LUTRA

Journal of the Dutch Mammal Society
Volume 66 – Number 2 – December 2023

LUTRA

Volume *Deel* 66 – Number *Nummer* 2 – December 2023

Lutra is a scientific journal published by the Dutch Mammal Society (Zoogdiervereniging). The society is dedicated to the study and protection of native mammals in Europe. Lutra publishes peer-reviewed scientific papers on mammals across all disciplines, but tends to focus on ecology, biogeography, behaviour and morphology. Although exceptions are made in some cases, Lutra generally publishes articles on mammal species native to Europe, including marine mammals. Lutra publishes full articles as well as short notes which may include novel research methods or remarkable observations of mammals. In addition Lutra publishes book reviews. Lutra publishes in British English and in Dutch. Lutra is an open access journal and Lutra has no page charges. Lutra publishes two issues per year and Lutra is indexed in 'Biological Abstracts' and 'Zoological Record' and 'Artik'.

Address *Adres*: P.O. Box 6531, NL-6503 GA Nijmegen, the Netherlands
e-mail: lutra@zoogdiervereniging.nl

Website: Lutra is available from the internet: www.zoogdiervereniging.nl

Subscription *Abonnement*: The annual fee for a subscription to Lutra is € 27,50
The annual fee for a Lutra subscription and Zoogdiervereniging membership is € 45,–. This also includes a subscription to Zoogdier, a journal that publishes in Dutch.
Students are entitled to a discount of € 4,50 for the first two years of their Zoogdiervereniging-membership.

To subscribe please visit https://www.zoogdiervereniging.nl/lidworden#no-back

DUTCH MAMMAL SOCIETY

Information *Secretariaat*: Zoogdiervereniging, P.O. Box 6531, NL-6503 GA Nijmegen, the Netherlands
tel. +31 (0)24 74 10 500
e-mail: lutra@zoogdiervereniging.nl
website: http://www.zoogdiervereniging.nl

Photograph cover by: Yves Adams / Vilda (Reeves' muntjac)

Art: Ed Hazebroek (p. 76, harbour porpoise; p. 122, raccoon dog)

ISSN 0024-7634

The Pleistocene overkill

More than half of the planet's large mammal species have become extinct since the last Interglacial, which ended about 120,000 year ago. Whilst this has happened all over the world, the extent of these extinctions is not geographically uniform, with Europe, northern Asia, the Americas and Australia experiencing a far greater number and proportion of mega-fauna extinctions than Africa and southern Asia.

For over fifty years there has been a heated debate about what has caused these extinctions. In 1966 Paul S. Martin (1966) formulated the Pleistocene overkill hypothesis in the journal Nature. This hypothesis has been tested in many publications. Almost ten years ago researchers at the University of Aarhus published the results of their examination of the correlations between the number of extinct large mammals, human pressure and changes in temperature and precipitation (Sandom et al. 2014). This month an article was published in the journal Anthropocene, that, again, presents good evidence that hunting by man, rather than climate change, was the main cause of these extinctions (Lemoine et al. 2023).

Africa is the continent of the origins of modern man. From there they first occupied southern Asia and then expanded in other directions. Remmert (1982) has put forward evidence that the reason for the relative richness of the African mammal fauna is a very early co-evolution between evolving man and the mega-fauna of this continent. Continents without such an early co-evolution, like the Americas, suffered severe losses of their native mega-fauna when early hunters invaded them. Hortolà and Martínez-Navarro (2013) put forward another explanation. They argue that mega-fauna have only survived until recent times in areas where modern man has not been able to thrive: basically the African savannahs and rainforests and the Southern Asian rainforests. Tropical rainforests are not the best habitat for *Homo sapiens* and its predecessors, so until recently they have remained sparsely inhabited. The vast African savannahs are areas where human settlement has been historically limited due to the tsetse fly (*Glossina* spp.), which transmits the deadly sleeping sickness.

It has even been suggested that Neanderthal man and the closely related Denisova man were also victims of the invasion of modern man into Eurasia. Hortolà and Martínez-Navarro (2013) argue that those two extinct archaic *Homo* species should be considered to be part of the Pleistocene overkill. Except in its native continent of Africa, in the other continents *Homo sapiens* could be considered as an invasive species, and since the Industrial Revolution, following its exponential demographic increase, as a worldwide pest species. It seems that Palaeolithic man did not exploit the mega-fauna in a sustainable way and depleted it, including some of history's most charismatic species. They were aggressive and skilful hunters, perhaps even eradicating archaic man.

Given the big impact of large-bodied animals on vegetation structure, plant dispersal, nutrient cycling and co-dependent biota, the simplification and downsizing of mammal faunas worldwide represents the first planetary-scale, human-driven transformation of the environment. It has been argued that the start of the Pleistocene overkill should be the beginning of the envisaged new geological epoch: the early Anthropocene (Malhi 2017). However this claim seems to be exaggerated, as it would mean that the Holocene should be ignored.

The Dutch atmospheric chemist and Nobel Prize laureate Paul J. Crutzen proposed taking the start of the Industrial Revolution in the 1780s as the starting point of the Anthropocene. He has widely popularised the term 'Anthropocene' and has argued that the influence of human behaviour on the Earth's atmosphere since the Industrial Revolution is so significant as to constitute a new geological epoch for its lithosphere (Crutzen 2002).

In 2009, the International Union of Geological Sciences (IUGS) created the Anthropocene Working Group. In May 2019 a large majority of this working group voted in favour of denoting the present geological time period as the Anthropocene, which started around the mid-twentieth century. This starting point is much later than the Industrial Revolution, as proposed by Paul Crutzen. The IUGS argued that the most notable changes in the lithosphere, such as the worldwide radioactive fallout from testing of hydrogen bombs, have happened from the 1950s, much later than the changes in the atmosphere. It is expected that the congress of the IUGS in 2024 will approve the recommendations of their Anthropocene Working Group. After the approval the Anthropocene will be official. This will be a 'late' Anthropocene.

On the subject of hunting large mammals, albeit marine mammals, this issue of Lutra contains an article by Koken et al. which presents a new reconstruction of a mass-stranding of long-finned pilot whales (*Globicephala melas*) in 1825 in the south-western Netherlands. After an extended study of sources, the authors conclude that at least some of the 38 stranded animals were victims of an opportunistic drive hunt.

There is more on sea mammals in this issue. For almost a hundred years the Netherlands has had a system for registering stranded cetaceans. However, until the 1970s the harbour porpoise (*Phocoena phocoena*) was not sufficiently registered, as their numbers were initially very high compared to the other cetaceans. Keijl and Niessen use the old notebooks of two birdwatchers to (partially) close the registration gap between 1931 and 1970.

The other two papers in this issue of Lutra highlight terrestrial mammals. Researchers from two Flemish institutes (the Research Institute for Nature and Forest and the Agency for Nature and Forests) present an account of attempts to control a population of the invasive Reeve's muntjac (*Muntiacus reevesi*) in a large park near the city of Antwerp (D'hondt et al). The authors also provide suggestions on how to improve control practices for this species.

In a final paper, van Manen describes the frequency pattern over time, and interactions of, scavengers, both mammalian and avian, visiting a carcass of a wild boar in a natural setting in a Polish forest. The scavengers were recorded by a camera trap continuously for two months, after which the carcass had disappeared.

References

Crutzen, P. 2002. Geology of mankind. Nature 415: 23. DOI: 10.1038/415023a

Hortolà, P. & B. Martínez-Navarro 2013. The Quaternary mega-faunal extinction and the fate of Neanderthals: An integrative working hypothesis. Quaternary International 295: 69-72. DOI: 10.1016/j.quaint.2012.02.037

Lemoine, R.T., R. Buitenwerf & J.-C. Svenning 2023. Mega-fauna extinctions in the late-Quaternary are linked to human range expansion, not climate change. Anthropocene 44: 100403.

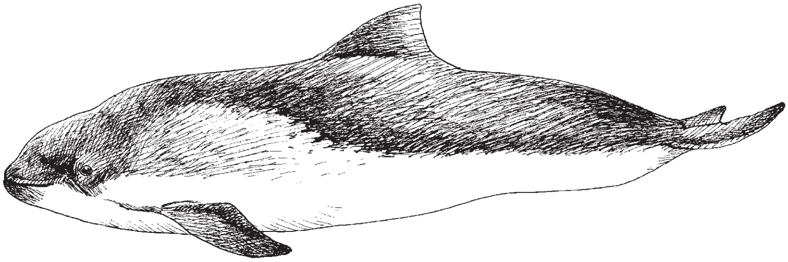
Malhi, Y. 2017. The concept of the Anthropocene. Annual Review of Environment and Resources 42: 77-104.

Martin, P.S. 1966. Africa and Pleistocene overkill. Nature 212 (5060): 339-342.

Remmert, H. 1982. The evolution of man and the extinction of animals. Naturwissenschaften 69: 524–527. DOI: 10.1007/BF00463496

Sandom, C., S. Faurby, B. Sandel & J.-C. Svenning 2014. Global late quaternary mega-fauna extinctions linked to humans, not climate change. Proceedings of the Royal Society B Biological Sciences 281: 20133254. DOI: 10.1098/rspb.2013.3254

Johan Thissen



A peek into the past – harbour porpoise strandings in the Netherlands during the mid-twentieth century

Guido O. Keijl[1] & Harm Niesen[2]

[1] Naturalis Biodiversity Center, Postbus 9517, NL-2300 RA Leiden, the Netherlands,
e-mail: guido.keijl@naturalis.nl
[2] Stierop 12, NL-1862 JL Bergen, the Netherlands

Abstract: Between 1931-1975 two birdwatchers visited the North Sea beach along the central west coast of the Netherlands, independent of each other, but overlapping in both time and geography. On their repeated trips they not only noted the location and length of the stretch of beach they visited, but also the number of dead harbour porpoises (*Phocoena phocoena*). This enables us to calculate the density, i.e. the average number of stranded porpoises per kilometre, which is considered more informative than absolute numbers. The calculated densities of both observers are comparable, as are the monthly and yearly patterns. Combined with the data from the national cetacean strandings database, the porpoise strandings during the study period show a recurrent undulating pattern, also after this period, from 1964 until the late 1980s, when the density was considerably lower.

Keywords: *Phocoena phocoena*, North Sea, mortality, monitoring, historical data.

Introduction

Mapping the at-sea distribution of cetaceans is a methodologically complicated (Buckland et al. 2015) and time-consuming affair. To gain at least some knowledge on cetaceans, an alternative to censusing live individuals is to count dead ones. Counting cetaceans washed on the coast does not give absolute information on the size of a population, but can be considered a finger on the pulse on its state. Also, censusing dead cetaceans is decidedy less costly, while strandings give ample information about the presence and status of various species (Pyenson 2011) as well as provide the opportunity to collect ecological information otherwise difficult to obtain.

In the Netherlands, harbour porpoises (*Phocoena phocoena*) (further: porpoises) have been present for a long time. For instance, they were ‘*fairly common along the entire coast*’ according to Van Bemmelen (1866). Whether or not this status fluctuated or otherwise changed since then is unknown, but during the early decades of the twentieth century Van Deinse (1924) still found the species to be ‘*always common along our coast, also in inland waterways as long as they can be reached from the sea*’. At that time, porpoises could be observed from the beach, from dikes and piers, apparently anywhere along the coast. Dead porpoises also featured regularly on the beach. For instance, Van Deinse (1924) found six dead porpoises between Katwijk and Scheveningen on 1 July 1923, a stretch of only 16 km, and Slijper (1936), when he needed them for study, simply collected three stranded neonates (newly born) on 8 July 1932 on a stretch of beach of 12 km in Noord-Holland, and a further seven in July 1932 on the beach elsewhere in the same province. In fact, dead porpoises were such a regular phenomenon, that there was a supposedly stable and

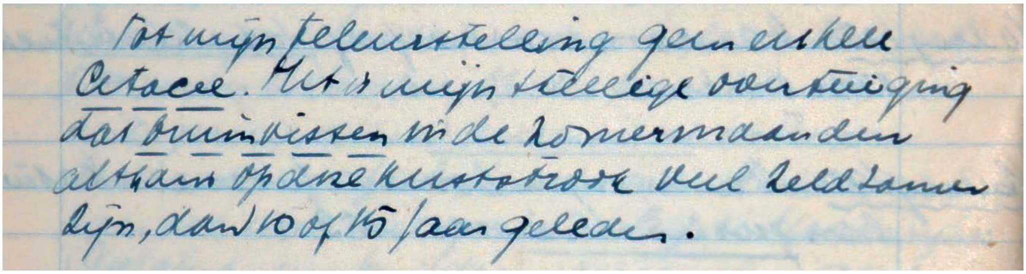

Tot mijn teleurstelling geen enkele
Cetacee. Het is mijn stellige overtuiging
dat bruinvissen in de zomermaanden
althans op deze kuststrook veel zeldzamer
zijn, dan 10 of 15 jaar geleden.

Figure 1. Notes from the diary of Fokko Niesen from 19 August 1950. Apart from notes on birds seen on this day, he mentions the absence of cetaceans (see text). In Dutch, he wrote: "Tot mijn teleurstelling geen enkele Cetacee. Het is mijn stellige overtuiging dat bruinvissen in de zomermaanden althans op deze kuststrook veel zeldzamer zijn, dan 10 of 15 jaar geleden."

pronounced seasonal pattern in strandings, with most encountered in July and August (Van Deinse 1945a). Hence, as is often the case with common species, little attention was paid to their presence and ecology, and porpoises were never mentioned in publications unless there was something special to report (e.g. Van Deinse 1945b). As a consequence, basic ecological information from the first half of the twentieth century, such as numbers, age or diet, is lacking.

Jan Verwey, having a life-long interest in porpoises (Verwey 1975), was one of the first to report a change in porpoise presence. He wrote to Van Deinse (1952) (in Dutch): '*The species (Phoc. phoc.) has decreased significantly in the Wadden Sea and its various entrances during the war. In 1945 they were definitely rare and even today I would call them rather scarce. This is not an impression, but a fact.*' Fokko Niesen, a self-made naturalist living in Haarlem, had noticed the decrease as well, although his data did not refer to live porpoises but to dead ones, and also, the decrease noted by him remained unknown to the general public at the time. After a visit to the beach on August 19th 1950 he wrote in his diary (in Dutch) '*To my disappointment no single cetacean. I strongly believe that harbour porpoises have become much rarer in the summer months, at least on this part of the coast, than 10 or 15 years ago*' (Figure 1).

The letter of Verwey stimulated Van Deinse, who had until then been collecting data on stranded cetaceans in the Netherlands *except* porpoises, to include dead porpoises in his study. He notified the people in his cetacean stranding network to not just report the rare species, but all cetaceans. The first year on which he published all stranded porpoises reported to him was 1951 (Van Deinse 1952). The result was a meagre 24 individuals, and even though Van Deinse stated that this number must certainly have been higher as some carcasses had likely remained out of sight, 24 corpses on over 500 km of coastline seems very low indeed for a species that is supposed to be common. During the years following this first complete report on stranded porpoises, rather few individuals per year were recorded, and even for the next thirty years numbers remained low. There were, for instance, 26 porpoises in 1953 (Van Deinse 1954), 13 in 1963 (Van Deinse 1964), 22 in 1973 (Van Bree & Husson 1974) and 26 in 1983 (Smeenk 1986). From the late 1980s onwards, porpoises increased again in Dutch coastal waters (Camphuysen 2004, IJsseldijk et al. 2020) and parallel to it the number of stranded individuals (www.walvisstrandingen.nl). The cause, or causes, for neither the demise nor the return of porpoises in Dutch waters have ever been elucidated.

So, even though the precise evolution of the Dutch porpoise population during the twentieth century remains unknown, there is no doubt that porpoises were common in Dutch waters in the early decades of the century, decreased strongly around the middle, were very scarce in the 1960s-1980s, and increased again from the late 1980s onwards. An analysis of strandings during the twentieth century revealed that not only had there been a shift in peak numbers from summer prior to the 1950s to winter in the years thereafter, but also that neonate porpoises had largely disappeared after the 1950s (Addink & Smeenk 1999). Anno 2023, living porpoises are again a common sight along the Dutch coast (Soldaat & Poot 2020, IJsseldijk et al. 2021, www.trektellen.nl, www.waarneming.nl), and also neonates are found regularly on the beach in summer (www.walvisstrandingen.nl). In countries neighbouring the Netherlands, a similar trend is observed (IJsseldijk et al. 2020).

Despite extensive research on Dutch porpoises in recent years (e.g. Jansen 2013, Leopold 2015, IJsseldijk 2021), the question as to why porpoises have disappeared and subsequently returned in national waters has not been answered yet (Camphuysen 2004, Camphuysen & Siemensma 2011). Among the many unknowns about porpoises in the Dutch part of the North Sea, a nagging question remains how the supposedly high numbers of dead porpoises on the shore today compare to those a century ago. Even though the national database (www.walvisstrandingen.nl) contains strandings of porpoises from the early twentieth century, it has until now been considered unfeasible to compare present day stranding patterns with those from former times, as the older data were thought to be largely incomplete and any resulting pattern should therefore be seen as unreliable (Smeenk 1987). Nevertheless, a continuous series of counts of stranded porpoises is available since the early 1950s until today, albeit with an annoying break between 1964 and 1970.

Monitoring dead cetaceans is nowadays carried out in most countries bordering of the North Sea. Generally, when the strandings are reviewed, it is common practice to present the total number per country per month or per year (e.g. Smeenk 2003 for the Netherlands, Siebert et al. 2006 for Germany, Leeney et al. 2008 for the United Kingdom, Haelters et al. 2018 for Belgium, Kinze et al. 2018 for Denmark). A more valuable measure for common species however is to present the density, i.e. the average number of animals per unit of length (for instance kilometre; cf. Camphuysen et al. 2008, Keijl et al. 2016, 2021, Kinze et al. 2021), as this enables the comparison of the stranding intensity in a geographical as well as a temporal context. A prerequisite to do so is to know the observation intensity. Although the observation intensity at present is rarely mentioned and usually unknown, most parts of at least the Dutch beaches are visited nowadays by people probably at least once a week, and many stretches daily, by numerous people. Hence, on most parts, it seems hardly possible for a porpoise carcass to remain undetected. We could call this continuous censusing effort.

Between the 1930s and the early 1970s two Dutch naturalists, Fokko Niesen and Henk Kortekaas, regularly visited the beach. They both kept a diary in which they took detailed notes about their natural history adventures, and they included dead cetaceans. Together they have collected a unique set of data on dead porpoises from around the middle of the twentieth century, an important era in the history of porpoises in the southern North Sea, but a period neglected by Van Deinse regarding this species. Here, we describe this recently discovered dataset. It enables us to calculate densities of dead porpoises on the beach during these years. Although densities of stranded individuals have not been calculated in earlier studies (Van Deinse 1952, Addink & Smeenk 1999), they suggest a serious decline of porpoises in the Wadden Sea and adjacent estuaries from the early 1940s onwards. By analyzing the data of Niesen and Kortekaas, we expect to better pinpoint the drop in strandings, either '*during the war*' (the early 1940s; cf. Verwey in Van Deinse 1952) or in '*the late 1950s/early 1960s*' (cf. Addink & Smeenk 1999). The densities of Niesen are also separately compared with those of Kortekaas, to check the validity of monthly and yearly strandings patterns. If they match, the calculated densities from Niesen and Kortekaas may be considered representative for the local situation at the time. The data can then also be compared with those from the national database, which are less systematically collected. Although the densities may differ between the Niesen/Kortekaas data on the one hand and the national database on the other, we expect to find similarity in patterns. The combined set can then be compared with the data of Addink & Smeenk (1999), who described the pattern of porpoise strandings in the Netherlands between 1920 and 1994, and, especially, with present day strandings. Hopefully, the results contribute to a better understanding of the sudden and steep increase in porpoise strandings in the south-eastern North Sea since 2006.

Methods

The study area considered spans the beach between Hoek van Holland and IJmuiden. The beach in this part of the North Sea is a fairly narrow sandy strip, on average about 90 metres wide. From the diaries of Kortekaas and Niesen, records of dead porpoise were extracted[1]. Niesen and Kortekaas visited the same parts of the Dutch coast, although never together, and their visits overlap in time. On most of their excursions they indicated which stretch of beach was visited, and they did so for decades. Although both men were interested in nature in general, their visits to the beach focused on birds. This resulted in a seasonal pattern of visits. Both Niesen and Kortekaas not only mentioned a dead porpoise in their diaries, but also wrote down their precise location (usually relative to the nearest numbered beach pole).

Fokko Niesen was born in Haarlem, Noord-Holland, in 1913 and lived there during his entire life. His diaries cover 1931-1975, a period of 45 years. When looking for birds along the sea shore, he usually entered the beach at Zandvoort, about six kilometres west of Haarlem. Later on, he worked in Katwijk, Zuid-Holland, and regularly traveled home from work on his bicycle along the beach from Katwijk to Zandvoort. He also visited the beach to look for birds during weekends. Niesen was very precise about his excursions. He specifically mentioned dead cetaceans on the beach and wrote down details such as the animals' sex and length. Niesen apparently carried a measuring device, as the measurements written down by him are very precise.

Henk L. Kortekaas was born in 1923 and lived in Den Haag, Zuid-Holland (Kortekaas & Peeters 2014). His diaries to our disposal span the years 1938-1958, a period of 21 years. Kortekaas's diaries contain less information on daily activities. He often merely wrote down the names of the birds he observed, without mentioning which part of an area was visited. Apart from the records from the diary of Kortekaas, we also have the list of cetaceans which he in 1978 sent to P.J.H. van Bree, then curator of mammals of the Zoological Museum of Amsterdam University, and compiler of reviews of dead cetaceans on the beach (e.g. Van Bree 1977). In this list there is sometimes more information than in the diaries, and the source containing most information was used.

Densities, i.e. the number of porpoises found per kilometre of beach, are calculated by dividing the total number of porpoises by the length of the trajectory visited. In a few cases, and only concerning the records of Kortekaas, the trajectory was not described in the diary nor in the letter to Van Bree, but could be inferred with near-certainty from the beach pole numbers noted during the visits. Only in two cases

[1] A few diaries of Kortekaas were missing from the archives of the Heimans en Thijsse Stichting during our visit to the library in July 2021.

dead porpoises found by Niesen are omitted because the trajectories are unknown. In their diaries Niesen and Kortekaas also mentioned the carcasses they had found during their earlier visits, so we are certain that the data do not include double counts.

Presently, the national strandings database, available at www.walvisstrandingen.nl[2], containing data on all cetaceans found in the Netherlands, is managed by Naturalis Biodiversity Center. The core is formed by strandings collected by A.B. van Deinse, and it has been extended by others after his death until present (e.g. Scheygrond 1964, Van Bree & Husson 1974, Keijl et al. 2021). The data rarely, if ever, provide information on which stretch of beach was searched for stranded cetaceans, hence the data of Niesen and Kortekaas, who usually visited a part of the beach between Hoek van Holland and IJmuiden, are not directly comparable. The beach in the area under consideration is narrow, flat and open, and a porpoise washed on the beach lies exposed and is very visible. As the beach in the study area is crowded nowadays, and most of it visited on a daily basis, the search effort can be considered continuous. Therefore, if data from the national database are used, the cumulative number of dead porpoises is divided by 62 (kilometres), which is the total length of the stretch of beach between Hoek van Holland and IJmuiden.

Results

The contributions of Niesen and Kortekaas

Between 1931-1973, Niesen found 216 porpoises on 127 trips in 28 years. Of these, 214 porpoises found on 125 trips in 28 years covering 909 kilometres are used for further analysis. Niesen's trips to the beach used for the analysis ranged between Scheveningen in the south to IJmuiden in the north. The stretch between Langevelderslag (north of Noordwijk) and Zandvoort was visited most by him (Table 1). Niesen went to the beach most frequently in the 1930s (Table 2), with a peak of 19 visits in 1934, and 5-10 visits in most of each of the following years. His average trip length was 7.3 km. This increased from 6 km in the 1930s to 11 km in the 1950s, after which it decreased to 5 km in the 1960s and 2 km in the 1970s. He found porpoises in every single year between 1931 up to and including 1942. His first visits to the beach after the Second World War were in 1945, but he reported his first post-war porpoise only in 1948. After the war the intervals during which he did not go to the beach increased, or he paid brief visits only. There were, for instance, no visits at all between July 1961 and October 1963. Still, he found porpoises in every single year between 1950 and 1958, and from then on intermittently until 1973.

