Enjoying Lutra!

Over the past four years I have had the great fortune to spend the late spring, until early autumn, in Norway in a house on the island of Sula, along the Hagenfjord, close to the mouth of the Sognefjord. In this time I have had around forty casual encounters with otters (*Lutra lutra*). All these encounters were special for me, even if most of the observations confirmed typical otter behaviour: a trail of air bubbles, clearly visible especially during calm weather, betraying the course the animal followed before surfacing again. Or, an otter dashing over and between the rockweed (*Fucus vesiculosus*) during low tide, sometimes playfully but now and then stopping to consume a small crab or fish racing for deeper water. Once I saw a couple of otters in the fjord, right in front of the house, diving and surfacing with small fish, making several wild bites, swallowing and diving again. When one caught a bigger fish, it was taken and devoured ashore. Afterwards I saw the same individual galloping inside a large concrete tube, obviously sprainting, before dashing out again and returning to the water. The other otter caught a fish in a water pool, killed it with a quick bite, swallowed the fish and returned into the water again. After watching them for more than an hour the two animals disappeared.

On two occasions I saw new (to me) patterns of otter behaviour. The first was a female with several youngsters in the water, regularly diving for food. The pattern displayed was: the female went down with the cubs following. Then the adult emerged, often without food, but sometimes with a fish. Usually the cubs had already surfaced, and when the female appeared, the youngsters raced towards their mother uttering high pitched squeaks and devouring pieces of the prey. And then they dived again from the same place. Once submerged, they spread out in different directions. During those dives each cub apparently followed its own centrifugal path, exploring the sea bottom. At the end of their exploratory dive, perhaps close to oxygen depleted, they instinctively went straight upwards and after surfacing gravitated towards their mother. This pattern repeated itself several times.

The locomotor activity of an otter at the surface, almost always follows the same pattern: emerging, swimming short distances at the surface, submerging with the middle of the back bending towards an angle of approximately 90º and starting their search for prey. After catching a bigger fish or when their search has ended, otters swim in a straight line towards the coastline, staying surfaced, devouring their prey ashore or just disappearing between the rocks. Last summer the yearly event of spawning mackerel entering the Hagenfjord was late. During these weeks no otters were observed. Then a single otter appeared in the water, right beyond the observation point, displaying a remarkable swimming behaviour that I had not noticed before. The otter stayed more or less at the surface, without diving, but instead of diving, only keeping its head under water and alternately swimming head down in bursts of straight lines for one or two metres and then heading up. This could be described as a 'dolphin stroke'. Then the otter followed a straight line towards the other side of the 400 m wide Hagenfjord using this same stroke. This was really unusual behaviour. At first, I thought this swimming stroke was because of the absence of fish: that he or she was 'fast scanning' the deeper waters in. Later, when the mackerel came by the thousands, another observation of an otter (the same specimen?) displayed the same type of locomotion. Was this otter, with its remarkable swimming behaviour, suffering from a highly advanced vertebral arthrosis? A disorder already reported from this area (Bekker 2019). I really do not know. Maybe somebody else has observed a similar type of swimming behaviour?

On all these occasions I felt very privileged to have had the opportunity to enjoy the presence of this beautiful mammal. And I hope that all readers of this edition of the *Lutra* journal will enjoy its contents as much as I have enjoyed observing individual *Lutra*, face to face.

This issue completes the 65th volume of *Lutra*. Whereas last October's special issue focused exclusively on bats, this issue covers a variety of mammals and subjects. Two contributions highlight marine mammals. Haelters et al. report on the extremely high number of grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) that washed ashore on Belgian beaches in 2021. From necropsies and photographs the authors found out that most deaths were human-related, which, they argue, stresses the need to re-evaluate the phenomenon of 'by-catch'. In another marine study, Raemakers & Oosterbaan investigate deformed whale bones of at least six species (mostly harbour porpoise - *Phocoena phocoena*), from the North Sea and discuss the possible influence that these malformations may have had on the whales' health.

This *Lutra* also dives into the past with Govaert's study of beavers' (*Castor fiber*) historical presence in the river IJssel. By meticulously studying preserved financial records, the author comes to the conclusion that, surprisingly, beavers, after (almost) being driven to extinction by the year 1400, must have been present in large numbers in the IJssel in the second half of the fifteenth century.

Bats also feature in this issue, albeit this time not as hibernators. Jonker et al. compare the activity of common pipistrelles (*Pipistrellus pipistrellus*) around white and the now widely-used bat-friendly, but expensive, amber street lighting, with a special kind of (phosphor converted) amber light. The latter is more energy-efficient, cheaper to run and also provides better visibility to humans. The authors give advice on how to repeat the experiment to arrive at more decisive conclusions, which they could not draw from their study.

Mammal ecologists nowadays commonly use (stand-alone) trail cameras to detect and monitor mammals. But these are suited mainly for animals of a certain size. In this issue Smaal & van Manen introduce a device, called a *Struikrover*, which includes an adjusted trail camera, to study mammals up to the size of a western polecat (*Mustela putorius*). They provide recommendations on how to best use Struikrover for the optimal results.

At the end of this year I will step down as a member of the editorial board of *Lutra*. Since I joined the board in 2003, when *Lutra* published a beaver special, I have felt a great camaraderie with my fellow editors, and especially from Ben Verboom, the current managing editor, with whom I closely collaborated to prepare and finalize *Lutra's* latest special issue, on hibernating bats. Over the years, the editors of *Lutra* have produced a wealth of inspiring issues, and I feel privileged to have taken part in this work. I wish the journal a prosperous future, full of sparklingly creative and appealing intellectual manuscripts, that will attract more and more readers.

References

Bekker, J.P. 2019. Skeleton of an otter (*Lutra lutra*) with some regular and remarkable alterations. Lutra 62 (2): 77-88.

Jan Piet Bekker

Historical presence of the Eurasian beaver (*Castor fiber*) in the IJssel River (the Netherlands) in 1450-1500

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Abstract: This article studies the presence of the Eurasian beaver (*Castor fiber*) in the IJssel River (the Netherlands) in the second half of the fifteenth century on the basis of preserved financial records. It argues that the beaver may have become functionally extinct in the Netherlands as early as 1500, several centuries before the last individual was reportedly killed (in 1826). The study also demonstrates the value of using medieval administrative sources to reconstruct the historical range of mammals in Western Europe. At least 153 beavers were presented to the city councils of Deventer and Zutphen in 1454-1489 in order to receive a financial reward. The species was hunted for multiple reasons, among which the prevention of economic damage was the most important. The introduction of a bounty system to capture beavers was probably a deliberate attempt to exterminate the animal. The presence of large numbers of beavers in the fifteenth-century Netherlands is remarkable, because the species may have become very rare or extinct in most of the Low Countries by 1400. Its possible reappearance and temporary recolonisation of large stretches of the IJssel River could be interpreted in the context of environmental changes. The digging of a new canal, which connected the city of Deventer with its German hinterland, may have created a new corridor that facilitated beaver migration from refugia in north-western Germany. The volume of water transported by the IJssel towards the Zuiderzee also declined significantly during the fifteenth century, which may have limited the species' dispersal options and exacerbated conflicts with humans.

Keywords: bounties, Middle Ages, Deventer, Zutphen, ecology, dispersion, migration, hunting, nuisance animal, biogeography.

Introduction

As a result of new European protection laws and effective reintroduction efforts the Eurasian beaver (*Castor fiber*) has rapidly recolonized most of Western Europe during the last three decades (Halley et al. 2021). In the Netherlands, for example, in 1988-1991 42 animals from the Elbe were released in the Biesbosch National Park, followed by reintroductions in the Gelderse Poort (1994) and the Leudal (2002). By 2003 there were 200-250 animals in the country, and in 2019 the population had grown to 2000-3500 animals (Sluiter 2003, Dijkstra 2019).

Knowledge about beavers' historical presence in Europe on the other hand is rather limited. It is well established that the European population had become fragmented into several distinct populations by the early twentieth century (Veron 1992, Halley et al. 2012, Horn 2014). The exact date when the species became extinct in a specific country is more controversial. For example, British scholars traditionally assumed that the beaver became extinct relatively early, around 1200 or 1300 AD in Wales and Southern England, and around 1600 in Scotland (Kitchener & Conroy 1997, Raye 2014). The archaeologist Bryony Coles challenged this view in 2006, by arguing that the beaver survived in Britain until at least the eighteenth century (Coles 2006, 2010). This 'late' extinction date has not been universally accepted. Coles' use of historical sources in particular has drawn criticism (Raye 2014).

Another issue is that many scientific studies simply accept extinction dates given in older literature, without critically analysing the historical sources on which these claims are based. For Belgium two distinct extinction dates are put forward: the fifteenth century (Libois 1982, Veron 1992), or the year 1848 (Halley et al. 2012, Rosell & Campbell-Palmer 2022). No beaver was seen in Belgium in 1848, it is simply the year Julien Deby's book on the natural history of Belgium was published. He mentions the beaver, but also notes that it became extinct a long time ago (Deby 1848). The idea that beavers were still present in late medieval Belgium is also based on Deby's book, and more specifically on his claim that the village of Beverlo got its name from a beaver population that lived in that area until the mid-fifteenth century (Deby 1848). However, this is a misinterpretation of toponymic evidence. The oldest reference to Beverlo dates back to the twelfth century, not the fifteenth (Gysseling 1960). If this name refers to actual beavers, which is far from certain, it can only be used as evidence for their presence during the eleventh or twelfth century.

Even if the date of extinction actually corresponds to the last recorded killing of a beaver, focussing on a single year can be misleading. The species may after all have been functionally extinct for a long time, perhaps even for centuries. Functional extinction occurs when '*a reduction in its population size, caused by an increase in its mortality rate or decrease in its fecundity, leads to the extinction of another species in the ecosystem*' (Säterberg et al. 2013). In other words, the animal has become so rare that it can no longer fulfil its ecological role (Säterberg et al. 2013, Sellman et al. 2016).

In the Netherlands the year 1826 is commonly accepted as the date the last beaver in the Netherlands was killed, more specifically in Zalk between Kampen and Zwolle. Yet beavers had been very rare in the country for almost a century, with killings being recorded in Gorinchem in 1742, Middagten (Rheden) in 1757, Moerdijk and Nieuwland in 1759, Hedel in 1770, the River Merwede in 1791, Epse in 1799, Doesburg in 1801, Gorinchem in 1819 and Zalk in 1826 (Martinet 1778, Pasteur 1796, Bonn 1806, van Wijngaarden 1966, Canters & Hoekstra 2019). The last record of a beaver family with offspring - two adults and six kits - comes from 1742 (Martinet 1778). It is also noteworthy that all beaver sightings occurred in two geographical areas: the Rhine-Meuse estuary (including the Biesbosch) and the IJssel River (Canters & Hoekstra 2019).

Current knowledge about the presence of beavers in Europe before 1900 is mostly based on early zoological studies, hunting manuals, travel accounts, and legislation. Such sources are relatively reliable for one specific geographical area or country, namely the one the author resided in or visited, but are of limited value when it comes to a European level.

Archaeozoological research can also provide proof for the presence of beaver populations in the past (Duval et al. 2011, Liarsou 2013, Çakirlar et al. 2019). Some caution is advised, as people may have transported body parts of beavers over large distances because of their economic or cultural value. A piece of wood with gnawing marks of a beaver offers more solid evidence (Manning et al. 2014).

It is clear that current knowledge of the beaver's gradual extinction in most of Europe during historical times is rather limited. In order to gain a better understanding of the geographical distribution and population dynamics of the Eurasian beaver in the past we need to consider the full range of available historical sources. Administrative documents, such as financial accounts, refer to the killing of individual animals and often mention specific locations. In this way they can complement the data provided by other historical sources and archaeozoological research.

The advantage of using such administrative sources is that the information obtained allows us to extent our historical inquiries to the Middle Ages. Medieval encyclopaedias, including Albertus Magnus' famous books on animals, are of limited use for biogeographical studies because they mainly rely on earlier Greek or Roman works rather than directly on observation (Hossfeld 1983).

However, only a very small part of medieval financial accounts provides substantial data on wild animals. These documents provide a systematic overview of an institution's or official's income and expenses during a specific year. They only mention animals if these were treated as commodities or gifts. So far, references to beavers in late medieval administration from the Netherlands have only been found in the accounts of the cities of Deventer and Zutphen, dating to the second half of the fifteenth century. Nineteenth-century naturalists already knew that these two cities paid bounties for beavers in the Late Middle Ages, but did not analyse their accounts in a systematic way (Molhuysen 1840, Groneman 1882).

The objective of this article is therefore to study the presence of beavers in the IJssel River (the Netherlands) in 1450-1500 by using preserved financial accounts from the cities of Deventer and of Zutphen. It will use the data gathered from these sources to reconstruct the species' historical dispersal patterns and ecology.

Materials and Methods

Study area

The River IJssel is a branch of the Rhine (figure 1), which flowed into the Zuiderzee until the twentieth century, and is now connected to the IJsselmeer. The cities of Deventer and Zutphen are located halfway the IJssel River, about fifteen kilometres from each other. Their financial accounts are a unique source for an historical analysis of beaver presence in the IJssel basin because both city councils paid financial rewards (bounties) for the catching of these animals.

Used sources

The study was conducted by systematically processing the financial administration (yearly accounts) of the cities of Deventer and Zutphen in 1448-1500. The accounts of Deventer for the year 1459-1460, and those of Zutphen for the years 1471-1472, 1473-1475, 1476-1477, and 1483-1489 have not been preserved. The accounts of both cities have been published for the years 1337-1447 and 1364-1446 respectively, but these do not mention beavers (van Doorninck et al. 1885-1914, Alberts 1959, de Meyer 1968-1985, Wartena 1977).

Medieval financial accounts are typically divided into different subheadings. In the great majority of cases payments for beavers were included in a rest category, called *'alrehande saken'* in Deventer and *'gemeyn onraed'* in Zutphen. These listed divers small payments not included in the main subheadings (construction works, wages for officials, etc.). In Deventer payments for caught beavers were sometimes also included under the subheading dedicated to payments for messengers. This may have been the case because messengers from nearby cities or noblemen regularly presented wild animals, such as roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), to the city council as gifts.

Deventer and Zutphen both used the Julian calender in the fifteenth century, and identified individual days by referring to the liturgical year. The account of Zutphen for the year 1482-1483 specifies, for example, that a beaver was presented to the city council on the 'Monday before Pentecost' (*des mandags voir pinxten*). In order to correctly identify the months

Figure 1. The IJssel River in the second half of the fifteenth century (© Hans Blomme, Ghent University). The map is based on the following datasets:
https://hdl.handle.net/10622/HPIC74
https://data.overheid.nl/dataset/11592-paleogeografische-kaarten---atlas-van-nederland-in-het-holoceen

beavers were captured, the dates mentioned in accounts were first calculated by using the Julian calendar, before converting them to their corresponding dates in the Gregorian calendar.

References to beavers in the accounts of Deventer and Zutphen were combined with a study of beaver bones found during archaeological research in the Netherlands (Database Boneinfo). An overview of this data is presented here. A literature study was conducted for use in the discussion.

Results

Beavers in the financial accounts of Deventer and of Zutphen

According to the financial accounts studied at least 153 beavers were presented to the city councils of Deventer and Zutphen from 1454 to 1489 (figure 2a). No beavers are recorded in the accounts covering the years 1490-1500. The actual number of bounties paid before 1490 was probably higher, given that several accounts have not been preserved.

There are also two references to non-lethal actions, both in Deventer: in 1449 Henrick '*den wruchter*' (an official tasked with managing the city's trees and wood supply) put thorns around willow shoots to protect them against beavers, and in 1471 the city paid two labourers to demolish four beaver dams. They needed two days to complete this task.

Of the 153 aforementioned animals, 79 were caught in Deventer and 74 in Zutphen, 36 were described as 'small' or 'young' beaver (figure 2b), 101 as 'beaver' and 16 as 'large beaver' (figure 2c). Deventer paid bounties for beavers from 1454 to 1480 and Zutphen from 1464 to 1489. The highest numbers of beavers were caught in Deventer in the year 1472 (13) and in Zutphen in 1477 (14).

Exact dates are indicated only occasionally. Of the 56 instances where the approximate date of capture of one or more beavers is known 33 (or 58 %) concern the months March-June (figure 3).

In Deventer the location where one or more beavers were caught is mentioned seven times. Most (four) refer to common lands to the southeast of the city, between two river arms of the IJssel (the 'old' and 'new' IJssel). These were known collectively as the 'Mars' or 'Marsch' (figure 4). Note that the 'old' IJssel no longer existed in the late sixteenth century, when Joannes van Doetecum made this map. He did draw its former riverbed, however.

The Marsch was largely uninhabited in the fifteenth century, but it formed an essential part of the city's rural hinterland, used for the pasture of livestock, stone production (brick kilns), and wood supply (Kronenberg 1902). On one occasion, dating to 1469, the accounts simply note that a beaver was caught on the 'Marsch', in the other three instances (dating to 1468 and 1469) the accounts refer to the 'wrucht' or 'wrocht' specifically. These were parts of the Marsch, located near the 'old' and 'new' IJssel, which were closed off by a ditch or fence to protect the trees growing there against livestock (Kronenberg 1902). The four beaver dams demolished in 1471 were also located here.

Beavers were also captured in three other locations. In 1467 one beaver was caught in the 'Worp', the name given to a strip of land in the IJssel floodplain, located on the left riverbank opposite the city centre. This area was originally connected to the right riverbank by a ferry, a wooden bridge was only built in 1482 (Poelhekke 1870). In 1469 another beaver was caught on the 'stad weerde', an island in the IJssel, to the southeast of Deventer (figure 4). One year later three young beavers were taken on the border of the city's territory: in an earthen embankment with hedges planted on top (a *landweer*) that served as its outer defence (Brokamp 2015).

In Zutphen the location of the capture is mentioned twelve times. Most beavers (seven) were caught in the floodplain of the River IJssel, to the northwest of the city (the '*stadsweerd*'). Three others were taken in the IJssel floodplain (*weerd*) without specifying the exact location. The final two were captured near a dike, and near brushwood located on higher ground (*bij dat veerste horst*). The landscape around Zutphen was similar to that around Deventer, and provided the city with access to pasture, hay, clay and wood. A least one basket weaver, one carpenter, and a pair of hunters were rewarded for presenting beavers to the city council. Given that fishermen also received bounties in 1466, 1468 and 1469 it is likely that some animals were caught in the River IJssel itself.

Archaeological finds of beavers in the Netherlands

Remains of beavers are rarely found in archaeological contexts dating to the High or Late

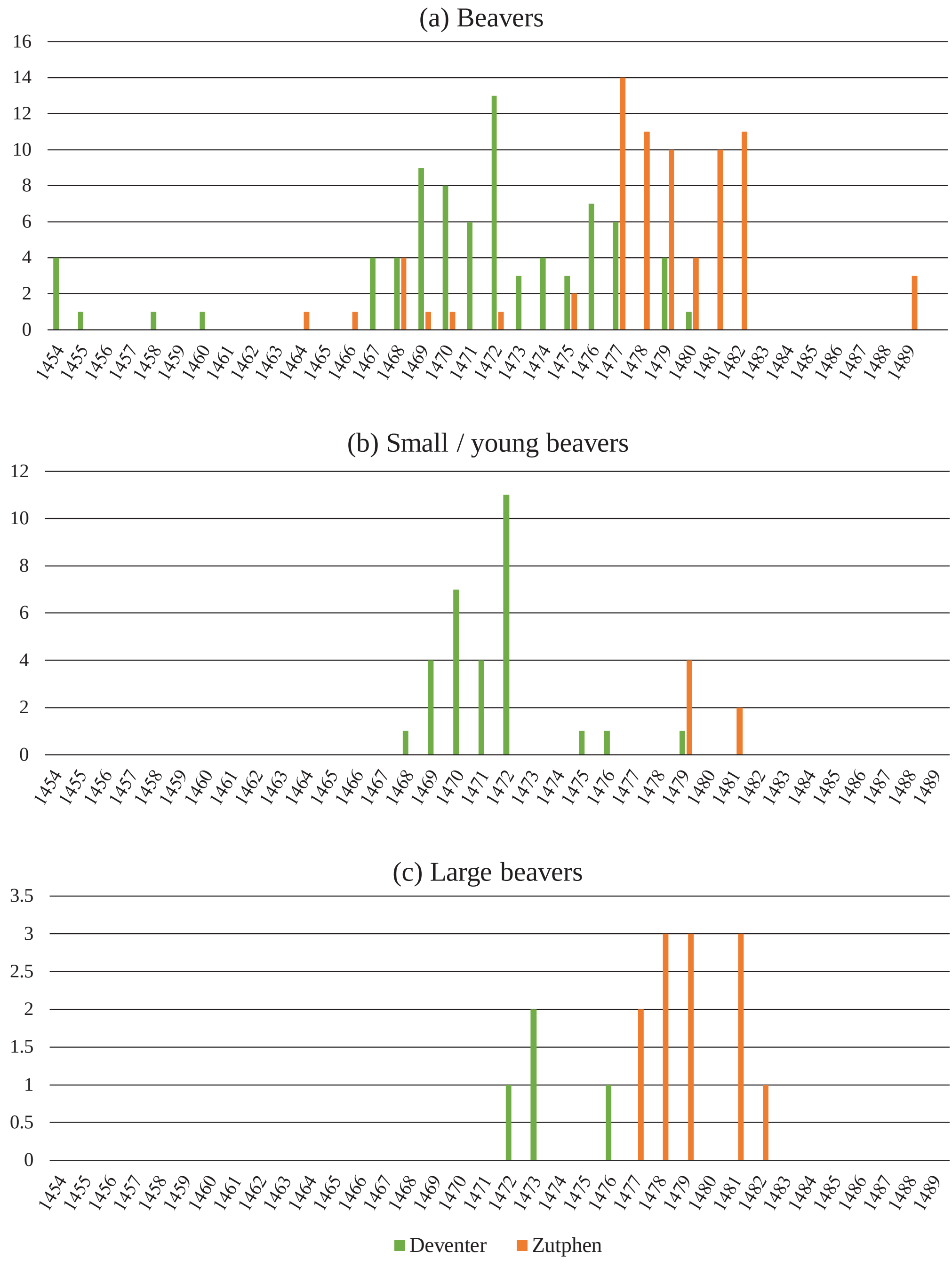

Figure 2. Bounties paid for captured beavers (a), 'small' and 'young' beavers (b) or 'large' beavers (c) in Deventer and Zutphen from 1454 to 1490.

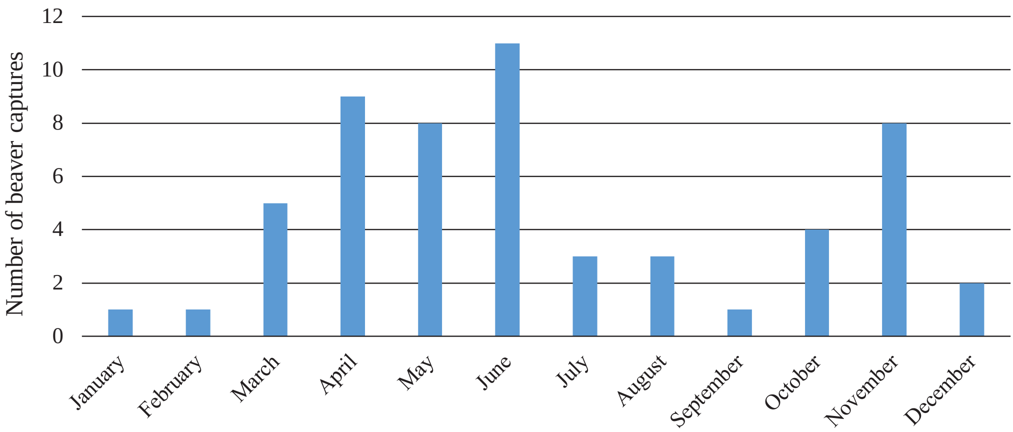

Figure 3. Distribution of beaver captures across the year in Deventer and Zutphen from 1454 to 1490.

