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Otto Plantema - Buiten-beeld (muskrat)

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Ed Hazebroek (p. 12, golden jackal; p. 54, narwhal), Bureau Endemica (p. 30, lynx)

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The Muskrat Conundrum

One of my favourite natural history books is "Monster of God", by David Quammen, subtitled "The Man-Eating Predator in the Jungles of History and the Mind". It tells the story of man's relationship with big, fierce animals, the ones that can kill and eat us. To illustrate his story, Quammen draws on four examples, three of them mammals (Romanian bears, Russian tigers and Indian lions). He describes the threats to these species, the conflicts that arise where humans and large predators live near one another and the efforts of conservationists.

Many large predatory species have now been driven to the edge of extinction due to habitat loss caused by human encroachment and poaching, but things were very different in our shared past. There was a time when we lived in both fear and awe of large predators, which were always near us, and not only in our dreams - or nightmares. In some parts of the world, large predators are still part of the ecosystem and that shared history continues, but these parts grow fewer and farther apart by the day. Our willingness to accept the danger presented by wild animals has waned and our ability to eradicate the danger has grown boundlessly. It's probably true that in this way the world has become a safer place for us. But what have we lost along the way? David Quammen quotes biblical and classical examples, such as Job, Leviathan and Beowulf to illustrate the role of large predators in our art and our stories, in the "jungle of our mind". But we need only switch to a nature TV channel to realise how we're still fascinated by big cats or sharks. But, whilst in the old days we might run into these monsters during a walk to the next village or while herding the cattle, large predators are now mostly encountered in zoos or in children's books. Nature has, for the most part, been tamed, especially in our part of the world, and space for wild things to live in is much reduced.

I was born and grew up on the Veluwe, the forested heart of the Netherlands. To call it a wilderness would require a considerable stretch of the imagination, but when we went on walks when I was little, the mere possibility of a sudden and unexpected encounter with wild boars was an exciting part of the experience. I was instilled with respect for these animals by the knowledge that they could and would defend themselves, in other words, by the potential danger they presented. Their wildness lends a special quality to the forest in a way a deer or squirrel, though wonderful creatures in their own right, never can. And today a walk on the Veluwe means a walk in wolf country and, even though the chances of seeing one are minute, just knowing that they are there is exciting. But not everyone is happy about the wolf's return. Some feel that the wolf does not belong here and that there is no place for it among us. In Germany, the Cabinet has approved a bill that will relax

the rules for culling wolves that have become 'problematic' and there are some who are strongly in favour of similar legislation in the Netherlands. In other words, while European protection has undoubtedly had a very positive effect on the wolf population in Western Europe and the general attitude towards wolves has improved, there are still those who take issues with the presence of wolves.

There are two articles in this issue of Lutra about other large predators that are present in, or near, the Netherlands: the golden jackal and the lynx. While the authors of the article about the first species conclude that the Netherlands could potentially support a sizeable population of golden jackals, those of the latter find that the fragmented forests of the Netherlands cannot support a viable lynx population. But the discussion about wolves tells us that it not just about these animals finding sufficient space to live in our fragmented landscape, but also about us giving them a place in our hearts and minds.

Also in this issue of Lutra is an article on damage caused by muskrats (*Ondatra zibethicus*). Coincidentally - and perhaps somewhat unexpectedly - there is a chapter in "Monster of God" called "The Muskrat Conundrum", in which Quammen describes the work of Paul Errington (1902-1962), an American wildlife biologist. During his youth, Errington spent much of his time as a fur trapper, but he later became a scientist and, among other things, studied muskrats and the predation of muskrats by minks (*Mustela vison*). Muskrat fur at that time was a staple of the fur trade, and so minks were unpopular with the industry. Errington's research showed that mink predation was unimportant as a factor limiting population size of muskrats. Muskrats are territorial and their population dynamics is density dependent. The number of muskrats in any given habitat is restricted by how many territories fit into it, which in turn depends on the availability of food and denning sites. Muskrats with a well-situated territory are by and large protected from predation. Their dens provide protection, their food is nearby and the routes between the two provide sufficient shelter. Muskrats without a territory or with one that is suboptimal are not so lucky and run a much greater risk of predation. In other words, the haves and have-nots of the muskrat society are defined by their territory or lack thereof and the have-nots are more likely to suffer predation. Quammen proceeds to draw a parallel with the relation of man with large predators and wonders whether it "... is inevitable that the costs exacted by alpha predators be borne disproportionately by poor people ...while the spiritual and aesthetic benefits of those magnificent beasts are enjoyed from afar." The question of how to better distribute the material, spiritual and aesthetic benefits is what he calls the Muskrat Conundrum and this brings me back to the return of the wolf in the Netherlands. If we cannot tolerate the presence of wolves in the Netherlands, how can we expect others to do so? Or ask Russians to live with tigers, Indians to put up with lions or Romanians to share their land with bears? We all benefit from afar from the existence of these phenomenal creatures in this world and it is no more than fair that we also share some of the costs by allowing the return of some wildness to our lands.

Eric Thomassen

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Molecular identification of sei whales (*Balaenoptera borealis*) from the Netherlands

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Abstract: Sei whale (*Balaenoptera borealis*) is a very rare species in the North Sea. The remains of four whales identified as sei whales, originating from the Netherlands, are preserved in the zoological collection of Naturalis Biodiversity Center, Leiden, the Netherlands. A single bone in the Naturalis collection, found on the Dogger Bank just outside Dutch waters, was also identified as sei whale. Because there were doubts about identification of several specimens, three of them were genotyped, using partial *16S, COI, ND4L, CytB* and *D-loop* sequences, which are standard DNA barcoding markers. The holotype of *Sibbaldius schlegelii* (Flower, 1864) [= *B. b. schlegelii*] from Pekalongan, Indonesia, and a fin whale (*B. physalus*) from the Netherlands were included for comparison. Three of the six specimens turned out to be incorrectly identified. The results underscore the added value of molecular identification of skeletons, and of museum collections. On the basis of our results, we cannot distinguish between the southern hemisphere subspecies of sei whale, *B. b. schlegelii* and *B. b. borealis*.

Keywords: baleen whale, rorqual, genotype, museum collection, DNA barcode.

Introduction

The baleen whales included in the genus *Balaenoptera*, also called rorquals, all have a torpedo-shaped body, more or less pointed snout, sickle-shaped dorsal fin, and gular grooves from chin to belly. The smaller species are quite similar in colour and body dimensions and may therefore pose identification problems. For instance, despite centuries of whale hunting, an extant *Balaenoptera* was described only in the twenty-first century: Omura's whale (*B. omurai*) (Wada et al. 2003). As living whales only show little of themselves when surfacing, and an observation usually lasts some seconds at most, specific identification at sea is difficult or even impossible. When stranded, rorqual identification can be even more challenging: corpses are frequently decomposed, discoloured and/or incomplete, while their skulls, if still present, can only be identified by specialists. As a consequence, knowledge on distribution and population size of several species is incomplete (e.g. Jung et al. 2016).

Sei whale (*Balaenoptera borealis*) has a worldwide distribution, but is still poorly known. At present, this species seems to have smaller populations than many of its relatives (Christensen et al. 1992, Prieto et al. 2012, Hammond et al. 2013) and it is currently categorised as 'endangered' (IUCN 2018). In order to be able to protect it, it is important to know its distribution, potential division into separate populations, (sub)specific sta-

tus and identifying characters. In the North Sea, sei whale is extremely rare, probably because the feeding conditions are not suitable for this species. In the southern North Sea five rorqual species have been recorded, among which sei whale, but out of 88 *Balaenoptera* carcasses stranded in the Netherlands up to April 2019, only four have been identified as sei whale (e.g. Reid et al. 2003, Smeenk & Camphuijsen 2016, www.walvisstrandingen.nl). The remains of these are preserved in the scientific natural history collection of Naturalis Biodiversity Center in Leiden, the Netherlands. In this note, we report on three of these four specimens. Some were incomplete when they washed ashore, and identification was problematic. Remains of a whale identified as sei whale from just outside the Dutch territorial waters at the Dogger Bank consists of a single vertebra only. Therefore we performed a DNA-analysis for identification. (The sei whale that stranded on Maasvlakte, Zuid-Holland, on 9 November 1986 was not included in the sample, as this specimen was fresh and complete when it washed ashore and good photographs are still available; hence its identification is beyond any doubt (figuur 1).) The analyses presented us with a challenge, because the first sei whale for the Netherlands dated back to 1811. As the Naturalis collection is also in possession of the holotype of *Sibbaldius schlegelii* (Flower, 1864), currently considered a subspecies of *B. borealis* (Perrin et al. 2009) occurring in the Southern Hemisphere, we included this specimen in our sampling.

Material and methods

Skeletal fragments of six different whales were investigated (table 1): the type specimen of the southern sei whale, *Sibbaldius schlegelii* Flower, 1864, originating from Indonesia, and four whales identified as sei whales: three that stranded in the Netherlands between 1811-2006 and one that was collected at the Dogger Bank. A whale identified as fin whale (*B. physalus*) that stranded in the Netherlands was included as well. We presume that sei whale specimens from the North Sea represent the nominate subspecies.

Bone samples were taken by breaking off pieces of bone from the ear region using a pair of pliers; the fragments were collected in Falcon tubes. The pliers were cleaned with bleach and meticulously rinsed with demi-water before sampling the next specimen. DNA extractions were carried out in a dedicated ancient DNA facility of Leiden University and Naturalis Biodiversity Center, where no prior work on whales had been performed. To prevent contamination, all work on the type

Table 1. *Balaenoptera* specimen data, sequence results and updated (sub)specific identifications. Except for the type specimen of *Sibbaldius schlegelii*, which is from Java, Indonesia, all specimens are from the Netherlands or very close by. Cases in which the analysis conflicted with the original identification are indicated in bold.
Museum ID = initial (morphological) identification; RMNH = Naturalis collection number; Genetic ID = the results of the DNA analysis; *CB* = cytochrome B, *CR* = control region D-loop.