Kortekaas found a total of 95 porpoises on 55 trips in 14 years between 1941-1961, of which 87 during 42 trips in 14 different years covering 411 kilometres are used here (Table 1). (The eight porpoises not used in the analysis were found elsewhere.) Most visited by him was the beach between Scheveningen and Katwijk, but his activities stretched between Hoek van Holland in the south to Bloemendaal in the north, so he has visited more different parts of the beach than Niesen. Kortekaas paid fewer visits to the beach (a maximum of six in both 1940 and 1954), but they were on average longer (9.9 km), especially in the 1940s (11 km). In the 1960s he only made a single trip (Table 2). He found his first porpoise on 14 September 1941, his second in 1947 and none in 1948. From 1949 until 1959 he reported porpoises in every year, and his last one dates from 1961.

During and immediately after the Second World War, between 1942 and 1946, vari-

[2] The website www.walvisstrandingen.nl will cease to exist early in 2024. From then on, dead cetaceans as well as other marine mammals will be recorded on www.stranding.nl

Table 1. Stretches of beach (and their length) visited by Niesen and Kortekaas between 1931-1973, arranged from south to north, the number of visits and the number of porpoises found. The total number of visits is lower than the accumulated number (142 instead of 125 for Niesen, 49 instead of 42 for Kortekaas) because on a single visit different stretches could have been visited.

Stretch	Length (km)	Niesen		Kortekaas	
		n visits	*n* porpoises	*n* visits	*n* porpoises
Hoek van Holland - Monster	6	0	0	3	3
Monster - Kijkduin	6	0	0	1	1
Kijkduin - Scheveningen	4	0	0	4	5
Scheveningen - Katwijk	16	2	2	31	57
Katwijk - Noordwijk	4	20	27	4	12
Noordwijk - Langevelderslag	7	20	30	3	6
Langevelderslag - Zandvoort	9	52	82	1	1
Zandvoort - Bloemendaal	6	37	52	2	2
Bloemendaal - IJmuiden	4	11	21	0	0
Total	62	125	214	42	87

Table 2. The number of porpoises (*n* porp) reported, the calculated average number of porpoises per kilometre, the total accumulated length surveyed, and the number of visits, for the whole observation period (All) and per decade, for Niesen and Kortekaas.

	Niesen				Kortekaas			
	n porp	Average porp / km	*n* km	*n* visits	*n* porp	Average porp / km	*n* km	*n* visits
All	214	0.24	909	121	87	0.21	406	41
1930-1939	118	0.29	413	70	-	-	-	-
1940-1949	27	0.19	143	15	20	0.17	119	11
1950-1959	57	0.19	306	28	66	0.23	284	29
1960-1969	9	0.21	42	9	1	0.29	3.5	1
1970-1979	3	0.50	6	3	-	-	-	-

ous parts of the beach, and finally the entire beach, were forbidden to enter (Figure 2). As a consequence, hardly any porpoises were reported during those years (Figure 3). Immediately after the war there was still unexploded ammunition on the beach or washing ashore and parts of the beach were still off limits to the public. These circumstances explain the gap in the sightings of Niesen and Kortekaas in these years: there are no data from 1943-1946.

There is a large overlap between the beach trips of Kortekaas and those of Niesen, in time as well as in geography. Still, from the date, the exact location, the state of the carcass, the length, and the sex, we were able to deduce whether different individuals were involved. Niesen and Kortekaas have added a total of at least 303 porpoises found between Hoek van Holland and IJmuiden in 1930-1975, which makes their contribution to the national strandings database considerable. Although it is difficult to be certain, because an individual porpoise may have been reported by various people while only the name of one of them was noted in yearly reports, Niesen and Kortekaas appear to have contributed almost half of all unique cases.

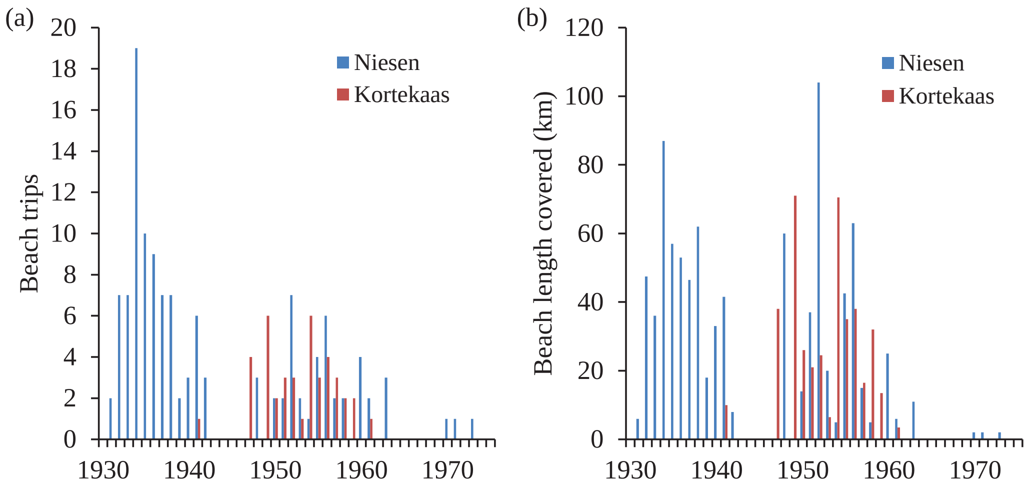


Figure 2. (a) The total number of beach trips per year by Fokko Niesen (blue, 125 trips between 1931-1973) and Henk Kortekaas (red, 42 trips between 1941-1961), and (b) the length of beach covered per year (in kilometres, blue - Niesen 909 km, red - Kortekaas 406 km) in the years during which they reported dead porpoises.

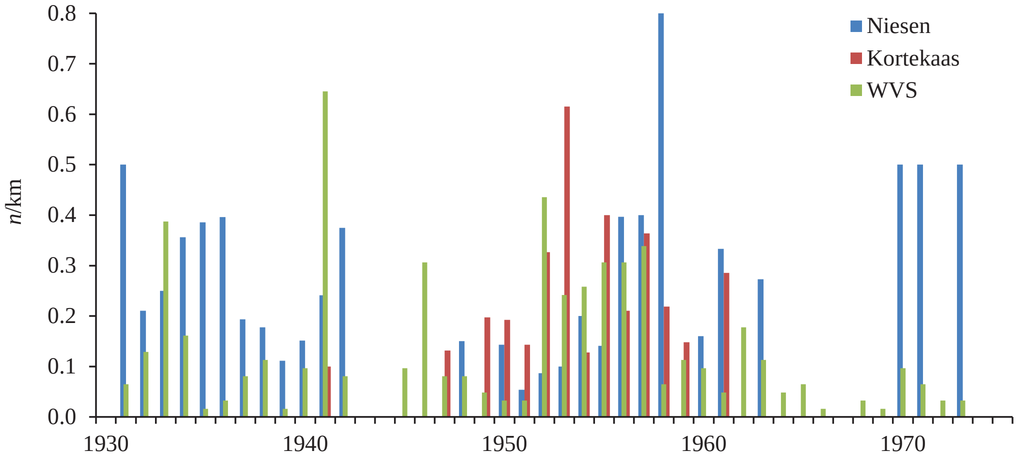


Figure 3. Average density of dead porpoises (*n*/kilometre/year) between Hoek van Holland and IJmuiden in 1930-1975 found by Fokko Niesen (blue, *n*=214) and Henk Kortekaas (red, *n*=88), and from the national database without the data of Niesen and Kortekaas (WVS, green, *n*=352). Although the data for WVS are calculated differently (see methods), the densities, and the resulting scale (y-axis), are the same.

Comparison between years

The average number of porpoises per visit found by Kortekaas was 2.1 and by Niesen 1.7. The small difference is possibly explained by the difference in average length of a visit, which was slightly longer for Kortekaas (9.9 versus 7.3 kilometre). The overall average porpoise numbers per kilometre per year are very close (0.24 by Niesen, 0.21 by Kortekaas), but fluctuate markedly in time (Figure 3). The average densities from Niesen show several peaks: in the mid-1930s, in the early 1940s, and in the late 1950s. The pattern from the data of Kortekaas, although it covers a shorter period, is comparable to that of Niesen. Unfor-

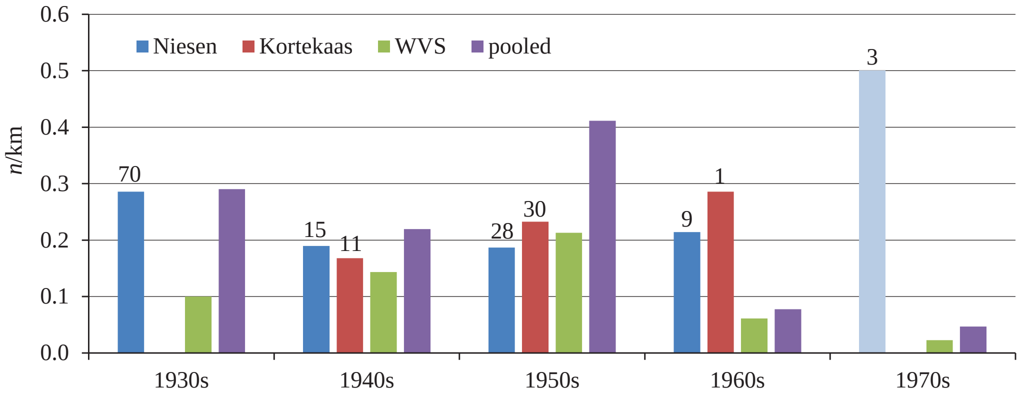


Figure 4. Average density of dead porpoises (*n*/kilometre) between Hoek van Holland and IJmuiden per decade in 1931-1973. Niesen: *n*=214; Kortekaas: *n*=88; the national database without data of Niesen and Kortekaas (WVS): *n*=352; and the three pooled: *n*=654. The bar for Niesen in the 1970s is made pale blue because it is based on only three counts of 2 km each. The number of trips of Niesen and Kortekaas are given above the bars.

tunately, neither reported any porpoises after 1961 (Kortekaas) or 1963 (Niesen). Although Niesen did find three more porpoises, in 1970, 1971 and 1973 respectively, they were found on just three trips, one in each year, with each trip covering two kilometres only, resulting in high densities. Surprisingly, the densities from the national database over the entire period, as well as the pattern, give the same result (Figure 3), even though the data are calculated differently (see Methods). Only in the years prior to the Second World War the more erratic pattern from the national database differs from that from Niesen.

If the data are displayed per decade, those of Niesen show a higher density in the 1930s, lower ones in the 1940s-1950s and a marginal increase in the 1960s (Figure 4, Table 2). The data of Kortekaas follow this pattern. The density from the national database now differs, with a lower average in the 1960s (Figure 4). This difference is caused by the data of Niesen and Kortekaas from this period onwards being less representative (Figure 2), as Kortekaas visited the beach in the 1960s only once (1961, one trip of 3.5 km, one porpoise), and Niesen only in three years (1960, 1961 and 1963; nine trips covering 42 km, nine porpoises). If the data of the three sources are

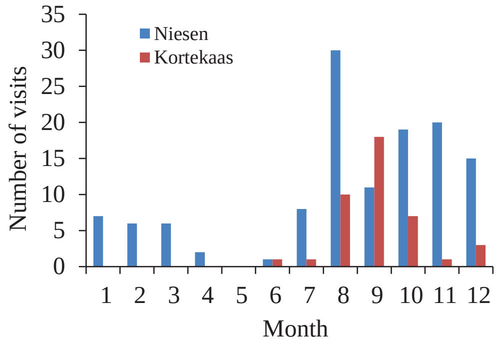


Figure 5. Number of visits per month by Fokko Niesen (*n*=125) and by Henk Kortekaas (*n*=45) during which they reported porpoises.

pooled (purple bars in Figure 4), it shows an increase from the 1930s to the 1950s and a drop in the 1960s.

Monthly pattern

Being birdwatchers, for both observers dead porpoises on the beach were merely 'by-catch'. Although peculiarities such as sex and length were often noted by them, neither had the intention to perform research on porpoises. The fact that they were looking for birds is likely the main explanation for the absence

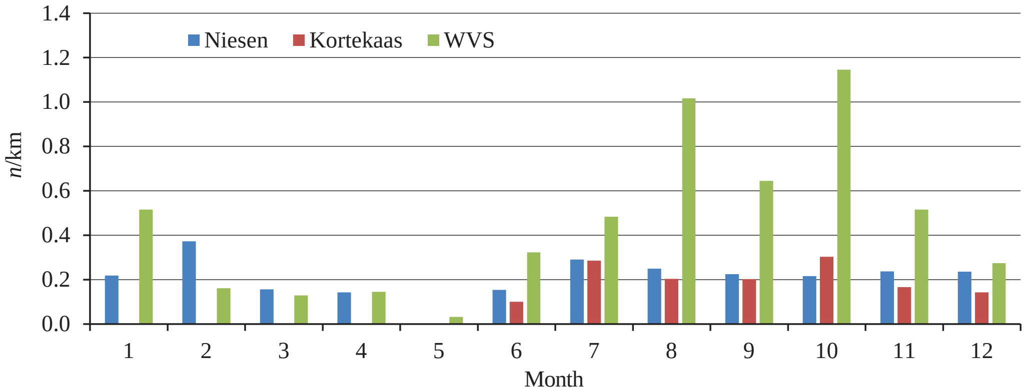


Figure 6. Average density of dead porpoises (*n*/kilometre) per month between Hoek van Holland and IJmuiden in 1931-1973 found by Fokko Niesen (*n*=214), by Henk Kortekaas (*n*=88) and from the national database (WVS, *n*=334, data of Niesen and Kortekaas excluded).

of visits in May (Figure 5). April and May are an excellent time for observing birds in the Netherlands. During these months a variety of bird species may pop up in vegetated places like the dunes. Hence, the beach during those months was probably deemed less interesting by them. From the diaries we learn that they indeed paid multiple visits to the dunes and other places in April and May, especially after 1945, but not to the beach. A visit to the beach in June is least appealing for observing birds. Autumn and winter on the contrary are more rewarding, particularly during stormy weather, with the possibility to see seabirds such as skuas and auks, hence both observers paid numerous visits to the beach during those months.

The presence (density) of dead porpoises found by Niesen was highest in February (0.37 porpoises per kilometre, six trips) and July (0.29, eight trips). Kortekaas found the highest densities in July (0.29, one trip) and October (0.30, seven trips) (Figure 6). As far as counts are available (Kortekaas did not visit the beach in January-May), the monthly averages for both observers show the same pattern, with low densities in March-June, a notable increase in July and a more or less stable pattern from then on until December. Only in October 1949 and October 1955 Kortekaas found higher densities (0.40 and 0.83 respectively). It is likely that both observers were more prone to visit the beach during strong onshore winds, when the chance of observing seabirds – as well as finding a porpoise – is higher. Because the number of visits during January-June is low (14.1% of the total number of visits), it is uncertain whether the calculated averages for these months are representative. The monthly pattern from the national database excluding the data of Niesen and Kortekaas however shows a similar pattern (Figure 6), with the lowest density between late winter and early summer, a peak in July-October, and a decrease from then on until January. The density calculated from the national database is much higher, despite the difference in calculation. Possibly, this is caused by the chance of finding several porpoises being higher on a longer trajectory (62 km).

The Second World War has caused an important caesura in the data (Figure 3) and we have used it to compare densities before and after this period. Although Niesen paid almost twice as many visits to the beach prior to 1943 than later on (82 versus 43, Figure 2a), and the total distance covered was somewhat higher as well (495.5 versus 413.5 kilometres), the number of porpoises (136 versus 78) seems

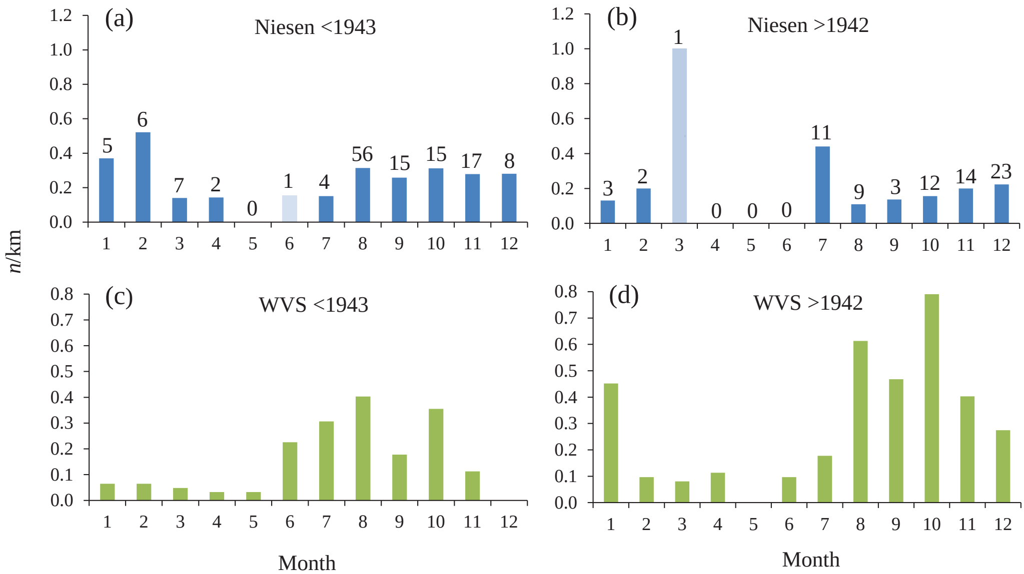


Figure 7. (a) Monthly pattern of dead porpoises (average/kilometre) found by Niesen before 1943 (1931-1942, *n*=136) and (b) after 1942 (1943-1973, *n*=78) compared to that in the national database (WVS) without the data of Niesen but including those of Kortekaas ((c): 1931-1942, *n*=113; (d): 1943-1973, *n*=221). The number of trips per month made by Niesen is indicated above the bars. The bar for Niesen in the 1970s is made pale blue because it is based on only three counts of 2 km each. Note the different scales.

large enough to allow for a comparison in monthly pattern between the two. The overall average density was lower during the second period (0.19 after 1942 *versus* 0.27 before 1943), while the density per month after 1942 was higher only in March and July (Figure 7a, b). The peak in March in the second period is based on a single trip on 23 March 1961, covering only one kilometre, during which Niesen found one porpoise (Figure 7b). (The peak in July after 1942 is based on five trips covering a total of 25 km.)

The number of porpoises in the national database is lower prior to 1943 compared to the years thereafter (113 versus 221) and the overall density two times higher during the second period (0.14 versus 0.28). Thus, the trend emerging from the data of Niesen is the opposite to that from the national database (Figure 7). This can probably be attributed mainly to the fact that Van Deinse only started to systematically collect and report records of dead porpoises from the early 1950s onwards. The pattern emerging from the national database however, especially after 1942, with a peak in October and elevated numbers from August extending up to and including January, while the higher numbers in summer had disappeared, is probably more reliable than that of Niesen. The number of visits to the beach made by numerous people has obviously been higher than those made by a single person, especially in summer, when people were on holiday and many visited the beach. Also, the absolute number of porpoises after 1942 in the national database is almost three times higher.

Discussion

The systematically collected data of Niesen and Kortekaas on dead porpoises, together with the more incidental observations mentioned in the introduction and below, are solid prove that porpoises were common along the

Table 3. Percentage of new-born calves (<90 cm) and sex ratio (% males) prior to 1943 and after 1942, both for the data of Niesen and for the national database (WVS; excluding Niesen's data). The two data sets are pooled to enlarge the sample size, while after 1942 (last column) the data of Kortekaas are added as well.

	<1943			>1942		
	Niesen	WVS	Pooled	Niesen	WVS	Pooled
% <90 cm	14.4 (97)	29.2 (72)	20.7 (169)	3.9 (51)	3.3 (92)	4.6 (219)
% males	67.7 (68)	77.4 (93)	71.5 (171)	70.6 (17)	59.3 (81)	55.0 (109)

Dutch coast during the first half of the twentieth century. Until now however, the intensity and number of porpoise strandings prior to the early 1950s, i.e. the period during which Van Deinse did not systematically collect data on this species, have been obscure. The numbers indicated in publications were therefore deemed unreliable for a country-wide impression of presence and mortality of the harbour porpoise in the Netherlands (Smeenk 1987, Addink & Smeenk 1999), and therefore densities have never been presented. Nevertheless, *ad hoc* data from which densities could have been calculated were actually already available, such as those presented in the introduction (0.38/km in July 1924, Van Deinse 1924; 0.25/km in July 1932, Slijper 1936). And there were more. For instance, A. van Wijngaarden found seven porpoises on a single trip of 16 km in October 1933, giving a density of 0.44/km, and J.P. Strijbos found five porpoises on a trip of 21 km in November of the same year, a density of 0.24/km (Van Deinse 1946). Even though it is obvious that small sample sizes may yield deceiving results (Figure 4, Table 3), we know now that all these densities were representative for the local situation. The fact that the independently collected data sets by Niesen and Kortekaas, compared to that of the national database, reveal the same pattern, suggests that the three sets merged could be sufficiently robust for an analysis of stranded porpoises in the period 1930-1970, as far as the coastline between Hoek van Holland and IJmuiden is concerned. This enables us for the first time to compare densities from the past with those from the present (Figure 8).

For this study, the present-day stranding data between Hoek van Holland and IJmuiden were divided by the length of the total stretch (62 km), because historical systematic counts have long seemed to be absent, and densities could therefore not be calculated otherwise. Although the excellent database on the Dutch dead beached bird surveys (cf. Camphuysen 1995) could have been of help to compare with the densities from the national database, as corpses of marine mammals are included in the counts, it was not, because nowadays dead marine mammals are usually removed immediately from the beach after they are reported. Although the methods of the data sets of Niesen/Kortekaas and the national database differ, the *patterns* of strandings within years and between years can be compared. It is interesting to note that despite the difference in calculation methods, the densities are virtually the same.

The change in abundance of dead porpoises on the beach during the past century has been striking enough to be noted, not just by Verwey (1975) and Niesen, and it has intrigued researchers through time (e.g. Van Deinse 1960, Husson & Van Bree 1972, Smeenk 2003, Camphuysen & Siemensma 2011). Smeenk (1987) attributed the increase in porpoise strandings around the mid-1950s entirely to an increase in observers, although this was not corroborated with data. In their analysis of historical porpoise strandings, Addink & Smeenk (1999) divided their study period, 1920-1994, into five periods of about fifteen years each for the sake of statistics. By analysing discrete sets of time as a single unit, however, there is a risk that any changing pattern within a particular set will be obscured.

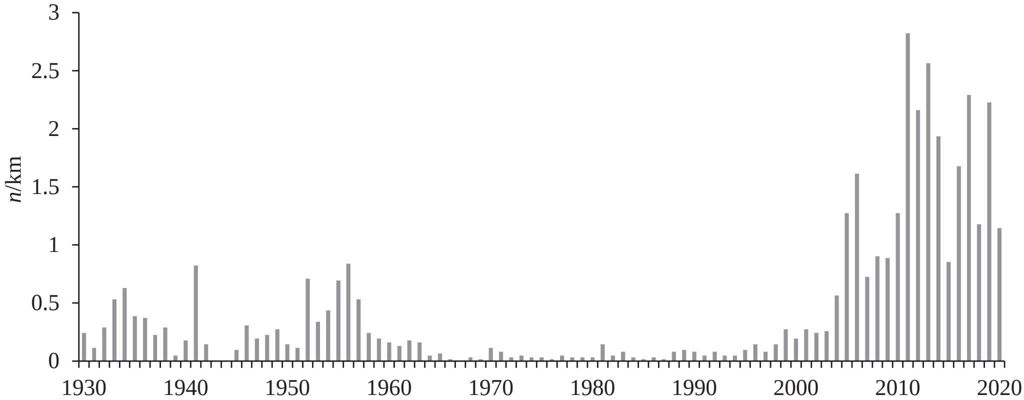


Figure 8. Density of stranded porpoises (*n*/kilometre) between Hoek van Holland and IJmuiden in 1930-2020 (*n*=2453), with the data from Niesen, Kortekaas and the national database combined.

Addink & Smeenk (1999) found '*a serious decline in numbers in the late 1950s/early 1960s*', which they attributed mainly to the disappearance of neonates. They also found a shift in strandings from summer to winter between the period prior to 1950 compared to that after 1970. (They did not include 1965-1969 because of a lack of data.) Despite their thorough analysis, they did not present densities, as data on search intensity from their area of study, i.e. the whole country, were not available, even though those of Kortekaas were included. Also, they did not especially focus on changing patterns, but rather tried to establish the cause of the decline in strandings. Their '*late 1950s/early 1960s*' fell within their single defined study period 1950-1964. The stranding data from the national database only covering the coast between Hoek van Holland and IJmuiden, now boosted with the data of Niesen, unveil that there was no decline in strandings during these years (Figure 8), at least not in this part of the country. The decline mentioned by Addink & Smeenk (1999) appears to have occurred after a period of six years with elevated numbers. It was not until 1964 when the density fell dramatically, and the total number of dead porpoises reported in that entire year along Hoek van Holland and IJmuiden was only three, the resulting density being 0.05 per kilometre. The undulating pattern in strandings density appears to continue even after 1970, with peaks, albeit marginal ones, around the early 1980s, early 1990s and around 2000, after which the numbers rise steeply. Also, the density of stranded porpoises from the late 1990s appears not to have been unusual up to and including 2004 compared to that prior to the Second World War. In 2005-2006 extremely high densities were reached. From 2010 onwards mortality along the Dutch coast has been excessive, especially in 2011-2013. Sighting rates of live porpoises from the coast show a comparable trend (IJsseldijk et al. 2021), although there are also some remarkable differences between the two data sets, for instance in timing.

