collision, North Sea.

Introduction

There has been an increasing interest in cetaceans in the North Sea over the past decades. For instance, three complete censuses, SCANS I, II and III, were executed (Hammond et al. 2002, 2013, 2017) and desk studies were performed to put these in a larger perspective, for instance for identifying areas of importance to cetaceans and human resources (Waggit et al. 2019). Also in the Dutch section of the North Sea, attention to cetaceans and other marine life has increased (e.g. Autenrieth et al. 2017, Foster et al. 2019) and national surveys are nowadays undertaken on a more or less regular basis (e.g. Scheidat et al. 2013, Aarts et al. 2016, Geelhoed & Scheidat 2016). Most of these are directed towards monitoring of populations as a basis for conservation. Focal species usually concerns harbour porpoise (*Phocoena phocoena*). However, surveys are costly, as they are often dedicated multi-day ship-based operations or aerial surveys, and/or require expensive equipment. A cost-effective way to monitor harbour porpoise presence, as well as that of other species, is the registration of stranded animals. It is difficult to understand how the number of animals on the beach relates to the population and there are several factors complicating the interpretation of rising and falling numbers (Peltier et al. 2013). Numbers however can be considered as relative counts and fluctuating numbers may be used as a proxy for local population trends.

Here we present numbers of stranded cetaceans on the Dutch coast, and of cetaceans brought in on the bulb of ships, from 2015 up to and including 2019. This report is the fourtieth in a series on cetacean strandings in the Netherlands over multiple years (e.g. van Deinse 1933, Husson & van Bree 1972, Camphuysen et al. 2008) and follows on that by Keijl et al. (2016), who reviewed seven years of strandings. Even though the above mentioned interest in whales and dolphins in the North Sea has resulted in a growing number of sightings of live animals, the rare species remain unrecorded during censuses. Documenting strandings appears to be the only way to record their presence (cf. Pyenson 2011) and therefore this list includes all records of cetaceans, also finds of loose bones and skulls.

A change in numbers of strandings of a particular species can be an indication of a shifting range, for instance due to changing conditions. There are aspects of cetacean ecology that can only be studied when the animals are dead, such as pregnancy rate, disease or diet. The Netherlands have ratified the Habitats Directive as well as the Marine Strategy Framework Directive and is thus obligated to maintain a favourable conservation status of the smaller cetacean species. Given the increasing human use of the North Sea, for instance for wind and solar energy production, it is expected that pressure on cetacean populations will increase.

The harbour porpoise is the most common Dutch cetacean, with hundreds of strandings per year, compared to a few individuals of any other species. The number of dead porpoises on the Dutch coast has increased from 53 in 1990 to 888 in 2011, the latter figure being the highest number recorded thus far. Since then, the number has decreased to a couple of hundred per year. Despite the impressive increase in elaborate and dedicated studies (e.g. Blom 1989, Addink et al. 1995, Addink & Smeenk 1999, ASCOBANS 2005, Murphy et al. 2010, Camphuysen & Siemensma 2011, Jansen 2013, Scheidat et al. 2013, Leopold 2015, Gilles et al. 2016, Hammond et al. 2017), it is still unknown what caused the fall and rise in numbers of porpoises in the southern North Sea in the 1950s and 1990s respectively.

In the following, all cetacean strandings are listed individually, with the exception of harbour porpoise. Although more details may be available on www.walvisstrandingen.nl, where peculiarities are mentioned on single animals, this multi-year overview aims at giving insight in changes that have occurred over the recent past, something that cannot be obtained by scrolling through individual cases. For general information on distribution, diet, habitat, biology and trends in strandings of cetaceans in the Netherlands up to 2012, we refer to Broekhuizen et al. (2016).

Methods

Methods for collecting data on strandings are the same as mentioned in the previous report (Keijl et al. 2016). People involved in the strandings network collect and report strandings of seals and cetaceans directly to www.walvisstrandingen.nl, to www.waarneming.nl or to Sealcentre Pieterburen. Reports are also received from day visitors. Data are stored in the national database and made available online at www.walvisstrandingen.nl, managed by Naturalis Biodiversity Center in Leiden.

The data in this report are presented per species; the taxonomic order and nomenclature follows Wilson and Reeder (2005), with the exception of *Balaenoptera* instead of *Megaptera* for humpback whale (following Sasaki et al. 2005, Miller 2007 and Árnason et al. 2018) and *Leucopleurus* instead of *Lagenorhynchus* for white-sided dolphin (following LeDuc et al. 1999 and May-Collado & Agnarsson 2006). Details are presented for all species with the exception of harbour porpoise, for which the data are summarised and analysed (table 1). Baleen whales caught on the bulb of ships and brought into Dutch waters are included in the report, as well as finds of loose bones of species other than harbour porpoise, as long as these cannot be linked to another strandings case.

It has been convention in previous reports to mention additions, omissions, misidentifications et cetera from the past. This has proven unfeasible; corrections on strandings in the near or far past are updated continuously. For the most recent situation on a precise number of a particular species, correct identification, or other information of individual specimens, it is recommended to consult www.walvisstrandingen.nl, or contact the database manager at Naturalis.

Area

The Dutch coast consists entirely of sandy (bordering the North Sea) or muddy (Wadden Sea proper, some intertidal parts in the southwestern Delta) substrate, but there are some dikes and piers scattered along the coast. Patterns of stranded harbour porpoise are described for three parts of the coastline differing in physical characters (table 2): A. The Delta area, in the southwest, from the Belgian border up to and including Maasvlakte. B. The mainland coast between Hoek van Holland and Den Helder. C. The Wadden Sea, from Razende Bol to Rottumeroog. The 'inner Delta' includes the borders of the rivers Western Scheldt and the partly closed Eastern Scheldt and Grevelingenmeer. The Wadden Sea is subdivided into the North Sea coast of the islands and the Wadden Sea proper, the latter of which includes the Wadden Sea side of the islands, the north-eastern part of province Noord-Holland, Afsluitdijk and the mainland coast of the provinces of Friesland and Groningen. The islet of Razende Bol is combined with Texel (North Sea coast), Griend with Vlieland (Wadden Sea), and Engelsmanplaat with Schiermonnikoog (North Sea coast), while the easternmost islets of Rottumerplaat and Rottumeroog are combined to 'Rottum' (Wadden Sea). The length of the coast of the subareas is given in table 2. See Camphuysen et al. (2008) for a map.

Coverage

Coverage of the complete Dutch coastline was probably similar to that during the previous reporting period (2008-2014). On the North Sea beaches of the Delta and mainland coast coverage is expected to be close to 100%, but it is lower on the North Sea beaches of the Wadden Sea islands, especially outside weekends, holidays and in summer. The coverage of the extensive Inner Delta and the Wadden Sea is low, but unfeasible to estimate. In these areas, beached carcasses are found only by chance, illustrated by the fact that fresh harbour porpoise carcasses are reported from the same locations through the years, for instance near a main entrance to the beach, near an access road, or bordering a harbour.

Research

A number of cetaceans has been collected for research. Smaller individuals are usually transported to the Faculty of Veterinary Medicine of Utrecht University, where they are necropsied to establish the cause of death, while basic data such as sex and length are standard recordings. Large cetaceans are sometimes investigated on the beach or at a more suitable place nearby. About half of the specimens found during 2015-2019 were not necropsied, but were transported to a destruction site (see under respective species). Some skeletons, or parts (mostly skulls), are collected and stored in the collection of Naturalis Biodiversity Center in Leiden, at nature museum Ecomare on Texel, or at other natural history museums.

Systematic list

During 2015-2019 a total of 2701 stranded cetaceans were reported, involving eleven species (table 1). Two of these concern recent or subfossil bones (not included in table 1), one a single tooth of a sperm whale, while nine are recent cetaceans which could not be identified. All species had been recorded previously in the Netherlands. Since 1900 and excluding harbour porpoise, a total of 974 individual cetaceans belonging to 22 species have been found on Dutch shores (figure 1). In 2015 six species were recorded (one by a bone only), in 2016 five, in 2017 nine (one by a single bone only), and four in both 2018 and 2019. The majority of records however consists of harbour porpoise (2651 individuals, making up 98% of the total number of cetaceans in 2015-2019).

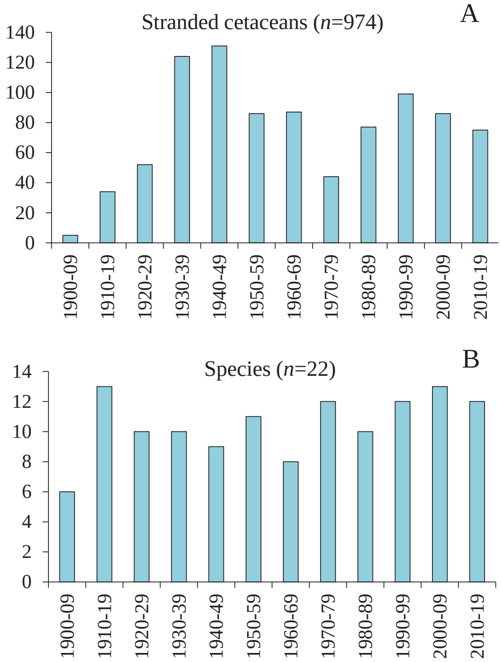


Figure 1. Number of all stranded cetaceans per decade since 1900 (A) and number of species per decade (B), both without harbour porpoise.

Common minke whale (*Balaenoptera acutorostrata*)

2015-2019: 8 records
2000-2014: 10 records
Before 2000: 27 records

7/11/2015 Rotterdam, Zuid-Holland. Female, 506 cm (measured), 910 kg (weighed). Fresh, complete. Skull, a few vertebrae, both flippers and remaining baleens collected (RMNH.5070448). Reported by J. van der Hiele and R. Duyndam. Necropsied by Utrecht University (case no. BA1).

12/12/2015 Razende Bol, Noord-Holland. Pregnant female, 880 cm (measured), 6400 kg (weighed). Rotten, complete. Fetus 200 cm (estimated). Entire skeleton and tissue collected (RMNH.5070317.a), fetus collected (RMNH.5070317.b). Reported by Hans Eelman and Bert Hollanders. Necropsied by Utrecht University (case no. BA2).

13/4/2017 Vrouwenpolder, Zeeland. Male, incomplete (skull 160 cm). Rotten. Not collected, not necropsied.

14/11/2017 Texel, Noord-Holland. Pregnant female, 700 cm (estimated). Rotten, head dam-

Table 1. Stranded cetaceans on the Dutch coast in 2015-2019, including unidentified species. The second last column gives the total per species in the past twenty years, the last column the average number per year. Five species reported in 2000-2014 but not during the last pentade, are presented in the lower part (in italics). Records of loose bones/skulls are excluded.

	2015	2016	2017	2018	2019	2000-2019	Average/ year 2000-2019
Common minke whale	2	-	4	-	2	18	0.9
Fin whale	1	-	1	-	2	15	0.8
Common dolphin	-	3	1	1	-	9	0.5
Long-finned pilot whale	2	-	-	1	-	6	0.3
White-beaked dolphin	-	-	1	-	1	58	2.9
Striped dolphin	-	2	1	-	-	6	0.3
Harbour porpoise	309	667	689	478	508	8962	448
Sperm whale	-	6	1	1	-	16	0.8
Sowerby's beaked whale	-	2	2	-	-	8	0.4
Unidentified Cetacea	0	3	-	0	5	28	1.4
Total	314	683	700	481	518	9126	
Humpback whale	-	-	-	-	-	6	0.3
Killer whale	-	-	-	-	-	1	0.05
Bottlenose dolphin	-	-	-	-	-	2	0.1
White-sided dolphin	-	-	-	-	-	4	0.2
Blainville's beaked whale	-	-	-	-	-	1	0.05

aged, not weighed. Fetus 170 cm (estimated). Complete skeleton (RMNH.MAM.60362.a), tissue (RMNH.MAM.60362.b), fetus skeleton (RMNH.MAM.60362.c) and fetus tail (RMNH.MAM.60362.d) collected. Reported by S. de Wolf and Rijkswaterstaat. Not necropsied.

9/12/2017 Zandvoort, Noord-Holland. Female. Rotten, incomplete (head missing), remainder 450 cm (estimated). Not collected, not necropsied. Reported by K. Kooimans and R. Noort.

12/12/2017 Neeltje Jans, Zeeland. Male, about 680 cm (measured), about 1900 kg (weighed). Rotten. Collected by Natuurhistorisch & Volkenkundig Museum Oudenbosch. Tissue sampled by Utrecht University (case no. BA3), no cause of death established due to the decomposition.

8/7/2019 Texel, Noord-Holland (figure 2). Female, 403 cm (measured), 530 kg (weighed). Fairly fresh, complete. Necropsied by Utrecht University (case no. BA4). Collected by Ecomare (no collection number yet). Reported by A. Oosterbaan.

9/7/2019 Schiermonnikoog, Friesland. Rotten, incomplete (head missing), remainder 350 cm (estimated). Nothing collected by institutions, but a single lower jaw of presumably this individual was found nearby by day visitors.

Despite being a regular inhabitant of the North Sea, minke whale is not recorded yearly on the beach. The species is fairly common in the northern part of the North Sea, especially in summer, but rare further south (Camphuysen & Smeenk 2016). However, the number of beached minke whales seems to be increasing (figure 3A).

Seven out of eight minke whales stranded during this period were sexed and only two

Table 2. Total number of harbour porpoise in 2015-2019 in the Netherlands per subarea. Also given are density (average density, *n*/km/year), percentage of males (with total number of sexed individuals between brackets), and age (as percentage per length class, in cm; see text). See also the Methods section for the geographic subdivision. Note: coastal length differs slightly from Keijl et al. (2016) because Grevelingenmeer and Haringvliet (both with 0 porpoises) are omitted.

