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Mammals, big mammals and statistics

The title of this editorial may look oddly familiar. That's because it riffs on the famous phrase "lies, damned lies and statistics," a quote of slightly uncertain origin (Mark Twain is one of the options, as seems frequently the case). It's often used to describe the persuasive power of statistics to bolster a weak argument. Weak arguments abound in today's media landscape, and reports on the state of biodiversity are no exception. The debate on it is often fierce and polarized, and accusations of either uncalled-for alarmism or opportunistic dismissiveness fly back and forth in the public debate. Statistics get thrown around with reckless abandon and there is something for every taste to be found for whoever is willing to do some cherry-picking. Since this is Lutra, let's take a look at the case for mammals.

Take the article on the Our World in Data website called "Wild mammals are making a comeback in Europe thanks to conservation efforts", republished in updated form in September 2022. As the title suggests, it presents genuinely good news: many populations of large mammals are on the rebound from the earlier effects of hunting and habitat loss. This was picked up by some to support the argument that there is no such thing as a biodiversity crisis, even though the article is very clear: this is about large mammals and the fact that they're doing better is actually proof that protective measures can be highly effective.

More recently, Statistics Netherlands (CBS) published data for the 1995–2022 period on numbers of mammals in the Netherlands. Again, the overall trend looks good, showing a nearly 50% average increase since 1995. And again there's a more nuanced message for anyone who reads beyond the headline. The trend is based on 35 species for which suitable data is available, 18 of which increased, five of those sharply so, and that's great news. However, populations of twelve species actually dropped, five of those are mouse species. Another four species were stable and data for the one remaining species (common vole) showed an unclear confidence interval due to strong fluctuations. Of the five species that showed the most marked increase, two (beaver and otter) are reintroduced species while the population growth of one (hamster) is due to yearly releases of captive bred animals. In other words, conservation measures that have proven to be effective. Five declining species are covered by the Habitat Directive: root vole, serotine bat, whiskered bat, brown long-eared bat and hazel dormouse. The latter three species were still increasing until 2011. The Netherlands has a special responsibility for the root vole, as it is a distinct subspecies (*Alexandromys oeconomus arenicola*) that's endemic to the Netherlands. The serotine bat is vulnerable to effects of cavity wall insulation, a measure the Dutch government wants to be taken in two million homes by 2030 to counteract climate change.

So yes, there really is good news when it comes to the state of mammals in the wild. But it's essential to look beyond the headlines, beyond the infographics that lump data for species with wildly varying trends and certainly beyond the (social) media one-liners.

This issue of *Lutra* does exactly that. The pine marten (*Martes martes*) is one of those species that has seen a marked increase in its distribution and population. They have been increasing for several decades in wooded parts of the Netherlands, but it was only in the twenty-first century that they gradually gained ground in the west of the country. Heemskerk here present the results of a four-year study of a population in a dune area that only began to establish itself from 2006 on. The author was able to monitor individual pine martens for long periods of time and gain insights into their population structure and spatial use of the area.

In a neighbouring dune area, the population of the introduced fallow deer (*Dama dama*) has also increased, but in this case it is not particularly favourable to the area's biodiversity. From the late 1990s on, the number of deer in the area exploded and along with it the grazing pressure, which resulted in negative effects on the area's flora and fauna. In his review, Van der Spek summarizes a number of studies on the subject, which mostly justify the control measures taken by the authorities.

Keijl et al.'s overview of stranded cetaceans on Dutch coasts in 2020-2023 comprises 14 species. By far the most commonly stranded species was (once again) harbour porpoise (*Phocoena phocoena*), and the authors discuss the population dynamics of the stranded animals and their causes of death.

The sperm whale (*Physeter macrocephalus*), which is also on Keijl et al.'s list, only irregularly strands on the Dutch coast. Historical stranding records are an important source for assessing their population dynamics and distribution in former times, which in the case of sperm whales have largely been impacted by whaling and its subsequent cessation and, probably, by climate change in more recent times. Kinze reviews such a list of 16th Century North Sea sperm whale strandings, and reveals three more strandings of this species on the East Frisian coast of Germany.

Another rare mammal in the Netherlands is the parti-coloured bat (*Vespertilio murinus*). Modderman et al., after a thorough search in the north-easternmost part of the country, rediscovered several roosts of the species. Maternity roosts are now known from two areas in the Netherlands.

The smallest mammals in the Netherlands, shrews and true mice, are represented in this issue by a study of Bekker, who dives into the hypothesis of the variability in size among shrews being smaller than among true mice. The author presents a method to quantify these differences and discusses possible explanations for this phenomenon.

The last paper in this issue, by Mostert & Bekker, describes the occurrence of the noctule (*Nyctalus noctula*) in the west of the Netherlands. Figures show that rising populations and the expansion of this tree-dwelling bat over de last decades has especially been apparent in that part of the country.

Eric Thomassen
Abstracts by Ben Verboom

The impact of fallow deer (*Dama dama*) grazing on the biodiversity of a Dutch coastal dune system

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Abstract: In the coastal dune system of Amsterdamse Waterleidingduinen (AWD), the Netherlands, numbers of the once introduced fallow deer (*Dama dama*) increased exponentially during the late 1990s and early 2000s. Thereby grazing pressure also increased. By the spring of 2016, the density was an estimated 190-220 deer/km². Several studies show that increased grazing pressure has resulted in loss of biodiversity. This was based on long-running monitoring networks of plant and animal species (including citizen science by volunteers), databases for sightings of plant and animal species, vegetation mapping, data modelling, small-scale field experiments and judgements by independent (inter)national experts. Studied species included mammals, birds, reptiles, butterflies, micro and macro moths, bees, bumblebees, hoverflies, butterflies and plants, as well as vegetation and habitats. Temporal comparisons were used in order to detect changes within the area over time, spatial comparisons for differences between AWD and other, comparable dunes systems with little or no fallow deer grazing. This review summarizes all published papers and reports on this subject up to 2024. These reports are all in Dutch, and therefore this review also makes the conclusions of these publications available for a wider audience. The correlation between increased deer numbers and strongly decreasing numbers of many species (groups) is such that it is justified to conclude that a high grazing pressure has led to significant biodiversity loss, and that strictly protected Natura 2000 habitats are under pressure. Partially based on the impact on biodiversity, the responsible authorities have granted permission for population control of fallow deer since 2016.

Keywords: fallow deer, *Dama dama*, Amsterdamse Waterleidingduinen, deer grazing, overgrazing, biodiversity loss, cascading effects.

Introduction

In temperate climates, large herbivores influence their ecosystems in multiple ways (Côté et al. 2004). They facilitate many plant and animal species, but can also disrupt the habitats they occur in when grazing pressure is too high. By grazing, they have an impact on the biomass and the vegetation height and structure, they produce degradable manure and treading disturbs the soil by either loosening or compacting it. This speeds up or slows down nutrient cycles, decreases litter accumulation and changes the microclimate. As a result the vegetation composition changes. Finally, they compete with, or facilitate other herbivores. Fallow deer (*Dama dama*) were first recorded in the coastal dune reserve of Amsterdamse Waterleidingduinen (AWD), the Netherlands, in the early 1970s. Their numbers increased significantly during the 1990s and 2000s. The increased grazing pressure lead to concerns about their impact on biodiversity. Therefore, a series of studies was set up in order to quantify the impact (if any). This paper reviews the findings of these studies up to and including 2024 and covers habitats, vegetation, plants, mammals, birds, reptiles and insects.

Site description

AWD (3390 ha) is a coastal dune reserve on the border between the provinces of Noord-Holland and Zuid-Holland (Figure 1). This mainly lime-rich, parabolic dune system was formed between 1200 and 1600 AC. At its widest point, it measures a little over 5 km and at its smallest point it is no more than 1.5 km wide. AWD is owned by the city of Amsterdam (12 km away between the nearest points) and managed by drinking water company Waternet. It serves as a vital source for drinking water. With a production of 70 billion litres a year, the area provides up to 70% of the drinking water for Amsterdam and its surroundings. The second main objective is to maintain and – whenever possible – improve the area's natural habitats and biodiversity. The impact of the water production is therefore brought back to a minimum. Roughly, half of the area comprises open habitats, 30% is half open and 20% is closed. From west to east, the habitats of the system change from the sandy beach and the sparsely vegetated foredunes dominated by marram grass (*Ammophila arenaria*) to dune grasslands and wet dune slacks, to dune scrub dominated by common sea buckthorn (*Hippophae rhamnoides*) and finally to dune woodlands. Furthermore, the area is interspersed with waterbodies like unpaved canals and small lakes that are part of the drinking water production facilities, with their own natural values. Coastal dunes support a high and partially endemic biodiversity, but have disappeared in much of Europe as a result of coastal development. It is a relatively rare ecosystem and therefore AWD is protected under the Habitats Directive of the European Union. The Natura 2000 area of Kennemerland-Zuid protects 8170 ha of coastal dune habitats, and AWD covers most of the southern part of the reserve. The Natura 2000 area has been designated to preserve eight habitat types and four species, of which respectively seven and two occur in AWD (Table 1). AWD is furthermore of importance for coastal security (natural sea wall), historical land use (with historical and cultural artefacts) and, with well over a million human visits a year, recreation. From an ecological point of view, issues besides high grazing pressure by deer include fixation of the outer dunes as a safety measure against the sea (turning a once dynamic system into a more static one), high levels of atmospheric deposition (most notably nitrogen), alien invasive plant species and past planting of e.g. pines for timber wood and against sand drift. In order to cope with these issues, sand drift is now being stimulated rather than prevented on a small scale by the removal of top layers in both the outer and inner dunes. An intensive program in order to eradicate alien invasive species has been largely successful. Cattle (cows, sheep) grazed in the area since 1986, but numbers were first lowered before cattle was finally banned in 2017 when grazing pressure from deer became too high.

History of fallow deer in AWD

Based on fossil records, fallow deer were native to the northern part of Europe (including the Netherlands) during the interglacial of the Pleistocene, and went extinct during the Last Glacial Maximum. Despite populations occurring on all continents except Antarctica, it is now considered native only to Turkey where only one undoubtedly natural population survives in the Düzlerçami Game Reserve. Hence, all populations outside Turkey originate from captive stock. It was already introduced across Europe by Phoenicians, Romans and Normans, but most populations are the result of later introductions, many from the 20th century (Masseti & Mertzanidou 2008). Around AWD, fallow deer were first introduced in the nearby Kennemerduinen (within the same current Natura 2000 reserve) around 1958, with about 20 animals present in 1974 (Lever 1985). The first sightings in AWD were in 1973. Fallow deer are not just browsers like the native roe deer (*Capreolus capreolus*), but are also grazers.

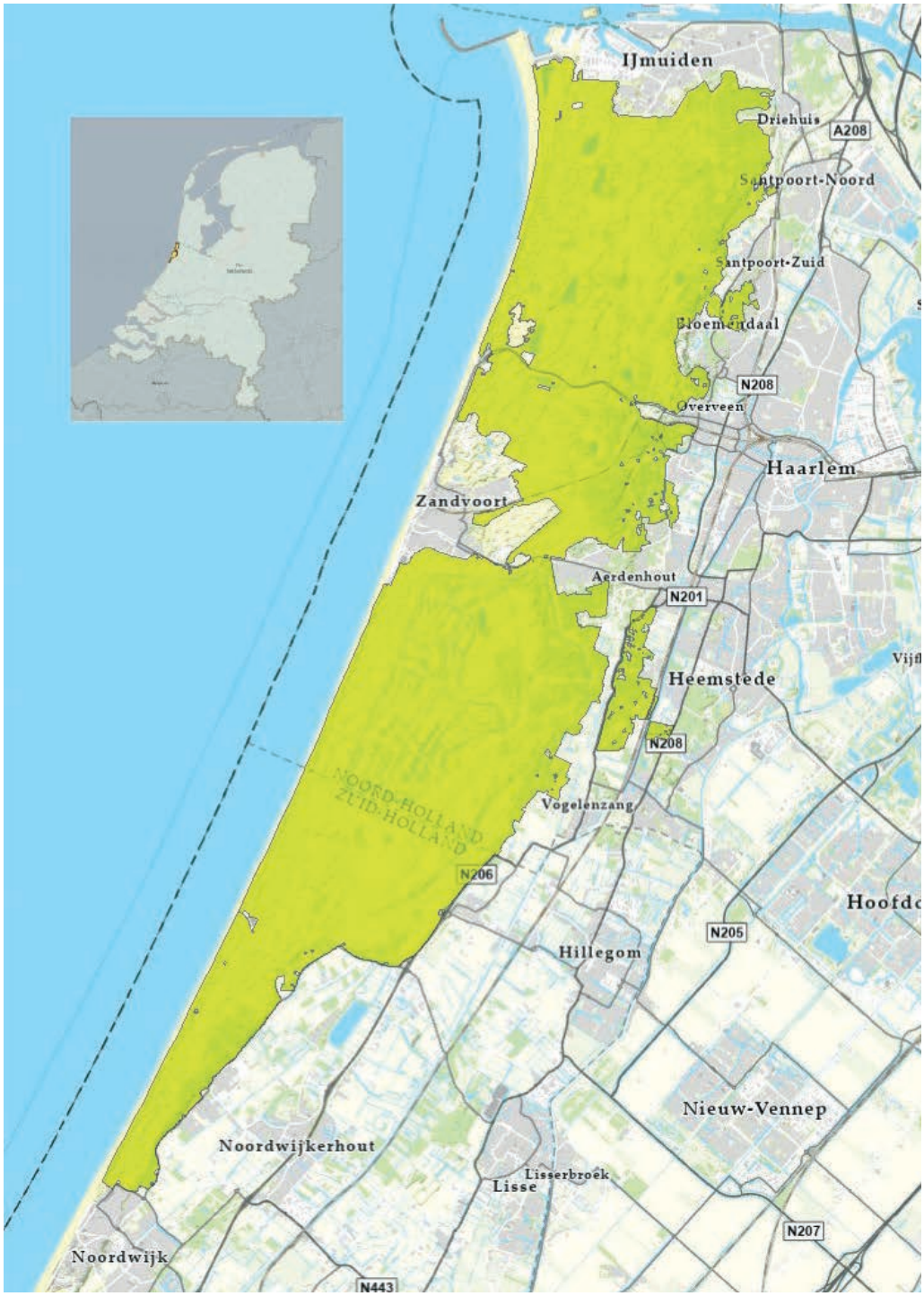

Figure 1. Map of Natura 2000 area Kennemerland-Zuid. Amsterdamse Waterleidingduinen roughly forms the lower half of the reserve. Inlay: position of the area in the Netherlands.

Table 1. Natura 2000 conservation objectives for Kennemerland-Zuid under the Habitats Directive of the European Union (EU).

Habitat types
H2110 Embryonic shifting dunes #
H2120 Shifting dunes ('white dunes')
H2130* Fixed coastal dunes ('dune grasslands' or 'grey dunes')
H2150 Atlantic decalcified dunes Calluno-Ulicetea ('dune heather')
H2160 Dunes with *Hippophaë rhamnoides* ('sea buckthorn scrub')
H2170 Dunes with *Salix repens* ssp. *argentea*
H2180 Wooded dunes of the Atlantic, Continental and Boreal region ('dune woodlands')
H2190* Humid dune slacks ('wet dune slacks')
Species
H1014 Narrow-mouthed whorl snail (*Vertigo angustior*)
H1149 Spined loach (*Cobitis taenia*) #
H1310 Pond bat (*Myotis dasycneme*)
H1903 Fen orchid (*Liparis loeselii*) #

** Habitat types marked with an asterisk (*) have priority*

 # Species or habitat types marked with an (#) occur elsewhere in the Natura 2000 area, but not in AWD

Unlike roe deer, fallow deer have no territorial system that limits population size (Chapman & Chapman 1987). Large predators do not occur in the area, therefore food availability is the main driver behind population densities. With rising deer numbers, collisions with cars in the region increased, and commercial bulb flower fields were damaged by grazing. In order to prevent traffic accidents and economical damage, fences were placed around AWD from 2007 onwards. Since 2012 the entire southern, eastern and northern parts are fenced, cutting the deer off from an important food source: the agricultural land and private estates east of AWD. With both increased numbers and a decreased range for roaming, the browsing pressure within AWD increased significantly. The population peaked with over 3900 counted in 2016. This raised concerns about their impact and therefore Waternet initiated studies and gave assignments to independent NGO's specialized in plant and animal species in order to measure the impact (if any) of deer grazing on the biodiversity of the area. Since 2016 population control within the entire Natura 2000 area (including AWD) was granted by the responsible authorities, partially based on biodiversity loss. The aimed (counted) population size for the AWD after management is determined at 600-800 individuals.

Methods

Studies included: 1. Analyses of existing, long-running standardized monitoring data mostly collected by volunteers (citizen science). 2. Field work in order to collect new monitoring data. 3. Small-scale field experiments. 4. Data modelling. 5. Judgements by independent (international) experts. Most studies in categories 1-4 were initiated by and paid for by Waternet, but were conducted by independent experts.

Deer monitoring

Numbers of fallow deer and roe deer have been monitored annually since 1969 based on a standardized method, carried out by Waternet during late March or early April, just before the vegetation starts growing

(high visibility), but before fawns are born. The area is divided over twelve sections, each covered by one team. The fixed routes cover almost the entire AWD. Whenever possible, each team identifies the age and sex of animals encountered. There are three consecutive counts: around dusk on the first day, and around dawn and dusk on the following day, all within set times. The highest tally of the three counts represents the number for that year. This is a monitoring method that only reflects the bare minimum number of deer present in a year. In order to get more insights into the actual number of deer present, experiments with drones, laser techniques (Lidar) from planes and population data modelling have been carried out. Since 1996, deer have also been counted during standardized transect monitoring of rabbits (*Oryctolagus cuniculus*) during spring and autumn, as part of the governmental national network for ecological monitoring (Netwerk Ecologische Monitoring; NEM). A transect of ca. 25 km divided over 35 parts is crossed after dark by car on a minimum of eight nights in both spring and autumn. All rabbits and deer seen in the headlights of the car are counted. Maximum counts per part are used to determine the maximum counts per season.

Existing monitoring data

Waternet has facilitated standardized monitoring of plant and animal species for nature management purposes for decades. In many cases data have been collected by volunteers (citizen science). Long-term data of plants, mammals, birds, sand lizards (*Lacerta agilis*), butterflies and moths were used. The bird, sand lizard and butterfly monitoring has been standardized within the NEM. Data analysis are being carried out by the Central Statistical Office (in Dutch: CBS). This has resulted in long-term series of data that allow both temporal (population trends and changes in species composition) and spatial analysis (comparisons with trends in other areas). For the latter analysis especially, data from National Park Zuid-Kennemerland (NPZK) were valuable: this roughly forms the northern half of the same Natura 2000 area, with the same habitat types, while fallow deer densities are much lower there. Most analyses were carried out by, or in collaboration with independent not-for-profit organizations that are specialized in specific species groups. Moths were not monitored within the NEM systematics, but a local group has conducted more or less standardized monitoring and they have analyzed their own results. Furthermore, the second form of citizen science was the use of online observation platform waarneming.nl (part of observation.org), that stores mostly unstandardized observation data. These data were used to determine species compositions. In order to monitor Natura 2000 objectives, the vegetation is mapped every 10-12 years. These data allowed comparisons within the area over time.

Modelling

No long-term monitoring data was available for bees, bumblebees and hoverflies, but past observations gave insight in the species composition. Species within these taxonomical groups show a variable amount of dependance on specific plant species, both as larvae (host plants) and imagoes (nectar). With preferred plant species in decline, it was expected that the dependant insects were also in decline. Based on flora monitoring data (Mourik 2015) combined with the ecology of the species, expected trends for bees, bumblebees and hoverflies were modelled.

Field studies

Waternet set up experiments with grazed and ungrazed control plots, using four small (1x1 m) exclosures on four different grasslands where smaller natural grazers like rabbits

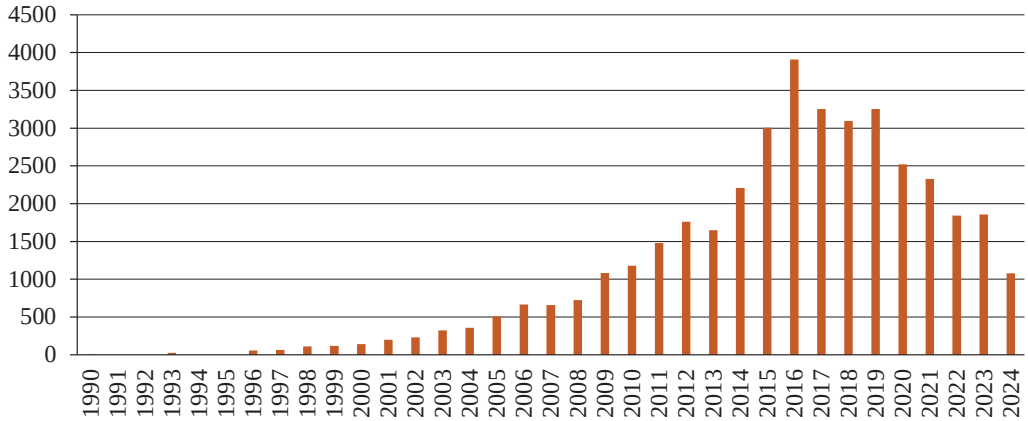

Figure 2. Early spring (pre-reproductive) population trend of fallow deer in Amsterdamse Waterleidingduinen 1990-2024. Population control started from late 2016 onwards.

did have access, but fallow deer did not. The effects on vegetation structure, coverage and species composition in grazed and ungrazed conditions could thereby be measured. In another small-scale experiment, three tiny (0.5 x 0.5m) exclosures were placed in 18 dune grassland plots. Also, several exclosures of different sizes were placed in the area in order to protect vulnerable plant species. Though not set up for a study, these offered an opportunity to measure the conditions of plants in and outside the exclosures. Finally, a past ant survey was repeated.

Expert judgement

The OBN Knowledge Network (OBN Natuurkennis) has ten national expert groups for the natural landscape types of the Netherlands, run by the Ministery of Agriculture, Fisheries, Food security and Nature and the twelve provinces. The OBN Dunes and Coastal Areas Expert Team visited the area twice in order to judge grazing effects by fallow deer. Also, foreign experts from the European Commission have judged nature restoration projects in AWD funded by the EU and carried out by Waternet.

Results

Deer monitoring

Up until spring 2016 there was no population control. For many years deer numbers remained low, but they gradually increased, eventually exponentially (Figure 2). The highest count was in spring 2016, when 3907 individuals were counted. Drone experiments failed to give useful additional insights (Waternet, unpublished data), but according to the Lidar data from 2020 and 2021 ~40% of the deer were missed during the official counts (unpublished data Kavel 10/Waternet). Population modelling showed that up to 48% is missed (FBE Noord-Holland 2024). This means that the population density in spring 2016 was an estimated 190-220 deer/ km^2. With fawns being born after the counts, the summer population density was even significantly higher. Among the adult deer, does formed the vast majority in 2016 (Figure 3), resulting in exponential population growth each year. Population control from November 2016 onwards focused primarily on the culling of does and fawns, since this lowers the yearly production and thereby is the most effective way to decrease numbers. Between 2016/2017 and 2023/2024, 1440 to 2315 deer

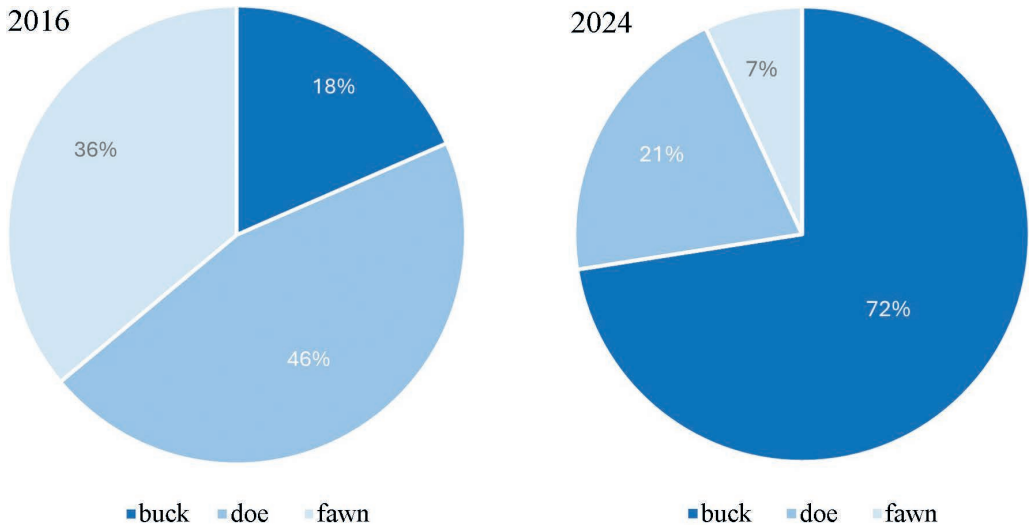

Figure 3. Ratios of bucks, does and fawns of fallow deer in Amsterdamse Waterleidingduinen in 2016 and 2024.

have been shot each winter. This strategy has resulted in both a population decline and a significant shift in the doe-to-buck ratio (Figure 3).

Effects of grazing on habitats, vegetation and plant species

In general, as explained into more detail below, the picture painted by Oosterbaan et al. (2018) and Oosterbaan & Mourik (2020) is that overgrazing has led to a huge impact on the vegetation and vegetation structure of the area. When deer numbers peaked, dune grasslands (H2130) and terrestrial parts of humid dune slacks (H2190) lost their structure and flower richness. Edible plants were grazed off to ground level, creating monotonous grassy lanes of the same height, with only small herbs still flowering. Thickets and shrubs had fallen apart on a large scale due to trampling. There was no rejuvenation in the forests (H2190). The lower layers of herbs and scrub were rare at best but absent in most forested areas.

Natura 2000 habitats

Oosterbaan et al. (2019) conclude that trampling greatly influenced Natura 2000 restoration projects. At sites where sod-cutting had been applied as a nature management measure, the vegetation did not recover. The same applied for the edges of restored pools. While not substantiated, the directorate of the European Commission that judges the execution of EU funded nature restoration projects noted that: "*The management of the site is very well done but overgrazing by fallow deer seems to jeopardise the favourable conservation status of the targeted priority EU habitat 2130 (Fixed coastal dunes with herbaceous vegetation - grey dunes) and the EU habitat 2160 (Dunes with Hippophae rhamnoides).*" (Anne Burrill, DG Environment European Commission, September 2015). Based on expert judgement, the OBN Dunes and Coastal areas Expert Team concluded that grazing had become too intensive and that this contributed to a negative impact on the natural quality of the area. With the grazing pressure at the time, they expected plant species to disappear (VNBE 2018). These expert judgements were later confirmed by data. Based on vege-

tation mapping, qualifying Natura 2000 habitats decreased significantly between 1997 and 2017. In 1997, 82.5% of the area was assigned to a Natura 2000 habitat type. In 2007, this had decreased to 77%, and in 2017 to 52.8% (Figure 4). The authors mention fallow deer grazing as the most important cause of the decline (Oosterbaan et al. 2018).

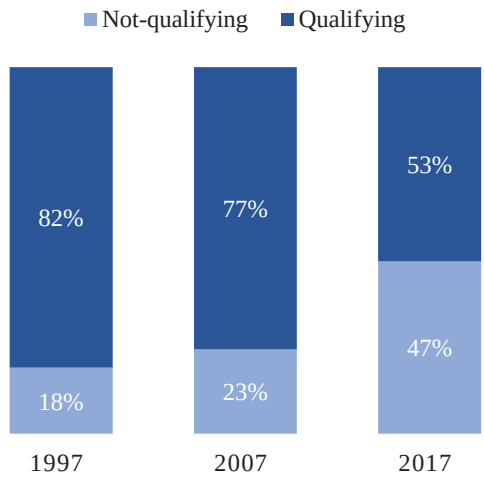

Figure 4. Qualifying Natura 2000 habitats in Amsterdamse Waterleidingduinen in 1997, 2007 and 2017, based on data from Oosterbaan et al. (2019).

Vegetation and plant species

Oosterbaan & Mourik (2020) showed that, based on flora and vegetation mapping in 1997, 2007 and 2017, high density fallow deer grazing has had an effect on three vegetation levels: 1. Biomass. 2 Vegetation forms. 3. Characteristic flora species. In this paper, level 4, 'Physical condition of plants' is added.

1. *Biomass*. The highest scale level is of the total amount of above ground biomass. This seems to have decreased significantly after 2007, correlating with increasing deer numbers. Forest rejuvenation (H2190) had been absent for a long period of time and plant height of all herbs and grasses combined decreased with 33%. This is supported by an additional small-scale field study by Aggenbach & Clevers (2020). Based on field work in 2018 and 2019 with tiny (0.5 x 0.5m) exclosures on 18 dune grassland plots (H2130), they concluded that after only one growing season without deer grazing, the plant biomass, the cover and height of flowering herbs was higher within the exclosures than in control plots.
2. *Vegetation forms*. Oosterbaan & Mourik (2020) grouped similar plant forms together in nine groups (Table 2). On this intermediate scale level, grasses, the poisonous species and mosses increased significantly in coverage (the latter nearly completely caused by one species: the neat feather-moss (*Pseudoscleropodium purum*)), whereas small scrub (H2160), large herbs and lichens steeply decreased. Trees and larger shrubs were unaffected by grazing and increased.

Table 2. Vegetation groups and difference in coverage in Amsterdamse Waterleidingduinen between 1997 and 2017 (based on Oosterbaan & Mourik 2020).

Vegetation group	1997	2017	Difference	
	ha	ha	ha	%
Trees	295	441	145	+49%
Large scrub	185	268	83	+45%
Small scrub	494	289	-205	-41%
Grasses	872	1086	214	+25%
Large herbs	414	213	-202	-49%
Small herbs	97	79	-18	-19%
Poisonous herbs	35	61	26	+26%
Mosses	779	1229	450	+42%
Lichens	171	34	-137	-80%

increase
decrease

Grasses and mosses benefited from shrub complexes like sea-buckthorn (H2160) falling apart by trampling, covering the newly created open spaces. Also, they benefited from the disappearance of species like European dewberry (*Rubus caesius*) and burnet rose (*Rosa pimpinellifolia*) that normally occur in dune grasslands (H2130). A steep decline of lichens was largely caused by trampling. Large herbs declined due to

grazing, and as a result, poisonous herbs benefited from the lack of competition. The latter was already shown in several earlier studies. Based on half a century of standardized flora monitoring, Mourik (2015, 2017) showed that only very small or poisonous species, some grasses and older trees and larger scrub with thick barks survived. No less than 66% of all common non-poisonous flowering plants measuring over 15 cm in height had decreased strongly between 2000 and 2013-2014. Species with large leaves or inflorescences decreased more than smaller species (that are less vulnerable to grazing). As expected beforehand, poisonous species did not decrease. Oosterbaan et al. (2019) state that based on flora mapping for the Natura 2000 monitoring system, virtually all plant species had been negatively affected by fallow deer grazing accept for the poisonous and very odorous ones.

3. *Characteristic flora species*. On the third scale level, Oosterbaan & Mourik (2020) concluded that coverage of characteristic dune plants had decreased in alarming rates. Out of 177 species mapped between 1997 and 2017, 72% decreased whereas only 24% increased. For species depending on pollination, even 76% decreased and only 19% increased.

   The effects of grazing on larger flowering herbs were already studied before deer numbers peaked. In a small-scale field experiment, using 16 1x1 m exclosures spread over four dune grassland sites, Reussien (2013) and Aldershof (2014) showed that deer grazing had a negative impact on flower richness and the occurrence of host plants for butterflies. In control plots, species normally very common in the dunes like viper's bugloss (*Echium vulgare*), common bugloss (*Anchusa officinalis*), common evening-primrose (*Oenothera biennis*) and greater mullein (*Verbascum thapsus*) were nearly impossible to find. If present, usually only rosettes were found, whereas these species grew abundantly within the small exclosures (Figure 5). In the control plots, only poisonous, very smelly and/or thorny species like common ragwort (*Jacobaea vulgaris*) and hound's tongue (*Cynoglossum officinale*) flowered. Mourik (2017) showed that the steep decline of 78 species between the 1996-2005 and 1996-2015 decades was much stronger than expected based on national trends, correlating with the strong increase of the deer population, and that the decrease intensified during the final years of the study (with deer numbers still growing). This also affected rarer species. For instance, in 2006-2014 there were still 54 sites with the nationally rare round-leaved wintergreen (*Pyrola rotundifolia*), but in 2015-2016 only six sites were left. A similarly alarming trend was seen in the localized *neerlandica* subspecies of the orchid broad-leaved helleborine (*Epipactis helleborine*), with 49 sites found in 2006-2014, but only two in 2015-2016. Wild basil (*Clinopodium vulgare*) decreased from 168 sites in 2002 to 15 in 2015-2016 (Mourik 2017). Oosterbaan & Mourik (2020) mentioned that due to an increase of small-scale sand drift caused by ecological restoration projects, pioneering species should have benefited, but didn't. These also decreased as a result of deer grazing.

4. *Physical condition of plants*. The fourth, smallest scale, that was not specifically categorized as such by Oosterbaan & Mourik (2020), is the physical state of plants. Many plants are still present, but do not or barely flower (Mourik 2015). Edible plants that have not (yet) been grazed off to the ground, are in a poorer physical state than those protected within exclosures. Oosterbaan et al. (2019) state that this even applies to normally very common species. During flora mapping, many were encountered in a vegetative state only. On transects used for standardized butterfly monitoring, the number of flowers (and thereby: nectar supply) strongly decreased. In 1992-1996 (hardly any fallow deer), 2007-2008 (mod-

Figure 5. In a field experiment with small exclosures (Reussien 2013, Aldershof 2014) unfenced control plots were grazed off to the ground, whereas inside small exclosures (1m x 1m) larger flowering herbs grew abundantly, in this example dominated by viper's bugloss (*Echium vulgare*), Amsterdamse Waterleidingduinen, 8 June 2016 (Vincent van der Spek/ Waternet).

erately high numbers) and 2015-2016 (peak numbers) the number of flowers along butterfly monitoring transects were counted. Between 2007-2008 and 2015-2016, the number of flowers suitable for butterflies decreased by 77%. Compared to 1992-1996, this was even 98% (Wallis de Vries 2017). Van der Spek & van der Voet (2018) used broad-leaved helleborine as an example species in order to measure the physical state of edible plants. The orchids within two 7x4 m exclosures were on average more than twice as large, the size of the leaves was nearly twice as long and the number of flowers was more than twice as high as in helleborines in the control plots. The number of flowering plants within the exclosures was 131, whereas only twelve were found in the control plots within the same humid dune slack (H2190). Oosterbaan et al. (2019) confirmed this by concluding that 95% of the broad-leaved helleborines inside exclosures flowered, opposed to only 5% outside the exclosures.

Effects of grazing on fauna

Mammals

The population of roe deer in AWD was at a maximum between 1996 and 2002, with up to 250 counted. With increasing numbers of fallow deer, roe deer rapidly declined and eventually disappeared altogether (Figure 6). Nowadays they are only very seldomly seen, whereas they do occur regularly in surrounding estates without fallow deer (personal observation). Rabbits are the other mammalian grazers of the area, but populations in the Netherlands including AWD have dwindled, in many places to near-extinction, due to the outbreak of variants of Rabbit Hemorrhagic Decease. Potential positive or negative effects in relation to fallow deer could therefore not be studied.

Birds

The nightingale (*Luscinia megarhynchos*) is on the Dutch red list of threatened birds. Nationally the numbers have declined, but

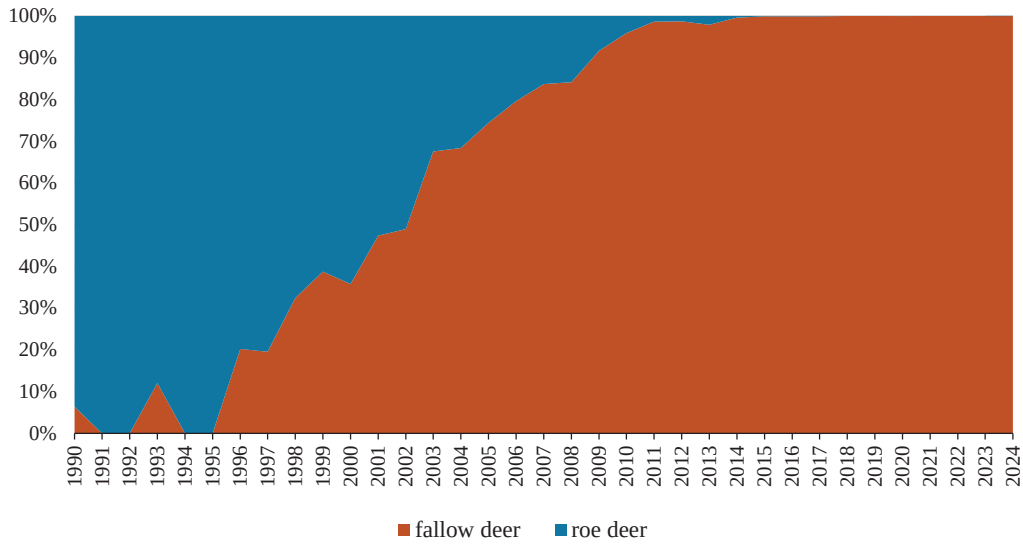

Figure 6. Ratio of roe deer (orange) vs. fallow deer (blue) during deer counts at Amsterdamse Waterleidingduinen 1990-2024. Roe deer have been outcompeted by fallow deer: they virtually disappeared after 2014.

the calcareous coastal dunes form the national stronghold, and densities are still high there. AWD however forms the exception. Noordzij & van der Spek (2017) showed that there is a significant negative correlation between deer and nightingale densities. The higher the deer densities, the steeper the declines. In 2015, the lowest number of nightingales since the start of the standardized breeding bird censuses in 1985 was reported. In Meijendel, province of Zuid-Holland, a geomorphologically similar dune system without fallow deer (save a few stragglers), the nightingale densities slightly increased during the same time span. In order to eliminate other causes, only areas without past large-scale nature restoration measures like removal of the invasive alien black cherry (*Prunus serotina*) or sod cutting were used in this study. Browsing and trampling by deer resulting in more open scrub with less cover was believed to be the determining factor for the declines within AWD (Noordzij & van der Spek 2017). Another example species dependant on scrub (H2160) for breeding is the dunnock (*Prunella modularis*). De Groot (2024) showed that based on breeding bird censuses between 1984-2022, the species declined steeply after 2010, whereas similar declines were not nearly as strong both in comparable areas just outside AWD and nationally. Based on aerial photographs, De Groot (2024) concluded that scrub with e.g. sea buckthorn and wild privit (*Ligustrum vulgare*) had declined and the quality of remaining scrub deteriorated (H2160), caused by fallow deer trampling and grazing.

Reptiles

Sand lizard is the only reptile species of the area. Coastal dunes form an important habitat for this strictly protected species under the Habitats Directive. Based on long-term monitoring the population in AWD increased between 1994 and 2012 (Ehrenburg & Janssen 2014). However, the population has declined between 2012 and 2023. Nationally, the population also declined since, so more factors seem to be at place, but Molenaar et al. (in press) showed that the population in AWD declined earlier, and that the decline was steeper, also compared to similar areas nearby with less or no fallow deer. They showed that

the habitat within lizard monitoring plots had changed and that habitat structure, which is of vital importance for sand lizards, had declined as a result of grazing.

Butterflies
Three studies based on long-term monitoring show that the butterfly population (all species combined) decreased by 76% between 2005 and 2016 (Wallis de Vries 2015, 2017, 2019). Fifteen out of the 23 species (65%) that are common in AWD declined. These declines were statistically significantly stronger than in the neighboring NPZK, where deer densities were much lower. The declines in AWD were also statistically significantly stronger than in comparable coastal dune systems without fallow deer elsewhere in the Netherlands. The declines intensified in 2015-2016, with deer numbers still on the rise, compared to 2014. Declines were strongest in species that, based on their ecology, *a priori* were classified as moderately to very vulnerable for grazing, whereas species marked as not vulnerable for grazing did not show such marked declines. This was further demonstrated by the fact that areas with higher deer densities showed stronger decreases. According to the author, this shows that the relationship between increasing deer numbers and declining butterfly population are causal. Finally, after the number of deer also increased in NPZK, species vulnerable to grazing also started to decline there.

Moths
For the macro moths, Wallis de Vries (2015) calculated that a larger number of species declined in AWD (30% out of 393 species) than in neighboring NPZK (13% out of 420 species). As in butterflies, the decline in species *a priori* marked as vulnerable for grazing was strongest. Moth monitoring between 2006-2019 showed that especially a group of species dependant of dune grasslands was in decline. Six out of seven of these species show more positive trends nationally, whereas they declined in AWD. Therefore the causes were thought to be local and the author links this to grazing by fallow deer (Kruijsen 2021).

Bees, bumblebees and hoverflies
With edible flora decreasing (see above), population declines of species dependant of plants as hosts or for nectar were expected. Smit (2015) calculated that out of 85 species of bees and bumblebees known to occur in AWD between 1980 and 2014, 65 must have decreased based on their ecology (dependance on nectar) in relation to long-term plant monitoring data (Mourik 2015). For ten species the decline was over 50%. In some species of hoverfly the larvae use specific host plants. Out of 105 species known to occur in AWD between 1980 and 2014, eleven species were thought to have shown a strong decline, whereas only two had increased. The estimated trends for bees, bumblebees and hoverflies were based on the absence or occurrence of plant species per km² grids and not on the actual numbers of plants, let alone the physical state of individual plants. Smit (2015) therefore stated that the actual declines must have been much stronger than calculated.

Ants
Ants are the only group studied for which negative effects that can be correlated with fallow deer were not found (Noordijk & van Loon 2015). Based on expert judgement however, the authors did raise concerns about scarce species with nests above the ground, since trampling by deer could disturb these.

Narrow-mouthed whorl snail (Vertigo angustior)
This tiny snail is a Habitats Directive species (H1014) and it therefore is of high nature management importance. Population sizes or trends are unknown, but in general grazing has a negative impact. Expert judgement by independent authorities on mollusks came to the conclusion that grazing pressure by fallow deer has created a 'savannah-like' habi-

tat (low vegetation with larger bushes), with a large impact on the structure and composition of the vegetation and the structure of the soil. Therefore a strong decrease of snails in general, including the narrow-mouthed whorl snail, was suspected (Boesveld & Gmelig Meyling 2018).

Discussion

Legal status

The Dutch legal status of fallow deer as a native, protected species can be challenged. Based on fossil records, fallow deer indeed once occurred in the Netherlands naturally. However, it also went extinct naturally under a climate change, and all current Dutch populations are of feral stock.

Population trends and number of deer counted

Using Lidar data for deer counts in a hilly terrain with forests and scrub is very much in its infancy and the value of the results need to be interpreted with caution. Two issues arise: in order to cover the entire area, a plane has to fly a total of 30 flight lines in order to cover the area. In the meantime, deer were expected to have moved around. Determining the number of double counts as well as the number of deer missed was impossible. Aerial photographs were made simultaneously. Artificial Intelligence could detect objects but was far from flawless, and deer had to be manually separated from other large living creatures like cattle, foxes, visitors etc., making it vulnerable to mistakes. Based on expert judgement, the hunters estimate 40-50% of the deer are missed during the official counts, in most years towards the higher end of this estimate. This matches the combined Lidar and population modelling data of 40-48%. The percentage of deer missed in the official counts varies from year to year: varying weather conditions are for instance of influence (Marcel Doornbosch, personal communication, 24 August 2024). Using the mean of the three counts instead of the highest number counted in a year could also be used as method, but the current method is used by all site managers in the region, as prescribed by the local authority responsible for fauna management (Faunabeheereenheid Noord-Holland). The current counts however give a good insight in the long-term population trend. Does are no longer in the vast majority, meaning the population has leveled off and the current numbers imply that the desired counted population size of 600-800 has come within sight. The trend is validated by the number of deer counted during rabbit transactions counts. Despite the numbers being much lower than in the official counts, the trends are extremely similar (Figure 7) and correlate statistically (Spearman's ρ=0.987).