If porpoise stranding density reflects population size, it is possible that numbers decreased because of the acts of war in the early 1940s, for instance because of underwater explosions or increased ship movements. This remains unknown, especially because survey data from the war are lacking, but the number of dead porpoises on the beach increased again immediately after the war. Establishing the population size of an elusive cetacean like the harbour porpoise is a challenge, but it makes sense to assume that in a larger population more animals die than in a smaller one. There are no estimates whatsoever for the historical North Sea porpoise population, and also nowadays science is struggling to estimate the present population size (Hiby & Hammond 1989, Northridge et al. 1995, Hammond et al. 2002). Between the 1990s and mid-2000s, and possibly irrespective of the population size, there seems to have been a shift in porpoise distribution within the North Sea from the north to the south (Geelhoed et al. 2022). The reason for this remains obscure, but the increase in strandings on the Dutch coast from the late 1990s onwards seems to support the assumption that when there are more porpoises, more will wash ashore (cf. Camphuysen & Siemensma 2011).

From the late 1950s onwards populations of piscivorous marine species such as common seal (*Phoca vitulina*) and sandwich tern (*Thalasseus sandvicensis*) in the southern North Sea crashed due to pollution by PCBs (Van Haaften 1974, Reijnders 1986, Brenninkmeijer & Stienen 1992). The decrease of the piscivorous porpoise partly preceded and partly coincided with that of these species. However, a link of a diet consisting of fish polluted with orchanochlorines as an explanation for increased mortality, decreased fertility, and the near-disappearance of a large part or most of the porpoise population, though likely, has yet to be proven. The recent findings of Van den Heuvel-Greve et al. (2021) suggest that increased mortality may especially have hit unborn porpoises, which in turn may be an explanation for the near-absence of neonates on the beach after the 1950s. On the other hand, if there would have been a rise in prematurely born – i.e. aborted, hence not viable – porpoises, the question rises why they were not encountered on the beach. Although the recent increase in porpoise abundance in the southern North Sea since the late 1980s could be explained by a cleaner environment, climate change, a southward shift of (part of the) North Sea population, or a difference in availability of preferred fish species, further analysis to unravel this phenomenon is beyond the scope of this paper.

Acknowledgements: Many thanks to Kees Camphuysen for unearthing the porpoise strandings from the diaries of Fokko Niesen. Kees also provided the porpoise stranding data from the NSO-archives. The diaries of Kortekaas are stored in the archives of Amsterdam University, the staff of which is thanked for access. Hundreds of people have reported dead porpoises on the beach, in the past as well as during the present; their efforts are invaluable in the monitoring of stranded porpoises in the Netherlands. Comments from Jeroen Creuwels, Eric Thomassen and an anonymus reviewer have greatly improved the manuscript.

References

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

Brenninkmeijer, A. & E.W.M. Stienen 1992. Ecologisch profiel van de Grote Stern (*Sterna sandvicensis*). RIN-rapport 92/17. DLO-Instituut voor Bos- en Natuuronderzoek, Arnhem, the Netherlands.

Buckland, S.T., E.A. Rexstad, T.A. Marques & C.S. Oedekoven 2015. Distance sampling: methods and applications. Springer.

Camphuysen, C.J. 1995. Olieslachtoffers langs de Nederlandse kust als indicatoren van de vervuiling van de zee met olie. Sula 9: 1-90.

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

Camphuysen, K.C.J. & M.L. Siemensma 2011. Conservation plan for the Harbour Porpoise *Phocoena phocoena* in The Netherlands: towards a favourable conservation status. NIOZ Report 2011-07. Royal Netherlands Institute for Sea Research, Texel, the Netherlands.

Camphuysen, K.C.J., C. Smeenk, M. Addink, H. van Grouw & O.E. Jansen 2008. Cetaceans stranded in the Netherlands from 1998 to 2007. Lutra 51: 87-122.

Geelhoed, S.C.V., M. Authier, R. Pigeault & A. Gilles 2022. Abundance and Distribution of Cetaceans. In: OSPAR 2023: The 2023 Quality Status Report for the Northeast Atlantic. OSPAR Commission, London, UK. Available at: https://oap.ospar.org/

en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/abundance-distribution-cetaceans/

Haelters, J., F. Kerckhof & T. Jauniaux 2018. Strandings of cetaceans in Belgium from 1995 to 2017. Lutra 61: 107-126.

Hammond, P.S., P. Berggren, H. Benke, D.L. Borchers, A. Collet, M.P. Heide-Jorgensen, S. Heimlich, A.R. Hiby, M.F. Leopold & N. Oien 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39: 361-376.

Hiby, A.R. & P.S. Hammond 1989. Survey techniques for estimating the abundance of cetaceans. Reports of the International Whaling Commission, Special Issue 11: 47- 80.

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

IJsseldijk, L.L. 2021. Living on a knife-edge. Unravelling harbour porpoise health through multidisciplinary and cross-border approaches. PhD thesis. Utrecht University, the Netherlands.

IJsseldijk, L.L., M.T.I. ten Doeschate, A. Brownlow, N.J. Davison, R. Deaville, A. Galatius, A. Gilles, J. Haelters, P.D. Jepson, G.O. Keijl, C.C. Kinze, M.T. Olsen, U. Siebert, C.B. Thøstesen, J. van den Broek, A. Gröne & H. Heesterbeek 2020. Spatiotemporal mortality and demographic trends in a small cetacean: strandings to inform conservation management. Biological Conservation 249. Https://doi.org/10.1016/j.biocon.2020.108733

IJsseldijk, L.L., K.C.J. Camphuysen, G.O. Keijl, G. Troost & G. Aarts 2021. Predicting harbour porpoise strandings based on near-shore sightings indicates elevated mortality rates. Frontiers in Marine Science 8. Https://doi:10/3389/fmars.2021.668038

Jansen, O.E. 2013. Fishing for food. Feeding ecology of harbour porpoises *Phocoena phocoena* and white-beaked dolphins *Lagenorhynchus albirostris* in Dutch waters. PhD thesis. Wageningen University, the Netherlands

Keijl, G.O., L. Begeman, S. Hiemstra, L.L. IJsseldijk, P. Kamminga & Seal Centre Pieterburen 2016. Cetaceans stranded in The Netherlands in 2008-2014. Lutra 59: 75-107.

Keijl, G.O., M.F. Bakker Paiva, L.L. IJsseldijk & P. Kamminga 2021. Cetaceans stranded in the Netherlands in 2015-2019. Lutra 64: 19-44.

Kinze, C.C., C.B. Thøstesen & M.T. Olsen 2018. Cetacean stranding records along the Danish coastline: records for the period 2008-2017 and a comparative review. Lutra 61: 87-105.

Kinze, C.C., R. Czeck, H. Herr & U. Siebert 2021. Cetacean strandings along the German North Sea coastline 1604-2017. Journal of the Marine Biological Association of the United Kingdom 101 (3): 483-502. Https://org/10.1017/s0025315421000503

Kortekaas, H. & H. Peeters 2014. Geheim vogeldagboek 1940-1945. Delft, the Netherlands.

Leeney, R.H., R. Amies, A.C. Broderick, M.J. Witt, J. Loveridge, J. Doyle & B.J. Godley 2008. Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. Biodiversity Conservation 17: 2323-2338.

Leopold, M.F. 2015. Eat and be eaten. Porpoise diet studies. PhD thesis. Wageningen University, the Netherlands.

Northridge, S.P., M.L. Tasker, A. Webb & J.M. Williams 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena*, L.), whitebeaked dolphins (*Lagenorhyncus albirostris*, Gray) and minke whales (*Balaenoptera acutorostrata*, Lacepede) around the British Isles. ICES Journal of Marine Science 52: 55-66.

Pyenson, N.D. 2011. The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. Proceedings of the Royal Society B 278: 3608-3616.

Reijnders, P.J.H. 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. Nature 324: 456-457.

Scheygrond, A. 1964. Vijftig jaren walvisonderzoek. Een gouden jubileum van Dr. A.B. van Deinse. Natura 61: 186-188.

Siebert, U., A. Gilles, K. Lucke, M. Ludwig, H. Benke, K.H. Kock & M. Scheidat 2006. A decade of harbour porpoise occurrence in German waters – analyses of aerial surveys, incidental sightings and strandings. Journal of Sea Research 56: 65-80.

Slijper, E.J. 1936. Die Cetaceen vergleichend-anatomisch und systematisch. Capita Zoologica 6/7: 1-590.

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

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

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

Soldaat, L. & M. Poot 2020. Analyse bruinvisgegevens en evaluatie monitoring Noordzee - kwaliteitsborging IHM 2019. Centraal Bureau voor de Statistiek, Den Haag, the Netherlands.

van Bemmelen, A.A. 1866. Lijst der zoogdieren, tot heden in den wilden staat in Nederland waargenomen. In: J.A. Herklots. Bouwstoffen voor eene fauna van Nederland: 228-254. Derde deel.

van Bree, P.J.H. 1977. Over strandingen van bruinvissen op onze kust. Natura 74: 20-24.

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

van Deinse, A.B. 1924. De bruinvisch. De levende Natuur 29: 195-203.

van Deinse, A.B. 1945a. De in 1944 bekend geworden vondsten van Nederlandse Cetacea. Het Zeepaard 5: 4-6.

van Deinse, A.B. 1945b. De staart der Cetacea en eenige gevallen van lintvormige staarten bij *Phocaena phocoena* (L.). Zoologische Mededeelingen 25: 23-35.

van Deinse, A.B. 1946. De recente Cetacea van Nederland van 1931 tot en met 1944. Zoologische Mededeelingen 26: 130-210.

van Deinse, A.B. 1947. Onze Cetacea vanaf 808 tot en met 1944. De Levende Natuur 50: 52-53.

van Deinse, A.B. 1952. De walvisachtige dieren in Nederland waargenomen in 1951, alsmede bijzonderheden omtrent onze oude en moderne walvisvaart. Het Zeepaard 12: 19-29.

van Deinse, A.B. 1960. Walvisnieuws over 1959. Lutra 2: 42-44.

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

van den Heuvel-Greve, M.J., A.M. van den Brink, M.J.J. Kotterman, C.J.A.F. Kwadijk, S.C.V. Geelhoed, S. Murphy, J. van den Broek, H. Heesterbeek, A. Gröne & L.L. IJsseldijk 2021. Polluted porpoises: generational transfer of organic contaminants in harbour porpoises from the southern North Sea. Science of the Total Environment 796. Https://doi.org/10.1016/j.scitotenv.2021.148936

van Haaften, J.L. 1974. Zeehonden langs de Nederlandse kust. Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging 101.

Verwey, J. 1975. The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Waddensea) in the years 1931-1975. Part I. Intern verslag. NIOZ-report 1975-17a.

Samenvatting

Een tipje van de sluier – bruinvisstrandingen in Nederland rond het midden van de twintigste eeuw

Het monitoren van walvissen op zee is ingewikkeld en omgeven met onzekerheden. Bovendien gaat het gepaard met hoge kosten. Tellingen van gestrande walvissen leveren geen kennis op omtrent de omvang van de populatie, maar kunnen wel worden gezien als een relatieve maat voor aanwezigheid. Bovendien kan onderzoek aan dode dieren kennis opleveren die niet op andere wijze kan worden verzameld, zoals sekseverdeling of dieet. De bruinvis (*Phocoena phocoena*) komt al lang in Nederlandse kustwateren voor en in de eerste helft van de twintigste eeuw was hij algemeen. Hoewel er al sinds 1915 een registratiesysteem voor dode walvissen in Nederland bestaat, zijn bruinvissen daarin aanvankelijk niet meegenomen, juist omdat ze zo algemeen waren. Het is daarom lastig om bijvoorbeeld de toename sinds de jaren 1990 en de schommelingen in aanspoelpatronen in context te plaatsen: betekent deze toename dat de populatie weer terugkeert naar de omvang van weleer, of is er wat anders aan de hand? In het begin van de jaren 1950 leken bruinvissen in aantal af te nemen, zowel levend in de kustwateren als dood op het strand. Vanaf die periode zijn dode dieren meegenomen in de strandingsregistratie, maar

het was aan de late kant, want bruinvissen bleken toen al erg schaars te zijn geworden. De aantallen die zowel uit de periode voor 1950 als de periode tot de jaren 1970 circuleren, en de schommelingen daarin, zijn in de literatuur als onvolledig en onbetrouwbaar benoemd. Zo is een toename van aangespoelde bruinvissen in de jaren 1950 toegeschreven aan een toename van dagjesmensen op het strand, en aan de extra aandacht voor de soort, niet aan een werkelijke verandering in talrijkheid. De dagboeken van vogelaars Fokko Niesen en Henk L. Kortekaas, die de periodes van respectievelijk 1931-1975 en 1938-1958 omspannen, blijken een belangrijke bron van informatie te zijn omtrent dode bruinvissen tussen Hoek van Holland en IJmuiden. Deze gegevens zijn hier verder uitgewerkt. Zowel Niesen als Kortekaas kwamen regelmatig aan het strand op zoek naar levende en aangespoelde vogels en noteerden niet alleen dode bruinvissen, maar ook waar precies ze het strand betraden en weer verlieten. Met hun gegevens is het gemiddelde aantal bruinvissen per kilometer te berekenen, een getal dat belangrijker wordt geacht dan een totaal aantal dode bruinvissen op een stuk kust van onbekende lengte, omdat gemiddelden beter met elkaar kunnen worden vergeleken. Niesen legde op 125 strandbezoeken in 28 verschillende jaren in totaal 909 kilometer af en vond daarbij 214 bruinvissen; Kortekaas bezocht het strand in 14 verschillende jaren 55 keer, legde daarbij 411 kilometer af en vond 95 bruinvissen. De gemiddelden van Niesen en Kortekaas worden hier onderling vergeleken, maar ook met die uit de nationale database uit dezelfde periode, en met die uit de jaren vanaf 1970 tot en met 2020. Het strandingspatroon per maand tussen beide waarnemers komt overeen, maar verschilt met de landelijke gegevens. Dit komt waarschijnlijk door de belangrijkste interesse (vogels) van de twee waarnemers, waardoor er weinig strandbezoeken in het voorjaar waren. Ook het aantal strandbezoeken per waarnemer per jaar, of de afgelegde afstand per bezoek, zijn van invloed op de gevonden patronen: hoe minder bezoeken per jaar, des te grilliger het verloop tussen jaren, en hoe kleiner de afgelegde afstand per bezoek, des te groter de schommelingen. Dat de gegevens uit de nationale database van voor 1950 lager uitkomen dan die van Niesen en Kortekaas komt doordat van Deinse, op wiens gegevens de database is gebaseerd, vóór dat jaar alleen bruinvissen noteerde als er iets bijzonders over te vermelden viel. De soort werd te algemeen geacht om alle gegevens te verzamelen. Toch liggen de kilometergemiddelden uit de drie bronnen (Niesen, Kortekaas, nationale bestand) dicht bij elkaar en geven de sterk vergelijkbare schommelingen in de tijd vertrouwen dat de gevonden patronen reëel zijn. Daarmee is een belangrijk instrument gevonden om de strandingspatronen door de tijd in een breder daglicht te plaatsen. Als de dichtheden van aangespoelde bruinvissen op de kust tussen Hoek van Holland en IJmuiden over de hele periode 1930-2020 wordt beschouwd, zien we een golvend patroon. Er is geen afname in strandingen na de Tweede Wereldoorlog, en hoewel er rond 1950 lagere dichtheden zijn geconstateerd, heeft een voortdurende afname van de bruinvis in de jaren 1950, zoals die bij eerder onderzoek is gevonden, niet plaatsgevonden: in de tweede helft van de jaren 1950 waren de aangespoelde aantallen juist hoog. De grootste afname vond plaats vanaf 1964, hoewel in de dertig jaar daarna, toen er hooguit enkele bruinvissen per jaar werden gevonden, nog altijd een golvend strandingspatroon zichtbaar is. Deze ‘magere’ periode komt overeen met de afname van andere mariene viseters zoals de grote stern (*Thalasseus sandvicensis*) en de gewone zeehond (*Phoca vitulina*), soorten waarvan is aangetoond dat ze te lijden hebben gehad van PCB-vergiftiging. Of dat ook de achteruitgang van de bruinvis in Nederland heeft bespoedigd, valt buiten het bestek van deze studie, net als de sterke toename van zowel levende als aangespoelde dieren sinds de jaren 1990.

Received: 20 June 2023
Accepted: 8 December 2023

An opportunistic drive hunt of long-finned pilot whales (*Globicephala melas*) in the Netherlands in 1825

Phil W. Koken[1], Justin J.F.J. Jansen[2] & Erwin J.O. Kompanje[3]

[1] Regulusweg 10, 3453 HK De Meern, the Netherlands, e-mail: catman@ziggo.nl
[2] Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands
[3] Natural History Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, the Netherlands

Abstract: In this article, a reconstruction is made of an opportunistic drive hunt of a pod of about 38 long-finned pilot whales (*Globicephala melas*) which took place on 9 April 1825 near St. Philipsland (Zeeland, the Netherlands). The reconstruction is based on published and non-published documents, artistic impressions, and five complete skeletons and one stuffed skin in Belgian and Dutch museums. For at least five, maybe even six but perhaps even up to twelve, whales of this drive hunt a partial or complete timeline is reconstructed.

Keywords: long-finned pilot whale, *Globicephala melas*, drive hunt, Tholen, Van Trigt, Ver Huell, watercolour.

Introduction

The long-finned pilot whale (*Globicephala melas*) is a highly socially cohesive oceanic dolphin species. Males measure from five to six metres in length. Females are significantly shorter, typically between four to five metres. They travel in groups (pods) in numbers ranging between about 20 and 1000 individuals. These groups are often genetically related, suggesting a matrilineal social unit in which males remain with their mothers for life. Pods are usually composed of around 60 percent female dolphins. Mating occurs in the spring or early summer, and births take place approximately twelve months later, in late summer or early autumn in the Northern Atlantic. Females can reach an age of up to 60 years, males around 45 years (NOAA 2022).

Long-finned pilot whales are the most common cetacean species involved in mass strandings. This often involves the whole pod. Most probably, their highly strong social bonds result in these mass strandings: if one animal strands, almost all others follow. Another form of mass stranding is as a result of human actions in the form of a drive hunt, of which the best-known example is from the Northern Atlantic Faroe-islands. Each year during summer, approximately 700 long-finned pilot whales and hundreds of Atlantic white-side dolphins (*Lagenorhynchus acutus*) are driven onto shallow shores and killed for their meat. Drive hunting involves men in several boats herding a large group of dolphins into shallow water; subsequently the animals are beached and slaughtered. The largest known catch of pilot whales on the Faroe Islands in a single season was 1203 animals in 2017. The hunting and killing of these highly social mammals is highly controversial, although more than 80% of the Faroe islanders still support this tradition (Mamzer 2021). More general information about today's drive hunts can be found elsewhere (Wikipedia 2023).

Two drive hunts of long-finned pilot whales in the Netherlands are documented. Both took place in the nineteenth century. The first, further discussed below, took place on 9 April 1825. It involved a pod of 36 or 38 individuals driven to shore between St. Annaland and St. Philipsland at Tholen, Zeeland (estimated GPS 51.612N, 4.145E) (Anonymous 1825a, Anonymous 1825b, Hoogkamer 1825).

The second (partial) drive hunt took place on 2 April 1856 when eleven whales were driven onto shore near Arnemuiden, Zeeland (estimated GPS 51.822, 3.905). In the 1856 event, the entire pod probably numbered between 300-400 animals in total. Besides the animals that were driven to shore, several groups of other individuals stranded alive at different locations in the same area. Sixty-one animals were reportedly stranded near Ouddorp, Zuid-Holland (estimated GPS 51.822N, 3.905E) (van Deinse 1931, Heerebout 2007) and eleven others were surrounded by fishermen in boats after which they came ashore with the low-tide on a beach close to Arnemuiden, Zeeland (estimated GPS 51.519N, 3.690E), where they were slaughtered (Anonymous 1856a, Heerebout 2007). We found only very limited information about the 1856 event, and do not describe it further.

The purpose of the present article is twofold:

1. The event of 1825 is mentioned in the literature as a 'mass stranding'. Our first aim is to correct this. It has the hallmarks of at least an opportunistic 'drive hunt'. The animals were surrounded by boats and driven onto shore, such that their escape was prevented by closing off the route to the open sea.
2. Our second aim is to describe the drive hunt of 9 April 1825, present a timeline of what happened to several of the killed animals and highlight its documentation in Belgian and Dutch museum collections.

Material & Methods

Internet sources, such as www.delpher.nl, were searched using terms such as the event date (9 April 1825), location (St. Annaland or St. Philipsland, Tholen, the Netherlands) and long-finned pilot whales. The majority of more than 25 Dutch archives were visited for published and non-published sources such as books, diaries and notes, book inventories and journal articles. Furthermore, the Ghent University Museum (Ghent, Belgium) and Naturalis Biodiversity Center (Leiden, the Netherlands) (hereafter referred to as Naturalis) were visited to study the collected skeletons and mounted skin of long-finned pilot whales from the 1825 event. Finally, the Arnhem Museum (Arnhem, Gelderland) and the Teylers Museum (Haarlem, Noord-Holland) were visited to study two preserved artistic impressions made within days after the drive hunt. A third artistic impression, made more than 100 years after the drive hunt, was found at Naturalis. Based on all uncovered sources, a chronological reconstruction of the drive hunt and the events which followed the stranding was made.

Measurements of the animals, such as size and weight, mentioned in the publications of 1825 and after are assumed to be according to the standardized Dutch metric system in 1820 unless indicated (Maenen 2002). These have been converted to the S.I. metric system, i.e., a 'Dutch pound' equals 1 kilogram and the 'Dutch el' equals 1 metre. It is of interest to note that even five years later after its introduction the standardized system was still not in common use, e.g., the measure of length in the text of an artist's impression by Stephanus van Trigt (see paragraph on 'Watercolour made by Stephanus van Trigt (1825)') mentions explicitly the "Rijnlandse voet", which equals to 0.3140 metres.

Results

Written evidence

According to two locals, 36 or 38 "*visschen*" (old Dutch plural for fishes) swam into the bay of Mosselkreek in the afternoon of 9 April 1825. The Mosselkreek is a sand trench not far from St. Annaland (north) but as shown in Figure 1 it appears to be closer to St. Philipsland, on the island of Tholen (just south of it) in the southwest of the Netherlands (Anonymous 1825a, 1825b, 1825c, Hoogkamer 1825). Local fishermen chased the animals with their boats until they were stranded on the beach after which they were killed for their flesh and other valuable body parts. Only one animal was able to escape the massacre (Anonymous 1825a, 1825d). The pod of animals was possibly observed earlier near Veere, about 33 km south-west of Tholen, after a heavy storm in February of 1825 (Anonymous 1825a).

Initially there was uncertainty and discussion about the identification of the species (Hoogkamer 1825). A correct determination of the "*visschen*" to be long-finned pilot whales was perhaps firstly made by Bonifacius den Jonge (1788-1854) after one of the animals had been transported to Middelburg for display (Anonymous 1825b). But even after this some newspapers would still refer to them using an incorrect species name, for example North Atlantic right whale (*Eubalaena glacialis*) (Anonymous 1825d, 1825e).

At the time of the drive hunting and beaching, the temperature was 9-10 °C (Anonymous 1825f). At this temperature, the whales would soon start to decay and to rot. Within a few days of the massacre at least five, possibly twelve, animals were transported elsewhere. Our findings did not give a conclusive answer as to who initiated and organised the transport.

Artist impressions

Two watercolours, which were made shortly after the drive hunting and slaughtering of the long-finned pilot whales, were discovered in collections of the Arnhem Museum (Arnhem, Gelderland) and the Teylers Museum (Haarlem, Noord-Holland) in the Netherlands. A third artistic impression, an ink drawing made in the twentieth century of one of the skulls preserved in Naturalis, was found in the archives of this museum. The latter impression will be described further on in the paragraph on 'Collected skeletons and skin'.