	Total	Densitiy	% males (*n*)	<90 cm	90-130 cm	>130 cm	(*n*)
Delta (408 km)	868	0.4	58.9 (643)	15.0	51.8	33.2	(247)
Zeeuws-Vlaanderen	31	0.4	55.0 (20)	0.0	50.0	50.0	(8)
Walcheren	273	1.3	58.8 (228)	12.7	47.3	40.0	(55)
Schouwen	172	1.4	61.9 (139)	12.2	51.0	36.7	(49)
Goeree	158	1.8	51.2 (86)	13.3	64.4	22.2	(45)
Voorne	35	0.8	78.3 (23)	30.8	15.4	53.8	(13)
Inner Delta	126	0.1	54.3 (94)	21.7	63.0	15.2	(46)
Maasvlakte	73	0.8	66.0 (53)	12.9	41.9	45.2	(31)
Mainland coast (153 km)	914	1.2	54.7 (512)	12.4	57.3	30.2	(354)
Zuid-Holland	510	1.4	54.4 (338)	12.7	60.8	26.5	(204)
Noord-Holland	404	1.0	55.2 (174)	12.0	52.7	35.3	(150)
Wadden Sea total (384 km)	869	0.5	62.4 (263)	10.9	55.6	33.5	(495)
North Sea coast (107 km)	745	1.4	61.5 (218)	10.5	55.6	23.9	(446)
Texel	210	1.3	56.9 (109)	15.8	53.3	30.9	(152)
Vlieland	276	1.9	64.7 (17)	4.9	56.8	38.4	(185)
Terschelling	96	1.7	65.5 (29)	9.4	53.1	37.5	(32)
Ameland	107	1.3	59.1 (44)	15.4	53.8	30.8	(52)
Schiermonnikoog	56	0.6	84.2 (19)	12.0	68.0	20.0	(25)
Wadden Sea (277 km)	124	0.1	66.7 (45)	14.3	55.1	30.6	(49)
Texel	27	0.2	71.4 (14)	14.3	64.3	21.4	(14)
Vlieland	6	0.1	100.0 (2)	0.0	50.0	50.0	(4)
Terschelling	23	0.2	54.5 (11)	0.0	50.0	50.0	(8)
Ameland	4	0.0	66.7 (3)	0.0	33.3	66.7	(3)
Schiermonnikoog	8	0.1	100.0 (2)	66.7	33.3	0.0	(3)
Rottum	18	0.4	- (0)	0.0	0.0	100.0	(1)
Noord-Holland	3	0.0	100.0 (2)	-	-	-	(0)
Friesland	22	0.1	42.9 (7)	16.7	58.3	25.0	(12)
Groningen	13	0.0	75.0 (4)	25.0	75.0	0.0	(4)
Total (945 km)	2651	0.6	58.0 (1418)	13.5	55.3	23.9	(1096)

were male. Of the four females investigated, two were pregnant. Two out of eight were fresh or fairly fresh when stranded, indicating that they had died in the vicinity of the Dutch coast. Out of the six that were (partly) investigated, two had likely been hit by a ship, and one had a broken back, although whether this had happened *post mortem* could not be established. The minke whale from 8 July 2019 had scoliosis (figure 2).

Fin whale (*Balaenoptera physalus*)

2015-2019: 4 records
2000-2014: 11 records

Figure 2. Common minke whale. Stranded on Texel, 8 July 2019. *Photo: Frouke Fey*.

Before 2000: 26 records

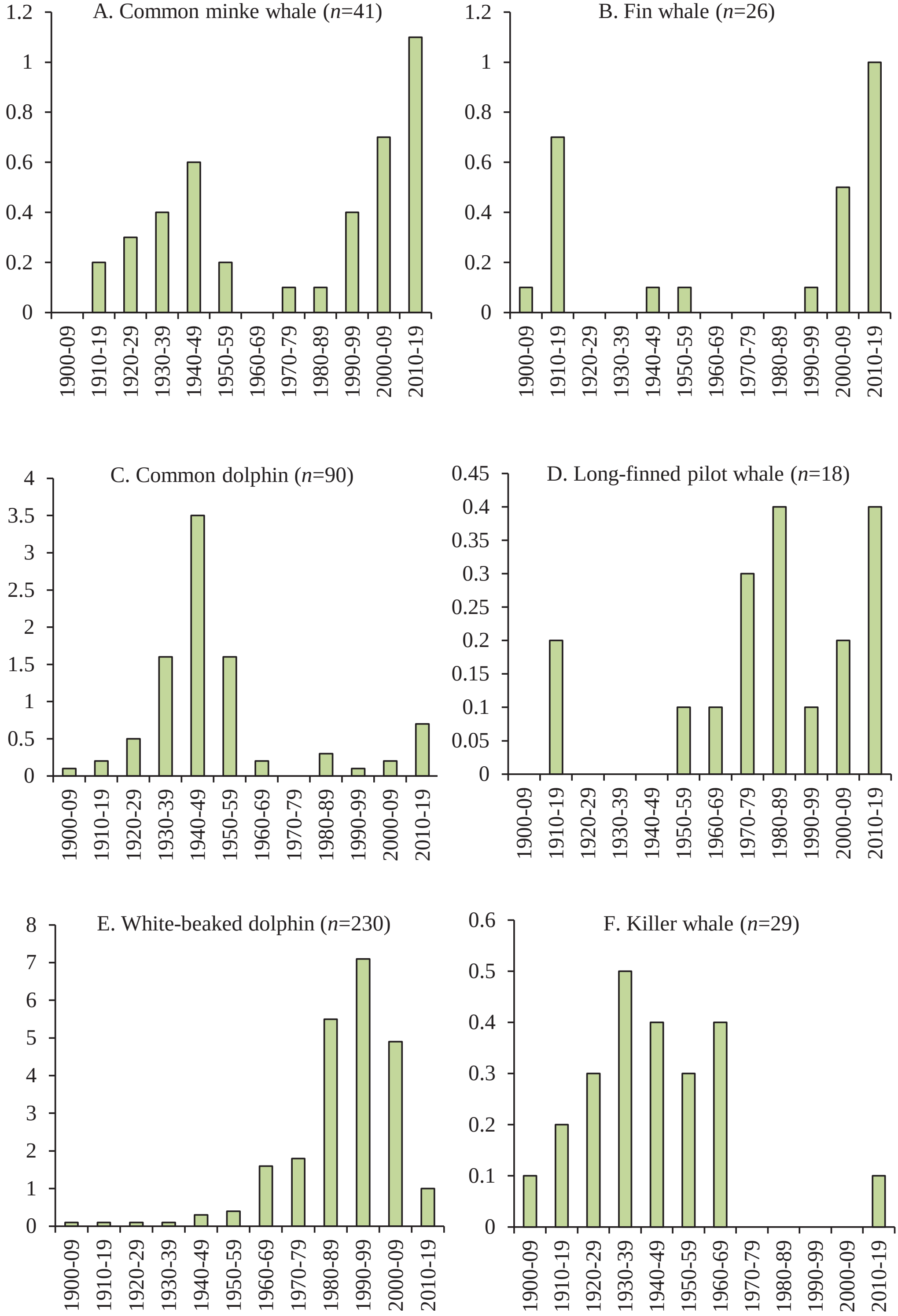
9/11/2015 Terneuzen, Zeeland. Male, 1160 cm (measured), 10,000 kg (weighed). Skeleton collected by the Faculty of Veterinary Medicine at Ghent University, Merelbeke, Ghent, Belgium. Reported by J. van der Hiele and R. Duyndam. Necropsied by Ghent University.

20/8/2017 Texel, Noord-Holland. Female, 1840 cm (measured). Complete skeleton collected by Ecomare, Texel (no collection number yet). Reported by Ecomare. Not necropsied.

7/6/2019 Vlissingen, Zeeland. Male, 1570 cm (measured), 16,000 kg (weighed), but part or most of abdominal organs missing. Not collected. Reported by J. van der Hiele. Necropsied by Utrecht University (case no. BP7).

10/9/2019 Ter Heijde, Zuid-Holland (figure 4). Female, 1440 cm (measured). Collected by Ecomare (baleens; no collection number yet) and Naturalis (bulla, hyoid, eye, left and right flipper, 1 scapula and tissue, RMNH.MAM.59671). Reported by K. Kooimans and R. Noort. Not necropsied.

Necropsy on the fin whale from June 2019 revealed that it was hit by a ship alive (IJsseldijk & Gröne 2019a). Even though only two out of the four fin whales were necropsied (Lempereur et al. 2017, IJsseldijk & Gröne 2019a), the other two were probably hit by a ship as well (see for instance Haelters et al. 2016 and figure 4). The same was suspected for all six fin whales found in 2008-2014 (Keijl et al. 2016). The fin whale that stranded on 20 August 2017 was recorded, and photographed, already on 7 August on a routine flight by the coast guard. It was floating in Dutch waters close to the British/Dutch border, almost 92 km west of The Hague, and as it posed no hazzard to ship traffic, it was left untouched. It was already discoloured and much of the skin was missing and it had thus been dead for several days. It was subsequently located and photographed from the air on four more days (Keijl 2017). At first, the carcass floated around in the same general area with an average speed of 3-6 km/day, but after 18 August it floated in a north-easterly direction with an average speed of 23 km/day, until it stranded on Texel two days later.


A. Common minke whale (n=41)
B. Fin whale (n=26)
C. Common dolphin (n=90)
D. Long-finned pilot whale (n=18)
E. White-beaked dolphin (n=230)
F. Killer whale (n=29)
1900-09
1910-19
1920-29
1930-39
1940-49
1950-59
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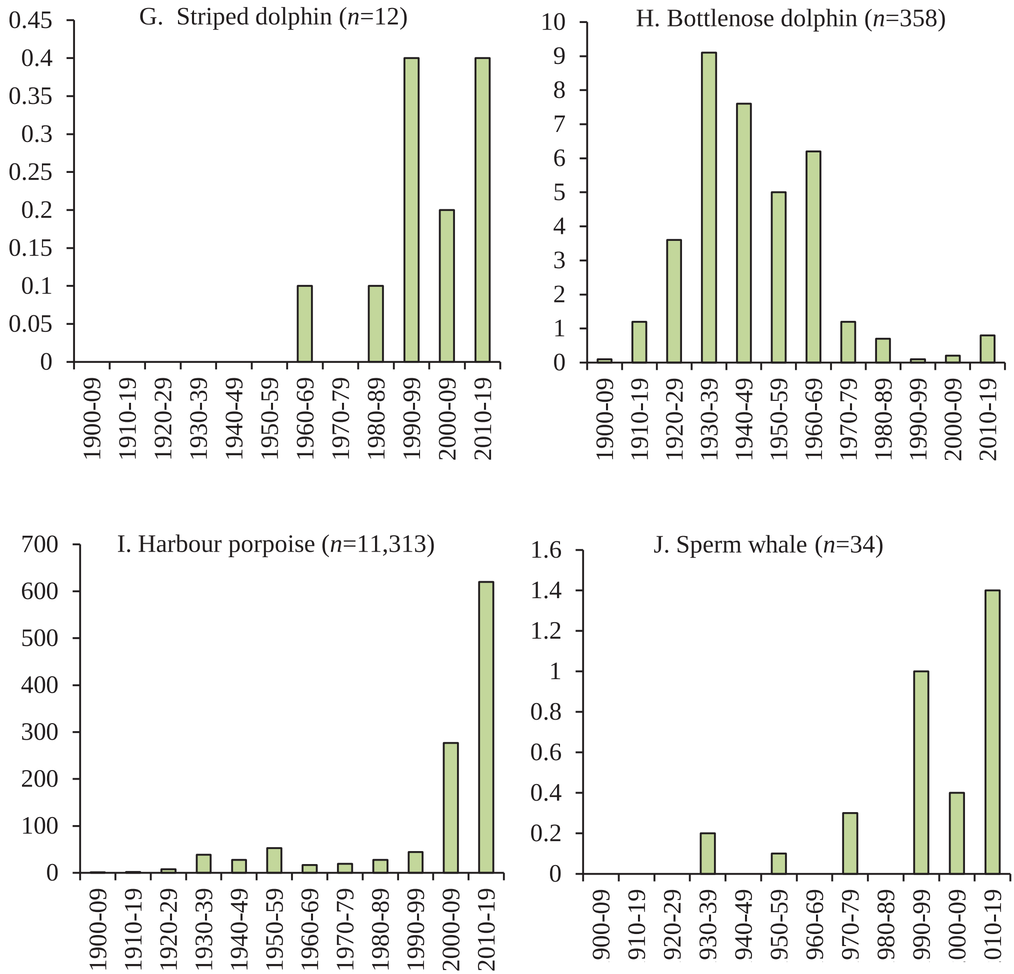
1990-99
2000-09
2010-19



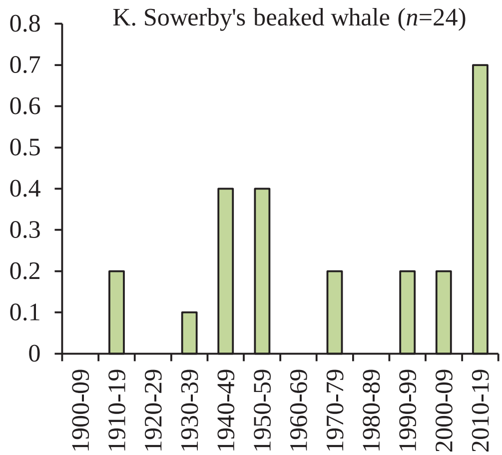


Figure 3A-K. Annual average number of stranded cetaceans per decade since 1900 for species found during 2015-2019.

Figure 4. Fin whale, Ter Heijde, 10 September 2019. *Photo: Rinus Noort*.

Numbers of stranded fin whales in the Netherlands are naturally low, since the species does not occur in the southern North Sea, but the number transported into the North Sea seems to be increasing (figure 3B). The graph of strandings shows a remarkable similarity to that of minke whale. The database contains 41 fin whale records, the oldest dating back to 1306. Between 1901-2000, there were eleven recordings (on average 1 per decade), with a peak in November, when six out of eleven were reported. Of these, four were found in 1914 and their death was ascribed to exploding sea mines (van Deinse 1915). From 2001-2010 there were five (0.5 per year), from 2011-2019 ten (1 per year). The monthly pattern seems to have shifted to the summer period, with five out of eleven strandings in August and another five in June and September combined (figure 5).

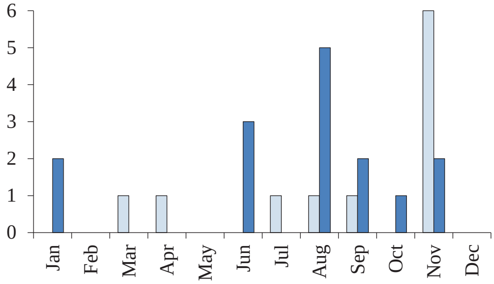


Figure 5. Strandings of fin whales per month in 1900-2000 (pale bars) and 2001-2019 (dark bars) in the Netherlands.

Common dolphin (*Delphinus delphis*)

2015-2019: 5 records
2000-2014: 4 records
Before 2000: 83 records

31/1/2016 Zurich, Friesland. No length reported. Fairly fresh, but washed away by the incoming tide. Reported by I. Ruivenkamp and M. Bakker Paiva. Not necropsied.

21/2/2016 Harlingen, Friesland. Female, 189 cm, 62 kg (but parts missing). Rotten. Entire skeleton collected (RMNH.MAM.60630). Reported by G. Hehenkamp and D. Visser. Not necropsied.

2/9/2016 Wassenaar, Zuid-Holland (figure 6). Male, 220 cm, not weighed, stomach contents

Figure 6. Common dolphin. Wassenaar, 2 September 2016. *Photo: Rinus Noort.*

collected. Skull and flipper collected (Utrecht University, collection number DD4). Reported by J. Warmenhoven and M. Groenenboom. Tissue sampled by Utrecht University (case no. DD4), no cause of death established due to the advanced state of decomposition.

11/4/2017 Nummer Eén, Zeeland. Female, 200 cm (estimated). Rotten. Skull, cervical vertebrae and flipper collected (RMNH.MAM.60364). Reported by P. Wolf. Tissue sampled by Utrecht University (case no. DD5), no cause of death established due to the advanced state of decomposition.