Museum ID	Locality	Year	RMNH	Reference	Sequence	Genetic ID
B.b. schlegelii	Pekalongan	1864	31166	Flower 1864	*16S, COI, ND4L*	***B. b. borealis***
B.b. borealis	Monnikendam	1811	31164	Weber 1922	*16S, COI, CR, ND4L, CB*	*B. b. borealis*
B.b. borealis	Dogger Bank	1953	11933	[unpublished]	*16S*	***B. acutorostrata***
B.b borealis	Rotterdam	1972	22579	van Bree & Husson 1974	*16S, COI, CR, ND4L, CB*	*B. b. borealis*
B.b. borealis	Texel	2005	41459	Camphuysen et al. 2008	*16S, COI, CR*	***B. acutorostrata***
B. physalus	Kwade Hoek	2006	41465	Camphuysen et al. 2008	*COI, CR B*	*B. physalus*

Table 2. Targeted region and primer sequences.

Gene	Primer name	Primer sequence (5'--> 3')	Length	Length amplicon	Without primers
16S	1081_16S_F	TACACCTAGAAGATTCCACAGTCC	24	121/122	70/71
	1201_16S_R	TCTCCTATACTTTAGATGTATGGTGAA	27		
COI	5875_COI_F	AATATAAAACCACCTGCCATGACC	24	124	77
	5998_COI_R	TAAGTAGCATGGTGATTCCGGCT	23		
ND4L	9998_ND4L_F	ACCTAATATCCGCACTACTCTGTC	24	103	55
	10100_ND4L_R	ATCATGTTAGCCAAGGTGAAGTGT	24		
CB	14437_CB_F	GATACCTACACGCAAACGGAGC	22	139	92
	14575_CB_R	GTGGCTATAACTGTGAATAGTAGGA	25		
D-loop	15649_D-loop_F	GCATTCAATTATTTTCACTACGAGCA	26	150	101
	15798_D-loop_R	TGGAGCGGCCATAAGAATCATTT	23		

specimen of *S. schlegelii* was carried out first, separate from the bone material of the other whales. Samples were ground using a mortar and pestle, while a Retsch Mill was used for larger fragments (collection numbers RMNH.MAM.41459 and RMNH.MAM.41465, table 1). Total genomic DNA was isolated using the silica extraction method from Rohland & Hofreiter (2007). Sequences obtained with this study have been deposited in GenBank (supplementary table S3: https://zoogdierwinkel.nl/content/lutra-62-1-2019).

Based on a MAFFT alignment (Katoh & Toh 2008) of full mitochondrial sequences of *Balaenoptera* from a number of studies (Arnason & Gullberg 1993, Arnason et al. 2004, Sasaki et al. 2005, 2006, Archer et al. 2013), primers targeting five small (103-150 bp) variable mitochondrial regions commonly used for DNA barcoding (*16S large ribosomal subunit*, *Cytochrome Oxidase subunit I*, *NADH dehydrogenase subunit 4L*, *Cytochrome B*, *control region D-loop*) were designed (table 2). PCRs were performed in 25 µl volumes using 1 µl template, 0.5 µl Phire® Hot Start II DNA Polymerase (Thermo Scientific), a final concentration of 1× Phire reaction buffer, 0.5 mM $MgCl_2$, 0.3 mg/ml BSA, 0.5 mM of each primer and 0.2 mM dNTPs. The used thermoprofile consisted of an initial denaturation for 3 minutes at 98˚C, followed by 40 cycles of – denaturation 5 seconds at 98˚C, annealing 10 seconds at 60˚C, extension 30 seconds at 72˚C – and a final extension of 5 minutes at 72˚C. PCR products were cloned with a TOPO® TA cloning kit (Life Technologies) following the manufacturer's protocol. Up to five colonies were picked to PCR the insert using primers M13-FP Forward and M13-pUC(-40) Reverse (Messing 1983). The colony-PCR amplicons were purified and Sanger sequenced in both directions on an ABI 3730xl sequencer (Applied Biosystems), using the last mentioned primers, at BaseClear (Leiden). The chromatograms were edited with Sequencher 4.10.1 (Gene Codes Corporation). For each marker the obtained sequences were aligned in Geneious v.10.2.3 (Kearse et al. 2012) with the corresponding regions from the full mitochondrial datamatrix, adding humpback whale (*Megaptera novaeangliae*) (Sasaki et al. 2005) as outgroup. These five alignments were subsequently concatenated.

Maximum likelihood phylogenies (100 bootstrap replicates) were generated with PhyML (Guindon et al. 2010) for both the alignment of the complete mitogenomes as well as the alignment of the selected regions. A comparison between these two should show whether the reduced dataset (together the selected regions representing ~2.4% of the complete mitogenome) would yield the same cladogram topol-

Figure 1. The sei whale that stranded on 9 November 1986 on Maasvlakte, Zuid-Holland. The picture is a bit blurry because it was taken during twilight, but the species is easily identified by the colours and pattern on flipper and throat and the length of the gular grooves. *Photo: A. Molenkamp (Naturalis).*

ogy. Uncorrected pairwise (P) genetic distances between species were calculated for each of the short targeted fragments, also in Geneious (same version). The number of variable and parsimony informative sites were calculated with PAUP 4.0a165 (Swofford 2003). Assignment of the obtained sequences to any of the known species of *Balaenoptera* was done based on NCBI nucleotide BLAST searches (https://blast.ncbi.nlm.nih.gov), assessing interspecific distances and the position of these sequences in the phylogeny reconstruction.

Results

Only three out of the six specimens appeared to be correctly identified. Two originally identified as sei whale turned out to belong to minke whale (*B. acutorostrata*) (table 1). The original identification as fin whale from the animal stranded at Kwade Hoek was confirmed by the analysis. The type of *S. schlegelii* could genetically not be discriminated from other sei whales.

There were strong fluctuations in amplification success between the different samples, which were not typically (collection) age related. In order of amplification success, the markers could be ranked (from highest to lowest success rate) as *16S,COI*, *CR, ND4L* and *CB*. Only for the sei whales of Monnikendam and Rotterdam all five markers were obtained. Least effective were the PCRs of the minke whale from the Dogger Bank. BLAST searches with each of the obtained sequences yielded unambiguous identifications (4e44 < E-value < 5e19; 99% < identity <100%; supplementary table S1: https://zoogdierwinkel.nl/content/lutra-62-1-2019). Also, there was no conflict in identification between the different markers. The selected regions showed some interspecific variation within *Balaenoptera*. Based on average uncorrected P-distances the markers could be ranked (from most to least informative) as *ND4, CR, 16S, CB* and *COI* (supplementary table S2: https://zoogdierwinkel.nl/content/lutra-62-1-2019). Within *Balaenoptera*, the average interspecific sequence divergence (all markers) was 11.7%. From a phylogenetic per-

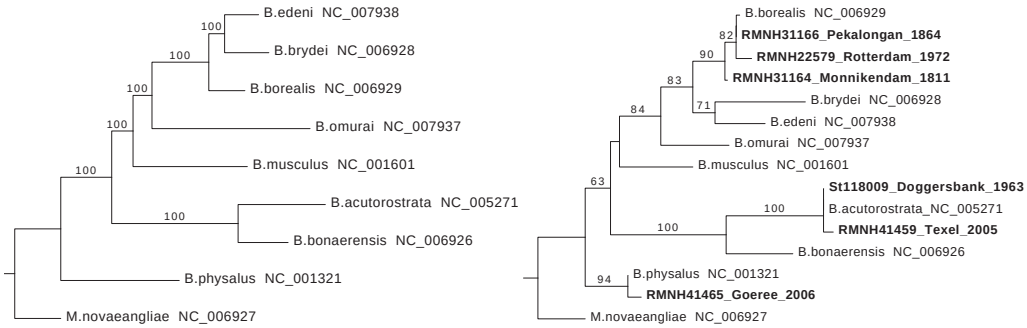

Figure 2. The left figure shows a fully resolved Bayesian phylogeny of *Balaenoptera* based on complete mitogenomic sequences (~16400 nt). The right figure shows the same phylogeny based on a subset of *16S, COI, CR, ND4L* and *CB* (sequences obtained in this study are indicated in bold).

spective the markers could be ranked (corrected for fragment length) from most to least parsimony informative: *ND4* (17,12), *CR* (37,21), *16S* (24,12), *CB* (25,12) and *COI* (16,10) (in parenthesis, the number of variable and parsimony informative characters, respectively). Fragment lengths without primers are given in table 2. The ML phylogeny inferred from full balaenopteran mitochondrial sequences was completely resolved (figure 2, left cladogram). The phylogeny based on the selected regions showed the same topology, although some nodes received lower bootstrap support (figure 2, right cladogram). Species clades, including taxa assessed in this study, were always highly supported.

Discussion

DNA analysis can aid accurate identification of historic cetacean specimens (e.g. Foote et al. 2012 and references therein), which (as in this case) may be up to 200 years old. The larger DNA-fragments in this study (*control region D-loop* and *cytochrome B*) amplified less successfully, yet no trend could be detected between amplification success and age of the specimens. Although the primers were generally designed to work for *Balaenoptera*, a bias in species specificity cannot be ruled out. For instance, PCRs with the *ND4L* and *CB* primers only resulted in amplicons for sei whale, while PCRs with *COI* and *CR* showed that these primers worked with one minke whale (RMNH. MAM.41459), but did not result in amplicons for the other one. Despite the successful amplifications, we could not separate the species pair minke whale – Antarctic minke whale (*B. bonaerensis*) with COI (table S2).

This study underpins the value of natural history collections. They offer the possibility to study material both morphologically and with DNA techniques: being stored in a suitable facility, specimens can be studied again and again if needed. Genetic analysis could result in successful identification when morphological characters are no longer available, for instance in case of incomplete or badly decomposed specimens. However, if conservation conditions are less than optimal, DNA can degrade quickly even in recently collected material and molecular analysis becomes impossible. Also, collecting cetacean bones from stranded animals is a costly affair, as is their storage. It is nevertheless recommended to store at least some parts of a stranded specimen, not only for *post hoc* identification, but also because new techniques could recover information that is presently impossible to get.