Watercolour made by Stephanus van Trigt (1825)

The Dutch surgeon and artist Stephanus Hendrik Willem van Trigt (1788-1840), who lived and worked in Dordrecht, not only made several hundreds of watercolours of Dutch and exotic birds but he also made watercolours of mammals. One of the latter concerns a dead male foetus of a long-finned pilot whale. Almost all watercolours made by van Trigt do not have a date or a description of the animal or the conditions during painting. It was therefore exceptional that the watercolour of the pilot whale foetus was accompanied by both a text and a date.

Since October 1897 this watercolour has been part of the collection of the Teylers Museum (collection item KT 2009 028-370) (Figure 2). The artwork is not signed, which is also typical for almost all of van Trigt's work. Besides the placenta, the non-rigid tail clearly shows the animal was unborn. Our translation of the Dutch text above the drawing is:

> *A young of Delphinus globiceps, about 2 metres long, taken out of the mother which was 5 metres long and 1,25 metres wide measured at the thickest place, the tail fin was 1 metre wide. The pectoral fins 1,15 metres. On April 10, 1825 this fish stranded together with 37 others of the same species in de Mosselkreek near Sint Annaland, and was slaughtered. The length of the others varied between 3.1 and 6.9 metres and their weight was estimated from 800 to 4000 kg (?). Multiple animals were pregnant.*

A non-specialist comparison (performed by the authors) of the text on this watercolour with other texts on van Trigt's works suggests

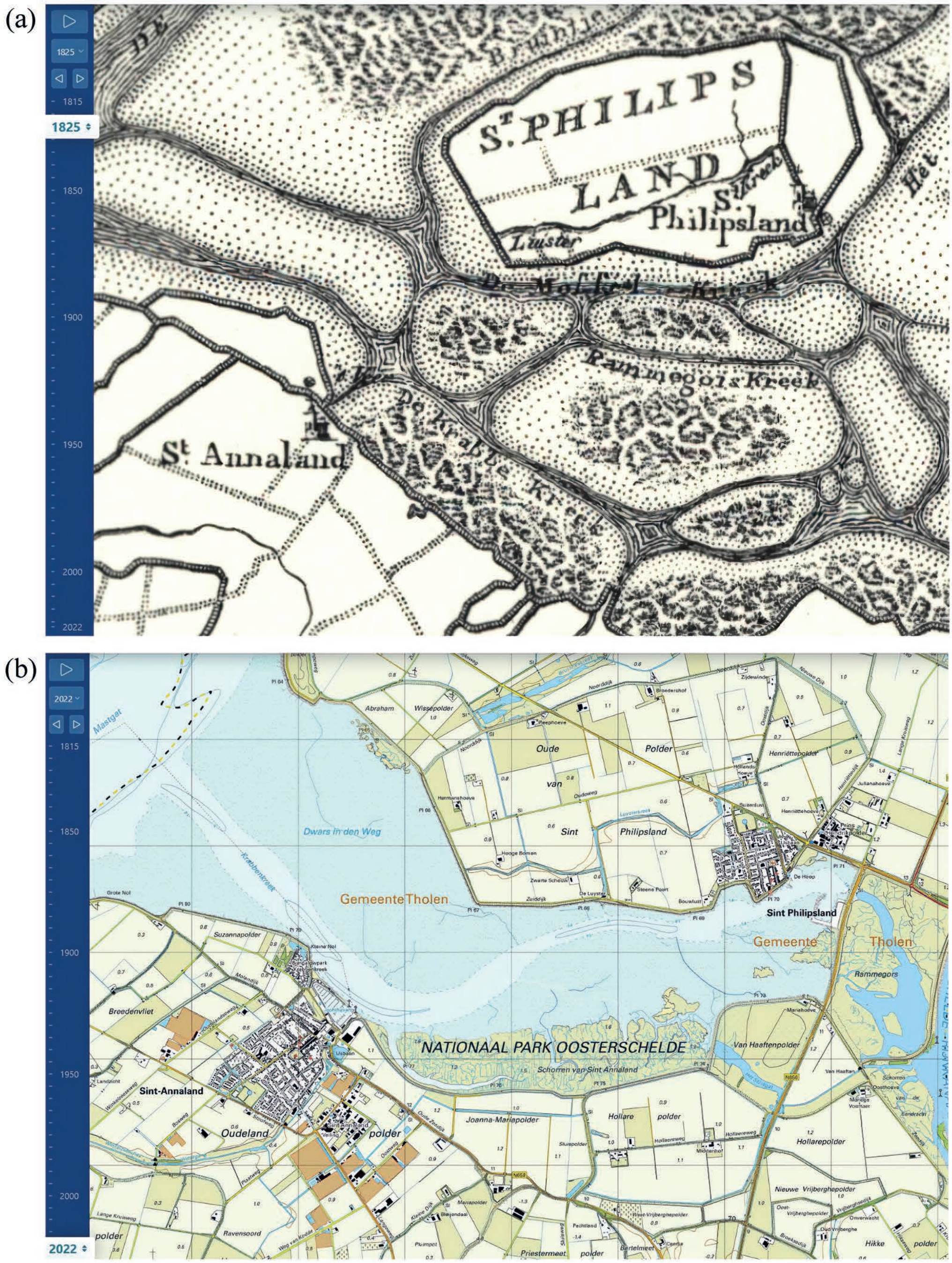


Figure 1. Topographic maps from the drive hunt in 1825. (a) shows the situation in 1825 and (b) shows the situation in 2022. It shows that in 1825 the Mosselkreek was nearer to St. Philipsland than to St. Annaland. Both maps were derived from topotijdreis.nl

Figure 2: Watercolour by Stephanus van Trigt, dated 10 April 1825. This is the first documented male foetus of long-finned pilot whale (*Globicephala melas*) in the Netherlands. It is possibly also the first document with the correct species determination (© Teylers Museum).

that the handwriting is by the same person. The year 1825 has been added later, and the handwriting suggests this was not done by van Trigt.

According to the timing of the slaughter, the foetus must have been approximately ten or eleven months old and almost mature, which is in accordance with van Trigt's watercolour (NOAA 2022).

Watercolour made by Quirijn Ver Huell (1825)

Quirijn Maurits Rudolf Ver Huell (1787-1860), a former marine officer and artist educated at the Royal Academy of Art in Amsterdam, made a watercolour of an adult long-finned pilot whale (Figure 3). The artwork is, since a bequest in 1897 by Ver Huell's son, located at the Arnhem Museum (Arnhem, the Netherlands, registration number GM 4446). The translated text left-below on the drawing says:

Q.M.R. Ver Huell – drawn to life on April 15, 1825.

The catalogue of an exhibition in 1989 in the Natural History Museum in Rotterdam mentions that Ver Huell most likely was present at St. Annaland (Reumer 1989). However, we think it is more plausible that Ver Huell made his watercolour in Rotterdam; Ver Huell lived in Rotterdam at that time and worked in the harbour after he returned from Indonesia (van Harderwijk 1860). A local newspaper report on 21 April 1825 describes the arrival of one of the whales in Rotterdam where it was shown for a limited time (Anonymous 1825d). Despite extensive research in archives no solid proof was found to support either of these two scenarios. However, since the drawing shows an intact whale, it must have been made within days after the stranding.

Collected skeletons and skin

Five complete skeletons and one mounted

Figure 3: Watercolour by Quirijn Maurits Rudolf Ver Huell, dated 15 April 1825. The work shows a complete rather fresh dead long-finned pilot whale (*Globicephala melas*) (© Museum Arnhem).

skin of long-finned pilot whales of the April 1825 drive hunt are still present in museum collections:

Complete skeleton, Ghent University Museum, Belgium
The Ghent University Museum owns a skeleton labelled MDV 50405. The skeleton with a length of 4.5 metres was acquired in 1825 by Jacobus Gijsbertus Samuël van Breda (1788-1867) (Anonymous 1825g, van Bree 1975). The notice of purchase states incorrectly that the stranding of 1825 took place near Bergen op Zoom, a town about 20 km south-east of St. Philipsland (Anonymous 1825g). It is more likely that the whale was transferred from St. Philipsland to Ghent through Bergen op Zoom.

Complete skeleton and stuffed skin, Naturalis
A complete skeleton of a juvenile whale (van Bemmelen 1864, van Oordt 1918) and a stuffed skin of a juvenile whale were found in Naturalis. Their registration numbers are RMNH.MAM.31215 and RMNH.MAM.31213b, respectively. The length of the skeleton measures 2.90 metres and the skin measures 2.70 metres. Comparison of the sizes of this skeleton and skin and matching the locations of the blowhole showed remarkable agreement, to within a few cm (<5 cm; Figure 4). Although a DNA analysis of the two items has not been made, we believe the skin and the skeleton belong to the same animal.

Schlegel (1862, page 93) wrote that several objects originating from the 1825 event were acquired by Naturalis (formerly named Rijksmuseum van Natuurlijke Historie (RMNH)):"… *the last example of this nature occurred in Zeeland near St. Annaland on April 9, 1825, where 35 individuals were killed at the same time, the largest of which had a length of 20 feet. Several of these objects were then purchased for the RMNH, where they are still located*". Schlegel does not mention the stranding of 1856 at all. He also does not specify the skin or number of skeletons. Neither in Naturalis nor in the Nationaal Archief (The Hague) acquisition data were found.

Figure 4: Comparison of skull skeleton RMNH.MAM.31215 and skin RMNH.MAM.31213b. The blow holes on the skin and skeleton matched with a few cm. *Photo: Phil W. Koken / © Naturalis.*

Complete skeleton, Naturalis
A complete skeleton with registration number RMNH.MAM.31214 was found in this museum (Schlegel 1862, van Bemmelen 1864, van Oordt 1918). The length of the skeleton is 5.4 metres.

Complete skeleton and 20th century ink drawing, Naturalis
A complete skeleton with registration number RMNH.MAM31213a was found in this museum (Schlegel 1862, van Bemmelen 1864, van Oordt 1918). Its length is 3.55 metres.

An undated and unsigned drawing was found in the van Deinse archive of the same museum. It has no collection item number but was made by Rob van Assen (1944-2022) (Chris Smeenk, personal communication 1995). The drawing shows the left upper and lower mandibula of a long-finned pilot whale (Figure 5a) with several distinct markings on the teeth and maxillary bone. Close comparison with the skulls of long-finned pilot whales at the Naturalis collection revealed that the drawing was made of RMNH.MAM3121a (Figure 5b).

Complete skeleton, Naturalis
The collection of Naturalis contains a complete mounted skeleton of an adult long-finned pilot whale with registration number ZMA.MAM.7858. Most likely the partly dissected animal with a length of about 4.5 metres was bought by Nicolaas Cornelis de Fremery (1770-1844) to Utrecht (de Fremery 1825). After his death, the skeleton was bought by Pieter Harting (1812-1885) at a public auction for fl. 50 and became part of the collection of the Zoological Laboratory in Utrecht (Anonymous 1856b, de Graaf 1856). Van Bree (1975) mentions that because of lack of space this skeleton was transferred to the Zoological Museum Amsterdam (ZMA) around 1960. In 2011 the ZMA collection was integrated into the collection of Naturalis (Goud 2011).

Discussion

We found two reports of local witnesses of the drive hunt of 1825 (Anonymous 1825a, Hoogkamer 1825). They mention different numbers of animals caught: respectively 36 and 38. Van Trigt mentions 38 animals. Later sources repeat similar numbers but some mention 35 animals (Schlegel 1862, De Smet 1974) or 37 animals (van Bemmelen 1864). Since the witness reports mention that one of the animals escaped, it could well be that these later sources only refer to the number of slaughtered animals.

Robson and van Bree (1971) suggested that the stranding might have been caused by a light seaquake, but we found no proof that such an event occurred. Besides, the drive

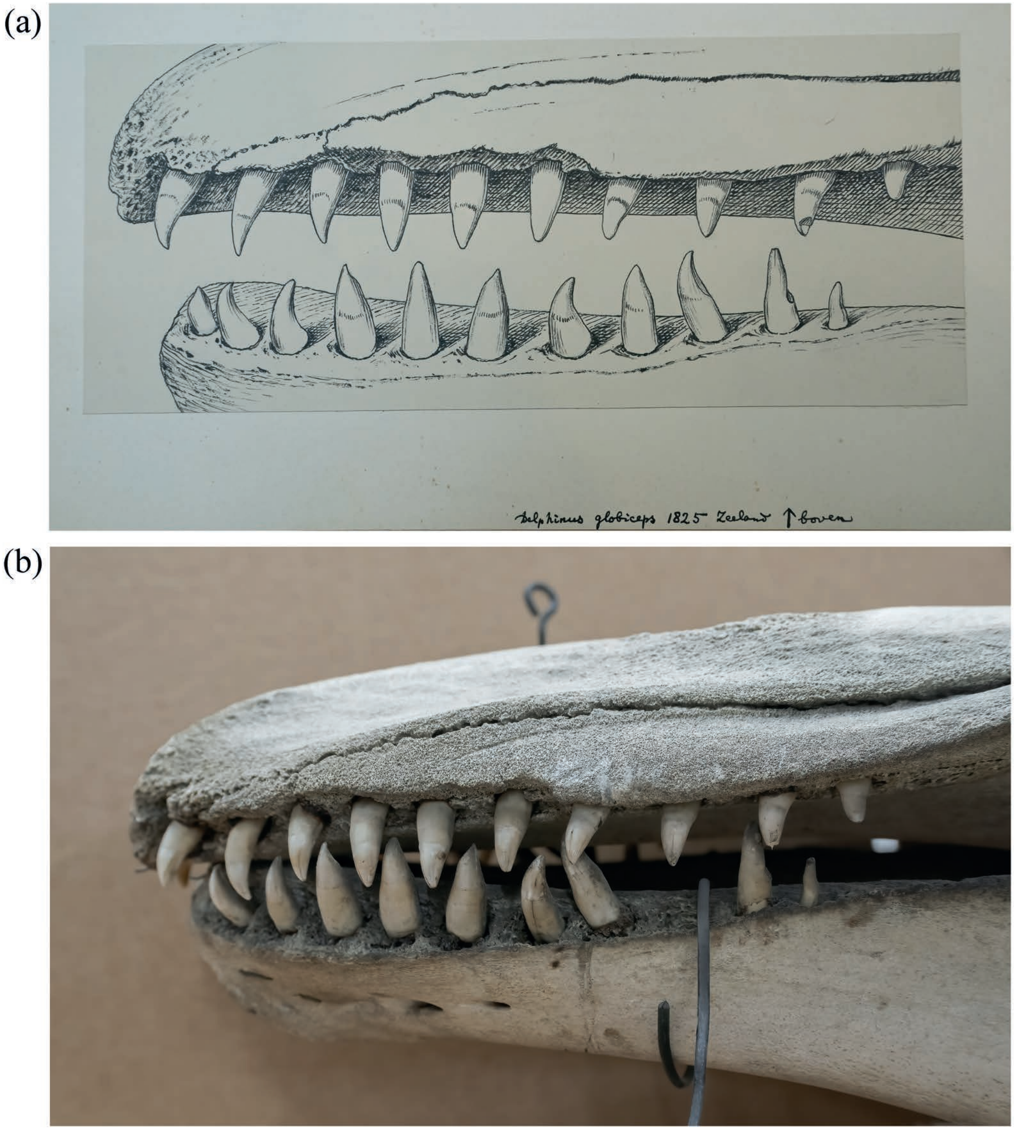


Figure 5. (a) Ink drawing by Rob van Assen, undated but created in the 20^{th} century. It shows the left mandibula of a long-finned pilot whale (*Globicephala melas*). Comparison of the drawing showed that it was made after the jaw of RMNA.MAM.31213a; (b) Detail of a skeleton RMNA.MAM.31213a. *Photos: Phil W. Koken / © Naturalis.*

hunt appears the actual cause of the stranding even though it is not sure whether or not the animals would also have stranded without the presence of the locals. Van Bemmelen (1864) mentioned that the group always follows their leader, irrespective of the cause of the stranding.

Based on old maps, acquired from topotijdreis.nl, the stranding took place at the Mosselkreek between St. Philipsland and St. Annaland; based these maps the Mosselkreek is a bit closer to St. Philipsland than to St. Annaland. In 1825, St. Philipsland was part of the isolated island of Tholen. We estimated the stranding and slaughter occurred near the Zuiddijk in St. Philipsland. We therefore refer to the location as St. Philipsland rather than St. Annaland in this article.

Van Trigt wrote on his watercolour that multiple animals were pregnant. The number of pregnant animals remains unknown. No solid proof was found as to where van Trigt observed the foetus; it is possible he depicted the watercolour at the scene near St. Philipsland. But he also could have done this in Rotterdam where a foetus was discovered when a female long-finned pilot whale was dissected (Anonymous 1825e, de Fremerij 1825).

The watercolour made by van Trigt is the first artistic impression accompanied by text of the event after the drive hunt. If the date mentioned in the text on the watercolour was also its creation date, then van Trigt's watercolour would be the first document mentioning the correct species.

Was van Trigt present at or near Tholen at the time of the stranding, and did he actually make his drawing the day after the stranding? Or was he elsewhere when he made his drawing? If he was at or near Tholen, he must already have been there before the stranding took place, given the time taken for news about the stranding to travel to Dordrecht and the logistics to travel from Dordrecht to Tholen which were too cumbersome to be completed in just a single day. Another possibility could be that van Trigt saw the foetus in Rotterdam where an adult pregnant female long-finned pilot whale was dissected after which it was displayed with its foetus in the centre of Utrecht (Anonymous 1825b, 1825h). Despite extensive research in multiple archives we have not found any solid proof for either of these two possibilities.

Van Deinse (1931) mentions in his thesis that an outline of a sea mammal was drawn on the wall of the fish market at Tholen. The drawing was coloured black and based on its size van Deinse reasons it might have been one of the long-finned whales of the 1825 drive hunt. The wall with this drawing was torn down in 1885.

Besides the RMNH.MAM-labels on the skeletons and skin and Schlegel's description no other specific proof was found that the skin and three skeletons originate from the 1825 drive hunt (Schlegel 1862, page 93). However, in the early years of the RMNH such data were not always as complete as they are nowadays. Schlegel (1862) does not mention the stranding of 1856 at all. All in all, we conclude that the labeled skeletons and skin are correctly dated, and therefore are part of the drive hunt of 1825.

We reconstructed timelines of at least five (perhaps six), and at the most twelve individual whales beginning directly after the mass stranding (Table 1). If skeleton RMNH.MAM.31215 and skin RMNH.MAM.31213b indeed belong to the same animal, then the number of six whales is reduced to five. Based on documents in archives and literature we could reconstruct a complete timeline after the stranding for one skeleton of a whale and a near-complete timeline for another, represented by skeletons labelled as ZMA.MAM.7958 and MDV 50405. Although we know the current location of three other skeletons (including a skin possibly belonging to one of them), we were not able to reconstruct their complete timelines between 1825 and 1862. But as argued above both were indeed part of the 1825 event.

Despite thorough investigations in more than 25 archives, we could not find solid evidence about who played a key role in what happened with the remains after the drive hunt. An indication could be a letter by Laurens Britting dated May 1825 suggesting that on behalf of government one or more animals were ordered to be transported to Naturalis (Gijssen 1938). Other details related to the drive hunting, but that are not relevant to this article, will be described separately (Koken et al. 2023).

In conclusion, our research has resulted in the first, and most complete, documented overview of a drive hunt of long-finned pilot

Table 1. Timelines of the fate of a number of dead whales after the drive hunting of April 1825. It is possible that animals 1 – 6 overlap with the remains in museum collections.

Specimen	Present location	Known history	Literature
1	-	Arrived in Middelburg on 12 April 1825 by ship, measured 5 m and weighed 1000 kg. Dissected three days after arrival.	Anonymous 1825a, Anonymous 1825b, van Deinse 1950
2	-	Shown in Rotterdam before 21 April 1825 at Westnieuwland, Beurs. It weighed about 1000 kg, indicating it was a non-dissected animal. Species incorrectly referenced to as right whale.	Anonymous 1825d
3	-	Shown in Brussels before 22 April 1825, measured 11 "ellen" [the Dutch standardized metrics of 1820 cannot be applicable here: length of 11 metres would be too much] and weighed 1500 kg, indicating it was a non-dissected animal.	Anonymous 1825i
4	-	Transported to Amsterdam before 22 April 1825, measured "more than 8 m" [most probably exaggerated], purchased for fl. 1000.	Anonymous 1825i
5	-	Exhibited in Maastricht before 28 April 1825 at Boschstraat in the city centre.	Anonymous 1825h
6	-	Adult pregnant female dissected in Rotterdam; displayed with its foetus in Utrecht city centre. Length was more than 5 m, weighed about 1000 kg. Wrong initial determination of right whale was corrected by De Fremery.	Anonymous 1825e, de Fremery 1825
7	Ghent	Skeleton MDV 50405, see paragraph 'Complete skeleton, Ghent University Museum, Belgium'	
8	Naturalis Biodiversity Center (Naturalis)	Skeleton RMNH.MAM.31215, see paragraph 'Complete skeleton and stuffed skin, Naturalis'	
9	Naturalis	Skin RMNH.MAM.31213.b, see paragraph 'Complete skeleton and stuffed skin, Naturalis'	
10	Naturalis	Skeleton RMNH.MAM.31213.a, see paragraph 'Complete skeleton, Naturalis'	
11	Naturalis	Skeleton RMNH.MAM.31214, see paragraph 'Complete skeleton and 20th century ink drawing, Naturalis'	
12	Naturalis	Skeleton ZMA.MAM.7958, see paragraph 'Complete skeleton, Naturalis'	

whales in the Netherlands. From the drive hunt of 9 April 1825, five skeletons, one mounted skin, and two drawings made within days after the stranding are still preserved in the collections of one Belgian and three Dutch museums.

Acknowledgements: Our study on the described mass stranding would not have been possible without the kind help of many. The authors thank the following institutions and their co-workers in alphabetic order: Dordtenazoeker.nl: Erica van Dooremalen; Erfgoedcentrum Rozet: Maria de Haan; Gelders Archief: Irene Rooker; Gemeente Tholen: Roy Hage; Gemeente Schouwen-Duivenland: Huib Uil; Ghents University Museum: Jo Vansteenkiste, Dominick Verschelde, Kristel Wautier; Het Utrechts Archief: Rune Sassen; Historisch Centrum Limburg: Julia Philippens; Independent researcher: Ruud Vlek; Koninklijke Archief: Geeske Bisschop; Museum Arnhem: Joanna Minderop, Sjoerd Popkema; Nationaal Archief: Jeroen van Luin; Naturalis Biodiversity Center: Pepijn Kamminga, Guido Keijl, Karien Lahaise, Steven van der Meije; Natuurhistorisch Museum Maastricht: Paul Beuk;

Noordhollands Archief: Lise Koning; Stadsbibliotheek Maastricht: Joes Minis; Teylers Museum: Celeste Langendijk; Universiteit Utrecht: Paul Lambers; Zeeuws Archief: Ilja Mostert, Anna Naerebout, Michiel van Wijngaarden; Zoogdiervereniging: Ruth Daalderop. The authors also thank both anonymous reviewers for their useful comments and suggestions. Last but not least we thank Max Dahele for correcting the British English language.

References

Anonymous 1825a. ‘sGravenhaagsche Courant, 18 april.

Anonymous 1825b. Middelburgse Courant, 14 april.

Anonymous 1825c. Walvischaardige dieren op de Zeeuwsche stroomen. Algemeene Konst en Letterbode, 22 april: 250-252.

Anonymous 1825d. Rotterdamsche Courant, 21 april.

Anonymous 1825e. Utrechtse Courant, 29 april.

Anonymous 1825f. Weather report. https://www.genealogieonline.nl/over-de-dag/1825/4/9 and https://www.genealogieonline.nl/over-de-dag/1825/4/10; viewed 2 September 2023.

Anonymous 1825g. Walvischaardige dieren op onze kusten. Algemeene Konst en Letterkonde, 13 mei: 302-303.

Anonymous 1825h. Journal de la Provence de Limbourg, 28 april.

Anonymous 1825i. ‘sGravenhaagsche Courant, 22 april.

Anonymous 1856a. Middelburgsche Courant, 8 april.

Anonymous 1856b. Catalogue des musées d’histoire naturelle et d’anatomie comparée délaissés par feu M.N.C. de Fremery et feu M.T.D. Schubärt. Item 352: 7.

de Fremery, N.C. 1825. Walvisaardige dieren op onze kusten. Algemeene Konst en Letterbode 20: 315-318.

de Graaf, N. 1856. Results public auction collection De Fremerij. Utrechts Archief, inv. nr. 4274 34-4.