Effects of deer grazing on biodiversity

In order to preserve Natura 2000 habitat types and their rich biodiversity, some degree of grazing is desired, especially as long as nitrogen deposition levels remain too high. Without grazing (and mowing), this leads to grass encroachment. But the exponential growth of the deer population has resulted in an imbalance. Surprisingly perhaps, four centuries ago the impact of fallow deer on the vegetation of a calcareous dune system was already acknowledged. At the start of the 17th century, one hundred fallow deer from England were introduced in the dunes near The Hague, the Netherlands. Twenty years later they were all shot, since the damage to the vegetation was considered too high (Chapman & Chapman 1980). Measuring biodiversity as a whole is practically impossible. The number of species (groups) studied is however believed to be diverse enough to form a good sample. Several studies show the negative effects of fallow deer

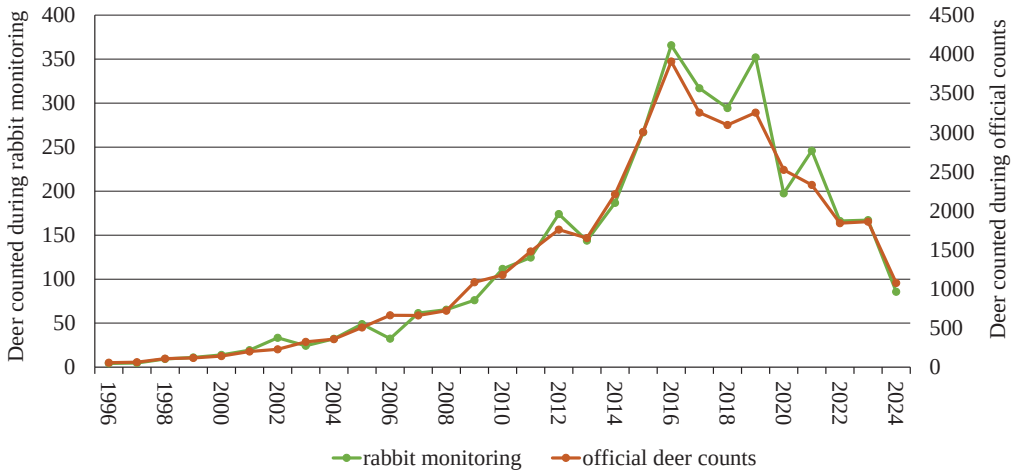

Figure 7. Fallow deer trends in Amsterdamse Waterleidingduinen are being monitored in two ways: 1. During area-wide official deer counts. 2. During transect counts designed for rabbit monitoring. The strong similarity in trends seems to validate both trend monitoring methods.

grazing and trampling on habitats and plant species, and that, as a consequence, there are cascading effects on a wide range of animal species, ranging from invertebrates to vertebrates. Since none of the studies show largely profiting species (groups), it seems justified to conclude that high-pressure deer grazing has caused broad biodiversity loss. Future monitoring will show if deer management was in time and if habitats and their plant and animal species will recover, and if an extinction debt was prevented. With deer numbers currently still being considered too high, signs of recovery have not yet been measured. For instance, the deer counts show that roe deer have not yet returned. Between 2017 and 2022, common nightingales decreased further (Waternet/Sovon, unpublished data), which is perhaps unsurprising since the scrubs where they normally breed in had not recovered from the trampling effects. The next vegetation mapping is scheduled around 2030. This will shed light on the extent of recovery of habitats. In 2024 the flora of the entire area was mapped. The results have not yet been analysed, but based on field impressions recovery of characteristic species was not noticed (Bernard Oosterbaan, personal comment, 7 November 2024). A renewed analysis of the butterflies is scheduled for 2025, but again the impressions from the field are not positive (Mark van Til, personal comment, 7 November 2024). Most of the studies show a correlation between an increase of deer on the one hand and a decrease of a (group of) species on the other. The field experiments with the small exclosures were very informative, but the scale was too small from a scientific point of view. Nonetheless, causal effects between high grazing pressure by fallow deer and biodiversity loss seem likely for two reasons:

1. The amount of studies showing declines of species (groups) and negative effects on habitats over time, that also differ from very similar areas with far lower deer densities or no deer at all; and 2. Many of the conclusions are supported by studies on (fallow) deer grazing elsewhere. In a worldwide review on deer overabundance, Côté et al. (2004) described the effects on the growth and survival of many herb, scrub, and tree species, and how this modified patterns of relative abundance and vegetation dynamics. As a consequence, there are cascading effects on insects, birds, and

mammals, in line with the findings in AWD. Several studies are directly related to specific species (groups) that have declined in AWD. Italian studies show that fallow deer are dominate over roe deer and that they outcompete them (Focardi et al. 2006, Feretti et al. 2011), and that this is not habitat-dependant (Feretti et al. 2012). It is known that high densities of deer in Britain negatively affect the populations of several passerine species (Newson et al. 2011). Palmer et al. (2015) showed when population trends for deer strongly increased (46%), the population trend across deer-sensitive birds dependant on understory vegetation declined much more than the trend for deer-tolerant birds. Causal effects have even been specifically studied in nightingales. An experiment shows that deer browsing reduces habitat sustainability for breeding nightingales. Densities within unbrowsed exclosures were 15 times higher than in browsed control plots (Holt et al. 2010). Invertebrate abundance and species density decreased with an increasing length of browsing history by introduced Sitka deer (*Odocoileus hemionus sitkensis*) on Canadian islands that were compared with neighboring islands without deer (Allombert et al. 2005). In Britain, red deer (*Cervus elaphus*) can negatively affect both the vegetation and invertebrates (Baines et al. 1994), and though depending on the local situation, butterflies can suffer from deer grazing, including by fallow deer (Feber et al. 2001). These are just examples; many more studies supporting the findings in AWD can be found.

Future perspectives

The aimed counted population size of 600-800 fallow deer was determined by the province administration, based on a report that modelled the population size in which fallow deer in AWD could co-exist without mutual competition (Groot Bruinderink et al. 2013). This roughly equals the population size of 2006-2008. This coincided with the fact that for many studied species, this was around the threshold of their declines. With an aimed population size of 600-800 counted deer, the actual density (including the 40-48% of deer missed during the counts) will then be an estimated 34-45 per deer/km². If this is low enough to stop a decline in biodiversity remains to be seen. Effects of deer grazing on open dune habitats have not been extensively studied elsewhere, but there are many studies on deer grazing and their effects on forests, of which over 700 ha is present in AWD. In a field experiment with white-tailed deer (*Odocoileus virginianus*) in the east of the United States, the threshold of a negative impact on forest vegetation was 8 deer/km² (Horsley et al. 2003). Though white-tailed deer are on average moderately larger and heavier than fallow deer, this is much less than the aimed for 34-45 fallow deer/km² in AWD. A British study states that forest regeneration is most likely impossible when deer densities, including fallow deer, are higher than 14 deer/km² (Gill & Morgan 2009). As shown by Oosterbaan et al. (2020), the habitats in AWD were impoverished by years of high-pressure grazing. In a growing population, 600-800 counted deer might have been around the threshold for biodiversity loss, but due to the impoverishment of the habitats, hysteresis might have taken place. Hence, it is likely that 600-800 deer is too many for full biodiversity recovery. A scientific study by University of Amsterdam, Stichting Bargerveen and De Vlinderstichting in collaboration with site managers Waternet en PWN (NPZK) has been conducted since 2020. In AWD 16 larger fenced exclosures covering 40 ha. have been placed, preventing deer from grazing (smaller grazers like rabbits can enter). Unfenced, grazed plots of a similar size in similar habitat serve as controls. Grazing effects on vegetation and invertebrates are being measured. The exclosures were only placed in the second year of the study, in order to carry out baseline measurements in the first year. This allows a comparison in both space and time of the grazed

and ungrazed plots. This study will thereby provide insights in causal rather that correlative effects. Furthermore it might give more insights into the question which deer densities are optimal in relation to both Natura 2000 objectives and biodiversity in general. After a population size of 600-800 has been achieved, ongoing analyses and evaluations should lead to adaptive deer management in order to find the right balance.

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Samenvatting

De invloed van begrazing van damherten op de biodiversiteit van een Nederlands duingebied

De Amsterdamse Waterleidingduinen zijn een grotendeels kalkrijk duingebied van bijna 3400 ha op de grens van Noord- en Zuid-Holland. In de jaren 1990 en aan het begin van deze eeuw, nam het aantal damherten (*Dama dama*) er exponentieel toe. De soort was eind jaren 1960 elders in de regio illegaal uitgezet. Met de toename van de herten nam ook de graasdruk in het gebied sterk toe. In het voorjaar van 2016 lag de dichtheid op 190-220 damherten/ km², wat op basis van onderzoeken elders zeer hoog is. Uit onderzoeken blijkt dat de toegenomen graasdruk een groot effect heeft op de flora en vegetatie, wat een cascade-effect veroorzaakt en waardoor ook diersoorten sterk afnemen. Dit artikel vat alle gepubliceerde onderzoeken samen. Naast planten en vegetatie zijn effecten gemeten op zoogdieren (reeën zijn geheel verdwenen), struikbroedende vogels, zandhagedissen, vlinders, nachtvlinders (zowel micro's als macro's), bijen, hommels en zweefvliegen. Van de onderzochte groepen werden alleen op mieren geen effecten gevonden. De correlaties (en in een enkel geval causale verbanden) tussen toegenomen graasdruk en afnemende biodiversiteit is gemeten aan de hand van langlopende monitoringsnetwerken van flora en fauna (dikwijls uitgevoerd door vrijwilligers), alsmede databases met losse waarnemingen zoals waarneming.nl, datamodellering, nieuw veldwerk zoals kleinschalige veldexperimenten naar graaseffecten en vegetatiekarteringen, en (internationale) externe expertmeningen. Veel onderzoeken zijn uitgevoerd door onafhankelijke kennisinstellingen. Daarbij zijn zowel vergelijkingen gemaakt in de tijd (voor en na toename van herten binnen het gebied) als in ruimte (vergelijkingen met zeer vergelijkbare gebieden zonder of met veel minder damherten). De onderzoeken wijzen dusdanig één kant op, dat het gerechtvaardigd is te concluderen dat begrazing door grote aantallen damherten leidt tot aanzienlijk biodiversiteitsverlies. Dit sluit aan bij internationale onderzoeken naar (dam)hertenbegrazing. Deels gebaseerd op het aangetoonde biodiversiteitsverlies wordt de populatie sinds het najaar van 2016 middels afschot in aantal teruggebracht. Een lopend wetenschappelijk onderzoek naar graasgedrag moet mede antwoord geven op de vraag welke hertenstand acceptabel is vanuit biodiversiteitsoogpunt.

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The pine marten (*Martes martes*) population in a wooded coastal dune area in the Netherlands

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Abstract: This article presents the findings of a long-term study on the population structure, social organization and spatial behaviour of pine martens (*Martes martes*) in a forest area in the Noordhollands Duinreservaat, a coastal dune reserve in the Netherlands. A rich dataset of the pine martens inhabiting the area was generated by using camera traps to record the individually unique bib patterns of the martens. Based on the data collected, a database was compiled that allowed analysis of where, and when, the individuals were registered. A total of 9892 images of pine martens were recorded, and in 78% of these cases, the pine martens could be individually identified. In the four-year period between 2020 and 2023, a total of 64 individuals were recognized in the research area, which covered about 1500 ha. Many of these individuals were followed for long periods of time and each had its territory or at least a home range, with a high population density of pine martens of 2.2-2.8/km2. On average, two different pine martens occurred at each camera trap location. At one location, seven different individuals were seen. However, at two locations no pine martens were registered. Recording the date and time of the recordings provided insights into the martens' activity patterns and allowed the creation of an extensive annual overview on a two-weekly and half-hourly basis. The individuals observed could be classified as kittens (first calendar year), territorial males, territorial females, and non-territorial (sub)adults. These non-territorial animals were females in their second or third calendar year and males in their second, third and one even in its fourth calendar year. By deploying camera traps, 32 subadult pine martens, which had a home range, but no territory, were monitored during these four years. Several were born in the research area, appeared on video for the first time with their mother and were followed in subsequent years. This provides insights into the social behaviour of pine martens in a family context. Usually, two female partners live in the territory of an adult male, together with several (sub)adult pine martens, each with their own home range within the boundaries of the territorial male. The number of (sub)adults in each adult male's territory can vary from year to year. Social interactions were filmed, including growing young males playing with their mother's new generation of kittens.

Keywords: pine marten, *Martes martes*, camera traps, bib patterns, population structure, reproduction, social organization, spatial behaviour, daily activity pattern.

Introduction

Historical pine marten sightings in the Dutch province of North Holland are rare. The first confirmed sighting of a pine marten in Noord-Holland was made in the mid-1990s (Broekhuizen et al. 2016). Since the turn of the Millennium, pine martens have begun to colonize Noord-Holland. A study of the population size and structure was started shortly after the first pine marten was seen in 2006 in the Noordhollands Duinreservaat (NHD), a nature reserve at the coast of the North Sea.

Pine martens are mainly active in the night, rather secretive and thus difficult to observe. It is only after the advent of transmitter technology, DNA analysis and camera trap tech-

niques that a comprehensive picture of how pine martens live have emerged. It is clear from the literature that the densities and size of pine marten home ranges and territories greatly depend on the habitat and the available food supply (Brainerd et al. 1994, Balestrieri 2023). Pine martens are omnivores, although their diet mainly consists of mice. Male pine martens will mate with several females in one breeding season. Pine martens often exhibit intra-sexual territorial behaviour: i.e. male territories exclude other males, and female territories exclude other females (Balharry 1993, Birks 2017, Balestrieri 2023). Young male pine martens have an extended subadult stage in which maturity is delayed until they have passed their third birthday. Young female pine martens reach sexual maturity in the year following their birth, but because of the long period of delayed implantation they do not first give birth until their third calendar years (Birks 2017). Little is known about the spatial behaviour of these non-territorial individuals compared to territorial male and female pine martens.

This study on pine martens started in 2007. It is important to record the pattern of their bib is in order to recognize pine martens individually. It has become clear that individual pine martens can be uniquely identified by their bib patterns (Birks 2017). This can be done by making pictures or videos during an encounter with a pine marten with good quality camera equipment, but until 2011 only few pine martens were photographed and individually recognized. In 2011, the first camera traps were deployed. In 2012, a large-scale study with camera traps was carried out. Many pine martens were recorded at different locations, but individual recognition of the bib pattern was not possible at that time (Hamers et al. 2013). It wasn't until 2019 that the method and technology of camera traps were good enough to identify martens individually using camera traps. The use of these new cameras in 2019 provided images of different male pine martens at the same location. This was a strong indication

Figure 1. Location of the study area.

that there were subadults in the study area. To improve our knowledge of how many individual pine martens were around we started to intensively use high-quality camera traps. A method that was continued in the following years. 'Using this technique, the goals of this study were to determine the number of pine martens in the NHD, to clarify family relationships and to determine population structure by sex and age classes of the pine marten population in the NHD.

Materials and methods

Study area

The Noordhollands Duinreservaat (a Natura 2000 site) is a 5300-hectare forest and coastal dune area between Wijk aan Zee and Bergen (in the province of Noord-Holland) (Figure 1). A third of this area consists of forest. Since 2007, research into the occurrence of the pine marten has been conducted in most of the forested part (87%, ca. 1500 ha) of the Noordhollands Duinreservaat.

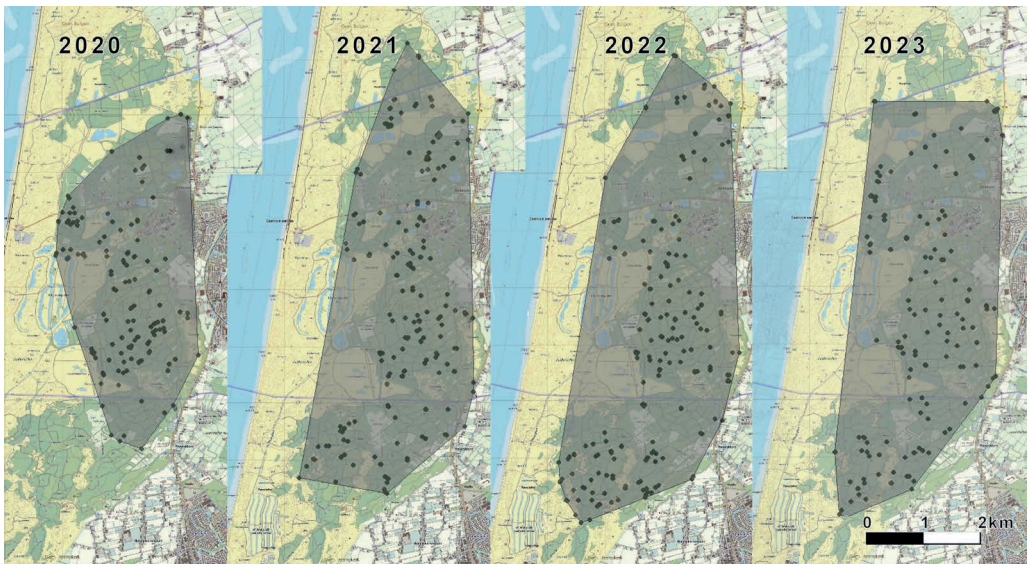


Figure 2. An overview of where camera traps were located each year. On average, the cameras remained at one location for three weeks.

The largest part of this forest was in use from 1820 and, until 1940, wood was harvested for various purposes. The forested surface consists of 12% coniferous wood and 88% deciduous forest. The deciduous trees belong to the native flora and are planted in places where they have been able to develop into natural dune forests. The most important tree species that occur are oak (*Quercus robur*) and birch (*Betula* spp.). In addition, species such as maple (*Acer* spp.), beech (*Fagus sylvatica*) and poplar (*Populus* spp.) occur. Provinciaal Waterbedrijf Noord-Holland (PWN), which combines the roles of being a drinking water company and nature management organization, has being trying to convert the coniferous forests into more natural deciduous forests. The coniferous tree species, mostly black pine (*Pinus nigra*), are not native flora. The shrub layer contains species such as hawthorn (*Crataegus* spp.), privet (*Ligustrum vulgare*), holly (*Ilex aquifolium*), dewberry (*Rubus caesius*), wild honeysuckle (*Lonicera periclymemum*), American bird cherry (*Prunus serotina*), alder buckthorn (*Frangula alnus*), wild rowan (*Sorbus aucuparia*) and spindle tree (*Euonymus europaeus*). To maintain openness, PWN uses large grazers, such as Exmoor ponies, Highland cattle, sheep, goats and Holstein-Friesian cattle, which are to be found in many places in the research area.

A main road runs along the east side of the site that separates the forest from residential areas and the agricultural landscape. The western border is the transition to an open dune landscape. To the north and south there is partly forest and open dune area. There are many walking and cycling paths in the area, which are used intensively between sunrise and sunset. There are three camping sites in the research area.

Camera trap set-up

From 2020 to 2023, ten camera traps were deployed throughout the year and were moved every three weeks (Figure 2). During the period with young pine martens, cameras of an older type were sometimes added. The following types of camera traps were used: Bushnell TROPHY CAM HD Brown, Bush-

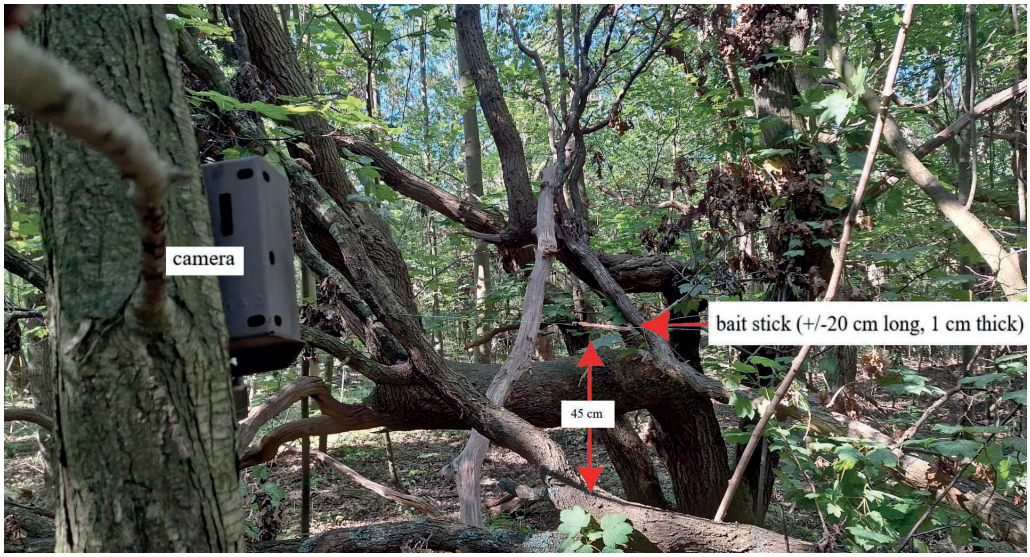


Figure 3. Camera trap set-up – location 23-116.

Figure 4. Camera trap setup snapshot location 23-116: night and day recordings.

nell Nature View HD Max, Stealth Cam DS4K, Reconyx Hyperfire 2 and Maginon WK4HD. These were replaced during the research by Browning 2021 Recon Force ELITE HP4 and Browning 2022 Recon Force Elite HP5 cameras. In front of the camera trap, a bait stick (ca. 20 cm long, 1 cm thick), was hung at 1.5 to 3 metres from the camera and approximately 45 cm above the ground, tree trunk or branch. A small amount of peanut butter was spread on the bait stick, but also on some branches / trunks that were visible on the camera, a dried plum was divided into four pieces and mounted on the bait stick and branches with a screw. This created a set-up in which a pine marten had to stand upright to reach the bait, allowing the camera to film the marten's bib pattern (Figures 3 and 4). The camera traps were checked twice a week. During the inspection new bait was applied, the images were viewed in the field and camera trap set-up adjustments were made where possible to increase the chance of making more recognizable images of the bib pattern.

Analysis

For the analyses of bib patterns, unique ID cards (Figure 5) were created by hand for each individual. ID cards consist of a standard pine marten drawing where the bib pattern is drawn plus a compilation of snapshots of this pattern from videos at different angles and

Figure 5. Example of an ID card. On the left a drawing of a bib, on the right compilations of stills from videos of the same individual taken during the day and at night and from different angles.

Table 1. Annual differences from four years of camera trap research: research year and area, number of locations, number of film observations, number of individuals recognized and density.

2020	2021	2022	2023
994 Ha	1553 Ha	1721 Ha	1575 Ha
137 unique locations 1622 images	211 unique locations 2725 images	230 unique locations 3050 images	176 unique locations 2495 images
22 unique pine martens	41 unique pine martens	49 unique pine martens	40 unique pine martens
Density 2.3 per km²	Density 2.6 per km²	Density 2.8 per km²	Density 2.5 per km²

lighting. This is manual work using a photo editing programme that can work with layers. In this way the bib pattern can be traced. The GPS location, camera name, individual ID and the date and time of each image were registered. Sex determination was mainly done by the visible scrotum of males and the puffy nipples of females. It often happened that the gender could only be determined after several registrations. In the second calendar year, especially during the mating season, this became easier. Kittens filmed with a female in May, June and July were assumed to be her offspring.

By plotting the GPS coordinates of each pine marten on a map, a picture emerged of which pine marten was observed where and which individuals shared locations. To estimate the size of the home range of individual martens, minimal convex polygons were calculated (Paterson 2018, https://www.r-project.org/). Although minimum convex polygons are commonly used to estimate home range sizes, they may potentially include areas that are not visited by the individual and thus result in an overestimation of the home range size. This also applies in reverse, i.e. pine martens can also occur outside the minimum convex polygon. Since data from open terrain and outside the research area are missing, it was not possible to make a good estimate of the home range for each individual.

Results

Overview of data per year

Over the study period (2020-2023), camera traps at 723 locations resulted in a total of 9892 registrations of pine martens. Of these registrations 78% were of sufficient quality to distinguish unique individuals, resulting in a total of 64 individuals (Figure 6, Table 1), with the exception of the kittens which were seen

Figure 6. Individual pine martens that were recognized over four consecutive years by their bib pattern. Each pattern has been traced using video fragments.

for only a short period and who probably died before becoming independent or dispersed from the study area.

Turnover in the pine marten population

In 2021, the survey area was extended by 559 hectares. The six females and three males seen in this area in 2021 were also present in the area before 2020. Figure 7a shows the total number of observations of pine marten individuals per quarter, classified by life stage per sex.

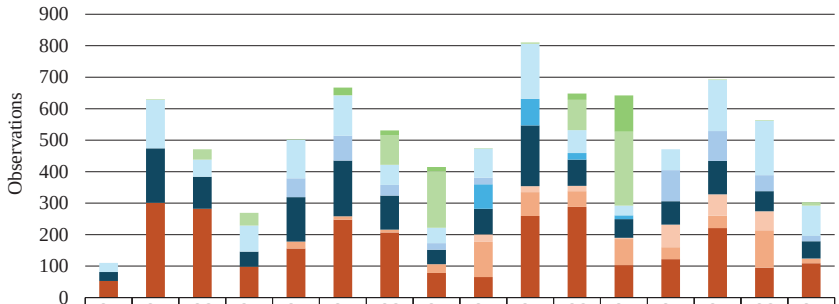
Not all 64 unique pine martens were present at the same time. On average, 15 territorial females, seven territorial males and ten subadults were recorded each year. In the four-year study period, five territorial females, three territorial males and 18 subadults disappeared without trace. During this period five traffic victims were found, two 2nd calendar year males (2 June 2021 and 22 June 2021), an unknown, presumably young, female (7 September 2022) (based on the slight wear of the teeth) and two adult females (8 July 2021 and 5-13 May 2023).

Subadults, especially males, may be present in their father's territory for several years. Figure 7b shows the number of individuals present in each quarter of each year. The unique individuals are divided into life stages and by gender. The 1st of January has been taken as the division date between the life stages. A pine marten in its first calendar year is classified as a kitten.

Young females become sexually mature in their 2nd calendar year. Nine 2nd calendar year females could be followed during this period, and all appeared on camera in their 3rd calendar year. Two of these young females appeared on camera with young. In spring (lactation period) lactation was observed in other young females, which may include phantom pregnancies. Adult females who gave birth to kittens that spring usually appeared on camera with kittens for the first time in early July, some time after their reproductive status was noticed by showing signs of lactation. These 3rd calendar year females had established their own territories at the edge of their mother's territories. One of these 3rd calendar year female pine martens disappeared from her territory in August 2022, eleven months later this "missing" female was caught by a camera trap in a narrow forest plot on the edge of the research area. She came in front of the camera together with a new young. She had changed her territory. Her young, born in 2022, were regularly seen in her parents' territory, where the neighbouring female was now staying.

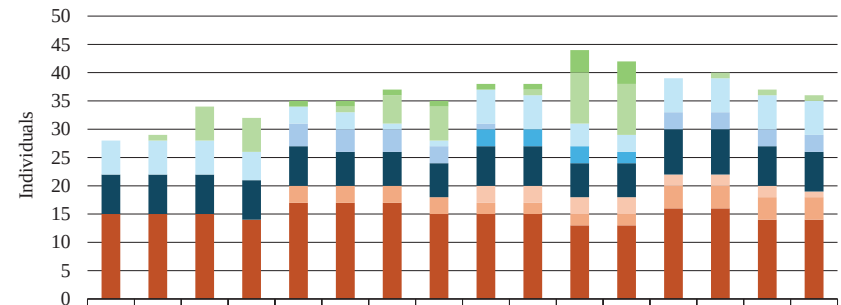
Males may reach sexual maturity in their 2nd calendar year (Stier 2012, Broekhuizen & Müskens 2000), but generally do not show signs of sexual activity until they reach the

(a)



	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
	2020				2021				2022				2023			
New	0	0	0	0	1	24	16	13	1	1	20	115	0	0	0	0
kitten	0	2	33	40	0	1	93	180	0	3	96	235	0	2	2	11
2nd calendar year males	29	154	54	83	122	128	64	49	92	175	73	31	66	162	173	96
3rd calendar year males	0	0	0	0	60	79	34	21	21	0	0	0	99	95	51	17
4th calendar year males	0	0	0	0	0	0	0	0	78	84	21	12	0	0	0	0
male adult	28	173	102	48	141	177	108	46	81	193	83	59	74	106	64	55
2nd calendar year females	0	0	0	0	0	0	0	0	24	19	17	4	72	68	60	1
3rd calendar year females	0	0	0	0	22	11	9	28	112	76	50	83	38	39	119	14
female adult	53	301	282	98	156	247	207	78	65	259	288	103	122	221	95	109

(b)



	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
	2020				2021				2022				2023			
New	0	0	0	0	1	1	1	1	1	1	4	4	0	0	0	0
kitten	0	1	6	6	0	1	5	6	0	1	9	9	0	1	1	1
2nd calendar year males	6	6	6	5	3	3	1	1	6	6	4	3	6	6	6	6
3rd calendar year males	0	0	0	0	4	4	4	3	1	0	0	0	3	3	3	3
4th calendar year males	0	0	0	0	0	0	0	0	3	3	3	2	0	0	0	0
male adult	7	7	7	7	7	6	6	6	7	7	6	6	8	8	7	7
2nd calendar year females	0	0	0	0	0	0	0	0	3	3	3	3	2	2	2	1
3rd calendar year females	0	0	0	0	3	3	3	3	2	2	2	2	4	4	4	4
female adult	15	15	15	14	17	17	17	15	15	15	13	13	16	16	14	14

Figure 7. Total number of observations of individual pine martens (a) and of individuals (b) per quarter, classified by life stage and gender. Q1, Q2, etc. refer to quarters of the year.

age of three years (Balharry 1993, Kleef & Wijsman 2015, Balestrieri 2023).

During this study, two 4th calendar year males established their own territories. A male born in 2019 was found in January 2022 at another location in the study area. Another male, born in 2019, took over a territory from his father. This father, who was followed from 2018, was seen in 2020 in several places outside his own territory and the last sighting was on 15 May 2022, limping in front of a camera trap. In 2018 this male had his own territory.

Table 2. Daily activity patterns of pine martens in the course of the year, by two-week period, cumulated over the years 2020-2023. Numbers represent the number of pine martens recorded by the camera traps. A darker grey hue indicates more records, i.e. a higher activity level. Recordings with imprecise times are not included.

week number / Time	01+02	03+04	05+06	07+08	09+10	11+12	13+14	15+16	17+18	19+20	21+22	23+24	25+26	27+28	29+30	31+32	33+34	35+36	37+38	39+40	41+42	43+44	45+46	47+48	49+50	51+52	Total
0:00	8	5	18	8	15	13	17	26	24	43	40	40	33	31	40	31	27	19	28	15	18	17	14	13	7	12	562
0:30	7	8	11	5	12	22	6	15	17	38	35	32	18	13	26	31	14	24	14	13	8	19	6	10	9	14	427
1:00	2	6	11	9	12	16	20	17	21	26	27	27	19	17	17	24	22	38	19	10	11	9	13	3	6	17	419
1:30	4	7	13	5	9	25	12	16	24	22	26	20	18	21	11	27	19	19	15	11	14	15	10	7	7	8	385
2:00	10	12	13	13	15	13	6	22	15	24	15	18	15	14	17	13	13	26	31	5	15	9	9	11	10	9	373
2:30	3	8	7	6	13	16	15	19	17	22	21	21	20	16	12	11	14	28	9	11	11	10	11	4	9	17	351
3:00	7	20	11	5	6	8	17	14	19	18	19	20	17	24	16	15	16	21	16	9	16	6	8	4	2	9	343
3:30	6	11	9	8	6	10	18	11	22	22	25	15	18	9	19	14	18	13	13	9	17	24	10	14	5	13	359
4:00	4	10	9	6	9	8	11	9	19	28	22	16	19	9	15	26	16	22	13	8	11	18	11	13	6	10	348
4:30	4	7	9	9	11	16	11	19	15	17	12	17	14	22	23	20	10	14	16	9	7	9	8	4	7	15	325
5:00	4	5	11	3	2	7	10	16	18	18	14	19	6	6	13	10	15	11	16	6	12	5	10	9	13	8	267
5:30	6	5	7	3	7	4	4	2	12	11	10	11	10	13	9	11	11	14	7	13	9	6	5	8	4	8	210
6:00	6	7	10	2	2	5	6	5	2	11	6	12	14	11	8	4	4	7	11	5	3	7	2	7	2	10	169
6:30	8	4	3	5	1	1	3	1	3	3	6	8	4	8	6	2	4	8	2	4	8	7	12	3	2	11	127
7:00	3	2	2	5			1	2	4	3	5	8	3	7	5	4	1	5	5	7	3	8	2		4	2	91
7:30		1	2	1						1	2	9	8	4	4	3	3	8	1	4	2		1	1	7	2	64
8:00	2	1	3						2	1	2	3	7	7	6	1	4	5	2	4			2		3	2	57
8:30									1	1	8	4	7	9	2	4	3	3	3			2	1	1		2	51
9:00									2	1	3	2	5	7	5	1	6	4	4	1	1	3				1	46
9:30							1				4	3	4	5	4	4	4	5	1	2				1			38
10:00									1		7	2	1	1	2	1	6	2	2	4	3						32
10:30					1				1	2	5	1	6	2	1	6	1	2			1						29
11:00				1			1			1	1		1	6	2	2		4	4		1						24
11:30								1			2	1	3		2	2		3	2	3							19
12:00											2	2	4		1	1	2	4	1	2							19
12:30								1			2	3		1	3	2		2			2						16
13:00										1	5	4		1	1		1	1									14
13:30										1	1		1	3	3			2									11
14:00					1							4	2		1		2	1	2								13
14:30										3	2	3	2	2	2		2		2	1	1					1	21
15:00										2	2	2	1	3	2	3		2		1	1						19
15:30											1	2	2		5	2		1	1								14
16:00										3		5	3	3	2		3										19
16:30				1						1	3	7	3	1	2												18
17:00							1	1	1	2	7	7	3	3	2	3	2			1						1	34
17:30	5	1			1	1	2	1	3	2	8	5	2	1	7	2	1	2					2	6	3	5	60
18:00	3	12	3		2				2	3	4	5	5	2	7	2	3			3			6	15	6	22	105
18:30	12	7	10		4	1	1		1	5	8	9	7	4	5	5	2	1	2			1	9	12	13	24	143
19:00	5	10	15	18	20	6	2	1	4	4	7	8	8	4	3	3	3	3	1	3		3	12	16	17	19	195
19:30	9	7	16	16	23	24	6	3	3	4	6	8	8	7	4	4	6	2	4	2	9	15	15	13	14	21	249
20:00	5	7	9	15	19	18	17	3	5	4	9	11	3	7	8	4	3	9	6	13	17	12	16	15	13	17	265
20:30	12	21	18	23	16	29	14	14	6	10	8	13	10	7	8	6	9	13	17	10	13	23	10	10	14	15	349
21:00	6	11	10	16	18	29	27	30	19	21	10	16	16	14	10	6	4	18	22	13	26	19	10	16	17	13	417
21:30	4	18	11	14	17	15	36	30	43	17	22	17	10	14	15	12	15	20	21	27	12	12	10	10	12	14	448
22:00	5	8	19	13	10	18	30	36	46	39	27	29	16	24	27	23	24	35	23	27	18	14	9	12	3	14	549
22:30	9	8	8	12	6	21	25	43	48	52	39	30	24	36	41	22	20	29	26	21	18	16	10	10	10	10	594
23:00	9	14	11	14	21	26	18	35	48	57	56	44	29	37	50	35	41	22	18	15	20	15	17	8	9	10	679
23:30	8	9	13	18	11	17	24	26	36	31	31	31	28	30	28	25	21	25	18	15	12	12	10	13	9	11	512
Total	176	252	292	254	290	369	362	419	504	575	577	574	457	466	502	427	395	497	398	307	320	316	271	269	243	367	9879

One 4th calendar year male (born in 2021) was, at the time of writing of this article (on 1 November 2024), still present in his father's territory. The father showed up at the same camera location. He came into view together with his father. This young male is now 42 months old.

The gender of four animals seen in 2022 could not be determined. A total of 27 females and 33 males were identified.

Activity patterns

The large number of observations made it

Figure 8. The female is on the left, kitten in the middle and 2nd calendar year male on the right. Only the kitten shows no moult contrast in the tail.

possible to create an overview of half-hourly activity patterns in the course of the year (in two-week periods) over the study period of 2020-2023 (Table 2). To create this overview the data was organized and summarized by two weeks and half hours. A pivot table was created from this.

Pine martens are more active during warmer weather than cold periods, but other events also have an influence, such as social interactions over the course of the year. In January nothing much happens. In February pregnancy begins with the implantation of blastocysts. The new kittens are usually born in early April, open their eyes and mothers go out more to find food for the kittens. At the end of June the kittens appear in front of the camera and sometimes encounters are filmed with the subadults living in the territory. In early July the mating season begins, which lasts for some weeks. In July, some kittens start dispersing and may be seen in other males' territories, while other kittens seek a home range in their father's territory. Each subadult, male or female, has its own home range within their father's territory. The mating season ends in August. In September some kittens still follow their mother on some days. Also new animals will appear in the area for a short period. Activity decreases in November and December. So far, the data show no particular period of the year for the subadults to leave the area to establish their own territory.

To determine the mother relationship, I registered which mother the kittens were seen with. The kittens were on camera from the beginning of June. Until August they are recognizable by their smaller size, uniform coat and thinner tail. Pine martens moult twice a year, in spring and late summer. Figure 8 shows the tail shape of a female, a kitten and a 2nd calendar year male. Only the kitten shows no moult contrast in the tail. The summer moult lasts until August. The old fur that still has to moult is long and fluffy and the difference in tail shape between kitten, subadult and adult is clearly visible in June and July. The males and subadults finish the summer moult at the end of July, and the females have their young a few weeks later. The distinguishing difference in fur between kittens, adult and subadults disappears by August.

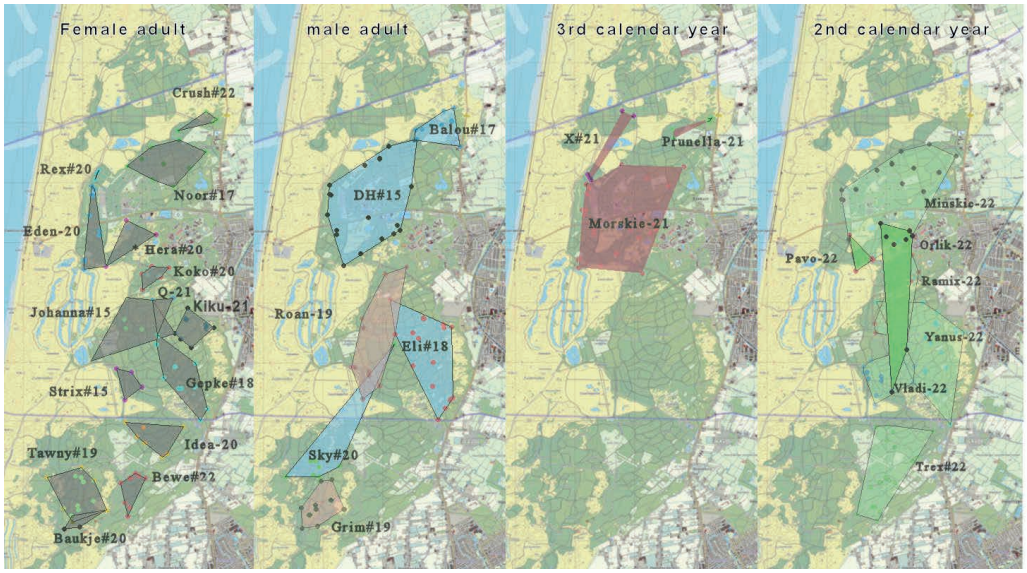


Figure 9. Spatial distribution of the home ranges of pine martens in 2023 (individuals recognized in camera trap images) in the NHD, divided into adult females, adult males and resident yearlings of one and two years old. The last two digits of a marten's name is the year of 1st recording. If the character before it is a dash (-) it means that it is seen together with its mother. # means it was unclear who the mother was.

Table 3. Overlap of home range/territory of different pine martens.

overlap of home range/territory of different pine martens	
Adult male – adult male	Males have their own territory. Occasionally an adult male was registered within the home range of another adult male. This was during the mating season.
Adult female – adult female	Females have their own territory. Sometimes there is overlap at the edges. Occasionally an adult female was registered within the territory of another adult female.
Subadults – adult males	Each subadult has its own home range. The home range is within the father's territory and may overlap with multiple female territories. Every now and then a subadult appeared together with the territorial adult male in front of the camera. The territorial of an adult male is larger than that the home range of a subadult. The home range of a subadult falls wholly or largely within the male's territory.
Subadult – adult females	The home range of subadults may overlap with multiple female territories. Every now and then a subadult appeared together with the territorial female in front of the camera.
Subadult – subadult	The home range of subadults may overlap with other subadults. One or several subadults together were regularly observed at camera locations. Subadults from different years of birth have appeared together in front of the camera. Subadults are tolerated in the territories of adults and the home ranges of other subadults. The size of the home range of a subadult increases as they grow older. Densities above 2 pine martens per km² are a sign that subadults are present in that area.

The kittens are still recognizable by their playful behaviour, which gradually decreases. In October one can hardly see any difference in behaviour in front of the camera. In this way the mothers of 23 kittens could be determined.

Table 4. Number and location of individual pine martens recorded in 2023. Once sufficient registrations and locations had been collected, the surface area (minimum convex polygone) was calculated in ha. When an individual was registered at only one of two camera locations, including one case of three locations, there is a question mark for 'surface area'.

Detailed data on pine martens registered in 2023 in the NHD									
individual	registrations	locations	ha	individual	registrations	locations	ha		
female adult				Subadult in 3rd calendar year				mother	Father ?
Crush#22	33	6	6.8	Eric#21	10	1	?		
Koko#20	41	7	8.5	Mart-21	17	3	?	Miep#21	?
Baukje#20	26	4	8.5	Morskie-21	210	30	225.1	Noor #17	DH#15
Q-21	63	5	10.2	Prunella-21	33	7	6.1	Crush#22	Balou#17
Strix#15	39	6	11.5	X#21	9	2	?		
Move#21	43	10	14.0	Subadult in 2nd calendar year				mother	Father ?
Kiku-21	137	12	21.4	Orlik-22	53	8	92.8	Hera#20	DH#15
Hera#20	9	3	22.5	Pavo-22	39	6	9.4	Hera#20	DH#15
Eden-20	62	15	27.4	Peppi-22	1	1	?	Koko#20	DH#15
Idea-20	31	7	27.9	Minskie-22	115	20	215.1	Noor #17	DH#15
Tawny#20	49	13	51.6	Olly-22	4	2	?	Miep#21	?
Gepke#18	54	10	53.7	Ramix-22	61	11	57.8	Johanna#15	Roan-19
Noor #17	49	9	56.5	Shawka#22	4	3	?		
Johanna#15	35	8	71.0	Trex#22	113	21	104.3		
Miep#21	2	2	?	Vladi-22	112	18	48.4	Daffy-20	Roan-19
Rex#20	54	2	?	Yanus-22	190	23	154.4	Gepke#18	Eli#18
male adult									
Balou#17	3	2	?						
DH#15	49	19	188.5						
Eli#18	44	18	111.8						
Grim#19	80	12	35.6						
Roan-19	69	13	100.4						
Sky#20	26	9	87.7						

Homerange of subadults

Little is known about the home ranges of young pine martens, but this study did shed some light on this (Table 3). With the collected data, the home ranges or territories of each individual can be plotted on a map (Figure 9) and an indication of the area of the habitat can be calculated. Using R-studio, the home ranges of the individuals that were observed at, at least, four locations were calculated (Table 4, showing the situation in 2023 for female animals that had given birth, adult males, one- and two-year olds). Only registrations from 2023 have been included. The home ranges at the edges of the research area indicate part of the territory, as adult males are known to make occasional forays into neighbouring territories (Birks 2017).

Martens most often appeared alone in front of the cameras. Only 1% of the registrations were of multiple animals, excluding mothers with their kittens, these are encounters between two resident pine martens or with yearlings or yearlings with a territorial pine marten. No territorial aggressive encounters were registered.

Some of these encounters were subadults with their mothers and kittens. These subadults played with the kittens.

Figure 10. Snapshot of film of a yearling (15 months old) making a suckling movement with its mother (standing in the middle). Right, a kitten from 2023. The QR code is a link to the film on YouTube - https://www.youtube.com/watch?v=2lZpSQaU--U.