As the marine environment changes, so does the distribution of cetaceans (e.g. Santos et al. 2008, Nøttestad et al. 2015). Identification should therefore be done on basis of characters of specimens, not on known

(=present) distribution. Monitoring of cetaceans is generally considered important, e.g. for detecting population changes and conservation issues, and several techniques are in use, including acoustic surveys, aerial surveys and strandings analyses (Evans & Hammond 2004, MacLeod et al. 2005, André et al. 2011, Scheidat et al. 2011, Hammond et al. 2013). However, cetaceans are known to sometimes wander away from their area of regular occurrence (van Oort 1926, Anonymous 2005), while distribution of several species is still incomplete due to identification problems. Omura's whale, for instance, described from the Indo-Pacific Ocean and overlooked for centuries, was recently shown to occur in both the Indian and Atlantic Oceans as well (e.g. Cerchio et al. 2015, Cypriano-Souza et al. 2016, Jung et al. 2016). As identification of dead whales on the beach or in a collection may be as difficult as that of live individuals at sea, easier access to important morphological characters, like an identification key of cetacean remains, would be of great help.

The whale delivered to the Leiden museum by C.G.C. Reinwardt from Java was described by Flower (1864) as a species new to science: *Sibbaldius schlegelii*. This name was later synonymised with *B. borealis* by Tomilin (1946), although he proposed to retain it as a subspecies. As a result, two subspecies of sei whale are recognised until present (e.g. Rice 1998, Wilson & Reeder 2005, Perrin et al. 2009, IUCN 2018), despite the fact that Tomilin (1946) states that the two are only separable on basis of (maximum) body length and geographical distribution. Perrin et al. (2009) are right in pointing out that samples from northern and southern hemispheres should be compared more closely to find potential differences. On basis of our analysis, it is not possible to differentiate between sei whales from the Atlantic Ocean and the type of *S. schlegelii*, which originates from the Indo-Pacific. In cetaceans, body size alone cannot be used as a distinguishing character between (sub)species. We cannot rule out the possibility that population genetic markers, like microsatellites or RAD sequencing (e.g. Palsbøll et al. 1997, Attard et al. 2018), would show a difference between northern and southern populations, but it is unlikely that those data can be obtained from the type specimen of *Sibbaldius schlegelii*.

The geographical distribution of sei whale is still poorly known in the Atlantic (e.g. Prieto et al. 2012), but even more so in the Pacific. The northern population of the latter is considered to stay north of 40 °N in summer, but migrates south in winter, apparently almost into the tropics, similar to sei whales in the North Atlantic (IUCN 2018). Southern sei whale spend the (southern) summer between 40-60°S, while they occur as far north as 7°S in (southern) winter, at least in the Atlantic (da Rocha 1983). So, the distance between the southernmost records of northern sei whales and the northernmost records of southern sei whales may be as little as 2500 km. With the type specimen from *Sibbaldius schlegelii* from Java washing ashore at 7°S, one may wonder whether it really belonged to the southern sei whale population.

Sei whale populations from the Atlantic and Pacific are genetically distinct (Huijser et al. 2018), but until present the two are not (yet) separated as subspecies. Genetically distinct populations of any species could merit (sub)specific recognition, for instance when both prove to represent monophyletic clades. Genetic distance could lead to follow-up research, perhaps even revealing distinct and constant morphological characters (cf. Baker et al. 2002, Baker & Bradley 2006, Zink 2015).

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Samenvatting

Moleculaire determinatie van noordse vinvissen (*Balaenoptera borealis*) uit Nederland

Van de vijf soorten vinvis (*Balaenoptera*) die in de zuidelijke Noordzee zijn waargenomen, is alleen dwergvinvis (*Balaenoptera acutorostrata*) een regelmatige gast. Deze soort komt er het hele jaar voor; zijn verspreidingsgebied in de Noordzee reikt zuidelijk tot aan de zuidelijke rand van de Doggersbank. Gewone vinvis (*B. physalus*) en noordse vinvis (*B. borealis*) komen onder andere voor in de diepe noordelijke Noordzee, Bultrug (*Megaptera novaeangliae*) is in de hele Noordzee zeldzaam en blauwe vinvis (*B. musculus*) is er zeer zeldzaam. Toch zijn al deze soorten op de Nederlandse kust gevonden. Van noordse vinvis zijn er tot nog toe vier meldingen uit ons land: een uit de 19e eeuw (1811), de andere uit 1972, 1986 en 2005. Skeletresten van deze vier worden bewaard in de collectie van Naturalis Biodiversity Center in Leiden. Daarnaast is er in Naturalis een wervel afkomstig van de Doggersbank uit 1953, juist buiten het Nederlandse deel van het Continentale Plat, die eveneens aan noordse vinvis is toegeschreven. Omdat er twijfels waren over de juistheid van de determinaties, en vanwege de grote zeldzaamheid van noordse vinvis in de zuidelijke Noordzee, is DNA uit botten van drie van de veronderstelde noordse vinvissen onderzocht aan de hand van vijf markers: 16S, COI, ND4L, CytB en D-loop. Het exemplaar van 1986 is niet onderzocht, omdat determinatie van dit dier vanwege de zeer verse staat bij stranden, compleetheid van het kadaver en goede foto's, buiten kijf staat. Wel is het holotype van *Sibbaldius schlegelii* Flower, 1864 meegenomen in het onderzoek. Dit exemplaar is in het midden van de 19e eeuw gevonden op Java en naar Leiden gestuurd. De naam *B. borealis schlegelii* wordt gebruikt voor de ondersoort van de noordse vinvis die op het zuidelijk halfrond leeft en men is er altijd van uitgegaan dat dit exemplaar uit die populatie afkomstig was. Uit de resultaten van de DNA-analyse bleek dat twee als noordse vinvis gedetermineerde dieren dwergvinvissen bleken te zijn. Op grond van de gebruikte DNA-markers is er geen verschil aantoonbaar tussen het type van *schlegelii* en de nominaat uit de Noordzee. Dit onderzoek toont het belang aan van DNA-onderzoek, dat bovendien mogelijk blijkt te zijn aan de hand van oud botmateriaal, mits dat onder de juiste condities bewaard wordt. Ook het belang van collecties is hiermee opnieuw aangetoond. Daarnaast wordt gesteld dat het belangrijk is om altijd enig materiaal van gestrande walvissen te bewaren, zodat het voor eventueel toekomstig onderzoek gebruikt kan worden.

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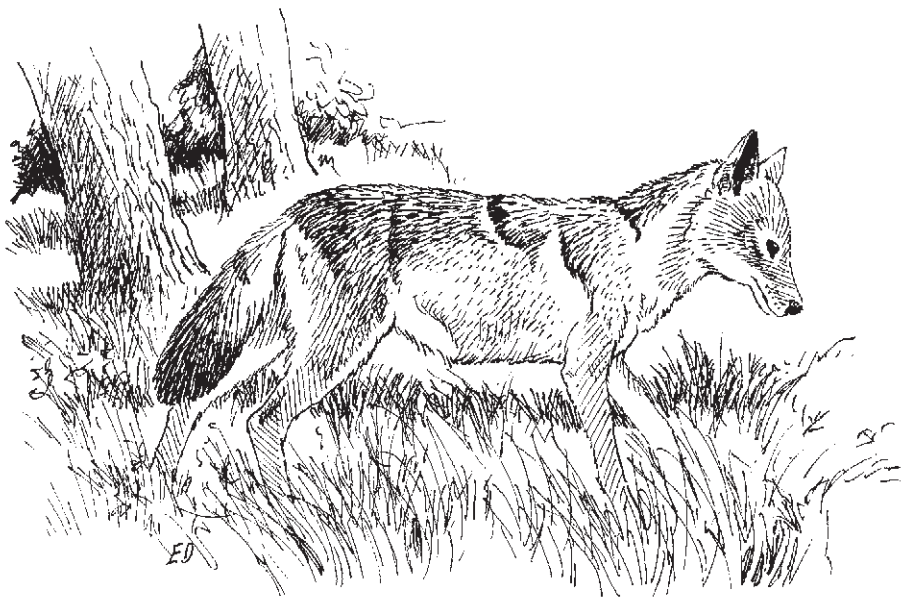

A Habitat Suitability Analysis for the golden jackal (*Canis aureus*) in the Netherlands

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Abstract: The golden jackal (*Canis aureus*) is expanding its range towards Northern and Western Europe. In these parts of Europe, there is a lack of substantial knowledge about this animal's ecology and habitat requirements. The aim of this study was to determine the potential location and numbers of territories in the Netherlands suitable for the golden jackal. This article uses a literature study to review the habitat requirements of the golden jackal. Factors such as diet, roads, habitat size, land use and potential wolf (*Canis lupus*) territories were taken into account to assess the quality of potential habitat for golden jackal in a Habitat Suitability Analysis (HSA). Maps of the Netherlands were created to visualise possible core areas, highly suitable, and suitable areas. The main factors limiting establishment of the golden jackal would seem to be urbanisation and the presence of wolves. The results show that core areas in the Netherlands could support more than a hundred family groups, while highly suitable areas could potentially support an additional 150 family groups. The remaining suitable areas were found to be able to support up to around 1200 more family groups. In total, the Netherlands could support around 1450 golden jackal family groups, although the re-establishment of wolves could decrease these numbers to around 800 golden jackal family groups. This study only considered the most important parameters, which were set quite conservatively, so it is likely that our assessment of the amount of suitable habitat and potential golden jackal numbers are an underestimation.

Keywords: Golden jackal, *Canis aureus*, Habitat Suitability Analysis, habitat requirements, the Netherlands.

Introduction

The golden jackal (*Canis aureus*) is a canid species with a widespread range. Up until the year 1950 their habitat ranged from Indochina (Sillero-Zubiri et al. 2004), in the east, to the Balkans in the northwest (Hoffmann et al. 2018). Since the 1980s, the species has been expanding north-westward in Europe, which has resulted in a genetic founder effect (Zachos et al. 2009): the golden jackal has established a thriving population in Hungary, with an estimated population in 2007 of more than 1500 individuals (Tóth et al. 2009). The first sighting in Germany was in 2000 (Möckel 2000). Reproduction of the golden jackal was confirmed in Italy in 2007 (Lapini et al. 2009) and in the Czech Republic in 2017 (Jirku et al. 2018). Factors that seem to drive the recent expansion of the golden jackal are land use change (Šálek et al. 2014), climate

change (Arnold et al. 2012) and the persecution of wolves (*Canis lupus*), which has eliminated mesopredator control (Krofel 2017).