De Smet, W.M.A. 1974. Inventaris van de walvisachtigen (Cetacea) van de Vlaamse kust en de Schelde. Bulletin Koninklijk Belgisch Instituut voor Natuurwetenschappen 50 (1): 1-156.

Gijssen, A. 1938. ’s Rijks Museum van Natuurlijke Historie 1820-1915. W.L. & J. Brusses’s uitgeversmaatschappij, Rotterdam: 246-247.

Goud, J. 2011. Samenvoeging van de collecties van ZMA en Naturalis van start / Integration of the collections of ZMA (Zoological Museum Amsterdam) and Naturalis has started. *Spirula 379:* 27.

Heerebout, G.R. 2007. Grienden op het strand. De Ouwe Waerelt. Historisch tijdschrift voor Goeree-Overflakkee 7 (19): 2-4.

Hoogkamer, W.R. 1825. Nederlandsche Staatscourant, 16 april.

Koken, Ph.W., J.J.F.J. Jansen & E.J.O. Kompanje 2023. Grienden stranding op 9 april 1825 nabij St. Philipsland. Heemkundekring ‘Philippuslandt’, Cronicke (in press).

Maenen, J. 2002. De invoering van het metrieke stelsel in Nederland tussen 1793 en 1880: aspecten van een beschavingsproces. PhD thesis. Radboud University Nijmegen, the Netherlands.

Mamzer, H.M. 2021. Ritual slaughter: the tradition of pilot whale hunting on the Faroe Islands. Frontiers in Veterinary Science 8: 552465

NOAA, 2022. National Oceanic and Atmospheric Administration website https://www.fisheries.noaa.gov/species/long-finned-pilot-whale#:~:text=The%20lifespan%20of%20long%2Dfinned,least%2060%20years%20for%20females.; viewed 15 September 2023.

van Bambeke, C. 1868. Quelques remarques sur les squelettes de cétacés, conservés à la collection d’anatomie comparée de l’Université de Gand. Bulletin de l’Académie royale des sciences, des lettres et des beaux-arts de Belgique, Bruxelles (2) 26: 20-61.

van Bemmelen, A.A. 1864. Lijst der zoogdieren, tot heden in den wilden staat in Nederland waargenomen. In: J.A. Herklots (ed.) 1866. Bouwstoffen voor een fauna van Nederland. Derde deel: 250. E.J. Brill, Leiden, the Netherlands.

van Bree, P.J.H. 1975. Over de skeletten van twee Grienden, *Globicephala melaena* (Traill, 1809), afkomstig van de massastranding op Tholen in 1825. Lutra 17: 6-8.

van Deinse, A.B. 1931. De fossiele en recente Cetacea van Nederland. PhD thesis. H.J. Paris, Amsterdam, the Netherlands.

van Deinse, A.B. 1950. Geen walvissen maar zwarte dolfijnen. NRC, 2 May 1950.

van Harderwijk, K.J.R. 1860. Levensberigt van Quirijn Maurits Rudolph Ver Huell. Gelders Archief, Inv. nr. 57: 2039.

van Oort, E.D. 1918. Over een te Noordwijk aan Zee aangespoelden *Lagenorhynchus albirostris*. Benevens een lijst van de Cetaceën-soorten, die tot heden aan de Nederlandsche kust zijn waargenomen. ‘s Rijksmuseum van Natuurlijke Historie: Zoölogische Mededeelingen 4: 54-62.

Reumer, J.W.F. (ed.) 1989. Vreemde en treffende natuurtonelen, de natuur op aquarellen van Maurits Ver Huell (1787-1860). Natuurmuseum Rotterdam, the Netherlands.

Robson, F.D. & P.J.H. van Bree 1971. Some remarks on a mass stranding of sperm whales, *Physeter macrocephalus* Linnaeus, 1758, near Gisborne, New Zealand, on March 18, 1970. Zeitschrift für Säugetierkunde 36 (1): 59.

Schlegel, H. 1862. Natuurlijke historie van Nederland – de dieren van Nederland: gewervelde dieren. Kruseman, Haarlem, the Netherlands.

Wikipedia. https://en.wikipedia.org/wiki/Dolphin_drive_hunting ; viewed 14 October 2023

Samenvatting

Een opportunistische drijfjacht van grienden (Globicephala melas) in Nederland in 1825

In dit artikel wordt een reconstructie gemaakt van een drijfjacht op een groep van circa 38 Grienden (*Globicephala melas*) welke plaatsvond op 9 april 1825 nabij St. Philipsland (Zeeland) in Nederland. De reconstructie is gebaseerd op gepubliceerde en niet-gepubliceerde documenten en artistieke impressies, aangevuld met vijf volledige skeletten en een huid van grienden in Belgische en Nederlandse musea die restanten zijn van deze drijfjacht. Van vijf, mogelijk zes en wellicht zelfs twaalf dieren gedood bij deze drijfjacht is een gedeeltelijke of complete tijdslijn gereconstrueerd.

Received: 19 September 2023
Accepted: 4 November 2023

Monitoring van een Vlaamse populatie van Chinese muntjak (*Muntiacus reevesi*) in het kader van bestrijding

Bram D'hondt[1], Patrick Engels[2], Bert Verbist[2], Jan Vercammen[1], Wouter Huygens[2], Tim Adriaens[1] & Jim Casaer[1]

[1] Instituut voor Natuur- en Bosonderzoek (INBO), Havenlaan 88 bus 73, 1000 Brussel, België,
e-mail: bram.dhondt@inbo.be
[2] Agentschap voor Natuur en Bos (ANB), Havenlaan 88 bus 75, 1000 Brussel, België

Abstract: *Monitoring of a population of Reeves' muntjac in the context of eradication (Flanders, Belgium)*
The emergence of Reeves' muntjac (*Muntiacus reevesi*) in mainland Europe is a major concern for the forestry, nature conservation and hunting sectors, among others. The species is therefore subject to international agreements aimed at preventing its further spread. Predicting the response of muntjac to management interventions is critical in developing effective strategies, but accounts are largely lacking. The muntjac is now an established species in Flanders (Belgium). Following the first observations in 2004 and 2005, the number of observations increased sharply from 2012 onwards, with a provisional peak in 2020 (over 60 1-km² grid cells). The ban on keeping muntjacs is strictly enforced, and inspection services have seized animals in dozens of cases since the ban entered into force (August 2016). Efforts are made to remove every animal from the wild, with 53 successful removals reported officially between January 2019 and July 2023. Most observations come from the eastern edge of the Antwerp agglomeration, where the species has escaped from a private estate (as confirmed by genetic analysis). To expand our understanding of this 'new' mammal, the muntjac is monitored, and also managed, in the nearby public domain Park Vordenstein (137 ha; municipality of Schoten). Monitoring is performed by means of camera traps (up to fourteen, November to June). Management is performed primarily through shooting from high seats (morning and evening, February to April). During this first campaign (2020-2022), muntjacs were observed frequently, albeit quite localized (615 sequences, second only to roe deer (*Capreolus capreolus*)). The species' diel activity pattern was clearly crepuscular, with a slightly stronger peak near dusk. The species appeared to avoid human disturbance temporally rather than spatially. The detections confirmed muntjac as a solitary species (more so than roe deer). Observations of behaviour (e.g. grazing, estrus, rut, conflicts) indicate a normal, healthy population. Two image sequences showed a red fox (*Vulpes vulpes*) chasing a muntjac. The control effort during the study period totalled 511 man-hours of occupying high seats and, as a trial, six hours of stalking. In total, ten animals were shot: eight bucks, two does. The data suggested a marginally significant shift in diel activity during periods of management. From the limited experience so far, culling of muntjac seems to benefit from a close exchange with the camera trap monitoring, an extended time window for shooting (two hours past sunset), and by stalking (as opposed to high seats). Although the culling campaign led to a notable decrease in the number of detections in each of both years, numbers quickly recovered. The population in the park thus appears to be resilient. Nevertheless, the current management results may help flatten population growth and spread (containment), or be of broader significance if the observed population recovery is partly due to immigration (source-sink dynamics).

Trefwoorden / keywords: muntjak, muntjac, cameravallen, camera traps, bestrijding, control, invasieve soorten, invasive species, Park Vordenstein, Agouti.

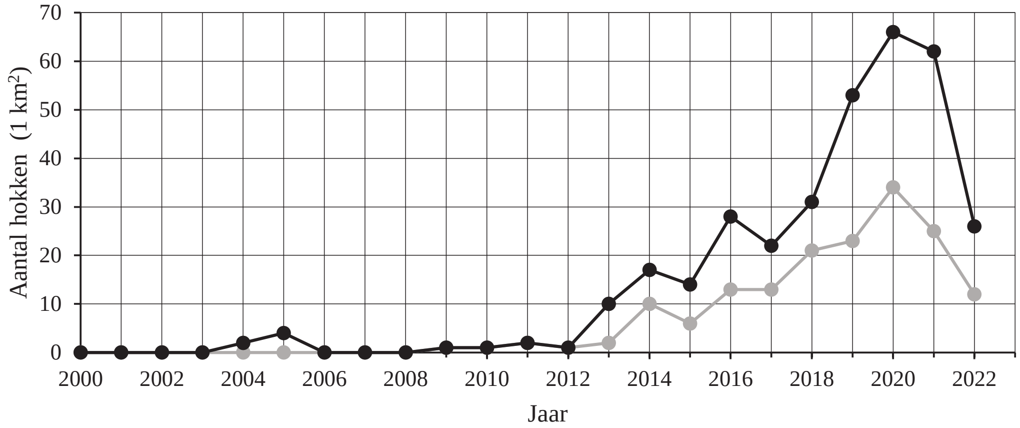
Inleiding

De Chinese muntjak (*Muntiacus reevesi*), verder kortweg muntjak genoemd, is een kleine hertachtige die inheems is in China en Taiwan (Smith-Jones 2022). De soort is door de mens naar Europa gebracht. In Groot-Brittannië is de muntjak sinds zijn introductie als sier- en jachtwild aan het eind van de 19de eeuw ondertussen zelfs uitgegroeid tot een wijdverspreide en abundante soort (Chapman 2021). Dit is niet zonder gevolgen gebleken: lokaal hoge dichtheden van muntjak leiden tot schade aan tuinen, parken, bossen en akkers, en tot risico's voor de verkeersveiligheid (aanrijdingen; Raymond et al. 2021) en ziekte-overdracht (McKillen et al. 2017, Chapman 2022). De meest rechtstreekse invloed laat zich voelen in de bosomgeving, waar vraat- en veegschade leiden tot wijzigingen in de boomlaag (verhindering van verjonging van hakhoutsoorten zoals hazelaar (*Corylus avellana*)), de struiklaag en de kruidlaag (selectieve vraat van oudbosplanten zoals boshyacint (*Hyacinthoides* spp.), bosbingelkruid (*Mercurialis pernennis*) of sleutelbloem (*Primula* spp.), ten voordele van ruigtesoorten zoals duinriet (*Calamagrostis epigejos*) of ruwe smele (*Deschampsia cespitosa*)). Deze effecten van muntjak worden uitvoerig behandeld in de monografie van Cooke (2019), op basis van decennialange monitoring in Groot-Brittannië. Wijzigingen in de vegetatie kunnen ook doorwerken bij de fauna, zoals in de lokale broedvogelgemeenschap (Palmer et al. 2015).

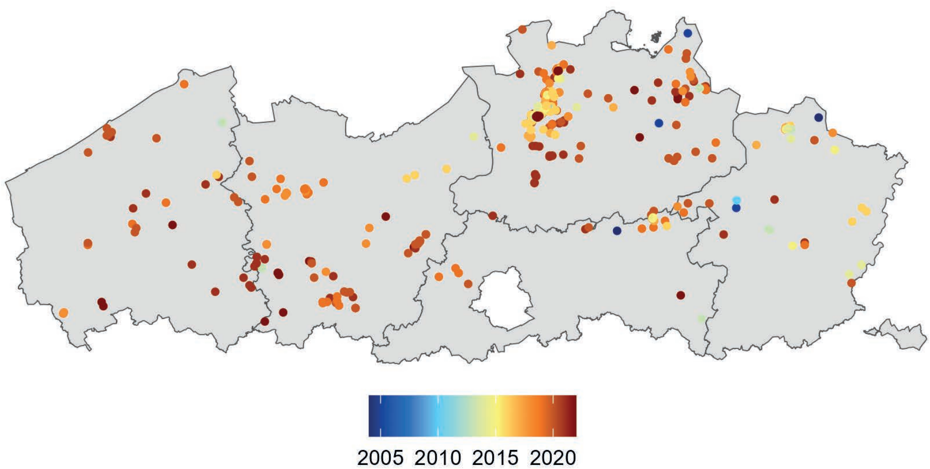
Deze effecten kunnen tot op zekere hoogte veralgemeend worden voor alle hertachtigen, en vaak is er dus sprake van een gecombineerd schadebeeld. Vooral in geëutrofieerde regio's (zoals Vlaanderen en Nederland) leidt een hoge vraatdruk door hoefdieren tot een degradatie van de bosomgeving (Segar et al. 2022). De mate waarin muntjak en ree elkaar aanvullen (cumulatie) dan wel vervangen (concurrentie) is niet éénduidig (Acevedo et al. 2010, Cooke 2019, Chapman 2022). Hemami et al. (2004) concludeerden uit een veldstudie in Engeland dat concurrentie om (voedsel) bronnen (exploitatiecompetitie) te verwachten is in gevallen van voedselschaarste (bv. 's winters in naaldbossen). Uit een grote dataset van een ree-, damhert- en muntjakpopulatie konden Zini et al. (2023) recent opmaken dat reeën minder nakomelingen hebben bij sterke aanwezigheid van muntjak, met aanwijzingen dat hiervoor niet exploitatie-, maar wel interferentiecompetitie doorslaggevend is. De auteurs verwijzen hiervoor naar stressinducerende interacties tussen beide soorten.

Om te vermijden dat het Britse scenario zich op het Europese vasteland zou herhalen, plaatste de Europese Commissie muntjak op de lijst van voor de Unie zorgwekkende, invasieve uitheemse soorten. De opname op deze lijst houdt middels een verordening (nr. 1143/2014) in dat muntjaks sinds 2016 niet langer mogen worden gehouden, gekweekt of verhandeld. Daarmee wordt een totale uitdoving van de gehouden populatie beoogd. Daarnaast is opgelegd dat alle lidstaten werk moeten maken van de wilde populatie op hun grondgebied. Indien de muntjak nog niet aanwezig is, moeten de nodige instrumenten worden ontwikkeld om dat ook zo te houden; indien de soort wel aanwezig is, moeten inspanningen worden geleverd om de populatie zo mogelijk te verwijderen, of op zijn minst te beheersen. Maar, zoals Barton et al. (2022) uit een review van het beheer van hertachtigen konden opmaken, is over de effectiviteit van muntjakbeheer bitter weinig gekend.

Voor Vlaanderen (België) geldt dat de soort onmiskenbaar in het wild aanwezig is. Van alle lidstaten binnen de Unie lijkt in geen enkele andere regio even standvastig melding te worden gemaakt van muntjak. Het



Figuur 1. Het aantal kilometerhokken binnen het Vlaamse Gewest waar muntjak is aangetroffen. Zwart: alle waarnemingen; grijs: gevalideerde waarnemingen. Bron: GBIF.org (2023), eigen data.
Figure 1. Number of grid cells from the Flemish Region where muntjac has been observed. Black: all observations; grey: validated observations. Source: GBIF.org (2023), own data.



Figuur 2. Kaart met cumulatieve waarnemingen van muntjak (2000 t/m 2022). Bron: zie Figuur 1.
Figure 2. Map with accumulated observations of muntjac (2000 up to and including 2022). Source: see Figure 1.

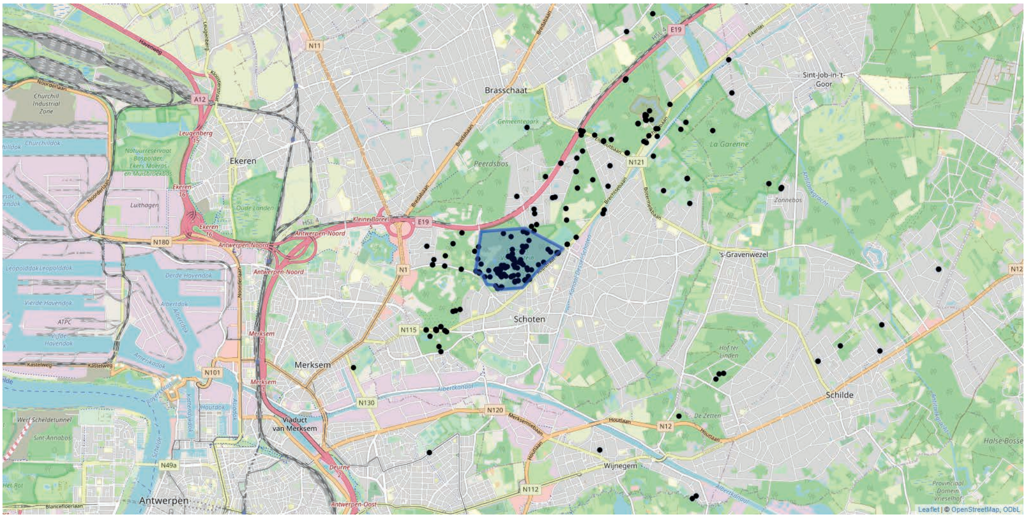
Vlaamse Gewest draagt daarmee een belangrijke, internationale verantwoordelijkheid om de vestiging van de muntjak in Europa te vermijden (Ward et al. 2021).

In dit artikel geven we een beknopte update van de situatie van de muntjak in Vlaanderen, en rapporteren we, voor het eerst, over de opvolging en het beheer van een gevestigde populatie nabij de Vlaams-Nederlandse grens.

De muntjak in Vlaanderen

In het Vlaamse Gewest werd de muntjak, na initiële waarnemingen in 2004 en 2005, met name vanaf 2012 in jaarlijks toenemende mate gemeld (Figuur 1, Figuur 2; Deflem et al. 2022). Een voorlopige piek kwam er in 2020, toen de soort in niet minder dan 66 kilometerhokken werd waargenomen.

De achterliggende dynamiek is redelijk goed



Figuur 3. De situering van Park Vordenstein (blauw) binnen de agglomeratie Antwerpen. Zwarte punten zijn waarnemingen van muntjak (zie Figuur 1 voor details).

Figure 3. The location of Park Vordenstein (blue) within the Antwerp area. Black dots are observations of muntjac (see Figure 1 for details).

gekend op basis van dossierkennis en onderzoek. Kort samengevat weerspiegelt de waargenomen verspreiding veeleer menselijke dan natuurlijke processen. Sinds de opname op de Europese lijst van invasieve exoten hebben de inspectiediensten tientallen dossiers van illegaal gehouden muntjaks vastgesteld. Door deze dossiers weten we dat de meeste waarnemingen van muntjak in het wild voortkomen uit dergelijke gehouden populaties. Dit wordt bevestigd door genetisch onderzoek: de totaalpopulatie is sterk gestructureerd, met duidelijk onderscheidbare clusters en familieverbanden die enkel door menselijk handelen kunnen worden verklaard (Deflem et al. 2022). De achterliggende intenties, nl. of dieren (onopzettelijk) zijn ontsnapt of (opzettelijk) zijn uitgezet, kunnen hieruit niet afgeleid worden. Dossierspecifieke details suggereren dat beide een rol speelden (Figuur 2).

De piek van waarnemingen in 2020 moet ook in het licht van deze handhaving worden gezien. Interventies hebben vermoedelijk heel wat houders ertoe aangezet zich pro- of reactief van hun dieren te ontdoen. Dit illustreert goed de risico's die met een nieuw verbod op soorten gepaard gaan (Hulme 2015). Toch lijkt deze handhaving, als noodzakelijke eerste stap, resultaat te hebben bereikt: het aantal dossiers van gehouden muntjaks is sterk gedaald, en de vaak geïsoleerde vaststellingen blijken van korte duur te zijn geweest (getuige een terugval in de jaren 2021-2022).

Parallel aan deze handhaving zijn ook initiatieven genomen voor het beheer van dieren in het wild (Casaer et al. 2015). In principe wordt bij elke vaststelling van een dier in het wild onder impuls van de overheid naar een oplossing gezocht. Dieren worden gevangen of geschoten, waarbij de uitvoering op overheidsdiensten, ordediensten, jagers of dierenopvangcentra rust. Er is geen verplichting tot rapportage, en ook acties door de overheid zijn in het verleden niet steeds bijgehouden. Dit laatste is veranderd met de opmaak van een specifiek meldingsformulier voor muntjaks. Voor de periode van januari 2019 tot en met juli 2023 zijn 53 verwijderde dieren gemeld (e-loket van het Agentschap voor Natuur en Bos).

De muntjak in de Antwerpse rand

Het zwaartepunt van de verspreiding van de muntjak ligt in de groene oostrand van de agglomeratie Antwerpen. Daar zijn de waarnemingen het meest aaneengesloten in locatie en tijd (Figuur 2, Figuur 3). De oorsprong van deze populatie ligt in een groot privaat domein in de gemeente Schoten. Het genetisch onderzoek van Deflem et al. (2022) bevestigde de nauwe verwantschap tussen dieren uit het wild en dieren die op dat domein in beslag zijn genomen. Diezelfde analyse bevestigde ook de verwantschap met dieren die tot op 10 kilometer afstand zijn gevonden, wat op een natuurlijke uitbreiding wijst.

In het vlakbij gelegen overheidsdomein Park Vordenstein werden vanaf 2012 regelmatig muntjaks gemeld. De betrokken overheidsdiensten wonnen in de daaropvolgende jaren de nodige adviezen in, en ondernamen bescheiden pogingen tot beheer (afschot). Hoewel deze muntjakpopulatie daarmee snel de best gekende van Vlaanderen werd, bleven tot voor kort echter nog vele, vaak essentiële vragen onopgelost.

Om daaraan tegemoet te komen, startte het Instituut voor Natuur- en Bosonderzoek (INBO), in nauwe samenwerking met het Agentschap voor Natuur en Bos (ANB), een studie naar het voorkomen van muntjaks in het park. Deze monitoring had het expliciete doel om het beheer van de soort te ondersteunen. In dit artikel gaan we in op het muntjakbeheer en cameravalonderzoek in de winters van 2020-2021 en 2021-2022. We hopen met dit beschrijvend onderzoek een goede basis te leggen voor een beter begrip van dit zoogdier in de Lage Landen.

Materiaal en Methoden

Park Vordenstein

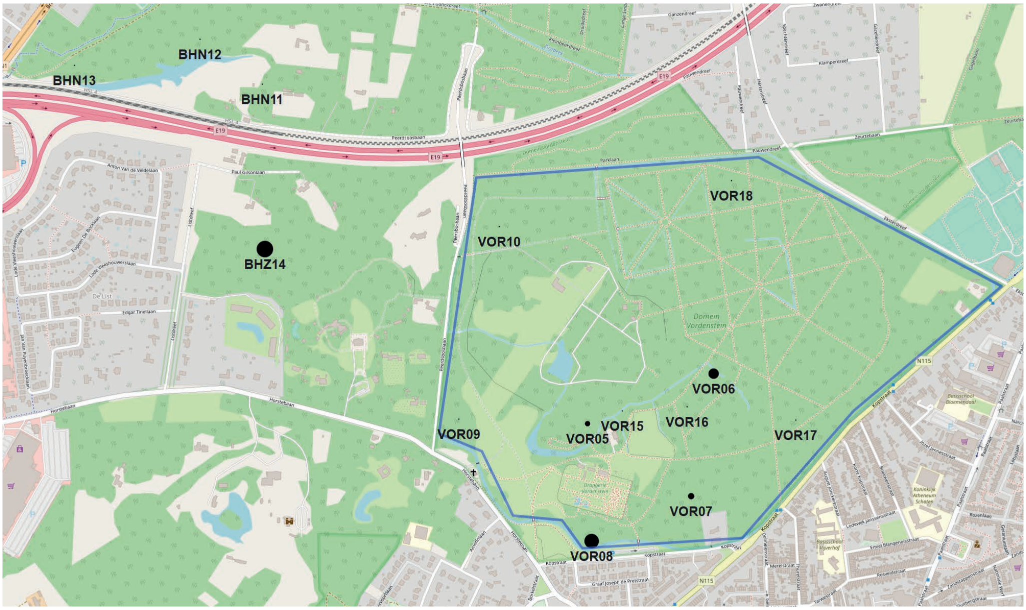
Park Vordenstein is een oud kasteelpark dat aansluit op andere groengebieden in een overigens (sub)urbane omgeving (Figuur 3, Figuur 4). Het 137 hectare grote domein is voor het grootste deel eigendom van het Vlaamse Gewest en in beheer bij het ANB. Het overig deel is privé-bezit. Het park kent een hoge esthetische waarde en combineert tal van vlak-, lijn- en puntvormige elementen die een kenmerkende landschapsstijl hebben (Geudens et al. 2009). Daartoe behoren onder andere een landschapspark naar Engels model, een arboretum en een sterk geometrisch drevenpatroon.