Middle Ages (1000-1500). In the Netherlands beaver bones deposited after the year one thousand have been found only four times: one bone fragment in Borsele (Zeeland) dating to 1050-1499, three bones in Houten-Loerik (Utrecht) dating to 900-1200, five bone fragments in Houten (Utrecht) deposited before 1250 and two deposited in 1350-1450 (Hazenberg 2000, Hielkema 2003, Dijkstra & van Benthem 2004). In Belgium, four beaver bones were recovered from the fortress of Franchimont in the Ardennes. These all come from the oldest archaeological layers, dating to the eleventh and twelfth centuries. None were found among the numerous animal bones deposited in the late fifteenth and early sixteenth century (Gautier et al. 2005).

Discussion

Several scholars have analysed motivations for hunting beavers during historical times (Delort 1978, Dieberger 2003, Duval et al. 2011). The economic value of their fur, meat (specifically the tail and hind legs), and castoreum, the widespread belief that they eat fish, and the damage they cause to woody plants and human infrastructure (dam building, burrowing) constituted the most important reasons for killing them. Damage to woody plants (willow shoots), and dam building are explicitly mentioned in the financial accounts of Deventer. Damage done to river dikes may have been an important consideration as well, but is not stated explicitly.

It is uncertain whether the species was hunted because of other reasons. In 1470 a furrier presented three young beavers to the city council of Deventer. He had captured them in the *landweer*. It is possible that this man also caught the parent animals, but did not bring them in because their fur was worth more as a trade object than the bounty. The financial accounts provide no explicit evidence that beavers were eaten by members of the city council or presented to noblemen living nearby as gifts. On only one occasion, in 1455, a financial account specifies that a man presented a beaver tail to the city council (Deventer).

As mentioned before, fishermen caught beavers on several occasions in Zutphen, but it is unclear whether they believed that the animal ate fish. Both Deventer and Zutphen paid only one bounty for the killing of an otter (*Lutra lutra*), in 1488 and 1473 respectively. This makes it unlikely that preservation of fish stocks was an important consideration. In fact, existing economic incentives to hunt beavers were probably considered to be not strong enough; otherwise the city councils

Figure 4. Map of the IJssel River and the city of Deventer in 1567 by Joannes van Doetecum in 1567. The original is preserved in Historisch Museum Deventer.

would not have deemed it necessary to pay a financial reward for each captured individual. Deventer paid one guilder as bounty for a beaver and Zutphen one pound. Both bounties are the equivalent of seven to fourteen working days' wages for a skilled labourer.

During the second half of the fifteenth century Deventer and Zutphen probably perceived the presence of beavers as a problem. The absence of any record of the species in the published financial accounts of both cities from the fourteenth and early fifteenth century could thus be taken as an indication that the beaver was either absent or very rare in the upper and middle part of the IJssel basin in the decades before 1449 (the first mention of beavers in Deventer). It is of course possible that the cities simply did not pay bounties for its capture. However, this leaves open the question why they suddenly started to do so in the second half of the fifteenth century. It also does not explain why so few beavers were captured in the first years after the bounty system was first introduced.

The fact that beavers are mentioned in the accounts in Deventer for more than a decade (from 1449 onwards) before one was caught in Zutphen (in 1464) rather suggests a gradual southward dispersal along the River IJssel. From 1454 to 1466 only seven beavers were reportedly killed in Deventer and two in Zutphen. Recent studies on reintroduced beaver populations also attest to a slow initial expansion, followed by a more rapid increase once the population has established itself (Bluzma 2003, Rosell & Campbell-Palmer 2022). Migrating beavers tend to occupy the most suitable habitats first which can result in irregular dispersal patterns with considerable distances between individual territories (Fustec et al. 2001). In this specific case, high hunting pressures may have been at least partially responsible for the slow population expansion.

The terminology employed in the financial accounts provides further evidence for a gradual expansion upstream along the IJssel, from north to south. Small and young beavers, possibly referring to kits, are mentioned for the first time in Deventer in 1468, and in Zutphen in 1479. The time lag between the first mention of a beaver, and the first mention of a kit, indicates that it took around 19 and 15 years before beavers actually reproduced near the respective cities. It is also revealing that 'large beavers' are only mentioned near Deventer and Zutphen from 1472 and 1477 onwards. These were probably fully grown adult beavers. If citizens typically encountered yearlings or subadult beavers searching for a territory of their own, they may very well have perceived a fully-grown beaver as 'large'.

Still, we should not rely too much on the distinction between 'beavers' and 'large beavers', for the clerks of Deventer seem to have been less consistent in making such distinctions. In Zutphen twelve 'large beavers' are recorded as opposed to only four in Deventer. Both Deventer and Zutphen paid the same bounty for a 'beaver' and a 'large beaver' (one *gulden* and one pound respectively), which means that the distinction between the two kinds may not have been considered essential from an administrative point of view. 'Young' and 'small' beavers were valued as one half or one third of a 'beaver' or a 'large beaver'.

The date of the capture, when known, further supports the hypothesis that most beavers captured near Deventer and Zutphen were yearlings or subadult animals trying to establish a territory of their own. When the exact date of the capture is mentioned, it is mostly (in 33 of 56 instances – ca 58 %) during the months March-June (figure 3). Several studies have noted that beavers leave their parental territory shortly before the arrival of a new litter (Hartman 1997, Sun et al. 2000, McNew & Woolf 2005, Mayer et al. 2017). Beavers typically give birth in the period mid-April to mid-August. The dispersal rate is mainly determined by population density. Beavers disperse at a younger age when the population density is low (Hartman 1997, Sun et al. 2000, McNew & Woolf 2005, Mayer et al. 2017).

High mortality due to human persecution probably explains the long time span between the first mention of a beaver in the accounts and the first mention of a kit (more than a decade in both Deventer and Zutphen). It may have taken several years before a beaver family was not only able to establish a territory near the city, but also reproduce successfully. Fully-grown adult beavers that survived their first encounters with humans could have had significant advantage over their competitors, and occupied the most optimal territories (Nimje et al. 2021).

The landscape around the cities of Deventer and Zutphen after all provided a very suitable habitat for beavers. The water level in the river IJssel would certainly have been higher than the minimal water level (0.6-1.0 m) required for the establishment of a territory (Rosell & Campbell-Palmer 2022) and there was plenty of food (herbaceous plants, willows and ash trees) (Hartman 1996). Both cities used lands near the river for the pasture of livestock, mainly cattle, and planted large numbers of willows and ash trees to secure their wood supply. The brick kilns located next to the river IJssel in particular needed access to large quantities of firewood. The fact that human presence in these areas was relatively limited may initially have been to beavers' advantage. Adult beavers with young show risk-avoiding behaviour when selecting habitats (Steyaert et al. 2015).

It is also noteworthy that most sites where beavers were caught were located to the southeast of Deventer's city centre and to the northwest of Zutphen's. In other words: many beaver territories, if not all, were probably situated in between the two cities. This part of the River IJssel may have been the most suitable for beavers because of several reasons. The first is political. Deventer was part of the Bishopric of Utrecht until it became a free imperial city in 1495, while Zutphen owned allegiance to the duke of Guelders. This made the lands in between the two cities a frontier zone, which was generally more sparsely populated by humans than a political 'core' area.

The second reason is connected to the River IJssel itself. The IJssel is a relatively young river that only developed from the ninth century onwards because of the establishment of a connection between its precursor and the Rhine (Makaske et al. 2008). In the fifteenth century the IJssel split into two river arms after passing Zutphen, which reconnected again near Deventer. The fact that these river arms were known as the 'old' and 'new' IJssel suggests that the river had started carving out a new riverbed. In 1395 larger seagoing ships already found it difficult to navigate the 'old' IJssel. During the fifteenth century the volume of water transported by both river arms declined further as a result of the so-called Elisabeth floods (1421 and 1424). In their aftermath, a new estuary emerged, the Biesbosch, which increased the volume of water flowing into the North Sea through the main river arms of the Rhine. By 1485 navigation difficulties had become so critical that cities located on the river IJssel organised a conference to discuss these problems. At some point between 1456 and 1485 the 'old' IJssel had become little more than a brook, and seagoing ships, such as cogs, could no longer pass through the 'new' IJssel either (van Doorninck 1839, Jordens 1852, Weststrate 2008).

This gradual lowering of the water level may have limited beavers' dispersal options, and simultaneously lowered human tolerance for their engineering abilities. It could also have contributed significantly to Deventer's and Zutphen's decision to pay bounties for the capture of beavers. The drying up of the riverbed of the 'old' IJssel may also explain the presence of four beaver dams in the 'wrucht' in 1471. The financial account of Deventer refers to the destruction of four dams 'that were still left', which suggests that there used to be more. Perhaps these four were the largest and most difficult to demolish.

Environmental changes are probably the main reason why beavers appear in the financial records of Deventer and Zutphen around the mid-fifteenth century. It is unlikely that beavers were common in the IJssel in the decades immediately preceding the introduction of bounties to catch them. As mentioned before, remains of beavers are rarely found in the Netherlands among animal bones deposited after the year one thousand. So far, they have been found once in Zeeland and three times in Utrecht. This could be taken as evidence that the animal was uncommon in the Low Countries during the late Middle Ages.

Historical sources confirm this impression. In the early thirteenth century the encyclopaedist Thomas of Cantimpré questioned the common belief that beavers castrate themselves to escape human hunters seeking castoreum by stating that people in Poland knew that beavers had their testicles inside their body (Boese 1973). The reference to Polish beavers may indicate that he did not know anyone in his own region (Brabant and northern France) who had seen beavers. Jacob van Maerlant, who made a Dutch translation of Cantimpré's book on animals while living on the island of Voorne in Holland, did not add any new information on the beaver (Verwijs 1878).

Surviving financial accounts demonstrate that Countess Mahaut of Artois kept a beaver in her menagerie in 1303-1306 (Delmaire 1977, Dowling 2012), and that Margaret of Flanders, Duchess of Burgundy, received one as gift from Champagne in 1376 (Delort 1978). The fact that a beaver was considered a worthy addition to a menagerie, which typically includes exotic animals, implies that very few people in northern France had seen it.

Even if beavers were rare or extinct in the Scheldt basin by 1300, substantial populations could have survived in the nearby Meuse and Rhine basins. Financial records of William II, Duke of Jülich and Guelders, show that he bought 553 beaver pelts in the cities of Utrecht and Arnhem in 1388 as preparation for his crusade to Prussia (van Hasselt 1807). The great majority, if not all, probably came from the Baltic (Delort 1978), but it is possible that some were locally procured. In 1482 a merchant from Bastogne (Luxemburg, Wallonia) agreed to supply furs to a colleague in Mons (Hainaut, Wallonia) at fixed prices (Slootmans 1952). The inclusion of beaver fur on this list suggests that beavers were still present in the Ardennes and Eifel in the late fifteenth century. However, given that beaver fur was the most expensive item on the list, being valued at the same rate as Eurasian lynx (*Lynx lynx*) fur, the species was probably not very common.

Archaeological and historical sources both suggest that beaver populations in northern France, Belgium, and the Netherlands declined significantly during the early Middle Ages, more specifically during the reign of the Carolingian dynasty (eighth-nineth centuries). Beaver bones are far more numerous in Dutch and French archaeological contexts from the early Middle Ages than after the year one thousand (Duval et al. 2011, Çakirlar et al. 2019). A palace ordinance written in 882, and supposedly based on the organisation of the Carolingian court under Charlemagne, also mentions beaver catchers (*beverarii*) who probably had to supply the court with beaver fur (Prou 1884).

It is possible that the IJssel basin, or the lands to the east of the Zuiderzee more generally, still provided a refugium for beavers. Emperor Otto I allowed the bishop of Utrecht to hunt large game, such as Eurasian brown bears (*Ursos arctos arctos*) and elk (*Alces alces*), in his hunting reserve near Vollenhoven according to a charter from 944, a privilege confirmed twice by his successors in the early eleventh century (Sickel 1879). If bears and elk survived in this area until at least the tenth century, it is likely that beavers did as well. However, this does not prove their continued presence into the 1400s. Very few administrative sources of this area have been preserved, which makes it very difficult to prove either beavers' presence or absence during the fifteenth century.

What these sources do suggest is that the arrival and subsequent spread of beavers in the IJssel River from 1449 onwards may have constituted a major recolonisation attempt, a population expansion that is particularly remarkable considering that beavers were probably more or less exterminated in most of the Low Countries around that time.

The question now remains why the southward dispersal into areas with a relatively strong human presence (near two city centres) occurred at all. The most likely explanation for this migration and population growth are changed environmental circumstances (Bowler & Benton 2005). A first possibility is the creation of a corridor that enabled migrating beavers to spread to an area that had previously been cut off by a barrier. In 1399-1404 the city of Deventer dug a canal called the Schipbeek, which connected the city to Diepenheim and its German hinterland. Although the canal was more or less complete around 1404, construction work continued until 1422. The creation of this canal may have allowed beavers from German populations to spread to the Netherlands. It could explain why beavers were recorded first in Deventer and later in Zutphen. Another, not necessarily mutually exclusive, explanation is that the southward migration of beavers was related to the aforementioned changes in the water level of the river IJssel after the so-called Elisabeth floods (1421 and 1424).

Beavers probably experienced and responded to changes in the water level decades before political elites in the region finally took action (in 1485). This would have been particularly so given that sedimentation builds up faster near beaver dams because they slow down watercourses (Rosell & Campbell-Palmer 2022). These changes may have had only a limited effect on beaver families established in the most optimal territories. Subadult beavers on the other hand could have been confronted by a decreasing number of dispersal options as the carrying capacity of the IJssel basin declined. It is also well established that beavers disperse more frequently when the population density is low (Hartman 1997, Sun et al. 2000, Mayer et al. 2017).

Finally, it is possible that beavers coming from northern Germany or a refugium near the Zuiderzee were joined by conspecifics dispersing from other, more southern, populations. Beavers remained after all present near Zutphen until at least the year 1487, while they are no longer mentioned in Deventer after 1480. This discrepancy can also be explained, however, by beavers establishing territories on tributaries of the IJssel, such as the Issel/Oude IJssel (not to be confused with the like-named river on which Deventer and Zutphen are located) during preceding years. Testing either hypothesis is difficult because the financial accounts of Zutphen for the years 1483-1489 have not been preserved. The financial accounts of the city of Doesburg for the years 1476-1484 do not mention beavers (Streekarchivariaat de Liemers en Doesburg). We do know that the last beavers in Nordrhein-Westfalen were reportedly killed in the nineteenth-century Möhne and Ruhr (Nitsche 2020). According to Conrad Gessner they could still be found in the Rhine in the mid-sixteenth century (Gessner 1551-1587). Theoretically, German beavers could have reached Zutphen from the south by swimming downstream along the Rhine.

Beavers are no longer mentioned in the financial administration of either Deventer or Zutphen from 1490 to 1500. This could mean that the species became locally extinct, or that its population had declined to such an extent that the city councils no longer felt the need to pay bounties. In the early sixteenth century beavers were again recorded in the area. According to financial accounts the Duke of Guelders received the tails and hind legs of three beavers in 1519 and one in 1522 (van Hasselt 1805, 1807). These animals were caught in or near Borucht ('s Heerenberg between the Rhine and Oude IJssel) and Wisch (Terborg on the Oude IJssel), and in marked contrast to their fifteenth-century predecessors, were treated as prestigious gifts and as a delicacy rather than a nuisance. This could be taken as evidence for the beaver's rarity. A shift towards beaver tails as high-status food is also visible in Germany and Latvia in the late fifteenth and early sixteenth century (Ehlert 2010, Mänd 2016).

As far as the seventeenth century is concerned, we have access to two important naturalist studies: the hunting treatise *Jacht Bedryff*, probably written by the deputy forester of Holland Cornelis van Heenvliet around 1635, and Ernst Brinck's notes on animals (dating to the 1630s and 1640s and stored at the Streekarchivariaat Noordwest-Veluwe). The *Jacht Bedryff* does not mention beavers at all, which is remarkable considering that it includes species such as the red fox (*Vulpes vulpes*), which was only seen in Holland as an occasional immigrant from neighbouring provinces (Swaen 1948). Ernst Brinck, scholar and mayor of Harderwijk, claims to have seen a living beaver in his native city in 1636. However, he does not give any information about the location where the animal was captured. Given that the rest of his notes only gives a brief description of the animal before specifying the number of pelts imported from North America in a certain year, the animal in question may have been imported from outside the Netherlands.

So far, one of the few explicit pieces of evidence that beavers might still have been present in the seventeenth-century Netherlands comes from Peter von Streithagen's poem on the Rur/Roer, published in 1638. It lists the beaver among several animals that could be found in this river, a tributary of the Meuse (Teschenmacher 1638). It is unclear if there were any beaver territories in the Rur at that time, perhaps the animal was only seen as a rare visitor.

As mentioned in the introduction, the last recorded killing of a beaver in the Netherlands dates back to Zalk, approximately 40 km north of Deventer, in 1826. At this moment there is very few evidence to support the permanent presence of beaver populations in the Netherlands between 1522 and 1826. Jan Floris Martinet, our main source regarding beavers in the eighteenth-century Dutch Republic, claimed in his 'Catechism of nature' that the beaver was not 'native' to the Netherlands ('*geen inboorling van ons Vaderland')* and only caught occasionally (Martinet 1778). In a later abbreviated version of this book, he noted that the beavers seen in the Republic were immigrants from Germany (Martinet 1779).

We should consider the possibility that all sightings of beavers in the Netherlands after 1500 or 1600 refer to immigrants from Germany and their immediate descendants. The species' gradual disappearance from western Europe may after all not have been a linear process, but included dispersal and recolonisation attempts. The evidence that is currently available indicates that the beaver may have become functionally extinct in the Netherlands before 1500, several centuries before the death of the last known individual.

Conclusions

The financial records of the cities of Deventer and Zutphen provide detailed evidence on the presence of Eurasian beavers in the IJssel River during the second half of the fifteenth century. Beavers may have been absent or very rare near these cities in the early fifteenth century, before migrating southwards along the IJssel around the middle of the century. This gradual expansion could be related to environmental changes: the creation of a new corridor, a canal linking the city of Deventer with Germany, and/or a significant decline in the water volume transported by the IJssel. Beavers reached Deventer by 1449 and Zutphen by 1464. The initial population expansion may have been slowed down by severe hunting pressure, namely the issuing of financial rewards for beavers' capture. The introduction of a bounty system was likely intended to exterminate the species. By 1490 it had achieved its purpose.

The beaver may have become functionally extinct in the Netherlands before 1500. The possibility that all references to beavers after 1500 or 1600 refer to immigrants and their immediate descendants merits further study.

This article demonstrates the value of using historical archives, more specifically financial accounts, for the study of the Eurasian beaver in the Netherlands, but can also serve as an example to conduct similar research on other species and geographical regions. Medieval administrative documents can be a valuable source for such research because they provide detailed information on a historical period for which few other records based on direct observation exist.

Acknowledgements: This study was made possible by a Junior Postdoctoral Research Fellowship of the Flemish Research Council (FWO), grant number 12W5622N. I would like to thank the anonymous reviewer and the corresponding editor for their helpful comments on an earlier version of this article.

Bibliography

Archival sources

- The financial accounts of Deventer are preserved in Deventer, Collectie Overijs-

sel, 0698 Cameraars, inventory numbers 1.20-1.28. They can also be accessed online: https://collectieoverijssel.nl/
- The financial accounts of Zutphen are preserved in Zutphen, Regionaal Archief Zutphen, 0001 Inventaris van het oud-archief van de stad Zutphen, inventory numbers 1037-1076. They can also be accessed online: https://erfgoedcentrumzutphen.nl/
- The financial accounts of Doesburg are preserved in Doesburg, Streekarchivariaat de Liemers en Doesburg, Oud Archief Doesburg. Inventory numbers 859-865 contain those of the years 1476-1484.
- Ernst Brinck's notes on the beaver can be found in Harderwijk, Streekarchivariaat Noordwest-Veluwe, Adversaria van Dr. Ernst Brinck, inventory number 2058 'Nieuwe Aenmerckongen over sommige Viervoetige Gedierten', f. 128r.- f. 129r. The document can also be accessed online: www.archieven.nl

Archaeozoological research

Database Boneinfo: https://www.cultureelerfgoed.nl/onderwerpen/bronnen-en-kaarten/overzicht/boneinfor

References

Alberts, W.J. 1959. De cameraarsrekeningen van Deventer betreffende het jaar 1447. J.B. Wolters, Groningen, the Netherlands.

Bluzma, P. 2003. Beaver abundance and beaver site use in a hilly landscape (Eastern Lithuania). Acta Zoologica Lituanica 13 (1): 8-14.

Bowler, D.E. & T.G. Benton 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biological Reviews 80: 205-225.

Bonn, A.C. 1806. Anatome Castoris, atque chemica castorei analysis, ejusque in medicina usus. Haak & co, Leiden, the Netherlands.

Brokamp, B. 2015. Der Stat lantweer' en de 'lantwerenvort lant van Zallant', De laatmiddeleeuwse verdedigingsgordels rond Deventer. Deventer Jaarboek: 19-34.

Çakirlar, C., J. van den Hurk, I. van der Jagt, Y. van Amerongen, J. Bakker, R. Breider, J. van Dijk, K. Esser, M. Groot, T. de Jong, L. Kootker, F. Steenhuisen, J. Zeiler, T. van Kolfschoten, W. Prummel & R. Lauwerier 2019. Animals and people in the Netherlands' past: >50 years of archaeozoology in the Netherlands. Open Quaternary 5 (13): 1-30.

Canters, K.J. & B. Hoekstra 2019. De bever van Zalk, 'de laatste bever van Nederland' nader onder de loep genomen. Overijsselse Historische Bijdragen 134: 11-55.

Boese, H. (ed.) 1973. Liber de natura rerum. Walter de Gruyter, Berlin, Germany.

Coles, B. 2006. Beavers in Britain's past. Oxbow Books, Oxford, UK.

Coles, B. 2010. The Eurasian Beaver. In: T. O' Connor & N. Sykes (eds). Extinctions and Invasions. A Social History of British Fauna: 104-115. Oxbow Books, Oxford, UK.

Deby, J. 1848. Histoire naturelle de la Belgique. 2 volumes. Brussels, Belgium.

Delmaire, B. (ed.) 1977. Le compte général du receveur d' Artois pour 1303-1304. Commission Royale d' Histoire, Brussels, Belgium.

Delort, R. 1978. Le commerce des fourrures en Occident à la fin du Moyen Age (vers 1300-vers 1450). Tomes 1 et 2. École française de Rome, Rome, Italy.

de Meyer, G.M 1968-1985. De stadsrekeningen van Deventer 1394-1440. 6 volumes. Wolters-Noordhoff, Groningen, the Netherlands.

Dieberger, J. 2003. Die Bejagung des Bibers (*Castor fiber* L.) von der Steinzeit bis zur Gegenwart. Denisia 9: 21-46.

Dijkstra, J. & A. van Benthem 2004. Definitief archeologisch onderzoek op terrein 9 in Houten. ADC-ArcheoProjecten, Amersfoort, the Netherlands.

Dijkstra, V. 2019. Beverpopulatie blijft groeien. URL: https://www.Zoogdiervereniging.nl/nieuws/2019/beverpopulatie-blijft-groeien; viewed 7 November 2022.