Historically, the golden jackal did not occur in these parts of Europe and therefore has not received much attention from ecologists or jurists compared to other terrestrial carnivores, such as the wolf (Chapron et al. 2014, Trouwborst et al. 2015). The golden jackal is included in the Annex V of the Habitats Directive of the European Union and thereby has less legal protection than the wolf (European Commission 1992). This indicates that Member States must ensure that their exploitation and hunting is compatible with maintaining a favourable conservation status of the golden jackal. This law requires Member States to anticipate what kind of management decisions will have to be taken for the golden jackal population in their State. For the Netherlands to meet this requirement it is necessary to identify what habitats the golden Jackal would find suitable if it were to settle here.

The first sighting of a golden jackal in the Netherlands was documented in February 2016 on the Veluwe by means of a camera trap (WUR 2016). These pictures have been verified by international experts on carnivores (personal communication G. Lelieveld). The apparent northwestwardly expansion of this species, combined with this first sighting, makes the arrival of the golden jackal in the Netherlands almost a certainty.

In anticipation of this, this study will review literature on the habitat requirements of the golden jackal and perform a Habitat Suitability Analysis (HSA) in order to answer the following questions: 1. Where would this species find suitable habitat in the Netherlands? 2. How large are the areas with different classes of quality of suitable habitat?

The literature review on the habitat requirements will focus on the behaviour of the golden jackal, its diet and habitat selection, including how they deal with competitors, such as the red fox (*Vulpus vulpus*) and the wolf. This literature review is then used to construct an HSA for the golden jackal.

The golden jackal's biology: a literature review

Social and hunting behaviour

The behaviour of the golden jackal is very similar to that of the wolf. The species lives in packs consisting of a breeding pair and the cubs of previous years that assist their parents by providing food for the current litter. There are known cases of jackal families hunting together, but this only occurs when there is a high density of golden jackal in an area (Markov 2012). Usually, the golden jackal hunts solitarily (Sillero-Zubir et al. 2004), which affects the prey size they can handle, the largest wild prey in Europe being red deer calves (*Cervus elaphus*; Boskovic et al. 2013). The rest of its diet is rather flexible and differs over the seasons. A study showed that the primary food of the golden jackal in winter consists of livestock carcasses, with small live mammals as a secondary food choice (Ciroviv et al. 2014). This study found golden jackals rarely eat plant materials during the winter. In contrast, a study on their diet over the whole year, conducted by Radovic & Kovačić (2010), shows a more varied diet. Meat was still the primary food source, but was supplemented by fruits, seeds and vegetables, which made up a third of their diet. A third study on their summer diet in an agricultural area, found small mammals to be their main food source (Markov & Lanszki 2012). Hence, most land use types in the Netherlands would provide some kind of food source for the golden jackal.

Golden jackal's ability to thrive on a wide food range indicates a high flexibility in habitat selection. Apart from forests, they can colonise agricultural areas where they hunt small rodents (Šálek et al. 2014). They sometimes even visit urban areas at night, where they forage for garbage (Giannatos 2004, Sillero-Zubir et al. 2004, Hoffmann et al. 2018). A study conducted in Greece found that the mean distance of observed jackal groups to the nearest human settlement was 2.61 km

(0.1-4.5 km; *n*=112; Giannatos 2004).

The habitat size and population densities (Šálek et al. 2014, Boyce et al. 2015) of the golden jackal correlates with the amount of food resources present in the area. For example, in Israel jackal densities became very high at a garbage dump (Reichmann 2013). Giannatos (2004) found one group within a 12 km^2 area of poor quality habitat but also found one group/1 km^2 in high quality habitat. The average number of groups that he found was 2-3 groups/10-12 km^2.

Habitat preferences

Giannatos (2004) also found that the golden jackal does not occur on high elevations or mountainous terrain, due to winters with extended periods of snow cover. The Netherlands does not have mountains or cold winters with long periods of snow cover so these factors would not limit the golden jackal's habitat options in the Netherlands and have been excluded from this study. The golden jackal prefers small forests with open canopies (Giannatos 2004) and has a tendency to settle in dense parts of small forest patches near human settlements (Markov 2012). A study performed by Lanszki et al. (2018) tracked a young female while she was dispersing to start her own territory. She crossed two highways and found her own territory about 230 km away from her parents' den with a significant lower density of golden jackal. This study confirms the golden jackal's high dispersal ability and shows that while roads are a potential threat they are not an obstacle to the ongoing expansion of the golden jackal's range.

Interactions with wolf and red fox

Golden jackals' flexibility also becomes evident in their interactions with the red fox. There is an overlap between golden jackal and the fox in their preferred food sources and feeding habits. When food sources are abundant, both species will consume small rodents (Lanszki & Heltai 2010). When they are less abundant, the two canids' food preferences seem to diverge. Lanszki et al. (2016) showed that this divergence leads to long-term coexistence of the two canids despite their apparent niche overlap. Another study supports this: they found that red foxes do not alter their behaviour when presented with the smell of the golden jackal but avoided an area where a golden jackal was present at that moment (Scheinin et al. 2006). This indicates that avoidance seems to lead to temporal divergence while their territories still have spatial overlap.

There has been less research on the interactions between the golden jackal and the wolf and the existing literature suggest that the two species do not readily co-exist. A study conducted by Mohammadi et al. (2017) observed a wolf kill a golden jackal in an agricultural area. Observations of an established golden jackal population in Greece, showed that it disappeared the moment a wolf pack of four individuals claimed the area (Giannatos 2004). These authors also observed that wolves were drawn to jackal sounds, presumably to chase them off.

To summarise, the literature shows that diet is not a limiting factor for the golden jackal due to its flexibility. The presence of foxes in their habitat is also no limitation to the golden jackal. However, presence of wolves can be fatal. The golden jackal prefers forested areas with clearings and near human settlements but can also thrive in agricultural areas. Urban areas are sometimes visited but do not provide rest areas and are therefore not permanently used by the golden jackal.

Method

Habitat Suitability Analysis

Our Habitat Suitability Analysis (HSA) (Boyce & McDonald 1999) is rule, or process, based,

Table 1. Habitat requirement rules.

Number	Rule	Explanation
1	Diet is not a limiting factor.	The literature indicates that the golden jackal is extremely adaptable in its diet and can adapt to seasonal changes (Markov & Lanszki 2012), the presence of the red fox (Lanszki & Heltai 2010) and the availability of different food sources in the area (Šálek et al. 2014).
2	Urban areas are not used as resting spots but will be visited during the night for foraging purposes.	The literature indicates that the golden jackal does not stay in prime urban areas. However, it will enter urban areas at night in search of garbage (Giannatos 2004, Sillero-Zubir et al. 2004, Hoffmann et al. 2018).
3	The territory of a family group in highly suitable areas is 6 km^2 and in suitable areas is 12 km^2.	The literature indicates that the smallest habitat size is 6 km^2 under natural conditions (Giannatos 2004, Šálek et al. 2014).
4	Roads are barriers but these are not insurmountable.	The literature indicates that roads pose a threat to the golden jackal but that it is able to overcome these (Lanszki et al. 2018).
5	Presence of wolves makes an area uninhabitable for the golden jackal.	The literature indicates that wolves actively chase and kill golden jackals (Giannatos 2004, Mohammadi et al. 2017).

Table 2. Summary of the basemap used, including a definition of the six suitability classes, population density and the corresponding ID codes from the LGN7.

Suitability class	Definition	Population density (family groups/km^2)*	ID codes from the LGN7**
0	The golden jackal cannot live here.	0	8, 16, 17, 18, 20, 25
1	The golden jackal cannot find food here but the area itself poses no limitation.	0	19, 24, 31, 35
2	The golden jackal is able to forage for food here but this is of low quality and there are usually no available resting areas.	0.01	3, 4, 6, 10, 26, 22, 23, 28, 32, 34, 36
3	The golden jackal is able to forage for food here, and resting areas are available.	0.08	1, 2, 5, 61, 9, 30, 33, 37, 38
4	The golden jackal is able to forage for food here, which is of good quality. There are resting areas.	0.16	62, 42
5	The golden jackal is able to forage for high quality food here and resting areas are abundant.	0.16	11, 12, 39, 40, 41, 43, 45

* Population density based on the studies from Giannatos (2004) and Šálek et al. (2014).

** The appendix describes the ID codes from the LGN7 and their reclassification in suitability classes.

due to the flexibility of the species and insufficient literature on the golden jackal to do any kind of powerful statistical analysis. Based on the available literature on the biology of the golden jackal (Giannatos 2004, Lanszki & Heltai 2010, Markov & Lanszki 2012, Šálek et al. 2014), it seeks to identify the factors that will limit the habitat of golden jackals in the Netherlands (table 1).