16/4/2018 Westenschouwen, Zeeland. Female, 154 cm (measured), 36 kg (weighed). Stranded alive, but died soon after. Skull collected (RMNH.MAM.60473). Reported by M. Henzel and L. Solé. Necropsied by Utrecht University (case no. DD6).

The stomach of the common dolphin from 2 September 2016 was filled with fish remains. The carcass was badly decomposed and it was impossible to establish the cause of death. The nature of the stomach contents suggests it had last fed in the southern British Channel or further south (M.F. Leopold & G.O. Keijl).

After a period of regular occurrence in the 1930s-1950s, common dolphin has become rare again in the North Sea (figure 3C).

Long-finned pilot whale (*Globicephala melas*)

2015-2019: 3 records
2000-2014: 3 records
Before 2000: 18 records (124 individuals)

11/1/2015 Hondsbossche Zeewering, Noord-Holland. Female, 417 cm (measured), 600 kg (weighed). Rotten, almost complete (fluke missing). Skeleton and tissue collected (RMNH.5069952). Reported by Van Oort/Boskalis and A. Gronert. Necropsied by Utrecht University (case no. GM2).

2/12/2015 Vlissingen. Male, 470 cm (measured), not weighed. Rotten, complete. Skull, cervical vertebrae, first and second ribs and hyoid collected (RMNH.MAM.60470). Reported by J. van der Hiele.

18/11/2018 Egmond aan Zee, Noord-Holland (figure 7). Male, 550 cm (measured), 2021 kg (weighed). Stranded alive, but died soon after. Skull and tissue collected (RMNH.MAM.59217). Reported by L. IJsseldijk. Necropsied by Utrecht University (case no. GM4).

Figure 7. Long-finned pilot whale. Egmond aan Zee, 18 November 2018. *Photo: Hans Verdaat*.

After some mass strandings in the nineteenth century, there have only been strandings of solitary animals. Between 1950 and 2019, there were on average 0.22 strandings per year; there were four strandings from 1981-1989, and only one from 1990-1999 (figure 3D).

The pilot whale that stranded in 2015 died due to asphyxiation after a common sole (*Solea solea*) had become stuck in its nasal cavity, similar to the one that stranded a month earlier (IJsseldijk et al. 2015). The animal stranded in 2018 had died as a result of infectious disease (IJsseldijk & Gröne 2019b).

White-beaked dolphin (*Lagenorhynchus albirostris*)

2015-2019: 2 records
2000-2014: 57 records
Before 2000: 173 records

8/12/2017 Wijk aan Zee, Noord-Holland. Male, 262 cm (measured), 280 kg (weighed). Fresh, complete, probably stranded alive. Collected by Het Natuurhistorisch (number 17-214). Reported by Ruud van Wilgenburg. Necropsied by Utrecht University (case no. LA10).

7/8/2019 Kijkduin, Zuid-Holland. Female, 234 cm (measured), 214 kg (weighed). Collected (RMNH.MAM.59788). Live stranded. Reported by SOS Dolfijn, K. Kooimans and R. Noort. Necropsied by Utrecht University (case no. LA11).

Two white-beaked dolphins in five years is a very modest number compared to former times, when sometimes up to 13 per year were reported. Between 1960-1980, the average number of stranded individuals rose above one per decade and was soaring to an average of almost seven per year between 1981-2000; in 2010-2019 it went back to one per year (figure 3E). A study on white-beaked dolphin strandings across the North Sea over a period of 27 years confirmed a northward shift, explained as a change in habitat due to climate change and its effect on distribution of prey (IJsseldijk et al. 2018a). See also MacLeod (2009) and Lambert et al. (2014) for more discussion on this issue and Schick et al. (2020) for causes of mortality of white-beaked dolphins in the southern North Sea.

Killer whale (*Orcinus orca*)

2015-2019: 1 record
2000-2014: 5 records

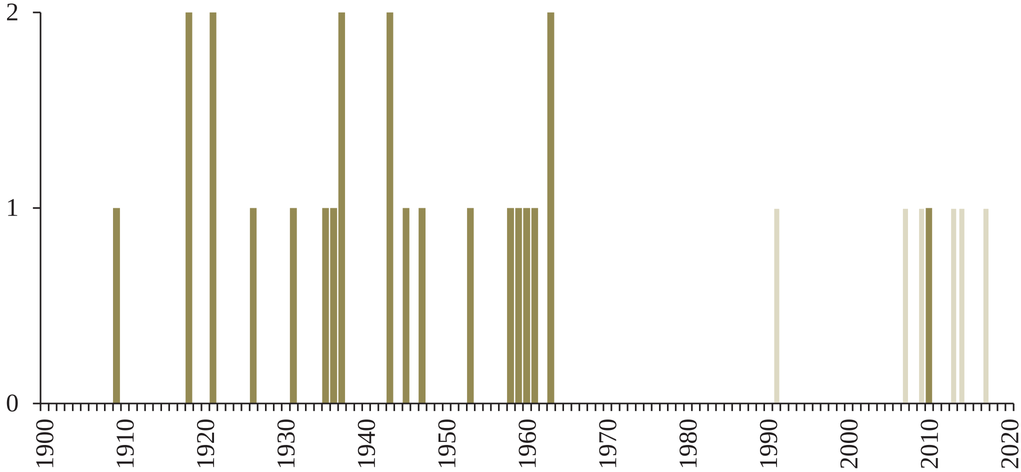


Figure 8. Strandings of killer whales (dark bars) and finds of bones (pale bars) in the Netherlands since 1900 (*n*=29).

Before 2000: 29 records

9/1/2017 Schiermonnikoog, Friesland. Part of skull. Reported by Thijs de Boer.

In the beginning of the twentieth century, some individuals apparently wandered south from the population present in the northern North Sea every now and then and got stranded in the Netherlands (figures 3f and 8). After the stranding in 1963 however, there has only been a single report, in 2010 (Keijl et al. 2016). All other records after 1963 refer to finds of bones or skulls only.

Striped dolphin (*Stenella coeruleoalba*)

2015-2019: 3 records
2000-2014: 3 records
Before 2000: 6 records

19/1/2016 Ameland, Friesland (figure 9). Female, 220 cm (measured), 120 kg (weighed). Lactating female, possibly stranded alive. Collected (no collection number yet). Reported by J. Krol. Necropsied by Utrecht University (case no. SC1).

19/1/2016 Ameland, Friesland. Female, 125 cm (measured), 29 kg (weighed). Female, possibly stranded alive. Skeleton collected (RMNH.5070365). Reported by J. Krol. Necropsied by Utrecht University (case no. SC2).

25/10/2017 Zoutelande, Zeeland. Female, 205 cm (measured), 77.5 kg (weighed, but incomplete). Rotten, virtually complete. Skeleton and tissue collected (RMNH.MAM.60361.a-b). Male fetus in uterus, length 50 cm (measured), collected (RMNH.MAM.60361.c), tissue sampled by Utrecht University (case no. SC3).

The two that stranded on 19 January 2016 were a mother and her calf. Striped dolphin has a tropical-temperate distribution. The number of strandings is increasing (figure 3G), probably due to a rising number of individuals wandering north (e.g. Santos et al. 2008, Coombs et al. 2019).

Bottlenose dolphin (*Tursiops truncatus*)

2015-2019: 3 records
2000-2014: 7 records
Before 2000: 359 records

Figure 9. Striped dolphin. Ameland, 19 January 2016. *Photo: Johan Krol.*

4/1/2015 Terschelling, Friesland. Only right jaw. Reported by D. Ruyg.

13/5/2015 Noordwijk, Zuid-Holland. Only left jaw, not very recent. Reported by R. Noort.

18/12/2015 Schiermonnikoog, Friesland. Single recent vertebra. Reported by T. de Boer.

Between 1980 and 1983 there were seven records. After 1983 and up to and including 2019, the species was recorded 'in the flesh' only in 1988, 1991, 2007 and 2013 (all single specimens) and it has become much rarer since the 1960s, after a period of regular occurrence during the decades before (figure 3H).

Harbour porpoise (*Phocoena phocoena*)

2015-2019: 2651 records
- 2015: 309
- 2016: 667
- 2017: 689
- 2018: 478
- 2019: 508

2000-2014: 6312 records
Before 2000: 2351 records

Numbers and density
Since the steep increase of stranded harbour porpoises in 2006, with 552 reported in that year, yearly totals have remained invariably high. The highest numbers were recorded in 2011 and 2013, with 888 and 875 respectively and, hence, the total number during 2010-2019 was much higher than that in 2000-2009 (figure 3I). The numbers, however, fluctuate between years (figure 10). The average number of 530 stranded porpoises per year during 2015-2019 was lower than the 709 during the previous period (2008-2014, Keijl et al. 2016). This is mainly caused by the extremely high numbers in 2011 and 2013 and the unexpectedly low number in 2015. It was exactly ten years back, in 2005, when a similar low number (310) was recorded. The monthly pattern, with peaks in March and July-September, did not differ significantly from that during the previous period of 2008-2014, although the

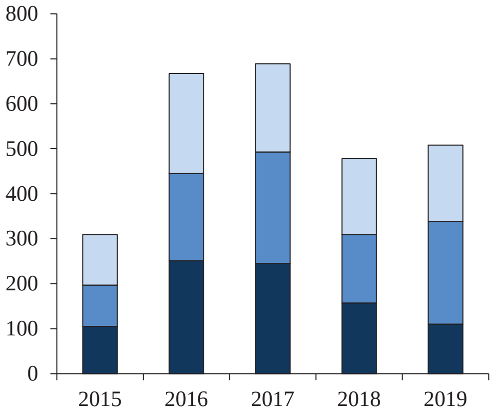


Figure 10. Number of dead harbour porpoise in 2015-2019 along the Dutch coast (www.walvisstrandingen.nl, *n*=2651). Dark blue=Delta, blue=mainland coast, light blue=Wadden Sea.

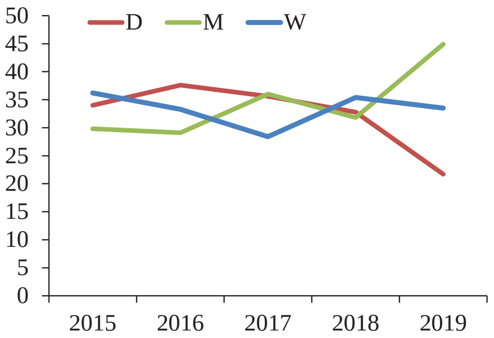


Figure 11. Proportion of dead harbour porpoise in three subareas in 2015-2019. D=Delta, M=mainland coast (= provinces of Noord-Holland and Zuid-Holland), W=Wadden Sea.

peak in March was lower and the one in summer more pronounced.

The percentage of harbour porpoise found in the three subareas – Delta, mainland coast and Wadden Sea – are comparable, with each making up about a third of the total (figure 11). This seems odd, as the coastline length of the Delta makes up 43% of the total coastline, and that of the Wadden Sea 41% (table 2). If the Western Scheldt, Eastern Scheldt and Wadden Sea proper are excluded, including the dead harbour porpoise (50 in Western Scheldt, 76 in Eastern Scheldt and 124 in Wadden Sea respectively, together making up 9.4% of the total), a higher proportion of harbour porpoise is to be found on the mainland coast, while the proportion on the beaches of the Delta and Wadden Sea islands drops slightly (table 3).

The density, expressed as the number of stranded harbour porpoise per kilometre per year, is 0.6 for the entire coastline, or 1.2 if the above mentioned 'inner waters' are excluded. The densities differ between subareas, with the highest density reported on the North Sea coast of the Wadden Sea islands (average 1.4), closely followed by the mainland coast (table 2). Within the Wadden Sea, the density is highest on the islands of Vlieland and Terschelling (close to 2). Areas with a density below 1.0 (Zeeuws-Vlaanderen, Schiermonnikoog) are probably under-recorded (Zeeuws-Vlaanderen, the beach of which is well visited, but largely by foreign tourists), or under-reported, because the area is extensive and difficult to survey (Schiermonnikoog).

Sex and age

Most people from the strandings network have seen hundreds of porpoises and are experienced in sexing individuals, even decomposed ones. However, there seems to be a tendency to report a male when a penis is visible, but to leave the sex undetermined if this is not the case. Also, some people are more prone to report the sex, or take measurements, than others. As reports of stranded harbour porpoises are frequently accompanied by digital photographs, it is often possible to sex an individual afterwards.

About half (53.5%) of the individuals in 2015-2019 was sexed, but the sexing rate differs clearly between subregions, with about three quarters sexed in the Delta and less than one fifth in Noord-Holland (even though this comprises 165 individuals). The proportion sexed has been fairly stable through the years (lowest in 2015 with 54.5%, highest in 2017 with 59.0%). The sex ratio seems to have

Table 3. Relative proportion of harbour porpoise (including number, *n*) found in the three subareas (% porpoise) compared to the relative proportion of coastal length (% km). The same is presented separately for the Delta (breakdown Delta), where the North Sea coast is seprated from the inner waters, and for the Wadden Sea (breakdown Wadden Sea), where the sandy North Sea side of the islands is separated from the generally more muddy Wadden Sea proper. At the bottom the same is presented for the three subareas without the inner waters/Wadden Sea proper.

Overall	% porpoise	% km	*n* porpoise
Delta	32.7	43.2	868
Mainland	34.5	16.2	914
Wadden Sea (total)	32.8	40.6	869
Breakdown Delta			
North Sea	85.5	30.9	742
Inner Delta	14.5	69.1	126
Breakdown Wadden Sea			
North Sea	85.7	27.9	745
Wadden Sea	14.3	72.1	124
Without inner waters			
Delta	30.9	32.6	742
Mainland	38.1	39.6	914
Wadden Sea	31.0	27.7	745

been stable during the past twenty years, with a slight skew towards males (58.0%) (58.2% in 2008-2015, 59.0% in 1998-2007). During 2008-2014, the percentage of males decreased from south to north, but this was not the case during the period under discussion, nor during 1998-2007.

From 41.3% we estimated the age (as deduced from length; <90 cm = neonate, 90-130 cm = immature, >130 cm = mature, *n*=1096; cf. Olafsdóttir et al. 2003). Over half were immature (55.3%), the minority neonate (8.7%). Of neonates 63.6% was male, of immatures 60.9%, of adults 46.5%. Most neonates are found in the Wadden Sea area (40%, *n*=135) and about a quarter (27.4%) in the Delta. The numbers however are low (only 27 per year). Between the subareas, there is not much difference in the percentage of neonates relative to the local (stranded) population (11-15%). The proportion of immatures along the coast of Zuid-Holland appears on the high side (60.8%, *n*=606) compared to the other subareas (51.8-55.6%), though lower than in the previous periods. Similar to the previous period, dead adults were (much) more common in the north of the country (46.8% compared to 14.1-23.1% in the other subareas).