Dowling, A. 2012. Landscape of luxuries: Mahaut d'Artois's (1302-1329) management and use of the park at Hesdin. In: C.R. Clason & A. Classen (eds): Rural space in the Middle Ages and Early Modern

Age: the spatial turn in premodern studies: 367-88. Walter de Gruyter, Berlin, Germany.

Duval, J., C. Callou & M.-P. Horard-Herbin 2011. Le castor *Castor fiber* Linnaeus, 1758 en France. Étude archéozoologique. Anthropozoologica 46 (2): 7-39.

Ehlert, T. (ed.) 2010. Küchenmeisterei: Edition, Übersetzung und Kommentar zweier Kochbuch-Handschriften des 15. Jahrhunderts, Solothurn S 490 und Köln, Historisches Archiv GB 4° 27; mit einen repographischen Nachdruk der Kölner Handschrift. Peter Lang, Frankfurt am Main, Germany.

Fustec, J., T. Lode, D. Le Jacques & J.P. Cormier 2001. Colonization, riparian habitat selection, and home range size in a reintroduced population of Eurasian beavers in the Loire. Freshwater Biology 46: 1361-1371.

Gautier, A., P. Hoffsummer & M. Vanguestaina 2005. Faune médiévale et post-médiévale du château de Franchimont (Theux). Vie Archéologique 64: 73-90.

Gessner, C. 1551-1587. Historia animalium. 5 volumes. Zürich, Switzerland.

Groneman, H.J.H. 1882. Bevers in Nederland. Album der Natuur 31 (1): 28-31.

Gysseling, M. 1960. Toponymisch woordenboek van België, Nederland, Luxemburg, Noord-Frankrijk en West-Duitsland (vóór 1226). 2 volumes. Belgisch Interuniversitair Centrum voor Neerlandistiek, Brussels, Belgium.

Halley, D., F. Rosell & A. Saveljev 2012. Population and distribution of Eurasian beaver (*Castor fiber*). Baltic Forestry 18 (1): 168-175.

Halley, D., A.P. Saveljev & F. Rosell. 2021. Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. Mammal Review 51 (1): 1-24.

Hartman, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. Journal of Zoology 240 (2): 317-325.

Hartman, G. 1997. Notes on age at dispersal of beaver (*Castor fiber*) in an expanding population. Canadian Journal of Zoology 75 (6): 959-962.

Hazenberg, T. 2000. Aanvullend archeologisch onderzoek op het tracé van de Noordoeverbinding van de Westerscheldetunnel, 1999 Borsele-Ellewoutsdijk. Archeologisch Diensten Centrum, Bunschoten, the Netherlands.

Hielkema J.B. 2003. Aanvullend archeologisch onderzoek op terrein 9 in Houten-Loerik, gemeente Houten (U.). ARC-Publicaties, Groningen, the Netherlands.

Horn, S. 2014. Ancient mitochondrial DNA and the genetic history of Eurasian beaver (*Castor fiber*) in Europe. Molecular Ecology 23: 1717-1729.

Hossfeld, P. 1983. Die eigene Beobachtungen des Albertus Magnus. Archivum fratrum praedicatorum 53: 147-174.

Jordens, E.A. 1852. De IJssel, als handelsweg en als waterweg van vroegere tijden tot heden: geschiedkundige proeve. Overijsselsche Almanak voor Oudheid en Letteren 17: 73-168.

Kitchener, A.C. & J.W.H. Conroy 1997. The history of the Eurasian beaver *Castor fiber* in Scotland. Mammal Review 27 (2): 95-108.

Kronenberg, H. 1902. Deventer weiderechten. PhD Thesis. Leiden University, Leiden, the Netherlands.

Liarsou, A. 2013. Interactions between the beaver (*Castor fiber* L.) and human societies: a long-term archaeological and historical approach. Archaeological Review from Cambridge 28 (2): 171-185.

Libois, R.M. 1982. Le castor. Les mammifères menacés de disparation en Wallonie. Service public de Wallonie. Direction générale opérationelle de l' agriculture, des ressources naturelles et de l' environnement, Namur, Belgium.

Makaske, B., G.J. Maas & D.G. van Smeerdijk 2008. The age and origin of the Gelderse IJssel. Netherlands Journal of Geosciences 87 (4): 323-337.

Mänd, A. 2016. Horses, stags and beavers: animals as presents in late-medieval Livonia. Acta Historica Tallinnensia 22: 3-17.

Manning, A.D., B.J. Coles, A.G. Lunn, D.J. Halley, P. Ashmole & S.J. Fallon 2014. New evidence of late survival of beaver in Britain. The Holocene 24 (12): 1849-1855.

Martinet, J.F. 1778. Katechismus der natuur. Tweede deel. Johannes Allart, Amsterdam, the Netherlands.

Martinet, J.F. 1779. Kleine Katechismus der natuur voor kinderen. Johannes Allart, Amsterdam, the Netherlands.

Mayer M., A. Zedrosser & F. Rosell 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. Animal Behaviour 123: 375-382.

McNew Jr, L.B. & A. Woolf 2005. Dispersal and survival of juvenile beavers (*Castor canadensis*) in Southern Illinois. American Midland Naturalist 154 (1): 217-228.

Molhuysen, P.C. 1840. Bevers in den IJssel. Overijsselsche Almanak voor Oudheid en Letteren 5: 95-98.

Nimje, P.S., M. Mayer, A. Zedrosser, M. Sæbø & F. Rosell 2021. Territory acquisition and mate choice in a monogamous mammal, the Eurasian beaver. Animal Behaviour 178: 165-173.

Nitsche, K.A. 2020. Historisch Nachrichten über Biber in Deutschland. Castor Research Society, Dessau, Germany.

Pasteur, I.D. 1796. Beknopte natuurlijke historie der zoogende dieren. Tweede deel. Honkoop & Dumortier, Leiden, the Netherlands.

Poelhekke, J. 1870. De Deventer Worp en zijne omgeving. Deventer, the Netherlands.

Prou, M. (ed.) 1884. De ordine palatii. Paris, France.

Raye, L. 2014. The early extinction date of the beaver (*Castor fiber*) in Britain. Historical Biology 27 (8): 1-13.

Rosell, F. & R. Campbell-Palmer 2022. Beavers: ecology, behaviour, conservation, and management. Oxford University Press, Oxford, UK.

Säterberg, T., S. Sellman & B. Ebenman 2013. High frequency of functional extinctions in ecological networks. Nature 499: 468-470.

Sellman, S., T. Säterberg & B. Ebenman 2016. Pattern of functional extinctions in ecological networks with a variety of interaction types. Theoretical Ecology 9: 83-94.

Sickel, T. (ed.) 1879. Die Urkunden der Deutschen Könige und Kaiser 1 Hannover, Germany.

Slootmans, K. 1952. Huiden en pelzen op de jaarmarkten van Bergen op Zoom. In: L.G. Verberne & A. Weijnen (eds). Land van mijn hart. Brabantse feestbundel voor Mgr. Prof. Dr. Th.J.A.J. Goossens op zijn zeventigste verjaardag (8 Februari 1952): 100-108. Henri Bergmans, Tilburg, the Netherlands.

Sluiter, H. 2003. The reintroduction and the present status of the beaver (*Castor fiber*) in the Netherlands: an overview. Lutra 46 (2): 129-133.

Steyaert, S.M.J.G., A. Zedrosser & F. Rosell 2015. Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia 179: 1023-1032.

Sun, L., D. Müller-Schwarze & B.A. Schulte 2000. Dispersal pattern and effective population size of the beaver. Canadian Journal of Zoology 78 (3): 393-398.

Swaen, A.E.H. (ed.) 1948. Jacht-Bedryff. Brill, Leiden, the Netherlands.

Teschenmacher, W. 1638. Annales Cliviae-Iuliae-Montiae, Marchiae, Ravensburgiae Antique et Modernae. Jacob van Biesen, Arnhem, the Netherlands.

van Doorninck, J. 1839. Welke zou de hoofdoorzaak van het verval der bevaarbaarheid van den IJssel zijn. Overijsselsche Almanak voor Oudheid en Letteren 3: 62-126.

van Doorninck, J.I., J. de Hullu & J.G.R. Acquoy (eds) 1885-1914. De cameraars-rekeningen van Deventer, 1337-1393. 9 volumes. J. de Lange, Deventer, the Netherlands.

van Hasselt, G. 1805. Bydragen voor d'oude Geldersche maaltyden. Arnhem, the Netherlands.

van Hasselt, G. 1807. Geldersch Maandwerk. 2 volumes. Arnhem, the Netherlands.

Veron, G. 1992. Histoire biogéographique du castor d' Europe *Castor fiber* (Rodentia, Mammalia). Mammalia 56 (1): 87-108.

Verwijs, E. 1878. Jacob van Maerlant's Naturen Bloeme. J.B. Wolters, Groningen, the Netherlands.

Wartena, R. 1977. De stadsrekeningen van Zutphen 1364-1445/46. 3 volumes. Gemeentearchief Zutphen, Zutphen, the Netherlands.

Weststrate, J. 2008. In het kielzog van moderne markten: handel en scheepvaart op de Rijn, Waal en IJssel, ca. 1360-1560. Verloren, Hilversum, the Netherlands.

Wijngaarden, A. van 1966. De bever, *Castor fiber* L., in Nederland. Lutra 8: 33-52.

Samenvatting

De historische aanwezigheid van de bever (*Castor fiber*) in de IJssel in 1450-1500

Dit artikel beschrijft de aanwezigheid van de

Euraziatische bever (*Castor fiber*) in de IJssel gedurende de tweede helft van de vijftiende eeuw op basis van middeleeuwse stadsrekeningen. Het beargumenteert dat de bever mogelijk al voor 1500 functioneel uitgestorven was in Nederland, verschillende eeuwen voordat het laatst bekende exemplaar werd gedood (1826). De studie toont ook het belang aan van middeleeuwse administratieve bronnen (rekeningen) voor de reconstructie van de historische aanwezigheid van zoogdieren in het verleden. Bevers worden in de stadsrekeningen van Deventer (de 'cameraarsrekeningen') vermeld van 1449 tot en met 1480 en in de stadsrekeningen van Zutphen (de 'overrentmeestersrekeningen') van 1464 tot en met 1489. Minstens 153 bevers werden in de jaren 1454-1489 aan de schepenen van beide steden getoond om een premie te krijgen. Bevers werden om meerdere redenen bejaagd, maar in dit geval was preventie van economische schade de belangrijkste motivatie. De invoering van een premiesysteem om bevers te vangen was waarschijnlijk een doelbewuste poging de soort uit te roeien. De rekeningen specificeren soms dat de getoonde bevers jong/klein of groot waren. Deze details geven een indicatie van de aanwezigheid van beverjongen en volwassen bevers in specifieke jaren. De meeste gedode dieren waren waarschijnlijk subadulte exemplaren. In twee gevallen, beide in Deventer, worden niet-dodelijke acties vermeld: het beschermen van wilgenpoten met doorns en de vernieling van vier beverdammen. Het voorkomen van relatief grote aantallen bevers in de IJssel is opmerkelijk, want historische en archeologische bronnen suggereren dat de soort rond 1400 grotendeels uit de Lage Landen verdwenen was. Zijn mogelijk opnieuw opduiken en tijdelijke rekolonisatie van grote delen van de IJssel kan verklaard worden door ecologische veranderingen. In de vroege vijftiende eeuw liet het stadsbestuur van Deventer een nieuw kanaal graven, de Schipbeek, dat de stad met Diepenheim en het Duitse achterland verbond. Dit kanaal kan als corridor gefungeerd hebben voor bevers uit populaties in Noordwest-Duitsland. Gedurende de vijftiende eeuw daalde het watervolume in de IJssel ook zeer sterk als gevolg van de Sint-Elizabethsvloeden van 1421 en 1424. Hierdoor werden dispersiemogelijkheden voor subadulte bevers mogelijk beperkt, terwijl het risico op mens-bever conflicten steeg. Een overzicht van zestiende- en zeventiende-eeuwse bronnen voor de aanwezigheid van bevers in Nederland suggereert dat individuele bevers, mogelijk immigranten uit Duitsland en hun nakomelingen, steeds zeldzamer werden, om in de achttiende en negentiende eeuw uiteindelijk helemaal te verdwijnen.

Received: 9 August 2022
Accepted: 22 October 2022

Detecting and monitoring small mammals with trail cameras

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Abstract: We have developed a device, the Struikrover®, for detecting and monitoring small mammals in the wild. This device is a trail camera encased in a tube. Through a study, covering 2590 trap nights and the analysis of over 130,000 pictures, we evaluate optimal camera settings and the intervals between refreshing the bait and compare our results with related studies in the Netherlands. We recommend taking pictures rather than videos, at a setting in which two pictures are taken each time the device is triggered, with a pause of one minute after the camera is first triggered. We also recommend leaving the Struikrover in place for 3-4 weeks to maximize its efficiency in terms of the number of species identified. The Struikrover proves to be a good option for detecting mammals up to the size of a western polecat (*Mustela putorius*). For larger animals we assume that a standard stand-alone trail camera is the better option. To cover the whole spectrum of mammal species a combination of Struikrover with a stand-alone trail camera would be ideal.

Keywords: methods, camera trap, monitoring, non-invasive, rodent, shrew, mustelid, Struikrover.

Introduction

One of the most fundamental challenges in conservation biology is how to determine species distribution and richness. For example, it is difficult to detect small mustelids in the field due to their unpredictable and mobile behaviour and low densities. In an earlier study (Smaal & van Manen 2017), in which we tried to collect data about the occurrence of weasels (*Mustela nivalis*) we experienced this low detection rate. In that study we tested several non-invasive and time efficient methods, such as track tubes and nest boxes with track tubes. Nest boxes proved to be relatively successful, but the results were not completely satisfactory, because the tracks of male weasels and female stoats (*Mustela erminea*) were hard to differentiate. Methods that use DNA identification (Jones et al. 2004) cannot be applied without the (expensive) aid of a laboratory, so we started experimenting with trail cameras. These are generally used for medium-sized to large mammal species (Hoffmann et al. 2010), but occasionally for species such as red squirrel (*Sciurus vulgaris*) and fat dormouse (*Glis glis*). In an Italian study small mammal species (weasel, shrews - *Sorex* spp.) were detected occasionally by other means, but were missed by the trail cameras (Di Cerbo & Biancardi 2013).

We started with standard stand alone trail cameras, but soon found out that problems arise with dense or tall vegetation, which hampers a trail camera capturing weasels. Focus distance, in most cameras more than one metre, turned out to be a second problem since, at that distance, small mammals may not be detected or when detected may not be identified.

In order to tackle these problems we have developed the Struikrover®: a tube with an internal trail camera. Struikrovers can provide clear pictures of almost all small mammal species that occur in a study area, allowing one to not only be able to capture weasels but, just as importantly, potential prey, competitors and predators. However since some small mammals, such as rodents, can be very numerous or persistently present, the processing of thousands of pictures can become a problem. This article describes the Struikrover and explains how to set up the cameras in order to reach a reasonable balance between the information obtained and the storage of, and time needed to process, data. We also compare results of Struikrover trials with those of other methods, such as stand-alone trail cameras and nest boxes for weasels.

The Struikrover concept

The Struikrover is a plastic tube painted in camouflage colours, with a diameter of 20 cm, with one end cut at an angle of 45°, and the other end closed (figure 1). Its longer side (the bottom) is 40 cm. The tube contains a tray with a trail camera at the closed end of the tube and a sardine can at the entrance. The tray fixates the distance between camera and sardine can, and can be attached to the tube preventing its removal by larger animals. On the top of the tube, just in front of the camera, there is a clear pane of plexiglass with a diameter of 10 cm, which provides the sensors in the camera with extra light, in order to avoid the overexposure of pictures in sunny conditions. The focus of the camera is adjusted with a reading glass (for most camera types +3 dioptres) in order to reduce the focal distance to 35 cm.

The tube is sufficiently robust to protect the camera from trampling (by cattle or sheep) and provides an unobstructed view. Vegetation in close range of the subject (which can cause overexposure at night) is thereby avoided. The tube also hides the camera (figure 2) and prevents the motion trigger from reacting to moving objects that are outside the camera's view range. The horizontal plane of the tube should be slightly angled towards the front end, to avoid rain entering it and the baited front end should be pushed a little into the soil or vegetation, so that small animals, such as shrews, will not be obscured by the rim of the tray. When the Struikrover is in position the sardine can is punctured at the top end without spilling the oil (as any spillage might lure the animals away from the camera's view).

Most camera types work with infrared led lamps in dark conditions. In some types the intensity of light can be reduced. Because a Struikrover takes pictures at very close range even the strongest light reduction is not sufficient to avoid overexposure. In most types of cameras we therefore reduced the light source by covering the lamps with (green) tape. The light sensors, however, should not be covered, otherwise the camera will always experience dark conditions and, especially during daytime, the pictures will be overexposed.

Methods

In order to test the Struikrover we set up a number in a study area, in and around the Drentsche Aa river valley (6.64°E, 53.03°N) where we had previously (in 2014-2016) set out nest boxes for weasels (Smaal & van Manen 2017). Most of the Struikrovers were in marshes and semi-natural grasslands, mown once a year in late summer or autumn. Some Struikrovers were placed in other habitats, such as heaths and woodland. In most cases we chose linear vegetation elements or vegetation transitions. A detailed description of the area can be found in Spek et al. (2015).

The data cover the period from 5 February 2018 to 19 January 2020. The Struikrovers were set out at 92 locations for 14-491 days, and the bait was refreshed 202 times (sessions), covering 2590 trap nights. A total of 131,717 pictures were taken and transcribed into a file. These could be reduced to 57,746

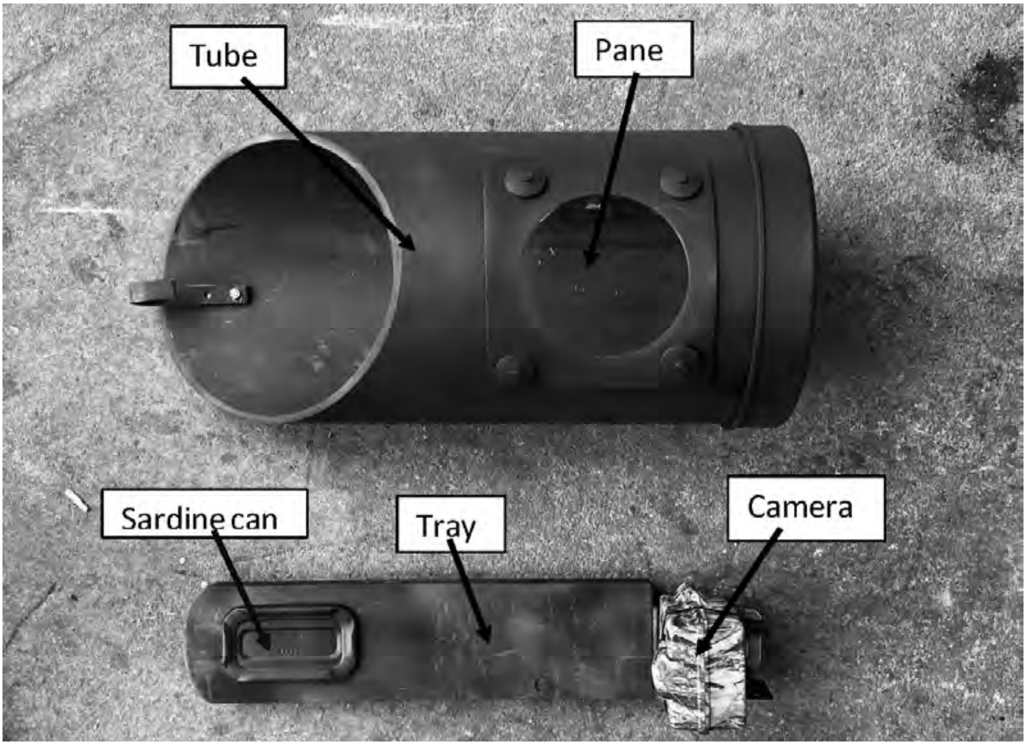


Figure 1. A Struikrover.

Figure 2. The 45° angel helps camouflaging the Struikrover and improves exposure of visiting animals during daylight. Taarlo 30-11-2022. *Photo: Matthijs Smaal.*

Table 1. Detection of mammal species in Struikrovers, expressed as the absolute number of sessions in which species were detected (number) and relative to the total of 202 sessions (%).

Species		Number	%
Western hedgehog	*Erinaceus europaeus*	3	1.5
Common shrew	*Sorex araneus*	56	27.7
Pygmy shrew	*Sorex minutus*	54	26.7
Water shrew	*Neomys fodiens*	12	5.9
Greater white-toothed shrew	*Crocidura russula*	2	1.0
Brown hare	*Lepus europaeus*	3	1.5
Rabbit	*Oryctolagus cuniculus*	2	1.0
Bank vole	*Myodes glareolus*	92	45.5
Common vole	*Microtus arvalis*	46	22.8
Field vole	*Microtus agrestis*	14	6.9
Water vole	*Arvicola amphibius*	1	0.5
Harvest mouse	*Micromys minutus*	31	15.3
Wood mouse	*Apodemus sylvaticus*	73	36.1
Yellow-necked mouse	*Apodemus flavicollis*	75	37.1
Brown rat	*Rattus norvegicus*	12	5.9
Weasel	*Mustela nivalis*	61	30.2
Stoat	*Mustela erminea*	12	5.9
Western polecat	*Mustela putorius*	10	5.0
Pine marten	*Martes martes*	17	8.4
Beech marten	*Martes Foina*	35	17.3
Otter	*Lutra lutra*	3	1.5
Badger	*Meles meles*	8	4.0
Red fox	*Vulpes vulpes*	8	4.0
Roe deer	*Capreolus capreolus*	9	4.5

moments when a camera was triggered (triggers). Triggers by an identified animal are referred to as ‘captures’. Calculations were made in Excel.

Results

Species range

During this study we recorded 24 species of wild mammals, of which small woodland species were most frequently captured (table 1). Other mammals included feral cats (*Felis catus*) and domestic dogs (*Canis familiaris*). Beside mammals we recorded 23 bird species, 2 reptiles and 2 amphibians.

Photo or video?

In the experimental stage we started with videos, but soon found out that extracting data from videos, even when they are very short, is extremely time consuming compared to processing pictures. Apart from the higher energy consumption (which has implications for the cameras’ battery life) and much larger file size, the videos took several seconds to start after the device was triggered. In pictures this was always less than a second, so videos (theoretically) miss more captures.

The number of pictures

Most camera traps have an option to take a series of pictures, often within one or two seconds, for each time the device is triggered. Multiple instant-pictures reduce the chance of missing an animal, but increase file size and the number of pictures to be analysed. During a pilot in the same area, when we still worked with three pictures per trigger and only some of the species captured were analysed (data not incorporated in the rest of this article) we checked the added value of more than one picture per trigger for captures of western hedgehog (*Erinaceus europaeus*) (13), water shrew (*Neomys fodiens*) (50), weasel (57) (*Mustela nivalis*), stoat (*Mustela erminea*) (19), western polecat (*Mustela putorius*) (1), pine marten (*Martes martes*) (4), beech marten (*Martes foina*) (42), otter (*Lutra lutra*) (1), badger (*Meles meles*) (4) and red fox (*Vulpes vulpes*) (8). Most animals were captured on the first picture (185 out of the total of 199). The second picture added 13 new captures (4 water shrews, 3 weasels, 3 stoats, 2 beech martens and 1 red fox). The third picture captured one additional weasel, that was not recorded on the first and second. This leads us to suggest a setting in which two pictures are taken each time the device is triggered.