Figure 11. Playful behaviour between 2nd calender year male or subadult (left) and two kittens. The QR code is a link to the film on You Tube: https://www.youtube.com/watch?v=SczghWI0Ovk&t

Several unique encounters have been recorded between subadult males playing with kittens in the presence of their mothers. The subadults displayed playful behaviour. In one film, a male subadult tries to drink from its mother (Figure 10). Subadults also display playful behaviour in the presence of adults (Figure 11). The adults did not respond to or correct this behaviour.

Table 5. The number of unique individual pine martens recorded during the day over the course of the year, by two-week period, cumulated over the years 2020-2023. The numbers reflect the pine marten recordings captured by the camera traps.

Number of days active unique pine martens in 2020/2023 biweekly	01+02	03+04	05+06	07+08	09+10	11+12	13+14	15+16	17+18	19+20	21+22	23+24	25+26	27+28	29+30	31+32	33+34	35+36	37+38	39+40	41+42	43+44	45+46	47+48	49+50	51+52	Total
New										1	1	1			1		1		3	1	1						7
kitten										1		1	2	3	2	3	6	7	2		1	2	1	1	1		13
2nd calendar year males				2	2	1	3	3	5	5	6	8	9	5	4	2	1	4	1	1					1	1	16
3rd calendar year males			1			1	2	1	1	2	3	5	4	3	3												8
4th calendar year males						1	1		1		2	2	1	1													3
male adult						3	4	4	4	7	6	8	8	5	4	4		2									9
2nd calendar year females					2	1	3	2	4	1	2	2	2	4	4	2	2	1									6
3rd calendar year females							1		1	1	1	2	3		1			2	2	1							5
female adult			1		2	6	6	9	11	14	10	10	10	10	8	9	7	6	6	3		1			1		19
Total			2	2	6	13	20	19	26	31	26	32	30	27	25	18	16	19	14	5	2	3	1	2	3	1	57

Discussion

The total number of bi-weekly registrations was lowest in January, with an increase from March onwards, and a peak from mid-May to late September, after which it gradually decreased (Table 2). Research in Białowieża National Park in Poland (Zalewski 2000, Zalewski & Jędrzejewski 2006, Balestrieri 2023), revealed that martens are active for an average of 8.5 to 9 hours per day. The duration of activity is lowest in winter (approx. 15% of the day cycle), and highest during the mating season (approx. 50%; Zalewski 2000). The mating season starts around the 1st of July and lasts for several weeks. These activities were measured differently in the two studies but the pattern of low activity in winter is similar.

Table 5 shows the number of unique individual pine martens recorded during the day over the course of the year, by two-week periods. In the period from late March to early August the number of active unique adult males is higher during the day, with a peak from mid-May to early August. This may indicate that the mating season starts earlier than in Poland. However, this peak is also seen in subadult males. Another explanation may be in the food supply. Birds, mainly Passeriformes, are on average the third item in order of importance in the pine marten's diet, especially in Mediterranean Europe, while medium-sized and large mammals (lagomorphs and ungulate carrion, respectively) are generally more frequently eaten at high latitudes (Zalewski 2004, Balestrieri 2023). In a breeding bird inventory in the NHD, Slaterus (2021) makes no special mention of (the arrival and increase of) pine martens as a possible explanation for declining bird populations, except for green woodpeckers (*Picus viridis*). For other individual bird species at a local level, a negative effect cannot be ruled out completely. Possibly, pine martens in the NHD eat fewer birds than other studies have shown. Future studies may shed more light on this.

Research in Białowieża National Park found that males show longer activity periods (four hours on average) than females (three hours) (Zalewski & Jędrzejewski 2006). In this study, the number of activity periods per day varied from one to six (average 2.6) and increased as the ambient temperature increased. In February-March it was 2.8 hours/day of activity and in June-July 12 hours/day. This method does not allow for measuring activity periods. Visits by the same pine marten were recorded for each day. However, since there were no start and end times, it is not clear whether a second registration is part of the same, or a new, activity.

In a study by Stier (2012) all pine martens, including the males, reached sexual maturity at the age of 1¼ year. Broekhuizen & Müskens

(2000) found that in the Netherlands females and males also reached sexual maturity in their second summer. Remarkably, in the NHD, young pine martens older than 1¼ years, both female and males, had home ranges in territories of adult male pine martens. These individuals were only seen within the confines of one territorial male, probably their father.

The density measured in the NHD (which, excluding kittens, varied between 2.3 and 2.8 pine martens per km^2) is high compared to other reported studies. Most other areas in the Europe have a much lower density (Balestrieri 2023). The National Pine Marten Population Assessment in Ireland assessed pine marten presence and densities at 19 wooded areas across Ireland, using non-invasive survey techniques. Hair samples from pine martens were collected and analysed using molecular methods to determine individual identity details for each pine marten. Pine marten densities ranged from 0 to 2.60 individuals per km^2 of forest habitat in randomly selected study sites (O'Mahony et al. 2017). In the Netherlands, some volunteers carry out annual inventories. The results are published in the annual newsletter 'Marterpassen' of the Dutch Pine Marten Working Group. The densities in the NHD of 2.3 and more also generally exceed their findings. However, Hartman (2023) reported 2.3 inhabitants/km^2 in De Bilt in 2022 (58 pine martens on 25 km^2).

A population density greater than two is an indication that there are growing young animals in the area. These subadults leave the parental territory at a certain age. Female subadults can stay for up to two years, males for up to three years, possibly four years.

Regarding the use of attractant: Not every pine marten reacts the same to attractant. It is possible that individuals were missed. The attractant was often eaten by other animals. This makes it possible that individuals were at the location but were not registered. If pine martens are used to the attractant, they will return more often to the location.

With this method it must be taken into account that errors can be made when analysing images. By irregularly plotting location data on a map, incorrectly written locations can be discovered. When creating the day and night activity table, AM-PM recording errors emerged. Multiple pine martens can occur at one location. When making an ID card, it sometimes happened that, at the entry of a new individual, an ID card was made of two individuals. When analysing new images, this error came to light and was corrected retroactively.

Young male pine martens have an extended subadult stage in which adulthood is delayed until they have passed their third birthday (Balharry 1993, Balestrieri 2023). In this study, a subadult in his fourth calendar year old lived in another male's territory until at least November. The underlying theory is that territorial males have significantly higher testosterone levels than subadults from May to July (Balharry 1993, Balestrieri 2023). It is not known whether this 4th calendar year old male had lower testosterone levels than normal. However, there were fewer visible bald spots around the abdominal gland, possibly indicating less friction with the abdominal glands (Figure 12).

Conclusions

The following conclusions can be drawn from this study,

- A healthy pine marten population lives in the forest area of the Noordhollands Duinreservaat.
- Camera traps can be used to determine the size of a local pine marten population, provided that the pine martens are individually recognizable. This also provides insight into the surface area of an individual's home range. The home range sizes of adult females and males in this study area are very small when compared to data from Birks (2017), which indicate that the smallest home range for a female is 70 hectares and 171 hectares

Figure 12. Compilation photo of the abdominal gland spots of four different males in late July. From left to right: a male of at least five years old, a 2nd calendar year male, a 4th calendar year male, and a male of at least ten 10 years old.

for a male. The research area contains a lot of food for the pine martens, which means that territories are small and several subadults can simultaneously grow up in such a space. Several subadults were registered at several locations. This study shows that a territorial male shares his territory with one or more females, plus the growing young of these females. There is a good chance that he is the father of these subadults.

- A territorial female shares her territory with one and sometimes two territorial males, plus young animals, that are not yet reproducing. These young animals are her offspring or from neighbouring females who share the same territorial male. Subadults are tolerated in the adult's territory for a quite long period of time. They prefer to grow up in a home range within the territory of one adult male.
- Subadults can play a role in raising the new generation. They play and eat together with the territorial female and her young. Yearlings follow the older animals.
- Pine martens live solitary lives, although it should be noted that pine martens tolerate each other within family bonds.
- Female pine martens have their first young when they are two years old (in their third calendar year). Because of the delayed implantation of the blastocyst these young females have mated for the first time in the year before, in their second summer.
- Subadults also have their own home range.

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Samenvatting

De boommarterpopulatie in het bosgebied van het Noordhollands Duinreservaat

Dit artikel presenteert de bevindingen van een langdurig onderzoek naar het voorkomen van boommarters (*Martes martes*) in het Noordhollands Duinreservaat. Het gaat specifiek om de verzamelde gegevens van 2020 tot en met 2023, waarbij een rijke dataset werd

gegenereerd met behulp cameravallen, gericht op het vastleggen van het individueel unieke befpatroon van de boommarters. In de loop van het onderzoek werd in totaal 9892 keer een boommarter geregistreerd, waarbij in 78% van de gevallen het dier individueel kon worden geïdentificeerd. In het onderzoeksgebied van ca. 1500 ha konden in totaal 64 individuen gedurende een bepaalde periode gevolgd worden. Dit resulteerde in een hoge dichtheid van boommarters van 2,3-2,8/km^2. Door de datum en het tijdstip van de opnames vast te leggen, werd inzicht verkregen in de activiteitspatronen van de marters zowel overdag als 's nachts, waardoor een uitgebreid jaaroverzicht op tweewekelijkse en halfuurbasis kon worden opgesteld. De waargenomen individuen konden per kalenderjaar worden ingedeeld in territoriale mannetjes, territoriale vrouwtjes en opgroeiende subadulte dieren, die gedurende enkele jaren konden worden gevolgd. Vier jaar lang werden gemiddeld tien camera's gebruikt die elke drie weken verplaatst werden en twee keer per week werden gecontroleerd. Bij controle werd nieuwe lokstof aangebracht, werden de beelden in het veld bekeken en de opstelling zo nodig aangepast. De camera's werden strategisch zo geplaatst dat de boommarters met hun unieke befpatroon gefilmd konden worden. Er zijn ruim 10.000 beelden verzameld en geanalyseerd. Hierdoor kwam een database tot stand die duidelijk maakte waar en wanneer welke boommarters werden gezien. Gedurende de onderzoeksperiode konden 32 sedentaire boommarters worden gemonitord. Deze dieren zijn geboren in het onderzoeksgebied, kwamen voor het eerst in beeld met hun moeder en konden in de jaren daarna gevolgd worden. Hierdoor ontstond een beeld hoe de boommarters gebruik maakten van het terrein en welke individuen er zich bevonden. De boommarters verschenen bijna steeds alleen voor de camera. Eén procent van de registraties betrof meerdere dieren, vrouwtjes met jongen niet meegerekend; het ging daarbij om vriendschappelijke ontmoetingen, territoriale interacties werden niet geregistreerd. Enkele van deze ontmoetingen waren subadulte boommarters die samen met hun moeder en haar jongen van enkele maanden oud gezamenlijk in beeld kwamen. Deze subadulte boommarters speelden regelmatig met hun jongere broertjes en zusjes. Door gebruik te maken van locatiegegevens was het mogelijk de omvang van het leefgebied van deze individuen te schatten. Subadulte dieren hebben hun eigen leefgebied wat zich in een mannelijk territorium bevindt en waar het territorium van de moeder onderdeel van uit maakt. De bevindingen werpen licht op het gedrag en de ruimtelijke dynamiek binnen boommarterpopulaties.

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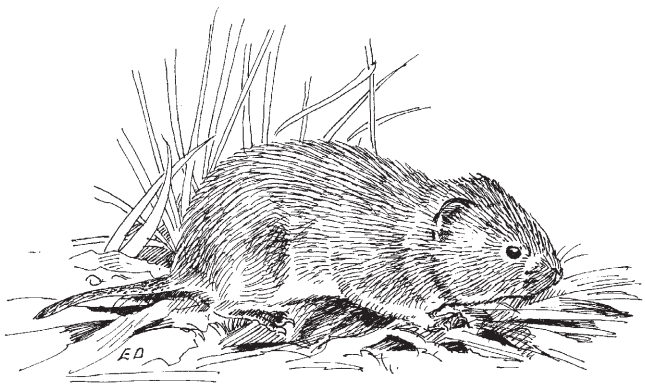

Variability of mandibular length in species of shrews and Myomorpha from the province of Zeeland, the Netherlands

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Abstract: Several studies have suggested that the variability in the size of shrews is less than in voles and true mice, as shown by the range differences of the mandibular lengths, which can be used as a proxy for body size. A smaller variability of the length of the mandibular is directly related with the variability of the total body length of micro-mammals. Young shrews have body-measurements almost similar to adults, whereas rodent species' body-measurements seem to vary more. This raises the questions as to whether the variation of the mandibular length differences in shrews is smaller than in Myomorpha and if these differences can be quantified. To address this question, a total of 6037 specimens of 14 different species of micro-mammals retrieved from owl pellets, all collected in the Province of Zeeland, the Netherlands, were analysed to determine their mandibular lengths. Using owl pellets for the sample meant that this was not a random sample, but a selection made by the owls, i.e. their preferred prey. The results reveal that the coefficients of variation of the mandibles of the shrews are significantly smaller than those of voles and other Myomorpha. For three of the species of the subfamily of the red-toothed shrews (Millet's shrew (*Sorex coronatus*), pygmy shrew (*S. minutus*) and water shrew (*Neomys fodiens*)) the coefficients of variation are at least twice as small as the other - non shrew - micro-mammals. In the white-toothed shrews (bi-coloured white-toothed shrew (*Crocidura leucodon*) and greater white-toothed shrew (*C. russula*)) and the common shrew (*Sorex araneus*), these coefficients are also smaller, but less markedly so. The differences between the shrews and Myomorpha are also reflected in the ranges of the percentages of the mandibular lengths of shrews (90-107%), voles (68-117%) and other Myomorpha (79-119%). Factors that might explain the differences between shrews and Myomorpha are discussed in the conclusions.

Keywords: coefficient of variation, mandibular length, skewness, red-toothed shrew, white-toothed shrew, voles, true mice.

Introduction

Anyone who has analysed substantial quantities of owl pellets may have noticed the lesser variation in measurements of skulls and mandibles of shrew species compared to rodent species. However, up to this moment this observation has not been described in the literature, let alone substantiated with figures.

Analyses of owl pellets in the Netherlands are usually aimed at revealing the diet of the raptor and/or the distribution of the small mammals (e.g. Tinbergen 1933, Wilmink 1944, Schreuder 1945), with some of the latter studies expanding their focus towards dental variants or molar aberrations (e.g. Ruprecht 1961, Jentzsch 2006, Kapischke et al. 2009).

A first indication of size variability in shrews being smaller than in voles and true

mice can be found in Husson (1962), who presented ranges of mandibular length for two species: the common shrew (*Sorex araneus*) (*n*=96; range 8.8-9.7 mm) and the common vole (*Microtus arvalis*) (*n*=117; range 11.5-15.5 mm) and from Reichstein (1978) who presented ranges of mandibular length for the house mouse (*Mus musculus*) (*n*=55; range 10.3-13.5 mm). These numbers result in differences of 9.3%, 29.6% and 26.7% respectively. It is important to mention here that Husson (1962) used the front side of the second tooth for measuring the mandibular length in shrews, instead of the front side of the alveolus of the lower incisor at the lingual side when measuring the mandibular length, as has been done in this article.

The differences in Husson's (1962) and Reichstein's (1978) findings raise questions about the differences in the variation of mandibular lengths between shrews (Eulipotyphla: Soricidae) and of small Myomorpha (Rodentia).

The variability of the total body length of micro-mammals, found or trapped outside the nest, is directly related with the variability of the mandibular length. Young shrews have almost adult body-measurements while rodent species seem to have more variable body-measurements. Almost a century ago Jackson (1928) remarked that it is the habit of young shrews to remain in the nest until they have almost reached maturity, which makes such youngsters so scarce in collections. The statement of Jeroen van der Kooij (personal communication) 'If you find a red-toothed shrew that is smaller than another one, you are dealing with a different species', hints in the same direction. This phenomenon of seemingly overlooking young shrews, is diametrically opposite the experience with other micro-mammals. A personal experience is the comparison of a range of head-body respectively tail lengths in a set of eight multi mammate rats (*Mastomys natalensis*) from two sites in Benin: Deme (100.1 - 133.6 and 97.1 - 117.4 mm respectively) and one specimen from Cotonou (52.0 and 52.0 mm respectively) (Bekker & Ekué 2004). Only after careful examination of the molar details, the specimen from Cotonou also turned out to be a multi mammate rat.

These considerations lead to the main hypothesis, that the variability in the populations of different species of shrews are expected to be lower than those of different species of small Myomorpha in the province of Zeeland.

Materials and methods

The selection of mandible specimens from the available material aims to maximize sample size (preferably from single locations) and, whenever feasible, consecutive years. This approach enhances the likelihood of achieving an optimal representation of the composition of the hunted population within a specific or consecutive year(s).

A large number of specimens (*n*=6037) of 14 different species of micro-mammals predominantly from barn owl pellets were studied. Samples contained at least 50 specimens per species, as suggested by Yablokov (1974). All owl pellets were collected in the province of Zeeland, the Netherlands, and were included in the terrestrial mammal collection of the Koninklijk Zeeuwsch Genootschap der Wetenschappen. Specimens available for this study belong to the following species of the red-toothed shrews (subfamily Soricinae): the common shrew (NHG26601-NHG26648), Millet's shrew (*Sorex coronatus*) (NHG26701-NHG26711), the pygmy shrew (*S. minutus*) (NHG26801-NHG26917) and the water shrew (*Neomys fodiens*) (NHG27001-NHG27062); as well as the white-toothed shrews (subfamily Crocidurina): the bi-coloured white-toothed shrew (*Crocidura leucodon*) (NHG27101-NHG27147) and the greater white-toothed shrew (*C. russula*) (NHG27201-NHG27206). Of the family Cricetidae, the bank vole (*Myodes glareolus*) (NHG27301-NHG27401),

Table 1. Numbers, by species, of the mandibulae studied across different regions in Zeeland: Schouwen-Duiveland (S-D), Tholen (T), Noord-Beveland (N-B), Walcheren (W), Zuid-Beveland (Z-B) and Zeeuws-Vlaanderen (Z-V); *: of five water shrews the location was missing.

	S-D	T	N-B	W	Z-B	Z-V	Total
Red-toothed shrews							
Common shrew	256	18	58	60	65	64	521
Millet's shrew	0	66	0	0	0	250	316
Pygmy shrew	250	45	31	64	9	61	460
Water shrew	0	17	4	28	7	31	92*
White-toothed shrews							
Bi-coloured white-toothed shrew	0	0	0	0	0	250	250
Greater white-toothed shrew	250	178	110	91	146	122	897
Voles							
Bank vole	62	19	49	51	62	179	422
Root vole	250	0	25	0	2	0	277
Field vole	0	125	66	67	66	59	383
Common vole	270	108	191	101	53	114	837
Common pine vole	0	0	0	0	10	254	264
True mice							
Harvest mouse	61	52	43	57	65	116	394
Wood mouse	78	114	131	80	115	78	596
House mouse	109	51	7	50	12	99	328

the root vole (*Alexandromys oeconomus*) (NHG27501-NHG27515), the field vole (*Microtus agrestis*) (NHG27601-NHG27617), the common vole (NHG27701-NHG27708) and the common pine vole (*M. subterraneus*) (NHG27901-NHG27950) were studied. Of the family Muridae, the harvest mouse (*Micromys minutus*) (NHG28001-NHG-28101), the wood mouse (*Apodemus sylvaticus*) (NHG28201-NHG28229) and the house mouse (*Mus musculus*) (NHG28301-NHG28366) were included.

Species per region

Not all the specimens of the studied species were present in all regions and/or evenly distributed in comparable numbers. At one end of the spectrum the bi-coloured white-toothed shrew, was only present in Zeeuws-Vlaanderen and the common pine vole, was only present in Zeeuws-Vlaanderen and Zuid-Beveland. At the other end of the spectrum three species of shrew (common shrew, pygmy shrew and greater white-toothed shrew), two voles (bank vole and common vole) and all three true mice (harvest mouse, wood mouse and house mouse) were present in all regions (Table 1).

Yablokov (1974) arranged the variability in mammals of structures, organs and body measurements in three classes, less than 10%, from 10 to 15% and at least 15%, respectively. Measurements in the <10%-class, where variability is smallest, were taken (in order of ascending variability) from the post-cranial skeleton, the skull and the body (*ibid.*). Using body length to assess the size of micro-mammals is thought to be unreliable for two reasons. First, living specimens, at the moment of investigation, almost always present themselves in postures with a more or less arched backbone. Secondly, in dead specimens the degree of relaxation after rigor mortis is not equal for all specimens. Yablokov (1974) esti-

mates the variability of body weight in mammals to be at least at 15%; in micro-mammals it is not a reliable measure for body size, as total weight is directly dependent of the general nutritional status or, in females, of pregnancy.

Therefore, in this study, the mandibular length in shrews and in rodents was chosen as a proxy variable for size, which is also supported by the following considerations. First of all, mandibles are osteological elements that are prone to growth, without epiphyseal discs, between well-defined functional landmarks in shrews as well as in Myomorpha. In shrews the mandibular length has been defined as the condylar length, following Krapp & Niethammer (1990) (Figure 1a) and not the incisive length, as in shrews the attrition of the lower incisors can sometimes be several millimetres. According to Niethammer & Krapp (1982b) the mandibular length in Myomorpha is defined as the distance between the anterior-most part of the irregularity of the symphysis mandibulae and the posterior-most part of the condyle (Figure 1b). Although measurements at the skull, such as the condylobasal length, may be longer, the skull comprises multiple bone components with sutures in between, leading to potential inaccuracies in measurements. Furthermore, each single mandible makes the ultimate determination of the species indisputable. The mandible is a long, firm bone element, arising secondarily by ossification of the connective tissue surrounding Meckel's cartilage (Langman 1976). Because of the robust nature of the mandible between its reference points for measurement (among other factors) this bone fragment seems less susceptible to post-mortem fractures.

All measurements were conducted using vernier callipers equipped with an analogue scale. This instrument can be read with an accuracy of 0.02 mm and was calibrated after each measurement. The measurement was taken after aligning the jaws of the callipers with the designated measuring points, while ensuring the mandible was lifted off the table.

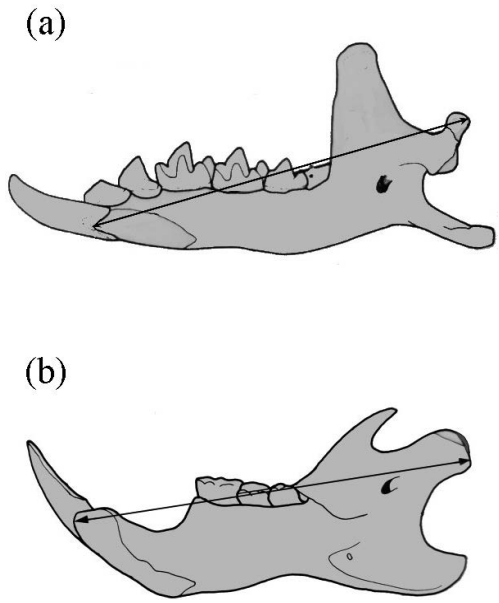

Figure 1. Measurement of mandibular length in (a) shrews (adapted from Krapp & Niethammer 1990) and (b) Myomorpha (adapted from Niethammer & Krapp 1982b).

Measurements were conducted on the right mandible, unless it was compromised by a fracture or was not available, in which case the left mandible of the same specimen was used.

To compare the measurements of all species in one frame, box plots of the percentages of the species measurements towards the species mean are presented in an overall comparison. Graphical methods are employed here to enhance the visual clarity (see Figure 2).

In addition, the traditional indices for a large series of measurements, such as the number of observations in a sample (*n*), the range (R), the population mean (μ), the population median (ų) and the standard deviation (sd) are presented, following Kirk (1999) (Table 2). Pearson's (sk_p) formula ($sk_p = 3*(\mu - ų) / sd$) was employed to measure skewness.

A negative value of sk_p indicates that the tail of the distribution is on the left side, which means that the distribution extends towards

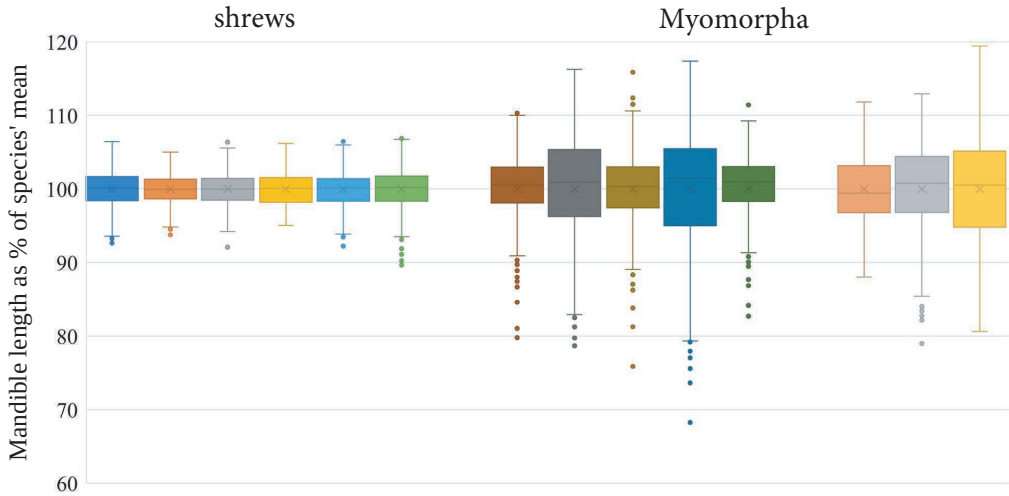

Figure 2. Boxplots of mandibular lengths of micro-mammals, as percentages of the species' mean. From left to right: shrews: common shrew (blue), Millet's shrew (orange), pygmy shrew (grey), water shrew (yellow), bi-coloured white-toothed shrew (light blue) and greater white-toothed shrew (light green) and Myomorpha: bank vole (brown), root vole (dark grey), field vole (sepia), common vole (dark blue), common pine vole (dark green), harvest mouse (orange), wood mouse (grey), house mouse (yellow).

Table 2. Key figures of mandibular lengths (in mm) in micro-mammals; CV: coefficient of variation, sd: standard deviation.

	n	CV (sd)	Skewness	Mean mandibular length in mm (and range)
Common shrew	521	2.46 (0.24)	-0.01	9.79 (9.11-10.42)
Millet's shrew	316	2.14 (0.20)	-0.09	9.42 (8.83-9.89)
Pygmy shrew	460	2.20 (0.16)	0.05	7.49 (6.90-8.01)
Water shrew	92	2.20 (0.25)	-0.12	11.19 (10.63-11.88)
Bi-coloured white-toothed shrew	250	2.54 (0.27)	-0.19	10.48 (9.67-11.16)
Greater white-toothed shrew	897	2.63 (0.27)	-0.22	10.35 (9.28-11.08)
Bank vole	422	4.57 (0.62)	-0.30	13.50 (10.77-14.89)
Root vole	277	7.38 (1.12)	-0.38	15.14 (11.91-17.60)
Field vole	383	5.05 (0.75)	-0.18	14.87 (11.27-17.21)
Common vole	837	7.94 (1.0.7)	-0.55	13.51 (9.22-15.86)
Common pine vole	264	4.58 (0.63)	-0.63	13.72 (11.35-15.29)
Harvest mouse	394	4.44 (0.40)	0.39	9.12 (8.03-10.20)
Wood mouse	596	6.18 (0.84)	-0.37	13.52 (10.68-15.27)
House mouse	328	6.68 (0.75)	-0.23	11.30 (9.11-13.49)

more lower values and vice versa. To compare the variability of different species the coefficient of variation (CV) was calculated as:
$CV = sd / \mu * 100$
To test for differences between the coefficients of variation of shrews and Myomorpha, data were measured on a continuous scale using a Student's two-sample *t*-test.

Results

The coefficients of variation of the mandible lengths of the shrews (range of CV 2.14-2.63) were smaller than those of the Myomorpha (range 4.44-7.94) (*t*-test, $t=0.00016$, $P<0.05$) (Table 2). Boxplots of the percentages of the mandibular lengths with whiskers of 90-107% for shrews and of 68-117% for voles and 79-119% for true mice (including outliers) for all 14 studied micro-mammals underline these statistical outcomes (Figure 2).

The skewness indices for shrews are negative, with exception of the pygmy shrew, and all are fairly symmetrical. For voles these values are between -0.63 and -0.18 (negatively skewed). The skewness for the harvest mouse, is positive (0.39) and fairly symmetrical. For the wood mouse and the house mouse the values are negatively skewed (see Table 2).

Discussion

The results clearly show that the variability of the mandibular length in the six species of shrews hunted by owls is smaller than those of species of other micro-mammals. For the investigated species of red-toothed shrews (common shrew, Millet's shrew, pygmy shrew and water shrew), the coefficients of variation are at least half as small as the other (non-shrew) micro-mammals except for the common shrew (see Table 2). In the white-toothed shrews (and the common shrew) these coefficients were less than 60% of them (see Table 2). The coefficients of variation of the mandible lengths of the shrews are significantly smaller ($P<0.001$) than those of the Myomorpha. The conclusions are, however, based on the species investigated, and do not necessarily apply to other shrews.

There are several factors that can explain the size variability in the hunted populations of micro-mammals. The first is growth during the pre-adult (sub-adult) period. Newborn micro-mammals (shrews and Myomorpha) are pink, more or less bean sized and typically meet the criteria of 'nestlings': hairless, large heads, extremities with fused toes, closed eyes and sealed ears (Bradley 2017, Burgin & He 2018). In that very first week competition in large litters of shrews (of between 6-9) is high and the smallest and weakest succumb (Churchfield 1990). Before the periods of leaving the nest, the opening of the eyes and ears, the completion of hair cover, the eruption of incisors, weaning and the intake of solid food, are all significant events that are reached before the third or fourth week[1]. Young shrews grow very rapidly until day 18 and then stop growing exponentially; at that moment the young are nearly as large as the mother. Fully weaned and with the start of solid food consumption at 20-25 days, the young grow to full size in about 30 days (Burgin & He 2018). On the other hand, Myomorpha have a much more extended growth curve. For example, at 43 days, bank voles weigh 13.7 g, and almost double their weight after one year (Bujalska & Gliwicz 1968). Another study showed that root voles gained approximately 150% in weight from between four to twelve weeks after birth. This period of intense growth in the condylobasal length of root voles persists up to the ninth month of their life, i.e. an increase of approximately 15% during the first nine months (Gebczyńska 1964). In 1-2 month old common voles an almost doubling

1 References for common shrew (Hausser et al. 1990, Burgin & He 2018), pygmy shrew (Hutterer 1990), water shrew (Spitzenberger 1990, Burgin & He 2018), bi-coloured white-toothed shrew (Krapp 1990), greater white-toothed shrew (Genoud & Hutterer 1990, Genoud & Perrin 1994), bank vole (Viro & Niethammer 1982), root vole (Frank & Zimmermann 1956, Tast 1982), field vole (Krapp & Niethammer 1982), common vole (Niethammer & Krapp 1982a), common pine vole (Niethammer 1982, Schröpfer 1977), harvest mouse (Böhme 1978, Ishiwaka & Mori 1999), wood mouse (Niethammer 1978, Owen & Trees 1998) and resp. house mouse (Reichstein 1978, Owen & Trees 1998).

of the weight has been registered after ca. one year, with the condylar basal lengths increasing by ca. 17% (Frank & Zimmermann 1957). Wood mouse and house mouse, which are weaned at 25-30 days, show a fast weight gain until day 50, after which their rate of weight gain decreases (Crowcroft & Rowe 1961).

In summary, Myomorpha continue to experience growth beyond the first month of their life, with their mandibles continuing to grow thereafter, surpassing the growth observed in shrews. This is an important factor in explaining the size variability.

Another factor that can account for size variability is sexual dimorphism, i.e. differences in the (mean) size between the sexes, or greater variability within either of the sexes. Sexual dimorphism in size might explain the size differences of mandibles in micro-mammals.

The owl pellet material used in this study was not differentiated according to sex, although in some species sex determination is occasionally feasible through the examination of the pelvis or scapulae from both *Sorex* and *Neomys* (Dolgov 1961). Overall, sexual dimorphism in common shrews is generally considered to be negligible (Polly 2007, White & Searle 2009). Zidarova (2015) showed no significant differences in the mandibular length between females and males in common shrews, pygmy shrews, water shrews and bi-coloured white-toothed shrews. In greater white-toothed shrews differences in mandible size were detected between sexes, with males exhibiting significantly larger mandibles than females (Sánchez-Chardi et al. 2018). This sexual size dimorphism in mandible size may contribute to the slightly higher coefficient of variation for greater white-toothed shrews (2.63) found in this study for the total hunted population. In several species of voles there is a sexual dimorphic difference in size. Although this significantly affects the average value of four somatic features, all of which attain higher values in male, than in, female Pannonian root voles (*Alexandromys oeconomus mehelyi*), this effect could not be demonstrated in the mandibular length (Baláž et al. 2021). On average the values, especially the length (and the height) of the mandible for adult and sub-adult females of *bank vole,* are higher than those for males (Csanády & Mošanský 2021a). A morphometric analysis of the common vole (Csanády & Mošanský 2021b) revealed sexual differences in the measured cranial traits, with the most pronounced disparity observed in the length of the mandible: values for adult males of this species were higher than those for females.

In wood mice, sexual dimorphism also has been registered for mandibular length: mean values in males exceeded those of females (Chassovnikarova & Markov 2007). Measurements of lower mandibular lengths in house mice exhibit sexual dimorphic outcomes across various populations, with results that are unequivocal (Csanády & Mošanský 2018): for adult males from Slovakia higher mean values in the mandibula length were found for house mice, while the Austrian population of this species showed a longer average mandibula length in adult females. All these sexual size differences in mandibular lengths contribute to higher (>4.44) coefficients of variation for Myomorpha, compared to the more modest coefficients in shrews, as listed in Table 2.

From day 7 until day 21 young greater white-toothed shrew can be observed 'caravanning' outside the nest (Jenkins 1977, Genoud & Hutterer 1990). In this behaviour each shrew youngster grasps the base of the tail of the preceding individual, with the mother running along with the young trailing in a line behind her (Churchfield 1990). Caravanning is well documented among several species of captive shrews (Burgin 2018) and has also been observed in the wild (Harper 1977). Available photographs of caravanning shrews show leading mothers with small youngsters (Genoud & Hutterer 1990, Burgin 2018). This behaviour could theoretically lead towards a greater proportion of youngsters being at risk, and, in the end, to a greater proportion of small mandibles in owl pellets; yet, as the low coefficients of variation show (Table 2), this

was not the case for shrews. An explanation for this discrepancy could be the continuous twittering of the leading individual (Harper 1977), a behaviour that can easily provoke aerial attacks of owls at the leading individual. Assuming the owls claws only grasp one shrew at the time, this 'self-sacrificing' behaviour of continuous twittering contributes towards prey selection of older individuals over young shrews. Myomorpha accompany their offspring outside the nest, but there are no reports of caravanning events as displayed by shrews. Thus, by venturing outside the nest, young Myomorpha are evenly at risk at being preyed upon by owls compared to older individuals. Therefore, the behaviour of caravanning in shrews, resulting in a preference by hunting owls of adult individuals instead of youngsters, could be a partial explanation of the smaller variability of mandibular length in shrews than in other micro-mammals.

The left-skewed distribution observed in almost all the investigated micro-mammals found in owl pellets (as indicated by the negative skewness values in Table 2) can be contributed to the population structures being dominated by young individuals. The skewness values of the three studied *Sorex* species are all close to zero: the common shrew and Millet's shrew are both just negative while the pygmy shrew is just positive. An explanation for the right-skewed distribution of the harvest mouse (skewness: 0.39) could be the marked seasonal fluctuation in the numbers of harvest mice taken by barn owls, rising in autumn and going down in spring (Buckley 1977, Darinot 2016). Besides, a high mortality of young individuals, in some years up to 80% of litters in their nests, which are usually located high (up to ca. 1 m) in reeds (*Phragmites australis*) and other grassy vegetation or shrubs, can succumb to poor weather conditions in autumn (Harris 1979) and are therefore not accessible to hunting owls. Both these factors can contribute to a harvest mouse population with a higher number of adult specimens with, on average, longer mandibles.

Conclusions

Based on a large sample of remains found in owl pellets, this study demonstrates that the variability of mandibular length in the hunted populations of all the studied species of shrews (common shrew, Millet's shrew, pygmy shrew and water shrew) is significantly smaller than those of eight studied species of other micro-mammals. For the red-toothed shrews investigated the coefficients of variation are at least half that of the other (non shrew) micro-mammals. The boxplots (shown in Figure 2) illustrate the statistical outcomes. The conclusions are however based on those species that were found in owl pellets in the province of Zeeland and may not apply to other red-toothed shrews.

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Samenvatting

Variabiliteit in de lengte van de onderkaak bij spitsmuizen en woelmuizen en ware muizen uit de provincie Zeeland

Verschillende studies suggereren dat de variabiliteit in grootte bij spitsmuizen kleiner is dan bij woelmuizen en ware muizen, wat onder meer blijkt uit de verschillen in range van de onderkaaklengtes. De onderkaaklengte wordt in deze studie gebruikt als een afgeleide voor de lichaamsgrootte. Jonge spitsmuizen hebben in de levensfase buiten het nest bijna volwassen lichaamsafmetingen, terwijl kleine knaagdieren meer variërende lichaamsafmetingen lijken te hebben. De vraag die hier rijst is: kan de variatie van de lengteverschillen in de onderkaak bij spitsmuizen en bij kleine knaagdieren (Myomorpha: woelmuizen en ware muizen) worden bevestigd en zijn deze verschillen te kwantificeren? Om deze vraag te beantwoorden, werd de onderkaaklengte van 6037 exemplaren van 14 verschillende soorten kleine zoogdieren bepaald. Deze onderkaken waren afkomstig uit braakballen van uilen en waren alle verzameld in de provincie Zeeland. Als gevolg van het gebruik van braakballen was dit geen willekeurige steekproef uit de populaties als geheel, maar een selectie gemaakt door de uilen, dus van de bejaagde populatie. De resultaten tonen aan dat de coëfficiënten van de variantie bij spitsmuizen significant kleiner zijn dan die van de woelmuizen en ware muizen. Voor drie van de onderzochte soorten van de onderfamilie van de roodtandspitsmuizen (tweekleurige bosspitsmuis, dwergspitsmuis en waterspitsmuis) zijn die coëfficiënten meer dan twee keer zo klein als bij de andere, niet-spitsmuissoorten. Bij de wittandspitsmuizen (huisspitsmuis en veldspitsmuis) - en ook bij de gewone bosspitsmuis - zijn deze coëfficiënten ook duidelijk kleiner, maar minder dan twee keer zo klein. Deze verschillen tussen de spitsmuizen en de woelmuizen en ware muizen worden ook weerspiegeld in de uitersten van de percentages ten opzichte van de soortgemiddelden van de onderkaaklengtes van spitsmuizen (90-107%), woelmuizen (68-117%) en ware muizen (79-119%). Onder de factoren die de verschillen in variabiliteit van de onderkaken tussen spitsmuizen en kleine knaagdieren kunnen verklaren, kan als eerste genoemd worden het doorgroeien van kleine knaagdieren na de eerste levensmaand, terwijl de spitsmuizen na die periode nog nauwelijks groeien. Verder vertonen roodtandspitsmuizen

nauwelijks geslachtsdimorfie, terwijl bij kleine knaagdieren een geslachtsdimorfie in de literatuur is aangetoond. Ook wordt aandacht gevestigd op risicovol gedrag bij volwassen vrouwelijke spitsmuizen door karavaanvorming: het gedrag waarbij jonge spitsmuizen zich vastbijten in de staartwortel van hun voorganger en de voorste aan die van het volwassen vrouwtje. Doordat het vrouwtje bij het voortgaan steeds geluid maakt, loopt juist dit exemplaar een grotere kans ten prooi te vallen aan (kerk)uilen, terwijl de jonge exemplaren dit moment van potentiële predatie juist overleven.

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Cetaceans stranded in the Netherlands in 2020-2023

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Abstract: Between January 2020 and December 2023 a total of 1940 (live and) dead stranded cetaceans were reported in the Netherlands, belonging to 14 species. With 1896 individuals, harbour porpoise (*Phocoena phocoena*) was the most commonly reported species. Most porpoises were found in the south-west of the country (Delta), but highest densities were encountered on the Wadden Sea islands. An Unusual Mortality Event (UME) occurred between 23 August and 4 September 2021, when 197 porpoises washed ashore on the Wadden Sea islands. They possibly originated from the Dogger Bank area and appeared to have died from a bacterial infection with *Erysipelothrix rusiopathiae*. Due to the UME, the strandings density of porpoises was especially high in the Wadden Sea area: 1.5 (individuals / km / yr), compared to 0.7 along the mainland coast and 0.2 in the Delta area. Despite the UME, the countrywide density decreased from 0.6 during 2015-2019 to 0.4 in 2020-2023. Since the unusually high number of strandings during 2011-2013, the average number of strandings per year is steadily decreasing. The proportion of males is decreasing (59% in 1998-2007, 56.2% in 2020-2023), the proportion of neonates is increasing (12.4% versus 14.9%). About 50 fresh porpoises per year are necropsied. Causes of death have changed slightly (bycatch from 16% during 2014-2019 to 12%, grey seal (*Halichoerus grypus*) predation from 24% to 19%, malnutrition/starvation from 17% to 15%, infectious disease from 32% to 37%), but whether this is influenced by selecting only fresh porpoises for necropsy is yet unclear. Rare species stranded were killer whale (*Orcinus orca*) and bottlenose whale (*Hyperoodon ampullatus*). The number of species is slowly increasing, the number of individuals other than porpoise only marginally. Other species were minke whale (*Balaenoptera acutorostrata*), fin whale (*B. physalus*), humpback whale (*Megaptera novaeangliae*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), and Sowerby's beaked whale (*Mesoplodon bidens*), all of which seem to be increasing (as strandings) in the south-eastern North Sea. Also reported, but decreasing as strandings, is white-beaked dolphin (*Lagenorhynchus albirostris*). Species stranded, but not showing any long term trend, during this period are long-finned pilot whale (Globicephala melas), white-sided dolphin (*Leucopleurus acutus*), sperm whale (*Physeter macrocephalus*) and bottlenose dolphin (*Tursiops truncatus*). The number of stranded cetaceans left unidentified increased from 17% since 2000 to 66% since 2020, for various reasons. Naturalis Biodiversity Center has stopped registering cetacean strandings as of 16 January 2024. Strandings can now be reported at and/or requested from www.stranding.nl. On this new platform the archive of www.walvisstrandingen.nl can also be found.

Keywords: Cetacea, harbour porpoise, *Phocoena phocoena*, UME, mortality, North Sea.

Introduction

We present a validated list of cetaceans stranded on the Dutch coast during the years 2020-2023. It follows the report on stranded

cetaceans summarizing five years by Keijl et al. (2021). The strandings during the focal period have again been reported by hundreds of people and various organizations and were collected by staff of the zoological museum of Naturalis Biodiversity Center in Leiden, the Netherlands. The reason for now summarizing four years instead of five, as in previous reports, is that Naturalis Biodiversity Center in Leiden, as of 16 January 2024, no longer supervises the cetacean strandings database.

Even with all single strandings being available on the internet and monthly reports produced, it is considered valuable to keep on reporting printed reviews instead of viewing single events or, at most, digital graphs summarizing years. Only an analysis of collated data of irregularly occurring stranding events may provide new insights in a slowly changing environment, although reviewing a few years only (such as this review) does not elucidate the larger picture. Strandings only form part of our knowledge on cetacean presence and ecology in the North Sea. Other important sources are observations of live animals and by-caught individuals. In the Netherlands, strandings and live observations are covered to a certain degree, the third source is still shrouded in mystery, with investigating stranded animals only partly elucidating bycatch events. By following strandings through time, as is happening in other countries bordering the North Sea, a picture is built from the cetacean community in the North Sea.

Methods

Stranding records have been verified by staff of Naturalis Biodiversity Center in Leiden. Records were received from people inside the regular strandings network, by day trippers filling in the form on the website walvisstrandingen.nl, and – increasingly – by records on waarneming.nl and in chat groups on whatsapp. Data collected are date, location, name of reporter, and, if possible, species name, sex, length, state, whether or not it was necropsied and/or collected, and other peculiarities (for instance entanglement). As most records are accompanied by photographs, information on state and sex can often be verified.

In this report, all individual records are presented, except for porpoises, for which this is unfeasible. Finds of loose bones or skulls are also mentioned, as well as live strandings, large whales caught on the bow of ships, or floating carcasses at sea, as long as they are found within Dutch waters. The results are summarized in Table 1. Unless stated otherwise, remains are destructed, but especially smaller whales (e.g. porpoises) are often buried locally. The taxonomic order follows Wilson & Reeder (2005).