Causes of death

During 2015-2019 244 harbour porpoises were examined *post-mortem* at Utrecht University, an average of 49 per year. The aim of this investigation is to determine the cause of death of each individual (see IJsseldijk et al. 2016, 2017, 2018b). A comparison of causes of death between 2008-2013 and 2016-2019 shows a modest rise in infectious disease (24% versus 30%), a decrease of by-catch (18% versus 11%) and a stable influence of grey seal attacks (25% versus 24%). There is however a notable difference in porpoises dying acutely from a grey seal attack, or dying from infection following a (failed) grey seal attack (see also Foster et al. 2019, Gilbert et al. 2020). In the first period 67% died acutely and 33% died of infected wounds (*n*=118), in the second period these percentages were virtually equal (51% *versus* 49%, *n*=55). Comparison among the causes of death between the two periods is hampered by a difference in selected harbour porpoise (all carcasses, or mainly fresh ones, in the first period, to exclusively fresh ones in the second). Other causes of death are food shortage/emaciation (15%) and 'other', among which trauma (10%) (IJsseldijk et al. 2016-2020a). The reason for investigating fresh harbour porpoise only is that it is difficult to get (all, or any) reliable pathological results from decomposed carcasses. However, it puts a bias on the results of both *post-mortem* examination and diet, because it is likely that fresh porpoise have died near-shore, and their cause of death may differ from those that have died offshore.

Sperm whale (*Physeter macrocephalus*)

2015-2019: 9 records
2000-2014: 9 records
Before 2000: 60 records

12/1/2016 Texel, Noord-Holland. Five males, stranded alive, all died within 12 hours. Lengths 960 cm, 1110 cm, 1010 cm, 1025 cm, 970 cm respectively. Tissue samples (RMNH.MAM.5070346 - 5070350, respectively) and stomach contents collected. Reported by R. Pop and S. de Wolf. Necropsied by Utrecht University (PM3-PM7).

14/1/2016 Texel, Noord-Holland. Male, 1100 cm (but measured inaccurately). Not collected, not necropsied but tissue collected by Utrecht University (case no. PM8). Reported by S. de Wolf.

6/5/2016 Schiermonnikoog, Friesland. Single tooth, probably from upper jaw. Reported by J. Loman-Bakkeveen.

1/12/2017 Domburg, Zeeland. Male, 1256 cm, 20,000 kg (weighed). Possibly stranded alive. Skeleton and tissue sample collected (RMNH.MAM.60366). Necropsied by Utrecht University (case no. PM9).

26/6/2018 Petten, Noord-Holland. Male, 1520 cm (measured), 47,000 kg (weighed). Alive, died same day. Complete skeleton collected (RMNH.MAM.60451). Necropsied by Utrecht University (case no. PM10).

In early 2016, an exceptional stranding of thirty sperm whales took place in the North Sea within a couple of weeks, with strandings spread over most countries bordering the south (see also figure 3J). Although five sperm whales on a single spot on a single day were a unique event for our country, we were 'outnumbered' by Kaiser-Wilhelm-Koog in Germany, where eight stranded. It was presumed a natural event (IJsseldijk et al. 2018c), with increased solar activity coinciding with the timing of southward migration supposedly being the cause of sperm whales swimming south-east into the North Sea instead of following the Faeroe-Shetland Channel in a south-western direction (Vanselow et al. 2017). The animal found in 2017 was emaciated and general debilitation likely resulted in its live stranding, whilst the sperm whale found from 2018 died as a result of infectious disease (IJsseldijk & Gröne 2018a, 2018b).

Sowerby's beaked whale (*Mesoplodon bidens*)

2015-2019: 4 records
2000-2014: 5 records
Before 2000: 16 records

7/3/2016 Borssele, Zeeland (figure 12). Male, 434 cm (measured), 930 kg (weighed). No bones collected. Reported by J. van der Hiele. Necropsied by Utrecht University (case no. MB2).

10/9/2016 near Hoorn, Terschelling. Male, 405 (measured), not weighed. Skull and tissue sample collected (RMNH.MAM.60000). Reported by SOS Dolfijn. Necropsied by Utrecht University (case no. MB3).

17/5/2017 Egmond aan Zee, Noord-Holland. Male, 323 cm (measured), 384 kg (weighed). Stranded alive, died soon after. Complete skeleton collected (RMNH.MAM.60001). Reported by M. Snijders. Necropsied by Utrecht University (case no. MB4)

31/8/2017 Serooskerke, Zeeland. Female, 349 cm (measured), 378 kg (weighed). Stranded alive, died soon after. Skeleton and tissue sample collected (RMNH.MAM.60360). Reported

Figure 12. Sowerby's beaked whale. Borssele, 7 March 2016. *Photo: Joop Fama.*

by A. Dijkstra & L. van Hoven. Necropsied by Utrecht University (case no. MB5).

Sowerby's beaked whale is a rare visitor to the southern North Sea. The number of stranded individuals is low, but there seems to be a slight increase in strandings, with sixteen during the past century, but nine since 2000 (figure 3K). Almost 80% of the Sowerby's beaked whales in the Netherlands stranded during July-September.

Small whale
1/5/2016 Texel, Noord-Holland. Part of skull only (basioccipitale) of a small whale, probably a toothed whale. Reported by W. van Setten.

Dolphin
13/8/2016, Ritthem, Zeeland. Floating in Westerschelde, also reported on 14 August, possibly Bottlenose dolphin. Reported by J. van der Hiele.

15/3/2019, Wijk aan Zee, Noord-Holland. Rotting flesh and bones, skull absent. Two vertebrae collected (no collection number yet). Reported by R. van Wilgenburg.

1/4/2019 Goeree, Zuid-Holland. Part of skull, possibly bottlenose dolphin or white-beaked dolphin. Reported by S. Bout.

2/4/2019 Wassenaar, Zuid-Holland. Part of skull, possibly bottlenose dolphin or white-beaked dolphin. Reported by A. Overklift and J. Seijn.

28/5/2019 Schiermonnikoog, Friesland. Shoulder blade, probably bottlenose dolphin. Reported by T. de Boer and Y. van den Hurk.

31/8/2019 Razende Bol, Noord-Holland. Reported as 'enormous dead animal, looked very much like long-finned pilot whale'. No photographs available. Reported to Zeehondencentrum Pieterburen.

Beaked whale (*Mesoplodon* spec.)
24/4/2016 Terneuzen, Zeeland. Female, 530 cm (measured). Not collected, not necropsied.

This whale unfortunately got lost. Judging from the photographs (see www.walvisstrandingen.nl), Sowerby's beaked whale is a likely candidate.

Discussion

Harbour porpoise is our commonest cetacean, and the commonest one found stranded on the beach, but there is a considerable number of species that also visits the southern North Sea on a more or less regular basis. Of the species that have occurred here since 1900, twelve may be regarded as more or less regular, as they have been recorded in ten or more years. Of these, bottlenose whale (*Hyperoodon ampullatus*) is nowadays probably the rarest. There have been twelve individuals of this species in ten different years, but seven strandings took place prior to 1960, while the last bottlenose whale prior to 2020 stranded more than 25 years ago (2, in 1993) (but see Keijl 2020).

It is likely that the (slight) increase of fin whales taken into the North Sea on the bow of ships is connected to both the increase of the species in the Bay of Biscay in late summer (Edwards et al. 2015, Authier et al. 2018), the increase in ship traffic (Sardain et al. 2019), and in faster ships (Martinez & Castells 2009). For protection of this species, it is important to establish their provenance, for instance by looking into the diet, and the cause of death. Examining a dead cetacean can provide us with ecological and life history data that are difficult or impossible to obtain in other ways. It is therefore recommended that all beached cetaceans are investigated by qualified researchers, and material saved for potential future research (cf. Keijl et al. 2019).

Recently, IJsseldijk et al. (2020b) have assessed patterns and biological parameters of harbour porpoise stranded between 1990-2017 on the North Sea shores of Scotland, England, Belgium, the Netherlands, Germany and Denmark. To make the data comparable to those of Hammond et al. (2017), the area was divided into six blocks. This resulted in the coast of the Netherlands being split into two sections (sections D and E), of which the southern section (D) formed a unity with Belgium and South-east England. The authors found the steepest increase in strandings in section E, the central and northern part of the Netherlands, while strandings in block D and in block F (the latter comprises the North Sea coast of Germany and Denmark), showed a less steep increase. The yearly pattern of strandings in blocks D and E were comparable, with two stranding peaks per year, as opposed to a single peak in the other blocks. Densities, expressed as number of strandings per kilometre per year, were not presented. They can, however, be calculated here for Belgium using the data from Haelters et al. (2018), who reviewed strandings during 1995-2017. The average density in Belgium increased through the years and varied between 0.05 and 2.28, being the lowest during the early years and the highest in 2013. As the pattern of strandings from the Belgian coast corresponded most with that of (the southern part of the British coast and) the southern half of the Netherlands (IJsseldijk et al. 2020b), we compared the density to the latter (figure 13). The pattern of strandings in Belgium indeed followed that from the Delta, although the density in Belgium was somewhat higher from 2003 onwards. Pattern and density however also correspond to other parts of the Dutch coastline. The strandings pattern per month in Belgium is also very similar to that in the Netherlands during 1995-2017, although the peak in spring in Belgium is slightly less pronounced.

Harbour porpoise is protected under several national and international legislation and agreements (e.g. Habitats Directive, ASCOBANS). Population structure, mortality, food quality, food availability, disturbance, habitat loss, pollution and health are important factors to be assessed in order to protect the species in the North Sea. Fishing gear, especially gill nets and trammel nets, still appear to be an important cause of death (e.g. Jefferson & Curry 1994, Bjørge et al. 2013, IJsseldijk et al. 2016-2019). Since in the Netherlands the municipalities instead of the national authority are presently responsible for the implementation of local recreational fishery legislation (www.decentraleregelgeving.overheid.nl), there is no insight in the impact of gill net and set net fisheries on harbour porpoise mortality on a national scale. Recently, a study on professional set net fishery was conducted, resulting in a calculated by-catch of on average 23 individuals per year (Scheidat et al. 2018). On basis of this study, it was concluded that the annual population mortality

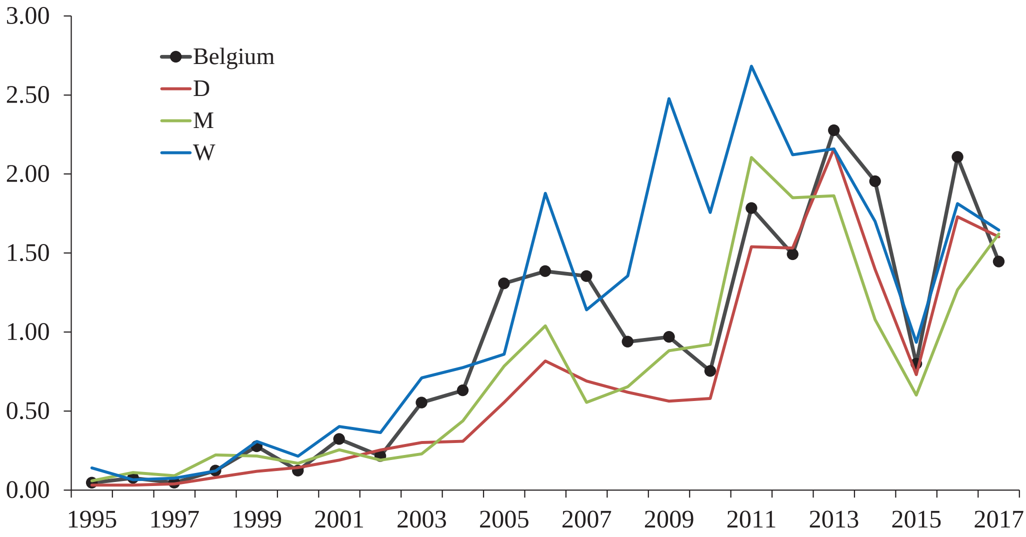


Figure 13. Density of stranded harbour porpoise in Belgium (*n*/km; Haelters et al. 2018) compared to the density in the Netherlands. D=Delta, M=mainland coast, W=Wadden Sea.

due to by-catch was lower than deemed unacceptable as defined by ASCOBANS (ASCOBANS 2005, 2016). However, only Dutch ships were monitored, while there is also extensive set net and gill net fisheries taking place in Dutch waters by foreign countries, and by local fisheries as mentioned earlier. Although harbour porpoise are notoriously difficult to count, there is, according to Hammond et al. (2017), no proof of change in the population of harbour porpoise in the North Sea. For the major shift in distribution (Hammond et al. 2002, 2013, 2017), presence (www.trektellen.nl), density (e.g. Hammond et al. 2017, Geelhoed et al. 2020) and mortality (www.walvisstrandingen.nl) between years and between seasons, several theories have been proposed.

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Samenvatting

Gestrande walvisachtigen op de Nederlandse kust in 2015-2019

Dit is de veertigste meerjarige rapportage van gestrande walvissen in Nederland. In deze rapportage, die de jaren 20015-2019 beslaat, worden 9 soorten gemeld met in totaal 2701 exemplaren. De talrijkste walvis was bruinvis met 2651 exemplaren (98,2%). Sinds 2001, het eerste jaar met meer dan 100 bruinvisstrandingen, zijn de aantallen gestegen via meer dan 500 in 2006 tot 'topjaren' 2011 met 888 en 2013 met 875. Sindsdien fluctueren de aantallen, waarbij vooral 2015 eruit springt als opmerkelijk 'mager' strandingsjaar met 309 bruinvissen. Het gemiddelde aantal per jaar in 2015-2019 was 530, lager dan de 709 in 2008-2014. Het maandelijks aanspoelpatroon, met pieken in maart en juli-september, is gelijk aan vorige jaren. Overal langs de kust lijken door de jaren heen ongeveer evenveel bruinvissen aan te spoelen: Delta, Hollandse kust en Waddengebied maken qua aantal elk ongeveer een derde van het totaal uit. Dit is opmerkelijk, want de kust van de Delta is 2,5 keer langer dan de Hollandse kust, en nagenoeg hetzelfde geldt voor het Waddengebied. Dit komt door de uitgestrekte oevers van de Westerschelde, de Oosterschelde en de Waddenzee, gebieden waar wel bruinvissen aanspoelen maar die veel slechter toegankelijk zijn voor potentiële bruinvisvinders. Dit blijkt ook uit de zeer lage aantallen, respectievelijk 50, 76 en 124 bruinvissen, slechts 9,4% van het totale aantal gevonden bruinvissen, terwijl de kustlengte van deze drie gebieden 59,2% van de totale kustlengte uitmaakt. Overigens zullen ook de aantallen bruinvissen die deze veelal brakke wateren bezoeken kleiner zijn. Als we zowel deze gebieden als de aantallen gevonden bruinvissen daar weglaten, valt het aandeel bruinvissen op de Hollandse kust wat hoger uit (38,1%), iets lager dan op grond van de kustlengte verwacht kan worden. Het aandeel bruinvissen op de Noordzeekust van de Waddeneilanden valt juist wat hoger uit dan verwacht, ook al is het aantal bruinvissen daar vermoedelijk wat onderteld. De dichtheid van aangespoelde bruinvissen, uitgedrukt als aantal per kilometer per jaar, is het laagst in de Delta (0,4) en het hoogst op de Noordzeekust van de Waddeneilanden (1,4); de Hollandse kust neemt een tussenpositie in (1,2). De dichtheid op Vlieland (1,9) en Terschelling (1,7) is het hoogst, en dat is al jaren zo. De laagste dichtheden vinden we in Zeeuws-Vlaanderen (0,4) en het Noordzeestrand van Schiermonnikoog (0,6). Dit is te wijten aan de samenstelling van het strandgaande publiek in Zeeuws-Vlaanderen (vooral buitenlandse toeristen) en aan het zeer uitgestrekte en onoverzichtelijke strand van Schiermonnikoog. Iets meer dan de helft van de bruinvissen is in de besproken periode gesekst (53,5%) en de digitale foto's die doorgaans worden meegeleverd dragen hier in hoge mate aan bij. De sekseverhouding blijft door de jaren onveranderd, met een klein mannenoverschot (58,0%). In de vorige besproken periode (2008-2014) was dit 58,2%, in de periode daarvoor (1998-2007) 59,0%. Omdat bruinvissen hun gehele leven groeien, het hardst in hun eerste levensjaren, kunnen ze op grond van lengte worden ingedeeld in leeftijdsgroepen: <90 cm noemen we hier pasgeboren, 90-130 cm onvolwassen en >130 cm volwassen. In de besproken periode kan 41,3% op deze manier worden ingedeeld. Meer dan de helft (55,3%) is onvolwassen, 8,7% pasgeboren. Van de pasgeborenen is 63,6% man, van de onvolwassen bruinvissen 60,9%, bij adulten 46,5%. Of dit de werkelijke situatie van de populatie weergeeft, of er seksegebonden sterfte optreedt, of dat er nog iets anders aan de hand is, is niet bekend. 40% van de pasgeboren bruinvissen wordt in het Wad-