Setting interval

Many animals visited the Struikrover only briefly. In the sample of 199 captures, most animals left the device within 1-2 seconds. Most camera traps have an option to set a minimum interval before the device will trigger again. Setting this interval reduces the number of redundant captures of the same individual (at the expense of battery life and memory space), but also may result in missing captures of new" species. To quantify the risk of setting an interval we analysed 61 sessions in which no interval was set. In these sessions traps were triggered 25,788 times, resulting in 301 session-species combinations. In 11,769 cases (46%) the devices were triggered within a minute from the previous trigger. In 11,558 cases, the species (and probably the individual) was the same as the previous one but in 211 cases the next species was a different one. This might have resulted in missing a species during the whole session, but effectively this was true in only four (1.3%) session-species combinations: one common shrew (*Sorex araneus*), one bank vole (*Myodes glareolus*), one common vole (*Microtus arvalis*) and one weasel would have been missed if an interval had been set.

In terms of reducing the number of pictures and missing valuable observations, we suggest setting the minimum interval at one minute. The benefits of having a longer interval are outweighed by the higher risk of missing species.

The duration of sessions

Since we worked with bait (canned sardine), it may be assumed that its attractiveness changed over the course of time. The period after which we removed the Struikrover or refreshed the sardine bait was not fixed, but ranged between 14 and 40 days. In some cases the session finished due to camera failure or dead batteries.

The increase in captures between day zero and day one partly resulted from switching on the devices around noon of day zero (figure 3), so day zero was actually only half a day. Since this initial increase was more than two-fold (actually three-fold) we believe that it took individuals some time to discover the Struikrover. Initially they returned often but after a few times probably learned that, despite the smell, there was no reward and lost interest. After 20 days interest levelled off and we assume that the local mammals no longer found the Struikrover an object of attraction. This pattern held true in new locations and sites where the bait was refreshed. The obtained pattern is mainly down to abundant species with small home ranges, such as bank vole, but the mechanism is probably valid for

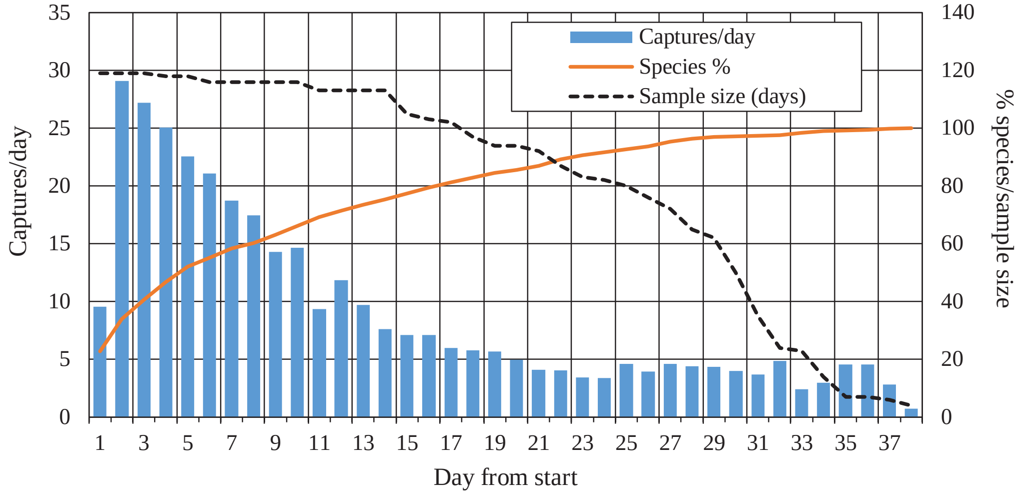


Figure 3. Number of captures and accumulated number of species by day after the start of a Struikrover session. The mean number of species per session had declined to 5.25 species by day 38.

most species attracted by the odour of canned sardine.

The mean cumulative number of species detected sharply increased during the first days a Struikrover was set out or after the bait was refreshed, and later levelled off, almost perfectly (R^2=0.988) following a logarithmic curve that can be expressed by the formula $y = 23.569\ln(x) + 15.114$. According to this model after one week 61% of all species had been recorded, 77% after two weeks, 87% after three, 94% after four and 99% of all species after five weeks.

Keeping in mind the reduction in attractiveness of the bait, we suggest a session duration of three or four weeks being optimal in terms of efficiency when one wants to cover many sample points with a restricted number of devices and in a limited time frame.

Comparing the detection rate of weasel for Struikrovers and nest boxes

We previously monitored weasels in the Drentsche Aa river valley using nest boxes (Smaal & van Manen 2017). Five of these nest boxes were still operational in 2018 and 2019 and a Struikrover was placed within ten metres of each one . We compared visits of weasels to the nest boxes with the paired Struikrover over the months in which the Struikrovers functioned for at least 21 days (n=67 months).

In 33 cases both devices recorded no weasels, in ten cases weasels were recorded in both, in eight cases weasels were recorded in a nest box, but not captured in the paired Struikrovers and in 16 cases they were recorded in the Struikrover but not in the nest box. The monthly numbers of visits of weasels in nest boxes and in paired Struikrovers were clearly correlated (figure 4) but Struikrovers proved to be about 50% more effective in registering weasels. In addition it was easier to distinguish weasels from stoats by photographs than by their tracks in the nest boxes.

Discussion

Comparing results with other trail camera research

The Struikrover is designed to detect small mammals up to the size of a marten and

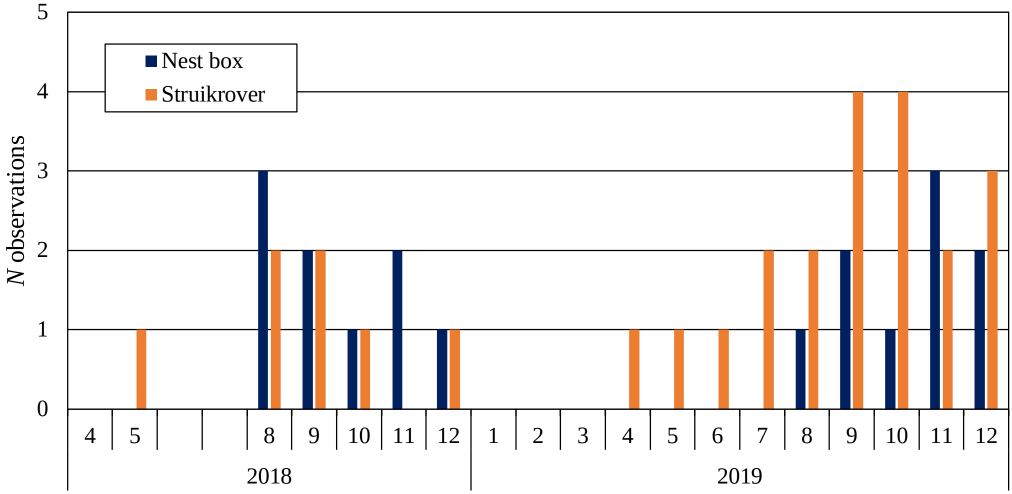


Figure 4. Monthly visits of weasels to five nest boxes, compared with captures in Struikrovers that were placed within 10 m from the nest boxes. Data are lacking for June and July 2018. In April 2018 and in January through to March 2019 no weasels were recorded by either method.

is actually quite similar to the TubeCam, described by Ratnaweera et al. (2017), developed to tackle similar problems that we faced in capturing small mustelids. Due to the short-distance focus and the restricted view the Struikrover is probably less effective in capturing larger animals such as red fox, badger and roe deer (*Capreolus capreolus*). We are not able to prove this since we did not set standard stand-alone trail cameras in the same area. Nevertheless there are a few data sets available that provide some circumstantial evidence. During the winter of 2014 a study was carried out close to our study area in the northern part of the province of Drenthe (Hasper & van Manen 2015) and during the winter of 2015 this was repeated in a more wooded part in the centre of Drenthe. In both cases the locations were baited with fish waste with a trail camera set at 1.2-2 m distance. Another study, in the north of the country (the provinces of Friesland, Groningen and Drenthe), was done by the Dutch Mammal Society in the context of the national survey of western polecat and pine marten, in which cameras were mounted at about 1.5 m from sardine cans, fixed to trees: the Bubo project. We compare the results of these studies noting that the duration of sessions was slightly higher in Struikrover (29 days) and Bubo (35 days) than in the two studies with fish waste (22 and 23 days respectively).

Although we tried to reduce the influence of regional differences on species composition by selecting only results from the northern part of the Netherlands, we cannot rule out an effect of specific location, habitat and season or year that may have affected the results obtained by the different methods. In general however standard stand-alone trail cameras captured relatively fewer small mammals up to the size of a weasel (table 2), either because these animals remain elusive or cannot be detected or identified from the pictures. The relative low presence of larger mammals in the Struikrover may be a result of the position, which is often in relatively dense vegetation. Larger animals probably prefer trails or shorter vegetation when exploring a home range. A prominent exception is the wood mouse (*Apodemus sylvaticus*), which is much more frequently captured by standard stand-alone cameras than would otherwise be expected by its size. Possibly this species is

Table 2. Species captured by Struikrover (only sessions of at least 21 days) compared to the results of the Bubo project and two studies with unmodified trail cameras baited with fish waste (see text). We present the mean number of sessions in which each species was recorded (1= in all sessions, 0= not recorded with this method).

Method	Struikrover	Bubo	Camera	Camera
Bait	Sardine oil	Sardine oil	Fish waste	Fish waste
Period	2018-19	2017-19	2013-14	2014-15
Sessions	89	27	49	35
Days	2590	942	1065	789
Western hedgehog	0.01	0.15	-	-
Common shrew	0.52	0.00	0.00	0.00
Pygmy shrew	0.49	0.00	0.00	0.00
Water shrew	0.06	0.00	0.00	0.00
Greater white-toothed shrew	0.02	0.00	0.00	0.00
Brown hare	0.03	0.26	0.16	0.09
Rabbit	0.02	0.00	0.02	0.00
Bank vole	0.87	0.22	0.00	0.11
Common vole	0.45	0.00	0.00	0.00
Field vole	0.12	0.00	0.00	0.00
Water vole	0.01	0.00	0.00	0.00
Harvest mouse	0.31	0.00	0.00	0.00
Wood mouse	0.70	0.59	0.35	0.89
Yellow-necked mouse	0.72	0.00	0.00	0.00
Brown rat	0.10	0.19	0.00	0.06
Weasel	0.49	0.04	0.00	0.00
Stoat	0.08	0.00	0.00	0.00
Western polecat	0.09	0.11	0.10	0.09
Pine marten	0.12	0.22	0.33	0.40
Beech marten	0.24	0.30	0.35	0.54
Otter	0.01	0.00	0.00	0.00
Badger	0.03	0.26	0.53	0.54
Red fox	0.03	0.37	0.73	0.57
Raccoon dog	0.00	0.00	0.12	0.03
Roe deer	0.09	0.70	0.65	0.69
n species	26	14	12	13
Maximum this method	14	5	2	4

not confined to denser vegetation like other small mammals. Also it is easily recognised, even from a distance, by its big, light-reflecting, eyes.

We advise using a Struikrover for detecting or monitoring mammals up to the size of a western polecat. For larger animals we suppose an standard stand-alone trail camera is the better option. To cover the whole spectrum of species a combination of both would be ideal.

In summary we recommend to:

- Use photos instead of videos;
- Set the camera for taking two pictures at each trigger, with an interval of one minute between triggers;
- Leave the device three to four weeks at one site or refresh the bait once a month;
- Use Struikrovers for detecting or monitoring species up to the size of a western pole-

Struikrovers proved to be effective in detecting animals up to the size of a western polecat, thanks to the shortened focus and the ability of operating in dense vegetation. Taarlo, 1-8-2021. *Photo: Matthijs Smaal.*

The Struikrover performs well in detecting small species like the pygmy shrew, that was registered 5.548 times during this study. Taarlo, 26-9-2021. *Photo: Matthijs Smaal.*

cat, but use standard stand-alone cameras when aiming for larger animals;
- List all recordings, since this may reveal interesting patters such as activity patterns over the course of a day or season, especially in abundant species (see van Manen & Smaal 2021).

Acknowledgements: We thank Staatsbosbeheer for giving permission to carry out the study in the Drentsche Aa Nature Reserve; Dick Bekker, Draak Den Hartog, Maurice La Haye, Tim Hofmeester, René Jansen, Hans Kleef and Aaldrik Pot for helping to identify some doubtful cases; Rob Bijlsma for commenting on a first draft of this article; Maurice La Haye and Dick Bekker of the Dutch Mammal Society for kindly providing us with the Bubo-data, Johan Thissen and an anonymous referee for improving the manuscript and Nicholas Parrott of TextualHealing.eu for English language editing.

References

Di Cerbo, A.R. & C.M. Biancardi 2013. Monitoring small and arboreal mammals by camera traps: effectiveness and applications. Acta Theriologica 58: 279–283.

Hasper, H. & W. van Manen 2015. Registratie van roofdieren met cameravallen in Noordoost Drenthe in de winter 2013-14. Stichting Boomtop, Assen, the Netherlands.

Hoffmann A., J. Decher, F. Rovero, J. Schaer, C. Voigt & G. Wibbelt 2010. Field Methods and Techniques for Monitoring Mammals. In: J. Eymann, J. Degreef, C. Häuser, J.C. Monje, Y. Samyn & D. VandenSpiegel (eds). Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring, Part 2: 482-529. Belgian National Focal Point to the Global Taxonomy Initiative, Brussels, Belgium.

Jones, C., H. Moller & W. Hamilton 2004. A review of potential techniques for identifying individual stoats (*Mustela erminea*) visiting control or monitoring stations. New Zealand Journal of Zoology 31: 193-203.

Ratnaweera, N., R. Ratnaweera & D. Früh 2017. Developing a new method to detect small mustelids. In: 32nd European Mustelid Colloquium 15-17 November 2017. Book of Abstracts: 27.

Smaal, M. & W. van Manen 2017. Monitoring weasels (*Mustela nivalis*) with nest boxes. Lutra 60: 19-26.

Spek, T., H. Elerie, J.P. Bakker & I. Noordhoff 2015. Landschapsbiografie van de Drentsche Aa. Van Gorcum, Assen.

van Manen, W. & M. Smaal 2021. Circadian and ultradian rhythms in free living bank voles (*Myodes glareolus*). Lutra 64 (2): 73-80.

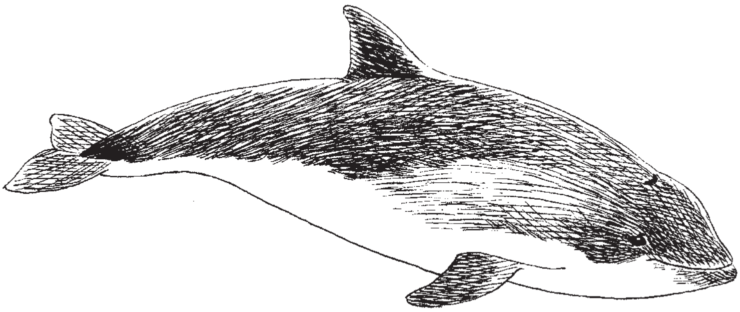
Samenvatting

Het registreren en monitoren van kleine zoogdieren met cameravallen

De meeste kleine zoogdieren brengen een groot deel van hun leven door in dichte vegetaties en zijn daardoor nauwelijks te registreren met standaard cameravallen. De focusafstand van cameravallen bedraagt meestal iets meer dan een meter en plaatsing in vegetaties levert veel valse triggers en onscherpe, overbelichte foto's op. Om deze problemen te tackelen, ontwikkelden we de Struikrover. Dit is een 35 cm lange, schuin afgezaagde pvc-buis met een diameter van 20 cm, aan het rechte einde afgedekt met een dop. In de buis ligt een plank, met aan het ene einde een cameraval en aan het andere einde een blikje sardine, waarin aan de kopse kant een gaatje is geprikt. Dit dient als lokmiddel, met name om dieren scherp en gecentreerd in beeld te krijgen. De lens van de cameraval is voorzien van een brillenglas dioptrie +3 en in de meeste gevallen is de infraroodbelichting van de camera afgeplakt met groene tape om overbelichting te voorkomen. Boven de camera zit in de buis een venster, om er overdag voor te zorgen dat, via de lichtsensoren, zoveel mogelijk in daglichtmodus wordt opgenomen. De schuin afgezaagde rand van de buis zorgt eveneens voor een betere belichting overdag en maakt de Struikrover minder opvallend in het veld. Tijdens een onderzoek in- en in de buurt van het beekdal van de Drentsche

Aa bij Loon (Drenthe) hebben we het gebruik van de Struikrover en met name de instellingen van de camera geëvalueerd, gedurende 2590 draainachten. We gebruikten de foto- in plaats van video-modus, omdat de camera bij foto's sneller aanslaat, foto's minder opslag en een lager batterijverbruik vergen en het minder tijd kost de informatie om te zetten naar een databestand. Veel cameravallen hebben de mogelijk om meerdere foto's te nemen per trigger. In een subset van 199 registraties, konden 185 op de eerste foto correct worden gedetermineerd. In 13 gevallen was een tweede foto nodig en in één geval leverde alleen de derde foto uitsluitsel. In termen van efficiency zijn twee foto's optimaal. Daarnaast kan bij de meeste cameravallen een rusttijd worden ingesteld nadat een opname is gemaakt, om teveel opnames van hetzelfde individu te beperken. In een subset van 61 gevallen hebben we geen rusttijd ingesteld en dit leidde tot 25.788 triggers (en een veelvoud aan opnames). In 46% van de gevallen werd binnen een minuut een nieuwe serie foto's gemaakt. Daarbij ging het in 98.2% om dezelfde soort en waarschijnlijk dus hetzelfde individu. In 1.3% werd binnen de rusttijd van een minuut een soort geregistreerd die anders op die locatie niet zou zijn vastgesteld. Door een rusttijd van een minuut in te stellen, kan veel batterij- en opslagcapaciteit en verwerkingstijd worden bespaard ten koste van gering informatieverlies. In de loop van de tijd waarin een Struikrover op dezelfde locatie lag zonder aas te verversen, liep het aantal waarnemingen terug, evenals het aantal nieuwe soorten dat werd geregistreerd. Na drie weken werd ongeveer 87%, na vier weken 94% van de soorten gedetecteerd. Bezoeken van wezels (*Mustela nivalis*) aan speciaal daarvoor ingerichte nestkasten (Smaal & van Manen 2017), vergeleken met registratie door een op enkele meters Struikrover, leverde een licht betere detectiekans door de Struikrover op. Hoewel vrijwel alle in het gebeid voorkomende zoogdiersoorten werden vastgelegd, waren Struikrovers minder effectief in het vastleggen van de grotere soorten dan los opgestelde cameravallen. Soorten kleiner dan een bunzing (*Mustela putorius*) werden, met uitzondering van bosmuis (*Apodemus sylvaticus*), echter zelden tot niet geregistreerd zonder Struikrover.

Received: 16 January 2022
Accepted: 20 November 2022



Deformed Cetacea bones from the southern North Sea

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Abstract: This study describes the occurrence of osteological pathologies in cetacean bones from the North Sea held in the collections of Vonk and Ecomare on the island of Texel, the Netherlands. Bone pathologies are mostly a congenital condition, a result of degeneration or a bacterial infection. More severe bone malformations can have serious consequences for the health of cetaceans. Previous research indicates that lesions in a cetacean skeleton can lead to a decrease in mobility and fitness of the animal. Besides affecting the locomotion, these animals are more exposed to predation as well. In total, 37 whale bones with abnormal conditions were found. The majority originated from the harbour porpoise (*Phocoena phocoena*) and accounted for 15 units. Vertebrae were the most common deformed bones with 24 units, mostly showing features of spondylodiscitis. As the studied collections primarily consist of fished up bone singletons instead of complete skeletons, it proved almost impossible to conclude if the observed pathologies had affected the health of the concerning cetaceans.

Keywords: Cetacea, osteological pathologies, pseudopathology, deformed bones, abnormalities, North Sea.

Introduction

The mammalian infraorder Cetacea comprises baleen and toothed whales, including dolphins and porpoises. These species evolved from quadruped terrestrial animals around 55.8 million years ago, in the early Eocene (Barnes 1984). The adaptation to the marine environment has been accompanied with several physical changes, such as the extension of the skull (also known as telescoping) with one or two dorsal blowholes for breathing, the disappearance of the pelvic limbs, and the transformation of the pectoral limbs into fins for locomotion. Nowadays, cetaceans move through the water by powerful vertical movement developed by their tailstock and the flukes (e.g., Camphuysen & Peet 2006, Cozzi et al. 2009). These movements are generated by very strong muscles, which are located along the spine. Hence the spine and its muscles can be assigned as the main locomotor organ in cetaceans (Cozzi et al. 2009) and the vertebral column of cetaceans is crucial for all their vital activities.

However, several studies have found different types of skeletal lesions (e.g. Kompanje 1995a, 1995b, 1996, 1999, Félix et al. 2007, Van Bressem et al. 2007, Groch et al. 2012, San Martín et al. 2016), raising the question whether these osteological pathologies affect the health of cetacean species. Based on previous studies, bone aberrations can be diagnosed as a consequence of: 1. Degeneration, related to age or as a result of direct damage due to abnormal forces around the joint or

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adjacent supporting structures. 2. Infectious spondylitis, often referred to as spondylo-osteomyelitis and used as an umbrella term for an inflammation of a vertebra as a result of a direct infection. 3. Spondylodiscitis, damage to the vertebral disc due to bacterial infection. 4. Congenital pathology. 5. Pseudopathology due to post-mortem disintegration, which are abnormalities that appear on the bone after the death of the animal, for instance due to the weathering process. Furthermore, osteophytes, which are bony outgrowths, and syndesmophytes occur often on the bones. Syndesmophytes are defined as osteophytes bridging between two vertebrae due to different ossification processes (François et al. 1995)

Here we report on the observed osteological pathologies of cetaceans held in the Vonk and Ecomare bone collections in spring 2021. For over thirty years, the Dutch fisherman Adrie Vonk has been collecting whale bones and other (marine) mammal remains found by fishermen as 'bycatch' at the North Sea. Vonk started this process in 1990 and kept everything he received from his fellow fishermen in his shed, called 'Groenland', on the island of Texel. No selection has been made in the incoming bones and every single bone ended up in Vonk's collection. Most bones are fished up in the period between 1980 and 2016 by beam trawl fishing in the area south of the Newcastle-Limfjord line in the southern half of the North Sea. In 2016, the extensive collection was donated to Ecomare, a nature museum on Texel. The collection consists of fished up recent bones but also fossils of all different parts of the skeleton. Currently, the collection is still being supplemented with new bones. The whole collection of around 5500 fished up bones has been identified, described, and catalogued with the help of a group of volunteers. The assessment of the entire bone collection consisted of the identification of the species, a rough estimate of the age, as well as defining from which part of the skeleton the bone originates, and the corresponding quantity.

Table 1. Number per pathology type found in the Vonk and Ecomare whale bone collections.
* deformed mandibles and scapulae

Pathology	Number
Congenital	3
Degeneration	1
Pseudopathology	6
Severe weathering	4
Spondyloarthropathy	2
Spondylodiscitis	17
Unknown bacterial infection*	4
Total	37

To further elaborate the research on the Vonk whale bone collection, this study will focus on the occurrence of deformed cetacean bones. The aim of this research is to document pathological aberrations observed in this whale bone collection and to diagnose the potential pathologies. In order to get an impression of how often osteological pathologies occur, which types are involved and whether there is a relationship with the age or the developmental stage of the animal, the Vonk bone collection is subjected to a closer inspection.