Ongeveer 87 hectare kan worden geklasseerd als bos. Dit bos varieert sterk in leeftijd (18de-eeuwse tot 20ste-eeuwse aanleg), structuur (hooghout, hakhout, of een combinatie), samenstelling (loof- vs. naaldhout), herkomsten (inheems vs. uitheems) en gelaagdheid (kruid- en struiklaag afwezig vs. dicht). In termen van volume zijn grove den (*Pinus sylvestris*), zomereik (*Quercus robur*), berk (*Betula* spp.) en beuk (*Fagus sylvatica*) de belangrijkste soorten. De oude, inheemse bosbestanden bevatten relatief veel dood hout. De belangrijkste planten in de ondergroei, in termen van dekking voor grondbewonende zoogdieren, zijn rododendron (*Rhododendron* spp.), braam (*Rubus* spp.) en adelaarsvaren (*Pteridium aquilinum*). Naast bos omvat het park ook hooiland (± 10 ha), weiland (± 2 ha) en heide (± 0,4 ha).

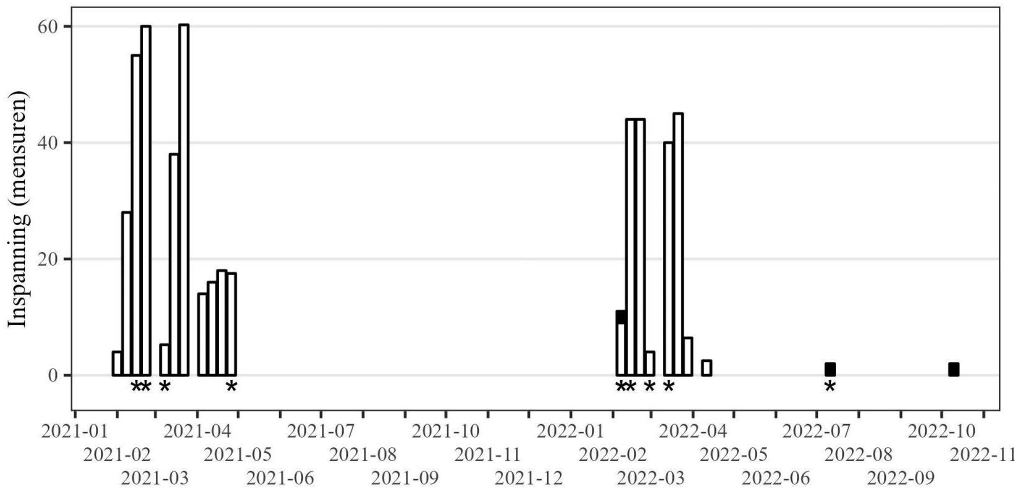
Rond het domein loopt een gracht die grotendeels de natuurlijke grens van het park vormt. Om de rust van het gebied te bewaren, wordt het park ’s nachts gesloten voor het publiek. De openingstijden variëren doorheen het jaar van 8u-17u (winter) tot 8u-22u (zomer). Bovendien zijn honden niet toegelaten, ook niet aangelijnd.

Beheer van muntjak

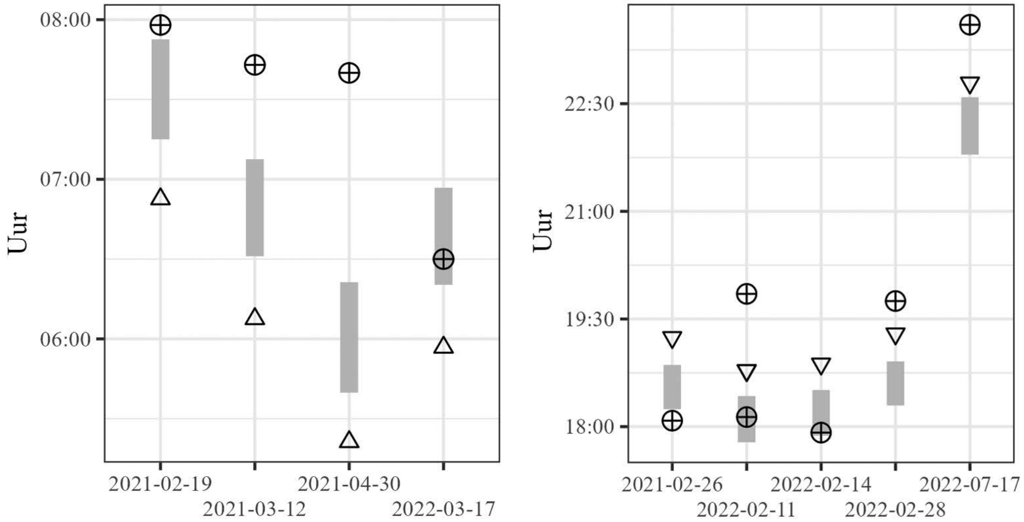
De bestrijding in Park Vordenstein omvatte twee perioden van aanzit in 2021 en 2022 (Figuur 5). Daarvoor werden zeven (2021) en tien (2022) locaties voor hoogzitten gekozen.



Figuur 4. Park Vordenstein (blauw), met de locaties van de cameravallen (VOR: Park Vordenstein, BHZ: Bonte Hanek Zuid, BHN: Bonte Hanek Noord). De cirkelgrootte is een maat voor het aantal sequenties met muntjak.
Figure 4. Park Vordenstein (blue), with locations of the camera traps (VOR: Park Vordenstein, BHZ: Bonte Hanek Zuid, BHN: Bonte Hanek Noord). The circle size is a measure of the number of sequences with muntjac.



Figuur 5. De bestrijdingsinspanning per week. De bersacties zijn weergegeven in het zwart. *: muntjak geschoten.
*Figure 5. The culling effort per week. Ground-level stalking is indicated in black. *: muntjac shot.*



Figuur 6. Tijdstippen van gerealiseerd afschot (links: ochtend, rechts: avond). Cirkels: tijdstip van afschot. Grijze balkjes: schemerperiode. Driehoekjes: start (ochtend) en eind (avond) van de afschotperiode volgens de wettelijke basisbepalingen. Gerealiseerd afschot buiten die periode valt onder de afwijking op die bepalingen.
Figure 6. Times of culling (left: morning, right: evening). Circles: actual times of culling. Grey bars: twilight. Triangles: beginning (morning) and end (evening) of the shooting period according to default legal provisions. Culling outside that period was granted by an exemption to those provisions.

Aanzitsessies werden steeds in de ochtend of de avond georganiseerd.

In 2021 varieerde het aantal op een ochtend of avond tegelijkertijd bezette hoogzitten van drie tot zes. Er werd in totaal 316 mensuren aangezeten (35 aanzitdagen, 45 aanzitsessies, 1 februari – 30 april). De ochtendlijke aanzit startte één uur vóór zonsopgang, en de avondlijke aanzit stopte één uur na zonsondergang, conform de basisbepalingen uit de Vlaamse wetgeving. Er werden in deze campagne bij het aanzitten 23 dieren gezien en vier dieren geschoten (twee geiten, twee bokken; 6,1-12,6 kg ontweid gewicht). Figuur 6 geeft details over de tijdstippen weer.

In de campagne van 2022 varieerde het aantal simultaan bezette hoogzitten van één tot zes. Er werd 195 uren aangezeten (24 dagen, 31 sessies, 11 februari – 12 april). Ten opzichte van het voorgaande jaar werden een aantal aanpassingen doorgevoerd. Het aantal hoogzitten werd verhoogd van zeven naar tien, voor een ruimere keuze (bv. in functie van de windrichting). Daarnaast werd de timing van de tussentijdse verwerking van de cameravallen nauwer afgestemd op de aanzitsessies. Ook werden de tijdsvensters voor aanzit uitgebreid (middels een afwijking op de wetgeving): van twee uur vóór zonsopgang, tot twee uur ná zonsondergang. Tenslotte werden er in dit jaar ook drie bersacties georganiseerd, als alternatieve vorm van bestrijding (bij bersen beweegt de schutter zich op grondniveau, i.p.v. stationair in de hoogte te wachten; zes mensuren; Figuur 5).

In 2022 werden 26 dieren gezien en zes dieren geschoten (allen bokken; 5,7-11,0 kg). Drie dieren werden geschoten in het uitgebreide tijdsvenster (Figuur 6). Twee dieren werden geschoten tijdens het bersen i.p.v. het aanzitten.

Uitgedrukt per eenheid van inspanning, werd dus één dier per 79 mensuren verwijderd tijdens de aanzitcampagne van 2021, en één per 49 uren tijdens het aanzitten in 2022. Voor het bersen (2022) was dit één dier per drie uren (enkel de tijd van schutters beschouwd, en niet van begeleiders en mede-zoekers).

Cameravalonderzoek

Cameravallen werden geplaatst van december 2020 tot juni 2021, en van november 2021 tot mei 2022. In het winterhalfjaar is de zichtbaarheid immers optimaal. De locaties worden getoond in Figuur 4. Drie camera's werden ten noorden van de E19 opgesteld (Bonte Hanek Noord, BHN11-BHN13). Eén cameraval werd geïnstalleerd ten westen van het park (Bonte Hanek Zuid, BHZ14). In Park Vordenstein zelf werden in de twee periodes respectievelijk zes (VOR05 t.e.m. VOR10) en tien cameravallen opgesteld (bijplaatsing van VOR15 t.e.m. VOR18). De locaties zijn deels willekeurig gekozen, maar niet volledig: met het oog op de bestrijding werden sommige camera's op wissels of open plekken in het bos gericht.

De cameravallen (Reconyx, HyperFire 2) werden op ongeveer een halve meter hoogte geïnstalleerd, en ongeveer noordwaarts gericht om tegenlicht of triggers door zonlicht te vermijden. De gevoeligheid werd als hoog ingesteld. Per detectie werd een reeks van tien foto's gemaakt. Indien de beweging aanhield, volgden reeksen elkaar zonder pauze op. Om de twaalf uur werd automatisch een foto gemaakt, die diende als controle voor de goede werking van de camera. De camera's werden regelmatig bezocht voor algemeen nazicht en tussentijdse uitlezing.

Alle beelden werden verwerkt met het online platform Agouti (Casaer et al. 2019). Beelden die elkaar opvolgen worden automatisch verzameld in een sequentie (dus een veelvoud van tien foto's) waaraan vervolgens waarnemingen kunnen worden gekoppeld (van dieren, met informatie over geslacht en gedrag). De resulterende datasets werden verwerkt in Rstudio (versie 2023.03.1, Posit Software), o.a. met behulp van de cameravalspecifieke pakketten *activity* (Rowcliffe 2023) en *camtraptor* (Oldoni et al. 2023).

Op basis van deze data beschrijven we onze waarnemingen van aantallen, geslachten, gedrag en dag-nachtritme bij de muntjak. Om het dag-nachtritme correct te interpreteren, corrigeerden we voor de variatie in daglengte binnen de studieperiode met de methode van Vazquez et al. (2019). Om na te gaan of dag-nachtpatronen tussen soorten verschilden, wordt de kans nagegaan dat beide patronen uit eenzelfde verdeling voortkomen (Ridout & Linkie 2009, Rowcliffe 2023; 999 iteraties).

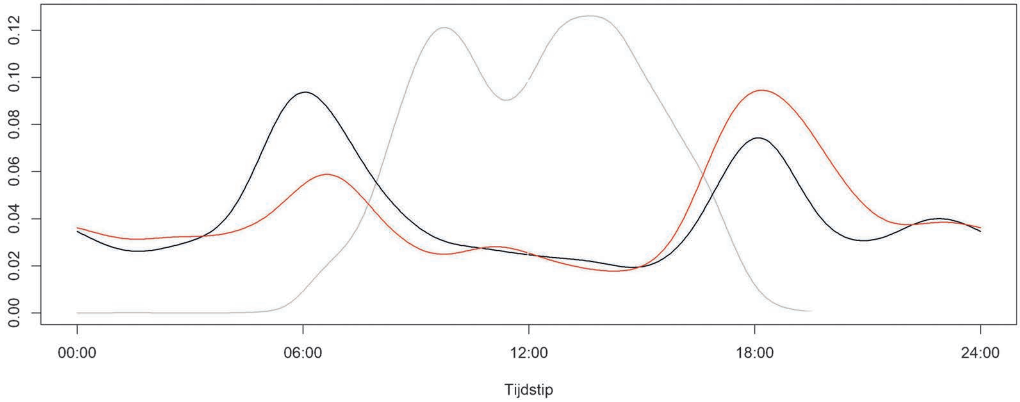
Voor een beschrijving van het aantal detecties doorheen de tijd maken we gebruik van het aantal sequenties met muntjak per tijdseenheid dat een camera effectief operationeel was (relatieve abundantie-index of RAI; Ferretti et al. 2023). Op die manier wordt gecorrigeerd voor ongelijke tijdstippen van opstelling en afbraak en (eventuele) tijdelijke defecten.

Resultaten

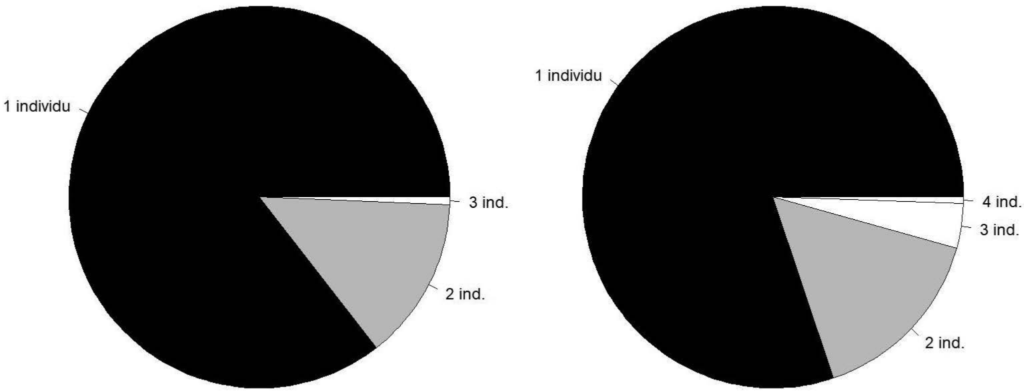
Waarnemingen: algemeen

In totaal werden 4637 sequenties met één of meerdere diersoorten bekomen (mensen en honden buiten beschouwing gelaten). Ree was met voorsprong de meest waargenomen diersoort (2444 sequenties, of 53% van het totaal). Muntjak volgt in de rangschikking, met 615 sequenties (13%). Vos (12%), houtduif (10%) en huiskat (3%) vervolledigden de top-vijf.

De ruimtelijke spreiding van muntjakwaarnemingen is opgenomen in Figuur 4. Er werden geen muntjaks waargenomen ten noorden van de E19 (Bonte Hanek Noord). De ene camera te Bonte Hanek Zuid registreerde daarentegen heel vaak muntjak. Alle camera's binnen Park Vordenstein registreerden muntjaks, maar het aantal sequenties verschilde zeer sterk (min. 3, max. 151 sequenties; maar let op de verschillende looptijden). Voor elk van beide jaren was duidelijk dat het zwaartepunt van de activiteit zich in de zuide-



Figuur 7. De dag-nachtactiviteit van muntjak (rood), ree (zwart) en mens (grijs), op basis van de data voor Park Vordenstein. Hoe hoger de y-waarde, hoe vaker de dieren op dat tijdstip werden gedetecteerd.
Figure 7. Diel activity pattern of muntjac (red), roe deer (black) and humans (grey), as based on data from Park Vordenstein. The higher the y value, the more often the animals were detected at that time.



Figuur 8. Taartdiagram van het aantal individuen per sequentie, voor muntjak (links) en ree (rechts).
Figure 8. Pie chart for the number of individuals per sequence, for muntjac (left) and roe deer (right).

lijke helft van het park bevond (omgeving van VOR05-06-07-08).

De activiteit van muntjaks gedurende een etmaal wordt getoond in Figuur 7. Het resulterend patroon is duidelijk crepusculair, dus met twee pieken, rond de ochtend- en avondschemer. Het patroon loopt sterk gelijk met dat van ree, maar kent een uitgesprokener avondpiek. De patronen van muntjak en ree zijn daarmee ook significant verschillend (P<0,01).

85,5% van de sequenties met muntjaks toonden één enkel dier, 13,8% toonden twee dieren (doorgaans een geit met kalf, of een bok en een geit) en 0,6% drie dieren (Figuur 8). Hoewel reeën ook het vaakst alleen werden gezien, is er toch een statistisch significant verschil tussen beide soorten, waarbij reeën vaker dan muntjaks samen worden gezien (chi-kwadraattoets, P<0,01).

Volwassen muntjakbokken zijn in voor- of zijaanzicht makkelijk te herkennen aan het (korte) gewei en de V-vormige koptekening (die de aanzet van het gewei accentueert; Shilai et al. 1986; Figuur 9). Geiten hebben geen gewei en vertonen een ruit- of diamant-

Figuur 9. Waarnemingen van muntjak. (a): bok achtervolgt bronstige geit; (b): conflict tussen twee bokken; (c): grazende geit en bok; (d): vos achtervolgt bok.

Figure 9. Observations of muntjac. (a): buck pursuing a doe. (b): two bucks in conflict. (c): grazing doe and buck. (d): fox chasing a buck.

vormige koptekening. Omdat het onderscheid tussen de geslachten niet bij alle dieren en op alle beelden even duidelijk is, kan over de verhouding niets worden besloten (behalve dat minstens 31% van de waarnemingen een bok betrof).

Vijf sequenties, uit de maanden februari, maart en mei toonden een achtervolging van een bronstige geit (met opgeheven staart) door een bok (Figuur 9a). Vijf sequenties, zij het van één enkele camera, toonden een conflict tussen twee bokken (Figuur 9b). Overigens laten de beelden geen sterk gevarieerd gedragsspectrum zien. In het merendeel van de sequenties waarbij het gedrag werd genoteerd (68%, n=114) passeerden dieren voor de camera, enigszins onderzoekend, snuffelend, mogelijk grazend op grondniveau, maar overigens zonder duidelijk gedrag. Begrazing van hogere struiken werd weinig geregistreerd (Figuur 9c). Muntjaks toonden ook interesse in een liksteen, die slechts op één locatie tijdelijk aanwezig was.

Slechts in enkele beeldreeksen kwam samen met muntjak ook een andere diersoort in beeld, het vaakst vogelsoorten. In dit opzicht zijn enkel ree en vos vermeldenswaard. In het eerste geval (drie sequenties) is er geen sprake van duidelijke interactie. In het geval van vos (twee sequenties) was er telkens sprake van een achtervolging van (één, respectievelijk twee) muntjaks door een vos (Figuur 9d).

Waarnemingen: beheer

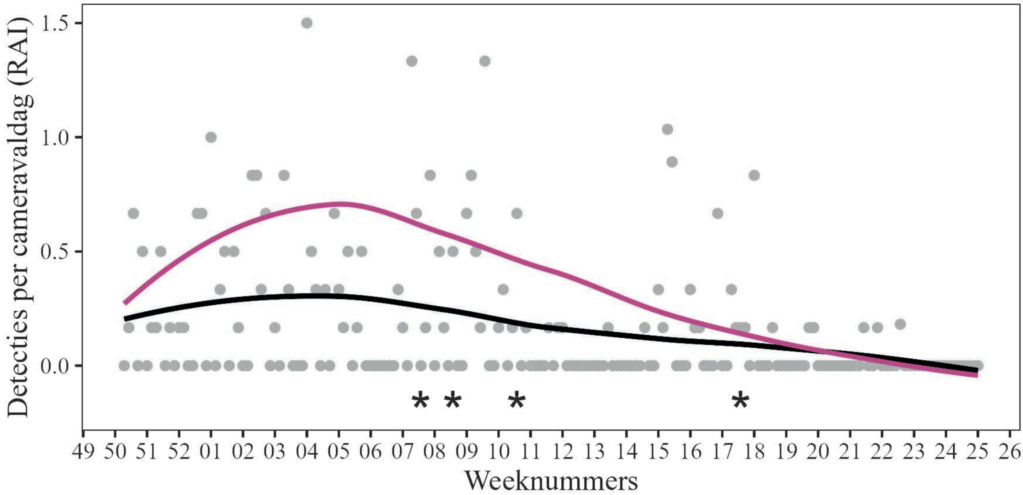
Het aantal detecties per tijdseenheid wordt getoond in Figuur 10 en Figuur 11. In de campagne van 2020-2021 is er sprake van een algemene achteruitgang: op het eind van de campagne werden muntjaks nog steeds waargenomen, maar beduidend lager dan vóór het eerste afschot. Tegen de aanvang van de campagne van 2021-2022 was het aantal detecties grotendeels hersteld tot het niveau van een jaar eerder. Het aantal detecties liep ook in deze tweede campagne sterk terug naargelang er dieren werden geschoten, maar dit aantal herstelde zich weer snel nadien. (Bemerk dat de trendlijnen in de figuren worden afgezwakt door de camera's met weinig waarnemingen.)

Zoals getoond in Figuur 12, lijkt de dag-nachtactiviteit van de muntjak iets gespreider te zijn gedurende perioden van afschot (gedefinieerd volgens de uiterste datums zoals vermeld onder 'Beheer van muntjak'), maar dit verschil is marginaal significant ($0{,}10 > P > 0{,}05$).

Discussie

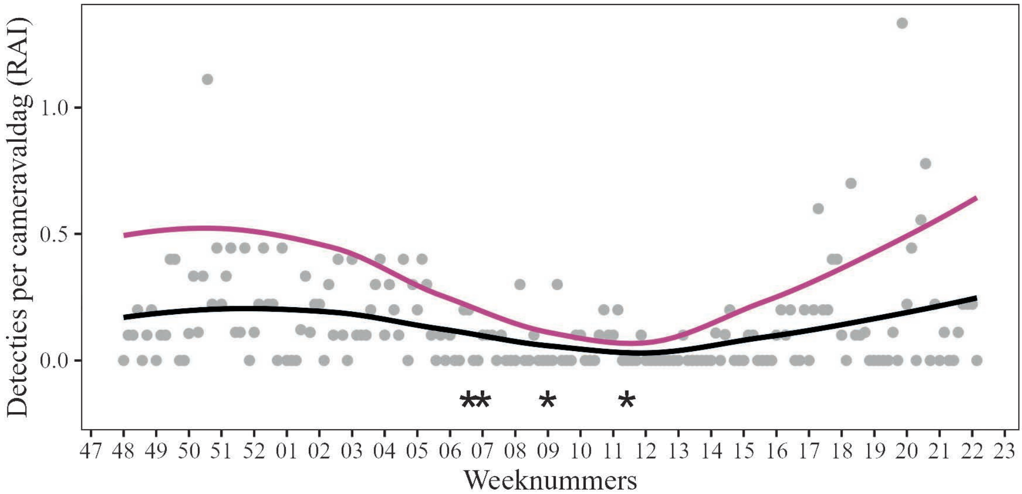
De structuur en vegetatie van Park Vordenstein kent tal van overeenkomsten met van Groot-Brittannië gekende, voor muntjak geschikte locaties (Smith-Jones 2004). De nachtelijke sluiting van het park en afwezigheid van honden dragen ongetwijfeld aan de geschiktheid bij. Overdag is het wel druk met wandelaars, maar muntjaks lijken deze met name temporeel (Figuur 7), eerder dan ruimtelijk (Figuur 4), te vermijden. De menselijke activiteit is namelijk ook in de zuidelijke helft het sterkst (o.a. loods, tuinonderhoud). Activiteit met een ochtend- en avondpiek is ook beschreven op basis van cameravalonderzoek in het inheemse areaal in China (Sun et al. 2022).