Area

The area from which strandings are reported stretches from the Belgian border in the south-west of the Netherlands to the German border in the north-east, and includes the inner waters of the Delta area in the south-west of the country and the entire Dutch part of the Wadden Sea. As the coast consists of parts of varying nature (sandy, muddy, stony) and exposure, it is subdivided into three parts following Camphuysen et al. (2008): 1. The Delta area, in the south-west, from the Belgian border up to and including the artificially created Maasvlakte. It includes the 'inner Delta', i.e. the borders of rivers Western Scheldt and the partly closed Eastern Scheldt (no strandings were recorded in Grevelingenmeer and Haringvliet); 2. The mainland coast, from Hoek van Holland to Den Helder; and 3. The Wadden Sea. This extensive area stretches from the sand spit Razende Bol in the west to the uninhabited islet of Rottumeroog in the east. The Wadden Sea is subdivided into the North Sea (mostly north-facing) coast of the Wadden Sea islands, and the Wadden Sea proper, the latter including the Wadden Sea (mostly

Table 1. Stranded cetaceans on the Dutch coast in 2020-2023, including unidentified ones. The third last column gives the total per species in the twenty years preceding the focal period, the last two columns the average number per year during two different periods. Records of loose bones/skulls are excluded.

						Average / year	
	2020	2021	2022	2023	2000-2019	2010-2023	1990-2009
Common minke whale	2	1	-	1	19	1.1	0.6
Fin whale	-	1	1	1	15	0.9	0.3
Humpback whale	-	-	1	1	7	0.4	0.2
Common dolphin	4	1	1	1	9	1.1	0.2
Long-finned pilot whale	-	-	-	1	6	0.4	0.2
White-sided dolphin	-	1	-	-	4	0.07	0.3
White-beaked dolphin	-	-	-	1	56	0.6	6.0
Killer whale	-	-	1	-	1	0.1	0.0
Striped dolphin	1	-	-	1	6	0.4	0.3
Harbour porpoise	433	715	423	325	8961	578	161
Sperm whale	-	1	-	-	15	0.9	0.7
Bottlenose whale	2	-	-	-	0	0.1	0.1
Sowerby's beaked whale	1	2	2	-	9	0.9	0.1
Blainville's beaked whale	-	-	-	-	1	0	0.05
Unidentified Cetacea	1	1	5	5	19	1.4	1.0
Total	444	723	434	337	9128		

south-facing) side of the islands, the north-eastern part of the province of Noord-Holland, Afsluitdijk and the mainland coast of the provinces of Friesland and Groningen. The uninhabited islets Razende Bol are combined with Texel - North Sea coast, Griend with Vlieland - Wadden Sea, and Engelsmanplaat with Schiermonnikoog - North Sea coast, while the easternmost islets Rottumerplaat and Rottumeroog are combined to 'Rottum' - Wadden Sea. The length of the coast of the subareas is given in Table 2.

Coverage and effort

Coverage is comparable with that in previous periods, see Keijl et al. (2016, 2021) for details. Only during the UME in late summer 2021 occurring on the eastern Frisian islands, daily surveys, or even multiple surveys per day, were undertaken by car to collect porpoise carcasses. Outside this period, no special activities have been undertaken to locate stranded cetaceans, although dedicated surveys are executed locally to locate abandoned seal pups or entangled seals.

Research

As in the previous period, research on stranded cetaceans was performed by the division of pathology of Utrecht University (e.g. IJsseldijk et al. 2020a, Keijl et al. 2021). This research focuses on the cause of death, following national and international rules of protection of marine mammals (Camphuysen & Siemensma 2011, Pierce et al. 2022). Species other than porpoise and animals too long to fit in a van are examined on the beach, when possible, or transferred to Utrecht University when smaller. Selection of carcasses of porpoise is done *ad hoc* and depends largely on the state of decomposition, but also on the location of stranding and associated logistics to retrieve specimens timely for post-mortem investigation. Approximately

Table 2. Total number of harbour porpoises in 2020-2023 in the Netherlands per subarea. Also given are density (average density, *n*.km^{-1} year^{-1}), sexual composition (percentage of males, with total number of sexed individuals between brackets), and age (as percentage per length class, in cm; see text). See also the Methods section for the geographic subdivision. A single porpoise found in inland waters (Elburg, IJsselmeer) is not included. No porpoises have been reported in Grevelingenmeer and Haringvliet, part of the inner Delta.

	Total	Density	% males (*n*)	<90	90-130	>130	(*n*)
Delta (408 km)	*387*	*0.2*	*57.0 (286)*	*17.2*	*34.5*	*48.3*	*(116)*
Zeeuws-Vlaanderen	15	0.2	63.6 (11)	33.3	33.3	33.3	(3)
Walcheren	156	0.7	54.0 (124)	14.8	40.7	44.4	(27)
Schouwen	53	0.4	61.1 (36)	22.2	55.6	22.2	(9)
Goeree	25	0.3	56.3 (16)	9.1	45.5	45.5	(11)
Voorne	19	0.4	66.7 (15)	30.0	40.0	30.0	(10)
Inner Delta	83	0.1	60.0 (60)	15.6	28.1	56.3	(32)
Maasvlakte	36	0.4	50.0 (24)	16.7	20.8	62.5	(24)
Mainland coast (153 km)	*569*	*0.7*	*59.9 (364)*	*17.2*	*43.0*	*39.7*	*(151)*
Zuid-Holland	299	0.8	62.9 (205)	14.9	45.9	39.2	(74)
Noord-Holland	270	0.7	56.0 (159)	19.5	40.3	40.3	(77)
Wadden Sea total (384 km)	*939*	*0.5*	*52.5 (421)*	*13.5*	*66.9*	*43.9*	*(446)*
North Sea coast (107 km)	*803*	*1.5*	*52.2 (356)*	*13.6*	*64.0*	*46.7*	*(390)*
Texel	184	1.2	53.9 (115)	19.2	49.5	31.3	(99)
Vlieland	194	1.3	50.0 (42)	9.2	30.0	60.8	(120)
Terschelling	145	2.6	47.6 (42)	13.8	62.1	24.1	(29)
Ameland	186	2.3	52.2 (122)	17.2	34.3	48.5	(99)
Schiermonnikoog	94	1.0	54.3 (35)	4.7	41.9	53.5	(43)
Wadden Sea (277 km)	*136*	*0.1*	*53.8 (65)*	*12.5*	*62.5*	*25.0*	*(56)*
Texel	29	0.2	37.5 (16)	5.0	75.0	20.0	(20)
Vlieland	3	0.1	33.3 (3)	0.0	0.0	100.0	(3)
Terschelling	15	0.1	33.3 (9)	66.7	33.3	0.0	(3)
Ameland	8	0.0	66.7 (3)	0.0	100.0	0.0	(4)
Schiermonnikoog	0	0.0	0.0 (0)	–	–	–	(0)
Rottum	28	0.6	66.7 (12)	15.4	38.5	46.2	(13)
Noord-Holland	7	0.1	66.7 (3)	0.0	50.0	50.0	(2)
Friesland	29	0.1	73.3 (15)	28.6	71.4	0.0	(7)
Groningen	17	0.1	50.0 (4)	0.0	100.0	0.0	(4)
Total (945 km)	*1895*	*0.4*	*56.2 (1071)*	*14.9*	*41.4*	*43.8*	*(1678)*

10-15% of all porpoises, about 50 (fresh) individuals per year, are assessed to determine causes of death, with only basic strandings data recorded from remaining cases. Apart from porpoises, 53% of the other species of stranded cetaceans were necropsied, with carcass freshness again as the most pressing criteria for selection. Information on results of necropsies of porpoises, and of individual cases of rare species, can be found at https://www.uu.nl/onderzoek/strandingsonderzoek.

The following zoological museums collected one or more (parts of) cetaceans stranded during the focal period:

- Ecomare at Texel, Noord-Holland (collection numbers starting with B),
- Het Natuurhistorisch in Rotterdam, Zuid-Holland (collection numbers starting with NMR),
- Naturalis Biodiversity Center in Leiden,

Zuid-Holland (collection numbers starting with RMNH.MAM), and
- Terra Maris at Oostkapelle, Zeeland.

Systematic list

In 2020-2023 1940 cetaceans were recorded, comprising 14 different species (Table 1). These strandings include recent bones of five different individuals (skull, rib, single vertebra, vertebral column, and a penis with pelvic bones still attached). They also include eight cetaceans not stranded but either accidentally brought in on the bulb of ships, found afloat nearshore or offshore (a large whale, three fin whales, one Sowerby's beaked whale *Mesoplodon bidens*), near-stranded (two or three Sowerby's beaked whales), or live-stranded and pushed back (striped dolphin *Stenella coeruleoalba*). New species for the Netherlands were not recorded during the present period, but there were several species which are not recorded yearly. Especially the strandings of a live killer whale (*Orcinus orca*) and of two bottlenose whales (*Hyperoodon ampullatus*) were notable events. Remarkable is the apparent increase in strandings of common dolphins. Thirteen cetaceans remained unidentified. As usual, the most common species was porpoise, with 1896 reported strandings (97.6% of all strandings in this period).

Common minke whale (*Balaenoptera acutorostrata*)

2020-2023: 4 records
2000-2019: 19 records
Before 2000: 27 records

12 July 2020, Schiermonnikoog, Friesland. Sex unknown, length unknown (but estimated 400 cm from a boat when the carcass was still afloat), weight unknown. Rotten, incomplete: skull and possibly one jaw missing. Reported by R. Arends and others, and coast guard Den Helder. Not collected, not necropsied, buried locally. Identification not certain.

25 November 2020, Rottumerplaat, Groningen. Male, 470 cm (measured), weight unknown. Decomposed, complete. Reported by J. Kostwinner and F.J. de Wal. Not collected, not necropsied. Entire carcass left above the high tide line on the island, rate of decomposition monitored until spring 2023, but skeleton still present in spring 2024.

14 April 2021, Razende Bol, Noord-Holland. Sex unknown, length 410 cm (measured from decomposed carcass), weight unknown. Reported by H. Eelman. Decomposed, fairly complete but tail fin and baleens missing (Figure 1). Part of the vertebrae, skull, mandibulae, tongue bone, jaws, and flippers collected by Ecomare Nature Museum (collection number B2-2122). Remainder buried locally.

20 December 2023, Brouwersdam, Zuid-Holland. Sex unknown, 750 cm (estimated), weight unknown. Decomposed, incomplete: jaws and baleens missing. Reported by R. van Aperen. Not collected, not necropsied, remains destructed.

The minke whale from 12 July 2020 was found floating between the island of Schiermonnikoog and Het Rif, to the west. It stranded nearby on the 14th. As the carcass was incomplete and discoloured, and because it was not seen by us and nothing was collected, identification based on the photographs alone could not be established beyond doubt.

Of the minke whale that stranded in November 2020, the process of decomposition was studied in detail, which had not been done before in the Netherlands. Apart from the rate of decomposition, nuisances brought about by a stranded whale, such as stench, the risk of explosion, pollution of the soil by heavy metals and DDT, and vertebrate and invertebrate biodiversity following decomposition, were evaluated by direct or remote observa-

Figure 1. Remains of a minke whale (*Balaenoptera acutorostrata*), Razende Bol, 14 April 2021. *Photo: Wilma Eelman.*

tion. Unfortunately, the carcass was not studied on the stranding site, but was taken to a different location on the same island and deposited far above the tide line, to prevent it from washing away. The trial lasted seven months, but the bones are still in the same location (September 2024), and are still being reported every once in a while (www.waarneming.nl and www.stranding.nl). See Baptist et al. (2024) for the full study report and Baptist & Leopold (2024) for an evaluation and recommendations for leaving cetacean carcasses to decompose in nature instead of destructing them.

None of the minke whales stranded between 2020-2023 were necropsied and, hence, no information is available on causes of death. None of the stomach contents were studied either. This is in stark contrast with the six studied out of the eight that stranded between 2015-2019. Two out of those six had been hit by ships.

The increase in minke whale strandings since the last century has been noted earlier (Keijl et al. 2021). Since 2000, an average of 0.95 minke whales stranded per year, which is considerably higher than before the turn of the century, when it was only 0.16 (1950-1999).

Fin whale (*Balaenoptera physalus*)

2020-2023: 3 records
2000-2019: 15 records
Before 2000: 26 records

27 July 2021, Terneuzen, Zeeland. Male, 1475 cm (measured), weight 15,000-17,000 kg (estimated). Not fresh, complete. Skull, one flipper, baleens, atlas, axis and tissue collected (RMNH.MAM.59331). Remainder destructed. Reported by H. Jonkers and J. van der Hiele. Necropsied by Utrecht University (case no. BP08).

2 October 2022, Westkapelle, Zeeland. Male, 1318 cm (measured), weight 13,000 kg (estimated based on weight of destructed material, so body fluids largely excluded). Not fresh, complete. Single tympanic bulla and tissue collected (RMNH.MAM.63697). Both mandibulae, baleen (part) and atlas and axis collected by Museum Terra Maris in Oostkapelle, Zeeland (no collection number yet).

Reported by J. van der Hiele. Necropsied by Utrecht University (case no. BP09).

29 August 2023, Zeeland (but discovered only in Antwerp, Belgium). Male, 1050 cm (measured), 9000 kg (estimated). Not fresh, complete. Parasites and tissue collected by Universities of Ghent and Liège, Belgium (no collection numbers), flippers collected by University of Antwerp, Belgium (no collection number). Necropsied by Universities of Antwerp, Ghent and Liège. Reported by J. Haelters.

All three fin whales concerned relatively small, and thus immature, individuals. The one from August 2023 at Terneuzen was the second smallest ever recorded in the Netherlands (the smallest one was a female from 15 January 2012 at Vlissingen (Flushing), measuring 877 cm). Fin whale calves are born in November-December and measure 600-700 cm at birth (Cawardine 2020), so individuals of this size are (less than) one or two years old.

All three were necropsied for establishing the cause of death (the one from August 2023 in Belgium), and all were probably hit by ships alive (see also Haelters & Kerckhof 2024). They were brought in during the now 'classic' period of the year, i.e. late summer/early autumn. Up to and including 2023, the average number of 'strandings' per year has risen from 0.75 since 2000 to 0.92 since 2010. There are now 44 registered 'strandings' of fin whales in the database, of which 31 have been sexed; 20 of these (70%) were males. Since 2000, 16 out of 18 have been sexed, resulting in 10 males and 6 females.

Humpback whale (*Megaptera novaeangliae*)

2020-2023: 2 records
2000-2019: 7 records
Before 2000: 0 records

5 July 2022, Vlieland, Friesland. Female, 638 cm (measured), 4000 kg (estimated on basis of destructed tissues, weight of skeleton and body length, but body fluids largely excluded). Slightly decomposed, complete. Complete skeleton and tissue collected (RMNH.MAM.63662). Reported by R. Bijma and J. Hoekendijk. Necropsied by Utrecht University (case no. MN02).

2 July 2023, floating at Steenbank, 7.5 mile north-west off Westkapelle, Zeeland. Female, 846 cm (measured), 5500 kg (estimated) (Figure 2). Decomposed, incomplete: baleens and stomach missing. Single flipper and tissue collected (RMNH.MAM.63882). Reported by P. van Leeuwen and T. de Ruiter. Necropsied by Utrecht University (case no. MN03).

Another two humpback whales, elevating the total number of stranded individuals in the Netherlands to eight (the one from March 2012 concerned a single vertebra). Since the first two strandings, both in 2003, humpbacks have been found in 2004, 2009, 2010, 2012, 2022 and 2023. Living and often apparently healthy humpbacks occur virtually yearly in Dutch waters since 2003 (Leopold et al. 2018, waarneming.nl) and although, based on their size, the stranded individuals seem to be mainly immature, large individuals, probably adults, have been observed in Dutch waters as well.

Common dolphin (*Delphinus delphis*)

2020-2023: 9 records
2000-2019: 9 records
Before 2000: 83 records

31 August 2020, Balgzand, Noord-Holland. Female, 201 cm (measured), 71 kg (weighed). Fairly fresh, complete. Skull and tissue collected (RMNH.MAM.59836). Reported by T. Zutt. Necropsied by Utrecht University (case no. DD07).

Figure 2. Humpback whale (*Megaptera novaeangliae*) at Steenbank, 7.5 mile north-west off Westkapelle, 2 July 2023. *Photo: coast guard*.

11 September 2020, Neeltje Jans, Oosterschelde, Zeeland. Female, 195 cm (measured), 42 kg (weighed). Incomplete: jaws, teeth and part of tissue missing. Dried out. Reported by J. van der Hiele.
Skull and flippers collected (RMNH.MAM.63844). Necropsied by Utrecht University (case no. DD08).

21 November 2020, Zierikzee, Zeeland. Male, 150 cm (measured), 35 kg (weighed). Fresh, probably live-stranded, complete. Skull, flipper and tissue collected (RMNH.MAM.59814). Reported by J. Dhont and R. van Aperen. Necropsied by Utrecht University (case no. DD09).

22 November 2020, Breskens, Westerschelde, Zeeland. Male, 173 cm (measured), 52,5 kg (weighed). Live-stranded, complete, died. Skull, neck vertebrae and tissue collected (RMNH.MAM.59815). Reported by J. van der Hiele. Necropsied by Utrecht University (case no. DD10).

28 November 2021, Westenschouwen, Zeeland. Sex unknown, 220 cm (measured, but tail missing), weight unknown. Old and incomplete carcass, teeth missing. Incomplete disarticulated skeleton collected by Het Natuurhistorisch (collection nr. NMR999000204210). Reported by R. van Aperen and W. Kraak. Not necropsied.

5 April 2022, Grevelingendam, Zuid-Holland. Male, 219 cm (measured), 88 kg (weighed). Decomposed, complete. Reported by RTZ Zuidwest. Complete skeleton collected (RMNH.MAM.63673). Necropsied by Utrecht University (case no. DD11).

10 January 2023, Texel, Noord-Holland. Male, 170 cm (measured), 47 kg (weighed). Not fresh, some tissue missing. Reported by J. Havermans and S. de Wolf. Collected by Ecomare Nature Museum (collection number B2-2123). Necropsied by Utrecht University (case no. DD12).

11 November 2023, Scheveningen, Zuid-Holland. Male, 187 cm (measured), 46 kg (weighed). Decomposed, complete. Reported by T. van Rijmenam. Not collected. Necropsied by Utrecht University (case no. DD13).

24 December 2023, Maasvlakte, Zuid-Holland. Male, 213 cm (measured), 72 kg (weighed). Fresh, complete. Reported by A.

Sajet and A. van den Berge. Tissue collected by Naturalis (RMNH.MAM.63895) and Utrecht University (no collection number). Necropsied by Utrecht University (case no. DD14).

The common dolphin from 24 December 2023 at Maasvlakte looked 'odd', and *D. capensis* was considered a possibility (even though the nearest area of occurrence lies off West-Africa, e.g. Morais Pinela 2015). It was necropsied, but the skull was not collected. DNA-analysis showed it to be *D. delphis*, but it is unknown whether the two are identifiable on the basis of the sequenced CO1-gene. Taxonomy of *Delphinus* is complicated, because different geographic forms are morphologically similar but appear to occur sympatrically. Researchers painstakingly try to find differences between them, usually on the basis of cranial measurements and/or DNA-analysis (e.g. Ngqulana et al. 2019). Recently, the long-beaked form occurring in the eastern Pacific has been re-named as *D. bairdii* (Jefferson et al. 2024), while the long-beaked form occurring in Senegalese waters appears to be distinct from both local short-beaked *D. delphis* and long-beaked forms elsewhere (but has not specifically been named yet, Becker et al. 2024). At present, *D. capensis* is (e.g. Wilson & Reeder 2005), or is not (e.g. Committee on Taxonomy 2024) accepted as a separate species. What is presently called *D. capensis* may be identifiable by DNA-analysis (Rosel et al. 1994), but possibly not in the Atlantic Ocean (Cunha et al. 2015). The species has not been recorded in Europe yet, but thorough inspection of skulls, perhaps in combination with DNA-analysis, could shed light on identification and distribution.

Two out of the nine common dolphins stranded alive. Several were emaciated and/or underweight. The weight of a healthy adult common dolphin lies between 100-200 kg (Cawardine 2020), although weight data in literature vary widely. In the Dutch strandings database, there are now 101 common dolphins, of which 26 males and 26 females (52% sexed). Also among the 18 common dolphins stranded since 2000, sex ratio is remarkably equal (seven males, seven females, four unsexed). Six out of the nine common dolphins stranded between 2020-2023 were necropsied.

Nine strandings in just four years is quite impressive, considering that the total number in the database amounts to only 101 individuals. Moreover, four stranded but unidentified dolphins during the focal period probably also concerned common dolphins, making a total of twelve strandings in just four years. During the 1930s-1950s, common dolphin was common in the central and/or southern North Sea, coinciding with Atlantic water extending further northward, but the species disappeared after that and the number of strandings decreased. Between 1925-1960, the average number of strandings per year was 2.06, between 1961-2000 0.15, and since 2001 0.75.

Long-finned pilot whale (*Globicephala melas*)

2020-2023: 1 record
2000-2019: 6 records
Before 2000: 18 records (124 individuals)

3 December 2023, Vlieland, Friesland. Female, 427 cm (measured), 1013 kg (weighed). Fresh, complete. Reported by F. Janssens. Entire skeleton collected by Ecomare Nature Museum (collection number B2-2124). Necropsied by Utrecht University (case no. GM05).

White-sided dolphin (*Leucopleurus acutus*)

2020-2023: 1 record
2000-2019: 4 records
Before 2000: 8 records

20 August 2021, Baarland, Westerschelde, Zeeland. Male, 245 cm (measured), 194 kg (weighed). Fresh, complete, probably live-

Figure 3. Killer whale (*Orcinus orca*), dying in the surf at Cadzand, 15 October 2022. *Photo: Jaap van der Hiele.*

stranded. Skull and tissue collected (RMNH. MAM.63677). Reported by J. van der Linden and J. van der Hiele. Necropsied by Utrecht University (case no. LA12).

White-beaked dolphin (*Lagenorhynchus albirostris*)

2020-2023: 1 record
2000-2019: 54 records
Before 2000: 173 records

20 February 2023, Engelsmanplaat, Wadden Sea, Friesland. Female, 202 cm (measured), 96.4 kg (weighed). Fairly fresh, complete, scavenged. Skull and tissue collected (RMNH.MAM.63879). Reported by T. de Vries and A. Dijkstra. Necropsied by Utrecht University (case no. LA13).

Only a single record in four years, but at least three unidentified dolphins (3 July 2022, Terschelling, Friesland, 5 July 2022, Dishoek, Zeeland, and 6 February 2020, Oostdijk, Zuid-Holland) probably also concerned this species.

In the previous review (Keijl et al. 2021), the total of 57 stranded white-beaked dolphins for the period 2000-2014 was erroneous. Prior to 1900, only two white-beaked dolphins had been identified, so 61% of the 282 strandings are from the twentieth century. Especially between 1980 and 2019, white-beaked dolphin was the most common cetacean on our beach next to harbour porpoise, with 182 strandings, so almost 80% of the total number of strandings was recorded in just 40 years. At present, the species is becoming increasingly rare in the southern North Sea. The average number of strandings per year has dropped from 6.1 between 1981-2000 to 2.4 since.

Killer whale (*Orcinus orca*)

2020-2023: 1 record
2000-2019: 6 records
Before 2000: 31 records

15 October 2022, Cadzand, Zeeland. Female, 517 cm (measured), 2003 kg (weighed). Fresh, complete, live-stranded (Figure 3). Complete skeleton collected (no collection number yet). Reported by J. van der Hiele. Necropsied by Utrecht University (case no. OO01).

Prior to 1964 there have been at least 24 strandings of killer whales in the Netherlands, the oldest in 1783, and five in the nineteenth century. Between 1920-1970, a relatively steady stream of on average 0.3-0.6 killer whales were found per decade. Since 1964, there has only been one stranding (22 June 2010, Lauwersoog, Friesland, also a live stranding), apart from a handful of records of loose bones and skull fragments.

The killer whale from Cadzand in 2022 concerned an adult female. She had not eaten for a considerable period, probably because of severe gingivitis (infection of dental gum), rotten, fractured and loose teeth, and infections in various organs. She was originally part of a pod of about 50 killer whales living in Iberian waters, known by her code name IB6, alias Gala, and usually in the company of a male coded IB13. Whether he was her mate or her son is unknown. Gala had been seen for the first time twenty years earlier, when she was already mature. This means that she could have been at least thirty years old when she died. Due to the severely damaged teeth, the animal's age based on dental growth layers could not be determined any more.

Striped dolphin (*Stenella coeruleoalba*)

2020-2023: 3 records
2000-2019: 6 records
Before 2000: 6 records

30 May 2020, Harlingen, Friesland. Sex, length and weight unknown. Live-stranded, pushed back into the Wadden Sea. Nothing collected, not necropsied. Reported by R. Oost.

8 June 2023, Domburg, Zeeland. Male, 210 cm (measured), weight unknown. Tissue collected (RMNH.MAM.63894). Reported by EHBZ zuidwest. Not necropsied.

14 July 2023, Vlieland, Friesland. Sex, length and weight unknown. Skull only, collected by Ecomare Nature Museum (collection number B2-2125). Reported by F. Janssens. Not necropsied.

The very decomposed and discoloured dolphin from 8 June 2023 found at Domburg could not be identified on the basis of morphological characters. Luckily, a tissue sample for DNA-identification could be collected and it turned out to be a striped dolphin, the fourteenth for the Netherlands and the eighth since 2000. (Note that the skull found on Vlieland in July 2023 possibly belonged to the striped dolphin that stranded alive nearby a month earlier and was pushed back into the sea. Hence, due to its rarity in the Netherlands, the two separate records are counted as one individual.) It was only the third cetacean in the Netherlands to be identified by DNA-analysis. The distribution of stranded striped dolphins along the coast of the Netherlands (with the first stranded in 1967) is somewhat peculiar for a species that is supposed to have a tropical/subtropical distribution: only four have been found in the province of Zeeland, in the south-west, one in (the south of) Zuid-Holland, and nine in the Wadden Sea area, in the very north of the Netherlands.

Bottlenose dolphin (*Tursiops truncatus*)

2020-2023: 2 records
2000-2019: 10 records
Before 2000: 360 records

12 May 2020, Wijk aan Zee, Noord-Holland. Male, not measured, not weighed (but see IJsseldijk et al. 2020b). Fresh, incomplete: tail and part of hind body missing. Entire skeleton collected (RMNH.MAM.59783). Reported by R. van Wilgenburg. Necropsied by Utrecht University (case no. TT02).

4 December 2021, Scherpenisse, Ooster-

schelde, Zeeland. Male, 274.5 cm (measured), 242 kg (weighed). Fresh, complete. Skull, neck vertebrae, flipper and tissue collected (RMNH.MAM.63674). Reported by foundation SOS Dolfijn. Necropsied by Utrecht University (case no. TT03).

The individual found in May 2020 concerned the fourteen year old bottlenose dolphin named Zafar (IJsseldijk et al. 2020b). This solitary living bottlenose dolphin, which preferred to mingle with humans rather than conspecifics since at least 2017, accompanied a sailing boat from the Atlantic coast of France through the Channel all the way to the (freshwater) port of Amsterdam, after which it was lured back to the North Sea through the Noordzee channel and the sluices at IJmuiden. It was last seen alive off Callantsoog, Noord-Holland, accompanying a beam trawler. It tragically died from a ship propeller strike, which cut off its tail.

The strandings database contains close to 400 bottlenose dolphins. Although the species has stranded in every decade since 1900, it has become particularly rare after the 1970s (on average 9.4 per year between 1931-1940, 1.3 between 1971-80, 0.5 since 2000).

Harbour porpoise (*Phocoena phocoena*)

2020-2023: 1896 records
2020: 433 records
2021: 715 records
2022: 423 records
2023: 325 records
2000-2019: 8961 records
Before 2000: 2371 records

Numbers and density

In 2020-2023 the average number of stranded harbour porpoises per year was 474. This is below the long-term average of 578 (2010-2023, *n*=8089) and also lower than the 552 during the previous period (Keijl et al. 2021). The yearly number of strandings fit in a trend with decreasing totals since the exceptional stranding numbers in 2011-2013.

A notable exception in the dwindling numbers was 2021, with 715 strandings. This number was surpassed only by the years 2011, 2012 and 2013 (with 887, 755 and 873 respectively). Note that without the unusual mortality event (UME) in 2021 (see below), the total number of strandings in this year would have still been higher than during 2020, 2022 and 2023. The stranding number of 2021 was elevated considerably by an UME occurring between 23 August and 4 September, when 197 decomposed porpoises stranded on the Wadden Sea islands of Vlieland, Terschelling, Ameland and Schiermonnikoog, an area of about 100 km wide. For comparison: in 2017-2020 in exactly the same area on the exact same dates a combined total of 83 porpoises was reported, i.e. an average of only 20.8 per year. During the 2021 event, the local density was elevated to 2.6 individuals km^{-1} $year^{-1}$, compared to 0.3 in the other years, again stressing the uniqueness of this event. The mass stranding was likely caused by an infection with the bacterium *Erysipelothrix rusiopathiae*, which had not previously been linked to mass strandings of marine mammals in the Netherlands (IJsseldijk et al. 2023a). Another unique characteristic of this event was that it predominantly hit adult females in good body condition (37.7% males, *n*=151 sexed individuals between 1 August and 30 September 2021, compared to 57.9% males in 2010-2023 in the same area and period excepting 2021, *n*=190 sexed individuals, and 80.0% adult females in 2021, *n*=65 measured, compared to 60.4% adult females, *n*=129 measured). Necropsies were conducted on a subset of 22 porpoises. Assessment of stomachs showed that none had eaten anything significant shortly before death. How the porpoises got infected by this bacterium remains unknown, and the same goes for why mainly adult females were involved. A model taking into account sea surface currents and wind direction, car-

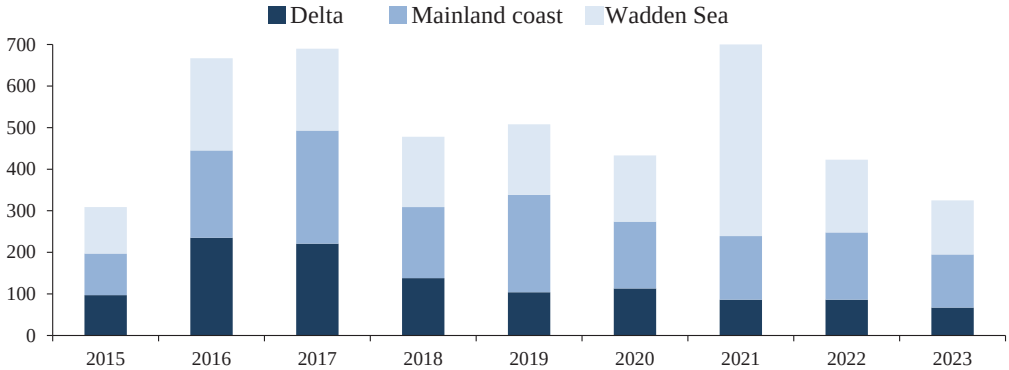

Figure 4. Number of dead harbour porpoises in 2020-2023 along the Dutch coast, with 2015-2019 added for comparison (www.walvisstrandingen.nl; *n*=4547).

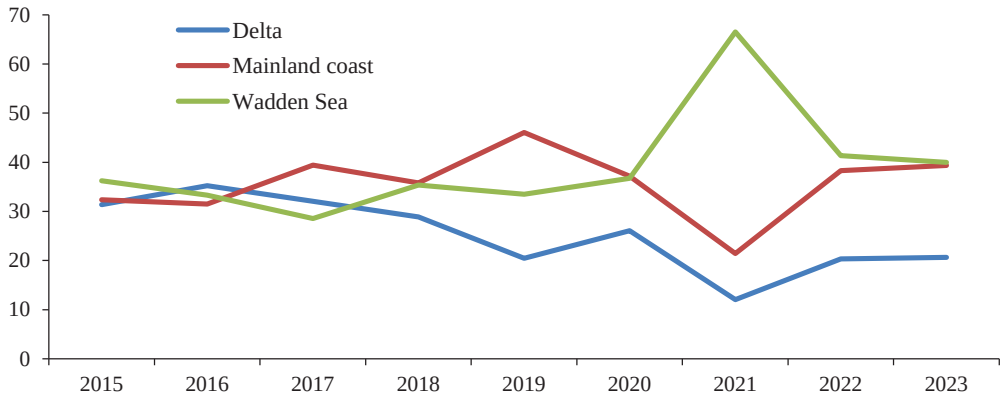

Figure 5. Proportion of dead harbour porpoise in three subareas (Delta, mainland coast and Wadden Sea area) in 2020-2023, with 2015-2019 added for comparison (source: www.walvisstrandingen.nl).

ried out by Rijkswaterstaat (part of the Dutch Ministry of Infrastructure and Water Management), indicated that the porpoises likely stemmed from a small area between the Frisian Front and Dogger Bank, about 100 km north-west of Texel and a bit further from the main area of the stranding (M.F. Leopold personal communication).

The country-wide average density of 0.4 porpoise is a third lower than during the previous period, when it was 0.6 (Table 2). The density in the Wadden Sea area remained the same, which can be ascribed to the UME described above. The normally high density on Vlieland however was lower than usual, while higher densities than normal were established at Terschelling and Ameland (2.6 and 2.3 respectively). Densities along the mainland coast were below 1.0. Compared to 2015-2017, when porpoises were spread about equal over the three areas (about one third each) (Figure 4), the total numbers are not just decreasing, but the proportion stranding in the Delta is decreasing to about a fifth of the countrywide total (Figure 5).

A single porpoise, found on 31 Mayt 2021 at Elburg, IJsselmeer (lake IJssel), was believed to have been placed there from an unknown location.

Sex and age

The proportion of males is decreasing through the years: it was 59% in 1998-2007

(Camphuysen et al. 2008), 58.2% in 2008-2014 (Keijl et al. 2016), 58.0% in 2015-2019 (Keijl et al. 2021) and 56.2% in 2020-2024, even though, as mentioned above, the mass stranding in 2021 involved only 32.5% males. The slow decrease of males (washing ashore) is intriguing and warrants further investigation to whether the sex ratio in the population is changing, whether there is differential mortality, or whether digital photography is still influencing the results (cf. Keijl 2022a).

The proportion of neonates (individuals <90 cm, Lockyer et al. 2001) on the other hand is increasing, albeit marginally: it changed from 12.4% before 2008 via 13.5% and 13.5% to 14.9% in the present (Camphuysen et al. 2008, Keijl et al. 2016, 2021 respectively) (and – again – despite the mass stranding involving mainly adults).

Causes of death

In 2020 49 porpoises were necropsied, in 2021 54, in 2022 57 and in 2023 47 by the division of pathology of Utrecht University (IJsseldijk et al. 2021, van Schalkwijk et al. 2022, 2023, 2024). The aim of the post-mortem investigation is to determine the cause of death of each individual. A comparison with the previous years shows a decrease in by-catch (from 16% to 12%, 2014-2019 compared to the focal period), grey seal predation (24% to 19%) and nutritional status (17% to 15%), but an increase in infection (32% to 37%) (*n*=474 porpoises). Porpoises from the UME from 2021 are not included in these figures.

A comparison can be made with the previous period as there is no difference in sampling methods any more (prior to 2016 also a proportion of decomposed porpoises was collected, from 2016 onwards fresh ones were preferred). However, by selecting only fresh porpoises, there may be a bias in causes of death: fresh individuals have died near-shore or onshore and/or have washed ashore soon after death, while decomposed ones (Figure 6) may come from farther away. This, for instance, could be an explanation for the decrease in by-caught

Figure 6. Decomposed male harbour porpoise *Phocoena phocoena*, 4 June 2021, Ameland, in a 'sea' of thorny sea mat (*Electra pilosa*). *Photo: Johan Krol.*

individuals, which may originate from further offshore and need time to make landfall (if at all). This issue has not been solved yet.

Sperm whale (*Physeter macrocephalus*)

2020-2023: 1 record
2000-2019: 18 records
Before 2000: 62 records

7 January 2021, Vlieland, Friesland. Male, 1364 cm (weighed), 35,000 kg (based on weight of destructed material, so body fluids excluded). Fresh, complete, live-stranded. Left flipper, four teeth and tissue collected (RMNH.MAM.59816). Reported by K. Venema and A. van den Berg. Necropsied by Utrecht University (case no. PM11).

Bottlenose whale (*Hyperoodon ampullatus*)

2020-2023: 2 records
2000-2019: 0 records
Before 2000: 21 records

7 September 2020, Terneuzen, Zeeland. Female, 700 cm (estimated), weight 6000 kg

Figure 7. Bottlenose whale (*Hyperoodon ampullatus*) washed ashore at Terneuzen, Zeeland, 7 September 2020. The oblique laceration all the way from the side of the left chest across the belly to the right flank has led to the acute death of this unfortunate whale. *Photo: Jeroen Hoekendijk*.

(estimated). Fresh, incomplete: part of organs missing. Skull, mandibulae, flipper, neck vertebrae and ribs collected (RMNH.MAM.59810). Reported by W.J. Strietman. Necropsied by Utrecht University (case no. HA01).

8 September 2020, Borssele, Zeeland. Female, length and weight unknown. Fresh, incomplete: cut into pieces by ship screw, only head and part of torso found. Skull, mandibulae, flipper, neck vertebrae and ribs collected (RMNH.MAM.59809). Reported by J. van der Hiele. Necropsied by Utrecht University (case no. HA02).

There are 23 stranded bottlenose whales in the database, but only once before was there a stranding of two more or less together (24 August 1956, Texel and 26 August 1956, Ameland). Remarkably, the bottlenose whales that stranded in September 2020 were observed alive on all days between 20 and 23 August 2020 in the partly closed Oosterschelde further north. They were elusive though and seemed to have disappeared after 23 August, despite thorough searches by multiple observers in the usually calm waters of Oosterschelde. The next time they popped up again they were in the river Westerschelde, on 6 September, which they almost certainly must have reached via the North Sea. (The alternative route, through the Rijn-Schelde channel, is extremely unlikely, as they then must have not just passed one or more sluices, but also done that undetected.) On 7 and 8 September however, they were dead, both unintentionally killed by ships. One had a large laceration expanding over the entire ventral body side and opening the abdominal cavity (Figure 7), the other was cut into three separate pieces, which stranded apart from each other. Stomach contents consisted of squid (*Gonatus fabricii*). See Keijl (2020) for more information on these and other bottlenose whales in the Netherlands. The previous strandings of this species were almost two decades earlier, in August and November 1993.

Sowerby's beaked whale (*Mesoplodon bidens*)

2020-2023: 5 records
2000-2019: 9 records
Before 2000: 16 records

17 August 2020, Neeltje Jans, Zeeland. Female, 382 cm (measured), 438 kg (weighed). Decomposed, complete. Skull, mandibulae and tissue collected (RMNH.MAM.59808). Reported by RTZ zuidwest. Necropsied by Utrecht University (case no. MB06).

5 October 2021, Ter Heijde, Zuid-Holland. Female, 473 cm (measured), 922 kg (weighed). Fresh, complete, live-stranded. Skull, mandibulae and tissue collected (RMNH.MAM.59830). Reported by K. Kooimans and R. Noort. Necropsied by Utrecht University (case no. MB07).

5 October 2021, Ter Heijde, Zuid-Holland. Female, 460 cm (measured), 799 kg (weighed). Fresh, complete, live-stranded. Skull, mandibulae and some vertebrae collected (NMR999000204890). Reported by K. Kooimans and R. Noort. Necropsied by Utrecht University (case no. MB08).

19 July 2022, Zandvoort, Noord Holland. Sex, length and weight unknown. Near-stranding. Reported by A. van den Berg. Not necropsied.

18 August 2022, Texel, Noord-Holland. Female, 400 cm (measured), 550 kg (weighed). Decomposed, complete (Figure 8). Reported by J. Hoekendijk. Necropsied by Utrecht University (case no. MB9).

The record of 19 July 2022 involved two, allegedly three, live individuals swimming very close to the beach at Zandvoort on a hot day. The animals were photographed and filmed from the shore, while there were many people bathing, but there is no material showing three different individuals, let alone three together. They were estimated by the public standing in the water to measure 2.5, 3 and 4 metres. The largest animal reportedly swam purposefully towards the beach and would probably have stranded, but several bathers could prevent that by physically redirecting it

Figure 8. Sowerby's beaked whale (*Mesoplodon bidens*), 18 August 2020, Texel. *Photo: Jeroen Hoekendijk.*

back towards the sea. It stranded again a while later on a flooded sand bar, and was set free again by hand. Then the animals swam away not to be seen any more. A report of a dead sea mammal measuring approximately 3.5 metres seen about eight kilometres away from where the whales near-stranded could not be confirmed (there were three floating dead porpoises at this site). See https://www.dumpert.nl/item/100036411_f0842381 and https://www.dumpert.nl/item/100036383_1985aa63 for video footage of the beaked whales. At least one of the Sowerby's beaked whales, showing very dark pigmented spots on the head, was not the same as the one that stranded in Wenduine, Belgium, on 8 August 2020.

The previously reported increase in strandings of this species seems to continue. Of the total of 30 records (32 individuals, and excluding one unidentified beaked whale in April 2016), almost half have been reported since 2000. Twenty-five out of thirty occurred in July-October. The majority are females (12 females, 7 males, 11 unknown), also since 2000 (6 females, 3 males, 5 unknown). The average length is 394 cm (only measured individuals (n=11); males 386 cm (n=4), females 405 cm (n=6)).

It is known that mass strandings of beaked

whales may be inflicted by sonar (low or mid-frequency active sonar, used by the military to detect submarines), which causes damage to the internal ears and/or causes the whales to leave the area (e.g. d'Amico et al. 2009, Chouinard et al. 2023). Beaked whales do not usually occur in the southern North Sea, they live in deep oceanic waters, for instance near Scotland and Norway. Naturally, one or two individuals cannot be considered a mass stranding, but the steady increase in strandings is worrying, as is the mass stranding of beaked whales scattered over a range of countries (among which the Netherlands) in the north-eastern Atlantic in summer 2020 (Dolman et al. 2021).

Unidentified cetaceans

2020-2023: 13 records
2000-2019: 19 records
Before 2000: 57 records

Small whale

14 January 2021, Noordwijk, Zuid-Holland. Single recent vertebra only, possibly from a *Balaenoptera spec*. or *Megaptera novaeangliae*. Reported by K. Kooimans and R. Noort.

Large whale

22 January 2022, Noordwijk, Zuid-Holland. Single rib from a large whale. Reported by R. and N. Burgler-van Dam.

Large balaenopterid

9 August 2022, Cleaver Bank, Dutch continental North Sea about 160 km north-west of Den Helder, Noord-Holland. Male, length and weight unknown. Reported by MV Capella. Not necropsied.

Rotten and inflated but apparently intact balaenopterid whale floating belly-up. Length estimate was not provided, photographs do not allow identification.

Harbour porpoise / unidentified dolphin

23 December 2023, Westkapelle, Zeeland. Sex, length and weight unkown. Decomposed and discoloured hump of meat, showing a row of small teeth, of which a few pointed and recurved. Reported by K. Nilsen. Not collected, not necropsied, left on the spot.

White-sided / White-beaked dolphin *(Leucopleurus acutus / Lagenorhynchus albirostris)*

6 September 2022, Texel, North-Holland. Sex and weight unkown, length estimated at 100 cm, but about one third of tail stock missing. Mummified, left on the spot. Reported by P. Bonnet.

Photographs offered to staff of Ecomare showed teeth resembling those of white-sided or white-beaked dolphin. Photographs not kept, a search on the beach remained unsuccessful.

Unidentified dolphin

6 February 2020, Oostdijk, Zuid-Holland. Penis and pelvic bones only. Reported by I. Scheijgrond.
Almost a copy of the penis attached to the pelvic bones found on 27 April 2011 at Terschelling, which at the time was identified as belonging to either a white-sided or a white-beaked dolphin, based on size and shape of the bones. A remarkable coincidence, since both species are uncommon at most in Dutch waters, while encounters of penises attached to the pelvic bones of the much more common

harbour porpoise have never been reported.

11 January 2022, Engelsmanplaat, Friesland. Incomplete vertebral column, fairly recent. Reported by Arjen.
Considering the size of the vertebrae possibly white-beaked or bottlenose dolphin.