Materials and methods

For this research, whale bone collections were assessed to study the occurrence of pathological conditions in cetacean species. We primarily used the Vonk collection, which comprises around 5500 bones. This collection was readily accessible because it was identified, classified, and photographed in the years 2017 and 2018. Moreover, during this identification, easily recognizable abnormal bones had been stored separately. For our study, a closer inspection of the entire Vonk collection was carried out in spring 2021 in order to find more whale bones with abnormalities. Previous research by François et al. (1995), Groch et al. (2012), Kompanje (1995a, b, 1996, 1999), and Nathan (1962) were

Table 2. The number of deformed bones per cetacean species found in the Vonk whale bone collection, and the corresponding percentages with respect to the total amount of bones. The total amount of bone data is retrieved from previous research by Oosterbaan (2018).

Species	Total amount of bones	Amount of deformed bones	Deformed bones (%)
Beluga *(Delphinapterus leucas*)	-	1	-
Bottlenose dolphin *(Tursiops truncatus*)	137	4	2.92%
Minke whale *(Balaenoptera acutorostrata*)	362	4	1.10%
Harbour porpoise (*Phocoena phocoena)*	± 4500	15	0.33%
Killer whale (*Orcinus orca)*	21	2	9.52%
White-beaked dolphin (*Lagenorhynchus albirostris)*	-	1	-
Unidentified	189	5	2.65%
Total	± 5500	32	0.58%

used to recognize pathologies. All deformed bones were representatively photographed using a digital photo camera. For each bone, the characteristics, species name, and object number were noted. As the Vonk collection is still growing, deformed bones added to the collection after 2018 were identified to species level using the cetacean vertebrae identification key from Houwertjes (2020) and with the expertise of Arthur Oosterbaan, Adrie Vonk, and Erwin Kompanje.

Besides the Vonk collection, this study also includes some material from the Ecomare museum on Texel. This museum owns a few complete whale skeletons from locally stranded specimens. While being on display for the public in 2021, these cleaned skeletons of different cetacean species were examined for pathological aberrations. Just as with the Vonk collection, all bones with pathological changes were photographed and characteristics were recorded for further study and elaboration. After a preliminary classification, all pathologies of both collections were revised or identified by Erwin Kompanje on basis of the photographs.

Results

Within the Vonk whale bone collection of approximately 5500 units, we observed 35 whale bones with abnormal conditions (table 1). As follows from spondylodiscitis being the main pathology, vertebrae were the most common deformed bones with 24 units (65%). Furthermore deformations were found in five skulls, two scapulae and two lower jaws. Among the vertebral anomalies, the most frequent occurred in lumbar vertebrae (n=11), followed by caudal (n=5), thoracic (n=4), and unidentified vertebrae fragments (n=4). These osteological pathological changes contained mostly fusion of the vertebrae, presence of osteophytes and syndesmophytes, and/or destruction of the vertebral bodies.

The majority of the deformed bones originated from the harbour porpoise (*Phocoena phocoena)* and counted for 15 units (table 2), followed by the white-beaked dolphin (*Lagenorhynchus albirostris*) with five units, the minke whale (*Balaenoptera acutorostrata)* and the bottlenose dolphin (*Tursiops truncates)* with both four units, and the killer whale (*Orcinus orca)* with three units. Other deformations belonged to one beluga (*Delphinapterus leucas)*, and one unidentified species. When the deformations are put into perspective with the total bone number per species according to the previous findings of Oosterbaan (2018) (table 2), the relatively low percentage of deformed bones in harbour porpoise stands out.

Three deformed vertebrae units were found

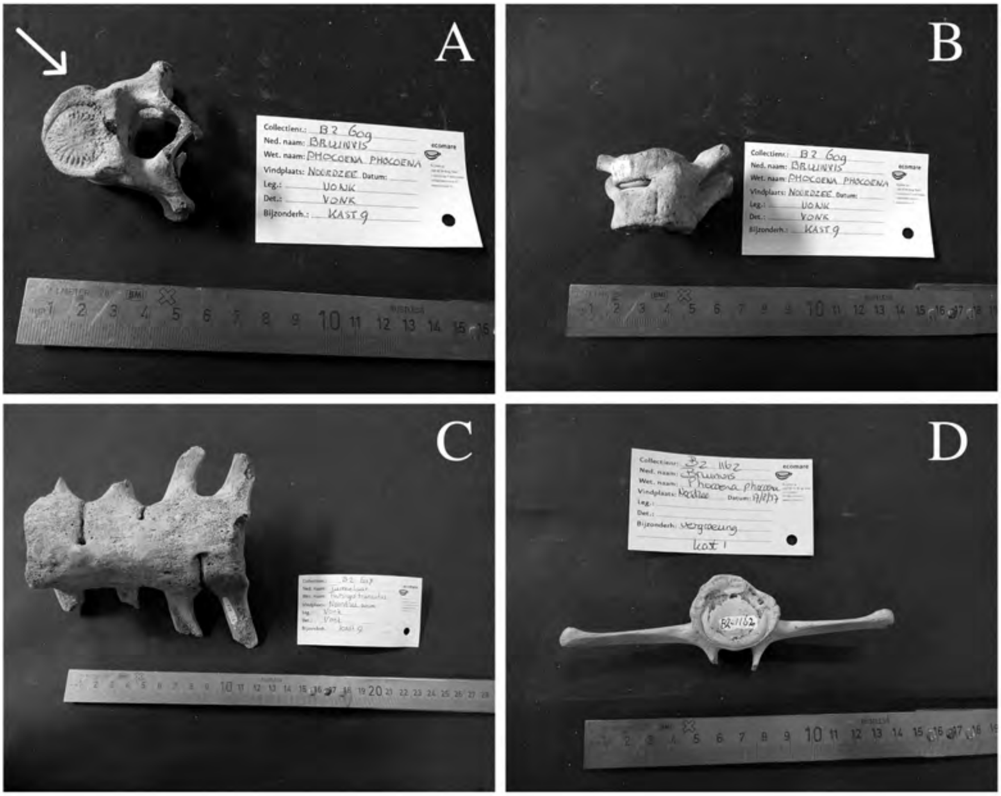

Figure 1. Deformed vertebral units of cetaceans. A: *Phocoena phocoena* (B2-0609), anterior view of two partly fused thoracic vertebrae. The arrow indicates the presence of marginal osteophytes. B: *Phocoena phocoena* (B2-0609), ventral view of two partly fused thoracic vertebrae with a syndesmophyte. C: *Tursiops truncatus* (B2-0617), ventral view of four partly fused thoracic vertebrae by new bone formation. D: *Phocoena phocoena* (B2-1162), posterior view of a lumbar vertebra, showing the growth of marginal osteophytes and pathological perforations of the intervertebral disc. *Photos: Maja Raemakers.*

with unfused growth plates (figure 1). Traditionally the extent of fusion of growth plates has been used as a coarse measure for age and specimens with unfused growth plates were commonly designated as juveniles. However, although this fusion is of course age related, the variation in timing of the process appears large and therefore does not enable a certain determination of life stage (Galatius & Kinze 2003). Figures 1A (anterior view) and 1B (ventral view) show a fusion of two thoracic vertebrae of a harbour porpoise (B2-0609). Furthermore, osteophytes on the margin of the vertebral body and the formation of a syndesmophyte have been observed. Figure 1C shows a fusion of four thoracic vertebrae of a bottlenose dolphin (B2-0617). These fused vertebrae have been developed through smooth new bone formation, which is not a typical sign of osteomyelitis. The last figure, 1D, shows a single lumbar vertebra originated from a harbour porpoise (B2-1162) with irregular thick osteophytes on the margins and an eroded/destructed vertebral endplate. These marginal osteophytes, and thereby the destruction of the vertebral body in immature cetaceans, are the results of an infection. The cavities, or so-called cloacae, found on the vertebral endplate are most likely caused by bacterial infection followed by the forma-

Figure 2. Deformed crania of *Lagenorhynchus albirostris* (B2-0259). Arrows indicate the cloacae. *Photo: Maja Raemakers.*

tion of pus. Therefore, it is likely that this harbour porpoise (B2-1162) suffered from a bacterial infection. This bacterial infection could be originated by penetrating a wound, and spreading from the urinary tract or by bacteremia, which are viable bacteria present in the bloodstream (Félix et al. 2007).

In the Vonk whale bone collection, five skulls originated from two minke whales, one white-beaked dolphin, one killer whale, and one unidentified skull fragment, which probably originates from a long-finned pilot whale (*Globicephala melas).* The skulls from a white-beaked dolphin and an unidentified cetacean showed deformations. However, due to the severe weathering features on these two crania it was difficult to identify the pathological cause. Although a few cloacae on the cranium of the white-beaked dolphin (B2-0259, figure 2) may have been the result of a bacterial infection, yet the very atypical location of these cloacae made it more plausible to diagnose these as pseudopathology.

Each of the other three skulls showed two remarkable holes on the posterior side right above the foramen occipital magnum, which consists of an oval or circular opening and passes through the spinal cord. In addition, two more skulls, originated from minke whales, with two similar holes on the back of the crania were found in the museum collection of Ecomare. This made a total of five cetacean skulls showing two additional holes around the same place on the skull. It seemed very plausible that these holes were located on fragile parts of the skull resulting in an increased chance of fracturing during the weathering process on the bottom of the seafloor. Although this phenomenon can be diagnosed as a pseudopathology, it is remarkable we found five nearly identical examples of this deformation. Because of the multiple occurrences, we used to call it the 'smiley phenomenon', since it resembles a little face (figure 3).

Figure 3. “Smiley” skulls of *Orcinus orca* (A) and *Balaenoptera acutorostrata* (B), posterior view. *Photos: Maja Raemakers.*

Figure 4. Deformed scapulae B2-1469 (A) and B2-1321 (B): osteolysis, resulting in complete loss of bone. *Photos: Maja Raemakers.*

Two deformed scapulae (figure 4) were also found. These scapulae were labelled as belonging to bottlenose dolphins (respectively B2-1469 & B2-1321), but after comparison with an intact skeleton, the latter one, B2-1321, was reidentified as a white-beaked dolphin. Both scapular blades showed deformations, however, only the fracture in object B2-1321 is diagnosed with a pathological cause due to the presence of several cloacae (figure 4B). It seems very plausible that this deformed scapula is the result of a bacterial infection. On the other hand, the fracture on the scapula with object number B2-1469 can be diagnosed as a post-mortem disintegration. Two deformed mandibles were identified as a white-beaked dolphin (B2-0634) and a bottlenose dolphin (B2-0618). The lower jaw of the white-beaked dolphin (figure 5A) showed an inner lesion at the top, possibly caused by a bacterial infec-

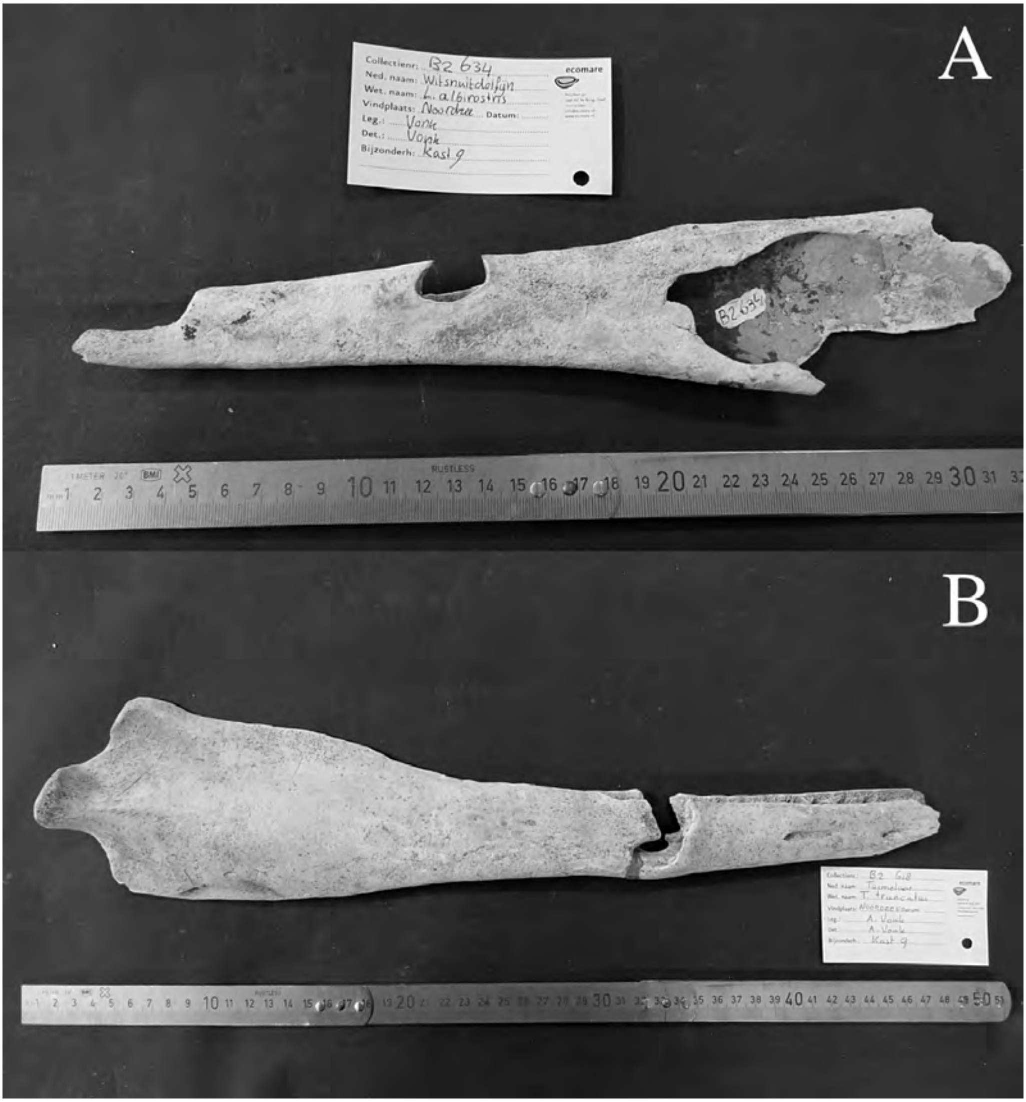

Figure 5. Deformed mandibles caused by a bacterial infection in the dental alveoli. A: white-beaked dolphin (B2-0634). B: common bottlenose dolphin (B2-0618). *Photos: Maja Raemakers.*

tion in the dental alveoli. Figure 5B shows a lesion in the mandible of the bottlenose dolphin, which almost reaches to the bottom of the mandible as a result of an infection. Note that the dark line at the bottom of the lesion is glued since the mandible has been broken during the identification process. Both mandibles were missing the tip, which is probably again no pathological cause, but is related with post-mortem disintegration.

In the collection of Ecomare, five other osteological deformations have been found. Of the cleaned skeletons, the specimens of one white-beaked dolphin and one killer whale showed both several skeletal abnormalities.

In the white-beaked dolphin skeleton, a congenital pathological change in the ribcage was observed (figure 6). Its sternum was asymmetrical and the proximal ends of two sternal ribs were fused leading to one attach-

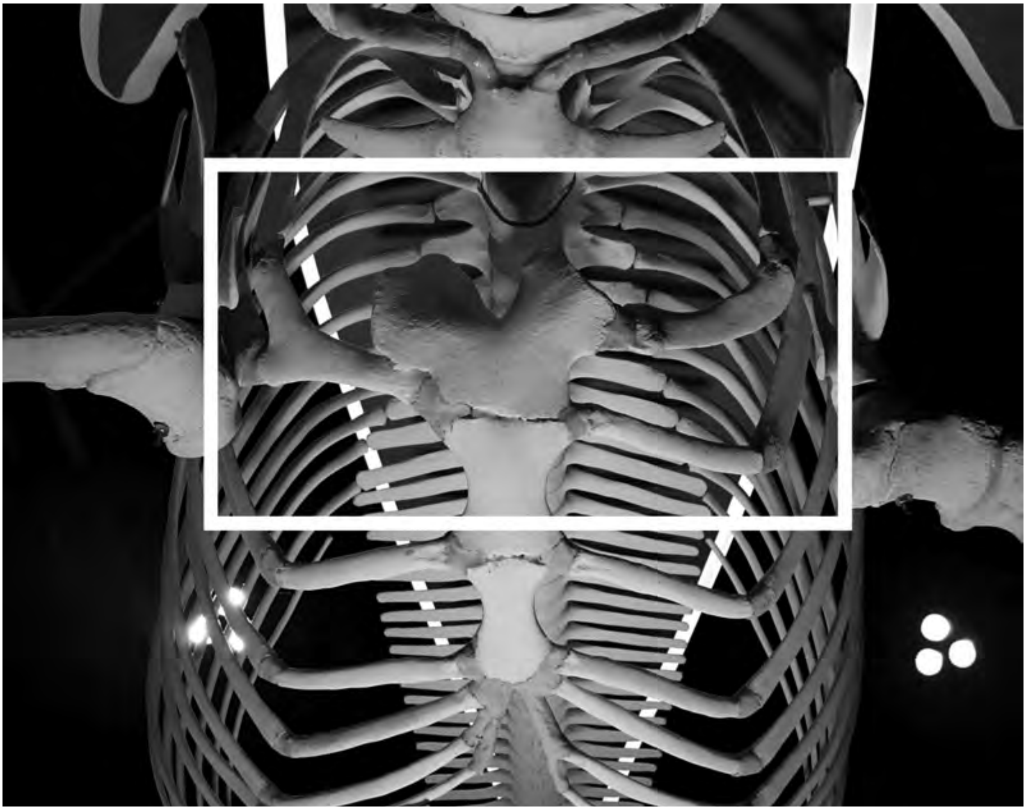

Figure 6. A skeleton of a white-beaked dolphin, *Lagenorhynchus albirostris*, stranded in 1996 on Texel with malformations of sternal ribs. The box indicates the pathological change in the upper part of the ribcage area: an asymmetric sternum and on the left side a fusion of the first and second sternal ribs. *Photo: Maja Raemakers.*

ments site on the sternum.

The killer whale showed a severe lesion in the fourth and fifth caudal vertebrae, which is caused by spondylodiscitis (figure 7A). The ankylosing spondylitis resulted in total loss of movement between these vertebrae. Furthermore, a congenital anomaly was found in the attachment of the last sternal rib on the sternum on the right side of the skeleton (figure 7B).

Discussion and conclusions

The goal of this research was to document the pathological observations that could be found in the whale bone collections of Vonk and Ecomare. A total of 37 osteological deformations were observed in the Vonk and Ecomare whale bone collections. The majority of the deformed bones originated from the harbour porpoise, which is in accordance with previous research on the Vonk whale bone collection (Oosterbaan 2018, 2020). As mentioned by Camphuysen & Peet (2006), the harbour porpoise is by far the most common cetacean species in the (Dutch part of) North Sea, which may explain its high occurrence in the Vonk collection. Moreover, spondylodiscitis occurred quite often in this study, especially in *P. phocoena* individuals, which can be explained by the aforementioned reason. Furthermore, vertebrae represent the majority of deformed bones in this investigation. A properly functioning spine is vital for the survival of cetaceans as the spine is crucial for loco-

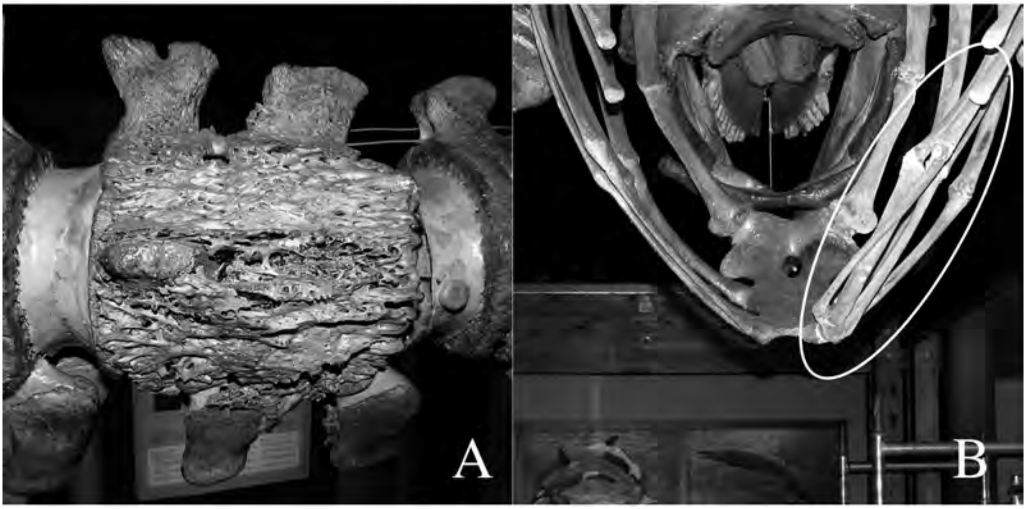

Figure 7. A killer whale (*Orcinus orca*) in the museum collection of Ecomare. A: a severe ankylosis between the two caudal vertebrae. The bizarre and extreme appearance indicates a spondylodiscitis. B: a congenital anomaly. The oval shape indicates the abnormality in the attachment of the last sternal rib on the sternum. *Photos: Maja Raemakers.*

motion (Cozzi 2009). Damage or fusion of vertebrae in particular can lead to a decrease in mobility in the spine. The eventual effect of this on vitality depends on the part of the spine affected and the severity of the damage. But it is clear that normal unobstructed locomotion is crucial for foraging and catching food, reaching the water surface for breathing, as well as for mating behaviour and avoiding danger. With regard to the latter, it is also important to mention that a damaged spine can also lead to a reduction in both manoeuvrability and tail mobility. Both these movement mechanisms are important in defence against predators, like larger sharks and, in the case of smaller species, other cetaceans, especially killer whales (Félix et al. 2007). Therefore, severe deformed bones are likely to lead to premature death of the animal, but the effect of limited osteological deformations is less clear. Probably many cetaceans will experience little hindrance of small lesions, but as lesions often indicate a chronical disease, with for instance the occurrence of bacterial sepsis, they can result in a lower fitness and higher predation risk as well. The deformations found in the Vonk and Ecomare collections are mainly small and can be assigned to the slight hinderance category. Interestingly, the percentage of deformed bones is remarkably lower in harbour porpoise than in the other species. Harbour porpoise is by far the most common and abundant cetacean in the North Sea, while it is rather unattractive to other cetaceans due to its shallowness. Therefore it might be hypothesized that less fit individuals of these other cetaceans (e.g. by illness or bone deformations) are more likely to turn up in the north sea, as more vital specimens prefer other sites. However, it should be noted that harbour porpoise has a low life expectancy (8-10 years) (Galatius & Kinze, 2003), which potentially could mean less time is available for the formation of obvious bone pathologies. It is not possible to estimate whether there is any relationship with the age or the developmental stage of the animal. Furthermore, it is unknown if these pathological aberrations have led to premature death.

Unfortunately it proved hardly possible to elaborate on the results due to usage of fished up separate bones instead of analysing the whole cetacean skeleton. This major diagnostic deficiency is an inherent characteristic of this method. The results are therefore a mere conservative estimate of the type of osteological pathology, since the condition of the entire animal is unknown. This leads to an absence of important information about the life history of the individual cetacean. Furthermore, the occurrence of pseudopathologies has been observed several times due to weathering and corroding. The weathering process on the seafloor results in the disappearance of characteristic features of certain osteological anomalies. This can make it difficult to indicate the type of pathological deformation and its accompanying inducement. Moreover, there are some uncertainties in the identifications of the species name and the type of bone, especially with the vertebrae series.