Study area and origin of data

The Habitat Suitability Analysis of the golden jackal in the Netherlands utilised the most recent land cover map of the Netherlands; "Landelijk Grondgebruiksbestand Nederland versie 7 (LGN7)" (Hazeu et al. 2014). Data regarding roads were retrieved from the Top10NL (Hazeu et al. 2014), the most recent and complete map of roads in the Nether-

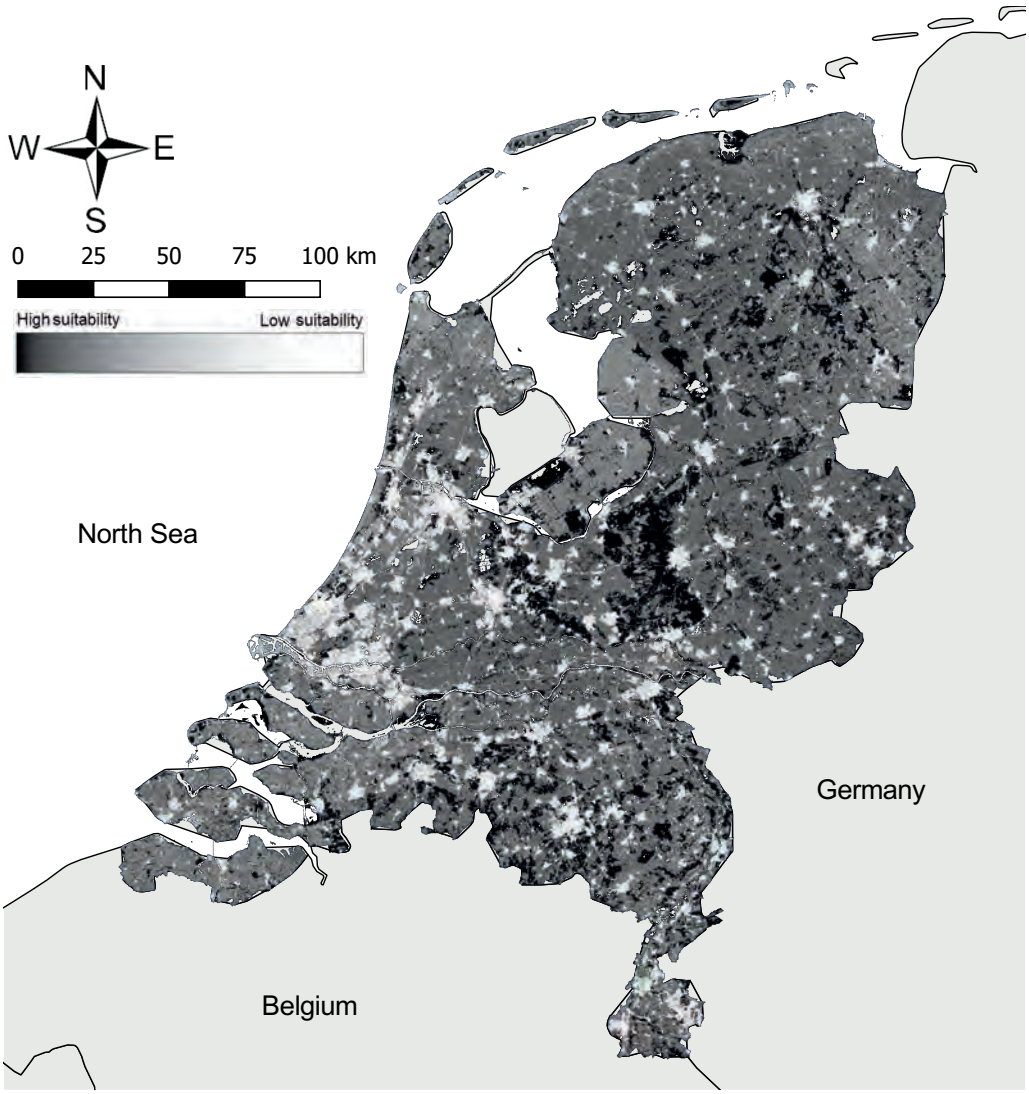

Figure 1. Habitat suitability for golden jackal in the Netherlands, based on land use types.

lands. The land cover of the LGN7 together with the road network from the Top10NL were combined to create a base map for this study. Data on potential wolf territories (derived from Lelieveld (2012), who found that the Netherlands can support at least 14 wolf packs with territories of at least 225 km^2) were then added. QGIS software was used to perform the HSA using the raster, rgdal, SDMTools, rgeos, units, smoothr, maptools and PBSmapping packages from R version 3.4.0.

Modelling strategy

Creating a base map

The first step was to reclassify the base map according to how suitable the areas would be for the golden jackal. With the detailed data on land use contained within the LGN7, we chose a resolution of 25x25 metres. Each of the 39 land use types defined within LGN7 was assigned a class based on habitat suitability from 0 to 5 (table 2; figure 1; appendix). 0

was considered the lowest suitability class and depicted as white in the map, 5 was considered the highest suitability class and depicted as black. Table 2 provides an explanation and estimated population density for each of the habitat suitability classes. The second step was to conduct a Focal Window Analysis. The goal of this analysis is to soften and reduce small spikes in the data. For example, we reduced the negative impact of a building in an otherwise suitable environment but did not reduce the negative impact of primary and secondary roads, which were added to the map after the Focal Window Analysis. The resulting map showed the habitat suitability for the golden jackal in the Netherlands.

Identifying three area types

Three different area types were created to estimate the suitable habitat for, and thus potential territory size of, the golden jackal. The core areas consisted of all areas that were assigned suitability class 4 and 5, which were single adjacent areas, based on Rook connectivity, larger than 6 km^2, without any primary or secondary roads, in an attempt to reach a low disturbance level (Giannatos 2004, Šálek et al. 2014). An area size of 6 km^2 is conservative for a golden jackal territory, considering that several studies have found multiple golden jackal groups within 6 km^2 (Giannatos 2004, Šálek et al. 2014). We chose, 6 km^2 as the Netherlands has a high human population density which would increase disturbance levels. The only difference in assessment criteria between highly suitable habitats and core areas was that the latter did not contain any roads. When the two areas overlapped, they were designated as core areas. To be conservative, any remaining highly suitable areas after this subtraction, that were smaller than 6 km^2, were excluded from the analysis. The third area type was suitable areas. These areas consisted of areas which were assigned class 3 to 5, single adjacent areas, based on Rook connectivity, that were larger than 12 km^2. When suitable areas and highly suitable areas or core areas overlapped, the suitable areas were considered to be less important. To be conservative, any suitable areas of less than 12 km^2 remaining after this subtraction, were excluded from the analysis. Lastly, potential wolf territories, derived from Lelieveld (2012) of 225 km^2 or more, were eliminated from the three area types to account for the effect wolves can have on golden jackals.

After the three area types were created, their total surface area and mean area size per polygon were calculated. Then a possible population density was estimated based on the two types of surface areas. First, the total surface area was multiplied by the corresponding population density (table 2). Second, the mean area size was divided by the corresponding territory size (6 km^2 for core and highly suitable areas and 12 km^2 for suitable areas) and then multiplied by the number of areas.

Results

The HSA showed that large parts of the Netherlands offer a potentially suitable habitat for the golden jackal, with the central, eastern and northern parts of the Netherlands providing more, and higher quality, habitat than other parts of the country. All urban areas are unsuitable for the golden jackal, while the forested and agricultural parts are more suitable (figure 1).

Figure 2 shows the next step in which the three area types in the Netherlands were created. Figure 3 shows the territory left for golden jackal to colonise after taking into account the likely re-establishment of wolves in the Netherlands. The distribution of the area sizes per area type shows that most of the areas are smaller than 100 km^2 (figure 4). The Pearson Chi-Square test for the core areas (X=240, df=225, P=0.235), highly suitable areas (X=1332, df=1296, P=0.238) and suitable areas (X=3080, df=3025, P=-0.238) showed that no significant differences were found whether or not wolves would be likely to be present.

The maximum amount of suitable habitat

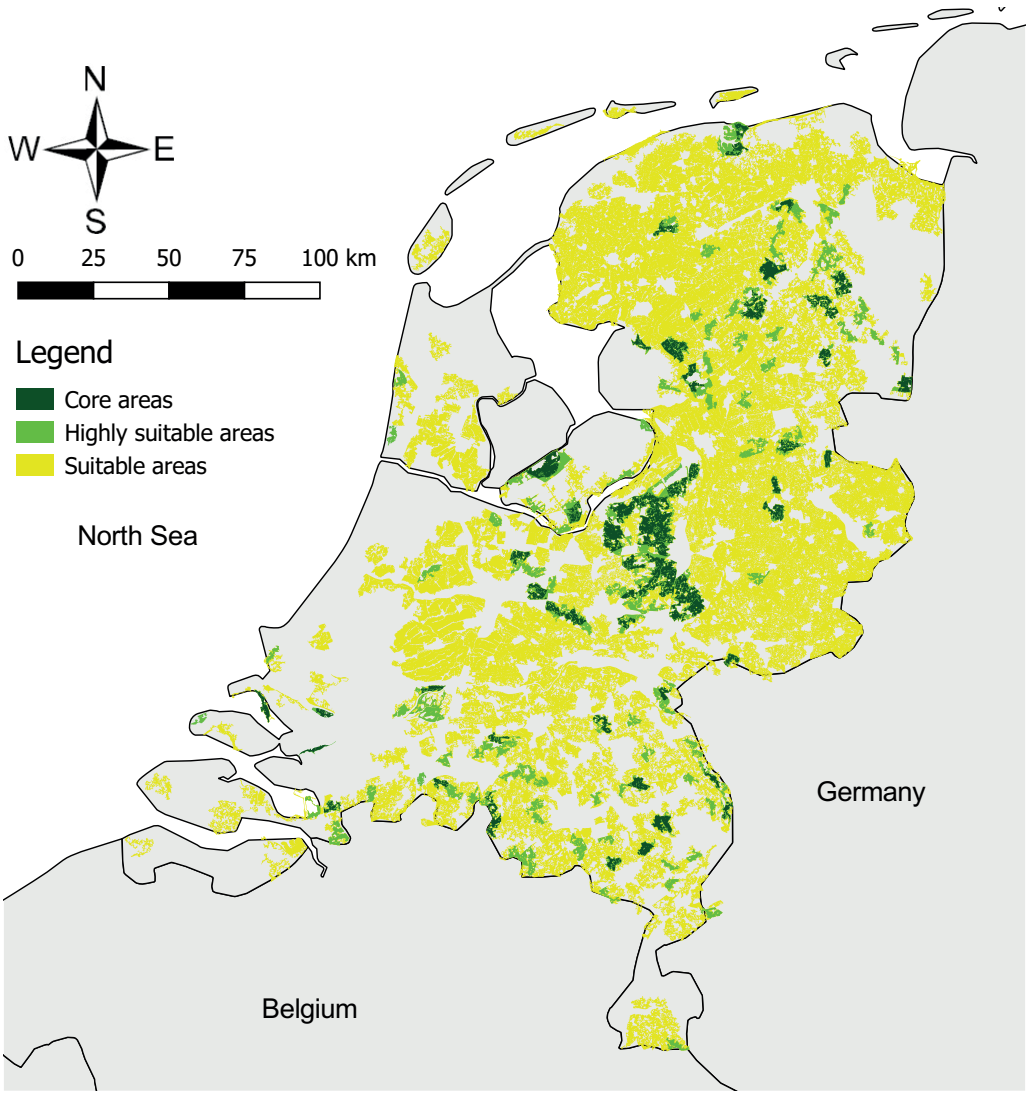

Figure 2. Potentially suitable habitat (core, highly suitable and suitable areas) for golden jackal in the Netherlands.

calculated per area and calculated from total area size show that the Netherlands could support 1432 to 1476 family groups. The first number was calculated with the minimum territory size in mind while the second was calculated from the total suitable area size. If wolves were to re-establish themselves in the Netherlands these numbers drop to 781 and 851 family groups respectively (table 3). Roughly half of the potential golden jackal population would disappear if, and when, wolves re-establish themselves in the Netherlands, although only a about a third of the total area would disappear. This is because mostly core areas of the golden jackal would be used by the returning wolves.