1 July 2022, Wadden Sea and Terschelling, Friesland. Male, 297 cm (measured), not weighed.
Decomposed, complete (Figure 9). Washed ashore on 3 July about 13 km east. Nothing collected. Reported by M. Poot and M. van der Meulen. Not necropsied.

5 July 2022, Dishoek, Zeeland. Male, 220 cm (measured), not weighed. Decomposed, complete. Reported by RTZ zuidwest. Nothing collected, destructed.
The dolphins of 1 July 2022 at Wadden Sea and (two days later) Terschelling, and 5 July 2022 Dishoek possibly concerned white-beaked dolphins. Unfortunately, the humpback whale that stranded on Vlieland a few days later attracted more attention, leaving the dolphins unidentified.

5 October 2023, Oostkapelle, Zeeland. Male, 220 cm, 200 kg (estimated). Reported by RTZ zuidwest. Nothing collected, not necropsied. Destructed. With near-certainty a common dolphin.

31 October 2023, Razende Bol, Noord-Holland. Sex, length and weight unknown. Reported by M. Staal.
The islet Razende Bol was visited as soon as the storm, which started on November 1st, had passed, but by then the sea had already washed the dolphin away. Possibly a common dolphin.

21 December 2023, Westkapelle, Zeeland. Sex, length and weight unknown. Reported by J. de Visser. Not necropsied. Possibly a common dolphin.

Figure 9. Unidentified dolphin, probably white-beaked dolphin (*Lagenorhynchus albirostris*), 3 July 2022, Terschelling. *Photo: Marjanna van der Meulen.*

Discussion

After the strong increase in strandings since 2006, and the exceptional numbers in 2011-2013, numbers are decreasing. These fluctuations are completely attributable to variation in the number of porpoise strandings. The increase in the number of different species per year however is continuing: since 1980, the average number of species per year was 4.9, since 2000 5.6, since 2010 6.1. The total number of cetacean species recorded in the Netherlands is 26. This includes remains of grey whale (*Eschrichtius robustus*), which has disappeared altogether from the Atlantic Ocean since the early 18th century. However, there have been recent confirmed records of living grey whales in the Atlantic (Scheinin et al. 2011, Manfrini et al. 2023, McCloud 2023). There are ten species that are regularly

recorded (yearly, or at least once every few years, see also Table 1) and another ten that have not been recorded for decades or longer. These are blue whale (*B. musculus*) (last recorded in 1840), rough-toothed dolphin (*Steno bredanensis*) (1877), narwhal (*Monodon monoceros*) (1912), Cuvier's beaked whale (*Ziphius cavirostris*) (1914), beluga (*Delphinapterus leucas*) (1919), pygmy sperm whale (*Kogia breviceps*) (1925), Gray's beaked whale (*Mesoplodon grayi*) (1927), false killer whale (*Pseudorca crassidens*) (1935), Risso's dolphin (*Grampus griseus*) (1970) and sei whale (*Balaenoptera borealis*) (1986). Note however that some of these have been recorded alive in Dutch waters in later years, for instance Risso's dolphin (1978 and 2004), while some species have been observed alive but never found dead, for instance Greenland whale *Balaena glacialis* (2017) (waarneming.nl, van der Meij & Camphuysen 2006). The last year when a stranded new species of cetacean for the Netherlands was found was in 2005 (Blainville's beaked whale (*Mesoplodon densirostris*)). The number of individuals per year of species other than porpoise has increased marginally since 2000 (average 9.9 since 1980, 10.0 since 2000, 10.4 since 2010). While some species are true vagrants in the south-eastern North Sea, showing no long-term trend in strandings whatsoever (e.g. long-finned pilot whale), (strandings of) other species are definitely decreasing (e.g. white-beaked dolphin) or increasing (e.g. minke whale) (Table 1).

Some cetaceans washed ashore cannot be named, for various reasons. In a few cases nothing recognizable remains. In other cases there are logistic and/or other circumstances preventing a visit to the carcass for identification. In fact, sometimes the primary goal appears to be to get a decomposed cadaver to a destruction site as soon as possible, with identification deemed as less important. Some of these stranded cetaceans can still be identified to the nearest taxon from photographs (for instance 'white-sided or white-beaked dolphin'), many only superficially ('dolphin').

Worryingly, the proportion of cetaceans remaining unidentified is increasing: since 2000, 42 non-porpoises (17.0%) remained unnamed, while this rose to 65.9% in 2020-2023 (see also Keijl 2022b). Due to their relative scarcity, detecting changes in distribution, abundance and species composition of cetaceans in a specific geographic area requires time, while only long-term trends can be used as indicators of a changing environment, and the same goes for evaluating protective measures (van der Meij & Camphuysen 2006, Coombs et al. 2019, Boyd & Punt 2021). Because all species except porpoise are uncommon or rare in the southern North Sea, it takes many years before any pattern in occurrence emerges, let alone changes therein. For many species stranded in the Netherlands, the North Sea lies on the edge of their current usual area of distribution, while this is exactly the area where changes in range shifts can first be detected (Simmonds & Isaac 2007, Pompa et al. 2011). Without a specific name, registering cetaceans is worthless. Nowadays, identification by DNA-analysis is not costly any more, while it is among the most robust methods to identify species. Hence, it is recommended to collect tissue from any cetacean carcass that will not be collected for necropsy or museum storage.

Although numbers of stranded porpoises have decreased since the high numbers in 2011-2013, porpoises are still common in Dutch waters, offshore (van Bemmelen et al. 2022) as well as coastal (trektellen.nl). Stranding numbers fluctuate largely between years, but it is only from 2001 onwards that numbers in excess of 100 per year are found. Analysis of strandings and sightings combined revealed that the high number of strandings in summer correlated well with increased presence in the preceding months (IJsseldijk et al. 2023). The peak in strandings in the summer of 2011 correlated with unusually high numbers of emaciated porpoises, hinting at food shortage and/or an inability to feed, and this mass stranding therefore qualified as an UME

(IJsseldijk et al. 2022b).

For long, the yearly pattern of porpoise strandings in the southern North Sea shows two peaks: one in March and one in summer (e.g. Camphuysen & Siemensma 2011, IJsseldijk et al. 2020). The previously established declining trend of strandings in March continued in 2020-2023. During the early years with elevated numbers since 2006, the March peak was pronounced and about half as high as the summer peak (e.g. Keijl 2009), but since 2017 the number of strandings in March is greatly reduced. In years with a high peak in March many porpoise strandings were recorded in a small area near Voorne-Goeree, and most of them had been attacked by grey seals. Therefore, we hypothesize that one, or a few at most, local grey seals stopped hunting porpoises at this location in March, moved elsewhere, or died. There are other explanations for the decline however, for instance that porpoises learned to avoid the area, or the number of porpoises has become so low that it is not profitable to hunt them in this area anymore.

It is not surprising that the number of porpoise strandings mirrors the numbers counted by bird observers from the coast (trektellen.nl), even though there is a mismatch in timing, with the highest number of strandings taking place in late summer, while most porpoises are seen from the coast in winter. A study combining sightings and strandings found that the number of strandings prior to 1990 and after 2010 could not be explained by increased presence in coastal waters, hinting at apparently prolonged and ongoing excessive mortality (IJsseldijk et al. 2023b), possibly influencing protective measures (Ten Doeschate et al. 2018). The fact that stranding numbers in recent times have been unusually high is corroborated by an analysis of recent strandings along the Dutch west coast with those from 1930-1970 (Keijl & Niesen 2023). For species other than porpoise, a connection between strandings and observations of live individuals seems to be absent due to their rarity, even though (living) cetaceans are occasionally observed from the coast (e.g. Hoekendijk et al. 2021).

The physical state of the Dutch coast, with narrow sandy beaches, makes it an excellent example for thorough long-term censusing of stranded marine mammals, as all parts of the coast are easily accessible, contrary to rocky coasts. However, in the Dutch part of the Wadden Sea, itself being a World Heritage Site (UNESCO 1972; Common Wadden Sea Secretariat and World Heritage Nomination Project Group 2008), stranded harbour porpoise seem to be underreported, not only along the extensive mudflats of the Wadden Sea proper but also on the North Sea-oriented sandy beaches, parts of which are only sparsely visited outside holidays and during the colder season. This situation is similar in Germany and Denmark, and it is recommended to join forces to tackle this problem in order to better assess the conservation status of porpoises as well as of common (*Phoca vitulina*) and grey seals (Scheidat et al. 2023).

The importance of a continuous, sound and thorough registration of cetacean strandings has been demonstrated repeatedly (e.g. Pikesley et al. 2011, Litz et al. 2014, Costa et al. 2017, Coombs et al. 2019, Peltier et al. 2019), even when strandings are used only as baseline information during unusual mortality events, such as the mass stranding in 2021 (Keijl 2021, and summarized above). Although there may be a danger of irregular and/or temporary underreporting during long-term research which leans heavily on data provided by the public (cf. Carmichael et al. 2022), just because of the sheer duration of the 'project', or due to a low stranding density, only long term trends in strandings provide the opportunity to detect changes in, e.g., species composition, abundance, or distribution (Camphuysen & Siemensma 2011).

Up to 16 January 2024 all strandings in the Netherlands, from the very first sperm whale in 1255 until the last harbour porpoise on 16 January 2024, have been individually con-

sultable on the website walvisstrandingen.nl, which was updated weekly by Naturalis Biodiversity Center. At the time, the database contained 14,389 strandings, virtually all consisting of single stranding events of 26 different species (among which five subfossil finds of grey whale), and 99 unidentified cetaceans (go to https://tinyurl.com/4akpn5cc for a download of all validated strandings up to and including 16 January 2024). Only seven records consisted of strandings of more than a single individual. The registration of cetacean strandings by Naturalis has stopped as of 16 January 2024. The strandings database however has not: it has been transferred to a newly created database managed by Foundation Observation International. The (old and new) data are now available from the website www.stranding.nl, a subsite of www.waarneming.nl. Similar to walvisstrandingen.nl, these data are open to the public. Registration of strandings on www.stranding.nl is left to personal initiative, while strandings may be validated by volunteers. Until December 2023, monthly updates on strandings and reports of notable or unusual events have been presented on the news page of walvisstrandingen.nl. Also this series has ceased to exist, but all reports can be freely downloaded from the website natuurtijdschriften.nl. By discontinuing the registration of cetaceans on the Dutch coast as of 16 January 2024 by a zoological museum, a 52 year old tradition has been broken (cf. Husson & van Bree 1972). This is the last report on cetacean strandings provided by Naturalis.

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Samenvatting

Gestrande walvissen op de Nederlandse kust in 2020-2023

In de jaren 2020-2023 zijn 1940 (overwegend dode) walvissen op de Nederlandse kust geregistreerd, behorende tot 14 verschillende soorten. Vooral de strandingen van orka en butskop vielen op vanwege hun zeldzaamheid. Een dolfijn die in december 2023 strandde op de Maasvlakte was misschien een Kaapse dolfijn, in dat geval een nieuwe soort voor Nederland. Helaas is deze dolfijn uiterlijk vrijwel niet te onderscheiden van gewone dolfijn. DNA-analyse wees op de laatste soort, maar of de achterliggende database (BOLD) beide soorten kan onderscheiden op basis van het onderzochte gen (CO1) is twijfelachtig. De schedel, waarop beide soorten wel kunnen worden onderscheiden, is niet bewaard. Kaapse dolfijn is nog niet in Europa vastgesteld, mogelijk omdat waarnemers niet bedacht zijn op deze soort. Het dichtstbijzijnde gebied van voorkomen, voor zover bekend, is West-Afrika. Andere bijzondere soorten die in deze periode zijn gestrand, en die bovendien de laatste decennia algemener lijken te worden, zijn bultrug, dwergvinvis, gestreepte dolfijn, gewone dolfijn, gewone spitssnuitdolfijn en gewone vinvis. Witsnuitdolfijn daarentegen lijkt, als enige soort in de rij van regelmatig aanspoelende soorten, in de zuidelijke Noordzee steeds zeldzamer te worden. Soorten als potvis, griend en tuimelaar, eveneens in deze periode gemeld, stranden onregelmatig.

Een deel van de walvissen (anders dan bruinvis) die aanspoelen wordt niet gedetermineerd. Hiervoor zijn diverse redenen aan te voeren, zoals een lastig te bereiken locatie, of gebrek aan tijd of middelen om het kadaver te bezoeken en/of te bewaren. Het is echter een bedenkelijke en kwalijke zaak dat het aandeel ongedetermineerde walvissen toeneemt, van 17% sinds 2000 naar bijna 66% sinds 2020. Naast genoemde oorzaken lijkt er een afnemende interesse te zijn om soorten te determineren en om materiaal te bewaren. Registratie van ongedetermineerde walvissen is zinloos, want elke soort heeft zijn eigen ecologie. Hier wordt dan ook de aanbeveling gedaan om uiterste inspanning te verrichten voor determinatie van álle aangespoelde walvissen. Determinatie aan de hand van DNA is tegenwoordig eenvoudig en betaalbaar.

De talrijkst aangespoelde soort in 2020-2023 was de bruinvis met 1896 exemplaren. De meeste bruinvissen zijn gevonden in het Deltagebied (387), maar de hoogste dichtheden zijn gemeld van de Noordzeekant van

de Waddeneilanden (gemiddeld 1,5 exemplaar per kilometer per jaar), vooral op Terschelling (2,6) en Ameland (2,3). Deze hoge dichtheid is toe te schrijven aan een opmerkelijke en nog niet eerder in deze omvang geregistreerde massastranding, die plaatsvond tussen 23 augustus en 4 september 2021, toen in totaal 197 rotte bruinvissen aanspoelden tussen Vlieland en Schiermonnikoog. Onderzoek wees uit dat de dieren waren gestorven aan een infectie met *Erysipelothrix rusiopathiae*. Deze bacterie, bekend van onder andere varkens en vissen, was tot dan toe in Nederland nog niet eerder in verband gebracht met een massastranding. Verder viel op dat bij deze stranding hoofdzakelijk volwassen vrouwtjes waren getroffen (67,5%, normaal gesproken is dat 33,3%). Ze waren in goede conditie maar hadden een lege maag en zijn dus een snelle dood gestorven. Een modelmatige analyse, waarin zeestroming en wind waren meegenomen, wees uit dat deze bruinvissen zijn omgekomen in een gebied tussen het Friese Front en de Doggersbank, ruim 100 kilometer ten noordwesten van de plaats van aanspoelen.

Dode bruinvissen zijn gedurende de onderzoeksperiode verspreid langs de hele kust aangetroffen. De landelijke dichtheid ligt tegenwoordig op 0,4 exemplaren per kilometer per jaar, een derde lager dan de 0,6 in 2015-2019. Alleen op de Waddeneilanden was de dichtheid hoger dan 1,0, wat deels is veroorzaakt door de massastranding van 2021. Langs de kust van Zuid- en Noord-Holland bedroeg de dichtheid 0,7, in de Delta was dit meestal nog lager. De reeds eerder geconstateerde afname van de strandingspiek in maart heeft zich in 2020-2023 voortgezet. Dit wordt toegeschreven aan afgenomen predatie van een of enkele grijze zeehonden, maar door de jaren heen neemt het aantal bruinvisstrandingen, na de piekjaren in 2011-2013, sowieso af. In het zuidwesten van het land nemen de aantallen aangespoelde bruinvissen sneller af dan in het midden en noorden.

Het aandeel mannetjes blijft dalen (59% in 1998-2007, 56,2% in de besproken periode; hierbij zijn de dieren van de massastranding in augustus-september 2021 niet meegerekend). De oorzaak blijft onduidelijk, maar zou veroorzaakt kunnen zijn door het nog altijd stijgende aandeel foto's, waardoor ook vrouwtjes nog vanachter het bureau als zodanig te herkennen zijn, terwijl het erop lijkt dat vinders op het strand meer moeite hebben met het herkennen van deze sekse dan van mannetjes. Er zijn natuurlijk ook alternatieve verklaringen te bedenken. Het aandeel pasgeboren bruinvissen is gestegen, zij het marginaal (12,4% in 1998-2007, 14,9% in 2020-2023).

Ook wat betreft doodsoorzaken zijn er kleine verschuivingen in de tijd zichtbaar. Zo is bijvangst als doodsoorzaak afgenomen (van 16% in 2014-2019 naar 12% in de huidige periode), net als predatie door grijze zeehond (24% naar 19%) en ondervoeding / voedseltekort (17% naar 15%), terwijl infecties lijken te zijn toegenomen (32% naar 37%; hierbij is de massastranding van augustus-september 2021 niet meegerekend). Er is echter een verandering opgetreden in het verzamelbeleid: tegenwoordig worden vrijwel alleen verse bruinvissen onderzocht, omdat daaraan de doodsoorzaak – het hoofddoel van de secties – beter te bepalen valt dan bij rotte bruinvissen. Het is daarom nog onduidelijk of de vastgestelde doodsoorzaken representatief zijn voor bruinvissen in de gehele Nederlandse Noordzee of alleen gelden voor de kustzone.

In de afgelopen 52 jaar zijn strandingen bijgehouden door de zoölogische musea van Amsterdam en Leiden. Met ingang van 2024 is een einde gekomen aan deze traditie. Vanaf nu worden strandingen van zeezoogdieren – dus ook van zeehonden – door vrijwilligers bijgehouden op www.stranding.nl, onderdeel van Waarneming.nl, eigendom van Stichting Observation International. Aan waarnemers wordt dan ook dringend verzocht hun vondsten daar te registreren.

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Review of 16th Century North Sea sperm whale strandings, including three recently re-discovered records from the East Frisian coast of Germany

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Abstract: A review of 16th Century sperm whale strandings in North Sea waters provided three additional and revealing stranding events from the German North Sea coast in 1511, 1577 and 1580, respectively and some valuable insights into historical stranding events.

Keywords: sperm whale, strandings, North Sea, 16th Century.

Introduction

Even today sperm whales continue to challenge the imagination of mankind. They have been doing so for as long as humans have been around, and it is therefore not surprising that information about the strandings of these enigmatic giants has been preserved in historical writings.

The data on past and present sperm whale strandings along the coasts of the greater North Sea from 1254 until 2016 have recently been reviewed and listed by Smeenk & Evans (2018) and by Kinze (2020) for the 18th Century. For the 16th Century, records have been documented for the following years: 1563, 1566, 1572, 1575, 1577, c. 1582 and 1598. Here, three additional records from the East Frisian coast of Germany, for the years 1511, 1577 and 1580 are presented along with a review of North Sea sperm whale strandings throughout the entire 16th Century.

Material and methods

A discovery of a hitherto overlooked German source (Wagner 1580) and the re-identification of a 1580 depiction of a 60 feet (ca. 18 m) toothed whale initiated a full review of 16th Century strandings, based on the work by Smeenk & Evans (2018) and the sources contained in their comprehensive review. The reliability of the recorded total lengths of the stranded sperm whales was assessed whenever both total length and the fluke span of the individual were available. Bartelmeß and Münzing (1991) found the fluke span to vary between 22.8 and 26% of the total length which fully matches modern standards as published by Fujino (1956) who found the fluke span to amount between 20 and 30% of the total length with a mean of 25%.

List of records

1511, January - Mid-East-Frisian coast, Germany. Total length 43 feet.
A 1580 treatise by Marcus Wagner on three large storm floods contained a description of

a sperm whale stranding that until now has been overlooked by natural historians. It concerns a 43 feet individual yielding a *Last* of oil (1 *Last* = 2 tonnes or 2.7 m^3 or 2700 litres of oil) which were sold domestically. The treatise stated the presence of white *rath* (= Walrath in German; spermaceti oil): a diagnostic feature of the sperm whale. The head of the whale was kept for some time in the *Kunstkammer* (natural history cabinet) in the castle of Jever, but a merchant seized it and possibly subsequently went 'on tour' with it. The present whereabouts of the head is not known and most likely the specimen got lost (for details view the original German text in Appendix 1).

Wagner stated the year of the stranding to be 1512, but since his treatise was written almost seven decades after the event, he may have referred to the so-called Antoni flood of January 1511 instead (Hamm 1976).

1563, December - Grimsby Lincolnshire. Total length 19 yards.
Smeenk & Evans (2018) quote Howes (2010) for this stranding event. Howes, however, only indirectly provided these details, which were available from his source for the stranding event (Southwell 1881). Here, the total length of the whale is given as 19 yards = 57 feet and the fluke span to 15 feet or 26.3 % of the total length.

1566, 11 March - Zandvoort, the Netherlands. Total length 42 feet.
Smeenk & Evans (2018) list Mulder (1836) as their earliest reference for this information, where it, however, is not contained. Instead, the information stems from Houttuyn (1762). A depiction of the whale is found in Adriaen Coenen's fish book of 1585 (Egmond & Mason 2003).

1572, 1-2 November (12/13 November) - Skallingkrog, Denmark. Three 'large whales'.
The source for this mass stranding is a Latin text published in Rørdam (1896). The text reads: *Vi tempestatum appulaerunt tria grandia cete quæ destita aqua et in sicco relicta emoribatur in littore Synderside udi Skallingkraag. [Due to the force of the storm, three large whales stranded on falling tide and were left on dry land to die on the shore of Synderside in Skallingkraag.]*

Such a multiple stranding event along with the season and a pre-stranding tempest are all indicative of sperm whales. Smeenk and Evans (2018) refer to this case *fide* Carl Kinze.

1575, month not known - Tønder (German name Tondern) Southern Denmark. Total length not known.
The township of Tønder/Tondern in the Duchy of Sleswick (Schleswig) during the 16th Century still had a seaport with direct access to the North Sea. The stranding site most likely lay in the former tidal estuary of the Vidå/Wiedau-river between the what is now the German island of Sylt and the present Danish island of Rømø. Duke Johan the Elder of Sleswick subsequently presented the cleaned head of the whale, considered an utmost rarity, to Duchess Anna of Saxony, who was residing in Dresden, Germany. She was the daughter of Christian III of Denmark and was married to the Prince Elector and Duke of Saxony (Mohr 1935, 1967). It is not known how the head was transported from Tønder/Tondern to Dresden but most likely it went up the River Elbe. The head of the whale was kept in the *Kunstkammer* of Dresden, and subsequently exhibited in the Dresden Zoological Museum (Anon 1894). The specimen was destroyed during the Second World War in February 1945.

1575, 9 July (Julian date 20 July) - Isle of Thanet. Total length 20 ells or 40 feet.
Thornburn (1921) refers to Baker's 1670 *Chronicle of the Kings of England* where reference is made to a stranding on the island of Thanet in the 17th year of the reign of Queen Elizabeth I (Baker 1670: 419-420). View the original text in Appendix 1. Elizabeth I ascended to the throne in November 1558. Counting 1558 as her first year, 1575 would be the most likely year.

Figure 1. Close-up of the whale depicted on David Fabricius' map (Sello 1896). Niedersächsische Staats- und Universitätsbibliothek Göttingen. Public Domain Mark 1.0.

1577, 2-5 July - Westerschelde. Belgium/ the Netherlands. Total length 58 feet.
This stranding event is well-documented by a series of temporaneous reports (Bartelmeß & Münzing 1991, Faust 2002).
There are two fluke spans reported for this individual: 14 feet (24.3% of the total length) according to Bartelmeß & Münzing (1991) and 13 feet, 3 inch (22.8%) according to Bartelmeß & Münzing (1991) and Faust (2002).

1577, 19 November - Between Jade and Rüstingen, Germany. Live stranding of a 52½ feet sperm whale.
A 1580 treatise by Marcus Wagner on three large storm floods contains a description of sperm whale strandings hitherto overlooked by natural history scholars. This individual most likely was part of the large group of whales of which several animals were subsequently stranded at Ter Heijde due to a large tempest also referred to by Wagner (1580). For details view the Appendix.

1577, 22-23 November - Ter Heijde, the Netherlands. Three animals of 48, 49 and 55 feet.
Several temporaneous reports document this mass stranding (see Bartelmeß & Münzing 1991, Faust 2002).
Houttuyn (1762) provided the total lengths of the three individuals. For one of the animals an apparently more precise total length of 49 feet, 5½ inch was given along with a fluke span of 11 feet, 3½ inch (22.8 % of the total length; Bartelmeß & Münzing 1991, Faust 2002).

1580, 26 November - between Dornumer and Frederikensiel on the East Frisian coast of Germany. Total length 60 feet.
Goethe (1983) listed this stranding as an unspecified whale, drawing on Hamm (1976). Kinze et al (2020) did not include this stranding in their review. However, a map produced by David Fabricius around 1592 (Sello, 1896) contains a drawing of a large whale with teeth, in the upper but not the lower jaw. Although hidden in the gum, these maxillary teeth indicate a sperm whale. A bulbous head is not depicted, but this could be due to the removal of the spermaceti organ. Details of the depiction are shown in Figure 1.

Around 1582 – Caister, Great Yarmouth. Total length not known.
Southwell (1881) researched this case in detail. Whilst the species determination is indisputable, an exact year of the event is lacking. It is not impossible that the event took place during 1580.

1598, 3 February – Berckhey (Berkheide), near Wassenaar, the Netherlands. Total length 52

feet.
This stranding event has been well-documented with several body dimensions given (Barthelmeß 1989, Bartelmeß & Münzing 1991, Faust 2002). The fluke span measured 13 feet, 2 inch, which is 26.0% of the total length.

Discussion and concluding remarks

With three re-discovered records for the 16th Century, it is clear that it is possible that further historical sperm whale strandings might be discovered in historical chronicles and other unpublished sources. Of the 16 strandings identified so far there is a lack of data regarding the month and also, in one case, the exact year. Notably the majority of strandings in the 16th Century occurred in November, but some also in July.

The total lengths of the individuals ranged from 40 to 60 feet with a mean of 52 feet. Additionally, the fluke span of four individuals was also measured. This ranged from 22.8 to 26.3% of the total body length, which is in accordance with the range of this measurement provided by Fujino (1956) from Japanese whaling operations. Therefore, the total lengths of these stranded sperm whales can reliably be compared with subsequent and more recent stranding events.

The November 1577 event, with the additional stranding from the present-day German North Sea coast, should be counted among the largest mass strandings of the species on record for the greater North Sea. Such sperm whale strandings might initially seem to be anecdotal. However, they can be interesting from another point of view. The data can provide not only insights into the historical stranding rate vs. the current one, but also about the size of the stranded animals in the past vs. the size of the animals we find on the same coasts nowadays. The population of sperm whales has gone through large changes in recent history, as a result of whaling, followed by its cessation and the subsequent recovery of the population (Smeenk & Evans 2018), possibly leading to a change in the population dynamics (i.e. the number of juveniles vs. adults). It is also possible that climate change is bringing about changes to the distribution of sperm whales with, for instance, the first record of a female sperm whale in the UK in July 2016 (Deaville et al. 2017), and to its migration patterns (i.e. overwintering immature and maturing male sperm whales in Norway (Pöyhönen et al. 2024), which possibly also influences strandings and the sizes of stranded whales.

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Samenvatting

Een overzicht van potvisstrandingen rond de Noordzee in de 16e eeuw, inclusief drie herontdekte strandingen langs de kust van het Duitse Oost-Friesland

In dit artikel worden alle tot nu toe uit de 16e eeuw bekende strandingen van potvissen op de kusten van de Noordzee besproken. Naast de reeds in de literatuur genoemde strandingen, worden drie aanvullende, middels historisch onderzoek ontdekte, potvisstrandingen in de jaren 1511, 1577 en 1580 gepresenteerd. Informatie over aantallen en lengtes van gestrande potvissen en over strandingslocaties in historische tijden zijn waardevol. We kunnen deze vergelijken met recentere strandingen, en ze relateren aan de opkomst en neergang van de walvisvaart en aan klimaatverandering.

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Appendix 1

Southwell's (1881) quote of the original text: *Description of a large Fish driven on shore at Great Grimsby in 1563*

In the month of December 1563 was drevyn on y^e^ at Grymsby in Lyncolneshire a great and monsterus fysh in length Xix yerdes his tayle 15 fete brode & of 6 yerdis between his 2 eyes he had in his lowar Jaws 92 tethe & none aboffe. Every to the weyed 1 lb & 1 oz in the the rofe of his mouthe he had a harp with a string naturally his heygth could not be then desernyd for that he lay so depe in the sande there might walke in a ranck 3 men between rib & robrt pinder habdasshr affermyd that he w^t^ other men did see 12 men stand in the monthe of here to saue the oyle that she had and & the toke out of her hed more than 2 tonnes of oyle. There was 14 days before the coming of the sayde pinder 30 men working about her & were not into ye rib of her. The townsmen of Grymsby did off 200£ for the oyle that was in her.

Baker, R. 1670. A Chronicle of the Kings of England: From the Time of the Romans Government, pp 419-420.

A mighty Whale taken in Thanet in Kent

In her seventeenth year, a mighty Whale was cast upon the Isel of Thanet in Kent, twenty Ells long, and thirteen foot broad from the belly to the back-bone, and eleven foot between the eyes, One of his eyes being taken out of his head, was more than a Cart with six Horses could draw. The Oyl being boyled out of the head, was Parmacetti [=spermaceti].

Wagner 1680. Einfeltige kurtze ... Historiae von den dreyen Wasserfluten in Phrißlandt, derer die erste ... 1512 ... ergangen : sampt Beschreibung zweyer grossen ungehewren Walfische.

Es ist desgleichen Anno 1512. Ein grosser Walfisch auch in der Flut gefangen/ und ins Landt bracht worden/ Nach dem er in stücken zertheilet worden ist/ und der Kopff ins Jeverische Schloss/ eine lange weil gewesen/ Aber endlich durch unachtsamkeit/ durch einen Kaufman/beybracht/ und hinweg gefurt worden/ der hat 43. Menschen Schuhe gehabt/ und auch schrecklich zu sehen gewesen/ welchen auch Leute/ so noch in frischer gedechtniß leben/gesehen/und iren Füssen gemessen haben.

Der todte Walfsich/ ist durch angeben und vorsichtigem weisen Rath/ dero Lender Rendmeister/ den Unterthanen zu nutz und aller bestem/ ins Land geschleppet/ und bescheidentlich verfasset/ und daraus groß Geldt gelöset haben. Denn es darvon den nutz hat/ das man Thron daraus machet/ so die Töpffer zu Ihrem Handwercke gebrauchen/ Und denn fort auch mehr/ als Schustern/ und andern opisïbus/ in hrer Narung kann und mag zu hülffe kommen/ und einen leiflichen Pfennig tragen. Weiviel nu Last ein Walfisch wol bringen/und haben kann/muß manvon den gewiß erkundigen/ und erfaren/ so sich der Narung gebrauchen/zu See warts/ Aber von diesem toten todten Walfisch hat man nicht mehr denn in die 30. Last Throns/ in fremde Landtverkeuffen lassen/ ohne was sie selbst behalten/und in den umligende Stedten/ ihren Handwercke zu gute/wiligliche nachnachgelassen und verkaufft haben […]

1577

Anno 1577 den 19. Novemberis. Ist ein groß Walfisch lebendig zwischen Jaget und Rustringer Land/ in Phrißland ankommen/ unf auff uberrahm ans Land angetrieben worden/ und mit sich eine grosse Flut bracht/ daven dem Lande groß schaden entstanden/welches in des orts Landesv vorhin niemals erhört worden ist, […]

Es ist aber der Walfisch lang gewesen/ zwey und funffzig/ und einen halben zimlichen Menschen Schuhe/ Und der Riebenfleisch eine so von unten am Bauch abgeschnitte ist/ heltet in die lenge/ drey und funffzig Schuhe. […]

Es haben solche thier/ viel Leute gesehen. Sonderlich der Wolgeborene un Edele Herr Johann/ Graffe zu Oldenborgk/ und Delmenhorst/ und Herr zu Jevera/ sampt ihren Gnaden Frewlein/ und andern viel vom Adel/ Bürger und Unterthanen. […]

Und nachdem sie eine gute weile daran gearbeitet haben sie biß 12 Thonnen abgefasset/ und in ein Gefeß gebracht

A preliminary inventory of the parti-coloured bat in the Eemshaven – Delfzijl area, Groningen, the Netherlands

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Abstract: The parti-coloured bat (*Vespertilio murinus*) has been considered a rare species in the Netherlands, with only one known nursery colony since 1998. A possible second colony was reported in 2002 in the north-eastern part of the province of Groningen, but it was not rediscovered afterwards. In 2016, a first systematic survey on the occurrence of the parti-coloured bat with hand-held and static bat detectors was conducted in the area of Eemshaven – Delfzijl in northeast Groningen. During the inventory, using a hand-held detector, three roosts belonging to two colonies, were found in the villages of Spijk and Bierum. In 2016, the highest number of departing parti-coloured bats in one night in Spijk was 29 and 12 in Bierum. In 2017 the highest figures were 61 and 12, respectively. Low numbers (1-4 individuals) of serotines (*Eptesicus serotinus*) were detected departing from the same roosts, always before the parti-coloured bats departed. There were indications of a possible third colony, but these could not be confirmed. We report observations showing that reproduction has taken place in the study area and occurred in or very close to the roosts that we observed. Automatic recorders detected much foraging activity in a relatively small area on the western shore of the river Ems, situated 2.5-4.5 km away from the roosts. During peak activity in this foraging area up to 71 recordings of nyctaloid bats (i.e. belonging to the acoustically similar genera of *Nyctalus*, *Eptesicus* or *Vespertilio*) in one 10-minute interval were recorded. In general, only a small proportion could be identified with certainty and we discuss the difficulties experienced with automatic identification of nyctaloid bat calls. In autumn the study area was surveyed for display calls and courting locations of males, especially in urban areas with high buildings. However, no courting male parti-coloured bats were found. Although the parti-coloured bat mostly lives in houses and buildings, the colonies are probably often overlooked and we suggest that the colonies found in this study have existed for decades.

Keywords: parti-coloured bat, nyctaloids, Chiroptera, automatic identification, bat detector, Batcorder, nursery colony, province of Groningen.

Introduction

The parti-coloured bat (*Vespertilio murinus*) is a relatively unknown species in the Netherlands. It is a medium-sized bat, comparable in size to the pond bat (*Myotis dasycneme*). It has a white to creamy-coloured belly, a black face and black ears. One characteristic of this species is the two-tone colour of the dorsal hairs: the hairs at the base are black and become white or silvery at the tips, which gives the species a special look. The ears are short and wide, with a short rounded tragus. Typically

the female has four nipples, which is unique among bat species in Europe (Baagøe 2001, Safi 2006, 2023). The parti-coloured bat normally gives birth to twins, sometimes to triplets, but rarely to a single young (Dietz et al. 2011, Safi 2023). The maximum recorded age is twelve years, which is low for a bat species, but the number of recaptures is very low (Baagøe 2001, Safi 2023). Therefore it is unknown whether this assumed relatively low life span is related to its specific reproduction biology and/or to its migratory behaviour (Dietz et al. 2011).

In May, females form nursery colonies of 20 to 60 females, in some areas up to several hundreds of females (Baagøe 2001, Safi 2023). The roosts are often situated under roofs and in crevices of buildings and, occasionally, in rock crevices and tree holes (Rydell & Baagøe 1994, Baagøe 2001, Safi 2023). Females and males live separately during spring and early summer. Males of parti-coloured bats show an atypical behaviour in comparison to other bat species: they form large, but flexible social aggregations between May and mid-July when they use a network of several summer roosts (Dietz 2011, Safi 2023). The male roosts are situated separately from the nursery colonies, but it is not known how far away and this may differ between locations (Zöllick et al. 1989, Baagøe 2001, Safi 2006). In the second half of July males adopt a more solitary lifestyle, coinciding with the start of the mating season (Safi 2023). In late summer and autumn (late August - December) males perform a conspicuous courting behaviour with display calls, mostly around high buildings in big cities (Baagøe 2001, Safi 2023). Hibernating individuals are found in high buildings, church towers and in rock crevices (Baagøe 2001, Dietz et al. 2011). Long-distance migration has been recorded from individuals reproducing in Eastern Europe, but in Western Europe these distances seem to be much shorter and populations may even be sedentary (Masing 1989, Rydell & Baagøe 1994, Markovets et al. 2004, Dietz et al. 2011).

The parti-coloured bat has a Eurasian distribution and occurs in a broad zone from the Netherlands and Belgium through Central Europe, southern Scandinavia, the Balkan countries and the Baltic states, Central Asia, Mongolia, northeast China and southern Siberia and as far as northern Japan (Kawai et al. 2015, Jansen 2016, Safi 2023). However, there are many vagrants that have been recorded in northern, western and southern parts of Europe and even on oil platforms at sea (Brabant et al. 2016, Boshamer & Bekker 2008)

The parti-coloured bat is considered to be a rare species in the Netherlands (Jansen 2016). The first observation in the Netherlands was in 1977, but since then the number of observations has been increasing (Lina 1991, Jansen 2016). Most individuals were observed in the western and northern part of the Netherlands. Until 2016, only two roosts had been found in the Netherlands. In 1998, a nursery roost was discovered in Maarssenbroek in the province of Utrecht (Jansen 2002, Jansen et al. 2017), which is still present. In 2002 a second roost with unknown status was found in Spijk in the province of Groningen. This colony, however, was not re-recorded and it is assumed that it has disappeared (Jansen 2016).

Very little is known about parti-coloured bats in the Netherlands. Therefore, it is not surprising that nearly all available information on the biology and ecology of this species comes from studies from abroad. In 2016 an attempt was made to systematically search for this species in the area where the second roost of the Netherlands had been located and where since 1995 observations of single individuals had been regularly reported. Thus, we systematically searched the area in the north-eastern part of the province of Groningen, around Delfzijl and the Eemshaven with bat detectors and series of automatic recorders for the presence of parti-coloured bats in an attempt to determine whether a population of this species was present in this area. We investigated the habitat use of the parti-

Figure 1. Study area in north-east Groningen and its position in the Netherlands (inset). Sources: Bing Aerial Maps, Microsoft; top10nl, PDOK.

coloured bat by locating the roosts and foraging areas and also by trying to find a courting area where males were performing their conspicuous courtship behaviour.

Material and methods

Research area and study period

The study area is located in the north-eastern part of the province of Groningen, the Netherlands, and consists of a 77 square kilometre area situated west of the mouth of the river Ems, including Eemshaven and Delfzijl (Figure 1). The study area can be described as a mostly rural area with large, intensive, agricultural holdings. It includes the villages Roodeschool, Oudeschip, Spijk, Bierum and Holwierde and a few smaller settlements. The study area also contains a large industrial area around the harbour of Eemshaven and one large residential area: the city of Delfzijl. Observations were made in 2016 from the end

of May until November. In 2017 the area was revisited from the end of June to the beginning of August for new counts of the colonies.

Surveys with handheld bat detectors

The research area was surveyed using a Pettersson D240x bat detector (Pettersson Elektronik AB, Uppsala, Sweden) with stereo headphones. In this way the heterodyne signal was heard on the left and the time expansion signal on the right. When possible, a sound recording was made and stored as a wav-file on a recording device (Zoom H1, Zoom Corporation, Tokyo, Japan). Recordings were made of all nyctaloids, the group of bats that includes the noctule (*Nyctalus noctula*), serotine (*Eptesicus serotinus*) and parti-coloured bat. These bats produce similar sounds that can be difficult to identify at species level.

In May, June and July 2016, four evening visits and five morning visits were made to the study area by bicycle (Appendix 1). During the evening visits, the locations where bats were foraging and commuting, were mapped. During the morning visits, particular attention was paid to swarming animals near roosts or nursery colonies. This swarming behaviour, with large groups of bats flying around the roost, usually takes place in a period starting two hours before sunrise. Swarming behaviour of a few individuals around nursery colonies occurs during the whole night as females return to nurse their young.

When roosts with parti-coloured bats were discovered, the individuals departing the roost were counted in the evening of the day of discovery. These counts took place from sunset to 1.5 hours after sunset. Additional counts at roosts with large groups of parti-coloured bats were conducted in July and early August. On 13 August a final simultaneous count was conducted at the major roosts found in that year.

During surveys in September and November we looked for courtship behaviour of parti-coloured bats, which mostly occurs near tall buildings in cities. Display calls could be heard by the naked ear and were detected with a bat detector. On 13 September 2016, the Eemshaven area was surveyed by bicycle, especially the areas around high buildings, such as the two power plants. On 22 September the areas around several apartment buildings in the northwest and in the city centre of Delfzijl were surveyed. The search for courtship behaviour was repeated on 11 November 2016.

Species identification of handheld bat detector surveys

The recorded bat calls from the Pettersson D240x detector were analysed in sonograms with Wavesurfer 1.8.8 (Centre for Speech Technology, KTH, Stockholm, Sweden) and Kaleidoscope 4 (Wildlife Acoustics, Maynard, USA) software. An FFT window of 512 points was used and the analysis window was also 512 points. Particular attention was paid to sonar pulses longer than 15 milliseconds, emitted in a slow rhythm of about 3 (2-4) pulses per second, with a quasi-constant frequency (QCF) and a peak frequency between 22 and 24 kHz. These frequencies are commonly used by the parti-coloured bat in open habitat and were used to distinguish the parti-coloured bat from the noctule and serotine. The serotine mostly uses shorter and higher pulses. In open habitat, it sometimes emits pulses with a maximum energy between 22 and 24 kHz, but then the bandwidth between the start and the end frequency lies above 2.5 kHz, whereas in the parti-coloured bat the bandwidth lies below 2.5 kHz (Barataud 2020). The pulses with a duration over 15 ms from the noctule are almost always lower compared to the parti-coloured bat, with a peak frequency below 22 kHz (Barataud 2020). The noctule also uses shorter and higher pulses with a larger bandwidth, making for the characteristic 'blip-blop' sound. This alternation

between higher and lower pulses is absent in the parti-coloured bat (Zbinden 1989, Russ 2021). Leisler's bat (*Nyctalus leisleri*) also emits alternating sonar pulses, of which the lower ones are 4-6 kHz higher than the noctule. However, at higher transition flight levels the higher and shorter pulses are often omitted, leaving only a slow rhythm of pulses in a frequency range that can be confused with parti-coloured bat. The pulses of Leisler's bat are mostly shorter than those of the parti-coloured bat (<15 ms), but when they last between 15 and 18 ms, which is the maximum for Leisler's bat, it is very difficult to discriminate between the two species and only a recording with alternating sounds can give a conclusive answer. Sonar pulses with a peak frequency of 22-24 kHz, that last over 18 ms, can be attributed to parti-coloured bat (Barataud 2020).

When no recording could be made, QCF sounds with a peak frequency between 22 and 24 kHz and a low bandwidth and without alternation were attributed to the parti-coloured bat. The low bandwidth can easily be recognized by listening through time expansion. In half-open and closed habitats, where the noctule alternates between two types of pulses (Barataud 2020), sonar sounds from the parti-coloured bat are more difficult to distinguish from those of the serotine. The pulses get shorter, higher and more frequent and start with an FM-component, during which the frequency falls from around 40 kHz to around 24 kHz (Russ 2021). These start and end frequencies are usually higher in the serotine with a higher bandwidth between them, but there is some overlap between the two species (Barataud 2020). During the field survey, but also when after sonogram analysis a sound recording could not be attributed to either of these species, such observations were classified as 'parti-coloured bat or serotine'.

On some occasions bats were seen in the twilight, near street lights or by using a torch. In these cases serotine and parti-coloured bats could be distinguished by their size, colour and flight pattern. Parti-coloured bats are smaller, fly faster than serotines and have a white belly.

Continuous monitoring of bat activity with Batcorders

Next to the handheld bat detector, the static detector Batcorder 2.0 (ecoObs GmbH, Germany) was used to continuously record during the night at a fixed location. This device automatically records ultrasonic sounds, especially targeting sounds emitted by bats. It consists of a microphone, a sound card, a processor and a SD card. Ultrasonic sound is continuously recorded and temporarily stored in the memory. If the detection algorithm of the Batcorder classifies a particular sound as a bat sound, this recording will be moved to an external memory for later analysis. If the recording does not resemble a bat sound, it is deleted from the temporary memory. These Batcorders are able to record sounds of parti-coloured bats up to circa 50 metres away.

The Batcorders were mounted on a pole at a height of 2.5-3.5 metre and were placed at 20 locations covering the study area (see Results, Figures 4 and 5). Each Batcorder was installed on a fixed location during a recording session, which comprised of two to three nights at the end of June or the beginning of July 2016 (Appendix 2). The Batcorders were set up to start logging roughly one hour before sunset and to end the session roughly one hour after sunrise. Because of a full memory card, recording sessions stopped prematurely during the second night at two locations: at Oostpolderdijk (PL09) at 03:22 AM and at the gas (compressor) station west (PL11) at 01:48 AM.