Besides that, there could be a bias in the Vonk whale bone collection since the size of the bones determines the chance of slipping through the fishing nets and the decision of fishermen if the bones are worth to collect. This can lead to a higher presence of certain bone types. As a result, it is not possible to determine with certainty the influence of deformities in the skeleton on the general health of cetaceans in the North Sea with the observations in the Vonk and Ecomare whale bone collections. A extrapolation to population effects of cetaceans in the North Sea is similarly impossible with these data. In conclusion, using whale bone collection for scientific analyses gives strongly limited information due to absence of the whole skeleton, weathering and corroding processes and a bias in the type of bones. Despite these drawbacks, the observations made in this study give an insight in the occurrence of osteological pathologies and their potential consequences for cetaceans in the North Sea. Without the impressive collecting effort of Adrie Vonk, this would not have been possible.

Acknowledgements: The authors wish to thank Adrie & Ineke Vonk for allowing access to the whale bone collections, Daphna Lavy (Ecomare) for the hospitality, Erwin Kompanje (Natuurhistorisch Museum Rotterdam and ErasmusMC) for helping with diagnosing the deformed bones. The first author would like to thank Jelle Reumer for the guidance during her bachelor thesis. We also appreciate the comments of the anonymous reviewers which greatly improved this paper.

References

Barnes, L.G. 1984. Whales, dolphins and porpoises: Origin and evolution of the Cetacea. Notes for a short course. Studies in Geology 8: 139–154.

Camphuysen, K. & J.G. Peet 2006. Walvissen en dolfijnen in de Noordzee. Fontaine Uitgevers B.V., Amsterdam, the Netherlands

Cozzi, B., S. Mazzariol, M. Podestá & A. Zotti 2009. Diving adaptations of the cetacean skeleton. The Open Zoology Journal 2 (1): 24-36.

Félix, F., B. Haase & W. Aguirre 2007. Spondylitis in a humpback whale (*Megaptera novaeangliae*) from the southeast Pacific. Diseases of Aquatic Organisms 75: 259–264.

Francois, R.J., F. Eulderink & E.G. Bywaters 1995. Commented glossary for rheumatic spinal diseases, based on pathology. Annals of the Rheumatic Diseases 54 (8): 615–625.

Galatius, A. & C.C. Kinze (2003). Ankylosis patterns in the postcranial skeleton and hyoid bones of the harbour porpoise (*Phocoena phocoena*) in the Baltic and North Sea. Canadian Journal of Zoology 81 (11): 1851–1861.

Groch, K., M. Marcondes, A. Colosio & J. Catão-Dias 2012. Skeletal abnormalities in humpback whales *Megaptera novaeangliae* stranded in the Brazilian breeding ground. Diseases of Aquatic Organisms 101 (2): 145–158.

Houwertjes, M. 2020. Determinatiesleutel voor wervels van walvisachtigen uit de Noordzee. Cranium 37 (2): 34–57.

Kompanje, E.J.O. 1995a. On the occurrence of spondylosis deformans in white-beaked dolphins *Lagenorhynchus albirostris* (Gray, 1846) stranded on the Dutch coast. Zoologische Mededelingen Leiden 69: 231–250.

Kompanje, E.J.O. 1995b. Differences between spon-

dylo-osteomyelitis and spondylosis deformans based on museum material. Aquatic Mammals 21: 199–203.
Kompanje, E.J.O. 1996. Intervertebral disc degeneration and discarthrosis in white-beaked dolphins (*Lagenorghynchus albirostris*). European Association of Zoo- and Wildlife Veterinarians (EAZWV): 21–25.
Kompanje, E.J.O. 1999. Considerations of the comparative pathology of the vertebrae in Mysticeti and Odontoceti: Evidence for the occurrence of discarthrosis, zygarthrosis, infectious spondylitis and spondyloarthritis. Zoologische Mededelingen Leiden 73: 99–130.
Nathan, H. 1962. Osteophytes of the vertebral column. An anatomical study of their development according to age, race, and sex with considerations as to their etiology and significance. Journal of bone Joint Surgery 44 (2): 243-268.
Oosterbaan, A. 2018. De walvisbottencollectie Vonk: nieuwe gegevens over het voorkomen van walvisachtigen in de Noordzee. Cranium 35 (2): 43-45.
Oosterbaan, A. 2020. Verdere analyse van de walvisbottencollectie Vonk. Cranium 37 (2): 58-66.
San Martín, A., S. Macnie, R. Goodall & C. Boy 2016. Pathology in skeletons of Peale's dolphin *Lagenorhynchus australis* from southern South America. Diseases of Aquatic Organisms 120 (1): 9–15.
Van Bressem, M.F., J.C. Reyes, F. Félix, M. Echegaray, S. Siciliano, A.P. Di Beneditto, L. Flach, F. Viddi, I.C. Avila, J.C. Herrera, I.C. Tobón, J. Bolaños-Jiménez, I.B. Moreno, P.H. Ott, G.P. Sanino, E. Castineira, D. Montes, E. Crespo, P.A.C. Flores, B. Haase, S.M.F. Mendonça de Souza, M. Laeta & A.B. Fragoso 2007. A preliminary overview of skin and skeletal diseases and traumata in small cetaceans from South American waters. Latin American Journal of Aquatic Mammals 6 (1): 1-14.

Samenvatting

Afwijkingen bij walvisbotten uit de zuidelijke Noordzee

Afwijkende botten worden wel vaker gezien bij walvisskeletten, maar in sommige gevallen lijkt er meer aan de hand te zijn. Zo bevinden zich in de walvisbottencollectie Vonk op Texel botten die vreemde uitstulpingen hebben of aan elkaar vastgegroeid zijn. Om de bottencollectie Vonk verder te analyseren, heeft dit onderzoek zich gericht op het voorkomen van misvormde walvisbotten. Het doel van dit onderzoek was om de afwijkende observaties te documenteren en de bijbehorende mogelijke pathologieën te bepalen. In totaal werden 37 vervormde walvisbotten gevonden, waarvan de meerderheid afkomstig is van de bruinvis (*Phocoena phocoena*; n=15). Het overgrote deel van de gevonden aandoeningen heeft een infectieuze oorzaak. Daarnaast representeren de wervels de meerderheid van de misvormde botten (n=24), waarbij spondylodiscitis het vaakst is geïdentificeerd. Dit is een aandoening waarbij de wervelschijf is aangetast als gevolg van een bacteriële infectie. Verder werden zeven schedels, twee schouderbladen en twee onderkaken gevonden met pathologische kenmerken. Hiervan werden de meeste vervormingen geïdentificeerd als pseudopathologie, waarbij de afwijkingen op het bot zijn ontstaan na de dood van het dier door verwering. Bij de schedels werd een ander opmerkelijk verschijnsel herhaaldelijk waargenomen. Aan de achterzijde, net boven de foramen occipitale magnum, werden twee extra gaten gevonden in de schedel. Het resulterende beeld was zo typisch dat we dit het 'smiley-fenomeen' genoemd hebben. Botaantastingen kunnen van grote invloed zijn op de overlevingskansen van de betreffende dieren. Met name een goed functionerende ruggengraat is van groot belang voor het overleven van walvisachtigen. Ernstige botvergroeiingen leiden daardoor hoogstwaarschijnlijk tot (vroegtijdige) sterfte. Bij beperkte vergroeiingen zullen de meeste walvisachtigen weinig hinder ondervinden, maar omdat het vaak om een chronische infectie gaat, kunnen bijkomende effecten, zoals bijvoorbeeld bacteriële sepsis, de overlevingskansen toch sterk reduceren. De aangetroffen vergroeiingen in de

collecties Vonk en Ecomare zijn over het algemeen minder ernstig en vallen daardoor in de beperkt hinderlijke categorie. Bij de beschreven resultaten moet er natuurlijk rekening mee worden gehouden dat onderzoek naar botafwijkingen in de walvisbottencollecties Vonk en Ecomare behoorlijke beperkingen heeft. Het gebruik maken van afzonderlijke opgeviste skeletdelen in plaats van het analyseren van het complete dier leidt tot verlies van veel waardevolle informatie. De resultaten geven dan ook slechts een grove schatting over het type botaandoening en de mogelijke bijbehorende oorzaak. Het heeft echter wel geleid tot een beeld van de botvervormingen die kunnen optreden bij walvisachtigen en de potentiële gevolgen ervan.

Received: 15 March 2022
Accepted: 12 December 2022

High prevalence of head and neck lesions in stranded seals: cause of death?

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Abstract: In 2021 Belgian beaches witnessed 101 deceased, washed ashore seals. This number is extremely high compared to the one in previous decades, with figures never exceeding 50. Of these animals, 21 grey seals (*Halichoerus grypus*), 13 harbour seals (*Phoca vitulina*) and 2 unidentified seals were collected for necropsy, and photographs were available for an additional 49 seals. Of the 90 animals that were necropsied or for which information was available, such as clear photographs, 58 (64%) presented severe head and neck lesions, which in 27 cases we described as a circular lesion around the neck, known in forensic medicine as ligature marks. Most of the animals with circular neck lesions were juveniles. We suspected that bycatch was the most probable cause of death in these 27 cases, though the characteristic lesions often seemed to have occurred post-mortem. Due to the nature of the lesions, we could exclude other possible backgrounds such as knife cuts or predation marks left by grey seals. We hypothesize that the animals were caught in nets and died due to asphyxia, while the hauling of the net caused the typical lesions. Some seals, however, survived: three live seals with similar neck lesions were found, still bearing parts of a nylon monofilament fishing net. The observations warrant a further investigation of the phenomenon, including of the system of bycatch, the spatial and temporal extent, the number of seals bycaught and the type of fishing vessel involved.

Keywords: *Phoca vitulina*, *Halichoerus grypus*, mortality, ligature marks, bycatch, Belgium.

Introduction

During the last decades, along with growing populations of seals in the southern North Sea (SCOS 2021, ICES 2022), there has been an increase of strandings of deceased seals at the Belgian coast, including both grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*). The number of seals rose steadily from less than ten per year in the 1990s and the first years of the 21[st] century to almost 50 in 2019 and 2020 (data RBINS). In 2021, however, a much higher than average number of seals washed ashore: 101 (figure 1). The high stranding rate, including many cases bearing strikingly similar lesions around the head and neck, prompted an exploratory investigation into the reasons for these deaths. This was fuelled by public outcry and wild speculation in social media about the origin of the ‘decapitations’ observed in many of the animals. We describe the strandings, assess the nature of the lesions observed and investigate possible causes of death.

Material and methods

The Belgian coast is short (67 km), easily accessible and the beaches are often crowded. There is a well-developed strandings network, and data on all marine mammal strandings are kept in a database managed by the Royal

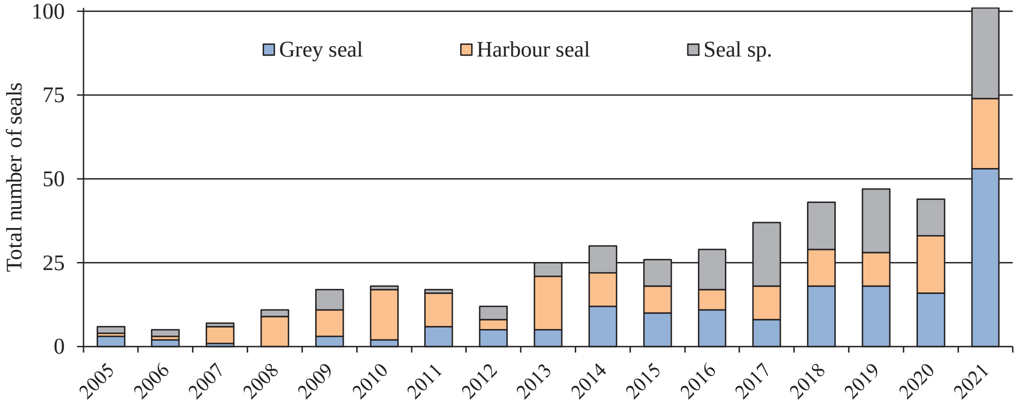


Figure 1. Total number of dead seals washed ashore in Belgium between 2005 and 2021.

Belgian Institute of Natural Sciences (RBINS). We are confident that nearly all stranded seals are registered and collected within an hour of reporting. Usually, the local fire brigade or communal technical services are the first responders. They, and/or the public, provide the RBINS with pictures of the animal, useful in case assessment as they provide information on species, lesions, sex and size/age. Based on species, size and state of decomposition, RBINS decides if the animal is useful for a further examination, with the latter as the decisive selection criterion. Carcasses in an advanced state of decomposition are sent to a destruction facility. Carcasses selected for necropsy are temporarily stored in a freezer (-20°C) prior to transport to the University of Liège (ULg) or the University of Ghent. The main objective of the necropsy is to determine the cause of death. Additionally, as part of long-term monitoring, information is collected about life history parameters, health prior to death, diet, the prevalence of parasites and disease agents, and levels of contaminants in tissues. A standardized protocol for marine mammal necropsy is used (Kuiken & Garcia-Hartmann 1991, Jauniaux et al. 2002, IJsseldijk et al. 2019). Four decomposition codes (DCC) are used here: DCC 1 live animal; DCC 2 freshly dead animal, intact carcass and no rotten smell; DCC 3 moderate autolysis, with organs still intact, moderate swelling due to gas, skin sloughing and discernible smell of decomposition and DCC 4 advanced decomposition, with major bloating, skin peeling, and organs beyond recognition.

Live stranded juvenile seals in difficulty (diseased, injured) are taken to a specialised rehabilitation facility (Sealife at Blankenberge) and released back into the wild after treatment. Adult animals in difficulty are usually left on the spot without further action, unless it concerns animals that can be assisted immediately, such as through disentanglement.

An identification to species level was not always an easy task, given the state of decomposition and in many cases the partial or complete absence of the head. Seal carcasses for which doubt existed, were tentatively identified based on the size of the animals vs. the date of stranding (period of pupping of grey vs. harbour seals), their girth/size and pelage, including remains of typical white fur indicating grey seal pups. Some animals remained unidentified; for these, no attempts were made to assess the species through e.g. a genetic analysis.

Results

Stranding records

In 2021, a total of 101 dead or dying seals

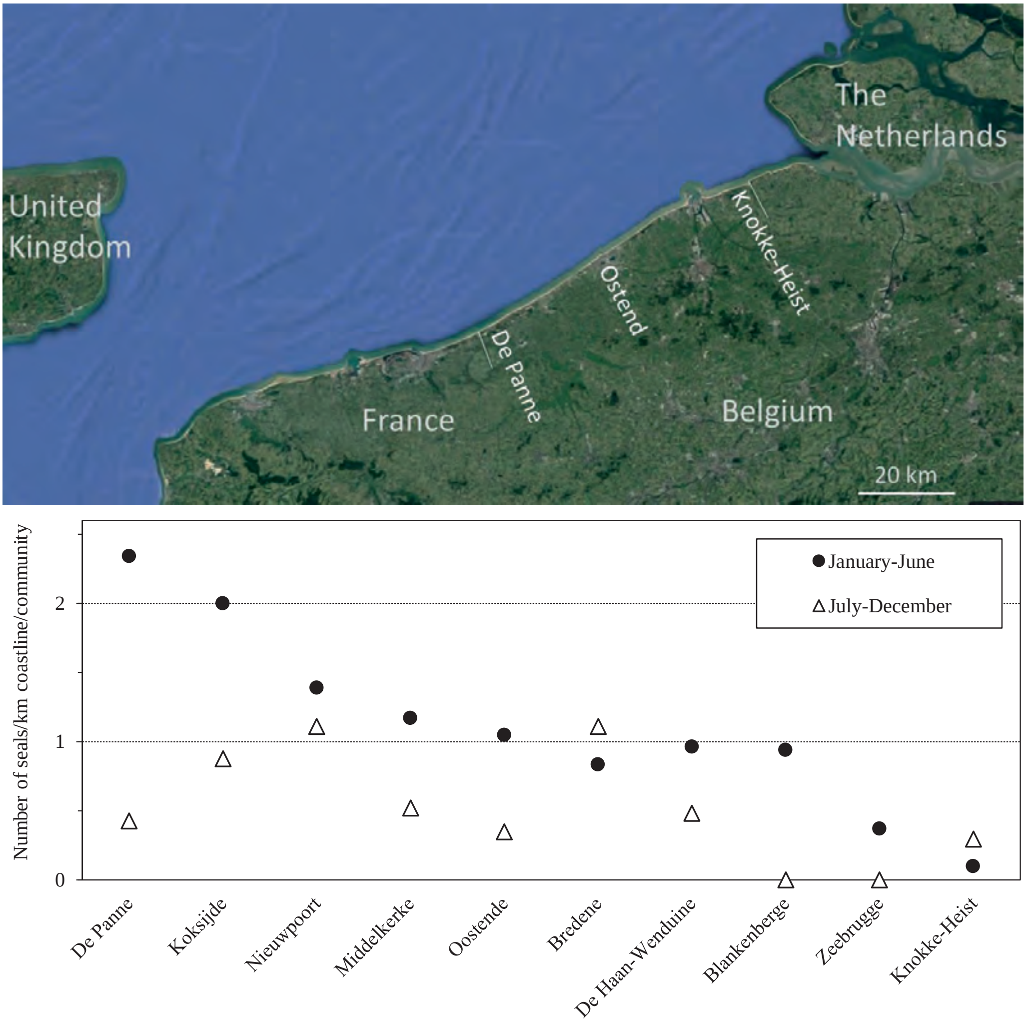


Figure 2. Location of (a selection of) coastal communities along the Belgian coast (top) and number of seals washed ashore per km coastline per coastal community, arranged on the x-axis from west to east.

washed ashore at the Belgian coast. This figure is more than twice as high as the highest number recorded during the last decades (figure 1). Next to this, Sealife took care of eight grey seals and ten harbour seals. Most of these were orphaned, injured or diseased, and only those cases relevant here are discussed further.

In total, 52 grey seals, 22 harbour seals and 27 unidentified seals were recorded dead ashore in 2021. The majority of the seals identified as grey seals were assessed as juveniles (74%), most of them in their first year of life, thus probably born in November or December 2020. A slightly higher percentage of the seals identified as harbour seals were juveniles (86%), born in the summer of 2020 or 2021. Out of the 97 animals we could classify for decomposition, 54 were relatively fresh (DCC 2-3; 30 grey seals, 16 harbour seals and 8 seal sp.) while 43 were very decomposed (DCC 4; 22 grey seals, 6 harbour seals and 15 seal sp.).

Most dead seals (69 animals; 68% of the total number of seals washed ashore in 2021) were found in the first six months of 2021,

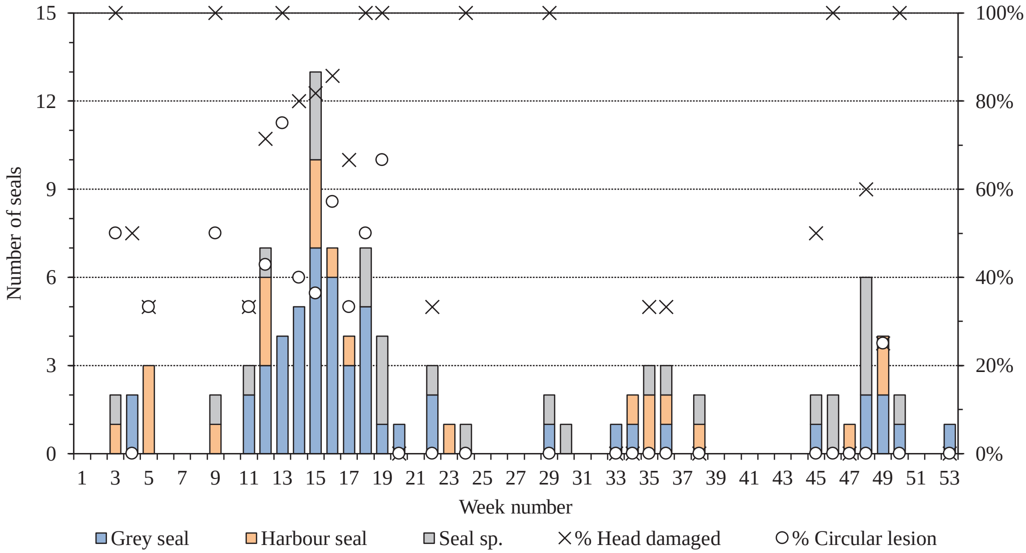


Figure 3. Number of seals per species washed ashore in 2021 (left axis), percentage of seals with damaged head (right axis, X) and percentage of seals with typical circular lesion around head or neck (right axis, ○).

with 50 of these (72% of the total number) found at the western half of the Belgian coast, between Oostende and De Panne, closest to the French border (figure 2). Moreover, strandings showed a distinct peak between week 11 and 19 (10 March to 7 May; 54 animals; figure 3).

We collected 21 grey seals (4 adults, 1 subadult and 16 juveniles), 13 harbour seals (3 adults and 10 juveniles) and 2 unidentified seals (1 adult and 1 juvenile) for necropsy. Additionally, photographs were available for 49 out of 65 animals that were discarded, and a description was provided for five additional animals. This allowed in many cases for identification, estimation of size and a basic assessment of lesions and decomposition (table 1).

External lesions

We were able to collect information on external lesions for 90 animals (89% of the stranded seals), based on the necropsy, photographs, a brief examination on the beach, or an oral description made by members of the public or the fire brigade. Of these, 58 animals (64 %; 31 grey seals, 11 harbour seals and 16 unidentified seals) had lesions to the head, ranging from small wounds to the head completely missing. In 27 of the animals (17 grey seals, 8 harbour seals and 2 unidentified seals) the lesion around the neck was remarkably circular (table 1; figure 4). For 18 additional seals (5 grey seals, 3 harbour seals and 10 unidentified seals) presenting a head trauma, a clearly circular lesion could not be verified due to decomposition or scavenging.

Ten grey seals, four harbour seals and one unidentified seal with the characteristic circular neck lesion were investigated more closely by scientists of RBINS and a veterinarian of the ULg, assisted by a forensic pathologist. The following observations were recorded for these animals:

- There were large skin and soft tissue lesions in the neck up to the skull, with no evidence of knife cuts: the injury could be described as a laceration, exposing fatty tissue in layers, and with no hairs cut. In an experiment trying to mimic the lesions using a sharp blade, hairs were cut. In some animals the

Table 1. Overview of seals that were included in this study and (in brackets) the number of seals presenting a circular lesion around the neck.

Species	Collected for necropsy	Photographs available and/or examination on the beach	No further investigation
Grey seal	21 (10)	31 (7)	0
Harbour seal	13 (4)	8 (4)	1
Seal sp.	2 (1)	15 (1)	10

Figure 4. Moderately decomposed seals identified as grey seals with characteristic circular head/neck injuries. Left: Ostend, 6 April 2021. Middle: Oostduinkerke, 20 March 2021. Right: Lombardsijde, 12 April 2021. Images provided by the communal fire brigades.

lesion could be described as a scalpation, exposing the upper part of the cranium. A striking feature was the almost perfectly circular neck lesion. In most animals the skull was partly present, with the lower jaw and part of the upper jaw missing.

- The body of the seals was mostly intact, with no evidence of fractures or amputations, though in relatively heavily decomposed animals sometimes skin from front and/or hind flippers was missing.
- In relatively fresh animals, the lesions seemed post-mortem, lacking haemorrhages in the exposed fatty tissue. The lungs were congested, with oedema and emphysema, and there was abundant haemorrhagic froth in the airways, indicating asphyxia.
- In general, the necropsied seals with these extensive head lesions were well-nourished. For example, seals of approximately 1 m had a dorsal blubber thickness of 20-30 mm. Due to decomposition (with only 4 out of 15 animals assessed as in DCC 2) other aspects, such as signs of disease, were not investigated.
- In one case, part of a fishing net consisting of monofilament twine was found buried deep into the neck lesion.