dengebied gevonden en ongeveer 25% in de Delta. Ook hier is weer niet bekend of in die gebieden ook meer jongen worden geboren (en de sterfte over de gehele kust gelijk zou zijn), of dat de jongensterfte in genoemde gebieden hoger is dan aan de Hollandse kust. Misschien worden estuaria zoals de Delta en het Waddengebied geprefereerd door vrouwtjes met pasgeboren jongen. De meeste dode volwassen bruinvissen komen eveneens uit het noorden van het land (46,8%). In de huidige periode zijn 187 – uitsluitend verse – bruinvissen professioneel onderzocht op doodsoorzaken. De belangrijkste doodsoorzaak is infectie (32,1%, vaak met verhongering of vermagering als gevolg), terwijl de grijze zeehond verantwoordelijk is voor 24,1% van de dode bruinvissen. In de besproken periode is het aandeel door bijvangst omgekomen bruinvissen gedaald naar 11%. In een recente studie, waarin strandingen van bruinvissen in 1990-2017 in de gehele Noordzee zijn geanalyseerd, blijkt de sterkste toename in aantallen te hebben plaatsgevonden in het gebied ten zuiden van IJmuiden/de Belgische kust/Zuidoost-Engeland. Daarnaast vertoont alleen in die sector én in de noordelijke helft van Nederland het jaarlijkse aanspoelpatroon twee pieken (in voorjaar en nazomer), terwijl er elders in de Noordzee steeds alleen een nazomerpiek in het strandingspatroon is en de voorjaarspiek ontbreekt.

Vondsten van bijzondere soorten in de besproken periode waren dwergvinvis (8; in 2000-2019 in totaal 18), gewone vinvis (4, 15), gewone dolfijn (5, 9), griend (3, 9), witsnuitdolfijn (2, 58), gestreepte dolfijn (3, 6), potvis (8, 16) en gewone spitssnuitdolfijn (4, 8). Er waren ook vondsten van ongedetermineerd gebleven walvissen (5), waarvan 1 misschien een gewone spitssnuitdolfijn was. Overigens zijn bij al deze getallen 10 botvondsten inbegrepen, waarvan orka de meest bijzondere was. Sinds 2000 zijn ook bultrug (6), orka (1), tuimelaar (2), witflankdolfijn (4) en spitssnuitdolfijn van de Blainville (1) gevonden, maar niet in de afgelopen vijf jaren. Gewone vinvis lijkt wat gewoner te worden (11 sinds 2000, daarvoor 26). Opvallend is dat, voorzover onderzocht, de meeste gewone vinvissen lijken te zijn aangevaren door een schip. Augustus is dé maand daarvoor (5 van de 11). Ook dwergvinvis lijkt vaker te zijn aangevaren naarmate een karkas vaker goed wordt onderzocht. Er is wel een opvallende tweedeling tussen beide onfortuinlijke soorten: gewone vinvis lijkt ons land overwegend per schip binnen te komen door het Kanaal; de soort wordt vooral in de zuidelijke helft van ons land aangevoerd of spoelt daar aan, met de Maasmond als favoriete regio. Ook de in augustus 2017 op Texel aangespoelde gewone vinvis is vermoedelijk door Het Kanaal de Noordzee binnengekomen. Dwergvinvis daarentegen spoelt vooral in de noordelijke helft van het land aan. Helaas worden nog altijd niet alle dode soorten anders dan bruinvis onderzocht; de score staat zelfs op een magere 58%. De rest wordt domweg verbrand. Dit heeft met financiën te maken maar is een gemiste kans, omdat er nauwelijks andere mogelijkheden zijn om aan een walvis sekse, lengte, gewicht, leeftijd, ziekte, parasieten, dieet enzovoort te onderzoeken. Een dode walvis op het strand is weliswaar jammer voor het individu, maar het biedt een unieke gelegenheid om meer over de soort te leren. Vanwege de toenemende druk op de Noordzee door de mens – denk aan recreatie, visserij, scheepvaartbewegingen, bouwprojecten – en vervuiling is het belangrijk een vinger aan de pols te houden van de stand van walvissen in de zuidelijke Noordzee.

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Diet of the first settled wolves (*Canis lupus*) in Flanders, Belgium

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Abstract: After a long period of absence, the wolf (*Canis lupus*) has made its comeback in Flanders, Belgium. Nevertheless, the proximity of a top predator in a human-dominated landscape could lead to a variety of conflicts, e.g. attacks on livestock and competition with hunters. This research describes the diet of the first settled wolves in Flanders in order to avoid misconception regarding this topic. From 2018 to 2021, 140 wolf scats were collected within the only wolf territory in Flanders. Prey species identification was based on hair features, and bone and tooth remains. Results are expressed as the frequency of occurrence of prey species relative to the total number of scats (=FO). Wild ungulates represented the largest part of the diet (FO=90.0%), with roe deer (*Capreolus capreolus*) (FO=69.3%) and wild boar (*Sus scrofa*) (FO=22.9%) as the main prey species of this category. Overall consumption of livestock was limited (FO=12.9%), but raised to 47.1% FO in autumn 2020. We believe that this phenomenon is explained by the presence of the first developing young which are not yet able to hunt, but still need to be fed. The large availability of unprotected livestock in the study area was therefore an easy and attractive alternative in case of higher energetic needs. Although the overall results indicate a rich wild prey base, this study addresses the necessity to further implement protective measures to prevent livestock predation. By the end of 2018, only 4% of randomly chosen pastures within a defined risk area were sufficiently protected.

Keywords: wolf, *Canis lupus*, diet, human-dominated landscape, Flanders, Belgium.

Introduction

The wolf (*Canis lupus*) in Europe is showing a marked recovery triggered by its protected status under the Bern Convention (1979) and the Habitats Directive (1992), together with the conservation of potential wolf habitat and growing prey supplies. Dispersing individuals originating from the Baltic and the Apennine relict populations gradually recolonised parts of Germany and France respectively, eventually leading to the recorded presence of both genetic lineages in Belgium (Everaert et al. 2018). In 2018, the first official settlement occurred in the north of the Flemish province of Limburg (Belgium), followed by successful reproduction in 2020. In addition, multiple dispersing individuals have been recorded in Flanders since 2018 (Gouwy et al. 2018, 2019, 2020a, 2020b). This ongoing recolonisation process towards human-dominated areas, could ratchet up the tensions again which historically led to the extermination of the wolf in most of Europe. Basis of conflict is the feeding ecology of the species, potentially causing economical and emotional damage due to attacks on livestock and pets, and competition with the hunting sector (Kleiven et al. 2004, Bergstrom et al. 2009, Kovařík et al. 2014). In addition, the question arises whether human-dominated landscapes offer a sustainable amount of wild prey. It is of great importance to obtain accurate information on this topic in order to guide policymaking and to avoid the spread of misconception among the general public, and as such, facilitate coexistence with a top predator (Everaert et al. 2018).

Previous studies on wolf diet in Europe show a flexible and opportunistic predator, enabling the species to persist throughout a wide range of ecological, even anthropogenic, conditions. The feeding ecology is predominantly driven by the spatiotemporal interplay of relative abundance and vulnerability of potential prey species, with an emphasis on wild ungulates (Peterson & Ciucci 2010, Zlatanova et al. 2014). Across Europe, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and moose (*Alces alces*) are identified as the major prey species (Okarma 1995, Jędrzejewski et al. 2000, Kübarsepp & Valdmann 2003, Nowak et al. 2005, Ansorge et al. 2006, Müller 2006, Barja 2009, Žunna et al. 2009, Nowak et al. 2011, Lanszki et al. 2012, Wagner et al. 2012, Sand et al. 2016, Mori et al. 2017, Sin et al. 2019). Other locally present ungulates, such as fallow deer (*Dama dama*) and mouflon (*Ovis orientalis*), are predated as well (Ansorge et al. 2006, Wagner et al. 2012). In addition, lagomorphs and Eurasian beaver (*Castor fiber*) could make a clear contribution to the diet, of which the latter appears to be a key prey species in wetland habitats (Okarma 1995, Andersone & Ozoliņš 2004, Sidorovich et al. 2017). If the availability of wild prey proves inadequate, livestock predation and waste consumption are adaptive foraging strategies. This phenomenon is particularly prevalent in certain southern European regions which are clearly characterised by a very low densitiy or a total lack of wild prey (Zlatanova et al. 2014). Nevertheless, when both wild and domestic prey are abundant, a preference for the former is generally observed (Sidorovich et al. 2003, Gula 2008, Barja 2009, Zlatanova et al. 2014, Imbert et al. 2016).

The feeding ecology of wolves is also well documented in recolonised regions. In Germany and western and central Poland, the wolf's diet mainly consists of wild ungulates while the contribution of livestock remains very limited (Nowak et al. 2005, Ansorge et al. 2006, Wagner et al. 2012). In Italy, a steady decline in livestock consumption has been observed during the recolonisation process (Meriggi & Lovari 1996, Meriggi et al. 2011). A meta-analysis conducted by Imbert et al. (2016), focusing on northern Italy, reveals multiple explanatory variables: the adoption of livestock protection measures, an increasing abundance of roe deer next to wild boar and the presence of stable wolf packs.

Although the wolf is indeed a well-studied species in terms of its feeding ecology, its increasing distribution corresponds to a growing proximity to human-dominated landscapes. Compared to studies conducted in Germany (Ansorge et al. 2006, Wagner et al. 2012), the northern part of the province of Limburg resembles a more anthropogenised region: highly fragmented nature areas, the absence of larger-sized ungulates (i.e. red deer), a lack of livestock protection measures and a high density of human population and traffic. In this context, our goal is to describe the diet of the first settled wolves in Belgium which should contribute to the understanding of wolf ecology in human-dominated landscapes. The results of this study should also be used to inform policymakers and the general public.

Materials and methods

Study area

The study was conducted in the north of the province of Limburg which is part of the Flemish Region of Belgium. It is the only region in Flanders where the wolf is settled. First, a female wolf appeared in the study area in 2018, which was joined by a male later that year. The female died in 2019 but successful reproduction occurred one year later after a new female made her appearance at the turn of the year 2019/2020. Derived from monitor-

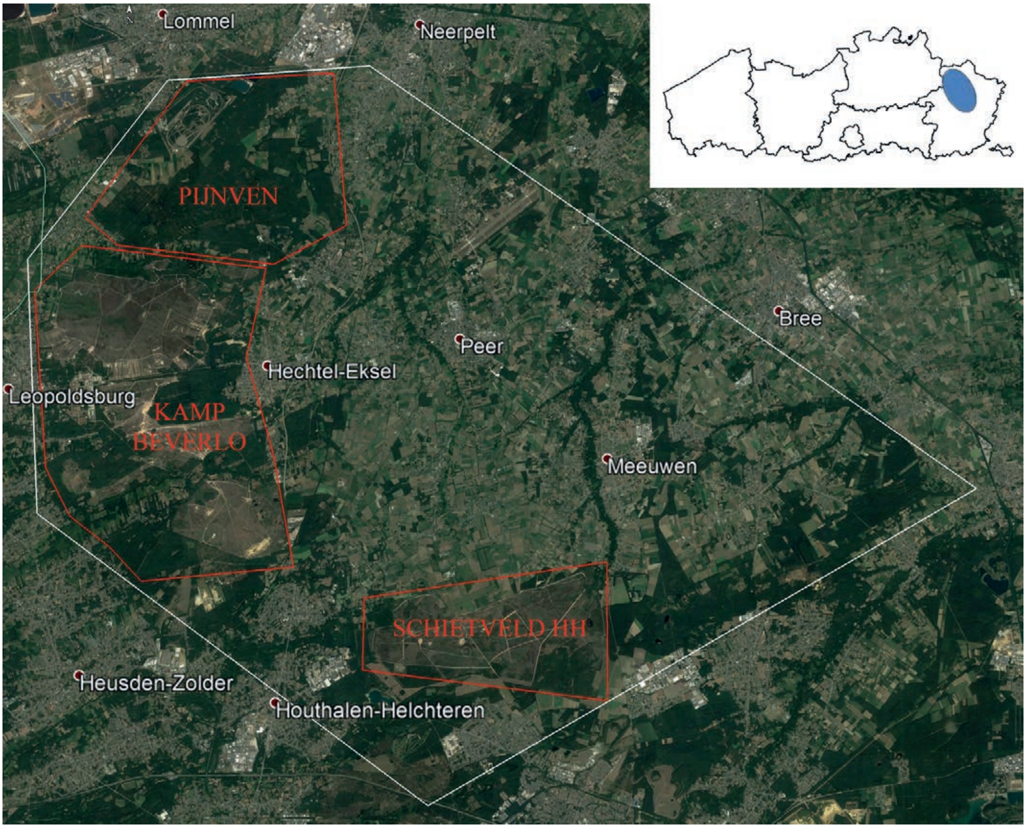

Figure 1. Indicative view of the study area (large white polygon and blue oval on the inset map) in the north of the province of Limburg, Belgium, with the three core areas circled in red.

ing studies, e.g. verified observations and damage records, the current wolf home range surrounds an area of ± 400km², including less suitable areas such as industrial, residential and intensive arable farming areas. The home range (partly) overlaps with the municipalities of Lommel, Hechtel-Eksel, Pelt, Leopoldsburg, Beringen, Oudsbergen, Peer, Heusden-Zolder and Houthalen-Helchteren and is indicatively represented in figure 1 by the polygon. Occasionally, the settled wolves are also observed outside of the polygon in the neighbouring municipalities of Balen, Bree, and Genk.