Discussion

This study has investigated (1) where the golden jackal could settle in the Netherlands and (2) how large the areas with different suit-

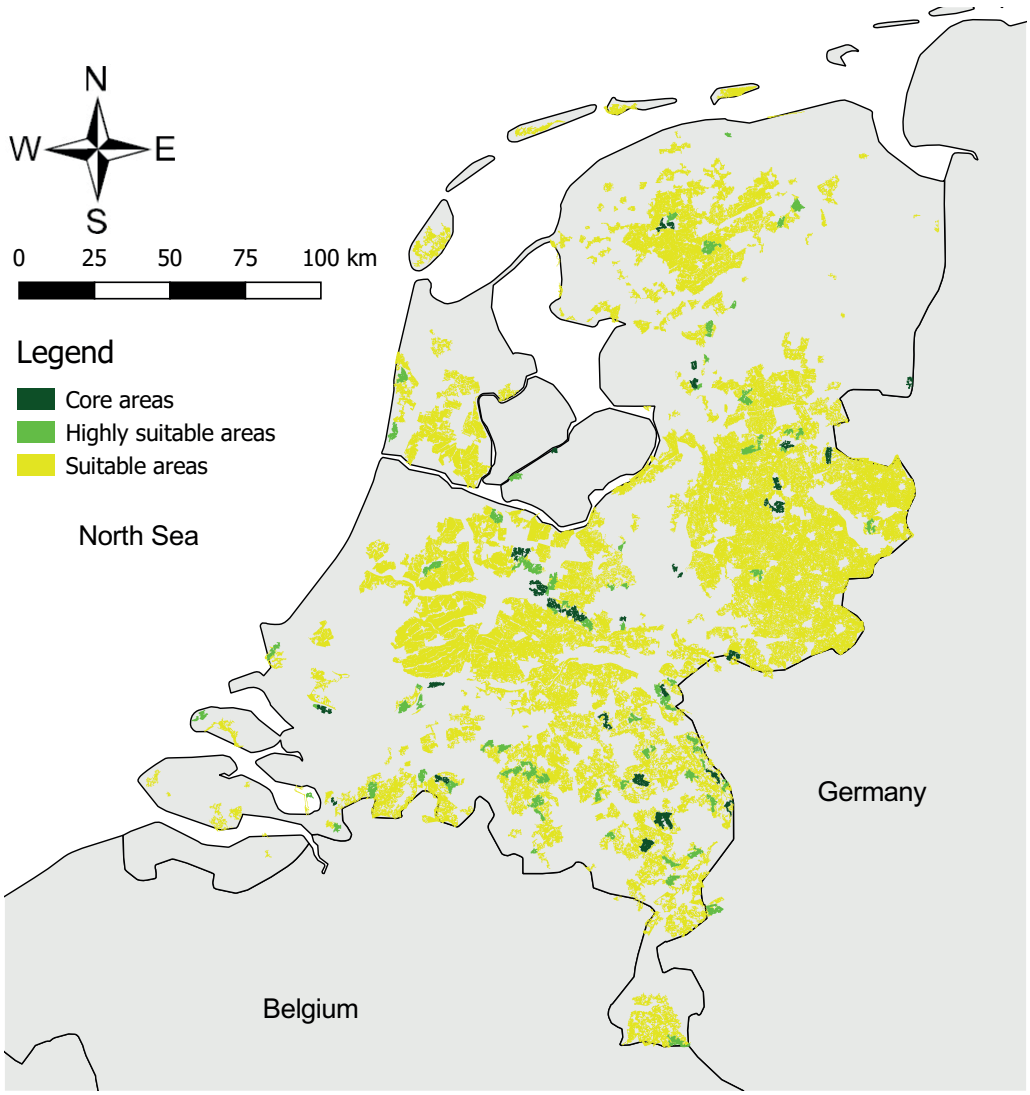

Figure 3. Potentially suitable habitat (core, highly suitable and suitable areas) for golden jackal in the Netherlands after excluding potential wolf territories.

ability classes are. Factors such as diet, roads, habitat size, land use and potential wolf territories were taken into account. The results show that the northern and eastern parts of the Netherlands, together with the Veluwe in the centre of the country, seem to be the best areas for the golden jackal (figure 1, figure 2). The potential re-establishment of wolves, would, however, reduce the suitable golden jackal areas by 6243 km^2. These potential wolf areas mainly coincide with core areas for the golden jackal (figure 3).

Even though this study applied conservative methods when assessing the quality of areas in the HSA, the results showed that the Netherlands has around 7000 km^2 of suitable habitat which could support at least 1432 family groups (table 3). Such groups on average consist of four adults; one breeding pair and the cubs of the previous year (Markov

2012). This results in a possible population size of up to 5728 individuals. The number of family groups calculated from the mean area size and the total area size only differ by 44 family groups. This shows that most of the suitable habitats are large enough to hold at least one family group. In addition, figure 4 shows that the area sizes are mostly within a 100 km^2 range, there are two very large outliers in terms of size within the suitable areas, respectively of 8053 and 2279 km^2. These outliers cover most of the northern and eastern parts of the Netherlands, which indicates a large area of well-connected suitable habitat there. Some areas, that provide suitable habitat, would be harder to reach for the golden jackal due to large surrounding water bodies, such as the Province of Zeeland, or large urban areas, such as the area to the north of the Amsterdam metropolitan region (Giannatos 2004, Šálek et al. 2014). Apart from this, most of the areas deemed suitable are reachable, although time and more research is needed to be conclusive on this. However, the potential reestablishment of wolves would reduce the 1432 possible golden jackal family groups to around 781 family groups.

Taken together the results show that the Netherlands has enough suitable habitat for a thriving population of golden jackal. Despite the high human and road density, there are enough sheltered areas and food sources. Lanszki et al's. (2018) tracking of a young dispersing female, which easily crossed highways in a cultural landscape, suggests a high flexibility in the dispersal of the species. The main reason why the Netherlands might become less suitable for the golden jackal would be the reestablishment of wolves in the country (Giannatos 2004, Mohammadi et al. 2017).

All the rules that we used for the HSA are supported by the literature. However, there is a serious lack of literature on the golden jackal in general, which means that this study is less well supported than we would prefer. As a result this study tried to be as conservative as

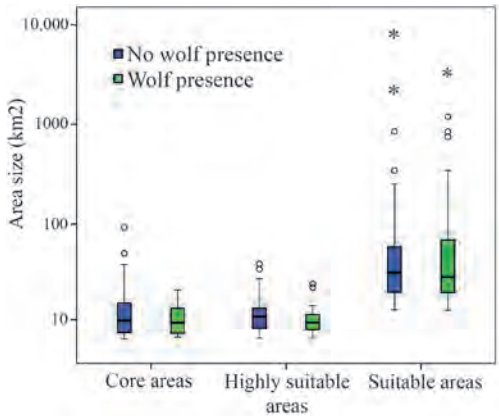

Figure 4. Boxplots (with median, first and third quartile, maximum and minimum) of area size per area type. Total core areas: *n*=58; Core areas with wolf presence (16); highly suitable areas: *n*=78; highly suitable areas with wolf presence: *n*=37; suitable areas: *n*=58; suitable areas with wolf presence: *n*=56. Y axis on logarithmic scale. Asterix * and circles ° are suspected outliers because these areas are larger than the other areas.

Table 3. Possible golden jackal population density per area (also accounting for potential wolf presence) in the Netherlands.

	No wolf presence				Including wolf presence			
	Core areas	Highly suitable areas	Suitable areas	Total	Core areas	Highly suitable areas	Suitable areas	Total
Number of areas	58	78	58	194	16	37	56	109
Average area size (km^2)	14.38	12.31	243.69	270.38	10.80	10.07	163.20	184.08
Total area size (km^2)	843.47	959.97	14133.81	15928.25	172.87	372.69	9139.15	9684.71
Potential number of family groups based on								
Average area size	116	156	1160	1432	16	37	728	781
Total area size	139	160	1177	1476	28	62	761	851

possible when assigning suitability classes to certain habitats. For instance, when there was any doubt about which suitability class should be chosen, we chose the lower class. This conservative method was also applied when assigning a population density to a certain suitability class. Therefore there is a strong possibility that we have underestimated the potential population size of the golden jackal in the Netherlands which could exceed the numbers that we have estimated, particularly when taking into account this species' flexibility with regard to habitat requirements, such as diet and resting areas (Lanszki & Heltai 2010, Markov & Lanszki 2012, Šálek et al. 2014). Other possible competitors such as the lynx (*Lynx lynx*) and brown bear (*Ursus arctos*) were not included because this study deemed it unlikely that these predators will reproduce sooner than the wolf or golden jackal in the Netherlands.

This study also excluded the border areas of the Netherlands from the HSA, although some golden jackal territories could overlap national boundaries with neighbouring countries

The future settlement of the golden jackal will have implications for Dutch society. The golden jackal is only slightly larger than a red fox and therefore is likely to be too small to be a direct threat to humans. However, it could be a potential threat towards sheep (Lanszki et al. 2006). Most literature on this topic is from eastern Europe, where herds are housed indoor during the night, protected by sheepdogs or electric fencing to keep the cattle save from wolves (Lanszki et al. 2006), which also prevents golden jackal from hunting sheep. However, sheep in the Netherlands are not protected and are therefore potential prey and this could potentially lead to high costs for farmers.