For the animals without a circular neck lesion, we add the following observations and conclusions for completeness:

- One juvenile grey seal was torn apart; it showed loose skin and tissue flaps, similar lesions as caused by attacks of a grey seal (see discussion).
- Three grey seals and five harbour seals had died due to other natural causes (age, disease, starvation).
- One juvenile grey seal probably died due to an attack of a dog on the beach.

Figure 5. Live stranded seals showing an extensive ligature mark caused by nylon monofilament twine (ligature) from a fishing net. Left: grey seal, De Panne, 11 April 2021. Right: harbour seal, Ostend, 23 April 2021. Images provided by Sealife.

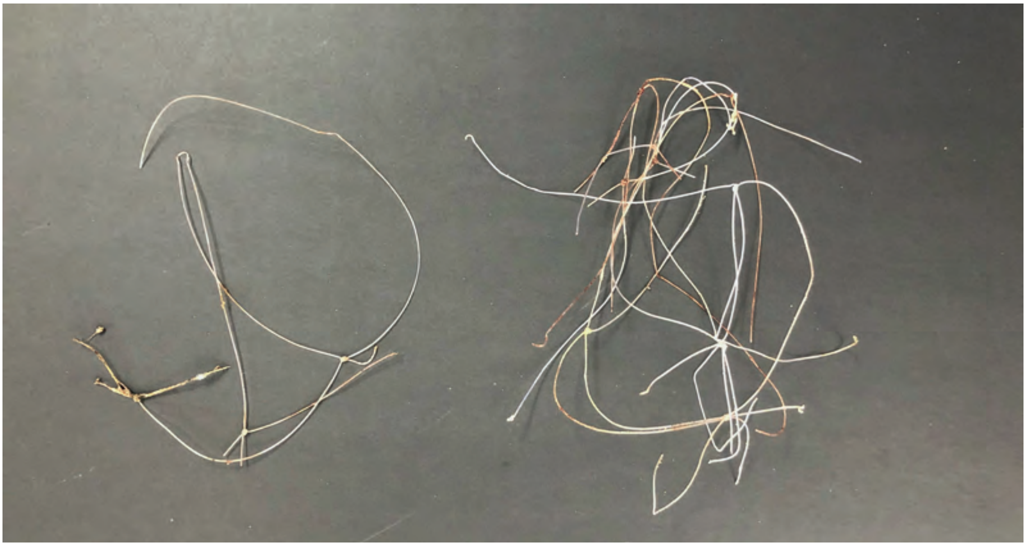


Figure 6. Part of the nylon net (ligature) removed from the neck of a live grey seal (7 April 2021; left) and a live harbour seal (23 April 2021; right); given the many cuts to the twine, it was not possible to measure mesh sizes. *Photo: RBINS.*

- For seven grey seals and four harbour seals not showing typical circular neck lesions, bycatch was suspected as the cause of death, with direct evidence (discovery within a fishing net) or indirect evidence such as lung congestion, the absence of disease agents, a full stomach and a general good body condition.
- In 13 cases (seven grey seals, two harbour seals and four unidentified seals), traces of

scavengers were found. They consisted of fresh lesions to the head and sometimes body (open abdomen), probable fox footprints around the carcass and traces of blood in the sand around the carcass. In two of the cases (juvenile grey seals that were found in dune areas), it cannot be excluded that they were actually killed by foxes. Traces of scavengers on the sand can easily be wiped away by wind, rain or incoming tides, and they were not always recorded prior to removal from the beach. Scavenging by seabirds could have occurred on the beach and at sea.

Strandings of live seals

During 2021, three live juvenile seals showing lesions similar to those observed in dead seals were found on the beach. Their age was estimated based on their size. They were gravely injured by a part of a monofilament fishing net, still around their neck and cutting deep into their tissues, exposing raw flesh (figures 5-6). The location of the injury was similar to the one in the deceased seals showing the circular neck lesion described above.

- Case 1. Juvenile grey seal, born in winter 2020-2021 (approximately 4 months old), stranded on 7 April 2021 at Koksijde. The animal showed a severe injury encircling its neck, caused by a piece of nylon monofilament fishing net; the net was removed on the beach.
- Case 2. Juvenile grey seal, born in winter 2020-2021 (approximately four months old), stranded on 11 April at De Panne. The animal showed a severe injury encircling its neck, caused by a piece of nylon monofilament fishing net. The net was removed and collected. The wound was 15 mm deep and 6 cm wide in the chin region and 3 cm wide in the neck region.
- Case 3. Juvenile harbour seal, born during the pupping season in summer 2020 (approximately ten months old), stranded on 23 April 2021 at Oostende. It suffered a similar lesion as in the two previous cases, with a severe injury encircling its neck caused by a piece of nylon monofilament fishing net.

All three animals were admitted to the rehabilitation facility at Sealife Blankenberge where their neck injuries were treated (which included stitching). After rehabilitation they were released into the wild.

Discussion

Assessment of the external lesions

Given the speculation about the seal deaths, we discuss different options for the origin of the typically circular lesions and their probability.

1. Incidental catch

We have good evidence of the cause of death in one dead animal. It had part of a monofilament net around its neck, buried deep within the neck tissue, so we suspect that it died directly or indirectly due to bycatch. However, given the very similar nature of the lesions in 26 other cases (animals necropsied or lesions clearly visible in photographs), and the nature of the lesions in the three live seals with the remains of fishing gear still around their necks, we suspect that circular head/neck lesions are a result of entanglement in fishing nets.

Typical circular neck lesions are well-known in forensic literature as ligature marks (Di Maio et al. 2001). They are caused by a piece of cord, string, nylon netting or similar material that has been used for strangulation or hanging. If the ligature is a hard and fine material, the groove is usually recognizable and clear, and deep, with well delineated margins (Di Maio et al. 2001), as was the case in many of our animals. In humans, suicide by hanging can even lead to a decapitation, although complete decapitation is very rare (e.g. Törö et al. 2008, Hejna & Bohnert 2013, Leccia et al. 2017). Also in this study we noted a (partial) decapitation of some animals. The

Figure 7. Fresh carcass of an emaciated, juvenile harbour seal suspected of having been scavenged or predated upon by foxes, 29 January 2021. Notice the traces of blood around the head and the irregular wound edges. The scavenging may have concealed primary lesions. Image provided by North Seal team.

crucial factor for the state of decapitation of the body is the kinetic energy, determined by the weight and the squared velocity of the falling body (Törö et al. 2008, Hejna & Bohnert 2013). Here, we hypothesize that this energy is obtained when the net in which a seal was entangled is hauled.

In this study, we could not definitely link the cause of death with the ligature marks. We suspect that the main cause of death was asphyxia due to entanglement, with the ligature causing deep lacerations peri- or post-mortem. To determine the exact cause of death, other, more sophisticated forensic techniques are needed.

2. Predation and scavenging by birds and foxes

Foxes are known to scavenge on grey seal pups and other stranded marine mammals (Haelters et al. 2016, IJsseldijk & Geelhoed 2016, Heers et al. 2017, ICES 2017) and even predate on unattended seal pups (Culloch et al. 2012). Also gulls are known to scavenge on stranded seals, often first damaging the head as this is the easiest way of entry (own observations; ICES 2017). Quaggiotto et al. (2016) investigated scavenging of seal carcasses and noticed that the umbilicus region and the eyes were the first areas to be fed upon. Birds often leave a ragged pattern of wounds corresponding with stabbing with their beaks. Van Neer (2021) described lesions induced by scavenging foxes to be characterized by skin and soft tissue missing on different areas of the body.

Unlike in the cases of scavenging described above, many of the dead seals in 2021 only presented typical lesions to the head area. Also, as the seals in this study were often collected upon stranding, land scavengers would hardly have had the opportunity to scavenge on the carcass. However, in a few cases, scavenging on the beach had clearly occurred, and even predation by foxes cannot be excluded (figure 7). Scavenging can mask traces that could have provided clues about the cause of death in some animals. We conclude however that it is very unlikely that scavenging was at the origin of the circular lesions.

3. Grey seal predation

Grey seals are known to prey on harbour and juvenile grey seals (van Neer et al. 2015, 2021, Bishop et al. 2016, Brownlow et al. 2016). In these cases, lesions were described as severe ‘corkscrew’ lacerations often following a helical course with smooth, linear and cut-like wound margins and the detachment of large parts of skin and underlying tissue extending from the head to the caudal region (Thomson et al. 2015, van Neer 2021). Such wounds were found in only one dead seal in 2021. In all others, the lesions were very different; for instance, skin and underlying tissue was only damaged in the head region, and unlike typical grey seal victims, no skeletal trauma was found.

4. Sharp trauma from anthropogenic origin

There were no amputations or fractures to the body of the seals, making propellor injuries or ship strikes unlikely. Also knife cuts are unlikely, given that the necropsies could not identify cut hairs, and the use of a blade to mimic the lesions did not result in a similar injury.

5. *Decomposition*
We consider that the lesions in 27 animals were too typical to have been the consequence of a random factor such as decomposition after a natural or anthropogenic cause of death.

Conclusion on cause of death

We conclude that the most likely cause of the circular lesions is entanglement and we therefore suggest that the cause of death of the seals was probably related to bycatch. We hypothesize that the ligature marks in 27 seals were most likely sustained post-mortem by the mechanical action of a fishing net. The net, consisting of fine monofilament twine (as observed in one dead and three live seals), would cause lesions on the head and/or neck when a strong force is exerted on it, such as when seals try to escape, or post-mortem during hauling, with additional damage caused by the hauling system (pulley/drum). In juvenile seals with relatively soft cranial bones, the lower and upper jaw would be crushed by a high tension on the twine, and the skin and underlying tissue of the upper skull could be removed, leading to a partial decapitation or a lesion that can be described as a scalpation.

Fine monofilament twine is used in bottom set gill- or trammel net fisheries. The mesh size for bottom set gill and trammel nets should be at least 120 mm, except for directed fishing for European bass (*Dicentrarchus labrax*), whiting (*Merlangius merlangus*) and dab (*Limanda limanda*) (100 mm) or for directed fishing for flatfish (Pleuronectiformes) (90 mm) (EC, 2019). Passive fishery with gill and trammel nets often involves setting many kilometres of net left in place for up to 24 hours.

The most important season for these passive fisheries in the southern North Sea is spring (March to May), when flatfish such as the highly prized Dover sole (*Solea solea*) enters shallower waters to spawn. This period concurs with the spring peak in strandings in 2021. While gill- and trammel net fishing is widely practiced in Belgian and adjacent waters, it is most popular in waters near the eastern Channel and further to the west. This could explain the fact that significantly more seals that are presumed to have died due to bycatch, had washed ashore in the western part of the Belgian coast vs. the eastern part. Though unassessed up to now, seals bearing similar lesions regularly wash ashore in neighbouring countries (social media communications from northern France, southern England and the Netherlands; personal communication Jacky Karpouzopoulos and Jaap van der Hiele; www.waarneming.nl; figure 8). SCOS (2021) assessed bycatch of seals around the UK, with observer schemes recording most cases in ICES area VII (south and south-west of the UK), with fewer seals caught in the eastern Channel and in ICES area IV (North Sea), but it also acknowledged that the eastern Channel and ICES area IVc (southern North Sea) would benefit from a better sampling, giving high fishing effort and a high density of seals.

High number of juvenile seals

It is striking that only relatively small seals that were presumed bycaught, showed typical ligature marks. Reasons for this can be: 1. Larger seals are less vulnerable to bycatch given their experience in the vicinity of nets and their strength to pull out and escape once bycaught. 2. The heads of larger seals do not fit into the maze. 3. Larger bycaught seals will fall out of the net due to their weight before high tension is exerted on the twine near the drum/pulley system. 4. The skull bones of juvenile seals are more fragile. Finally, it is possible that in the area high numbers of dispersing juvenile seals were present. Also SCOS (2021) mentioned that the majority of bycaught seals

Figure 8. Two examples of seals found live stranded in neighbouring countries, and presenting similar lesions. Left: harbour seal, Vlieland, the Netherlands, 4 April 2022. *Photo: Anthony Grymonprez*. Right: grey seal, Cap Blanc Nez, France, 20 March 2016. *Photo: Jacky Karpouzopoulos*.

around the UK were small animals.

A new phenomenon?

Checking strandings data and images of seals stranded in previous years (database of stranded animals kept by the RBINS, including images) yielded a few seals with similar lesions; these had remained mostly uncollected due to their state of decomposition, and their cause of death remained unassessed. However, their number is negligeable compared to the number in 2021.

It seems unlikely that fishing activity, including the type of net deployed, effort and fishing areas, would have changed profoundly in 2021 compared to previous years. A possible background for this striking phenomenon in spring 2021 can be a combination of the following:

1. There were more juvenile grey seals present in the southern North Sea with growing populations and steadily increasing numbers of pups being born in the November – December pupping season, including at colonies on land such as Donna Nook, Blakeney Point and Horsey where seals became habituated to human disturbance. In 2019, more than 10,000 grey seals were born in the colonies in eastern England (ICES 2022).
2. There were more grey seals present in the southern North Sea due to a changed dispersal pattern after weaning; this can be confirmed by more observations than ever before of live grey seals on Belgian beaches in winter 2020/2021 and spring 2021. These seals can be considered as occasional visitors, with only two permanently used haul-out sites in Belgium holding very few seals (Nieuwpoort: maximum 20 harbour seals; Ostend: <5 seals, mixed grey/harbour seals).
3. The southern North Sea experienced continued periods with meteorological conditions favouring strandings in Belgium – an objective assessment of this, using data on wind direction and wind speed, was however not made for this study.

Conclusions

The number of dead seals stranded on Belgian beaches during 2021, especially in the first half of the year, was unprecedented. A large proportion of the animals were juvenile grey seals. Many of the seals (27) presented characteristic ligature marks, of which we hypothesize that they can be attributed to bycatch in gill or trammel nets in the southern North Sea and eastern Channel.

The recovery of seal populations in the southern North Sea leads to conflicts: more seals are incidentally caught in fishing gear (data RBINS 1995-2021). The number of bycaught seals washed ashore is an unknown fraction of the total number of seals caught incidentally but based on the figures from a relatively short stretch of coastline it can be safely assumed that in the southern North Sea and eastern Channel hundreds of juvenile seals were bycaught in spring 2021.

The high level of bycatch in 2021 could in theory be explained by either more intense use of trammel- and/or gillnet fisheries during the first months of the year, but there is no evidence for this. It is more likely that there was a higher influx of especially juvenile grey seals after record-high numbers of pups born in colonies around the southern North Sea, and that additionally, or alternatively, long periods of northerly winds, which characterized late winter and spring 2021, drove carcasses to the Belgian coast. Potentially, different dispersal patterns of young grey seals or other prevailing wind directions in former years might have prevented or obscured this bycatch.

Both harbour and grey seal populations have recovered from near extirpation in the southern part of the North Sea. Given possible effects on the resilience of populations to future threats, animal welfare considerations and commitments and obligations in international fora protecting marine mammals, the suspicion of a high bycatch rate warrants further investigation. In addition, bycatch can also affect fishermen, including through loss of time and damage to gear and catches, but also through public perception of fisheries and the sale of fishery products that require proof of sustainability.

Incidental catches of marine mammals are assessed by the OSPAR Convention, the International Council for the Exploration of the Seas (ICES) and in reports to the European Commission. However, on board observer schemes in which bycatch is assessed are generally in place only in larger vessels, while trammel and gillnets are typically operated from small ships. Given the commitments made, there should be a further investigation of the causes of death of seals washed ashore. In cases of suspected bycatch, the fishery and net type involved, the bycatch mechanism, the location of bycatches, the origin of the animals bycaught (colony) and the effect on populations should be assessed. The evaluation of the number of bycaught seals washed ashore should be extended to cover the coastlines of neighbouring countries, with as an objective to assess mortality covering a larger area. To this end, fishermen should also be encouraged to report and document bycatches. Reverse drift modelling of stranded animals could help elucidating areas with high bycatch rates (Peltier et al. 2013, 2016). This information is essential when assessing bycatch against precautionary thresholds, such as potential biological removal (PBR) levels.

Our findings could aid to shed light on cases of similarly mutilated marine animals in other parts of the world. Indeed, the phenomenon of strandings of (partly) decapitated marine mammals and of live seals or sea lions with severe neck injuries is apparently a worldwide one not limited to the southern North Sea or to the species described here, with a search on the internet revealing tens of pictures of a variety of marine mammals showing similar severe injuries. Because of their gruesome appearance and their exposure on the Internet and in press articles, these photos often spark outrage and speculation about the possible perpetrators and the methods used. It is up to scientists to try and explain '*beheadings*', '*decapitations*' and '*laser-precision cuts*'.

Acknowledgements

We thank Dr Thierry Jauniaux for providing the results of the seals that were necropsied at the University of Liège. RBINS would like to thank the many volunteers who reported strandings, especially those from the North-SealTeam, the technical services and fire brigades of the coastal municipalities, and the forensic pathologist for their cooperation. We thank the personnel of Sealife for their information on the live stranded seals. We thank all reviewers for their valuable questions, comments and suggestions. RBINS, together with several scientific institutes, carries out research on marine mammals stranded in Belgium since the early 1990s. Results are regularly reported in journals and in the framework of international obligations. Since 2014, the Institute also publishes annual reports on marine mammals. These can be consulted at www.marinemammals.be/reports.

References

Bishop, A.M., J. Onoufriou, S. Moss, P.P. Pomeroy & S.D. Twiss 2016. Cannibalism by a male grey seal (*Halichoerus grypus*) in the North Sea. Aquatic Mammals 42: 137–143.

Brownlow, A., J. Onoufriou, A. Bishop, N. Davison & D. Thompson 2016. Corkscrew seals: grey seal (*Halichoerus grypus*) infanticide and cannibalism may indicate the cause of spiral lacerations in seals. PLoS ONE 11: e0156464.

Culloch, R., P. Pomeroy, R. Lidstone-Scott, L. Bourne & S.D. Twiss 2012. Video evidence of a potential terrestrial predator (*Vulpes vulpes*) within a grey seal (*Halichoerus grypus*) breeding colony on the UK mainland. Aquatic Mammals 38: 81-85. DOI:10.1578/AM.38.1.2012.81.

Di Maio, V.J.M. & D.J. Di Maio 2001. Forensic Pathology, 2nd ed. CRC Press: Boca Raton, FL, USA.

EC 2019. Regulation (EU) 2019/1241 of the European Parliament and of the Council of 20 June 2019 on the conservation of fisheries resources and the protection of marine ecosystems through technical measures.

Haelters, J., E. Everaarts, P. Bunskoek, L. Begeman, J.W.J. Hinrichs & L. IJsseldijk 2016. A suspected scavenging event by red foxes (*Vulpes vulpes*) on a live, stranded harbour porpoise (*Phocoena phocoena*). Aquatic Mammals 42 (2): 227-232.

Heers, T., A. van Neer, A. Becker, M.L. Grilo, U. Siebert & A. Abdulmawjood 2017. Loop-mediated isothermal amplification (LAMP) assay - A rapid detection tool for identifying red fox (*Vulpes vulpes*) DNA in the carcasses of harbour porpoises (*Phocoena phocoena*). PLOS ONE 12: e0184349.

Hejna, P. & M. Bohnert 2013. Decapitation in suicidal hanging - vital reaction patterns. Journal of Forensic Sciences 58, Suppl. 1: 270-277. Doi: 10.1111/1556-4029.12001. Epub 2012 Nov 5. PMID: 23127190.

ICES 2017. International Council for the Exploration of the Sea. Report of the Workshop on predator-prey interactions between grey seals and other marine mammals (WKPIGS), 30 April 2017, Middelfart, Denmark. ICES CM 2017/SSGEPD: 18.

ICES 2022. Working Group on Marine Mammal Ecology (WGMME). ICES Scientific Reports 4: 61. Http://doi.org/10.17895/ices.pub.20448942

IJsseldijk, L.L. & S.C.V. Geelhoed 2016. Fox scavenging mutilations on dead harbour porpoises (*Phocoena phocoena*). Report C036/16. IMARES Wageningen UR, Texel / Den Helder, the Netherlands.

IJsseldijk, L.L., A.C. Brownlow & S. Mazzariol (eds) 2019. Best practice on cetacean postmortem investigation and tissue sampling. Joint ACCOBAMS and ASCOBANS document. ACCOBAMS-MOP7/2019/Doc 33.

Jauniaux, T., M. García-Hartmann, J. Haelters, J. Tavernier & F. Coignoul 2002. Echouage de mammifères marins: guide d'intervention et procédures d'autopsie. Annales de Médécine Vétérinaire 146: 261-276.

Kuiken, T. & M. Garcia-Hartmann 1991. Cetacean Dissection techniques and tissue sampling. European Cetacean Society (ECS) Newsletter: Special Issue.

Leccia, C., V. Alunni & G. Quatrehomme 2017. Suicidal hanging resulting in decapitation: A case report and review of the literature. Forensic Science International 279: e10–e13. Https://doi.org/10.1016/j.forsciint.2017.07.016

Peltier, H., H.J. Baagøe, K.C.J. Camphuysen, R. Czeck, W. Dabin, P. Daniel, R. Deaville, J. Haelters, T. Jauniaux, L.F. Jensen, P.D. Jepson, G.O. Keijl, U. Siebert, O. Van Canneyt & V. Ridoux 2013. The stranding anomaly as population indicator: the case of harbour porpoise *Phocoena phocoena* in North-Western Europe. PLoS ONE 8: e62180.

Peltier, H., M. Authier, R. Deaville, W. Dabin, P.D. Jepson, O. Van Canneyt, P. Daniel & V. Ridoux 2016. Small cetacean bycatch as estimated from stranding schemes: the common dolphin case in the northeast Atlantic. Environmental Science & Policy 63: 7e18. DOI:10.1016/j.envsci.2016.05.004.

Quaggiotto, M.M., L.R. Burke, D.J. McCafferty & D.M. Bailey 2016. First investigation of the consumption of seal carcasses by terrestrial and marine scavengers. The Glasgow Naturalist (online 2016) 26: 3.

SCOS 2021. Scientific advice on matters related to the management of seal populations: 2021. Natural Environment Research Council (NERC), Special Committee on Seals (SCOS).

Törö, K., I. Kristóf & E. Keller 2008. Incomplete decapitation in suicidal hanging - report of a case and review of the literature. Journal of Forensic and Legal Medicine 15: 180–184.

van Neer, A., L.F. Jensen & U. Siebert 2015. Grey seal (*Halichoerus grypus*) predation on harbour seals (*Phoca vitulina*) on the island of Helgoland, Germany. Journal of Sea Research 97: 1–4.

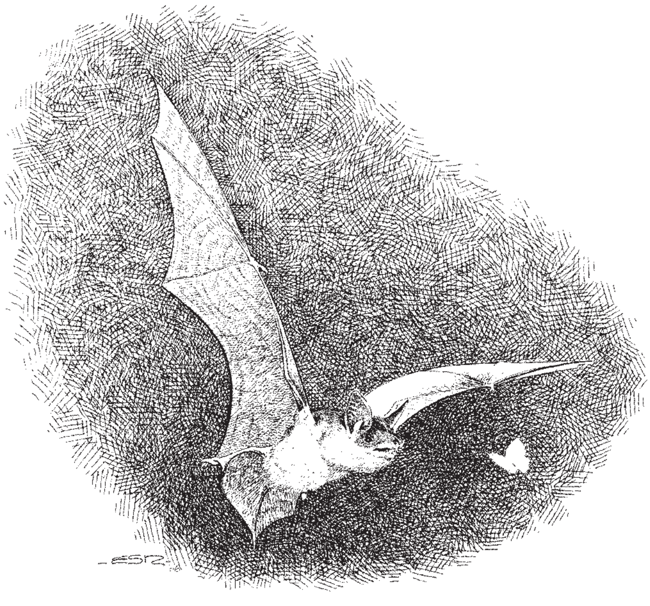
van Neer, A., S. Gross, T. Kesselring, M.L. Grilo, E. Ludes-Wehrmeister, G. Roncon & U. Siebert 2021. Assessing seal carcasses potentially subjected to grey seal predation. Scientific Reports 11: 694.