Within the wolf home range, three large nature areas are distinguished. Namely, the Pijnven state forest and its direct surroundings, and two military bases, 'Kamp Beverlo' and 'Schietveld Houthalen-Helchteren'. These core areas belong to the intensively used habitat of the settled wolves, together with the open agricultural habitat south of Peer.

The predominantly flat study area lies at an altitude of 50-90 meters above sea level and consists almost entirely of sandy soils and locally some small areas of peat. The vegetation is composed of dry and wet heathland, pine and deciduous forest on dry soils, patches of marsh forest in river valleys and a small area of grassland. Yet, most of the study area, i.e. within the polygon, is made out of arable and urban land.

The ungulate community mainly consists of roe deer and wild boar. Escaped fallow deer regularly appear in the study area although its share to the ungulate community is low. In one instance, a red deer was captured on camera trap. Presumably this individual was an escapee, but dispersal from a small population in the north-east of Limburg cannot be ruled out. Other potential prey species in the study area are rabbit (*Oryctolagus cuniculus*) and brown hare (*Lepus europaeus*). Presence of beaver was observed along three small rivers crossing the study area, however the species is not abundant in the wolf core areas (red polygons): only one territory was registered.

Across the study area, sheep (*Ovis aries*) are kept by both hobbyists and professionals. A small number of captive mouflon is present in at least one place. Other medium-sized (domestic) animals in captivity are goat (*Capra hircus*), fallow deer, red deer, alpaca (*Vicugna pacos*) and Bennett's wallaby (*Macropus rufogriseus*). In addition, both dogs (*Canis familiaris*) and (stray) cats (*Felis catus*) are common in the study area. Dogs must be leashed by law, although unleashed, or even escaped dogs are occasionally observed during day and night (INBO, own observations). Holvoet (2019) showed that only 4% of randomly chosen pastures were sufficiently protected against wolf attacks by the end of 2018.

Data collection and analyses

The wolf diet was examined based on scats collected from May 2018 to February 2021 within the wolf territory described above. Scats were detected randomly during the entire study period and the distinction between scats of wolf, domestic dog, red fox or other species, was based on expert judgement. In addition, a dog called Wietse was used to actively search for scats starting from December 2020. This dog was trained to recognise the scent of wolf scats and to discriminate them from other species under different treatments: e.g. age of scats, different locations, leashed or unleashed. Reliability was successfully demonstrated by means of a blind test. Expert judgement was used as a double check in the field, but there were no disagreements. As part of the wolf monitoring study, 19 scats were also checked for DNA in order to identify individual wolves since the first young started to move around in 2020. Of these, all appeared to be from wolf.

The scats were collected in their totality or to the greatest extent possible. Place and date of collection were subsequently noted. Next, the scats were stored at a temperature of -80 °C for at least eight days. This freezing process was intended to neutralise possible pathogens, especially eggs of *Echinococcus multilocularis*, a small cyclophyllid tapeworm. After thawing, the scats were soaked in water for approximately one hour and then rinsed over a 0.5 mm sieve to remove mud and debris. During rinsing, a distinction was made between hairs, bone and tooth fragments, vegetation and other substances. Subsequently, the residue was dried at room temperature after which the hair residue was examined under a stereomicroscope. Hairs were randomly isolated and classified according to shape, diameter, length and colour, with particular attention to guard hairs. Selected hairs were cleaned by rinsing with a detergent solution and then left to dry on absorbent paper. Cleaned hairs were macro- and microscopically identified using an own reference collection and the determination keys of Teerink (1991) and Tóth (2017). Microscopic hair features were visualised using the methods described by Teerink (1991). Additionally, tooth and bone fragments were identified using the reference collection of the Royal Belgian Institute of Natural sciences (KBIN). If species identification was still not possible, the highest taxonomic rank was determined. In case of wild boar, a distinction based on hair features was made between juveniles (< 3-5 months) and sub(adults). Results are expressed as the frequency of occurrence (FO) which is calculated by the relation of the number of scats containing a certain prey item to the total number of scats analysed:

$$FO = ni/N$$

Where *ni* is the total number of scats that contained a certain prey item *i* and *N* is the total number of scats analysed. Frequency of occurrence was calculated by prey species and by prey category. Based on the identified prey species, the following categories were distinguished:

- Wild ungulates (wild boar, roe deer, fallow deer, unidentified deer)
- Lagomorphs (brown hare, rabbit, unidentified Lagomorph)
- Livestock (sheep, goat, domestic pig)
- Domestic dog
- Domestic cat
- Small rodents
- Birds
- Fruits and seeds

Two or more different prey species belonging to the same prey category encountered in one scat, were reduced to a single prey item when calculating the frequency of occurrence at the category level. Fallow deer was assigned to 'Wild ungulates' due to both the escaped and captive status of this deer species and methodological constraints, i.e. the inability to distinguish between hairs of juvenile deer species with sufficient certainty (De Marinis & Asprea 2006).

Differences in the diet composition between 2018-2019 and 2020-2021 (before and after the arrival of the second female) and between seasons were analysed using Fisher's exact test. The following prey categories were used:

- Deer
- Wild boar
- Lagomorphs
- Livestock

Assignment to season was meteorologically based, e.g. spring begins on 1 March and ends on 31 May. Data was statistically analysed using RStudio (version 4.0.2) (R Core Team 2020).

Results

A total of 202 prey items out of 140 wolf scats were identified (table 1). The majority of the scats contained remains of only one prey item (65.7%). Presence of two prey items was recorded in 27.1% of the samples. Three and four items were found in 4.3% and 2.9% of the scats, respectively. The number of scats gathered in 2018-2019 (n=51) was notably lower compared to 2020-2021 (n=89). Date of collection was not known for three scats collected in 2019.

Wild ungulates clearly represented the largest part of the wolf diet (FO=90.0%). Within this category, roe deer was the most frequent prey species (FO=69.3%) followed by wild boar (FO=22.9%). More than half of the prey items identified as wild boar (59.4%), originated from juveniles with a maximum age of three to five months. Fallow deer was recorded in 7.1% of the scats. Seven prey items identified as deer, could not be specified at the species level.

With a frequency of occurrence of 13.6% and 12.9% respectively, lagomorphs and livestock were found about equally often. Within the latter, sheep was the most frequent prey species (FO=8.6%), followed by goat (FO=4.3%). A third species belonging to this category is domestic pig (*Sus domesticus*), which was observed in just one scat (FO=0.7%). Prey remains of domestic dog and domestic cat were each found once as well. Other prey items like small rodents, birds and fruits were recorded in low amounts.

There was no significant difference in diet between 2018-2019 and 2020-2021 (P=0.835) considering the following prey categories: 'deer', 'wild boar', 'lagomorphs' and 'livestock'. Analysis of the data by season did indicate a significant difference (P=0.003), based primarily on the higher proportion of wild boar and livestock during spring and autumn, respectively. In both cases, this effect was largely attributed to the composition of the diet in 2020. Frequency of occurrence of wild boar in spring 2020 was 61.5% (# scats=13), all of them being juveniles. In spring 2018 and 2019 combined, this was 18.2% (# scats=11), with one out of two being juveniles. Frequency of occurrence of livestock in autumn 2020 was 47.1% (# scats=17). This was 28.6% when

Table 1. Wolf diet of the first settled wolves in Flanders, Belgium, based on 140 scats collected from May 2018 to February 2021, expressed as the frequency of occurence (FO). Season of collection was not known for three scats.

	FO				
Prey items	Winter	Spring	Summer	Autumn	Total
Wild ungulates	90.0	83.3	97.4	83.3	90.0
Roe deer (*Capreolus capreolus*)	78.0	50.0	76.9	54.2	69.3
Fallow deer (*Dama dama*)	8.0	12.5	2.6	8.3	7.1
Unidentified deer	-	-	7.7	16.7	5.0
Wild boar (*Sus scrofa*)	12.0	41.7	25.6	16.7	22.9
Lagomorphs	18.0	16.7	5.1	16.7	13.6
European hare (*Lepus europaeus*)	10.0	4.2	2.6	12.5	7.1
European rabbit (*Oryctolagus cuniculus*)	4.0	12.5	2.6	4.2	5.0
Unidentified Lagomorph	4.0	-	-	-	1.4
Livestock	6.0	8.3	5.1	41.7	12.9
Sheep (*Ovis aries*)	4.0	8.3	5.1	20.8	8.6
Goat (*Capra hircus*)	2.0	-	-	20.8	4.3
Domestic pig (*Sus domesticus*)	-	-	-	4.2	0.7
Domestic dog (*Canis familiaris*)	-	-	2.6	-	0.7
Domestic cat (*Felis catus*)	2.0	-	-	-	0.7
Small rodents	16.0	8.3	2.6	4.2	8.6
Bank vole (*Myodes glareolus*)	4.0	4.2	2.6	-	2.9
Field vole (*Microtus agrestis*)	6.0	-	-	4.2	2.9
Unidentified vole (*Microtus* sp.)	6.0	-	-	-	2.1
Wood mouse (*Apodemus sylvaticus*)	-	4.2	-	-	0.7
Birds	4.0	4.2	-	-	2.1
Fruits and seeds	-	-	-	2.5	0.7
Black cherry (*Prunus serotina*)	-	-	-	2.5	0.7
# prey items	34	50	40	72	202
# scats	24	39	24	50	140

autumn 2018 and 2019 were taken together (# scats=7). Before and after autumn 2020, frequency of occurrence was clearly lower to absent (table 2).

Roe deer appeared to be a stable and frequent prey species throughout the entire study period, whereas prey items identified as fallow deer were found to be more concentrated in time, namely April 2019, August-September 2020 and January-February 2021.

Discussion

The present study provides initial insights into the diet of the first settled wolves in Flanders. Notwithstanding the prevailing anthropogenic influence within the study area, wild ungulates are by far the most frequent prey category. This result is similar to studies conducted in areas characterised by a sufficient prey supply (Zlatanova 2014). Just like in the recolonised areas of Germany (Ansorge et al. 2006, Wagner et al. 2012), roe deer appears to be the dominant prey species in Flanders. This was to be expected as roe deer generally reaches high population densities in semi-natural and heavily modified forest and agricultural landscapes (Gill et al. 1996, Melis et al. 2009). Overall, the composition of wild ungulate communities across Europe is diverse which is clearly reflected in the flexible diet

Table 2. Frequency of occurence (FO) of livestock throughout the study period May 2018-February 2021.

Period	# scats	FO livestock (%)
May 2018 – Feb 2018	15	13.3
Jan 2019 – Dec 2019	36	11.1
Jan 2020 – May 2020	15	0.0
Jun 2020 – Aug 2020	21	4.8
Sep 2020 – Nov 2020	17	47.1
Dec 2020 – Feb 2021	36	8.3

of the wolf. For example, red deer appears to be the main prey in several forest-rich areas of Central and Eastern Europe (Okarma 1995, Jędrzejewski et al. 2000, Nowak et al. 2005). In Scandinavia, the wolf feeds mostly on moose (Müller 2006, Sand et al. 2016). When the smaller-sized roe deer is available at sufficiently high densities however, it usually makes up a large to the largest part of the diet and often becomes positively selected in a multi-prey system (Bunewich 1988, Ansorge et al. 2006, Barja 2009, Nowak et al. 2011, Milanesi et al. 2012, Wagner et al. 2012, Figueiredo et al. 2020). For example, Sidorovich et al. (2011, 2017) conducted an extensive analysis on prey preference in the deciduous woodlands of central-western Belarus (Eastern Europe) where European beaver, roe deer, red deer, wild boar, moose and European bison (*Bison bonasus*) are all abundant. Both European beaver and roe deer appeared to be the preferred prey species. Larger-sized ungulates only became more significant after a sudden decline of the roe deer population. Similarly, the importance of moose as a prey species in Scandinavia is driven by the local population density of roe deer (Sand et al. 2016). This preference is generally explained by a risk-aversive strategy among wolves: the medium-sized roe deer is unlikely to cause severe injuries when predated. Also, the proportion of prey biomass lost to scavengers increases with prey size, suggesting that the actual amount of available food for wolves in both medium-sized and larger prey is more similar, while it is riskier to catch the latter (Sidorovich et al. 2011, Sand et al. 2016). The strong emphasise on roe deer in (recent) literature, additionally indicates that the absence of larger-sized ungulates (e.g. red deer and moose in Flanders) does not necessarily equate to an insufficient prey supply.

Being dependent on only one prey species implies a risk as the population may suffer a decline due to (random) events such as overhunting or unfavourable climatic conditions. A multi-prey system is indeed thought to be more sustainable in terms of food supply (Mech & Peterson 2010). However, the local wild ungulate community is also characterised by wild boar, which was found as a prey item in almost a quarter of the analysed scats. In Europe, this species is often avoided because of the dangerous anti-predator behaviour of adults (Okarma, 1995). Predation of wild boar is therefore mainly focused on vulnerable juveniles in spring (Jędrzejewski et al. 2000, Ansorge et al. 2006, Wagner et al. 2012). Indeed, this was also observed in our analysis, but only during 2020 when the majority of the scats was collected. We believe that a more representative result was obtained in 2020, explaining the absence of this phenomenon in previous years (2018-2019). In spring 2018, only a few scats of a solitary female that just started to settle were collected. In 2019, this female died shortly after she was observed pregnant, again resulting in a low number of scats. Despite a common avoidance, wild boar appears to be the dominant prey species of wolves in certain European regions (Zlatanova 2014). In Italy, this is explained by the high abundance of wild boar and its year-round reproduction. Inexperienced sub-adults are assumed to be an easy and profitable prey after leaving the matriarchal groups in response to a new reproduction event (Heck & Raschke 1980, Mauget et al. 1984, Capitani et al. 2004, Meriggi et al. 2011, Imbert et al. 2016). Year-round reproduction is also observed in our study area (INBO, own observations), indicating the potential importance of wild boar. Of the remaining wild prey species, mostly lagomorphs contributed to a further diversification of the diet, which in all likelihood reflects a high abundance. Especially brown hare is observed in remarkably high numbers on the heathland of the two military bases 'Kamp Beverlo' and 'Schietveld Houthalen-Helchteren' (personal communication Eddy Ulenaers and Michel Broeckmans).

Livestock made up a distinct component of the wolf diet, although a large part is explained by autumn 2020. It is to our belief that the strong and sudden increase in livestock predation during this period, is caused by the presence of the first developing young which are not yet able to hunt, but still need to be fed. The availability of unprotected livestock was therefore an easy and attractive alternative in case of higher energetic needs. This hypothesis is further supported by the decrease of livestock predation in winter, as the young started to move around with their parents more often, presumably learning to hunt wild prey. Throughout the preceding time period, the amount of livestock appeared to be notably lower to absent, rather indicating opportunistic predation. Hereby, it is noteworthy to mention that the calculated frequency of occurrence of livestock in autumn 2018/19 should not be considered representative due to the small sample size (FO=28.6%, # scats=7). Scientific research points out a general preference for wild prey over livestock if both are abundant. The presence of adequate protection measures further facilitates this relationship (Meriggi & Lovari 1996, Sidorovich et al. 2003 Gula 2008, Meriggi et al. 2011, Imbert et al. 2016, and others). Nevertheless, only 4% of randomly chosen pastures within a defined risk area were sufficiently protected against wolf attacks by the end of 2018 (Holvoet 2019). More recent numbers, by the end of 2020, show that barely 119 of the 1,455 (8%) small livestock owners within a risk area defined by INBO have applied for financial support to safely enclose their animals.