De waarnemingen bevestigen het solitaire karakter van de muntjak. Dit volgt de vaststellingen uit Groot-Brittannië, al zagen onze camera's relatief vaker dieren per twee (P<0,05, chi-kwadraattoets met gerapporteerde frequenties van Cooke 2019, tabel 2.8). Bij het merendeel van de waarnemingen werden dieren langzaam lopend geobserveerd, zonder duidelijk gedrag. Dit sluit subtiele, weinig zichtbare activiteiten niet uit. Vermoedelijk wordt vaak zeer laag bij de grond gezocht naar voedsel, waarbij ook kiemplanten en gevallen vruchten (bv. eikels) worden geconsumeerd. Dit is belangrijk, omdat de schade aan de vegetatie ten gevolge van vraat kan worden onderschat indien enkel naar



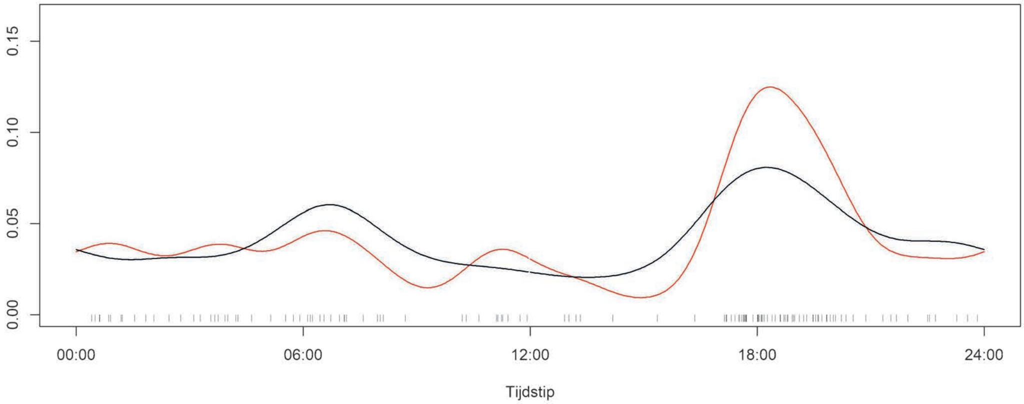
Figuur 10. Aantal detecties van muntjak per tijdseenheid (nl. per 24 uur operationele cameratijd), voor de campagne 2020-2021 te Park Vordenstein. De punten zijn de ruwe waarden per camera en per dag. Zwarte lijn: LOESS-regressie over alle camera's heen. Paarse lijn: regressie voor de camera's met de meeste detecties (VOR08 en VOR06, samen goed voor 60% van alle detecties). *: muntjak geschoten.

*Figure 10. Number of detections of muntjac per time unit (i.e. per 24 hours of operational camera time), from the 2020-2021 campaign in Park Vordenstein. The points refer to the raw data per camera and per day. Black line: LOESS regression across all cameras. Purple line: regression for the cameras with the most detections (VOR08 and VOR06, accounting for 60% of the total number). *: muntjac shot.*



Figuur 11. Aantal detecties van muntjak per tijdseenheid (nl. per 24 uur operationele cameratijd), voor de campagne 2021-2022 te Park Vordenstein. Details: zie vorige figuur.

Figure 11. Number of detections of muntjac per time unit (i.e. per 24 hours of operational camera time), from the 2021-2022 campaign in Park Vordenstein. Details: see previous figure.



Figuur 12. De dag-nachtactiviteit van muntjak in Park Vordenstein, tijdens (rood, *n*=126 detecties) en buiten (zwart, *n*=311) perioden van afschot. Hoe hoger de y-waarde, hoe vaker de dieren op dat tijdstip werden gedetecteerd. De verticale streepjes onderaan geven de ruwe gegevens weer van tijdens perioden van afschot.
Figure 12. Diel activity pattern of muntjac in Park Vordenstein, during (red, n=126 detections) and outside (black, n=311) periods of management. The higher the y value, the more often the animals were detected at that time. The black dashes at the bottom represent the raw data during periods of management.

uiterlijk waarneembare schade op gevestigde struiken en bomen wordt gezocht.

Intrigerend zijn de beelden met een achtervolging van een muntjak door een vos (Figuur 9d). Inderdaad is vos bekend als de vermoedelijk belangrijkste predator van muntjakkalfjes (Chapman 2022). Het is echter zeer de vraag of een vos ook (sub)adulte muntjaks aankan. Alvast lijkt in één van de twee gefilmde gevallen dezelfde muntjak later ongedeerd langs de camera te wandelen. Er zijn in de studie geen aanwijzingen gevonden voor een effect van muntjak op ree.

Waar het afschot in 2021 aanvankelijk tot een sterke terugval leek te leiden in het aantal detecties van muntjak (Figuur 10), bleek dit aantal in het begin van het volgende seizoen reeds hersteld te zijn. Bovendien veerde het aantal detecties veel sneller op na de aanzitperiode van 2022 (Figuur 11). Dit snelle herstel in detecties kan het gevolg zijn van succesvolle reproductie, en/of van immigratie van dieren uit de omgeving. Het eerste speelt haast met zekerheid een rol, aangezien in de laatste periode enkel bokken zijn geschoten, waardoor de dracht van geiten en de voortplanting (indien een seksueel actieve bok is overgebleven) niet onderbroken was.

De voortplanting bij muntjaks is niet aan seizoenen gebonden. De dracht duurt zeven maanden en geiten kunnen na een geboorte snel opnieuw bevrucht worden (Chapman et al. 1997). Op elk gegeven tijdstip is de meerderheid van de vrouwelijke dieren in een florerende populatie dan ook drachtig. Een worp bestaat in de regel uit één kalf (Chapman 2022).

Indien het snelle herstel enkel het gevolg is van lokale reproductie, lijkt het gerealiseerd afschot in deze jaren niet tot een afname (hoogstens tot een stabilisatie) van de populatie te hebben geleid. Om een afname te bekomen, zouden meer dieren geschoten moeten worden, geiten in het bijzonder. Hiervoor zou het aanzitten verder kunnen worden verfijnd en uitgebreid doorheen het jaar. De uitbreiding van het tijdsvenster per dag is alvast zinvol gebleken (Figuur 6), al suggereert het waargenomen dag-nachtritme meteen ook dat dieren zich dieper in de nacht niet vaker voor hoogzitten zullen laten zien (Figuur 7). Mogelijk verschuiven de dieren hun activiteit ook naargelang hoogzitten zijn bemand, wat erop zou wijzen dat de dieren de menselijke aanwezigheid gewaar zijn (Figuur 12). Bestrijding door bersen zou in dit opzicht effectiever kunnen zijn om dieren op te sporen. Dit blijkt voorzichtig uit het aantal geschoten dieren per eenheid van inspanning in de campagne van 2022, al is de omvang en opzet van deze 'test' voorlopig niet toereikend.

Indien het snelle herstel ook deels het gevolg is van immigratie, wordt met de bestrijding in Park Vordenstein een effect op bredere schaal bereikt. Dit is waarschijnlijk, omdat van de muntjak bekend is dat ze een zogenaamde 'source-sink'-dynamica vertoont: deelpopulaties waar het aantal muntjaks afneemt, worden in stand gehouden door immigratie vanuit deelpopulaties waar het aantal muntjaks toeneemt (Wäber et al. 2013). Indien afschot in het park vrije territoria creëert voor dieren uit de omgeving, wordt de verdere uitbreiding van muntjak op regionaal niveau mogelijk afgeremd of verhinderd. De omgeving van Park Vordenstein kent enkele sterke barrières (snelweg E19 annex spoorweg; kanaal Dessel-Schoten; stedelijk milieu), die voor immigrerende dieren net zo spelen als voor emigrerende dieren, maar niettemin overbrugbaar zijn gebleken (Figuur 3, Deflem et al. 2022).

Overigens kent het gebruik van RAI-waarden zijn beperkingen voor het bepalen van trends. Met het oog op de verwijdering van de populatie, zou de monitoring gebaat zijn met een schatting van de populatiegrootte, via censustechnieken of op basis van cameravallen. Dit is het onderwerp van vervolgonderzoek in het park en de directe omgeving.

Conclusie

De aanwezigheid van de muntjak op het Europese vasteland is een risico voor het bos- en natuurbehoud, naast andere sectoren. Dit geldt ook voor Nederland (Hollander 2015), Frankrijk (Hurel et al. 2018) en Duitsland (Schulz & Borkenhagen 2021). De meeste meldingen komen echter uit België, waar de soort in toenemende mate wordt bestreden. Over de effectiviteit van muntjakbeheer is in Europa echter heel weinig bekend (Barton et al. 2022). De monitoring annex bestrijding in Park Vordenstein helpt die kennislacune op te vullen. Deze eerste periode van monitoring heeft ons basisbegrip van de lokale populatie alvast aanzienlijk verbeterd, o.a. van voorkomen, activiteit en gedrag van de dieren. Het beheer lijkt dan weer gebaat te zijn bij een nauwe aansluiting met de cameravalverwerking, een uitgebreid tijdsvenster voor afschot, en bestrijding door middel van bersen.

Dankwoord: De auteurs danken Axel Neukermans en Sander Devisscher (INBO) voor ondersteuning van dit onderzoek. Ellen Blomme en Emily Laenen verrichtten stagewerk binnen dit project. De ANB-faunabeheerders en de Jonge Jagers Antwerpen leverden een zeer geapprecieerde bijdrage aan het beheer van muntjak. Bijzondere dank gaat uit naar Gerrit Huybreghts, die als vrijwilliger veel van het cameravalwerk op zich heeft genomen. Deze studie maakte gebruik van data en infrastructuur die beheerd worden door het INBO en gefinancierd zijn door het Fonds Wetenschappelijk Onderzoek - Vlaanderen (FWO), als onderdeel van de Belgische bijdrage aan LifeWatch. We danken een (anonieme) reviewer voor suggesties ter verbetering van het manuscript.

Referenties

Acevedo, P., A.I. Ward, R. Real & G.C. Smith 2010. Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. Diversity and Distributions 16: 515-528.

Barton, O., A. Gresham, J.R. Healey, L.S. Cordes & G. Shannon 2022. The effects of population management on wild ungulates: A systematic map of evidence for UK species. PLoS One 17: e0267385.

Casaer, J., N. Boone, S. Devisscher, J. Vercammen & T. Adriaens 2015. Best practice voor beheer van Chinese muntjak *Muntiacus reevesi* in Vlaanderen. Instituut voor Natuur- en Bosonderzoek, Brussel, België.

Casaer, J., T. Milotic, Y. Liefting, P. Desmet & P.

Jansen 2019. Agouti: A platform for processing and archiving of camera trap images. Biodiversity Information Science and Standards 3: e46690.

Chapman, N.G. 2021. History of introduction of Reeves' muntjac in Great Britain and ecological characteristics facilitating expansion of feral populations. European Journal of Wildlife Research 67: 33.

Chapman, N.G. 2022. Reeves' Muntjac *Muntiacus reevesi* (Ogilby, 1839). In: L. Corlatti & F.E. Zachos (red.), Terrestrial Cetartiodactyla: 29-50. Springer Nature, Cham, Zwitserland.

Chapman, N.G., M. Furlong & S. Harris 1997. Reproductive strategies and the influence of date of birth on growth and sexual development of an aseasonally-breeding ungulate: Reeves' muntjac (*Muntiacus reevesi*). Journal of Zoology 241: 551-570.

Cooke, A. 2019. Muntjac and water deer: natural history, environmental impact and management: Pelagic Publishing, Exeter, VK.

Deflem, I., B. D'hondt, Z. De Corte, C. Mouton, A. Van Breusegem, S. Neyrinck, T. Adriaens & J. Mergeay 2022. Een genetische studie van Chinese muntjak in Vlaanderen. Instituut voor Natuur- en Bosonderzoek, Brussel, België.

Ferretti, F., L. Lazzeri & N. Fattorini 2023. A test of motion-sensitive cameras to index ungulate densities: group size matters. The Journal of Wildlife Management 87: e22356.

GBIF.org 2023. GBIF Occurrence Download. Https://doi.org/10.15468/dl.gfgf4b

Geudens, G., D. Van Eykeren, S. Laureys, A. Ghekiere & L. De Bosscher 2009. Vordenstein, Harmonisch Park- en Groenbeheerplan & Geïntegreerd bosbeheerplan. Agentschap voor Natuur en Bos, Antwerpen, België.

Hemami, M., A. Watkinson & P. Dolman 2004. Habitat selection by sympatric muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) in a lowland commercial pine forest. Forest Ecology and Management 194: 49-60.

Hollander, H. 2015. Reeves' muntjac (*Muntiacus reevesi*) and sika deer (*Cervus nippon*) in the Netherlands. Lutra 58: 45-50.

Hulme, P.E. 2015. New law risks release of invasive species. Nature 517: 21.

Hurel, P., M. Terlin, F. Derré & A. Barboiron 2018. Le muntjac de Reeves, un nouveau cervidé exotique envahissant nécessitant une réaction rapide. Faune Sauvage 321: 22-25.

McKillen, J., K. Hogg, P. Lagan, C. Ball, S. Doherty, N. Reid, L. Collins & J.T. Dick 2017. Detection of a novel gammaherpesvirus (genus *Rhadinovirus*) in wild muntjac deer in Northern Ireland. Archives of Virology 162: 1737-1740.

Oldoni, D., P. Desmet & P. Huybrechts 2023. *camtraptor*: read, explore and visualize camera trap data packages. R package version 0.20.0.

Palmer, G., P.A. Stephens, A.I. Ward & S.G. Willis 2015. Nationwide trophic cascades: changes in avian community structure driven by ungulates. Scientific Reports 5: 15601.

Raymond, S., A.L. Schwartz, R.J. Thomas, E. Chadwick & S.E. Perkins 2021. Temporal patterns of wildlife roadkill in the UK. PLoS One 16: e0258083.

Ridout, M.S. & M. Linkie 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14: 322-337.

Rowcliffe, M. 2023. *activity*: animal activity statistics. R package version 1.3.3.

Schulz, B. & P. Borkenhagen 2021. Muntjaks (*Muntiacus reevesi*) in Schleswig-Holstein – Beginn einer Invasion, erfolgreiche Bekämpfung oder beides ein bisschen? Faunistisch-Ökologische Mitteilungen: 83-92.

Segar, J., H.M. Pereira, L. Baeten, M. Bernhardt-Römermann, P. De Frenne, N. Fernández, F.S. Gilliam, J. Lenoir, A. Ortmann-Ajkai & K. Verheyen 2022. Divergent roles of herbivory in eutrophying forests. Nature Communications 13: 7837.

Shilai, M., W. Yingxiang & X. Longhui 1986. Taxonomic and phylogenetic studies on the genus *Muntiacus*. Acta Theriologica Sinica 6: 191-208.

Smith-Jones, C. 2004. Muntjac: managing an alien species. Coch Y Bonddu Books, Machynlleth, VK.

Smith-Jones, C. 2022. A guide to the deer of the world. Quiller Publishing, Merrywalks, VK.

Sun, Y., H. Hu, C. Gong, D. Yang, L. Su, P. Li, Y. Li, Y. Liu, X. Wu & H. Zhang 2022. Diversity and vertical distribution patterns of wildlife in Tianzhushan, Shaanxi Province, China. Biodiversity Data Journal 10: e79923.

Vazquez, C., M. Rowcliffe, K. Spoelstra & P.A. Jansen

2019. Comparing diel activity patterns of wildlife across latitudes and seasons: Time transformations using day length. Methods in Ecology and Evolution 10: 2057-2066.

Wäber, K., J. Spencer & P.M. Dolman 2013. Achieving landscape-scale deer management for biodiversity conservation: The need to consider sources and sinks. The Journal of Wildlife Management 77: 726-736.

Ward, A.I., S. Richardson & J. Mergeay 2021. Reeves' muntjac populations continue to grow and spread across Great Britain and are invading continental Europe. European Journal of Wildlife Research 67: 34. DOI: 10.1007/s10344-021-01478-2

Zini, V., K. Wäber & P.M. Dolman 2023. Relative influence of inter-and intraspecific competition in an ungulate assemblage modified by introduced species. Journal of Mammalogy 104 (4): 879-891. DOI: 10.1093/gyad030

Samenvatting

De Chinese muntjak (*Muntiacus reevesi*) is in Vlaanderen inmiddels een gevestigde soort. Het aantal waarnemingen is sterk toegenomen vanaf 2012, met een voorlopige piek in 2020. Het zwaartepunt van de waarnemingen ligt in de oostrand van de agglomeratie Antwerpen, waar de soort uit een groot privaat domein is ontsnapt. Om ons begrip van deze exoot uit te bouwen, wordt de muntjak in het domein Park Vordenstein (gemeente Schoten) gemonitord, en ook bestreden. De monitoring gebeurt door middel van cameravallen, de bestrijding door middel van afschot. In deze campagne (2020-2022) werden muntjaks in het park frequent, maar eerder lokaal waargenomen. De soort is vooral tijdens de schemering actief (met name 's avonds) en vermijdt daarmee mensen eerder in de tijd dan in de ruimte. De beelden bevestigen de muntjak als een solitair dier. Het gedrag (bv. bronst, conflicten) in Park Vordenstein wijst op een normale, gezonde populatie. Op twee beeldsequenties werd een muntjak achtervolgd door vos. Tijdens de campagne werden tien dieren geschoten, voornamelijk door aanzit (511 mensuren). Hoewel de ervaring nog beperkt is, lijkt aanzit gebaat te zijn bij een nauwe aansluiting met de analyse van de cameravallen, een uitgebreid tijdsvenster voor afschot, en een aanvulling met bersen. Hoewel afschot in beide jaren leidde tot een terugval in het aantal waarnemingen, geraakten de aantallen gauw hersteld. De plaatselijke populatie blijkt dus veerkrachtig, al is over het aandeel van immigratie voorlopig niets bekend. Gelet op de internationale verplichting om de zorgwekkende uitbreiding van de muntjak af te remmen, zullen acties worden voortgezet.

Ontvangen / Received: 12 september 2023
Geaccepteerd / Accepted: 24 oktober 2023

Scavengers at a carcass of wild boar (*Sus scrofa*) in winter

Willem van Manen

Talmastraat 99, NL-9402 HD Assen, the Netherlands, e-mail: willemvanmanen@hotmail.com

Abstract: After a fresh carcass of a wild boar (*Sus scrofa*) was discovered in a northwest-Polish woodland in winter, a trapcam was installed to record the scavenging process. The carcass was monitored until it had disappeared two months later. It was scavenged by twelve species, of which red fox (*Vulpes vulpes*), common raccoon dog (*Nyctereutes procyonoides*) and common buzzard (*Buteo buteo*) were the most frequently recorded. Scavenging intensified after substantial opening of the carcass and during spells of cold weather or snow cover. In some cases individuals or species were observed together more often than expected, despite frequent antagonistic behaviour.

Keywords: scavenger, wild boar, *Sus scrofa*, camera trap, competition, Poland.

Introduction

In terms of mass, animal carcasses may be a relatively small part of the total detritus pool, but for some species or individuals they may be an important food source, at least during periods when other food resources are scarce or inaccessible. Scavenging has always been difficult to study in detail, especially when it occurs at night or in a closed landscape such as a woodland. What exactly happens at a carcass used to be studied through indirect evidence, such as reading tracks (Selva et al. 2005) and recording the disposal of a carcass over time, rather than describing the real time behaviour of scavengers (DeVault et al. 2003). The advent of trapcams has heralded a step change, allowing descriptive studies of disarticulation, scattering and removal of carcasses by vertebrate scavengers (Young et al. 2014, Probst et al. 2019). In the present study a trapcam was used to register the decomposition of a natural cadaver of a wild boar (*Sus scrofa*) in winter. The study focuses on changes in scavenging intensity and scavenging guild through the course of time and related to weather conditions as well as on intra- and interspecific interactions among scavengers.

Methods

The fresh carcass of a female wild boar in apparently normal condition was discovered on 27 December 2017. The estimated weight was 60 kg. Cause of death was unknown, and wounds that could have indicated killing by a predator or a gunshot were absent.

The carcass was found at the foot of a forested hill, bordering a small peat bog (53.8345°N, 16.2093°E, 100 m a.s.l.) near the village of Borzęcino in NW-Poland. The local woodland here is half open, consisting of mainly Scots pine (*Pinus sylvestris*), oak (pedunculated and sessile) (*Quercus robur/petraea*), beech (*Fagus sylvatica*) and some Norway spruces (*Picea abies*). The surrounding area is slightly hilly, and consists of large tracts of woodland interspaced with fields, meadows, hamlets and villages. Soils are sandy, nutrient-poor and dry, apart from peat bogs and brook valleys. The location of the cadaver was 163 m away from the nearest arable field, 1170 m from the nearest inhabited house and 2400 m from the nearest village of 30 houses and a lumber mill.

On 27 December a Bushnell Trophy Cam was placed at 2 m from the carcass with a view width of 2.5 m at 2 m distance. It was triggered by motion and set to take one photo, followed by a 10 second pause. On 7 January 2018 memory card and batteries were replaced. The camera was removed on 25 February, when the carcass had disappeared. The camera took 4496 pictures, only two of which did not show a recognisable scavenger. On 229 photo a second species could be identified and on eight a third species, totalling 4731 time/species events.

Identification of visitors at the carcass was in most cases straightforward, except differentiation between yellow-necked mouse (*Apodemus flavicollus*) and wood mouse (*A. sylvaticus*), both of which occur in the region. In the results they are listed as *A. flavicollus*.

Each time/species event was filed as a record, with precise date and time. Daily minimum temperature (recorded by the trapcam) and snow cover were recorded in and read from the pictures.

In order to be able to analyse scavenging intensity through the course of the day and relative to sunrise and sunset, an Hourly Scavenging Index (HSI) was calculated by taking the maximum number of individuals per species recorded on a single picture during a certain hour. To calculate the scavenging intensity in the course of the study period, a Daily Scavenging Index (DSI) was calculated by summing HSI per species per calendar day.

To calculate the duration of a foraging session of an individual or a group of scavengers, start and end time of nonstop series of images with the same species were calculated. A series of the same individual was defined as nonstop when intervals between consecutive images were 15 minutes or less.

To calculate the probability of co-occurrence of two species on one photo the general product-rule was applied, in which the total number of pictures represented pool size. In this way the expected co-occurrence of species was calculated and compared to the actual number of photos showing the two species together. The significance of the difference between expected and observed number was tested using a Chi^2-test. For measuring the difference between scavenging intensity on days with and without snow cover the a two-tailed Z-test was applied, assuming HSI might be higher as well as lower on days with snow cover. The relationship between temperature and scavenging intensity was calculated by applying a regression analysis. Calculations were done in Microsoft Excel.

Results

The carcass

When found on 27 December 2017 the carcass was almost intact, apart from a small hole (3 cm) in the lower belly near the genitalia. The boar may have been dead for several days and was lying on its right side. On 9 January the abdominal cavity had been emptied through the enlarged hole and a passage to the anus, the latter proved by a yellow-necked mouse that peeped out of the anus with its brightly reflecting eye. Also on this day, parts of the contents of the thoracic cavity had been consumed. On 13 January the thoracic cavity seemed to be empty. On 16 January the flesh from the ribs at the left (upper) side was consumed. On 17 January some flesh was taken from the chest and forelegs. On 21 January the hind legs were partly eaten, from the side of the belly. On 26 January the forelegs were fully eaten (removed). On 2 February the backbone was detached from the skin and on 3 February the hind legs had been completely defleshed. On this date the carcass consisted of skeleton and strips of skin, probably with some remains of flesh. On 8 February the carcass was briefly beyond the view of

Parameter/Species		Days	Max ind.	Max DSI	Pattern DSI 27 dec - 23 feb
Snow cover		18			
Minimum temperature (min=-10, max=6°C)					
Carcass visible		45			
White-tailed eagle	*Haliaeetus albicilla*	2	1	2	
Common buzzard	*Buteo buteo*	24	3	14	
Eurasian magpie	*Pica pica*	11	2	5	
Common raven	*Corvus corax*	17	9	26	
Red fox	*Vulpes vulpes*	54	3	15	
Wolf	*Canis lupus*	1	1	1	
Domestic dog	*Canis familiaris*	7	2	2	
Common raccoon dog	*Nyctereutes procyonoides*	21	2	12	
Western polecat	*Mustela putorius*	4	1	2	
Pine marten	*Martes martes*	32	2	15	
Eurasian wild boar	*Sus scrofa*	8	5	5	
Yellow-necked mouse	*Apodemus flavicollus*	7	1	2	
All species		59	2	54	

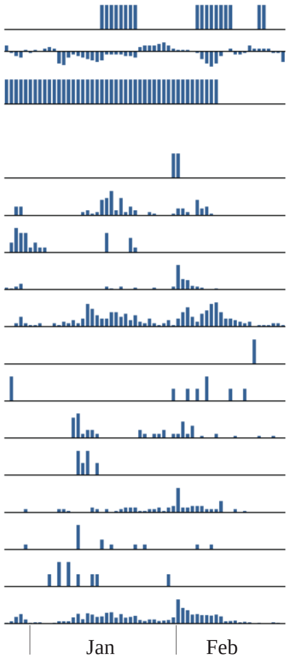


Figure 1. Temporal presence and abundance of species observed near or on the carcass, and the maximum number of individuals recorded on a single photo (max ind). Max DSI = maximum daily scavenging index (see Methods).

the camera, but reappeared for four hours on 9 February after which it remained out of sight. On 25 February, when removing the trapcam, no remains were found in the vicinity. The consumption of soft parts had taken about 45 days.