Samenvatting

Hoge prevalentie van hoofd- en neklaesies bij gestrande zeehonden: doodsoorzaak?

In 2021 werden op de Belgische stranden 101 dode zeehonden aangetroffen. Dit aantal is extreem hoog in vergelijking met dat van de vorige decennia, waarbij de aantallen nooit boven de 50 uitkwamen. Van de aangespoelde dieren werden 21 grijze zeehonden (*Halichoerus grypus*), 13 gewone zeehonden (*Phoca vitulina*) en 2 niet-geïdentificeerde zeehonden verzameld voor het uitvoeren van een autopsie, terwijl van nog eens 49 zeehonden foto's beschikbaar waren. Van de 90 dieren waarbij een necropsie werd verricht of waarvan informatie zoals duidelijke foto's of beschrijvingen beschikbaar waren, vertoonden 58 (64%) ernstige letsels aan kop en nek. In 27 gevallen kon die beschreven worden als een cirkelvormige laesie rond de nek, in de forensische geneeskunde bekend als een spoor van een ligatuur. De meeste dieren met cirkelvormige nekletsels waren jonge dieren. We besluiten dat bijvangst de meest waarschijnlijke doodsoorzaak was in deze 27 gevallen, hoewel de kenmerkende letsels vaak post-mortem leken te zijn ontstaan. Door de aard van de letsels konden wij andere mogelijke achtergronden uitsluiten, zoals insnijdingen met een mes of predatie door grijze zeehonden. Wij vermoeden dat de dieren in netten werden gevangen en stierven door asphyxie, terwijl het ophalen van het net mede verantwoordelijk was voor de typische letsels. Sommige zeehonden overleefden echter: er werden drie levende zeehonden met soortgelijke nekletsels gevonden; delen van een nylon monofilament visnet waren nog aanwezig, diep in de weefsels doorgedrongen. De waarnemingen rechtvaardigen een nader onderzoek van het verschijnsel, inclusief naar het systeem van bijvangst, de ruimtelijke en temporele verspreiding, het aantal gevangen zeehonden en de betrokken typen vissersvaartuig.

Received: 6 September 2022
Accepted: 8 November 2022



Potential effects of PC-amber on the activity of common pipistrelles (*Pipistrellus pipistrellus*)

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Abstract: Artificial light at night (ALAN) is known to have an impact on the environment. Adapted to the dark, nocturnal animals are likely to be strongly influenced by ALAN. For bats this means potential effects on the functionality of roosts, flight paths and foraging areas. When conducting construction work, a certain amount of light is required to ensure a safe working environment for humans. To limit the potential negative effects of ALAN on the environment colour spectrum light solutions have been implemented in the past. There is a trade-off between environmental impact, safety and costs. In this study, in close proximity to a specific construction site, we were interested in the effect of phosphor converted (PC) amber on the activity of common pipistrelles (*Pipistrellus pipistrellus*). PC-amber is cheaper and more energy-efficient than amber light and gives people more visibility. We conducted an experiment with four different light regimes: PC-amber, amber, white and natural darkness as a control, and measured the activity of common pipistrelles. We included several environmental variables in the analyses and used a negative binomial mixed-effect regression model with a log-link function. Neither colour treatment nor distance to the light source significantly explain the observed variation in common pipistrelle activity. The variance in data is partly explained by environmental factors as bat activity significantly decreased with precipitation, increasing wind speed and increasing moon illumination. Based on this experiment, no firm conclusion can be drawn on the effect of PC-amber coloured light on the activity of common pipistrelles. To be able to make a statement with more certainty, more replicates on multiple locations are needed.

Keywords: common pipistrelle, *Pipistrellus pipistrellus*, Chiroptera, Anabat, light experiment, Amber, PC-amber, bat friendly lighting, ALAN.

Introduction

Bats are nocturnal animals and as such are affected by artificial light at night (ALAN). Bats can experience nuisance from ALAN and in the course of spatial developments the degree of disadvantageous effects of light must be assessed and mitigated if necessary. Bats avoid light on flight paths (Verboom & Huitema 2010, Voigt et al. 2018, 2021). However, some light tolerant bats are also attracted by potential increased prey availability in proximity of lights. Different bat species show differences in response towards light. Common pipistrelles (*Pipistrellus pipistrellus*) are considered quite light tolerant species, however openness and light can have negative effects on flightpaths (Jansen & Limpens 2012, Jansen et al. 2014, Hale et al. 2015).

To have safe conditions for humans to work in the dark there must be a certain amount of light. On the other hand, the impact on nocturnal animals has to be reduced. At the same time the aim is to save costs by using energy efficient technologies. In other words, there is a trade-off between security and environmental impact. The background of this study

Table 1. Overview of test set-up and expectations regarding bat activity at positions 1 to 5 for the different light treatments. Detector 3 refers to the position of the lamp, i.e. the light source. A higher number of '+' means more activity. The symbols indicate the expected relative activity to the other treatments or positions; they do not indicate absolute differences.

	detector 1 far	detector 2 close	detector 3 light source	detector 4 close	detector 5 far
Dark	+/-	+/-	+/-	+/-	+/-
PC-amber	+	++	+	++	+
Amber	+/-	+	+/-	+	+/-
White	++	+++	+	+++	++

was a specific case of construction work close to the Beatrixsluis in Nieuwegein (Province of Utrecht, the Netherlands) (exemption FF/75C/2014/0294). The use of conventional bat-friendly light (Philips Clearfield) in the whole area would lead to a high cost in energy, an alternative option could be a more broadband, energy efficient PC-amber (Veltman 2018). Based on expert judgement, mitigation with PC-amber lights was considered a practical solution for this situation where safety and costs are balanced with limited negative effects of light on wildlife. However, empirical data of PC-amber light on bat activity was lacking. Spoelstra et al. (2017) suggested that white and green light should be avoided in order to limit the negative impact of light at night on bats. In this study we tested the effect of different light regimes on common pipistrelle activity in a field experiment and compared four light regimes: darkness, white, amber and phosphor converted amber (hereafter PC-amber). Our hypotheses are summarized in table 1, which shows the expected effects on bat activity in different light conditions and distances to the light source. The assumption is that common pipistrelles are, as a consequence of a balance of energy uptake and predation risk, ambivalent toward light. They will avoid illuminated flightpaths, but also hunt the insects that are attracted to the light. However they will not stay in the light cone, hence we expect bigger effects on intermediate distance to the light source (see hypotheses table 1). A light spectrum that is supposed to attract less insects (amber and PC-amber) is assumed to have less effects on hunting bats than white light.

Methods

Acoustic data was collected using automatic bat recorders (Anabat Swift) in the summer of 2019 (15 May – 29 June) from 30 minutes before sundown until 30 minutes after sunset. The study was conducted in close proximity of the Beatrix locks situated between the cities of Nieuwegein and Houten, on the east bank of the canal named 'Lekkanaal' (52.0329°N, 5.1149°E). Five poles with an automatic bat recorder were placed along the vegetation with 25 metre intervals, the light source was located at a height of approximately 8 metres, near the central pole (figure 1). The light regime changed every night using a Latin square scheme to select the colour treatment: white (*Philips Mini Luma,* with a correlated colour temperature (CCT) of 4000 K), amber (*Innolumnis Nicole,* CCT 2200 K), PC-amber (*Holophane V-Max,* CCT 2900 K) or the control condition: darkness (Veltman 2018). Acoustic data was analysed by a trained ecologist using the program 'bat classify' with a certainty threshold of at least 90%.

Data analyses

In total, 39 nights were used for the analy-

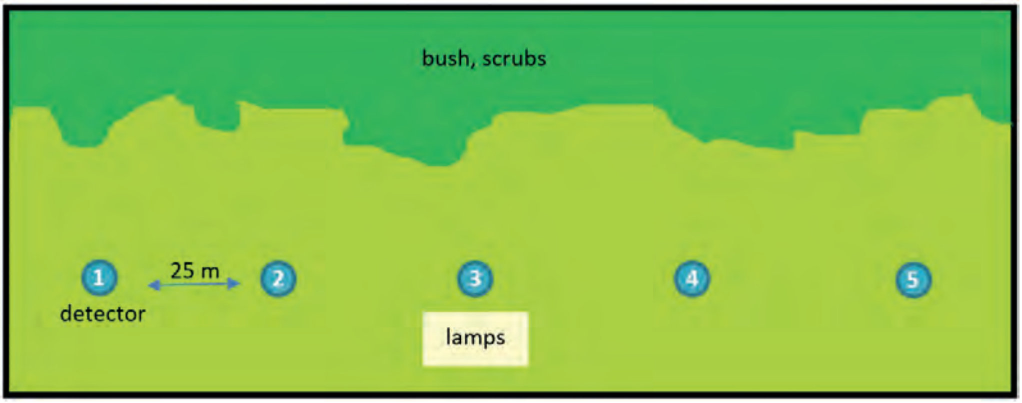

Figure 1. Schematic experimental set-up: Five poles with an automatic bat detector in a row (numbered 1–5 from north to south). With the light source at the centre (pole 3), two at an intermediate distance of 25 m (pole 2 and 4) and two further away from the light source at a distance of 50 m (pole 1 and 5).

ses. Some nights had to be removed from the analyses due to technical malfunctioning and unfavourable weather conditions. A filter was used to select common pipistrelle recordings, from now on referred to as 'bat activity'. The final data frame contained 195 recordings of bat activity (sum of detections per night) and nine predictor covariates. The response variable, i.e. the sum of bat activity per night, had a variance far exceeding the mean (647 >> 48). Frequency distributions of covariates were assessed, and none of the covariates were problematic in terms of a strongly unbalanced design. Collinearity was checked by calculating pair-wise correlations among the predictors, without detecting any problems.

To account for this over dispersion we used a negative binomial regression model. All data analyses were performed using R version 4.0.3 (R Core Team 2020). To investigate the effect of light treatment and distance to the light source on bat activity in dependence of other environmental confounders, we used negative binomial mixed-effect regression models with a log-link in R package lme4 (Bates et al. 2015). The final model had the following structure: fm1 = glmer.nb (bat.activity ~ treatment * DisTreat + wind.speed + moon.phase + temperature + night.duration + night.duration^2 + rain + (1|detector.ID)). The ID of the detector was included as a random intercept term. This accounts for systematic differences between the detector poles. The model fit was validated by plotting residuals vs. expected values and assessed the normal distribution of the random intercepts. Predicted model effects are visualized by producing conditional effect plots, using the effects library to average predictions across factor levels (Fox & Weisberg 2019).

Results

There was no significant difference in bat activity between light treatments, nor did we find a significant effect of the distance to the light source or the interaction of the two (table 2). There were trends indicating higher bat activity at distances 'intermediate' and 'far' from the light source and differences in the effect pattern of distance between light types, in particular the colour 'amber'; however, the associated variance was large (figure 2). Bat activity significantly decreased with wind speed and increasing moon phase. A negative effect of temperature was almost significant (table 2). There was a significantly lower activity during nights with rainfall. There was a significant non-linear effect of night duration,

Table 2. Model results of the negative binomial mixed-effect model explaining bat activity at detector poles as a function of light, distance to light as well as other environmental confounders. Coefficient estimates, associated standard errors and *P*-values are provided. Note that the category combination of 'no light' with 'at the light source' and 'no rain' are contained in the model intercept.

Covariate	Estimate	SE	z-value	*P*-value
(Intercept)	3.38423	0.17918	18.887	<0.001
treatmentAM	0.25332	0.20815	1.217	0.223595
treatmentPC	-0.11481	0.25331	-0.453	0.650375
treatmentW	0.13212	0.21971	0.601	0.547596
DisTreat-far	0.23005	0.19196	1.198	0.230767
DisTreat-intermediate	0.26038	0.19131	1.361	0.173490
wind.speed	-0.15465	0.04145	-3.731	0.000191
moon.phase	-0.15038	0.06518	-2.307	0.021054
temperature	-0.10041	0.05218	-1.924	0.054340
night.duration	-0.22879	0.07229	-3.165	0.001552
night.duration^2	0.28499	0.07266	3.922	<0.001
rain-Yes	-0.38424	0.10092	-3.807	0.000140
treatmentAM:DisTreat-far	-0.07680	0.25206	-0.305	0.760613
treatmentPC:DisTreat-far	-0.11324	0.30876	-0.367	0.713802
treatmentW:DisTreat-far	-0.06930	0.26516	-0.261	0.793821
treatmentAM:DisTreat-intermediate	-0.17809	0.25200	-0.707	0.479736
treatmentPC:DisTreat-intermediate	-0.03440	0.30841	-0.112	0.911187
treatmentW:DisTreat-intermediate	-0.03610	0.26478	-0.136	0.891564

with more bats recorded during short and long nights, and fewer in between (figure 3).

Discussion

This study was conducted in a relatively open habitat, therefore weather conditions could have had a relatively big impact on bats. Also, recent changes in the surrounding of the study site included an increase of light and a more open vegetation structure, which is likely to have altered the behaviour of the bats. Furthermore, it is likely that the spatial context had a significant influence. The design could be improved by taking into account behaviour and the different functional habitats so that it is possible to disentangle effects on flightpaths and foraging area.

All manufacturers were asked to supply a lamp with a luminous output of 3185 lumen. Although all three manufacturers indicated to comply with this, during the experiment a control illuminance measurement indicated differences between the light treatments. In future experiments we would recommend to control for this.

Conclusions

The current experiment does not allow to draw a firm conclusion on the effect of PC-amber coloured light on the activity of common pipistrelles compared to white light or darkness in general. We found no significant difference between the treatments. Weather conditions (most notable windspeed and rainfall) and moon phase had a significant effect.

The lack of significance of the light treatment can be due to the large associated variance. In other words, there were large differences in how many bats flew over the recorders each night, inflating the confidence intervals

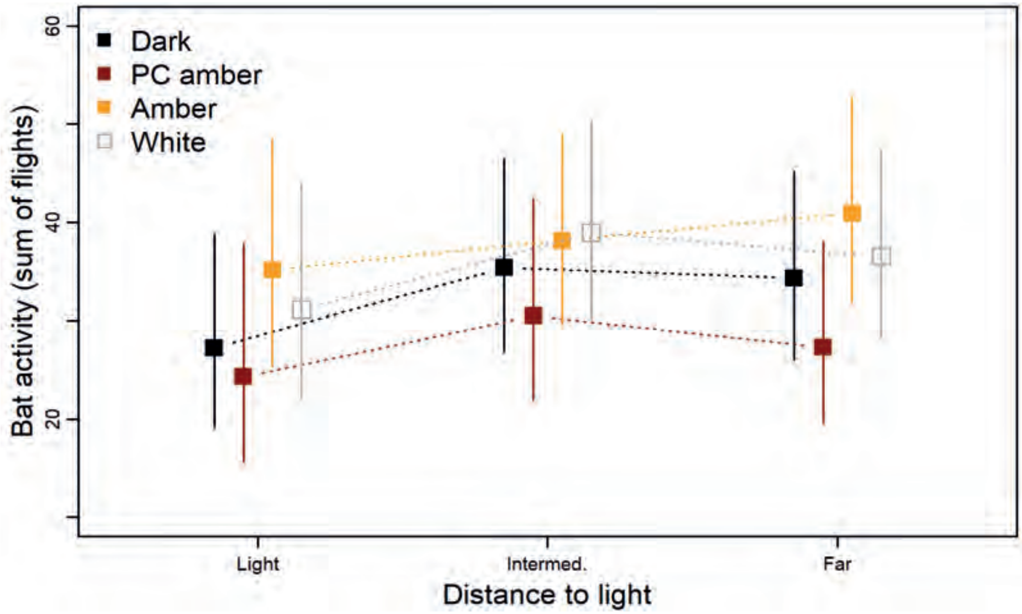

Figure 2. Conditional effect plots of the interaction term between distance to the light source and light treatment as predicted by the final model. Effects were obtained by averaging across the remaining covariates.

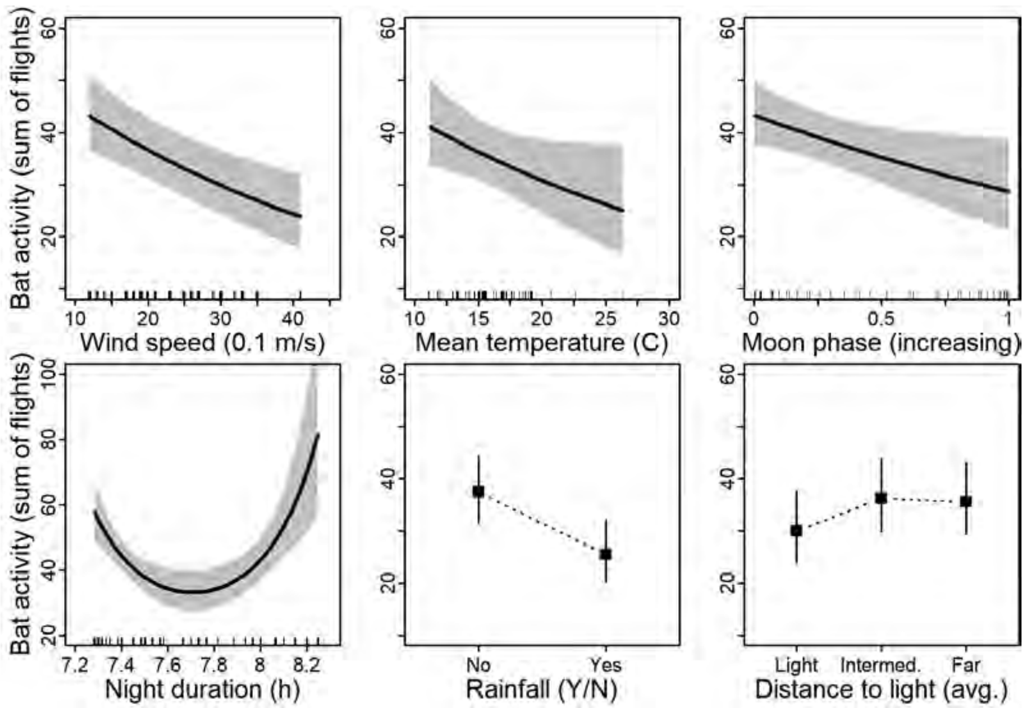

Figure 3. Conditional plots of the effects of additional covariates on bat activity as predicted by the final model. Effects were obtained by averaging across the remaining covariates. Note the different y-axes range for night duration. The single plot for distance to light (bottom right) was obtained by averaging across the colour treatments.

and leading to *P*-values exceeding the threshold. There is no clear signal in these results for the effect of the light treatment; to be able to make a statement with more certainty, more replicates on multiple locations are needed.

Acknowledgements: This experiment was commissioned by Rijkswaterstaat, Sas van Vreeswijk, Agidens en Holophane. We thank Lino Kämmerle for the help with the statistics and with R, and we thank Eric Jansen, Marinus-Jan Veltman and Benjamin Brandt for their fieldwork and placing the lighting and detectors, managing the light/detector set up and retrieving data. Eric Jansen, as well as Benjamin Brandt and his team at Habitus are thanked for their help in the analyses of the raw data.

References

Bates, D., M. Maechler, B. Bolker & S. Walker 2015. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software 67 (1): 1-48. Https://doi.org/10.18637/jss.v067.i01

Fox, J. & S. Weisberg 2019. An R Companion to Applied Regression. 3rd Edition. Sage Publications, Thousand Oaks, USA.

Hale, J.D., A.J. Fairbrass, T.J. Matthews, G. Davies & J.P. Sadler 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. Global Change Biology 21: 2467–2478.

Jansen E.A. & H.G.J.A Limpens 2012. De vleermuisfuncties van het Lekkanaal - Uitwerking mitigatie- en compensatieplan voor de 3e kolk Beatrixsluis en de verbreding Lekkanaal. Rapport 2012.11 Zoogdiervereniging, Nijmegen, the Netherlands.

Jansen E.A., H.G.J.A Limpens & M.J. Schillemans 2014. Uitwerking mitigatieplan vleermuizen Lekkanaal. Rapport 2013.23. Bureau van de Zoogdiervereniging, Nijmegen, the Netherlands.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Spoelstra, K., R.H.A. van Grunsven, J.J.C. Ramakers, K.B. Ferguson, T. Raap, M. Donners, E.M. Veenendaal & M.E. Visser 2017. Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. Proceedings of the Royal Society B 284: 20170075. Https://doi.org/10.1098/rspb.2017.0075

Veltman, M.J. 2018. Beoordeling aanpak voortschrijdend inzicht verlichting Beatrixsluizen, Nieuwegein. Notitie Ecosucces. Commisioned by Habitus.

Verboom, B. & H. Huitema 2010. The influence of treeline structure and wind protection on commuting and foraging common pipistrelles (*Pipistrellus pipistrellus*). Lutra 53 (2): 63-80.

Voigt, C.C., C. Azam, J. Dekker, J. Ferguson, M. Fritze, S. Gazaryan, F. Hölker, G. Jones, N. Leader, D. Lewanzik, H.J.G.A. Limpens, F. Mathews, J. Rydell, H. Schofield, K. Spoelstra & M. Zagmajster 2018. Guidelines for consideration of bats in lighting projects. EUROBATS Publication Series No. 8. UNEP/EUROBATS Secretariat, Bonn, Germany.

Voigt, C.C., J. Dekker, M. Fritze, S. Gazaryan, F. Hölker , G. Jones, D. Lewanzik, H.J.G.A. Limpens, F. Mathews, J. Rydell, K. Spoelstra & M. Zagmajster 2021. The impact of light pollution on bats varies according to foraging guild and habitat context. BioScience 71 (10): 1103-1109. Https://doi.org/10.1093/biosci/biab087

Samenvatting

Het effect van breedbandig amberkleurig licht op de activiteit van gewone dwergvleermuis (*Pipistrellus pipistrellus*)

Verlichting kan invloed hebben op de functionaliteit van vliegroutes en foerageergebieden van vleermuizen. In het projectgebied bij de Beatrixsluizen gaat het over concrete vliegroutes en oversteekplaatsen van de gewone dwergvleermuis over het Lekkanaal en foerageergebied van deze soort. Toepassing van breedbandig amberkleurig licht ('phosphor converted (PC) amber') voor alle nieuwe verlichting in het gehele projectgebied biedt mogelijk een oplossing, omdat deze ten opzichte van wit licht mogelijk minder verstorend is op de functionaliteit van de omgeving voor vleermuizen, en een goedkoper (energiezuiniger) alternatief is voor amberkleurig licht. In dit experiment is gekeken naar de activiteit van gewone dwergvleermuizen bij de drie verschillende kleurenspectra, wit, amber en PC-amber ten opzichte van de controleconditie zonder verlichting. Tevens is er gekeken naar het effect van afstand tot de lichtbron. We vonden geen significant verschil in vleermuisactiviteit tussen de verschillende lichtbehandelingen. Er was een grote spreiding in de data, die deels verklaard kon worden door omgevingsfactoren zoals neerslag, wind en maanfase. De proefopzet bestond uit slechts *één locatie, waardoor de individuele variatie binnen deze locatie effecten kan hebben gemaskeerd.* Om meer zekerheid te krijgen adviseren we de proef te herhalen op verschillende locaties en gedurende meer nachten.

Received: 26 April 2022
Accepted: 25 October 2022

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Editorial

Research Papers