In September, this scheme of recording sessions was repeated and each recording session lasted three nights. All sessions ended before the end of September, but the exact dates of each individual recording session were not recorded. Although the original sound files from June, July and September 2016 could not

Table 1. Start and end dates and times of the batcorders used on the buildings in Delfzijl. Each recording session was scheduled at 19:00 until 7:00 the next morning (Naterij and Dijkzicht), until 8:00 (Oldiek and Kadijk) or until 9:00 (De Vennen). At Naterij, Oldiek and Kadijk the battery ran out of power before the end of a session.

Building	Floor	Start date	Start time	End date	End time	# nights
Naterij	7	17-10-2016	19:00	22-10-2016	04:16	5
Dijkzicht	7	17-10-2016	19:00	24-10-2016	07:00	7
Oldiek	7	17-10-2016	19:00	22-10-2016	19:42	6
Kadijk	8	17-10-2016	19:00	23-10-2016	19:15	5
De Vennen	6	17-10-2016	19:00	31-10-2016	09:00	12

be retraced, the results of the automatic identifications of the sound files were not lost.

In the second half of October 2016 Batcorders were attached to high apartment buildings to look for courtship behaviour by recording display calls. These buildings were located in the northern part of the city of Delfzijl along the sea dyke, with regular distances between the buildings from the north-western part of Delfzijl to the north of the city centre. A total of five Batcorders were attached to balconies of apartments situated on the 6th, 7th and 8th floors of five apartment buildings in October. The start and end dates of these recordings are given in Table 1. The Batcorders were installed on 17 October and ran for as long as there was sufficient battery power.

Analysis and visualisation of the Batcorder recordings

All Batcorder recordings were analysed by bcAdmin3 and batIdent1.5 (ecoObs GmbH, Germany) to classify each sound to a certain species or species group. BatIdent calculates a probability for the classification of each call based on comparison with a set of reference calls. We used the default setting for the probability of 60%, above which the call was classified to a species or species group.

Some of the results apply to species that do not live in the research area or are very rare. In the nyctaloid group this includes Leisler's bat and the northern bat (*Eptesicus nilsonii*). Using the 'batch replace' function those results were changed into mid-sized nyctaloids and serotines respectively. The number of recordings recorded by the Batcorders was almost 15,000 and could not all be analyzed manually.

Graphs about the nightly activity of nyctaloid bats were created with the 'night graph' function in bcAdmin4. If the recordings could not be identified to a certain species, the following species groups were created: mid-sized nyctaloid bats, including serotine, parti-coloured bat and Leisler's bat, and all nyctaloids which also includes the noctule and three species that do not normally live in the Netherlands. Total recordings per species on each location were calculated and plotted with geographic software package QGIS 3.36.

Results

Surveys with the bat detector

In total 392 observations of bats were made with a bat detector: 328 in the period May until the end of July and 64 in the period August-September. Each observation consisted of one or more individuals or a group of bats. The vast majority of observations was of common pipistrelles (*Pipistrellus pipistrellus*) and Nathusius' pipistrelles (*Pipistrellus nathusii*). Only 44 sightings were classified as being certainly parti-coloured bats. Another 23 observations of nyctaloid bats were uncertain, but most likely also of parti-coloured bats (Table 2). Other species that were iden-

tified include serotine and Daubenton's bat (*Myotis daubentonii*).

In total 100 time-expanded recordings at 54 observations were made and analysed. Twenty eight of these observations were identified as parti-coloured bat (60 recordings) and five observations (7 recordings) as serotine, and 13 (22 recordings) could not be identified as being either of those two species. Also six observations of Daubenton's bat were identified from twelve time-expanded recordings (Table 3).

In July 2016 three large roosts of parti-coloured bats were found by searching for swarming individuals in the morning: two roosts in Bierum and one in Spijk (Figure 2). The number of parti-coloured bats departing from their roosts were counted during two (Bierum B) or three (Bierum A en Spijk) evenings in July and August. The roost at location A in Bierum consisted of twelve animals at the beginning of July. At the end of July there were no bats present, but twelve animals were counted at location B in Bierum. The roost in Spijk consisted of 29 departing animals at the end of July (Table 4). Two colony counts in Spijk and Bierum led to a relatively high summed value of 100 parti-coloured bats in May-July 2016 (Table 2). After departing their roosts, the bats were seen flying over open fields to their foraging grounds at a height of 20-40 metres.

Serotines were found in all roosts. Table 4 shows that between one and four serotines were observed departing the roosts. They could be distinguished by their larger size and slower flight, and they departed the roost earlier in the evening. By mid-August 2016 the three roosts were deserted, but commuting and foraging parti-coloured bats were still found in Bierum: seven individuals, one of which was spotted leaving the barn behind one of the roosts. In September, no bat detector survey was conducted around the roost areas. In June and July 2017, the colonies were revisited once again. In Bierum twelve parti-coloured bats were counted departing roost B

Figure 2. The roost locations and the maximum number of bats (parti-coloured and serotines) that departed the roosts in 2016. The colony in Bierum moved around mid July from location A to B. Source: Luchtfoto Actueel (Current Aerial Map), PDOK.

and in Spijk 61 individuals departed the roost. At the beginning of August only nine individuals were left in the Spijk roost.

The roosts were all located at the edge of the village in houses consisting of one or two floors and a gable or hip roof. At Bierum A bats flew out of both chimneys, one of which looked like a small ridge turret ('dakruiter' in Dutch). At the other location in Bierum and the location in Spijk, the bats flew out from openings over the full length of the roof between the ridge tiles and the top layer of roof tiles. Some left the roost near the end of the ridge tiles ('eindvorsten'), but most bats departed from other places on the roof.

All three houses that hosted parti-coloured bats colonies had concrete roof tiles ('sneldekkers'). In addition to these roosts, swarming individuals or small groups of the parti-coloured bat were observed around houses in Bierum (five individuals), Spijk (two individuals) and in Holwierde (three individuals). Most of these houses were similar to the houses with the colonies: low-rise houses with a gable or hip roof and two floors or less and

Table 2. Number of observations of different species in May to July (nursery period) and August to September (migration period) and the range (min-max) of the number of individuals per observation. The total number of individuals in those periods are also given.

	Total	May-July			August- September		
Species	Observations	Observations	Range	Sum	Observations	Range	Sum
Common pipistrelle	212	189	1-26	258	23	1-2	27
Nathusius' pipistrelle	83	56	1-3	63	27	1-2	31
Parti-coloured bat	44	39	1-30	100	5	1-2	7
Parti-coloured bat or serotine	23	18	1-3	48	5	1	5
Serotine	19	18	1-3	21	1	1	1
Daubenton's bat	9	6	1-2	7	3	1	3
Myotis (unidentified)	2	2	1	2	-	-	-

Table 3. Number of observations with time expansion recordings, the minimum and maximum number of recordings per observation and the total number of recordings per species.

Species	Observations	Min	Max	Sum
Parti-coloured bat	28	1	10	60
Parti-coloured bat (maybe serotine)	13	1	8	22
Serotine bat	5	1	3	7
Nathusius' pipistrelle	1	3	3	3
Common pipistrelle	1	6	6	6
Daubenton's bat	6	1	6	12

Table 4. Numbers of bats (parti-coloured and serotines) departing the roosts in 2016 and 2017. Vmur = parti-coloured bat, Eser = serotine.

Date	Location	Vmur	Eser	Remarks
09-07-2016	Bierum A	9-12	1-4	
14-07-2016	Bierum A	0	0	Foraging bats were observed at the gas compressor station despite heavy drizzle and a high wind of 5 Beaufort
22-07-2016	Bierum B	12	2	
13-08-2016	Bierum A	0	0	One from the barn behind the roost
13-08-2016	Bierum B	0	0	
22-07-2016	Spijk	23	0?	
23-07-2016	Spijk	29	1	
13-08-2016	Spijk	0	0	
23-06-2017	Bierum A	0	0	
31-07-2017	Bierum B	12	0	
08-07-2017	Spijk	61	2	
02-08-2017	Spijk	9	0	From the ridge of the house

generally located on the edge of the villages.

Foraging parti-coloured bats have mainly been observed at a height of 5 to 30 metres above wide waterways, the sea dyke and the inland dyke, but they were also seen in the villages and along tree avenues (Figure 3). This figure shows the observations of parti-coloured bats and nyctaloids, which were

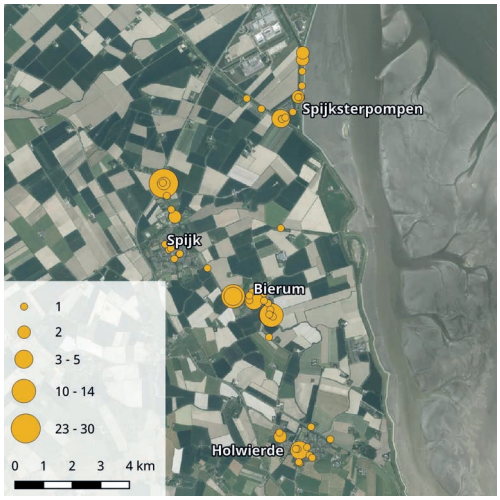


Figure 3. The number of bat detector recordings of parti-coloured bats in the study area. Source: Luchtfoto Actueel (Current Aerial Map), PDOK.

most likely parti-coloured bats. Looking at the characteristics of the foraging habitat, 17 individuals were seen above water, 2 individuals near agricultural area (inland dyke), 2 individuals near tree avenues and 17 individuals in the villages. Away from the colonies and the village of Holwierde, all the foraging activity was observed near the gas compressor station northeast of Spijk, the adjacent pumping station (Spijksterpompen) and Oostpolderdijk, the dyke along the river Ems. These locations are situated at 2.5–4.5 kilometres from the colonies.

Surveying the study area with Batcorders

In June-July, all Batcorders, except one, recorded sounds produced by nyctaloid bats (Table 5). The highest numbers of calls that we classified as parti-coloured bats were recorded by three Batcorders northeast of Spijk: Oostpolderdijk (PL10) and the gas compressor station (PL09, PL11). In addition, the two Batcorders in the villages of Spijk (PL13) and Holwierde (PL15) recorded relatively high numbers of parti-coloured bat (Figure 4). Nine Batcorders recorded only one or two recordings of the parti-coloured bats and six Batcorders did not record a recognisable parti-coloured bat sound.

In September, 11 out of 20 Batcorders recorded sounds of the parti-coloured bat (Figure 5). The numbers are overall a bit lower and recordings were more equally distributed over the study area. There was no concentration of recordings around the gas compressor station and Oostpolderdijk, as was seen in June-July. Interestingly, at Uiteinderweg (PL19), a relatively high number of parti-coloured bat sounds was recorded, whereas there were none there in June and July. In addition, there were more recordings in September than in June-July in the Eemshaven area (PL03-PL06). Only in Bierum (PL14) were individuals observed near a colony site in September. All Batcorders with high numbers were located at different locations than in July, except the Batcorder at the gas compressor station west (PL11).

The temporal distribution of the bat sound recordings

The nocturnal activity of the nyctaloid bats at eight locations is shown in Figure 6. Only a small proportion of the recorded bat calls were identified to a certain species. These recordings included noctule, serotine and parti-coloured bat and they were present in varying proportions at different locations. The majority of calls, however, was designated to the group of mid-sized nyctaloids (Nycmi), to which the parti-coloured bat belongs.

The peak activity differed between the locations. At Borkumkade (PL05) and Marsum (PL17) an early peak occurred around 23:00 hours (Figure 6, H and G). At Oostpolderdijk (PL09) and gas station west (PL11) the numbers were very high with a clear peak between 24:00-01:00 hours and a somewhat smaller peak between 03:00 – 04:00 (Figure 6, A and

Table 5. Number of batcorder recordings made per nyctaloid species in two periods in 2016. Automatic identification by batIdent: Vmur = parti-coloured bat, Nnoc = noctule, Eser = serotine, All nyct. = all recordings with any species of nyctaloid bat, including Vmur, Nnoc, Eser and nyctaloid bats, not identified at species level.

		June-July				September
Code	Location	Vmur	Nnoc	Eser	All nyct.	Vmur
PL01	Oudeschip	0	0	0	1	1
PL02	Roodeschool (Greedeweg)	1	3	0	6	1
PL03	Middenweg	1	5	4	23	5
PL04	Emmapolderdijk	0	2	0	3	1
PL05	Borkumkade	1	40	31	85	0
PL06	RWE-centrale	1	1	2	13	6
PL07	Synergieweg	0	0	0	0	1
PL08	Eemscentrale	2	0	0	4	2
PL09	Oostpolderdijk (Binnenbermsloot)	63	37	27	381	0
PL10	Gas (compressor) station east	8	2	78	228	0
PL11	Gas (compressor) station west	45	117	61	573	6
PL12	Oosteinde (Lage Trijnweg)	0	5	0	12	0
PL13	Spijk	3	6	3	48	0
PL14	Bierum (campsite Kiek op Diek)	1	0	0	14	8
PL15	Holwierde	10	35	22	134	0
PL16	Losdorp	1	18	18	82	1
PL17	Marsum	1	35	17	158	0
PL18	Uitwierde	1	1	5	18	0
PL19	Uiteinderweg	0	1	2	10	9
PL20	Hoogwatum	0	1	0	8	0

Table 6. The total number of recordings per apartment building and the number of recordings of the common pipistrelle (Ppip), Nathusius' pipistrelle (Pnat) and serotine (Eser). For the common pipistrelle the number of recordings with courtship behaviour (mating calls) is also given. For all species the maximum number of individuals per recording is also included.

Building	Recordings		Ppip			Pnat		Eser	
	Total	#/night	Total	Courtship	Indiv.	Total	Indiv.	Total	Indiv.
Naterij	19	0 – 12	17	7	1	2	1		
Dijkzicht	842	11 – 686	816	648	3	19	1	7	1
Oldiek	872	1 – 574	864	805	3	8	2		
Kadijk	91	3 – 57	85	6	3	6	1		
De Vennen	31	0 – 14	29	11	2	2	2		

E) It should be noted that gaps in recordings at Oostpolderdijk and gas station west occurred because the memory cards were already full halfway through the second night. At Holwierde (PL15) and Losdorp (PL16) calls were recorded during the whole night, without steep peaks in the number of calls (Figure 6, D and F). At gas station east (PL10) there was a clear peak between 02:00-03:00 (Figure 6, C). At Spijk (PL13) most calls were recorded between 01:00 – 04:00 hours, without a clear peak (Figure 6, B).

At all other locations there were no or only few calls recorded. Their total number was

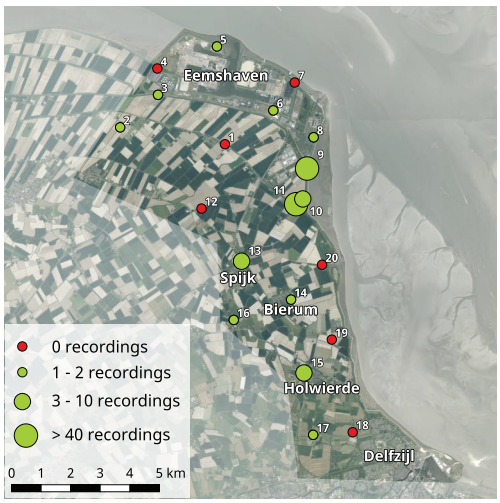


Figure 4. Overview of batcorder locations in July 2016. Green dots show locations with recordings identified as parti-coloured bats. Red dots show locations where no parti-coloured bats were recorded. The numbers on the map correspond with the numbers in the location codes of Table 5 and Appendix 2. Source: Luchtfoto Actueel (Current Aerial Map), PDOK.

Figure 5. Overview of batcorder locations in September 2016. Dots in green show locations with recordings identified as parti-coloured bats. Red dots show locations where no parti-coloured bats were recorded. The numbers on the map correspond with the numbers in the location codes of Table 5 and Appendix 2. Source: Luchtfoto Actueel (Current Aerial Map), PDOK.

always less than 25 recordings, except at Middenweg (PL03) with 28 recordings. Middenweg is situated southwest and in the direct neighbourhood of Borkumkade (PL05). At both Middenweg and Borkumkade a peak occurred around 23:00. Of the locations that are not shown in Figure 5, a high peak number of 15 recordings during one hour was found at Middenweg.

Monitoring courtship behaviour

The five Batcorders attached to high apartment buildings in Delfzijl did not record any parti-coloured bat sounds, and certainly no display calls. Other bat species, however, produced many calls. The vast majority of recordings were of the common pipistrelle and included many social calls (Table 6). Only a few sounds of Nathusius' pipistrelles were recorded and none were social calls. Seven recordings with sonar pulses below 30 kHz were made at an apartment building in Dijkzicht, but they were most likely from serotines. The number of recordings of the common pipistrelle varied greatly per night, and also between the apartment buildings. Most recordings were made on the balconies of the Dijkzicht and Oldiek apartment buildings, where 816 and 864 series of calls were recorded, of which, 648 (79%) and 805 (93%), respectively, contained display calls. On the Naterij, De Vennen and Kadijk building complexes there were 17, 29 and 85 recordings respectively, of which 7 (41%), 11 (38%) and 6 (7%) were display calls.

Discussion

Although there have been various scattered observations of individual parti-coloured bats, this inventory is the first effort to systematically search for this species in north-east Groningen. In 2016 and 2017 we surveyed the

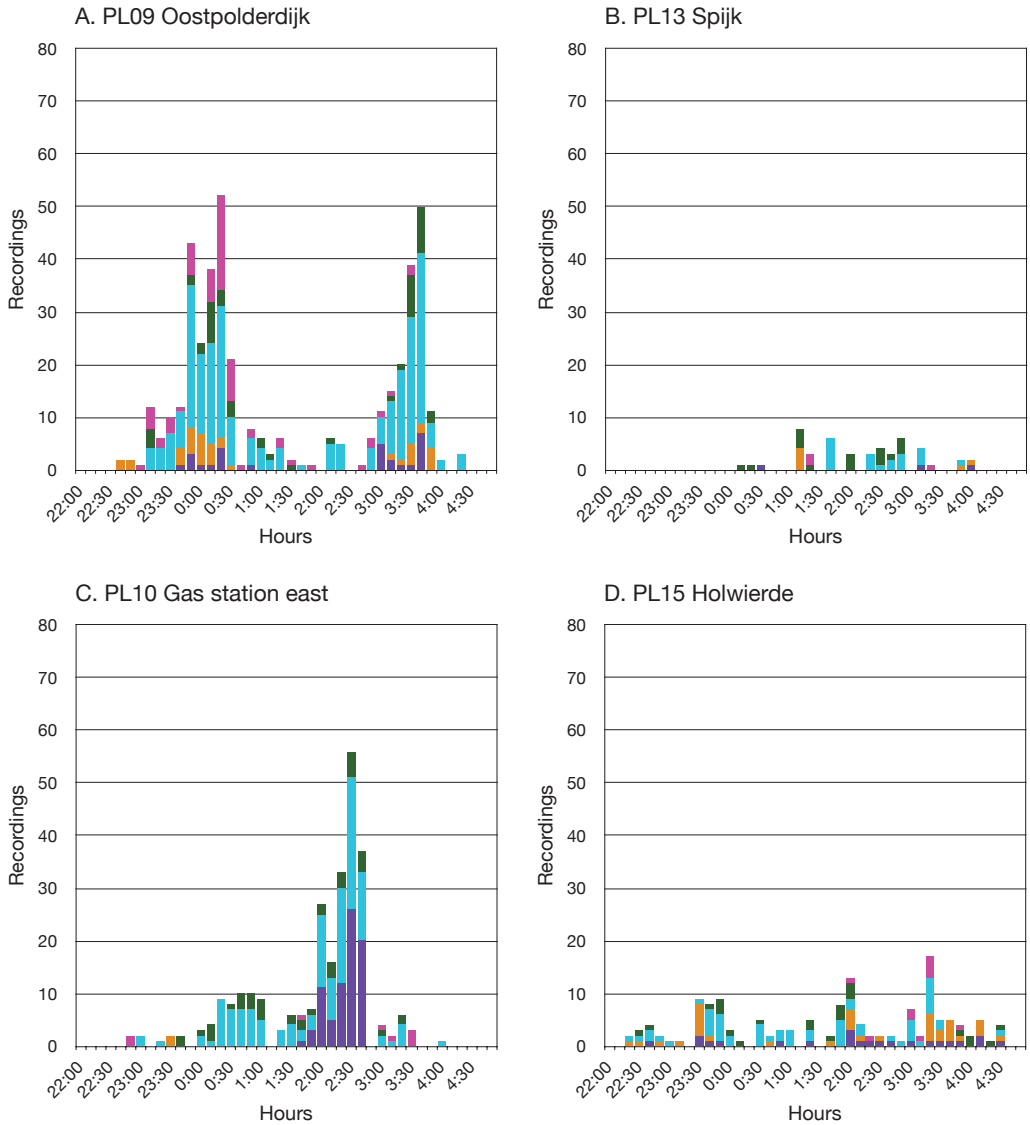
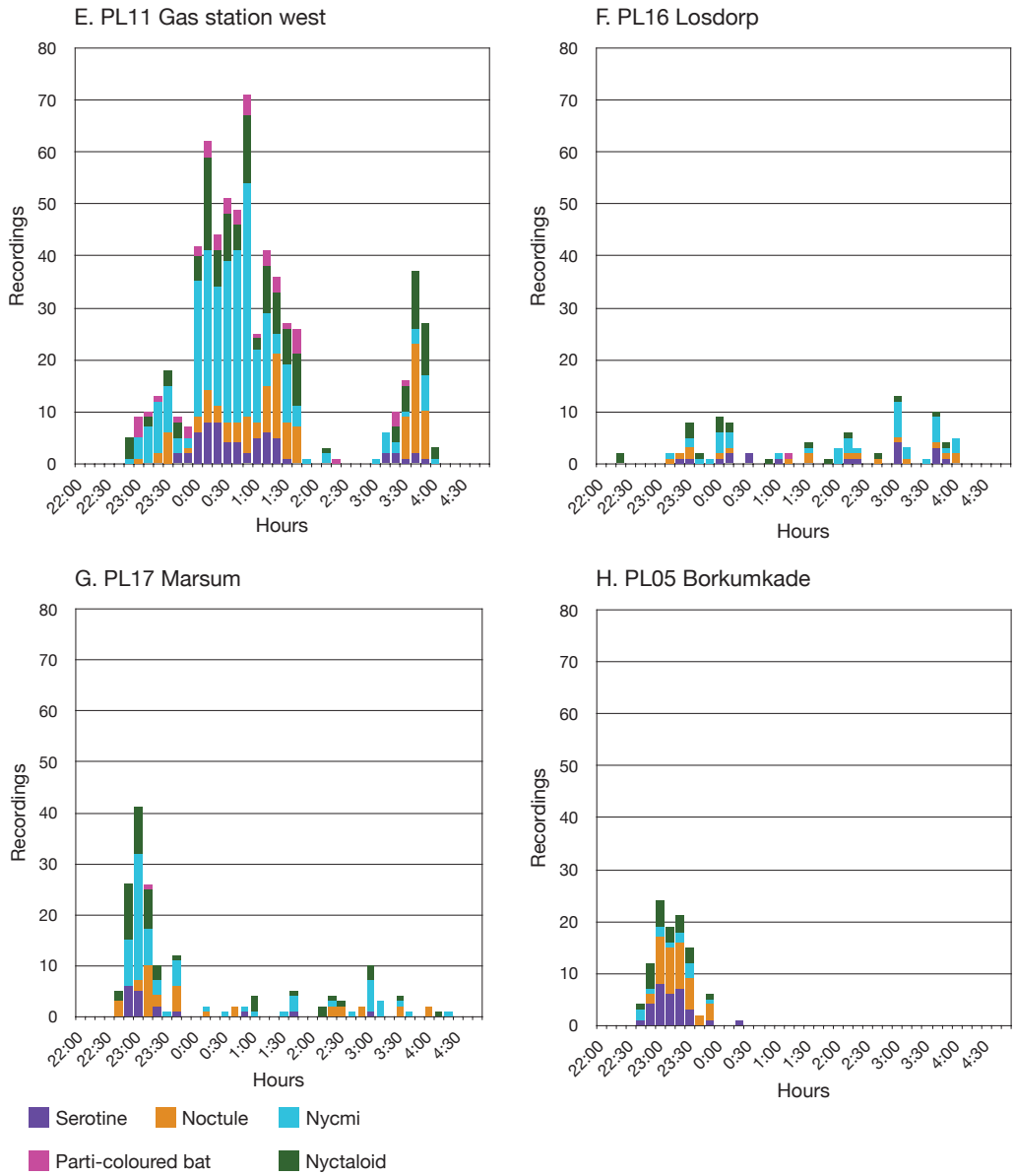


Figure 6. Night activity of nyctaloid bats. For each location recordings were aggregated in 10-min intervals. The recorded bat calls were identified by automatic identification software to different species or species groups: serotine, noctule, parti-coloured bat, Nycmi = mid-sized nyctaloid bat, and Nyctaloid = any nyctaloid bat (see text for further explanation). Locations with very few records are not shown.

study area of Eemshaven-Delfzijl with mobile bat detectors and Batcorders at fixed positions. We found roosts of parti-coloured bats in villages and much foraging activity in one particular area along the coast, but no courting males with their conspicuous display calls were observed in the area.

Roosts of parti-coloured bats in north-east Groningen

Houses in which the roosts have been found are modern single family houses, consisting of one or two storeys with a multi-pitched (gable or hip) roof. The landscape and this type of



houses are quite similar to northeast Zealand (Denmark), where there are many nursery colonies of parti-coloured bats (Baagøe 1986, 2001). Two colonies of parti-coloured bats were found in our study area, one in Spijk and another one in Bierum. After 2002, when a roost with 25 individuals in Spijk was found, no new observations of roosts have been reported until this study. Although no systematic survey of the area has been done before, we think that a summer population of this species may have been present for a long period, but not noticed. The roost found in Spijk in 2016 was situated in a similar house along the same street, roughly 250 metres from the location in 2002. The residents of the new location mentioned that in summer seasons they were having bats under the roof of

both their home and the adjacent garage for 20 to 30 years. They also found many droppings after each breeding season. It is not fully certain which bat species inhabited the space under the roof, but it is most likely that it was a colony of the parti-coloured bat. In 2016 the maximum total of individuals that departed the roost was 30. In 2017 this number was 63.

The locations of the roosts in Bierum were previously unknown. In 2007, two individuals were found in the same part of the village as roost Bierum B (waarneming.nl 2024). The maximum number of parti-coloured bats that departed both roosts in Bierum was twelve. Roost Bierum A appeared abandoned five days after its discovery in the beginning of July. Later that month roost Bierum B was discovered. Towards the end of the nursery period in 2016 the location of the colony apparently switched within Bierum (from Bierum A to Bierum B) over a distance of nearly 750 metres. By the end of July 2017 twelve parti-coloured bats departed from Bierum B. When the young become independent, females and their young often move to other locations (Safi 2023). In Maarssenbroek the main group of the nursery colony stayed in the same building block during the nursery period, but in the course of July, small groups were found in other blocks in the neighbourhood. On three occasions the nursery colony moved to one of the other blocks in the following year. Nursery colonies often change roosts within the same building block during the nursery period (Jansen et al. 2017).

A potential location for a nursery roost is Holwierde. A relatively high number of recordings of parti-coloured bats were made at several locations in this village using a handheld bat detector. In addition the Batcorder on location PL15 in Holwierde recorded more calls of the parti-coloured bat and other nyctaloids, not identified at species level, than the Batcorders in Spijk (PL13) and Bierum (PL14) did. Commuting and foraging individuals were seen, and potential swarming behaviour was observed. However, no colony was confirmed in this village in 2016 or 2017. In 2022 and 2023 a colony with unknown reproduction status was discovered in Holwierde, occupying two roosts that were located close to each other (Jonge Poerink 2024).

Reproduction status of the roosts

The roosts in Bierum and Spijk were not discovered until July 2016. Normally most young parti-coloured bats start to fly in July, which means that there were already flying young present when we started the roost counts. Therefore we were not able to compare these counts with counts of only flying adults in the first half of June. This means that our counts could not be used to establish the reproduction status of the colonies. Due to time constraints we were also not able to do early roost counts in 2017.

We received more information from a bat rehabilitation centre in the province of Groningen that gave us more insight in the reproductive status of the roosts in the study area. On 20 June 2017, a young female, of around two days old, was found in a house across the street from the Bierum A roost. Three days later we looked for a nursery colony there, but did not see any bats flying out at either location. On 30 July 2017, a young male, which was born the same year and already able to fly, was found near the village centre of Spijk. On 31 July 2018, a weakened lactating female from the roost in Spijk was brought to the rehabilitation centre. These findings show that reproduction takes place in the study area and in, or very close to, the roosts that were found in this study.

Foraging

The main hotspot of the nyctaloid bat recordings is the western shore of the river Ems, around the Oostpolderdijk and the gas compressor station. This area is situated only 2.5-

4.5 km away from the roosts in Spijk and Bierum. The importance of the western shore of the river Ems for nyctaloid bats is very clear (Figure 6 A, C and E), especially when taken into account that at two locations in this area the memory cards were already full halfway by the second night. Although these two Batcorders have the highest number of recordings, they were only active for 51% and 57% of the planned recording time, respectively. Figure 6 shows high numbers of nyctaloid bat calls in several peaks over the night. Up to 71 recordings in one 10-minute interval were recorded. The highest peaks in the number of recordings occurred between 00:00 and 04:00 hours. Before 0:00 hours lower numbers were found and after 04:00 hours the recordings ended rather abruptly. It is possible that the early foraging bats were mainly serotines, which were consequently replaced by parti-coloured bats. Hessing & Hinkel (2006) note that serotines leave the foraging area when parti-coloured bats arrive. However, all nyctaloid bats that were seen at Oostpolderdijk and around the gas station, were visually identified as parti-coloured bats due to their comparably small size in combination with their fast foraging flight. At the dyke this species was seen foraging in the evening twilight, shortly after 23:00 hours, at a height of over 20 metres, which is normal for the parti-coloured bat. The serotine is much larger and normally forages at lower heights (Haensel 2007).

Interestingly, there are relatively few recordings from the area around the colonies in Spijk and Bierum. Nearly all calls in the villages were recorded after midnight, and especially after 02:00. Parti-coloured bats are known to fly high and straight to foraging areas (Haensel 2007) and their calls are probably not picked up by the Batcorders, as the detection distance in these situations is only 50 metres. The Batcorders need to be placed straight below a commuting route to be able to record parti-coloured bats.

Parti-coloured did not seem especially attracted to street lamps, as we did not observe higher foraging activity close to street lamps. The rural area outside villages in northeast Groningen is quite dark, and artificial illumination in villages may lure insects from their normal environment. Although this 'vacuum cleaner effect' (Lewanzik & Voigt 2017) in residential areas could be a reason why parti-coloured bats are often observed in the villages, it is more likely that the nearby roosts explained their presence. Most of the bat detector observations occurred near open water (45%) and in the villages (45%). Within the villages the bats were observed at different locations: near canals, buildings or tree lines. Far fewer observations were found in agricultural land (5%) or along tree avenues outside villages (5%).

Rydell (1992) suggested that the street lights may partly have caused the increase of parti-coloured bat population in Sweden. We doubt whether this is the case in northeast Groningen. New research shows that artificial light at night might have little impact on foraging of fast-flying open-space foragers such as the parti-coloured bat (Straka et al. 2019). A stable high density of swarming insects above a large open water body is probably more important for parti-coloured bats, especially when located at a short distance from a nursery colony (Jaberg 2003). In our opinion this is the case in our study area, where the open water of the Ems-Dollard provides good foraging conditions with a high abundance of insects. The agricultural land, which covers a large proportion of the study area barely seems to be used for foraging by the parti-coloured bat.

Identification of nyctaloid bat sounds

Acoustic research of nyctaloid bats is challenging because of the overlap of the ultrasonic sounds produced by the different species. Automatic identification reveals many uncertainties and probably wrong identifications (Straka et al. 2019, Vandendriessche

2020). In our study many recordings could not be classified to certain species, but to species groups such as Nycmi or Nyctaloid, which shows that the automatic identification software of batIdent is not very precise for this group of bat species. Straka et al. (2019) arrived at the same conclusion after using the same Batcorders and identification software for automatic recording of bat calls in Berlin. The authors found also that recognition between nyctaloid species was problematic and therefore created species complexes: calls from *Nyctalus* spp., *Eptesicus* spp. and *Vespertilio murinus* were combined in the group NEV, and all calls from *Myotis* species were combined in one *Myotis* group. In a comparative study of four auto-identification programmes, Brabant et al. (2018) found that most false identifications occurred with nyctaloid species: Leisler's bat, serotine and parti-coloured bat.

One reason for the problematic identification is that batIdent uses individual calls, and therefore misses alternating calls ('blip-blop') which are characteristic of the noctule and Leisler's bat (Barataud 2020, Russ, 2021). An observer with a bat detector and a headphone will almost automatically pick up the alternating calls and interprets these sounds correctly. Unfortunately, as the original Batcorder recordings were lost, we were not able to re-analyse these sounds manually. In the bat detector survey, however, we never heard alternating sounds in the sonar of any nyctaloid bats. Therefore, we assumed that the noctule and Leisler's bat were absent during the nursery period. In August and September 2016, which is the migration period, we did not observe either of these species.

Generally, recordings in open habitat are most suitable for a reliable identification for nyctaloid bats (Russo et al. 2017, Brabant et al. 2018). For example, when parti-coloured bats and serotines are flying low and near clutter they may use very similar echolocation sounds. Although serotines in these circumstances usually emit sonar pulses with a higher peak frequency, the large variation in their pulses still creates some overlap with the parti-coloured bat (Barataud 2020). When flying at higher altitudes and in open habitats both species normally use pulses with different bandwidths and only little overlap occurs (Barataud 2020, Russ 2021).

Interaction with serotines in the study area

Baagøe (1986) suggested an allopatric distribution pattern between serotine and parti-coloured bats in Zealand, Denmark. Interestingly, he mentioned in his study one nursery roost of parti-coloured bat with three to five serotines. In our study in northeast Groningen we observed serotines departing from all the parti-coloured bat roosts, but always in low numbers. This is in accordance with other studies where serotine and parti-coloured bats were found in the same roost (Baagøe 1986, Hermanns et al. 2001, Jonge Poerink 2024). In Mecklenburg-Vorpommern, Germany, Hermanns et al. (2001) found a small group of serotines close to a nursery roost of parti-coloured bats in the same building complex. They also found parti-coloured bats in a serotine nursery roost. In the same study 15 serotines were observed in a large (probable) nursery roost of parti-coloured bats in Białowieża, Eastern Poland. In Holwierde, at a roost located in our study area, Jonge Poerink (2024) observed a few serotines flying out before 31 parti-coloured bats departed.

In contrast to Baagøe (1986), we found both serotines and parti-coloured bats in considerable numbers in our study area. A nursery colony of serotines has been discovered in Holwierde in 2024 (personal observation). In 2016, we saw serotines flying through Spijk, Bierum and Holwierde, mostly in the evening or morning twilight. Other observations in the evening twilight included a small group of serotines commuting along a tree line from Bierum in the direction of the sea dyke of the

Ems and serotines commuting and foraging near Roodeschool, at the western border of our study area. Parti-coloured bats and serotines were never visually observed together during our study, except at the roost locations. Serotines leave the colony and start foraging much earlier than parti-coloured bats (Hessing & Hinkel 2006; personal observation). This means that clear peaks of bat recording early in the night, might indicate the presence of serotines (Hessing & Hinkel 2006; personal observation). This is the case at both the north-western end of the study area (Borkumkade and Middenweg) and south-eastern corner of the study area (Marsum and Uitwierde). Here we also made only a few recordings after midnight.

Courting behaviour of males and hibernating roosts

Despite our systematic search for courtship behaviour of the male parti-coloured bats no display calls were found. Sexes are segregated in summer season, but they meet each other in autumn at display locations where males sing for long periods on mild evenings in the period from October to December. These display calls are typically heard near high buildings, often in larger cities and towns (Baagøe 2001, Dietz 2011, Safi 2023). We found no evidence that apartment buildings in Delfzijl, nor other areas in the study area are used as courting roosts by the parti-coloured bat. There were various other species recorded and one or two buildings seemed to be used as display areas and possibly winter quarters of the common pipistrelle. The number of recordings varied greatly per night, which was probably mainly caused by the large variation in weather conditions in autumn. The only published occurrence of display calls of the parti-coloured bat in the Netherlands is near a light house at the Maasvlakte to the west of the Rotterdam seaport (Mostert & Wondergem 1993). The harbour area around Eemshaven was systematically surveyed, both with hand-held bat detectors and Batcorders, with no signs of singing males. With the exception of the observation by Mostert and Wondergem, no display calls were reported in Belgium and the Netherlands until 2017.

Since the overall numbers of recordings were much lower in the northeast of Groningen in September, we assume that most individuals migrated and left the area. We presume that they flew to courtship areas or hibernating roosts, especially in larger cities, often located hundreds of kilometres away. For example, Groningen, which is a relatively large city with many high buildings, could be a possible courtship and hibernating location. However, bats are actively monitored in this city and no display calls have been recorded there. Further away, larger cities in northwest Germany could harbour mating locations. In Hamburg single males and females have been found in winter, and in Bremen a single pregnant female was found in 1997 (Hessing & Hinkel 2006). It should be noted that it is also unknown where the females of the Maarssenbroek colony go after their nursery period (Jansen et al. 2017).

Conclusions

Our preliminary inventory revealed three roosts of parti-coloured bats, used by two colonies in the study area in 2016 and 2017, where reproduction does occur. We do not know the population size of the parti-coloured bats in this area, or if it is growing or declining. Therefore, regular counts of parti-coloured bats departing their roosts before the nursing period and during the nursing period are recommended to monitor the population status.

We propose that roosts of the parti-coloured bat may have been present for several decades in this area, although remained unnoticed. The species might have been overlooked because of the problematic identification of echolocations sounds of nyctaloid bats,

in particular the parti-coloured bat, serotine, Leisler's bat and noctule. A new generation of acoustic identification has been developed which uses machine learning techniques to increase the accuracy in acoustic species recognition. Hopefully with this software the parti-coloured bat will be better recognized and more roosts discovered in other parts of the Netherlands. Only one main foraging area for the parti-coloured bats was found, which was located at the western shore of the river Ems. Further research is needed to establish whether and which other bat species were using this spot.

There is still much to learn about the males of the parti-coloured bats. We were not able to determine if there were also adult males present in the nursery roosts, and if there are all-male colonies in the study area, which would be typical for this species (Safi 2006). To gather this information, bats have to caught with nets or traps and sexed. Ideally, also some bats could be provided with radio transmitters to be able to follow individuals and get an insight in their nightly behaviour. In late summer when individual males migrate to their courting places, the females will migrate to these display areas not only to mate but often also will hibernate in or nearby these places. In north-western Europe these locations are often situated in high buildings in big cities. We observed declining numbers of parti-coloured bats in the area after August, and no courting display area has been found in this part of the Netherlands.

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Samenvatting

Een eerste onderzoek naar het voorkomen van de tweekleurige vleermuis in het gebied Eemshaven-Delfzijl, Groningen

De tweekleurige vleermuis (*Vespertilio murinus*) wordt in Nederland als een zeldzame soort beschouwd met maar één kraamkolonie, die in 1998 werd ontdekt. Een mogelijke tweede kolonie werd gemeld in Noordoost-Groningen in 2002, maar is daarna niet meer teruggevonden. Deze studie is een eerste systematische inventarisatie naar het voorkomen van de tweekleurige vleermuis in het gebied Eemshaven – Delfzijl, die in 2016 werd uitgevoerd met een mobiele batdetector en automatische recorders op vaste locaties. Met de batdetector werden drie verblijfplaatsen, behorend tot twee kolonies, aangetroffen in de dorpen Spijk en Bierum. In 2016 was het maximale aantal uitvliegende tweekleurige vleermuizen in Spijk 29 en in Bierum 12, terwijl in 2017 de maximale aantallen 61 respectievelijk 12 bedroegen. We zagen ook kleine aantallen, 1 tot 4 individuen, van de laatvlieger (*Eptesicus serotinus*), die eerder dan de tweekleurige vleermuizen uit dezelfde verblijfplaatsen uitvlogen. Er waren aanwijzingen voor een mogelijke derde kolonie, maar deze konden tijdens deze studie niet worden bevestigd. In dit artikel gaan we ook in op observaties van anderen die laten zien dat er voortplanting heeft plaatsgevonden in of heel dichtbij de kolonies die we in het studiegebied hebben gevonden. Met automatische recorders werd veel foerageeractiviteit geregistreerd in een relatief klein gebied aan de westelijke oever van de rivier de Eems. Deze foerageerlocatie was gelegen op 2,5-4,5 km afstand van de kolonies. Hier zijn foeragerende tweekleurige vleermuizen gezien op 5 tot 30 meter hoogte boven water. Tijdens de piek van de foerageeractiviteit werden in intervallen van 10 minuten maximaal 71 opnames gemaakt van de sonar van nyctaloïde vleermuizen (d.w.z. behorend tot de geslachten van *Nyctalus*, *Eptesicus* of *Vespertilio*, die vergelijkbare geluiden produceren). Over het algemeen kon slechts een klein deel met zekerheid op soortniveau worden geïdentificeerd en we bespreken de moeilijkheden die wij ondervonden bij de automatische identificatie van de echolocatiegeluiden van nyctaloïden. In de herfst zochten wij in het studiegebied naar baltsgeluiden en baltslocaties van mannetjes van de tweekleurige vleermuis, die in dat jaargetijde vooral in stedelijke gebieden met hoge gebouwen voorkomen. Er werden echter geen baltsende mannelijke tweekleurige vleermuizen aangetroffen. Hoewel deze soort voornamelijk in huizen en gebouwen en dus in menselijke nabijheid leeft, worden de zomer- en winterverblijven waarschijnlijk vaak over het hoofd gezien. In het geval van tweekleurige vleermuis in Noordoost-Groningen hebben we het vermoeden dat er al tientallen jaren kolonies aanwezig zijn.

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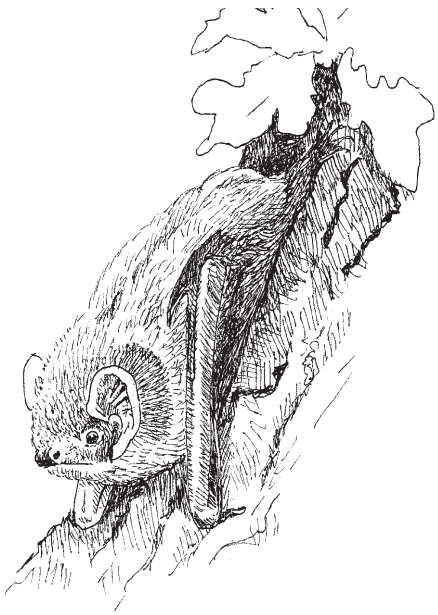
Appendix 1. Visiting dates and times, locations that were visited and the weather conditions during the visits

Date	Time	Temp. (°C)	Wind (Bft)	Locations/remarks
26-05	21:30 - 01:05	15 > 11	2 - 3	Eemshaven, Polen, Oudeschip
27-05	21:30 - 01:05	16 > 13	3 - 4	Spijk, Nieuwstad, Hoogwatum, Spijksterriet, Bierum
28-05	21:30 - 01:05	19 > 14	3	Delfzijl, Hoogwatum, Bierum, Holwierde, Nansum
01-06	21:55 - 00:10	20 > 18	4 - 5	Delfzijl, Farmsum, industrial area
08-07	01:20 - 05:20	15	0 - 1	Eemshaven, Polen, Oudeschip
09-07	01:15 - 05:15	15	3 - 4	Delfzijl, Nansum, Holwierde, Bierum, Spijk
09-07	22:00 - 23:30	18	3 - 4	Roost Bierum A
14-07	22:00 - 23:00	17	5	Roost Bierum A, foraging area gas compressor station Spijk, overcast with sometimes drizzle and rain
21-07	01:15 - 05:15	18	1	Delfzijl, Holwierde, Bierum, Appingedam
22-07	02:00 - 05:00	19	1 - 2	Spijk, Bierum
22-07	21:30 - 23:15	19	2 - 3	Roosts Bierum B and Spijk
23-07	21:30 - 23:00	18	0 - 1	Roost Spijk
25-07	03:00 - 05:00	19	0	Holwierde
13-08	21:10 - 22:20	18	1 - 2	Roosts Bierum A en B, roost Spijk
13-09	20:00 - 22:00	28 > 24	2 - 4	Eemshaven ZO, Spijksterpompen, Polen, Oudeschip
22-09	20:40 - 22:55	15 > 14	1 - 2	Delfzijl
11-11	18:15 - 20:25	2 > -1	2	Eemshaven, Delfzijl

Appendix 2. Locations of batcorders in June and July with the dates and times when the recording started, and the dates and times when the recording ended.