Dismantling the carcass was mostly the work of a pair of common raccoon dogs (*Nyctereutes procyonoides*); compared to their rough treatment, the changes red foxes (*Vulpes vulpes*) inflicted were delicate.

Scavenging patterns over time

Most species visiting the carcass were recorded eating, except wild boar and – probably – wolf (*Canis lupus*). Wild boars visited the carcass but were never recorded touching or feeding upon the cadaver, as evident from the unchanged configuration of the carcass and untouched snow after departure. A wolf showed up once, after the carcass had gone out of view of the camera.

During the 45 days that the carcass was visible on camera, it was visited daily by vertebrate scavengers (Figure 1). Peak attention coincided with spells of snow cover and low temperatures (not necessarily overlapping as periods with snow cover were not colder than the periods in between; Z=0.168, P=0.43), at least during the period the carcass was permanently visible, up to 8 February. A more intensive scavenging during snow cover was particularly evident in common buzzards (*Buteo buteo*). This species visited the carcass six times more often (Z=8.54, P<0.001) during 12 days with snow cover (mean DSI 6.25, sd=4.03) than during 31 snowless days (mean 1.06, sd=1.60). Similarly, red foxes also showed a significant increase of visits at the carcass during snow cover, with a mean DSI of 7.54 (sd=3.02) on days with snow cover versus 3.90 (sd=3.59) on days without (Z=-6.50, P<0.001). However, Red fox was the only

Species		Session (min) 0 10 30 60 >60	N	Duration (H) Max.	Duration (H) Total	Pause (H) 1 24 >24	N
White-tailed eagle	*Haliaeetus albicilla*		4	0.16	0.42		2
Common buzzard	*Buteo buteo*		68	2.82	24.04		67
Eurasian magpie	*Pica pica*		28	1.91	3.55		27
Common raven	*Corvus corax*		30	0.30	2.10		30
Red fox	*Vulpes vulpes*		190	1.90	37.83		190
Domestic dog	*Canis familiaris*		5	0.82	1.58		5
Common raccoon dog	*Nyctereutes procyonoides*		34	1.33	10.63		34
Western polecat	*Mustela putorius*		6	0.66	0.87		5
Pine marten	*Martes martes*		81	0.68	7.92		81
Yellow-necked mouse	*Apodemus flavicollus*		9	0.05	0.05		8

Figure 2. Duration of scavenging sessions of 0 (single picture), 1-10, 10-30, 30-60 en >60 minutes, longest session, total duration and pauses between scavenging sessions of 0-1, 1-24 and >24 hours between 27 December 2017 and 8 February 2018, the period during which the carcass was in view of the camera.

carcass visitor whose presence (DSI) correlated negatively with minimum temperature (r^2=0.22, F=12.16, P=0.001).

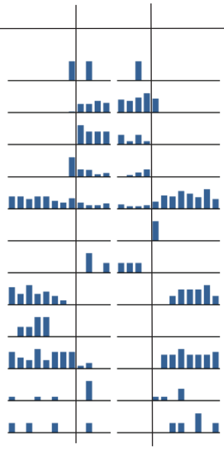
After the carcass had disappeared permanently from camera view on 9 February, only mammalian scavengers continued paying short visits for up to two weeks, after which the site apparently lost its attraction.

Individuals

Some visitors to the carcass could be distinguished individually with certainty. Of the dogs, one was brown/white and present only on 28 December when in company of a black dog; the latter returned on six days during 31 January through 15 February. The same juvenile white-tailed eagle (*Haliaeetus albicilla*) was present on two consecutive days. Of common buzzards at least four individuals were present: three in dark adult plumage, one in intermediate juvenile plumage. From 29 December onwards at least two adults were recorded, from 16 January onwards the juvenile and on 17 January a third adult was seen in company of the other buzzards (but may have been present earlier because the adults could not be differentiated). Red fox showed up as a single individual up to 19 January, but from then on a second one was frequently recorded simultaneously. On 8 February, the last day the carcass was more or less permanently in view, three red foxes showed up. Pine marten (*Martes martes*) was usually recorded singly except on 2 and 5 February when two individuals were recorded simultaneously. Raccoon dogs almost always showed up as a (the same?) pair. Ravens (*Corvus corax*) in most cases operated as a group and all other species not mentioned here as single individuals; whether individuals were the same across time remained unclear.

Duration of scavenging sessions

Almost all species visited the carcass for ten minutes or less (Figure 2). Taking into account the arbitrary decision that an interval of more than 15 minutes was regarded as a pause between scavenging sessions, unbroken spells at the carcass were longest for common buzzard, followed by Eurasian magpie (*Pica pica*) and red fox. During the period the carcass was in view of the camera, scavengers were present during 8.6% of the time.



Species		Duration (hr)		Ultimate times (min)	
		Day	Night	Sunrise	Sunset
White-tailed eagle	*Haliaeetus albicilla*	0.27	0.15	-20	-70
Common buzzard	*Buteo buteo*	22.97	1.07	-1	40
Eurasian magpie	*Pica pica*	3.55	0.00	14	-53
Common raven	*Corvus corax*	1.73	0.38	-23	-3
Red fox	*Vulpes vulpes*	3.23	36.00	-	-
Wolf	*Canis lupus*	0.00	0.01	-	34
Domestic dog	*Canis familiaris*	1.64	0.00	79	-61
Common raccoon dog	*Nyctereutes proc.*	0.00	10.82	-67	168
Western polecat	*Mustela putorius*	0.00	0.87	-194	-
Pine marten	*Martes martes*	0.41	7.63	90	60
Eurasian wild boar	*Sus scrofa*	0.02	0.12	62	51
Yellow-necked mouse	*Apodemus flavicollus*	0.00	0.05	63	124

Figure 3. Activity (cumulative Hourly Scavenging Intensity) of species relative to sunrise and sunset, total time present during day (between sunrise and sunset) and night and latest times (minutes relative to sunrise or sunset). Due to the increasing daylight period between 27 December and 23 February, hours at the extreme ends of the periods around sunrise and sunset are removed from the data as shown in the pattern. The break in the middle of the graphs refers to 12:00.

Diurnal and nocturnal rhythm

In general, mammals restricted their scavenging activities largely or exclusively to the night (except free ranging and probably owned dog), avian scavengers to the daylight hours (Figure 3). Within each class, small differences were noted. Among the mammals, red foxes were observed at the carcass throughout day and night, but night time visits were about three times more common. Dogs were exclusively recorded during daylight. Raccoon dogs and Western polecats (*Mustela putorius*) were largely nocturnal, visiting the carcass not even close to sunrise or sunset. A polecat paid visits on four days between 11 and 15 January, consistently between 3 and 6 hours before sunrise, suggesting the same individual which followed a strict routine. Pine martens visited the carcass almost exclusively at night, with a few exceptions just after sunrise.

Among birds, white-tailed eagle fed in the evening and in the early morning the next day (Figure 3), suggesting it roosted in close vicinity of the carcass. Common buzzards never arrived very early, and only once before sunrise, but used the carcass increasingly throughout the day till long after sunset, in almost complete darkness. Foraging after sunset was recorded on ten days, almost invariably following prolonged foraging in the afternoon. Magpies and ravens more often visited the carcass in the morning than in the evening. Ravens were present before sunrise on seven days.

Interactions

All species which regularly visited the carcass were sometimes observed in the presence of congeners, even usually solitary ones like common buzzard, pine marten and red fox (Table 1). Common buzzards invariably showed antagonistic behaviour, resulting in one individual feeding whilst the rest waited around. Red foxes initially (on 19 and 23 January and 3 February) seemed not to tolerate each other, taking aggressive postures when more than one individual was present. In the morning of 7 February, at 5:53, two were actually fighting, after which one retreated to a dis-

Table 1. Co-occurring of individuals and species at the carcass, expressed as the percentage of images on which the species was in the presence of its own or other species (*N* = number of pictures showing the species).

Species		Ha	Bb	Pp	Cc	Vv	Cl	Cf	Np	Mp	Mm	Ss	Af	*N*	% social
White-tailed eagle	*H. albicilla*	-	-	-	75.0	-	-	-	-	-	-	-	-	16	75.0
Common buzzard	*B. buteo*	-	10.1	5.2	3.3	-	-	-	-	-	-	-	-	1166	18.6
Eurasian magpie	*P. pica*	-	55.0	0.9	3.6	-	-	-	-	-	-	-	-	111	59.5
Common raven	*C. corax*	3.5	39.0	3.5	43.4	3.5	-	-	-	-	-	-	-	113	92.9
Red fox	*V. vulpes*	-	-	-	0.2	2.3	-	-	0.1	-	-	-	-	2385	2.6
Wolf	*C. lupus*	-	-	-	-	-	-	-	-	-	-	-	-	2	0.0
Domestic dog	*C. familiaris*	-	-	-	-	-	-	23.7	-	-	-	-	-	97	23.7
C. raccoon dog	*N. procyonoides*	-	-	-	-	0.5	-	-	82.2	-	-	-	-	387	82.7
Western polecat	*M. putorius*	-	-	-	-	-	-	-	-	-	-	-	-	18	0.0
Pine marten	*M. martes*	-	-	-	-	-	-	-	-	-	2.8	-	-	398	2.8
Eurasian wild boar	*S. scrofa*	-	-	-	-	-	-	-	-	-	-	40.0	-	30	40.0
Y.-necked mouse	*A. flavicollus*	-	-	-	-	-	-	-	-	-	-	-	0.0	10	0.0

tance of about 10 m where it reposed. Almost an hour later two foxes (the same?) worked on the carcass without apparent antagonistic behaviour. On 8 February even three foxes fed simultaneously on the last remains of the carcass. In raven, wild boar and raccoon dog no intraspecific antagonistic behaviour was recorded.

As for interspecific behaviour, white-tailed eagle and raven foraged together, but the eagle was clearly dominant. Ravens kept a distance of at least half a metre. Buzzards were seen simultaneously at the carcass in the company of one or two magpies on three days. In most cases magpies kept a distance of several metres, and once a magpie was chased from the carcass by a buzzard. Although raven activity peaked in the early morning and common buzzards mostly showed up at the end of the day, simultaneous carcass attendance was noted on six days. Even when six ravens were present, a single buzzard apparently was still able to dominate the scene whilst eating from the carcass with the ravens waiting around. Sometimes ravens pecked at the carcass from the opposite side of the carcass and less than a metre from the buzzard. In a few cases a buzzard performed a feeble attack towards one or more ravens. Magpies kept their distance from ravens.

Only once were a bird and a mammal recorded simultaneously at the carcass., i.e. on 9 February when a raven was displaced by a red fox. The raven kept a horizontal position at a distance of 5 m from the fox, as if preparing for flight.

Interspecific interactions between mammal species were rare (Table 1). In the night of 3 February a fox returned to the carcass after a pause of 36 minutes. One minute later a raccoon dog entered the scene. The (larger) fox flattened its ears and showed its teeth, but nevertheless disappeared. The raccoon dog foraged for 30 minutes, after which the fox shortly reappeared. The next image showed the raccoon dog again at the carcass, and the fox watching from 10 m distance.

Avoidance or attraction between species

The chance of co-occurrence of species, as based on the number of photos with and without other species, was calculated separately for night and day. Eurasian magpies and common ravens were more often recorded in each other's presence and in the presence of a common buzzard than expected. Common buzzards however avoided the company

Table 2. Expected and observed co-occurrence of species on the images, based on chance, expressed as % of images in the presence of the other species, relative to all images of the species, during day (sunrise to sunset) and night (sunset to sunrise). Only data of species which occurred on more than 90 pictures are presented. Percentages of observed co-occurrence may slightly differ from Table 1, because of the separation between day and night in Table 2. * and ** represent Chi^2 significance levels of $P<0.05$ and $P<0.01$ respectively for avoidance or attraction.

Species A	Species B	Co-occurrence (%)		
		Expected	Species A	Species B
Day (*N*=1528 photos)				
Common buzzard	Eurasian magpie	9.8	5.4**	58.6**
Common buzzard	Common raven	8.6	3.7**	47.3**
Common buzzard	Red fox	15.2	0.0**	0.0**
Common buzzard	Domestic dog	8.6	0.0**	0.0**
Eurasian magpie	Common raven	0.9	3.6*	4.4*
Eurasian magpie	Red fox	1.6	0.0	0.0
Eurasian magpie	Domestic dog	0.9	0.0	0.0
Common raven	Red fox	1.3	4.4	2.3
Red fox	Domestic dog	1.4	0.0	0.0
Night (*N*=3196 photos)				
Common buzzard	Red fox	5.8	0*	0**
Common buzzard	Common raccoon dog	1.0	0	0
Common buzzard	Pine marten	1.0	0	0
Red fox	Common raccoon dog	16.8	0.1**	0.5**
Red fox	Pine marten	16.8	0.0**	0.0**
Common raccoon dog	Pine marten	2.9	0**	0**

of corvids. Most other species-combinations indicate avoidance, sometimes significantly so (Table 2).

Discussion

The scavenger guild recorded at a single carcass of a wild boar largely reflected the assemblage of facultative carrion feeders typical for Central Europe. However local densities are unknown, all recorded species are commonly found in the area. Remarkable for being absent were European badger (*Meles meles*), Eurasian jay (*Garrulus glandarius*) and hooded crow (*Corvus cornix*), the first usually entering a state of semi-hibernation in winter (and therefore less likely to visit carrion in winter), the last being scarce >1 km beyond the range of human habitation. Of the scavengers recorded, several were of minor importance in terms of carcass consumption, or were not involved in scavenging at all, notably wolf and wild boar. Although the latter is omnivorous and noted for scavenging carcasses of ungulates (Wenting et al. 2022), the species avoids scavenging on congeners (Probst et al. 2017, 2019, Häkkä 2021), as was confirmed in this study. Avoiding scavenging on congeners is probably a general strategy among many species to reduce risks associated with parasites (Gonzálvez et al. 2021).

Carcass attendance showed a distinct dichotomy between avian and mammalian users, birds being active during daytime, mammals mostly at night. The carcass was probably discovered by birds (magpies and buzzards) on sight rather than by smell. When a carcass is covered by snow, mammals are more likely to detect it by using olfactory cues (Enari & Enari 2021). Usually, the sudden appearance of a highly nutritious carcass

Wild boars gathering around the carcass, smelling, but not touching it (11 January 2018).

Juvenile white-tailed eagle and common ravens waiting (1 February 2018).

Raccoon dogs, typically foraging pair-wise, keep a red fox at distance (2 February 2018)

An uncommon situation with three red foxes foraging simultaneously (8 February 2018).

leads to intense competition between microbial decomposers and invertebrate and vertebrate scavengers. The decomposing role of microbes and arthropods is much smaller in winter, when temperatures are low, than during summer, when competition is fierce and vertebrate consumption much reduced as a result of the highly efficient decomposition of carcasses by microbial and arthropod assemblages (Gu et al. 2014, Rivers & Dahlem 2014). In the present case, much of the carcass was consumed by vertebrates, notably red fox and raccoon dog. Most scavengers in this particular setting played a minor role in the later stages of decomposition.

Although the carcass was available for at least 45 days, only 8.6% of the time it was scavenged actively. This suggests low competition among vertebrate scavengers. It is however possible that some individuals spent much more time at the carcass while 'guarding' it, beyond the view of the camera, and only approaching the carcass to feed or to defend it. This may explain why often several common buzzards were present and why magpies and ravens were much more often recorded in the presence of a common buzzard than expected. By night, red foxes may have guarded the carcass. Feeding on carrion may seem cheap, but at the same time demands a lot of energy by having to deal with competitors. Particularly the smaller species may run a high risk, because meeting a potential predator is more likely near a carcass than elsewhere. It is possible that no matter how many individuals visit a carcass, few will really profit from the "free" meal.

The carcass was discovered while still fresh by diurnal opportunists such as common buzzard, magpie, raven and red fox, resulting in a flurry of activities during the first five days when mainly soft parts were targeted (abdominal cavity). This was followed by a period of poor interest until frost kicked in and access to the carcass was further facilitated by a pair of raccoon dogs that showed up on day 14. Their disarticulation of the carcass improved access for other animals, as suggested by an increase of scavenging intensity by a diverse assemblage of carrion-eaters. Contrary to expectation, domestic dogs were not involved in this process, although present at day 2 for 15 minutes. At a much later stage, when mostly just skeletal parts, tendons and skin remained, domestic dogs were observed feeding for longer periods of time (>30 min). Carcass attendance was highest during periods of frost and snow, illustrated by the lapse of activities during a spell of high temperatures when interest of scavengers temporarily faded (Figure 1). Nutritional demand may be higher during periods of sub-zero temperatures, when also availability of prey will be restricted (less activity, frozen ground). Common buzzards were a case in point, with intensive scavenging during periods of snow cover but near-absence during snowless intervals. This is in agreement with the absence of common buzzards on wild boar carcasses in a German study in summer, whereas it was the commonest scavenger in winter (Probst et al. 2019). Other scavengers are also noted for intensified scavenging at low temperatures, as in Selva et al. (2005).

A trapcam is a wonderful, patient and non-invasive device. However, meaningful interpretation of the images is fraught with its own methodological problems (Caravaggi et al. 2017), as exemplified by the absence of the Eurasian jay. In East Poland it was frequently recorded on large carcasses (Selva et al. 2005), in line with my own chance observations at left-overs of ungulates after hunting in NW-Poland. The jay was also absent in an extensive (122,160 images) trap cam study in the north of Germany (Probst et al. 2019), where, as in my study, the camera was triggered by motion. In a Norwegian study, where cameras were activated at fixed intervals (Gomo et al. 2020), jays were the third most common scavenger. At a carcass distance of 2 m jays probably do not easily activate a trapcam, unlike the slightly larger magpies. A methodological study of use of trapcams in the Netherlands, showed that mammals up to polecat size were less likely to be detected visiting camera-baits at distances of 1.2-2 m, than at a distance of 35 cm (Smaal & van Manen 2022). When striving to record the entire scavenger's guild, taking pictures at fixed intervals instead of using motion-trigger may be the smarter option, not just for recording small species, but also for reducing methodological problems when analysing the data.

Acknowledgements: I am grateful to Rob Bijlsma for kindly improving on a first draft of this article. An anonymous reviewer and Eric Thomassen and Ben Verboom of the Lutra editorial board are thanked for further improvements to the manuscript. I thank Han te Seldam for providing me data about the weight of wild boars.

References

Caravaggi, A., P.B. Banks, A.C. Burton, C.M.V. Finlay, P.M. Haswell, M.W. Hayward, M.J. & M.D. Woods 2017. A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation 3 (3): 109-122.

Carter, D.O., D. Yellowlees & M. Tibbett 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94: 12-24.

DeVault, T.L., O. Rhodes & J.A. Shivik 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102: 225-234.

Enari, H. & H.S. Enari 2021. Mammalian scavengers efficiently consume carcasses under heavy snowfall: a case for northern Japan. Mammalian Biology 101: 419-428.

Gomo, G., L. Rød-Eriksen, H.P. Andreassen, J. Mattisson, M. Odden, O. Devneau & N.E. Eide 2020. Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia. Ecology and Evolution 10 (23): 12860–12869. doi.org/10.1002/ece3.6834

Gonzálvez, M., C. Martínez-Carrasco, J.A. Sánchez-Zapata & M. Moléon 2021. Smart carnivores think twice: Red fox delays scavenging on conspecific carcasses to reduce parasitic risks. Applied Animal Behaviour Science 243: 105462. https://doi.org/10.1016/j.applanim.2021.105462

Gu, X., D. Haelewaters, R. Krawczynski, S. Vanpoucke & H.G. Wagner 2014. Carcass ecology – more than just beetles. Entomologische Berichten 74: 68-74.

Häkkä, S.S.S. 2021. Animal species scavenging on wild boar carcasses on island Hiiumaa (Estonia). BSc thesis. Estonian University of Life Sciences, Tartu, Estonia.

Probst, C., A. Globig, B. Knoll, F.J. Conraths & K. Depner 2017. Behaviour of free ranging wild boar towards their dead fellows: potential implications for the transmission of African swine fever. Royal Society Open Science 4 (5): 170054. https://doi.org/10.1098/rsos.170054

Probst, C., J. Gethmann, S. Amler, A. Globig, B. Knoll & F. Conraths 2019. The potential role of scavengers in spreading African swine fever among wild boar. Scientific Reports 9: 11450. https://doi.org/10.1038/s41598-019-47623-5

Selva, N., B. Jędrzejewska, W. Jędrzejewski & A. Wajrak 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology 83: 1590–1601.

Smaal, M. & W. van Manen 2022. Detecting and monitoring small mammals with trail cameras. Lutra 65 (2): 247-257.

Young, A., R. Stillman, M.J. Smith & A.H. Korstjens 2014. An experimental study of vertebrate, scavenging behavior in a Northwest European woodland context. Journal of Forensic Science 59: 1333-1342.

Wenting, E., S. Rinzema & F. Langevelde 2022. Functional differences in scavenger communities and the speed of carcass decomposition. Ecology and Evolution 12. https://doi.org/10.1002/ece3.8576

Samenvatting

Aaseters bij een karkas van een wild zwijn in de winter

Op 27 december 2017 werd in een bos in Noordwest-Polen bij een bijna intact en vers dood wild zwijn (*Sus scrofa*) met een geschat gewicht van 60 kg een wildcamera geplaatst. De camera stond op 2 m van het zwijn en werd door beweging getriggerd om één foto te maken, gevolgd door een pauze van 10 s. Op 9 februari werd het zo goed als ontvleesde karkas definitief uit beeld gesleept. Op 25 februari werd de camera weggehaald en werden in de omgeving geen resten van het zwijn teruggevonden. De camera nam 4496 foto's, waarvan slechts twee zonder determineerbare aaseter. Er werden twaalf soorten vastgesteld. Vooral een paar wasbeerhonden speelde een belangrijke rol in het openen van het karkas. In perioden met sneeuw steeg de bezoekfrequentie van met name buizerd en vos, vossen kwamen ook vaker naarmate het kouder was. De meeste bezoeken duurden korter dan tien minuten, de langste bezoeken kwamen van vos en buizerd, waarbij de laatste tot langer dan een uur onafgebroken bij het karkas kon blijven. Veel soorten hadden een expliciet bezoekritme, waarbij de vogels overdag, en de zoogdieren 's nachts langskwamen. Vossen foerageerden meest 's nachts, maar kwamen ook overdag regelmatig langs. De meeste individuen opereerden alleen, met uitzondering van de raven, die slechts in enkele gevallen alleen werden gezien, en wasbeerhonden, die vrijwel altijd met z'n tweeën (in paren) langskwamen, wat overigens gebruikelijk is bij deze soort. Wanneer de overige soorten met meerdere individuen tegelijk werden gezien, ging dit vaak gepaard met dreigen en slechts zelden werd simultaan gefoerageerd op het karkas. Ook verschillende soorten werden soms tegelijk bij het karkas gezien, maar vrijwel altijd was er dan sprake van een zekere rangorde. Zo werden eksters en raven vaak tegelijkertijd gezien met een buizerd, waarbij de laatste at, terwijl de rest toekeek. Bij de combinatie wasbeerhond – vos, die enkele malen voorkwam, keken de vossen toe van een afstand. Bij een analyse op basis van kansberekening bleken de meeste soorten elkaar te mijden, alleen eksters en raven waren vaker present in gezelschap van elkaar en van een buizerd dan verwacht. Omdat buizerds de raven en de eksters weghielden van het kadaver, bestaat het vermoeden dat buizerds (waarschijnlijk een enkel exemplaar) het karkas van een afstandje bewaakten en ingrepen zodra er eksters of raven arriveerden. Vermoedelijk namen vossen (of meer waarschijnlijk een enkele vos) deze taak 's nachts voor hun rekening. Verdediging van het karkas zou kunnen verklaren waarom er slechts gedurende 8.6% van de totale tijd aaseters bij aanwezig waren. Tenslotte werden er opvallend weinig kleine dieren bij het karkas opgemerkt. De lokaal algemene gaai bijvoorbeeld, werd in het geheel niet waargenomen. Mogelijk was dit een gevolg van de instelling van de camera, waarbij die werd getriggerd door beweging en dit bij kleinere soorten gewoonweg niet plaatsvindt. Gaaien werden bovendien wel waargenomen in een vergelijkbare Noorse studie, waarbij de camera met vaste tussenpozen een opname maakte. Het is dus belangrijk te overwegen welke instelling een camera wordt meegegeven, afhankelijk van het doel van het onderzoek.

Received: 5 October 2023
Accepted: 28 December 2023

Contents of Volume 66 (2023)

Editorials

Research Papers

Short Note