Further research could expand this study to the whole of Europe, since the expansion of the golden jackal is on-going. Factors such as elevation and cold winters would then be necessary to take into account. Also studies on potential diet composition, specifically tailored to the Netherlands, could add value to the conclusions of this study. Findings from these kind of studies could strengthen the argumentation behind our assignment of suitability classes to certain habitats.

The main conclusion from this, conservative, study is that the Netherlands has suitable potential golden jackal habitats that could support at least 1432 family groups. This leads to an estimated population size of at least 5728 individuals. The central, northern and eastern parts of the Netherlands are the most suitable for this species. However, the potential re-establishment of wolves in the Netherlands would reduce the available habitat for the golden jackal, reducing the number of possible family groups from 1432 to 781 and the potential population size to around 3124 individuals. This study considered as many parameters as possible and used conservative parameter settings, so it is likely that we have underestimated suitable habitats and potential golden jackal numbers.

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Samenvatting

Habitatgeschiktheidanalyse voor de goudjakhals in Nederland

De goudjakhals (*Canis aureus*) verspreidt zich op natuurlijke wijze vanuit de Balkanlanden in noordwestelijke richting. Daarmee komt de soort ook richting Nederland. In deze studie vragen we ons af wat geschikt leefgebied is voor de goudjakhals en waar in Nederland potentieel geschikte leefgebieden aanwezig zijn. Allereerst is een literatuuronderzoek gedaan, om meer zicht te krijgen op de ecologie en habitatvoorkeuren van de goudjakhals. Vervolgens is een een habitatgeschiktheidanalyse uitgevoerd, waarbij allereerst is gekeken naar het landgebruik in Nederland. Aan elk type landgebruik werd een waarde toegekend voor de mate van (potentiële) geschiktheid voor de goudjakhals. De hieruit voortkomende kaart vormde de basis voor het verdere onderzoek. Er werden drie verschillende typen gebieden aangewezen waar de goudjakhals zou kunnen leven. 1. Kerngebieden: hier is het landgebruik optimaal, zijn de gebieden minimaal 6 km^2 groot en komen geen primaire wegen (snelwegen en andere doorgaande wegen) voor. 2. Zeer geschikte

gebieden: deze lijken sterk op de kerngebieden, maar hierin komen wel primaire wegen voor. 3. Geschikte gebieden: het landgebruik is hier minder geschikt, gebieden zijn minimaal 12 km^2 groot en er komen primaire wegen in voor. Als volgende stap is uitgerekend hoeveel familiegroepen van de goudjakhals er in theorie in Nederland zouden kunnen leven wanneer potentiële wolfterritoria niet zijn meegerekend. Uit deze analyse blijkt dat Nederland ruimte heeft voor maximaal 1432 geschikte jakhalsterritoria, hetgeen zou betekenen dat er in ons land 5728 goudjakhalzen kunnen leven. Als wolven terugkomen zal dit aantal afnemen naar maximaal 781 territoria en 3124 dieren. Bij onze berekeningen zijn wij bij elke keuze steeds van de meest conservatieve optie uitgegaan. De hier gepresenteerde aantallen zijn daarom waarschijnlijk nog een onderschatting.

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Appendix

Description of the reclassification of the ID codes of the LGN7 in suitability classes
The LGN7 was used as a base map for this study. Each of the 39 land use types were classified according to their suitability for the golden jackal.

Code 1 - Agricultural grass
Grassland utilised by farmers. This includes pastures for cattle and areas used to grow hay, including dikes, road sides and other grass covered areas. Graveyards outside urban areas are also included in this class.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012), thus reducing pests (Cirovic et al. 2016). Therefore the assigned suitability class is 3.

Code 2 - Corn
All areas utilised by farmers for growing corn.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012), thus reducing pests (Cirovic et al. 2016). Therefore the assigned suitability class is 3.

Code 3 - Potatoes
All areas utilised by farmers to grow potatoes.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012) and thus reducing pests (Cirovic et al. 2016). Therefore the assigned suitability class is 3.

Code 4 - Beets
All areas utilised by farmers to grow beets.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012). But rodent density is lower than with other crops. Therefore the assigned suitability class is 2.

Code 5 - Crop plants
All areas utilised by farmers to grow crop plants. This includes wheat, barley, hay, rye, etcetera.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012) and thus reducing pests (Cirovic et al. 2016). Therefore the assigned suitability class is 3.

Code 6 - Other crops
All areas with agricultural crops that do not fall within the previous classes, excluding flower bulbs. Examples include horticultural crops, cabbages, hemp, oilseed rape, etcetera.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012). The rodent density of these areas is difficult to determine. Therefore the assigned suitability class is a conservative 2.

Code 61 - Orchards (tree)
All areas utilised by farmers to grow trees (other than fruit trees).

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki

2012). Therefore the assigned suitability class is 3.

Code 62 - Orchards (fruits)

All areas utilised by farmers to grow low-growing fruit trees. No distinction between different kinds of fruit are made.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012) and eating fallen fruit (Radovic & Kovačić 2010). Therefore the assigned suitability class is 4.

Code 8 - Greenhouses

All areas utilised by farmers by growing crops in greenhouses.

It is assumed that the golden jackal cannot enter these buildings and is therefore unable to utilise these areas. Assigned suitability class for this habitat is 0.

Code 9 - Orchards

All areas utilised by farmers to grow trees.

The golden jackal can utilise these areas by hunting rodents (Markov & Lanszki 2012). Therefore the assigned suitability class is 3.

Code 10 - Flower bulb fields

All areas utilised by farmers for growing flower bulbs.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012) and thus reducing pests (Cirovic et al. 2016). Therefore the assigned suitability class is 2.

Code 26 - Construction in rural area

All buildings classified for agricultural, forestry and nature purposes.

The golden jackal can utilise these areas by feeding on garbage but will not rest here (Giannatos 2004). Assigned suitability class for this habitat is 2.

Code 11 - Deciduous forest

This concerns deciduous forests outside urban areas. Forests in marshland and peat moor areas have gotten their own classes. Deciduous forest can have the function of nature but not *per sé*.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012), larger mammals (Boskovic et al. 2013) and foraging for fruits and seeds (Radovic & Kovačić 2010). In addition this habitat can provide resting spots which consist of dense vegetation and thereby difficult to penetrate by humans and domestic animals (Giannatos 2004). Therefore the assigned suitability class is 5.

Code 12- Coniferous forest

Coniferous forests outside urban areas. Forests in marshland and peat moor areas have their own classes. Deciduous forest can have some natural characteristics but are not natural *per se*.

The golden jackal can utilise these areas by hunting small mammals (Markov & Lanszki 2012), larger mammals (Boskovic et al. 2013) and foraging for fruits and seeds (Radovic & Kovačić 2010). In addition this habitat can provide resting spots which consist of dense vegetation which are difficult for humans and domestic animals to penetrate (Giannatos 2004). Therefore the assigned suitability class is 5.

Code 16 - Fresh water

All inland areas covered with fresh water, such as rivers, lakes, ditches, etcetera.

The golden jackal will drink from these areas but cannot live here. It is a land mammal. Therefore the assigned suitability class is 0.

Code 17 - Salt water

All areas covered with salt water such as the North Sea, Wadden Sea, Oosterschelde, Westerschelde, etcetera.

The golden jackal cannot live here because it is a land mammal. Therefore the assigned suitability class is 0.

Code 18 - Buildings in prime urban areas

All buildings within prime urban areas. Prime urban areas consist of shops, restaurants, company and industrial sites. These are typically located in the center of urban areas.

These areas generally have a high density of human population. Therefore the golden jackal will not enter these areas (Giannatos 2004). Therefore the assigned suitability class is 0.

Code 19 - Buildings in secondary urban areas

All buildings within secondary urban areas. Examples are airports, camp sites, buildings within military zones, buildings for electricity, etc. These are typically located at the edge of urban areas or not connected to cities.

These areas have a fluctuating human population. The golden jackal will enter these areas if the number is low to forage for garbage (Giannatos 2004, Sillero-Zubir et al. 2004, Hoffmann et al. 2018). Therefore the assigned suitability class is 1.

Code 20 - Forest in prime urban areas

All forests located within prime urban areas.

The golden jackal will not enter these areas due to the high human population density (Giannatos 2004). Therefore the assigned suitability class is 0.

Code 22 - Forest in secondary urban areas

All forests located within secondary urban areas.

The golden jackal will enter these areas to hunt for small rodents (Markov & Lanszki 2012) and forage for fruits and seeds (Radovic & Kovačić 2010). The quality of these areas is difficult to determine. However, these habitats do have potential to be of high quality. Therefore the assigned suitability class is 2.

Code 23 - Grass in prime urban areas

All grass areas within prime urban areas. These areas are construction sites, parks and sports facilities.

The golden jackal will visit these places at night, when there are less people around, to forage for garbage (Giannatos 2004, Sillero-Zubir et al. 2004, Hoffmann et al. 2018) and hunt small rodents (Markov & Lanszki 2012). Therefore the assigned suitability class is 2.

Code 24 - Bare soil in urban outskirts

All areas covered with bare soil in urban areas.

The golden jackal will not be able to forage for food in these areas. However, it is also not a limiting factor to them. Therefore the assigned suitability class is 1.

Code 28 - Grass in secondary urban areas

All grass areas within secondary urban areas. These areas are typically sports facilities, recreation areas, golf courts and garbage dumps.

The golden jackal will visit these places at night, when there are less people around (Giannatos 2004) to forage for garbage (Reichmann 2013) and hunt small rodents (Markov & Lanszki 2012). Some of these areas can be of high quality while others are of lower quality. Therefore the assigned suitability class is 2.

Code 25 - Infrastructure

This includes all major roads and train tracks. Highways, major roads and all roads broader than 7 meters are included. All roads are assumed to have a buffer zone that extends them to 12.5 meters. Train tracks have different buffer zones, depending on their type.

The golden jackal can profit from roads by feeding on roadkill, such as red fox (Douglas et al. 2011). However, roads can be lethal, therefore the assigned suitability class is 0.

Code 30 - Saltmarsh

All grass areas beyond the dikes.