Code	Location	Start date	Start time	End date	End time
PL01	Oudeschip	27-06-2016	21:00	30-06-2016	06:00
PL02	Roodeschool (Greedeweg)	09-07-2016	21:00	12-07-2016	06:00
PL03	Middenweg	27-06-2016	21:00	30-06-2016	06:00
PL04	Emmapolderdijk	27-06-2016	21:00	30-06-2016	06:00
PL05	Borkumkade	06-07-2016	21:00	09-07-2016	06:00
PL06	RWE-centrale	06-07-2016	21:00	09-07-2016	06:00
PL07	Synergieweg	27-06-2016	21:00	30-06-2016	06:00
PL08	Eemscentrale	27-06-2016	21:00	30-06-2016	06:00
PL09	Oostpolderdijk (Binnenbermsloot)	12-07-2016	21:00	14-07-2016	03:22
PL10	Gas (compressor) station east	03-07-2016	21:00	06-07-2016	06:00
PL11	Gas (compressor) station west	09-07-2016	21:00	11-07-2016	01:48
PL12	Oosteinde (Lage Trijnweg)	09-07-2016	21:00	12-07-2016	06:00
PL13	Spijk	03-07-2016	21:00	06-07-2016	06:00
PL14	Bierum (camping Kiek op Diek)	06-07-2016	20:00	09-07-2016	06:00
PL15	Holwierde	12-07-2016	21:00	15-07-2016	06:00
PL16	Losdorp	06-07-2016	21:00	08-07-2016	06:00
PL17	Marsum	12-07-2016	21:00	15-07-2016	06:00
PL18	Uitwierde	03-07-2016	21:00	06-07-2016	06:00
PL19	Uiteinderweg	03-07-2016	21:00	06-07-2016	06:00
PL20	Hoogwatum	03-07-2016	21:00	06-07-2016	06:00



De aantalsontwikkeling van de rosse vleermuis (*Nyctalus noctula*) in West-Nederland

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Abstract: *Changes in numbers and distribution of the noctule in the west of the Netherlands*
The occurrence of the noctule (*Nyctalus noctula*) in the west of the Netherlands, including the provinces of Noord-Holland (excluding Het Gooi), Zuid-Holland and Zeeland is for the most part limited to the wooded inner dune area. Until the late 1970s, data on the occurrence of this species were mainly based on casual finds and social calls and squeaks around colony trees, which alerted observers to the presence of the species. Since the early 1980s, the advent of the bat detector has made it possible to more effectively study areas for the occurrence of noctules, among other bats. The Dutch population in the 1990s was estimated at 6000 to 8000 animals, of which 810-1030 were recorded in the inner dune area. No maternity colonies of noctules were found outside the inner dune area. Since the 1980s, there have been three periods of monitoring of noctules in the western part of the Netherlands: 1986-1993 (period 1), 1998-2002 (2) and 2013-2018 (3). The area around The Hague, Rijswijk and Voorburg was studied in four separate periods: 1986-1993 (period A), 1998-2002 (B), 2008-2012 (C) and 2015-2018 (D). In that area in Zuid-Holland, systematic surveys of maternity colonies, summer roosts and foraging animals were conducted in suitable areas, including outside the inner dune area where the species was initially absent. The number of noctules emerging from their roost in the west of the Netherlands over periods 1 to 3 shows a definite, significant increase. Even so, the numbers of colonies increase over periods 1 to 3. Similarly, in The Hague, Rijswijk and Voorburg, both the numbers of emerging noctules and the number of colonies show an increase over periods A to D. Furthermore, between the periods of 1986-1993 and 2013-2018 the number of kilometre squares where noctules were heard in the west of the Netherlands increased significantly. The eventual establishment of a maternity colony is often preceded by years of observations of foraging animals and the establishment of roosts with one or a few animals. The population of noctules in the period 2013-2018 is estimated at 2600-2850 adult females compared to 800-1000 animals in the 1990s. This means a significant increase in the number of animals in recent decades. In addition to an increase in the number of maternity colonies and the number of foraging animals, an expansion and new settlements in areas outside the inner dune area were also observed. For example, new colony settlements were found in the vicinity of Zoetermeer, Rotterdam, Schiedam and 's-Gravenzande and also in the inner dune area of the former island of Voorne, areas in Zuid-Holland where the species was not found in the 1990s despite targeted efforts to find colonies. In Noord-Holland, new colonies were found in the Amsterdamse Bos and in a northerly direction in the vicinity of Alkmaar, north of Schoorl and in the Wildrijk. In Zeeland, however, the few formerly known colonies in the border area of Zeeuws-Vlaanderen and Flanders seem to have disappeared, while the area around Hulst has not been sufficiently investigated. The causes of the increase in the number of bats in the west of the Netherlands in the periods studied are related to both a general aging of the country estates and the forest, as well as to the greater availability of foraging areas, such as recreational forests and lakes. An increase of the number of recreational lakes was especially apparent in the western parts of the Netherlands, while the increase

of recreational forest was greatest in Zuid-Holland, compared to other parts of the Netherlands. For these reasons, the observed increase in the number of noctules is not necessarily representative of other parts of the Netherlands. A changing forest management since the 1970s, which took place nationally, with a greater emphasis on the preservation of old and dead trees, can also be mentioned as a cause of the increase. Felling of old trees, however, remains a concern. Forests containing such trees are important: the noctule seems to mainly appear in forests that are older than 80 years. In addition to logging during World War II, urbanization, leading to loss of hunting grounds, had a major effect on the populations of noctules in the west of the Netherlands. The bans on insecticides in 1968 and 1973 may have had a positive effect on noctule numbers, although there is no prove to support this. Another factor in favour of the noctule may have been the scharp increase in numbers since the 1970s of the great spotted woodpecker (*Dendrocopos major*), being the main supplier of tree cavities suitable for roosting noctules. The expansion of the ring-necked parakeet (*Psittacula krameri*) may have a negative effect on noctules locally, but does not seem to be affecting the noctule population for the time being. Remarkably, the Eurasian nuthatch (*Sitta europaea*) seems to have the same requirements as the noctule regarding age and size of trees and the required area with suitable trees. It is of great importance that new systematic area inventories are carried out on noctules throughout the Netherlands.

Trefwoorden / keywords: rosse vleermuizen, noctules, uitvliegers, fledglings, kraamkolonie, colony, binnenduinen, inner dunes, landgoederen, estates.

Inleiding

De rosse vleermuis (*Nyctalus noctula*) is een boombewonende soort. In het westen van Nederland is het voorkomen van deze soort grotendeels beperkt tot het bosrijke binnenduingebied. Tot eind jaren 1970 berustten gegevens over het voorkomen van deze soort voornamelijk op toevallige vondsten, vaak meldingen na het omzagen van bomen waar vleermuizen uit tevoorschijn kwamen. Wel kan de rosse vleermuis luidruchtig zijn en konden waarnemers die bekend waren met de (met het blote oor hoorbare) geluiden die zij produceren ook overdag kolonies vinden. Bels (1952) maakte veelvuldig gebruik van deze manier van inventariseren bij zijn onderzoek naar trekgedrag van de rosse vleermuis in de jaren 1940.

Door de komst van technische middelen als de bat-detector, waarmee de waarnemer ook ultrasone geluiden kan horen, is het sinds begin jaren 1980 mogelijk effectiever gebieden te onderzoeken op het voorkomen van vleermuizen, gebaseerd op de methodiek van Helmer et al. (1987) waarbij landgoederen en bossen systematisch worden geïnventariseerd met bat-detectors. De Nederlandse populatie rosse vleermuizen werd in de jaren 1990 op 6000 tot 8000 dieren geschat (Boonman 1993), waarvan een belangrijk deel voorkwam in het binnenduingebied (810-1030 dieren).

Sinds de jaren 1980 zijn er in West-Nederland drie perioden geweest waarin intensieve monitoring van (kraam)kolonies en andere verblijfplaatsen van de rosse vleermuis heeft plaatsgevonden. Monitoring in de eerste periode in de jaren 1986-1993 werd vooral uitgevoerd in het kader van de Atlas van de Nederlandse vleermuizen (Limpens et al. 1997). De tweede periode, 1998-2002, had vooral betrekking op Zuid-Holland en de derde, meest recente monitoringperiode in de jaren 2013-2018 viel grotendeels samen met inventarisaties in het kader van de Atlas van de Nederlandse zoogdieren (Broekhuizen et al. 2016). In de omgeving van Den Haag, Rijswijk en Voorburg, is in vier aparte perioden intensief naar kolonies en verblijfplaatsen gezocht: van 1986-1993 (periode A), van 1998-2002 (periode B), van 2008-2012 (periode C) en van 2015-2018 (periode D).

Onder West-Nederland worden hier de provincies Noord- en Zuid-Holland en Zeeland

verstaan. Het Gooi, het meest oostelijke deel van de provincie Noord-Holland, sluit qua fysiologische geografie meer aan bij de pleistocene zandgronden van de Utrechtse Heuvelrug en is hier buiten beschouwing gelaten. Bovendien zijn in Het Gooi geen gegevens verzameld sinds de jaren 1990. Van Texel (en de andere Waddeneilanden) zijn alleen incidentele waarnemingen van rosse vleermuizen bekend in de migratieperiode en ontbreken verblijfplaatsen en kolonies. Dit geldt ook voor het aangrenzende zeeklei- en kustgebied in het noorden van Nederland (Lagerveld & Mostert 2023).

In dit artikel worden de in de genoemde drie perioden verzamelde gegevens van de rosse vleermuizen in West-Nedeland en de gebruikte methoden uiteengezet en bediscussieerd. Hierbij is ook gebruik gemaakt van literatuurbronnen en soms van aanvullende gegevens van individuele waarnemers. Veel 'nulwaarnemingen' blijken niet te zijn gerapporteerd en zijn via gerichte vragen aan waarnemers achterhaald.

Geleidelijk aan kwam het beeld naar voren dat de rosse vleermuis steeds vaker werd waargenomen in West-Nederland en het areaal met zomerkolonies zich daar aan het uitbreiden is. In de Atlas van de Nederlandse zoogdieren wordt geconcludeerd dat tellingen van uitvliegende dieren in de zomer landelijk geen duidelijke indicaties opleveren voor een toe- of afname (Spoelstra 2016). Op basis daarvan is geconcludeerd dat er voor het bepalen van de staat van instandhouding van de rosse vleermuis landelijk onvoldoende gegevens bekend zijn (Rode Lijst: van Norren et al. 2020).

Habitat en levenscyclus

De rosse vleermuis, een soort die in hoofdzaak boomholten bewoont, maakt zowel in het zomerseizoen als in de winter gebruik van oude holle bomen, voornamelijk oude eiken (*Quercus* spp.) en beuken (*Fagus sylvatica*)

Kolonie rosse vleermuizen in een boomholte. *Foto: Kees Mostert.*

Colony of noctules in a tree cavity. Photo: Kees Mostert.

op landgoederen en in andere bossen (Boonman et al. 1997); gebouwbewonende rosse vleermuizen zijn, als bijzonderheid, in Nederland beschreven door Voûte (1977, 1990). De soort maakt veel gebruik van verlaten spechtenholten, waarbij de openingen zich meestal bevinden tussen de 5 en 22 meter hoogte (Kronwitter 1988). De groepsgroottes variëren van 10 tot 125 dieren (Boonman et al. 1997).

De groepen leven vaak verdeeld over een netwerk van meerdere verblijfplaatsen en verhuizen relatief vaak. Roepende territoriale mannetjes en paarverblijven in het najaar worden gevonden in boomholtes en ook wel in nest- en vleermuiskasten.

De rosse vleermuis jaagt veel boven wateren, zoals meren, open vijvers en rivieren en vaak op grotere hoogte van 10 tot 100 meter. Foerageergebieden kunnen tot tientallen kilometers van hun verblijfplaats liggen. De dieren zoeken soms verlichting, zoals straatlantaarns, op om te jagen op insecten die hierdoor worden aangetrokken. De grootste aantallen rosse vleermuizen zijn te vinden daar waar oude landgoederen grenzen aan waterrijke gebieden (Boonman et al. 1997).

De vrouwtjes vormen in de loop van april kraamkolonies, die in de loop van juli, na het zelfstandig worden van de jongen, weer uit elkaar vallen. Gemiddeld bestaat een kraamkolonie uit 30 volwassen vrouwtjes (Boonman et al. 1997). Volwassen mannetjes leven tijdens de kraamperiode in aparte kleine groepjes, meestal bestaande uit enkele dieren, vaak in de buurt van kraamkolonies. Niet zelden voegen deze zich ook bij kolonies van andere soorten zoals de watervleermuis (*Myotis daubentonii*). De eerste jongen kunnen al uitvliegen voor 10 juli, maar doorgaans wordt 15 juli aangehouden als uiterste datum waarop volwassen dieren nog zonder jongen uitvliegen. Het Vleermuisprotocol (Netwerk Groene Bureaus 2021) hanteert voor tellingen de periode van 15 mei tot en met 15 juli als de kraamperiode.

Uit ringonderzoek van zowel Bels (1952) als Sluiter & van Heerdt (1966) blijkt dat kolonies van rosse vleermuizen in het zomerhalfjaar regelmatig van boom verwisselen binnen hetzelfde landgoed maar veel minder naar naburige landgoederen. In de omgeving van Groenekan (Utrecht) werd vastgesteld dat een kolonie een leefgebied met een straal van circa vijf kilometer bewoont (Sluiter & van Heerdt 1966). Dit komt overeen met de opgave van ca. 200 ha voor kraamkolonies (Kronwitter 1988). Voor seizoensmigratie in het najaar en voorjaar gelden uiteraard andere afstanden. Seizoensgebonden migratie laat in centraal Europa patronen zien met zeer variabele afstanden. Rosse vleermuizen blijken trouw te blijven aan de individuele migratieafstanden, die variëren tussen regionale (< 50 km) en langeafstandmigratie (>400 km). Deze migratie leidt tot een uitgesproken vermenging van verschillende bronpopulaties in overwinteringsgebieden, waar ook paring plaatsvindt. De meeste individuen (namelijk 86%) waren consistent in hun migratiestrategie in de loop van de tijd (Lehnert et al. 2018).

De rosse vleermuis overwintert in holle bomen. Deze worden niet, zoals veel bunkers en andere "ondergrondse" winterverblijven, jaarlijks onderzocht. Hierdoor zijn er maar heel weinig meldingen van rosse vleermuizen in winterslaap en is derhalve nauwelijks bekend waar de populatie overwintert; vermoedelijk is dit grotendeels in hetzelfde gebied als waar de dieren 's zomers aanwezig zijn, maar langeafstandmigratie over meer dan 500 km is ook vastgesteld (Bels 1952). In de weinige bekende zogenaamde winterbomen met rosse vleermuizen worden meestal grote aantallen bij elkaar gevonden.

Methode

Systematisch zoeken naar kolonies en verblijfplaatsen

Door het gebruik van bat-detectors sinds halverwege de jaren 1980 konden voor het eerst gebieden systematisch geïnventariseerd worden op kraamkolonies en andere verblijfplaatsen. Een veel gebruikte methode om deze kolonies te vinden was, en is, de volgende. Als eerste stap wordt een onderzoeksgebied, zowel in de (voor)avond als in de vroege ochtend afgezocht. Rosse vleermuizen kunnen in de zomermaanden, vooral op warme dagen en avonden, luidruchtig zijn. Een deel van de kolonies wordt dan ook zonder gebruik van apparatuur ontdekt: dieren kunnen zonder batdetector tot op meer dan honderd meter te horen zijn (Helmer 1983).

Vervolgens wordt er in de avond gepost met bat-detectors bij kansrijke bomenlanen en in de vroege ochtend worden dieren terug gevolgd naar de kolonies. Een bosgebied of landgoed wordt gedurende de ochtendschemer herhaaldelijk doorkruist met detectors om zo het zwermen van de dieren bij de kolonies op te sporen. Afhankelijk van de grootte en de structuur van het betreffende onderzoeksgebied en indien er voldoende geschikte bomen aanwezig zijn op een landgoed wordt een indeling gemaakt tussen de beschikbare aantallen waarnemers. Omdat kolonies kunnen verhuizen worden kort daarna, zo mogelijk de daar-

Karakteristieke beuken- en eikenlaan met een kolonie van rosse vleermuizen op een landgoed in het binnenduin tussen Den Haag en Wassenaar. *Foto: Kees Mostert.*
Characteristic lane with beech and oak with a noctule colony on an estate in the inner dunes between The Hague and Wassenaar. Photo: Kees Mostert.

opvolgende avond, de uitvliegende dieren bij de ontdekte verblijfplaatsen simultaan geteld. Rosse vleermuizen vliegen meestal vroeg uit en zijn vaak in korte tijd uitgevlogen.

Van een deel van de gevonden kolonies zijn dieren afgevangen middels mistnetten en gecontroleerd op geslacht. Uit deze informatie kon worden afgeleid dat kraamkolonies in de regel uit groepen van tien of meer dieren bestaan. Voor het bepalen van de populatiegrootte van volwassen vrouwtjes is 15 juli als uiterste datum aangehouden. De eerste meevliegende jongen zijn overigens eenvoudig te herkennen aan hun geringere grootte en hun onhandige gedrag tijdens het uitvliegen waardoor ze niet zelden op een (kolonie)boom belanden.

Verwarring met andere soorten (met name bosvleermuis) is nauwelijks van belang: de frequentie van de constante roep van de bosvleermuis is hoger, rond 24 kHz, en duurt korter, tot 20 ms, dan die van de rosse vleermuis, die een frequentie heeft tussen de 19-22 kHz en waarvan de roep tot 28 ms duurt (Dietz et al. 2007).

Systematisch zoeken naar foeragerende dieren

Er is uitgebreid met bat-detectors gezocht naar foeragerende dieren. In Zuid-Holland zijn hiertoe in de periode 1986-1993 en in de periode 2013-2018 in het kader van de atlasprojecten de meeste kilometerhokken in de provincie tenminste driemaal geïnventariseerd op aanwezigheid van vleermuizen; voor beide onder-

zoeksperioden was de onderzoeksinspanning vergelijkbaar. In Noord-Holland heeft in de jaren 1988 tot en met 1993 een uitgebreid onderzoek plaatsgevonden (Kapteijn 1995). In Zeeland werd in de periode 1989-2008 ook op uitgebreide schaal naar foeragerende vleermuizen gezocht ten behoeve van de landelijke atlasprojecten en de regionale atlas (onder meer Bekker et al. 2010).

Waarnemingen buiten de trekperiode zijn aangevuld op basis van de gegevens van de NDFF (NDFF 2015). Batdetectorwaarnemingen in de trekperiode zijn buiten beschouwing gelaten.

Resultaten

Historische gegevens: voor 1985

Er zijn slechts weinig gegevens te vinden over kolonies en vondsten van rosse vleermuizen van voor 1985. Om deze boven tafel te krijgen werden de collectie van Naturalis en oudere literatuurbronnen geraadpleegd, onder meer Van Wijngaarden et al. (1971). Deze meldingen berusten op toevallige vondsten en geven daarom een summier en onvolledig beeld van het voorkomen van de soort.

De oudst bekende vondst van de rosse vleermuis in West-Nederland heeft betrekking op twee dieren (een man en een vrouw) die werden verzameld op 31 januari 1877 in de gemeente Leiden (Bels 1952); deze auteur vermeldt ook vondsten bij Rotterdam en Utrecht uit 1886 en Schiedam uit 1887.

In de collectie van Naturalis zijn tussen 1912 en 1966 vier vondsten bekend, waarvan er drie betrekking hebben op kraamkolonies. Het betreft de gemeenten Wassenaar, Leiden, Warmond en Noordwijk, alle vier gemeenten met oude landgoederen. In het Haagse Bos werd in juni 1941 een es gekapt met ongeveer 300 rosse vleermuizen (Kapteijn 1995).

In Noord-Holland werd bij Haarlem (Haarlemmerhout en Bloemendaalse Bos) in de jaren 1936 tot en met 1946 uitgebreid onderzoek aan rosse vleermuizen gedaan door Bels (1939, 1952). In de Haarlemmerhout wist hij 20 koloniebomen te lokaliseren door op warme middagen en avonden door het bos te lopen en naar de sociale geluiden van rosse vleermuizen te luisteren. Er waren vermoedelijk 400 tot 600 volwassen dieren aanwezig (Kapteijn 1995). Sluiter & van Heerdt (1966) vermelden kolonies voor Amsterdam, Badhoevedorp en Velzerbeek. Boven het Noordzeekanaal werden in deze periode enkele kolonies gemeld bij Bergen (aantal onbekend) en Marquette (twaalf dieren).

In de jaren 1930 was het verspreidingsgebied van de rosse vleermuis in West-Nederland aanzienlijk kleiner dan in de jaren 1980, maar lokaal waren toen wel bijzonder hoge dichtheden aanwezig. Dit geldt met name voor de omgeving van Haarlem. Hier werden regelmatig groepen van meer dan 100 exemplaren geteld, bijvoorbeeld de 198 stuks die Bels (1939) telde in de zomer van 1938. Ook in het Bloemendaalse Bos werden in de zomer van 1938 79 uit een boom uitvliegende dieren geteld (Bels 1939). Bels (1939) vond zelfs een keer een boom waar er "ongeveer 400 in zaten". Sluiter en van Heerdt (1966) constateerden later dat de kolonies in en om Haarlem grotendeels verdwenen waren. Ook waren er kraamkolonies (en blijkbaar dus geschikte biotopen) in en om steden als Leiden en Amsterdam waar de soort vervolgens langdurig afwezig is geweest.

Opvallend aan enkele oude vindplaatsen (Badhoevedorp en Leiden) is dat hier in de jaren 1980 met intensief bat-detectoronderzoek geen kolonies werden gevonden. Wel was er blijkens een vondst van twee juveniele dieren een kraamkolonie aanwezig in het Oosterpark in Amsterdam, en waren vooral in het najaar ook elders in Amsterdam, onder meer in de tuin van Artis en op de Oude Oosterbegraafplaats enkele paargroepen aanwezig (Kapteijn 1995). In Badhoevedorp werd op 4 september 1941 een holle wilg gekapt waaruit 30 exemplaren tevoorschijn kwamen. In Leiden werd een kraamkolonie gevonden in juli 1913, in Wassenaar in mei 1915 en in Warmond in juni 1936.

Van Wijngaarden et al. (1971) vermelden voor West-Nederland in de periode 1946 tot en met 1970 slechts drie kraamkolonies in het binnenduingebied bij Haarlem en een in gemeente Den Haag. Uit Zeeland waren behalve enkele vondsten bij Goes geen rosse vleermuizen bekend.

Periode 1: 1986-1993

In de periode 1986 tot en met 1993 is een groot aantal gebiedsinventarisaties met bat-detectors verricht in het kader van de Atlas van Nederlandse Vleermuizen (Limpens et al. 1997). Deze periode vormt de eerste referentieperiode voor de aantalsontwikkeling van de rosse vleermuis in West-Nederland, omdat daarbij voor het eerst op grote schaal geïnventariseerd kon worden met behulp van bat-detectors.

In de periode 1986-1993 is voor West-Nederland een aantalsschatting gedaan van circa 800-1000 volwassen dieren. Deze schatting is gebaseerd op 15 kolonies in Noord-Holland (425-525 dieren), 14 kolonies in Zuid-Holland (300-400 dieren) en twee kolonies in Zeeland (84 dieren). De verspreiding van de kolonies en van foeragerende rosse vleermuizen is weergegeven in Figuur 1. De weergegeven foeragerende dieren zijn door de NDFF gevalideerde waarnemingen.

De 15 kolonies (425-525 dieren) in Noord-Holland werden gevonden in het binnenduingebied tussen Haarlem en Bergen (Kapteijn 1995). Het zwaartepunt van de verspreiding lag in de landgoederen tussen Bloemendaal en Vogelenzang (250-325 dieren). Kolonies werden gevonden op de landgoederen Vogelenzang, Engelse Bos, Leyduin, Berkenrode, Huis te Manpad, Iepenrode, Groenendaal, Elswout, Bloemendaalse Bos, Nova Zembla (Duin en Kruidberg) en Velserbeek, Heiloo (Heilooër bos) en Heemskerk (Marquette). De meest noordelijke zomerverblijfplaatsen werden gevonden in Bergen (Oude Hof en Bergerbos). Een simultaantelling in 1994 leverde tussen Schoorl en Heiloo een aantal op van 125 uitvliegers.

In Zuid-Holland werden 14 kolonies (300-400 dieren) gevonden in het binnenduingebied van Zuid-Holland tussen Den Haag en Noordwijkerhout (Mostert 1990b, 1991a, 1993, Van der Kuil et al. 1996). In deze periode werden in de meeste van deze kolonies enkele dieren afgevangen om de determinatie te bevestigen (in verband met uitsluiting van bosvleermuis) en het geslacht te bepalen.

Kraamkolonies werden aangetroffen in het binnenduingebied tussen Den Haag en Wassenaar (acht kolonies met 130-150 volwassen dieren), Ockenburgh (40-50 dieren), Berbice bij Voorschoten (20 dieren) en Keukenhofbos (Houwelingen & Hassefras 1996 en Kosterman 1998, beide in de jaren 1994-1997).

Op meer dan de helft van de andere landgoederen werden ondanks intensieve inventarisaties geen kolonies van deze soort aangetroffen (Tabel 1, Appendix). Enkele potentieel geschikte landgoederen waren afgesloten voor publiek en daarom niet toegankelijk voor onderzoek.

In Zeeland werden uitsluitend kolonies gevonden in Zeeuws-Vlaanderen, en wel op landgoed Elderschans bij Aardenburg (28 volwassen dieren) en langs de Damse Vaart bij Sluis (16 dieren). Het bosgebied ten zuidoosten van Hulst (Clinge) werd niet onderzocht. In de geschikt ogende binnenduingebieden van de Zeeuwse Eilanden werden geen aanwijzingen voor de aanwezigheid van de rosse vleermuis gevonden (Twisk 1989, Mostert 1989, 1991b, Bekker & Mostert 1995).

Periode 2: 1998-2002

In de periode 1998-2002 is een beperkt aantal tellingen uitgevoerd, waardoor een vergelijking met eerdere en latere jaren niet goed mogelijk is. Toch zijn deze tellingen interessant omdat er nieuwe vestigingen van rosse vleermuizen werden gevonden in een aantal gebieden waar in de periode 1987-1993 niets was gevonden.

Figuur 1. De verspreiding van de rosse vleermuis in West-Nederland in de jaren 1986-1993.
Figure 1. The distribution of noctules (bats and colonies) recorded between 1986 and 1993.

Figuur 2. De verspreiding van de rosse vleermuis in West-Nederland in de jaren 2013-2018.
Figure 2. The distribution of noctules (bats and colonies) recorded between 2013 and 2018.

Tabel 1. Samenvattend overzicht van uitvliegers en kolonies van rosse vleermuizen op landgoederen en in bossen in West-Nederland (1986-1993, 1998-2002 en 2013-2018).

Table 1. Overview of counted emerging bats (uitvliegers) and colonies (kolonies) in estates and forests in the west of the Netherlands in three monitoring periodes between 1986 and 2018.

	Periode 1: 1986-1993		Periode 2: 1998-2002		Periode 3: 2013-2018	
	Uitvliegers	Kolonies	Uitvliegers	Kolonies	Uitvliegers	Kolonies
Noord-Holland (noord van Noordzee-kanaal)	175-200	6	>200	>3	310-320	12-13
Noord-Holland (zuid van Noordzeekanaal)	250-325	9	>100-450	>4	600-700	15-17
Zuid-Holland (vastelands binnenduinen)	300-400	14	535	22	1350-1450	40-44
Zuid-Holland (Rijswijk-R'dam-Zoetermeer)	0	0	65	3	341	10
Zuid-Holland (voormalige eilanden)	0	0	0	0	25	1
Zeeland	84	2	?	?	0	0
Totaal	800-1000	31	900-1250	>32	2600-2850	78-85

In Noord-Holland werden op landgoederen bij Heemstede kolonies van rosse vleermuizen gevonden in het Engelse Bos, Iepenrode en Leyduin (Haarsma 2000). Op het landgoed Marquette werd een kolonie gevonden met 57 uitvliegers en in het Heilooër Bos ging het om twee kolonies, zonder opgave van aantallen. Van een aantal andere landgoederen zijn in deze periode geen goede tellingen van kolonies van de rosse vleermuis uitgevoerd, waardoor aantalsschattingen voor deze periode nogal uiteenlopen.

In Zuid-Holland werden in 2001 in totaal 50 landgoederen in het binnenduingebied tussen Den Haag en Noordwijkerhout onderzocht op het voorkomen van rosse vleermuizen. Er werden op 18 landgoederen in totaal 30 verblijfplaatsen opgespoord (Haarsma 2001); 24 daarvan zaten in eiken en zes in beuken. De verblijfplaatsen bevonden zich op hoogtes variërend van 5-13 meter. Het aantal dieren varieerde van 9 tot 90. De populatiegrootte in de binnenduinrand tussen Den Haag en Noordwijkerhout werd geschat op 600 dieren, wat aanzienlijk meer is dan de 300-400 dieren in de periode 1986-1993.

In Oegstgeest werden voor het eerst kolonies van rosse vleermuizen gevonden in het Bos van Wijckersloot en Oud-Poelgeest, landgoederen waar eerder geen verblijfplaatsen aanwezig waren (Mostert 1990a, Van Meurs 1999). Op de landgoederen in Rijswijk werd in 1999 voor het eerst een grote kolonie met 60 uitvliegers gevonden in een oude eik en in het Keukenhofbos werden drie kraamkolonies gevonden met in totaal 89 uitvliegers (Kosterman 1998).

Periode 3: 2013-2018

Aantalsschattingen voor West-Nederland in de periode 2013-2018 komen uit op circa 2600-2850 dieren in 75-85 kraamkolonies. Deze schatting is gebaseerd op 27-30 kolonies met 910-1020 dieren in Noord-Holland. In Zuid-Holland gaat het om 51-58 kolonies met een totaal van 1600-1800 dieren. In Zeeland zijn na 1988 geen kolonies van de rosse vleermuis meer bekend. De kolonies en de (gevalideerde) foeragerende rosse vleermuizen in West-Nederland in de jaren 2013-2018 staan weergegeven in Figuur 2.

Noord-Holland

In de periode 2013 tot en met 2018 is er in Noord-Holland niet overal systematisch gezocht naar kolonies en andere verblijfplaatsen. Voor een aantalsbepaling is het daarom

noodzakelijk om van enige schattingen uit te gaan. De populatie wordt op 910 tot 1020 dieren geschat, verdeeld over 15-17 kolonies (600-700 dieren) ten zuiden en 12-13 kolonies (310-320 dieren) ten noorden van het Noordzeekanaal.

Ten zuiden van het Noordzeekanaal werd een kolonieboom gevonden in Duin en Kruidberg met 157 uitvliegers (Kooij et al. 2013). Vanuit Schapenduinen en het Bloemendaalse Bos werden in de avond vliegroutes van tientallen rosse vleermuizen richting het duingebied vastgesteld waarbij aannemelijk was dat deze afkomstig zijn van kolonies. Dit geldt ook voor landgoed Velserbeek bij Driehuis (J. Wondergem, mondelinge mededeling). In de Haarlemmerhout werden in 2015 twee kolonies gevonden in een eik en een beuk, een telling van uitvliegers is niet bekend. In het Amsterdamse Bos werd in mei 2017 een kolonie met 47 uitvliegers geteld.

Ten noorden van het Noordzeekanaal werden kraamkolonies aangetroffen in het Heilooërbos, het Alkmaarderhout, bij Schoorl, en in het Wildrijk bij St. Maartenszee. Op landgoed Maquette en in het Oude Hof bij Bergen konden echter geen van de kolonies worden teruggevonden die bekend waren uit respectievelijk de perioden 1 en 2 en periode 1.

Zuid-Holland

In de periode 2013-2018 werden vrijwel alle potentieel geschikte landgoederen systematisch onderzocht op het voorkomen van rosse vleermuizen. De inventarisaties van de landgoederen tussen Den Haag, Wassenaar, Leiden en Oegstgeest werden samengevat (Mostert 2016, Mostert & van der Kuil 2018), aangevuld met gegevens uit een onderzoek naar de validatie van het vleermuisprotocol (Lips 2014).

Van de rosse vleermuis werden in deze periode in totaal 51 kraamkolonies aangetroffen, het merendeel in oude eiken en beuken. Er werden in totaal ca. 1700 uitvliegers geteld. De grootste van deze kolonies bevond zich op landgoed Zuydwijk (112 dieren).

Een klein aantal potentieel geschikte landgoederen kon niet worden geïnventariseerd, omdat er geen toestemming werd verkregen. Dit geldt onder meer voor de Horsten en Duindigt bij Wassenaar en Oosterhout bij Warmond. In deze gebieden zijn ongetwijfeld kolonies rosse vleermuizen aanwezig, zoals bij de Horsten ook in eerdere jaren werd geconstateerd. Het werkelijke aantal rosse vleermuizen zal dus naar verwachting wat hoger liggen (naar schatting ca. 55 kolonies met ruim 1800 dieren).

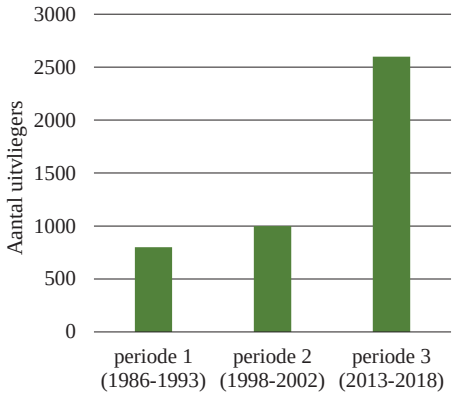
Zeeland

In Zeeuws-Vlaanderen werden ondanks diverse onderzoeken in 2017 geen kolonies of andere verblijfplaatsen van rosse vleermuizen meer gevonden op de eerder bekende locaties Elderschans en Sluis. Ook in andere potentieel geschikte binnenduinbossen op de Zeeuwse Eilanden, zoals het Slotbos te Haamstede op Schouwen-Duiveland en de Manteling, Oranjezon en het Veerse Bos op Walcheren werden geen nieuwe waarnemingen of vestigingen van rosse vleermuizen vastgesteld.

Samengevat vertonen de aantallen uitvliegende rosse vleermuizen in West-Nederland over de perioden 1-3 een afgetekende stijging. De verschillen van de aantallen tussen de perioden 1-2 ($P<<0{,}001$), 2-3 ($P<<0{,}001$) en ook 1-3 ($P<<0{,}001$) zijn significant (Figuur 3). De aantallen kolonies namen ook toe, zij het dat alleen de verschillen tussen periode 1-3 ($P<<0{,}001$) en 2-3 ($P<<0{,}001$) significant zijn (Figuur 4).

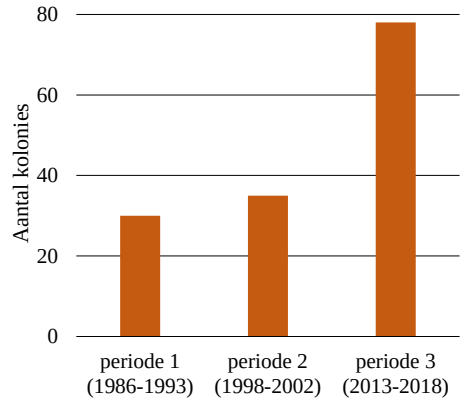
Uitbreidingen in Noord-Holland in 2013-2018

Hoewel in Noord-Holland niet overal systematisch is gezocht naar kolonies in de jaren 2013-2018, zijn er duidelijke uitbreidingen van het leefgebied van de rosse vleermuis geconstateerd, in vergelijking met voorgaande perioden



Figuur 3. Aantal getelde uitvliegende rosse vleermuizen in de drie onderscheiden periodes in West-Nederland (details: zie Appendix).

Figure 3. Number of emerging noctules counted in three monitoring period in the west of the Netherlands.



Figuur 4. Aantal kolonies van de rosse vleermuis in drie perioden in West-Nederland (details: zie Appendix).

Figure 4. Number of maternity colonies counted in three monitoring periods in the west of the Netherlands.

(vergelijk Figuur 1 met Figuur 2). Het Heilooerbos tussen Alkmaar en Heiloo is een van de kerngebieden ten noorden van het Noordzeekanaal. De populatie is hier gegroeid van 60-70 dieren in de periode 1986-1993 naar 220 dieren in 2006. In 2011 werd tevens voor het eerst een kraamkolonie gevonden in het nabijgelegen Alkmaarderhout (Witte 2016). In 2017 werd een deel van dit bos, het Westerhout, geïnventariseerd en werden drie koloniebomen gevonden met tenminste 20 dieren. Andere nieuwe vestigingen zijn gevonden in het duingebied bij Schoorl, in de Alkmaarderhout, 't Zand en ook kleine verblijfplaatsen in het Robbenoordbos en Dijkgatsbos bij Den Oever. De kolonie ten noorden van Schoorl werd bij toeval gevonden in augustus 2011 en het bleek hier om een kraamkolonie te gaan van 27 dieren.

In juni 2016 werd in Het Wildrijk bij St. Maartenszee een kolonie rosse vleermuizen met 29 uitvliegers gevonden in een abeel (van den Tempel 2016). Aan de kolonievondst in Het Wildrijk gingen meldingen vooraf van paarplaatsen in vogelnestkasten in 2013 en 2015. De locatie ligt 20 km noordelijker dan de meest noordelijke melding in de jaren 1990 in Bergen (Kapteijn 1995) en 10 km noordelijker dan de kolonievondst in 2011 bij Schoorl. Daarnaast is de rosse vleermuis aangetroffen in vleermuiskasten in de bossen bij Den Oever (J. Boshamer, mondelinge mededeling).

In het Amsterdamse Bos, ten zuiden van het Noordzeekanaal, werd in 2014 voor het eerst in een kraamkolonie gevonden. Mogelijk was deze kolonie al enige jaren aanwezig aangezien er steeds meer foeragerende rosse vleermuizen werden gehoord. In mei 2017 werden hier 47 uitvliegers geteld.

In de Haarlemmerhout werden sinds een lange periode van afwezigheid weer een grote kraamkolonie en meerdere verblijfplaatsen teruggevonden. Ook in de Schapenduinen werden aanwijzingen gevonden voor een kraamkolonie die hier nog niet eerder was aangetroffen.

Bij de vestiging van kolonies in nieuwe gebieden is door diverse waarnemers (mondelinge mededelingen Anton van Meurs en Rudy van der Kuil) geconstateerd dat deze vooraf wordt gegaan door waarnemingen van een of enkele foeragerende dieren. Vervolgens vindt vestiging plaats in verblijfplaatsen van een of enkele dieren en dan pas de uiteindelijke vestiging van een kraamkolonie. Het proces van verkenning en vervolgens definitieve vestiging kan in sommige gevallen jaren duren (Tabel 2).

Tabel 2. Overzicht van nieuwe vestigingen van 1986-2018 met vermelding van resp. eerste onderzoek, eerste waarneming, eerste vondst van een verblijfplaats en eerste vondst van een kolonie (>10 dieren).
Table 2. Years of first recording of noctules (waargenomen), roosts (verblijfplaats) and maternity colonies (kolonies) (>ten bats) in a number of estates and forests in the west of the Netherlands between 1986 and 2018.

	Onderzoek sinds	Waargenomen	Eerste verblijf-plaats	Eerste kolonie
Amsterdamse Bos	1986	1988	2015	2015
Alkmaarderhout	1986	?	?	2011
Schoorl	1990	?	?	2011
Wildrijk, St. Maartenszee	1990	?	2013	2016
Dijkgatsbos, Den Oever	1990	?	2016	-
Kralingse Bos, Rotterdam	1985	1985	1985	2010
De Tempel, Rotterdam	1986	1998	2013	2016
Schiebroekse Park, Schiedam	1990	2004	2014	2016
Staelduinse Bos, Gravenzande	1986	2008	2010	2012
Voorne	1992	2008	2010	2010
Van Tuyll Park, Zoetermeer	1988	2002	2017	2017

Uitbreidingen in de omgeving van Rotterdam 2013-2018

In de jaren 1990 werden in het Kralingse Bos in Rotterdam af en toe enkele rosse vleermuizen in het najaar gevonden in vleermuiskasten (P.H.C. Lina, mondelinge mededeling). Tijdens een uitgebreide inventarisatie in 1993 werden hier echter geen verblijfplaatsen aangetroffen en alleen enkele foeragerende dieren gehoord (Wondergem & Mostert 1993). Tijdens een inventarisatie in 2010 werden meerdere kraamkolonies gevonden in het Kralingse Bos, waar in totaal 70 dieren uitvlogen. In de daaropvolgende jaren werden nog meer nieuwe verblijfplaatsen ontdekt, maar er heeft geen simultaantelling meer plaatsgevonden (G. Bakker, mondelinge mededeling).

Op het nabijgelegen landgoedje Buitenplaats de Tempel werd in augustus 2013 voor het eerst een klein groepje rosse vleermuizen gevonden in enkele oude eiken (Mostert 2013). In 2016 en 2017 werd hier ook een eerste kraamkolonie aangetroffen. In het Schiebroekse Park werden in april 2014 20 rosse vleermuizen aangetroffen in vleermuiskasten.

Het Staelduinse Bos ligt geïsoleerd in het Westland bij 's-Gravenzande. Tijdens inventarisaties in de jaren 1980 en 1990 werden hier nooit rosse vleermuizen waargenomen en ook niet in 2010 toen het bosgebied uitgebreid werd geïnventariseerd. De eerste aanwijzingen voor bewoning kwamen in 2013 toen bij de Oranjeplassen bij Maassluis tientallen langsvliegende rosse vleermuizen werden opgemerkt uit de richting van het bos. In 2017 werd in het Staelduinse Bos voor het eerst een kraamkolonie gevonden, met 69 uitvliegers.

Tijdens een inventarisatie van vleermuizen in het binnenduingebied van Voorne werden in de zomer van 2012 voor het eerst verschillende verblijfplaatsen gevonden op het landgoed Mildenburg (Mostert 2012a). Het ging om een kraamkolonie van 28 dieren in een oude linde en om twee verblijfplaatsen van ca. drie dieren (vermoedelijk mannetjes) in oude eiken. De dieren vlogen zowel naar het Brielse Meer als naar het binnenduingebied van Voorne om er te foerageren.

Op 19 sep 2017 werd in de omgeving van Zoetermeer een kolonie van 27 dieren gevonden in een oud spechtengat in een dode tak van een populier (G. Bakker, mondelinge mededeling).

Tabel 3. Uitvliegers en (tussen haakjes) het aantal kolonies van rosse vleermuizen in vier perioden tussen 1986 en 2018 in de omgeving van Den Haag, Rijswijk en Voorburg.
Table 3. Number of emerging noctules and (in brackets) colonies in four monitoring periods between 1986 and 2018 in the Den Haag-Rijswijk-Voorburg area.