Fallow deer is an ambiguous prey species. On the one hand, (recently) escaped individuals are often observed in the wolf territory. However, several attacks on fallow deer in captivity were reported during the study period. It is not possible to distinguish between these two possibilities solely on the basis of prey remains found in scats. But taking into account the date of collection and officially reported wolf damage, consumption of captive fallow deer seems highly probable during August-September 2020 and January-February 2021. Although there is no data available on the number of escaped fallow deer in the wild, we are confident that their share to the ungulate community is still very low based on camera trap survey (INBO, own observations). Nevertheless, predation may be disproportionally high, as it may concern half-tame and easy to catch specimens due to a prior history in captivity (cf. Okarma 1995).

The killing of dogs by wolves is not an isolated case in Europe (Butler et al. 2014 and references herein). This aggressive behaviour is explained by their resemblance, which means that dogs are probably considered to be conspecifics. As such, dogs are seen as intruders within wolf territory or as competitors for prey or potential partners. In addition, dogs are often eaten after being killed, indicating the possibility that they are also perceived as prey (Kojola & Kuittinen 2002, Backeryd 2007). Although the number of cases may increase under conditions of poor prey supply (Sidorovich et al. 2003), dogs are not considered a frequent prey species (Butler et al. 2014). Nevertheless, in certain regions of Spain and Russia it is believed that the wolf suppresses the population of feral dogs, whether as a food source or not (Bibikov 1988, Blanco et al. 1992). Attacks on dogs have been extensively documented in Finland and Sweden by Backeryd (2007). In the period of 1995-2005, 152 official attacks were recorded, 86% of which were on hunting dogs during the hunt. The remaining attacks took place in forests when the dog was unleashed (5%), and in gardens (7%) or were unspecified (2%). Similar results were obtained in Wisconsin, United States of America (Treves et al.

2002). Concerning this study, there were no official records of a wolf killing a dog prior to collection of the particular scat containing dog remains. Escaped and unleashed dogs are not an exception however, as shown by camera trap surveys (INBO, own observations).

Conclusion

This study addresses the necessity to further implement protective measures for livestock, and other captive species such as fallow deer. It also shows the importance of a greater awareness of the dog-wolf relationship. Conflicts about both can strongly steer public opinion with adverse effects on the acceptance of the wolf in Flanders.

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Samenvatting

Het dieet van de eerste wolvenroedel in Vlaanderen

Sinds de wolf (*Canis lupus*) officieel beschermd is, vertoont de soort een voorzichtig herstel in Europa. Op 3 januari 2018 kwam dan ook, voor het eerst sinds meer dan een eeuw, een wilde wolf in Vlaanderen terecht om er zich vervolgens te vestigen,

meer bepaald in het noorden van de provincie Limburg. Succesvolle reproductie in 2020 leidde uiteindelijk tot de eerste wolvenroedel. Andere zwervende individuen vormen sindsdien een extra aanwijzing voor een blijvende of, op zijn minst, regelmatige aanwezigheid in Vlaanderen. De nabijheid van de wolf in een door de mens gedomineerd landschap kan echter aanleiding geven tot conflict, bijvoorbeeld aanvallen op vee en huisdieren. Om speculatie over de omvang te vermijden, heeft onderhavig onderzoek tot doel het dieet van de wolf in Vlaanderen te beschrijven.

Van mei 2018 tot en met februari 2021 werden 140 wolvenuitwerpselen ingezameld binnen het enige territorium in Vlaanderen. Identificatie van prooisoorten gebeurde aan de hand van micro- en macroscopische haarkenmerken en bot- en tandresten. De resultaten worden uitgedrukt als de frequentie van voorkomen van prooisoorten/-categorieën ten opzichte van het totale aantal uitwerpselen (=FO). Wilde evenhoevigen vertegenwoordigden veruit het grootste deel van het dieet (FO=90,0%) met ree (*Capreolus capreolus*) (FO=69,3%) en everzwijn (*Sus scrofa*) (FO=22,9%) als vaakst aangetroffen prooisoorten. De consumptie van vee was beperkt (FO=12,9%), maar steeg sterk tot 47,1% FO in de herfst van 2020. Dit wordt verklaard door de aanwezigheid van een eerste nest opgroeiende wolven die nog niet zelf kunnen jagen maar wel gevoed dienen te worden. Het beschikbaar zijn van onbeschermd vee is bijgevolg een gemakkelijk alternatief bij een hogere energetische nood. Onderzoek wijst uit dat, indien zowel wilde prooien als vee abundant zijn, er een voorkeur is voor de eerste. Aanwezigheid van beschermingsmaatregelen versterkt en bestendigt deze relatie. Een evaluatie van schapenweides gaf aan dat slechts 4% in de risicozone afdoende beschermd was in het najaar van 2018. Naast vee, werd bovendien eenmaal een hond als prooi geïdentificeerd.

Hoewel de resultaten een rijke basis van wilde prooidieren reflecteren, wordt evenzeer aangetoond dat de hernieuwde aanwezigheid van de wolf verdere inspanningen vraagt om het samenleven te bevorderen. Dit dient in de eerste plaats te gebeuren onder de vorm van meer afdoende maatregelen ter bescherming van vee. Ook wordt de nood aangetoond van een nadrukkelijker bewustzijn omtrent de hond-wolf-relatie. Conflicten omtrent beide kunnen sterk de publieke opinie sturen ten nadele van de wolf.

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Activity patterns of otters (*Lutra lutra*) in De Onlanden Nature Reserve, the Netherlands

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Abstract: The otter (*Lutra lutra*) population in the De Onlanden Nature Reserve (Province of Groningen, the Netherlands) has been monitored for four years using seven cameras placed at locations where otters regularly passed. Analyses of the recordings of these cameras showed that otters were present and active throughout the year and were mainly active in the dark period of the day. Males were found to be most active in the late summer months, while family groups were seen mostly in the winter months and were absent in the summer period. During the long winter nights, activity was spread out over the whole night and family groups and 'other' otters continued to be active at a low level in the daytime hours. Males were not active in daylight. Both males and family groups seemed to have short breaks during their night time activity. In the short summer nights the otters started being active a little (1-2 hours) before sunset and were most active at the start of the dark period. Activities diminished gradually during the night, continuing until approximately one hour after sunrise. Almost no activity was recorded during the long daytime period in summer. Comparison of locations with and without human disturbance (i.e. traffic) showed that in the absence of human disturbance the otters (especially families) were significantly more active during the daytime period.

Keywords: otter, *Lutra lutra*, De Onlanden, monitoring, camera, activity patterns, disturbance.

Introduction

Between 2002 and 2008 otters (*Lutra lutra*) were successfully reintroduced in the Netherlands with the release of 31 individuals in de Weerribben-Wieden National Park (Kuiters et al. 2011). Migration from this new and rapidly growing population brought otters into the De Onlanden Nature Reserve in 2013, where they flourished, due to the favourable environment, that offers plenty of food and is relatively undisturbed by human presence. In a few years the population in De Onlanden had grown to a more or less stable size of one to three males and five to eight females with their cubs (van Boekel 2016-2020). Yearly DNA-analysis of otter spraint samples showed that one dominant male was present in the largest, central part of De Onlanden, while the other males were living on the outskirts of the reserve (Kuiters et al. 2015-2020). The dominant male remained the same individual (labelled NB351 by Kuiters et al.) in all the years between 2014-2020, but the other males were often replaced by newcomers. DNA-analysis and monitoring with cameras showed that the females had their territories throughout the reserve, although most of them lived in the central part. Each year three to five females had litters of one to (exceptionally) four cubs. Some females were present over longer periods, as shown by DNA-analysis, but some changes in the female population occurred over the course of time too (for full details on the development of otter population in De Onlanden, see van Boekel 2016-2020).

Monitoring of the otters in De Onlanden was started in 2014 with one wildlife camera. By 2016 seven cameras were in use permanently throughout the year. The primary purposes of the monitoring were to follow the development of the otter population and the distribution of the individuals over the reserve. However, the large dataset that was collected over the years can also be used to try to answer some questions on otter activity patterns in De Onlanden. At what part(s) of the day are otters most active? Are there differences in activity patterns between sexes and/or other subgroups? Do activity patterns change over the seasons? Does human presence influence otter activity patterns? This study uses the dataset of recordings of otter activity in De Onlanden to address these questions.

Methods

Study area

The De Onlanden Nature Reserve is situated in the northern part of the Netherlands (figure 1). It consists of approximately 3000 ha of marshlands and grasslands with a large system of interconnected small rivers, canals and other water courses (for a full description of the origin and structure of De Onlanden, see van Boekel 2015). Surface water levels are high and fluctuate continuously in a natural way, depending on rainfall and transport downstream. Water levels are lowest in the summer period and can be up to 50 cm higher in the winter period. Fish can migrate freely both within as well as towards and from De Onlanden and find good spawning grounds in the large shallow water areas in the reserve. They are thus abundant in all the waters in

Figure 1. Location of De Onlanden Nature Reserve, which is situated in the northern part of the Netherlands (inset), also showing the positions of the permanent wildlife cameras (numbered 1-6).

the reserve (R. van Hezel, aquatic ecologist, Noorderzijlvest Regional Water Authority, personal communication). Wherever main roads in De Onlanden, with a high density of motorised vehicles, cyclists and/or pedestrians, cross the main water courses, the safe migration of otters (and other water-connected large animals) is secured by large sandy banks under the bridges (fauna passages, see figure 2). Human presence in the reserve is largely restricted to the roads and a few paths that run through it. Activities such as fishing, canoeing or swimming are prohibited in most watercourses. Maintenance activity is restricted to a small part of the reserve where cattle graze and the grasslands are mown once a year. Because of these restrictions, human activity and disturbance is minimal throughout the year in the most of the reserve.

Monitoring

The monitoring of otter abundancy and activity in De Onlanden was done with wildlife cameras at six fixed locations. The cameras were placed at locations with high level of otter activity (i.e. where many fresh spraints were found) in different parts of De Onlanden (the locations are shown in figure 1). Three of these locations were situated at fauna passages under road bridges with much traffic (locations 1-3 in figure 1), the other three fixed locations were situated far from human disturbances along water courses and at a dam in a watercourse (locations 4-6 in figure 1). Another (seventh) camera was placed in succession at changing locations in the reserve where new or a higher level of otter activity (visible as spraints or other traces) was found. Bushnell cameras of different types were used. All were so-called 'no glow' cameras, with special filters to reduce the visibility of the infrared light of the camera for animals. All cameras made 30 second video films at a 'normal' sensor level, with a reactivation time of 1 second after each recording. The batteries and SD cards of all cameras were replaced every two weeks. No measures were used to encourage the otters to visit the camera sites more often (such as spreading fish oil), so all the behaviour of the animals can be considered natural.

For this study all the data of otter activity gathered between 1 January 2016 and 31 January 2020 were used. For each occurrence of one or more otters at a camera site, the date, time of day, number of otters and (if possible) sex of the animal was recorded. All time-data from the summer season were adjusted to Dutch winter time. For the comparison of activity in winter and summer the data from the months November–January (winter) and May–July (summer) in all years were combined. In the dataset three otter subgroups were distinguished: 'male', 'family' (mother with one or more cubs), and 'other'. The sex of the animal could only be recorded with certainty for males with clearly visible genitals as the size of individuals was found to be an unreliable criterion for distinguishing between male and female otters. Families were defined as two or more otters, appearing in the record together and clearly being a mother with cubs, i.e. a large otter with one or more clearly smaller otters and/or showing the typical behaviour of family groups (much harmonious and playful interaction, frequent communication sounds, swimming side by side, etc.). All otters that could not be identified as either male or family were defined as 'other' otters. This group thus included single females and solitary youngsters, but also males and families that could not be identified as such. Often the quality of the camera recordings was not good enough (due to weather conditions or only partly visible animals) to derive detailed information. Otters on these recordings were also classified as 'other'. On the rare occasions that two adult otters were visible at the same time (distinguishable from a family by their size and, often aggressive, behaviour), they were recorded as two sepa-

Figure 2. A. View of the fauna passage at location 2 (see figure 1) in April 2012, shortly after it was constructed. In later years the vegetation around the passage became much higher. B. The sandy bank on the northern shore of the fauna passage at location 1 in April 2020, with clear signs of otter activity such as the scraped heaps of sand used for sprainting.

rate individuals. During the research period data from cameras that were placed temporarily in De Onlanden by other persons were sometimes added to the dataset, but only after review by the author of the recordings made by these cameras. These data make up less than 4% of the total.

To demonstrate the degree of similarity between two rankings, Spearman's rank correlation coefficient was used to assess the significance of the relation between them. To determine if two categorical variables from the same population have a significant correlation, the Chi-square test was used. For both tests a Bonferroni correction for repeated tests was applied and the probability of obtaining a difference by chance was set at P<0.01.

Results

Number of recordings per year/ subgroup

In the research period (January 2016-January 2020) a total of 6092 unique recordings of one or more otters were registered with the cameras. Of these, 626 recordings were of families (female with one or more cubs) and 761 recordings were of otters that could be identified as males. The largest part of the recordings (5140 in total) were made at the fauna passages (locations 1-3 in figure 1) that were often used by the otters not only for passing safely under the roads, but also for leaving their scent marks and sometimes for hunting, grooming or even sleeping. At location 1, in the central area of the reserve, the camera registered otters almost every night during the research period and sometimes up to five recordings of passing otters were made in one night.

The recordings of males showed a clear peak during the late summer period, while recordings of families peaked during the winter period. The recordings of 'other' otters were distributed fairly evenly over the months of the year (figure 3). These patterns were the same every year and were not correlated with each other, Spearman rank correlation; n=12; male–family: -0.343 (n.s.); male–other: -0.021 (n.s.); family–other: -0.028 (n.s.), so the peaks of recordings found for males and families in summer and winter respectively can be considered to be realistic.

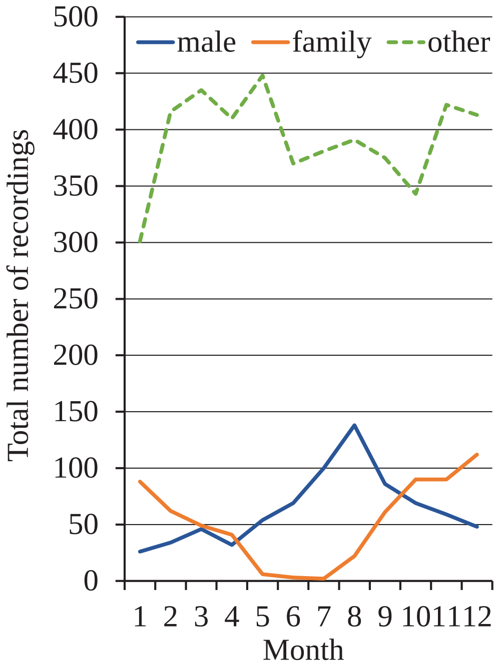

Figure 3. Distribution of unique recordings per month (as total recordings for each month over the research period) for male otters, families and other otters.