	Periode A 1986-1993	Periode B 1999-2002	Periode C 2008-2012	Periode D 2015-2018
Den Haag				
Ockenburg-Hyacintenbos	50 (2)	24 (1)	163 (5)	92 (5)
Meer & Bosch	-	-	60 (1)	92 (5)
Zorgvliet	-	-	-	37 (1)
Scheveningse Bosjes	-	-	-	35 (1)
Arendsdorp-Oostduin	-	-	25 (1)	-
Haagse Bos	-	-	77 (3)	27 (1)
Clingendael	-	55 (1)	99 (3)	103 (3)
Marlot/Reigersbergen	-	-	-	81 (1)
Voorlinden	32 (1)	31 (1)	18 (1)	27 (1)
Rijswijk				
Voordes	-	65 (1)	32 (2)	80 (2)
Te Werve	-	-	21 (1)	28 (1)
Dom Bosco	-	-	-	6
Voorburg				
Vredenoord	-	-	-	5
Arentsburg (Hoekenburg)	-	>4	-	-
Vreugd & Rust	-	-	3	8
Aantal kolonies	3	4	17	24
Totaal	82	175	495	605

Ontwikkelingen in Den Haag, Rijswijk en Voorburg in 1986-2018

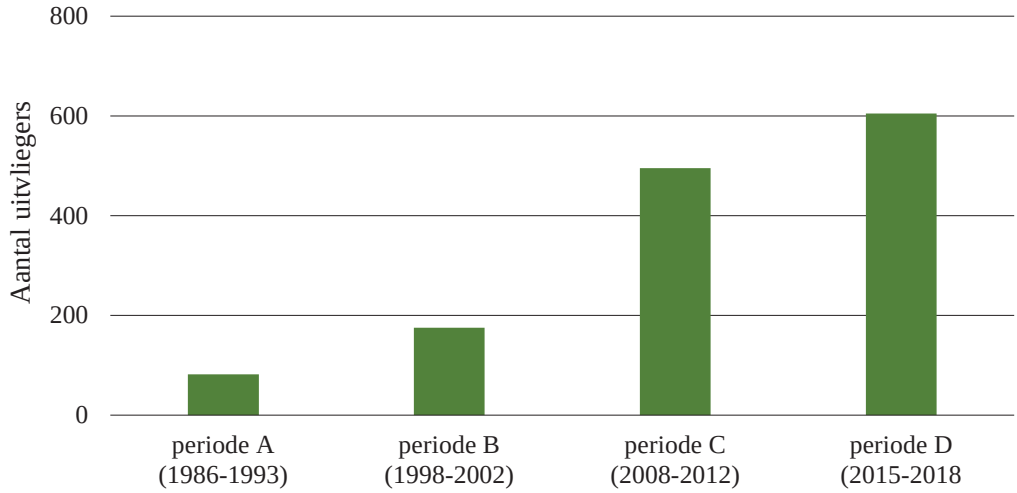
De omgeving van Den Haag, Rijswijk en Voorburg is sinds 1986 periodiek intensief onderzocht op boombewonende vleermuizen (Mostert 1993, 2012b, 2020). Er zijn vier perioden (A-D) te onderscheiden waarin een aantal bossen en landgoederen werden geïnventariseerd (Tabel 3).

Samengevat vertonen de aantallen uitvliegende rosse vleermuizen in Den Haag, Rijswijk en Voorburg over de perioden A tot en met D steeds een stijging. De significante verschillen tussen de aantallen uitvliegers over de perioden A-B (Chikwadraattoets: P<<0,001), A-C (P <<0,001), A-D (P <<0,001), B-C (P <<0,001), B-D (P <<0,001) en C-D (P <<0,001) geven aan dat de aantallen toenemen (Figuur 5). Ook de aantallen kolonies over de perioden A tot en met D nemen toe, met significante verschillen tussen de perioden A-C (P <<0,005), A-D (P <<0,001), B-C (P <<0,05) en B-D (P <<0,001) (Figuur 6).

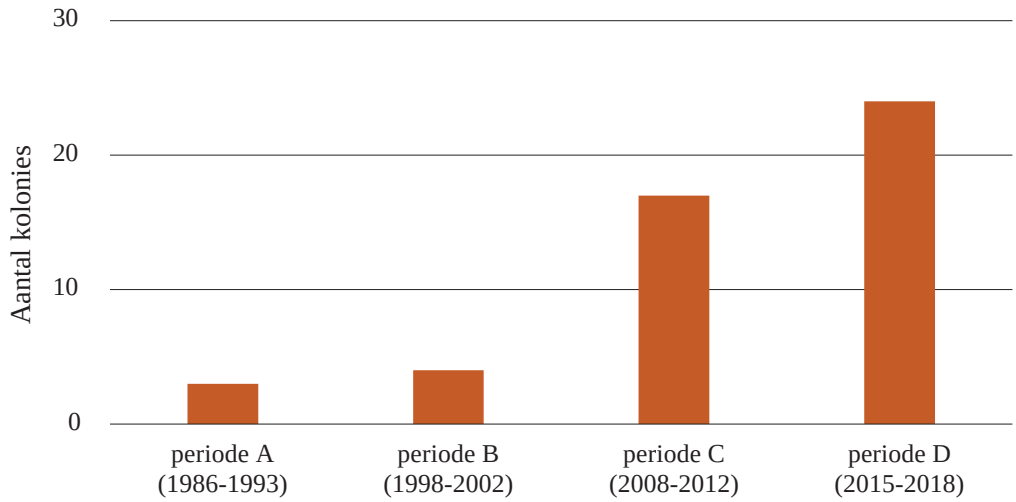
Toename aantal foeragerende dieren

In de periode 1986-1993 werden in Zuid-Holland in het kader van de eerste landelijke zoogdierenatlas (Limpens et al. 1997) voor het eerst vleermuizen geïnventariseerd met bat-detectors (Figuur 1).

De meeste waarnemingen van foeragerende dieren werden verricht in het binnenduingebied tussen Den Haag en Vogelenzang. Daarnaast zijn er ook relatief veel waarnemingen gedaan boven de aangrenzende plassen in de



Figuur 5. Aantal uitvliegende rosse vleermuizen per periode in Den Haag en omstreken (details: zie Appendix).
Figure 5. Number of emerging noctules counted in four monitoring periods in the The Hague area (see Appendix for details).



Figuur 6. Aantal gevonden kolonies van de rosse vleermuis voor vier perioden in Den Haag en omstreken (details: zie Appendix).
Figure 6. Number of emerging noctules counted in four monitoring periods in the The Hague area (see Appendix for details).

omgeving van Delft en Zoetermeer. Een klein aantal waarnemingen betreft foeragerende dieren langs de noordrand van Rotterdam, in de omgeving van Alphen aan de Rijn en rond de Nieuwkoopse Plassen.

In de periode voorafgaand aan de tweede landelijke zoogdierenatlas (Broekhuizen et al. 2016) werden in Zuid-Holland opnieuw inventarisaties per regio op vergelijkbare wijze uitgevoerd om foeragerende vleermuizen te inventariseren (Figuur 2).

Wanneer de kaarten uit beide perioden met

elkaar worden vergeleken is het opvallend in hoeveel nieuwe gebieden rosse vleermuizen zijn waargenomen. Er zijn relatief veel gebieden met waarnemingen waar de soort voor 2000 nauwelijks of helemaal niet werd waargenomen, zoals Midden-Delfland, de omgeving van Rotterdam, omgeving Zoetermeer, Reeuwijkse Plassen en op Voorne.

In de periode 1986-1993 bedraagt het aantal km-hokken waar rosse vleermuizen zijn gehoord in West-Nederland 293 (bron: NDFF / Zoogdiervereniging). In de periode 2013-2018 bedraagt dit aantal 944 (bron: NDFF / Zoogdiervereniging); het verschil tussen deze perioden is significant ($P<<0{,}001$).

Conclusies en discussie

Uit bovenstaande gegevens blijkt dat de rosse vleermuis sinds de jaren 1980 duidelijk is toegenomen in West-Nederland. Deze toename blijkt uit een groter aantal gevonden kolonies (bij een vergelijkbare telmethode), een groter aantal uitvliegende dieren en uit een veel groter aantal foeragerende dieren, onder meer boven een groot aantal plassen en watergangen.

Uitgaande van de kolonietellingen voor 15 juli (voordat jonge dieren meevliegen) kan de huidige populatie in West-Nederland op 2600-2850 volwassen vrouwtjes worden geschat, waarvan 1700-1800 in Zuid-Holland en 910-1020 in Noord-Holland (zonder Het Gooi). Dat is ruim drie keer zoveel als in de periode 1986-1993 toen de populatie op 800-1000 volwassen vrouwtjes werd geschat.

De uitbreiding van het door rosse vleermuizen bewoonde leefgebied is vooral goed zichtbaar in gebieden waar de soort tot voor kort ontbrak, zoals in de omgeving van Zoetermeer en Rotterdam, in het binnenduingebied van Voorne en boven het Noordzeekanaal (Figuren 1 en 2). Maar ook in gebieden waar al veel langer populaties bekend zijn, zoals de omgeving van Den Haag, Wassenaar en Leiden, is meer geschikt habitat beschikbaar gekomen voor de rosse vleermuis (zie verderop in de discussie).

De populatie is in alle deelgebieden toegenomen, met uitzondering van Zeeland. Op de Zeeuwse Eilanden zijn tot op heden nog geen vestigingen geconstateerd. De twee kleine populaties in het grensgebied van Zeeuws-Vlaanderen, welke in de jaren 1980 werden aangetroffen, zijn verdwenen, terwijl in het bosgebied bij Clinge (Zeeuws-Vlaanderen) en bij Reimerswaal (Zuid-Beveland) alleen foeragerende dieren zijn aangetroffen. Er is in het bosgebied bij Clinge niet systematisch naar kolonies gezocht.

In de perioden 1998-2002 en 2013-2018 zijn er hogere aantallen in de verschillende koloniebomen geteld dan in de periode 1986-1993 (zie ook de Appendix).

Ook het aantal kilometerhokken waarin de soort is aangetroffen is toegenomen: 944 kilometerhokken in 2013-2018 en 293 in 1998-2002 (zie ook Figuren 1 en 2).

Mogelijke oorzaken

Sinds de jaren 1980 is er in West-Nederland een toename gaande, zowel in het aantal kolonies van de rosse vleermuis als van de koloniegroottes. Deze toename hangt vermoedelijk samen met zowel een algehele veroudering van het landgoederenareaal als met een meer ecologisch beheer van deze gebieden, waar ook andere bossoorten van profiteren. Daarnaast speelt een uitbreiding van het bosareaal, meer specifiek van het aantal recreatiebossen, waarvan een groot deel in de jaren 1960 en 1970 werd aangeplant, een rol. De aanleg van recreatieplassen heeft de foerageermogelijkheden voor rosse vleermuizen verbeterd.

Verreweg de belangrijkste leverancier van geschikte boomholten voor kolonies rosse vleermuizen is de grote bonte specht (*Dendrocopos major*). Deze soort is in Nederland sinds de jaren 1970 sterk in aantal toegenomen (Vogelwerkgroep Avifauna West-Nederland 1981, SOVON Vogelonderzoek 2018). Zo is het aantal broedparen in Zuid-Holland toegeno-

men van 330-390 paar in de jaren 1970 naar 4460-6000 paar in 2018-2020.

Ouderdom bossen

Het Nederlandse bos wordt sinds de Tweede Wereldoorlog steeds ouder en bevat steeds meer dikke bomen (Schelhaas et al. 2022). De oudste bossen bestaan uit inlandse eiken en beuk. Een belangrijk deel hiervan is eigendom van natuurbeschermende organisaties, landgoederen en overige particuliere organisaties (Schelhaas et al. 2014). Tijdens de laatste decennia van de vorige eeuw verschoof het bosgebruik van houtproductie als primaire bosfunctie naar meervoudig gebruik, waarbij meer belangstelling ontstond voor bos als drager van biodiversiteit (Mohren et al. 2021). Sinds 1982 nam de oppervlakte bos in Nederland toe met gemiddeld 1434 ha per jaar. De grootste bosuitbreiding in Nederland vond plaats in Zuid-Holland (Dirkse et al. 2003). In de periode 1986-1993 waren kolonies vrijwel geheel beperkt tot oude eiken en beuken op de oude landgoederen in het binnenduingebied van Zuid-Holland en Noord-Holland.

In het algemeen worden vooral bomen van 80 jaar en ouder gebruikt door boombewonende vleermuizen (Mostert 1993). Door de ouder wordende bossen en het meer ecologisch gerichte beheer, waardoor meer gaten, spleten en holten in bomen beschikbaar komen, ontstaat er een steeds groter en dichter netwerk van bossen met voldoende oude bomen en geschikte boomholten die plaats bieden aan vleermuizen.

Bosgebieden buiten het binnenduingebied, zoals het Amsterdamse Bos, het Kralingse Bos in Rotterdam en de bossen in Wieringen in de Kop van Noord-Holland, waren in de jaren 1980 vermoedelijk nog te jong voor vestiging van rosse vleermuizen. De aanleg van het Amsterdamse Bos begon in 1934 en het Kralingse Bos is ook aangelegd rond de jaren dertig (eerste aanplant in 1928). Kolonies zijn hier voor het eerst gemeld in resp. 2010 en 2015 (Tabel 2). Anno 2018 zijn de bomen ouder geworden en zijn aldaar, maar ook in het Robbenoordbos en het Dijkgatsbos, beide bij Den Oever, de eerste rosse vleermuizen vastgesteld in vleermuiskasten. Rosse vleermuizen lijken zich in deze bosgebieden te hebben gevestigd nadat de bomen ongeveer 70-80 jaar geleden geplant werden.

In dat opzicht is het interessant om na te gaan hoe de kolonisatie van de bossen in Flevoland verloopt. De polders zijn in 1942 (Noordoostpolder), 1957 (Oostelijk Flevoland) en 1968 (Zuidelijk Flevoland) drooggelegd en enkele jaren later gedeeltelijk aangeplant met bos. De oudste bossen hebben momenteel een leeftijd van circa 60 jaar. Reinhold et al. (2007) vonden in de jaren 2005 tot en met 2007 de eerste paarplaatsen van rosse vleermuizen. Verblijfplaatsen werden toen vermoed op grond van vroeg in de avond vliegende dieren, maar niet gevonden. Vanaf 2022 zijn kraamkolonies gevonden in het Kraggenbos in de Noordoostpolder, niet ver van al langer bekende kolonieplaatsen in Noordwest-Overijssel (Mostert et al. 1989). De verwachting is dat de bossen in de Flevopolders binnen een periode van 10 tot 20 jaar verder worden gekoloniseerd door rosse vleermuizen. De in de afgelopen decennia toegenomen aanwezigheid van de grote bonte specht in Flevoland (https://www.vogelatlas.nl/atlas/soorten/soort/8760) lijkt in dat opzicht gunstig.

Uitbreiding bosareaal en foerageergebieden

Sinds de jaren 1970 zijn in West-Nederland veel recreatiegebieden aangelegd. Grotendeels zijn dit bossen op klei en veen. Veelal bestaan deze bossen uit wilgen (*Salix* spp.), populieren (*Populus* spp.), essen (*Fraxinus excelsior*) en iepen (*Ulmus* spp.), maar in toenemende mate ook uit eiken. Veel van deze bossen zijn, vanwege het kleine aandeel beuken en eiken (vooral beperkt tot zandgronden), in eerste instantie niet geschikt om uit te groeien tot

bossen waar kolonies van boombewonende vleermuizen zijn te verwachten. Toch lijken in de loop van de decennia steeds meer van deze bossen geschikter te zijn geworden voor vestiging van rosse vleermuizen. Dit speelt vooral in gebieden waar meer boomsoorten een zekere ouderdom hebben bereikt.

Hierbij is het ook opvallend dat een recent aantal gevonden kolonies op nieuwe locaties zich, behalve in eik en beuk, die lang het beeld bepaalden, ook in andere boomsoorten hebben gevestigd, met name in es, maar ook in populier, abeel (*Populus* spp.), wilg en linde (*Tilia* spp.) en zelfs in esdoorn (*Acer* spp.). Het toegenomen aantal oudere bomen van deze soorten zal hierbij zeker een rol spelen. Veel rosse vleermuizen maken daarbij gebruik van verlaten nestholten van de grote bonte specht, zoals gezegd een belangrijke leverancier van nestholten voor boombewonende vleermuizen. Deze vogelsoort is sinds de jaren zeventig fors in aantal toegenomen in Nederland (10.500-17.000 paar in de jaren 1970 en 97.000-130.000 in de jaren 2018-2020) en komt inmiddels talrijk voor, feitelijk overal waar sprake is van enige vorm van bos (SOVON 2018).

Rosse vleermuizen jagen bij voorkeur boven grote watergangen en plassen. In de afgelopen decennia zijn veel nieuwe recreatiegebieden met plassen en vijvers, plassen en waterbergingsgebieden aangelegd in West-Nederland. Vooral in en om de Randstad in Zuid-Holland en in Noord-Holland ten zuiden van het Noordzeekanaal gaat het om vele tientallen nieuwe plassen die vooral in de jaren 1970 en 1980 werden aangelegd. Veel van deze plassen zijn erg in trek bij rosse vleermuizen als foerageergebied. In gebieden als de Starrevaart, de Vlietlanden bij Voorschoten, Valkenburgse Meer, Dobbeplas, Delftse Hout, Noord-Aa, Benthuizerplas, Voorhovense Plas en Floraplas, Plas van Poot bij Zoetermeer, Oranjeplassen en Krabbeplas bij Vlaardingen, Toolerburgerplas en Haarlemmermeerse plas in de Haarlemmermeerpolder werden vele tientallen jagende exemplaren vastgesteld. In de vele recreatiegebieden zijn ook kleinere plassen en kreken verschenen die een bijdrage leveren. Ook rond de oudere plassen als Kagerplassen, Braassemermeer, Nieuwkoopse Plassen, Rottemeren en Westeinderplassen wordt veel gefoerageerd. De aanleg van nieuwe moerassen en waterbergingsgebieden zoals in de Zuidplaspolder bij Zevenhuizen en de Nieuwe Driemanspolder ten westen van Zoetermeer speelt eveneens een gunstige rol.

Betrouwbaarheid aantalsschattingen

Kolonies worden vaak gevonden langs bosranden en, vooral, in lanen (Kapteijn 1995, Boonman 2000). Kolonies van de rosse vleermuis zijn relatief eenvoudig te vinden. Hierdoor is de kans naar verwachting niet groot dat forse kolonies over het hoofd zijn gezien. Desalniettemin geven de tellingen van uitvliegende dieren geen volledig beeld van het aantal rosse vleermuizen in een gebied, en moeten ze met een zeker voorbehoud worden bezien. Hiervoor zijn verschillende redenen. Het aantal getelde uitvliegers hoeft niet overeen te stemmen met het aantal vleermuizen dat daadwerkelijk in de boomholte aanwezig is. Bij slecht weer, of om onbekende redenen, kan een deel van de dieren, of kunnen zelfs alle dieren, in een verblijfplaats niet blijken uit te vliegen. Dieren blijven dan hoorbaar in de boomholte en zijn soms ook te zien. Het aantal getelde dieren dient dan ook als een minimum aantal te worden opgevat. Verder is het aannemelijk dat niet alle door vleermuizen bezette bomen worden gevonden en geteld. Tenslotte kan er ook nog verhuizing plaatsvinden tussen boomholten, waardoor er sprake kan zijn van dubbeltellingen of waardoor juist dieren worden gemist .

De betrouwbaarheid van telresultaten zou kunnen worden verbeterd door alleen met gunstig weer tellingen uit te voeren, en vooral door een systematische simultaantelling te verrichten waarbij alle bekende bezette vleermuizenbomen in een betreffend landgoed of

deelgebied tegelijkertijd worden geteld.

Aangezien in de drie in dit artikel onderscheiden perioden in vooral Zuid-Holland en Zeeland door grotendeels dezelfde waarnemers op dezelfde wijze is geïnventariseerd, verwachten we geen effect op de resultaten in deze provincies op grond van de gebruikte methode.

Achteruitgang voor 1980

Hoewel de houtkap tijdens de Tweede Wereldoorlog ongetwijfeld een groot effect heeft gehad op de populaties van boombewonende vleermuizen, verklaart het verlies van oude bomen en boomholten wellicht niet helemaal de enorme achteruitgang in, bijvoorbeeld, de omgeving van Haarlem (voormalig onderzoeksgebied van L. Bels) in de jaren 1960. Verstedelijking, met als gevolg areaalverlies door het verdwijnen van bos en oude bomen, verlies van jachtgebieden en doorsnijding van gebieden door wegen, hebben waarschijnlijk ook een rol gespeeld (Kapteijn 1995).

Het Haagse Bos en de naburige Scheveningse Bosjes werden in de Tweede Wereldoorlog op enkele randzones na gekapt (Laan & Sauren 2013, Beekman 2024). Ook in Amsterdam heeft in die tijd grootschalige kap van oude bomen plaatsgevonden. Na de Tweede Wereldoorlog zal ook hier stedelijke uitbreiding effect hebben gehad op de populaties rosse vleermuizen (Kapteijn 1995).

Sluiter & van Heerdt (1966) veronderstelden dat de door hen geconstateerde achteruitgang in de jaren 1960 voornamelijk een gevolg is geweest van het grootschalig kappen van bomen tijdens en kort na de Tweede Wereldoorlog. Toch resteerden er ook in hun tijd hier en daar nog wel lanen en bossen met oude, holle bomen.

Wellicht is onderbelicht gebleven hoe de groot de rol van organochlorides, zoals van DDT en andere gewasbeschermingsmiddelen, is geweest voor de rosse vleermuis. DDT is op grote schaal toegepast in de jaren 1950 en 1960, juist de periode waarin een enorme achteruitgang van de rosse vleermuis (en andere vleermuissoorten) werd opgemerkt. Het gebruik van DDT is in Nederland sinds 1973 verboden. De effecten van DDT door bio-accumulatie op roofvogels en insectenetende vogelsoorten als boerenzwaluwen in de afgelopen decennia, zijn aangetoond (Carson 1962, Newton 2013, Guldemond et al. 2021). Daan (1980) zag aanvankelijk nog geen duidelijk keerpunt in de aantalsontwikkelingen van vleermuizen als gevolg van het verbod op insectenbestrijdingsmiddelen in 1968 (op aldrin en dieldrin) en in 1973 (op DDT). Er is een relatie gelegd tussen DDT- en lindaangebruik en gebouwbewonende soorten als meervleermuis (Voûte 1980) en grootoorvleermuis (Braaksma & van der Drift 1972). Hoewel vanuit Nederland ons geen studies bekend zijn waarin rosse vleermuizen zijn onderzocht op insectenbestrijdingsmiddelen, is door Luftl et al. (2005) deze belasting in de lever van vleermuizen (ook bij rosse vleermuizen) wel aangetoond in andere Europese landen. Insecten kunnen door verwaaiing in laanbomen grenzend aan landbouwpercelen, of boven deze percelen die werden bespoten met DDT, deze pesticiden hebben opgenomen. Deze insecten kunnen ook door (rosse) vleermuizen worden gegeten (Guldemond et al. 2021). In een internationale studie (Bayat et al. 2014) is vastgesteld dat in de perioden 1970-1980 en 1981-2000 het gehalte aan DDT in acht verschillende insectenetende vleermuissoorten, waaronder de in Nederland voorkomende tweekleurige vleermuis (*Vespertilio murinus*) en watervleermuis, sterk is verminderd. Schmidt (1997) ziet het verbod op de distributie van DDT als oorzaak van het regionaal stabiliseren en zelfs toenemen van populaties rosse vleermuizen, die over meer dan 20 jaar zijn gevolgd.

In de Haarlemmerhout en het Groenendaalse Bos bij Heemstede vond omstreeks 1960 een rigoureuze verjonging plaats, waarbij vele bomen van honderden jaren oud werden gekapt. Op andere plekken in deze regio werden lanen helemaal gekapt en ingeplant

met populieren. Een drukke verkeersader verdeelt de Haarlemmerhout nu in tweeën. Toch zijn er tegenwoordig weer voldoende oude holle bomen aanwezig in de omgeving van de bebouwde kom van Heemstede en Haarlem. De open ruimtes in het binnenduingebied zijn echter steeds verder bebouwd geraakt. Desondanks is de rosse vleermuis in recente jaren teruggekeerd naar de Haarlemmerhout, hoewel nog lang niet in de aantallen van tijdens het onderzoek van Bels in de jaren 1930.

Een mogelijke oorzaak van achteruitgang van aantallen rosse vleermuizen als gevolg van uitzonderlijk strenge winters werd eerder naar voren gebracht door Van Wijngaarden en Schuilenburg (1958) en is mogelijk ook een factor die de aantalsontwikkeling van rosse vleermuizen negatief heeft beïnvloed. Door klimaatverandering zijn strenge winterperioden tegenwoordig echter tot een minimum beperkt, waardoor de kans op massale sterfte door lage temperaturen tijdens de winter klein is geworden. Klimaatverandering heeft daardoor mogelijk een gunstig effect op de populaties van de rosse vleermuizen.

Concurrentie met en predatie door andere diersoorten

Concurrentie om boomholten met vogelsoorten, zoals spreeuwen (*Sturnus vulgaris*), kan een effect hebben op het voorkomen van rosse vleermuizen (Mason 1972). De halsbandparkiet (*Psittacula krameri*) kwam in de jaren 1980 in Den Haag en Amsterdam-Haarlem voor het eerst met circa 15 respectievelijk 10 paren tot broeden. Halverwege de jaren 1990 nam de populatie een grote vlucht en momenteel komt de soort in heel de Randstad talrijk voor. Momenteel vindt verdere expansie plaats zowel ten noorden van het Noordzeekanaal als in oostelijke en zuidelijke richting. In 2022 werden 22.000 exemplaren geteld op de bekende slaapplaatsen in de Randstad en is het aantal in 10 jaar tijd bijna verdubbeld (Sovon 2018). In de jaren 2018-2020 werden zowel in Noord- als Zuid-Holland 2500-3000 paar geteld en in Zeeland worden ook steeds vaker zwervende dieren gemeld. De concurrentie tussen halsbandparkieten en rosse vleermuizen kan zich voordoen door directe verstoring of doordat halsbandparkieten boomholtes minder geschikt maken voor de rosse vleermuis door vergroting van de invliegopening en egalisatie van wanden, met als gevolg een minder gunstig microklimaat; de egalisatie van de wanden heeft ook een verlies van wegkruipmogelijkheden tot gevolg (Haarsma & van der Graaf 2013). Door de toename van de aantallen van deze exoot zijn minder lege boomholten beschikbaar, maar het is niet duidelijk in hoeverre dit het leefgebied en de populaties van de rosse vleermuis negatief beïnvloedt. De uitbreiding van deze sterk toegenomen soort kan lokaal een negatief effect hebben op boombewonende vleermuizen, maar lijkt de populatie van rosse vleermuizen vooralsnog niet te deren (Haarsma & van der Graaf 2013).

Predators als uilen of boomvalken (*Falco subbuteo*) spelen een ondergeschikte rol (Bekker & Mostert 1991). Van de recent in West-Nederland verschenen boommarter (*Martes martes*) zijn vooralsnog geen predatiewaarnemingen bekend. Deze predator kan niet door een gat van een grote bonte specht en zal naar verwachting geen grote rol spelen.

De verspreiding en de toename van de boomklever (*Sitta europaea*) in West-Nederland vertonen opvallend grote overeenkomsten met die van de rosse vleermuis. De boomklever lijkt in dat opzicht dezelfde eisen als de rosse vleermuis te stellen aan de ouderdom en grootte van eiken en beuken, en aan het beschikbare areaal aan geschikte bomen, dat tenminste vele tientallen bomen moet zijn (Mostert 1990b, Broekhuizen et al. 1992). In de jaren 1970 kwam de boomklever, een vogelsoort die ook verlaten spechtengaten gebruikt, vooral voor in het binnenduingebied, tussen Vogelenzang en Velsen (in 1975 300 paar) en tussen Den Haag en Leiden (80-125 paar). Vanaf de jaren 1980 breidde de soort zich in noordelijke richting uit langs de binnenduinrand en werden de eerste

paren opgemerkt in het Amsterdamse Bos. In Zuid-Holland heeft de boomklever zich vanaf de jaren 1990 vooral in oostelijke richting uitgebreid en steeds meer bossen rond Rotterdam gekoloniseerd. In 2005 werd de oversteek naar het binnenduingebied van Voorne gemaakt en vanaf 2015 werd ook de Biesbosch gekoloniseerd. In Zeeland was de soort buiten het grensgebied van Zeeuws-Vlaanderen afwezig, maar in de laatste jaren zijn er vestigingen in het duingebied van Schouwen en Walcheren. In de jaren 2013-2018 ging het om 850-1850 paar in Noord-Holland, 340-410 paar in Zuid-Holland en paar 65-85 paar in Zeeland.

Concurrentie tussen de rosse vleermuis en andere boombewonende vogels zoals spechten en kraaiachtigen komt wel voor, maar lijkt beperkt (Bekker & Mostert 1991).

Bedreiging en bescherming

Ondanks het feit dat de rosse vleermuis zich in West-Nederland goed lijkt te handhaven, blijft kap van oude bomen een punt van zorg. Dit omdat er zich concentraties van honderden dieren in een enkele boom kunnen bevinden. Ook tijdens dit onderzoek zijn tussen 2000 en 2018 diverse bekende koloniebomen gekapt terwijl de locaties van de bomen waren aangeduid en in rapporten waren weergegeven (Rudy van der Kuil, mondelinge mededeling).

Tijdens migratie en, in mindere mate, tijdens het foerageren is de rosse vleermuis kwetsbaar voor windturbines op land (Cryan & Barclay 2009) en mogelijk zelfs op zee (Lagerveld & Mostert 2023). Windturbines vormen een toenemende bedreiging door toename van de aantallen en de hoogte van de turbines. Omdat rosse vleermuizen foerageervluchten maken op rotorhoogte en zij daarbij grote afstanden kunnen afleggen, kan de sterfte door windmolens ook effecten hebben als voortplantingsgebieden op grote afstand van windmolens liggen.

Aanbevelingen en toekomstperspectief

Nieuwe systematische gebiedsinventarisaties van rosse vleermuizen in heel Nederland zijn nodig voor toekomstige inschattingen van hun status en bepaling van de benodigde mate van bescherming. In West-Nederland geldt dit vooral voor gebieden die van belang worden geacht voor deze soort maar waar tellingen in recente jaren ontbreken, zoals het Heilooërbos bij Alkmaar en het Kralingse Bos bij Rotterdam. Het Gooi, dat net ten oosten van het in dit artikel behandelde gebied ligt, is met de geconstateerde populatie van 700-975 dieren in de jaren 1986-1993 een belangrijk bolwerk voor deze soort in Nederland: naar verwachting bevindt zich hier 10% van de Nederlandse populatie. Ondanks het veronderstelde landelijke belang van Het Gooi voor de rosse vleermuis, zijn hier na 1993 geen tellingen meer uitgevoerd en is onbekend hoe deze populatie zich heeft ontwikkeld.

Opvallend is dat de aandacht voor boombewonende vleermuizen de afgelopen decennia grotendeels is weggeëbd door de focus op de gebouwbewonende soorten, vanwege juridische zaken met betrekking tot de natuur- en milieuwetgeving (Flora- en Faunawet, Wet Natuurbescherming, Omgevingswet) rond bouwen en isolatie. Hierdoor zijn van veel belangrijke gebieden buiten West-Nederland al decennialang geen gegevens meer voorhanden over de rosse vleermuis. Het is daarom van groot belang dat er nieuwe systematische gebiedsinventarisaties worden uitgevoerd naar rosse vleermuizen in heel Nederland.

In overig Nederland zijn ook de randen van de Veluwe en de Utrechtse Heuvelrug van belang, evenals Noordwest-Overijssel, de omgeving van Groningen-Haren en mogelijk ook de landgoederen ten zuiden van Bergen op Zoom. Het gaat met name om bosgebieden die nabij grote wateren en moerasgebieden liggen. Een inventarisatie van deze gebieden zou niet alleen informatie opleveren over de rosse vleermuis, maar ook over andere boombewonende soorten zoals franjestaart, water-

vleermuis, baardvleermuis, gewone grootoorvleermuis en wellicht nog andere soorten.

Bij toekomstige inventarisaties van deelgebieden is het daarom van groot belang om simultaantellingen te organiseren. In juni dienen dan binnen enkele dagen alle beschikbare landgoederen in de vroege ochtend systematisch te worden afgezocht met bat-detectors. Aanvullend kunnen in de namiddag of vooravond bezoeken worden gebracht om luidruchtige groepen op te sporen. De gevonden kolonies en verblijfplaatsen dienen in de daaropvolgende avond simultaan geteld te worden, waardoor de kans op tussentijdse verplaatsingen zo klein mogelijk blijft.

Het is de vraag of de vastgestelde toename en uitbreiding van de rosse vleermuis ook representatief is voor andere delen van Nederland. Dit ligt niet zomaar voor de hand, om de volgende reden. In West-Nederland zijn zowel het (oude) bosareaal als het aantal watergebieden (vooral in de vorm van recreatieplassen) relatief sterk uitgebreid sinds de jaren 1970. Deze ontwikkelingen hebben in andere delen van Nederland maar beperkt of helemaal niet plaatsgevonden. Daarnaast zijn er landelijke ontwikkelingen, zoals het veranderde bosbeheer, dat sindsdien veel meer is gericht op ecologisch beheer, waarbij veel meer oude en dode bomen langer in stand worden gehouden en waarbij onder meer wordt gestreefd naar meer gemengd bos en een groter aandeel loofbomen. Mede hierdoor nam het areaal oud bos toe.

Of de toename van de aantallen en de uitbreiding van het leefgebied van rosse vleermuizen, zoals deze zich over de perioden 1986-1993 tot 2013-2018 heeft afgetekend, zich gaat voortzetten, zal moeten blijken uit aanvullende recente inventarisaties. De uitkomsten uit de omgeving van Den Haag laten zien dat er eerder sprake is van stabilisatie dan een verdere toename (Mostert & van der Kuil 2024).

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Samenvatting

Het voorkomen van de rosse vleermuis in het westen van Nederland, hier afgebakend als de provincies Noord-Holland (uitgezonderd Het Gooi), Zuid-Holland en Zeeland, - is grotendeels beperkt tot het bosrijke binnenduingebied. Tot eind jaren 1970 berustten gegevens over het voorkomen van deze soort voornamelijk op toevallige vondsten en op luid gepiep rondom koloniebomen, waardoor waarnemers geattendeerd konden worden op de aanwezigheid van de soort. Door de komst van de bat-detector is het sinds midden jaren 1980 mogelijk gebieden effectiever te onderzoeken op het voorkomen van rosse vleermuizen. De Nederlandse populatie werd in de jaren 1990 op 6000-8000 dieren geschat, waarvan 800-1000 in het binnenduingebied. Buiten het binnenduingebied werden in die tijd geen kolonies van rosse vleermuizen aangetroffen.Sinds de jaren 1980 zijn er drie perioden geweest waarin de rosse vleermuis in West-Nederland werd gemonitord: 1986-1993 (periode 1), 1998-2002 (periode 2) en 2013-2018 (periode 3). De omgeving Den Haag, Rijswijk en Voorburg, werd in vier aparte perioden onderzocht 1986-1993 (periode A), 1998-2002 (periode B), 2008-2012 (periode C) en 2015-2018 (periode D). Er werd systematisch onderzoek gedaan naar kraamkolonies, overige verblijfplaatsen en naar foeragerende dieren in geschikte gebieden, ook buiten het binnenduingebied waar de soort aanvankelijk ontbrak. De aantallen uitvliegende rosse vleermuizen in West-Nederland over de perioden 1-3 vertonen een afgetekende, significante stijging. Ook de aantallen kolonies namen toe, zij het dat alleen de verschillen tussen periode 1-3 en 2-3 significant zijn. De aantallen uitvliegende rosse vleermuizen in Den Haag, Rijswijk en Voorburg over de perioden A tot en met D vertonen steeds een gestage stijging, evenals de aantallen kolonies. In de periode 1986-1993 bedroeg het aantal km-hokken waar rosse vleermuizen waren gehoord in West-Nederland 293 (bron: NDFF / Zoogdiervereniging). In de periode 2013-2018 waren dit er 996 (bron: NDFF / Zoogdiervereniging), een significante stijging. Er is geconstateerd dat de uiteindelijke vestiging van een kraamkolonie doorgaans wordt voorafgegaan door jaren met uitsluitend waarnemingen van foeragerende dieren, gevolgd door vestiging van verblijfplaatsen van een of enkele dieren. De populatie rosse vleermuizen in de meest recente monitoringperiode, 2013-2018, is op basis van tellingen geschat op 2600-2850 volwassen vrouwtjes tegenover 800-1000 dieren in de jaren 1990. Dit betekent een forse

toename van het aantallen dieren in de afgelopen decennia. Behalve een toename van het aantal kraamkolonies en het aantal foeragerende dieren werden ook uitbreiding en vestiging in gebieden buiten het binnenduingebied geconstateerd. Zo werden kolonies gevonden in de omgeving van Zoetermeer, Rotterdam, Schiedam en 's-Gravenzande en ook in het binnenduingebied van het voormalige eiland Voorne, gebieden in Zuid-Holland waar de soort in de jaren negentig niet werd gevonden ondanks gerichte inventarisaties aldaar. In Noord-Holland werden nieuwe kolonies gevonden in het Amsterdamse Bos en in noordwaartse richting in de omgeving van Alkmaar, ten noorden van Schoorl en in het Wildrijk. In Zeeland lijken de enkele kolonies die in de jaren 1980 nog aanwezig waren in het grensgebied van Zeeuws-Vlaanderen en Vlaanderen echter te zijn verdwenen, terwijl de omgeving van Hulst onvoldoende is onderzocht. Als waarschijnlijke oorzaken van de toename van de rosse vleermuis in West-Nederland in de onderzochte perioden komen een aantal factoren in aanmerking. Allereerst een algehele veroudering van het landgoederen- en bosareaal, zowel als een grotere beschikbaarheid van foerageergebieden (recreatieplassen) is een factor. Ook een veranderend bosbeheer sinds de jaren zeventig waarbij de nadruk meer op behoud van oude en dode bomen is gericht, heeft bijgedragen aan de toename van de soort. De kap van oude bomen blijft echter wel een punt van zorg. Oude bossen zijn belangrijk: de rosse vleermuis lijkt te verschijnen in bossen die ouder zijn van 80 jaar. Om die redenen is de geconstateerde toename van de rosse vleermuis niet vanzelfsprekend representatief voor andere delen van Nederland. Nieuwe recreatieplassen werden vooral veel in West-Nederland aangelegd. Daarnaast was de toename van recreatiebossen relatief groot in Zuid-Holland, vergeleken met de rest van Nederland. Naast houtkap tijdens de Tweede Wereldoorlog, verstedelijking en, mede als gevolg daarvan, verlies van jachtgebieden hebben ook insectenbestrijdingsmiddelen waarschijnlijk een groot effect gehad op de populaties rosse vleermuizen. Het verbod op deze middelen in 1968 en 1973 hebben naar verwachting positief bijgedragen aan de aantalsontwikkelingen van rosse vleermuizen. De grote bonte specht, als de belangrijkste leverancier van geschikte boomholten voor kolonies rosse vleermuizen, is sinds de jaren 1970 sterk in aantal toegenomen. De uitbreiding van de halsbandparkiet kan lokaal een negatief effect hebben op rosse vleermuizen, maar lijkt vooralsnog geen bedreiging. Opmerkelijk is dat de boomklever, die ook sterk in aantal is toegenomen en zijn leefgebied heeft uitgebreid, dezelfde eisen lijkt te stellen als de rosse vleermuis aan zowel de ouderdom en omvang (met name dikte) van bomen als de oppervlakte van het aantal geschikte bomen. Opvallend is dat de aandacht voor boombewonende vleermuizen de afgelopen decennia grotendeels is weggeëbd door de juridische focus op de gebouwbewonende soorten vanwege de problematiek rond woningisolatie. Hierdoor zijn van veel belangrijke gebieden al decennia lang geen gegevens meer voorhanden. Het is daarom van groot belang dat er nieuwe systematische gebiedsinventarisaties worden uitgevoerd naar rosse vleermuizen, en naar en andere boombewonende soorten, in heel Nederland.

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Appendix

Overzicht van kolonies op potentieel geschikte landgoederen en in bossen in West-Nederland in de perioden 1986-1993, 1998-2002 en 2013-2018.
Number of emerging noctules counted and (in brackets) colonies on estates and in forests in the west of the Netherlands in 1986-1993, 1998-2002 and 2013-2018

Het weergegeven aantal berust op het aantal daadwerkelijk uitvliegende dieren. Tussen haakjes is het aantal kraamkolonies vermeld.
- = wel bezocht, maar geen dieren aangetroffen
* = gedeeltelijk onderzocht
? = niet bezocht
kol = aantal kolonies, geen uitvliegers geteld

Noord-Holland	1986-1993	1998-2002	2013-2018	aantal kolonies
Ten noorden van Noordzeekanaal				
Wildrijk, St Maartenszee	-	-	29	1
Schoorlse bos	25 (2)	?	27 en 152	2
Oude Hof, Bergen	10 (1)	-	-	-
Heiloerbos	60-70 (2)	116-120 (2)	220	6
Alkmaarderhout	-	-	20-30	3
Marquette, Heemskerk	57 (1)	52 (1)	-	0-1
Ten zuiden van Noordzeekanaal				
Beeckensteijn, Waterland	35 (1)	?	ca. 30	1
Duin & Kruidberg (Nova Zembla)	kol (1)	?	157	1
Schapenduin	-	?	ca. 30	1
Bloemendaalse Bos	33 (1)	?	ca. 30	1
Elswout	33 (1)	?	24	1
Haarlemmerhout	-	?	71	1
Iepenrode	kol (1)	17	?	0-2
Leyduin, Vinkenduin	22 (1)	27, 26	97, 10, 48	3
Engelse Bos, Vogelenzang	18 (1)	31	10	1
AWD, Vinkeveld	-	?	13 en 15	2
Groenendaalse Bos	kol (1)	?	>6	1
Bennebroek	22 (1)	?	64	1
Amsterdamse Bos	-	-	47	1
Totaal Noord-Holland	425-525	>300-650	910-1020	27-30

Zuid-Holland	1986-1993	1998-2002	2013-2018	aantal kolonies
Bollenstreek				
Nieuw-Leeuwenhorst	-	46 (1)	84	3
Keukenhofbos	64 (3)	89 (3)	34	1-2
Offem	?	27 (1)	25	1
Overbosch, Voorhout	-	5 (1)	26	1
Park Rusthoff, Sassenheim	?	kol (1)	28	1
Leiden – Oegstgeest-Warmond				
Huys te Warmond	>15 (1)	>12 (2)	100	4
Oostergeest	-	*47 (1)	?	0-1
Oud-Poelgeest	-	79 (1)	56	1
Leidse Hout	-	*25 (1)	-	
Bos van Bosmanpark	-	-	43	1
Bos van Wijckersloot	-	36 (1)	11	1
Endegeest / Rhijngeest	-	25 (1)	20	1
Voorschoten				
Berbice / Beerensteijn	20 (1)	?	80	2
Duivenvoorde	-	>9 (1)	30	1
Wassenaar				
Panbos	-	-	98	2
Horsten	38 (2)	?	?	0-2
Zuydwijk	23 (2)	32 (2)	112	1
Duinrell	kol (1)	?	15	1
Backershagen	-	22 (1)	-	
Hertenkamp, Wassenaar	-	-	25	1
Rust & Vreugd	25(1)	33(1)	28	1
Voorlinden	32(1)	31(1)	27	1
Den Haag				
Ockenburg	40-50 (2)	24 (1)	92	5
Meer & Bosch	-	-	95	2
Zorgvliet	-	-	37	1
Scheveningse Bosjes	-	-	35	1
Arendsdorp-Oostduin	-	-	25	1
Haagse Bos	-	-	27	1
Clingendael	-	55 (1)	103	3
Marlot/Reigersbergen	-	-	81	1
Duindigt	?	?	?	-
Rijswijk				
Voordes	-	65 (3)	80	2
Te Werve	-	-	28	1
Rotterdam				
Kralingse Bos, Rotterdam	-	-	70	3
Schiebroekse Park, Rotterdam	-	-	35	1
De Tempel, Rotterdam	-	-	32	1
Staelduinse Bos, Naaldwijk	-	-	69	1
Van Tull Park, Zoetermeer	-	-	27	1

Voorne				
Mildenburg	-	-	25	1
Overig				
Bisdom Haastrecht	-	-	-	-
Huis ten Donck	-	-	-	-
Kasteelbos, Rhoon	-	-	-	-
Dordwijk	-	-	-	-
Totaal Zuid-Holland	300-400	600	1600-1800	51-55

Zeeland	1986-1993	1998-2002	2013-2018	aantal kolonies
Steenen Beer, Sluis	16	?	-	-
Elderschans, Aardenburg	68	?	-	-
Bosgebied Clinge	?	?	?	-
Manteling en Oranjezon	-	-	-	-
Slotbos, Haamstede	-	-	-	-
Totaal Zeeland	84	?	-	-
Totaal West-Nederland	800-1000	900-1250	2600-2850	78-85

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