Daily patterns

In general, the otters were most active in the dark. This resulted in a clear difference in activity patterns of the otters between seasons. In the short summer nights (figure 4A) the otters became active approximately one - two hours before sunset and were most active at the start of the dark period. The activity level fell gradually during the rest of the night until approximately one hour after sunrise. Daytime activity was very low. There was

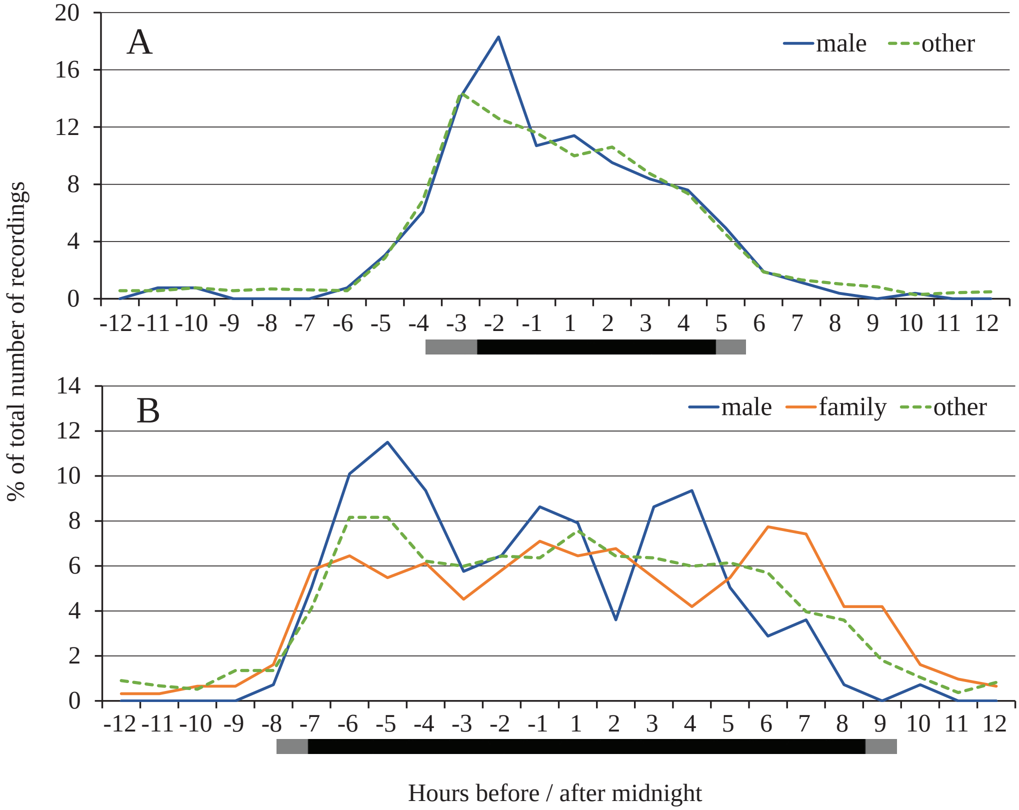

Figure 4. Distribution of recordings per hour (as % of total recordings over this part of the research period) in: A. The summer period (May-July) for male and other otters. B. The winter period (November-January) for males, families and other otters. Black and grey bars on the X-axis respectively show the minimum length and the maximum length of the dark period during the summer (A) and winter (B) period.

no clear difference in the daily activity pattern between males and other otters (Spearman rank correlation 0.905, *P*<0.01). The total number of recordings of family groups in the summer period was too low to analyse. During the long winter nights (figure 4B) all otters (males, families, and others) became active at sunset and remained active during the whole dark period. The heterogenous 'other'-group showed no distinctive pattern in activity during the night. The male otters seemed to have periods with higher activity interspersed by periods of low activity. This pattern suggests that the males took breaks between hunting sessions for grooming and/or sleeping. Families also showed this pattern of alternating higher and lower activity, although not as distinctly as the males. Both the males and families displayed this high-low activity pattern each winter, but the variation in these patterns between winters was large and the number of recordings for males and families was too small to confirm any statistically significant pattern of high and low activity in the data. In winter, males stopped activity well before sunrise and were not active during daytime hours. Families remained highly active for some time into the light period. Both families and the other otters were active at a low level during the light period.

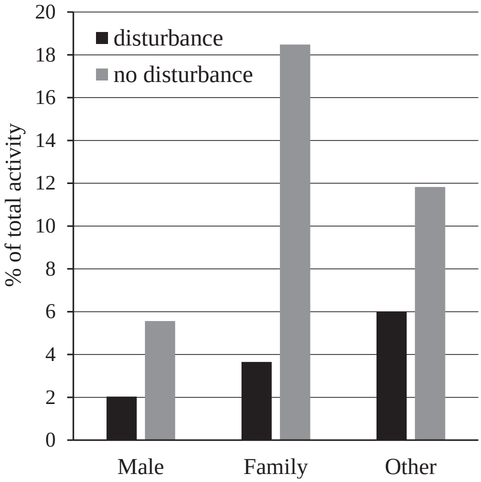

Figure 5. Daytime activity (as % of total activity at the given locations in the research period) of males, families and other otters at locations with human disturbance and with no human disturbance.

Relation with disturbance

The influence of disturbance by human presence (in the form of vehicle, bicycle and pedestrian traffic) on the activity patterns of the otters was analysed by comparing the daytime activity of the animals between sites with relatively high disturbance levels (locations 1-3 in figure 1) and undisturbed sites (locations 4-6 in figure 1). Figure 5 shows that all groups of otters were clearly more active during daytime at locations without human disturbance. This difference proved to be significant for families and other otters, but not for the male group (family χ^2 (df=1): 29.095, P<0.01; male χ^2 (df=1): 3.516, P=0.061 (n.s.); other χ^2 (df=1): 24.87, P<0.01).

Discussion

The large dataset of camera recordings of otters in De Onlanden showed the clear preference of this species for night-time activity. This nocturnal way of life has also been found in studies of otters in Portugal (Beja 1996, Quaglietta et al. 2018) and Scotland (Garcia de Leaniz et al. 2006), although Kruuk (2006) mentioned that otters living on the shores of the Shetland islands were active during the daytime. Here otters foraged for fish in the seawater around the islands. These fish were sleeping on the ocean floor during the day, so otters could easily catch them. In fresh water, the many fish species show no clear or uniform patterns of daily activity (Reebs 2003). For most fresh water fish species the preference for day or night time activity depends on other variables such as water temperature, the time of year, food conditions and/or predator activity and abundance. Otter activity patterns in fresh water therefore cannot easily be linked to the activity of their prey. In De Onlanden there is a great variety and abundance of prey available for the otters throughout the reserve, ranging from many different fish species, occurring often in large numbers, to amphibians, crayfish and waterbirds (personal observations). The otters were often seen hunting and catching fish, seemingly without effort, in front of the cameras. It can well be assumed that food availability was not the key factor determining their preference for night time activity.

Another explanation for their nocturnal life could be the avoidance of human presence. Otters are known to be shy animals, that flee immediately if disturbed by human activity. Only a few other otter studies have considered the influence of human presence on otter behaviour, possibly because most studies were done in areas with very limited human presence. Beja (1996) found that human activity had an influence on the selection of resting places by the otters living on the coast of Portugal, but not on their daily activity pattern. Kruuk (2006) found no relation between human activity and the location of the daytime resting places of otters living in Scottish fresh water lochs. He also mentioned examples of otters living and hunting in close proximity to humans, even in cities, and sug-

Wildlife camera view of an otter on the bank of the fauna passage under the main road at location 2 in De Onlanden during daytime, looking up at cyclists passing over the adjacent cyclists bridge.

gested that abundance of food is the key factor for the presence (or absence) of otters in any area. In the city of Groningen, close to De Onlanden, two different male otters were found living in the canals in the centre of the city in wintertime (H. Jansma, personal observation). DNA monitoring showed that one of these otters relocated to De Onlanden in the following two years (van Boekel 2020, Kuiters et al. 2020). Possibly, the otters in the city were young males without territory that preferred to follow their fish prey into the warmer waters and accept human presence. These city-otters were also only active during the night, probably to avoid the attention of humans. In De Onlanden, otter families and ‘other’ otters were significantly more active during daytime hours at locations without human disturbance compared to locations with regular human disturbance (motorcars, cyclists and pedestrians passing over the bridges). For the male otters this difference in daytime activity was found to be (just) not significant, but possibly this is an effect of the relatively small number of recordings for this group in the statistical analysis. Human disturbance may be a factor influencing the daily activity pattern of the otters in De Onlanden, resulting in the animals being most active in the dark period when human presence is minimal, but more research is needed to determine the extent of this influence.

Most recordings of male otters in De Onlanden were made during the late summer period, and they were rarely seen during the winter months. The recordings of otter families showed an almost opposite pattern. Although Eurasian otters have no strict reproductive season (Kruuk 2006), in De Onlanden most females had their litters at approximately the same time. The mothers and cubs started to appear on camera in late autumn and were seen all winter. In the next spring the young otters appeared progressively more solitary on the camera recordings and eventually they were no longer present in the area or could at least no longer be distinguished as youngsters in the recordings. The peak of male otter recordings in late summer may partly be explained as the appearance of young solitary male otters in the area, originating both from within and outside (migrat-

Wildlife camera view of an otter at location 5 on the bank of the main small river (Peizerdiep) in De Onlanden during daytime.

ing youngsters) De Onlanden. Possibly the dominant male also expanded and intensified his activity at that time in reaction to the presence of these young males in his territory.

During the short summer nights in De Onlanden, with only seven hours of darkness, the otters apparently were able to find enough food to help them through the long period of inactivity during the day. Their activities started before it was getting dark, possibly because human disturbance was already low at that late hour and the otters were eager to catch food after the long daylight period. After sunset the otters immediately showed a high activity level that gradually diminished towards the end of the night. There was no significant difference in this pattern between males and other otters, although the males seemed to be more active at the start of the night. In the long winter nights the otters were active during the whole dark period of approximately 16 hours. Males became less active at the end of the dark period, possibly because they had caught enough food to get them through the day. Families remained highly active well into the light period, possibly because a mother with cubs needs more time to catch enough food. The relatively large (but statistically not significant) differences in activity found during the night for both males and families suggests that the otters alternated periods of high activity with short periods of less or no activity. Kruuk (2006) described the necessity for otters to take breaks between feeding sessions in order to restore their body temperature after cooling down in the water. For the otters in De Onlanden this could also be an explanation for the apparent pattern of alternating activity and resting during the nights in the cold winter months. In Portugal, otters fitted with radio transmitters were also found to have an activity pattern with two peaks during the night time in the winter period (Quaglietta et al. 2018). Their activity continued at a low level into the light period. In the summer period Quaglietta et al. found one activity peak in the night and almost no activity in the daytime period. The authors explain the absence of daytime activity in the summer as avoidance of the period with high temperatures by the otters. In the Netherlands, with a more temperate climate, high summer temperatures cannot be assumed to have a relevant influence on otter behaviour. It seems more likely that the abundance of fish and other prey provided the otters with enough food in both summer and winter to be able to stay in their resting places for most of the daytime period. Comparison of the results presented here with activity patterns of otters living in temperate climate environments with less available food would be welcome, but no relevant data are available yet from such locations.

Monitoring otters with the use of strategically placed wildlife cameras over a period of several years proved to be a relatively easy method to collect a large dataset on otter activity that can be used to show and compare the activity patterns of otters living in different environments. If, in future studies, this method can be combined with techniques to identify the individual otters in the images (i.e. computerised identification) much more could be learned about the behaviour of this elusive species.

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Samenvatting

Activiteitspatronen van otters in natuurgebied De Onlanden

In natuurgebied De Onlanden werd de otterpopulatie (*Lutra lutra*) gedurende vier jaar gevolgd door middel van zeven wildcamera's. Drie camera's waren geplaatst bij bruggen met faunapassages onder wegen waar jaarrond veel verkeer (auto's, fietsers, wandelaars) pas-

seerde. Drie andere camera's stonden op locaties langs waterwegen waar juist geen mensen in de omgeving kwamen. Eén camera werd op steeds wisselende plekken met veel (nieuwe) otteractiviteit geplaatst. Van elke cameraopname van één of meerdere otters werden datum, tijdstip en aantal otters genoteerd. Ook werd genoteerd of het een mannetje betrof (genitaliën zichtbaar) of dat het om een familiegroep ging (moederotter met één of meer jongen). Vaak liet de kwaliteit van de opname niet meer toe dan de vaststelling dat het om een otter ging. Deze groep wordt hier 'overige otters' genoemd. De monitoring leverde in totaal 6092 afzonderlijke opnames op, waarvan er 761 van een herkenbaar mannetje waren en 626 van families. De opnames van de overige otters waren redelijk gelijk verdeeld over de maanden van het jaar, maar bij de mannetjes piekte het aantal opnames in de late zomerperiode terwijl in de wintermaanden relatief weinig opnames werden gemaakt. Families werden juist veel in de wintermaanden gezien en vrijwel niet in de zomermaanden. Alle otters waren gedurende het hele jaar vooral in het donker actief, maar in de (korte) zomernachten begon de activiteit al ruim (1-2 uur) voor zonsondergang, waarna direct aan het begin van de nacht een activiteitspiek bereikt werd. De activiteit nam daarna geleidelijk af tot een uur na zonsopkomst. Tijdens de lange winternachten werden de otters pas in het donker actief en ging de activiteit het grootste deel van de nacht in wisselende mate en zonder duidelijke piek door. Families bleven na zonsopkomst nog enige tijd actief, maar mannetjes stopten hun activiteit al ruim voordat het licht werd. Op de locaties met veel verstoring door verkeer waren alle otters significant minder vaak actief in de lichtperiode dan op de locaties zonder menselijke activiteit in de buurt. Vooral otterfamilies waren op de locaties zonder verstoring veel vaker overdag te zien op de camerabeelden. De otters in De Onlanden lieten activiteitspatronen zien die ook al bij otters in andere leefgebieden gevonden werden. De seizoenspatronen in de waarnemingen van zowel mannetjes als families zijn, voor zover bekend, nog niet eerder gemeld. De voorkeur voor nachtelijke activiteit wordt soms verklaard als een nachtelijk voordeel voor de otters bij de jacht op vis, maar deze koppeling kan in De Onlanden niet met zekerheid gemaakt worden. De resultaten tonen wel aan dat otters in De Onlanden overdag meer actief zijn op plaatsen waar verstoring door menselijke activiteit ontbreekt. Of dit ook in andere leefgebieden van otters zo is zou onderzocht moeten worden.

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