The golden jackal can hunt for small rodents (Markov & Lanszki 2012) and seabirds in these areas (Lanszki et al. 2009). Therefore the assigned suitability class is 3.

Code 31 - Open sand

All areas along the coast without any vegeta-

tion, such as beaches and open dunes.

The golden jackal will not find any food here but this is also not an absolute limitation since human population is low (Giannatos 2004). Therefore the assigned suitability class is 1.

Code 32 - Dunes with low vegetation (<1 m)

Dunes in coastal areas with low vegetation <1 m.

The golden jackal can hunt for small rodents (Markov & Lanszki 2012) and birds (Lanszki et al. 2009). Therefore the assigned suitability classification is 2.

Code 33 - Dunes with high vegetation (>1 m)

Dunes in coastal areas with high vegetation >1 m.

The golden jackal can hunt for more rodents than in dunes with low vegetation (Markov & Lanszki 2012). Therefore the assigned suitability classification is 3.

Code 34 - Dunes with heathland

Dunes covered with heath.

The golden jackal can hunt for rodents here (Markov & Lanszki 2012). However, heathland is has a low production speed. Therefore the assigned suitability classification is 2.

Code 35 - Open sand (drift/ river sand)

All areas covered with open sand with no to almost none vegetation, not situated in coastal dunes. Mostly drift planes but also beaches along rivers.

The golden jackal cannot forage for food in these areas but they are not limiting since the human population is low (Giannatos 2004). In addition, beaches along rivers can provide carrion. However, the basemap did not differentiate between drift sands and beaches along rivers. Therefore the assigned suitability class is 1.

Code 36 - Heathland

All areas covered with heathland with less than 25% grass.

The golden jackal can hunt for small rodents but heathland is of poor quality (Markov & Lanszki 2012). Therefore the assigned suitability class is 2.

Code 37 - Moderate grassy heath

All areas covered with heathland with grassy elements making up between 25-75%.

The golden jackal can hunt small for rodents. While heathland is of poor quality, grassland is not (Markov & Lanszki 2012). Therefore the assigned suitability class is 3.

Code 38 - Grassy heath

All areas covered with heathland with more than 80% grassy elements.

The golden jackal can hunt for rodents. Heathland is of poor quality but grassland is not (Markov & Lanszki 2012). It is difficult to determine whether the slight increase in grass will affect the hunting possibilities of the golden jackal. Therefore the assigned suitability class is 3.

Code 39 - Peat moor

All areas covered with peat moor.

The jackal can hunt for rodents (Markov & Lanszki 2012), birds (Lanszki et al. 2009) and forage for fruits and seeds (Corlett 2017). In addition, this habitat can provide resting spots which consist of dense vegetation and thereby difficult to penetrate by humans and domestic animals (Giannatos 2004). Therefore the assigned suitability class for this habitat is 5.

Code 40 - Forest on peat moor

All areas covered with forest, situated on peat moor.

The jackal can hunt for rodents (Markov & Lanszki 2012), birds (Lanszki et al. 2009) and forage for fruits and seeds (Radovic & Kovačić 2010, Corlett 2017). In addition, this habitat can provide resting spots which consist of dense vegetation that are difficult for humans and domestic animals to penetrate (Giannatos 2004). Therefore the assigned suitability class for this habitat is 5.

Code 41 - Other marsh vegetation

All areas covered in vegetation that is not forest or reed. These vegetation types mainly consist of grasslands within marsland.

The jackal can hunt for rodents (Markov & Lanszki 2012), birds, water fauna (Lanszki et al. 2009) and forage for fruits and seeds (Radovic & Kovačić 2010). In addition, this habitat can provide resting spots which consist of dense vegetation that are difficult for humans and domestic animals to penetrate (Giannatos 2004). Therefore the assigned suitability class for this habitat is 5.

Code 42 - Reed vegetation

All areas covered with reed, situated in marshland.

In several countries the nickname of the golden jackal is reed wolf (Tóth et al. 2009). The jackal can hunt for rodents (Markov & Lanszki 2012), birds, water fauna (Lanszki et al. 2009) and forage for fruits and seeds (Radovic & Kovačić 2010). However, resting spots are less abundant as most of the ground is usually wet. Therefore the assigned suitability class for this habitat is 4.

Code 43 - Forest in marshland

All areas covered in forest, situated in marshland.

The jackal can hunt for rodents (Markov & Lanszki 2012), birds (Lanszki et al. 2009) and forage for fruits and seeds (Radovic & Kovačić 2010). In addition, this habitat can provide resting spots which consist of dense vegetation that are difficult for humans and domestic animals to penetrate (Giannatos 2004). Therefore the assigned suitability class for this habitat is 5.

Code 45 - Nature grasslands

Nature areas covered with grass. These areas are not managed intensively.

The jackal can hunt for rodents (Markov & Lanszki 2012) and forage for fruits and seeds (Radovic & Kovačić 2010). In addition, this habitat can provide resting spots which consist of dense vegetation that are difficult for humans and domestic animals to penetrate (Giannatos 2004). Therefore the assigned suitability class for this habitat is 5.

No place to hide: Limited forest cover hampers the availability of suitable habitat for lynx in the Netherlands

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Abstract: In Europe, centuries-long of overharvesting and hunting of large herbivores and carnivores has resulted in extinctions of large mammals, such as the lynx (*Lynx lynx*). With the expansion of lynx distributions via recolonisation and reintroduction programmes, it is possible that the lynx will again recolonise the Netherlands. This study identified the most important predictors for lynx habitat suitability in the Netherlands and areas in the Netherlands where the ecological requirements of the lynx are met. The habitat suitability model showed that forest cover is the most important factor limiting the potential for the lynx in the Netherlands. The model shows that only four patches with suitable habitat of sufficient size to support at least one female lynx. Only one patch, covering the Veluwe, has enough room for four female territories and one male territory. The total range of suitable lynx habitat in the Netherlands amounts to 1054 square kilometres, although these patches are disconnected. While the species' selectiveness for forest might decrease over time through increased plasticity, the Netherlands has a very limited of amount of forestland, which is highly fragmented. We therefore conclude that the Netherlands' fragmented forests are not suitable for sustaining a viable lynx population at this moment.

Keywords: Eurasian lynx, recolonisation, reintroduction, habitat suitability model, the Netherlands.

Introduction

In Europe, centuries-long of overharvesting and hunting of large herbivores and carnivores has resulted in the local, regional and/or complete extinctions of large mammals, such as auroch (*Bos primigenius*), tarpan (*Equus ferus ferus*), lynx (*Lynx lynx*), brown bear (*Ursus arctos*) and wolf (*Canis lupus*) (Szafer 1968, Vereshchagin and Baryshnikov 1984, Berger et al. 2001, van Vuure 2002), although remnant populations of lynx have managed to survive in the Carpathian Mountains, the Balkans, Scandinavia and Eastern Europe (Breitenmoser 1998). In the second part of the 20th century, the Bern Convention and later the European Habitats Directive gave species such as the lynx some legal protec-

tion (Trouwborst 2010). Although poaching is still a threat to large carnivores (Liberg et al. 2012), lynx populations have increased and expanded their distribution throughout Europe over the last four decades. In the European large carnivore census of 2012, lynxes were distributed over 23 countries and can be grouped into ten subpopulations, five of which are the result of reintroduction programmes (Kaczensky et al. 2013). This information has recently been updated for 2012-2016, and according to this latest update the total number of lynxes in Europe (excluding the populations in Russia and Belarus) is estimated to be between 8,000-9,000 individuals (European Commission 2019; figure 1).

With the expansion of lynx distributions via recolonisation and reintroduction programmes, and the knowledge that the lynx lived in the Netherlands in the past (Groot Bruinderink 1997), it is possible that lynx will again recolonise the Netherlands in the future, be it naturally or through human intervention (Groot Bruinderink 1997, Groot Bruinderink et al. 2006). Because of this, it is of scientific interest to identify areas where lynx could most likely live in the Netherlands. An earlier exploratory study, based on literature analysis and expert judgement, assessed the possibilities of reintroducing the lynx in the Netherlands (Mulder 1992). However, this study was limited to the Veluwe (the Netherlands' largest forest) and was not able to make use of the potential of currently available geographical information systems (GIS) to fully assess the potential of the Netherlands for lynx.

GIS analysis can assess the potential distribution of lynx populations by using habitat suitability models. Hirzel & Le Lay (2008) define habitat suitability models as operational applications of the ecological niche, using environmental variables to predict the presence/absence and the abundance of a species throughout a study area. A habitat suitability model can cover both natural and man-made, environments and take into account constraining factors, such as the presence

Figure 1. Eurasian lynx distribution in Europe 2012-2016. Dark blue cells: permanent occurrence. Light blue cells: sporadic occurrence. *From: European Commission 2019.*

of urban areas, geographical barriers and human disturbance, and beneficial factors, such as vegetation type, food availability and corridors. To accurately predict the suitability of habitats, current habitat use is analysed, often by use of multivariate analysis, after which a predictive model can be produced and validated (Mladenoff et al. 1999, Schadt et al. 2002, Huck et al. 2010).

In this study, we try to identify the most important predictors for lynx habitat suitability in the Netherlands and to identify areas in the Netherlands that meet the ecological requirements of the lynx.

Methods

To build the habitat suitability model of lynx in ESRI ArcGIS 10.0, we used the parameters that have been found to be the best predictors in validated habitat suitability models of the lynx in Europe and North America: land use, human population density, road density

and forest cover (Glenz et al. 2001, Schadt et al. 2002). Prey density was not considered a potential limiting factor, as the main prey species (roe deer, hare and rabbits) are abundantly available throughout the Netherlands.

The land-use map used in this study was the LGN6 map from Alterra Wageningen UR. We transformed all land use classes into five general classes: agricultural land, urban areas, water bodies, forest and other nature areas. For computational reasons, we reduced the resolution from a 25x25 metre to a 250x250 metre grid. When multiple land types of land cover existed in one grid cell, the most dominant was expressed.

Human population densities were extracted from data from the Dutch Agency for Statistics (CBS). The vector-based map was converted into a 25x25 metre grid map and the resolution of the grid map was then reduced to a 250x250 metre grid to align the scale with the land use map. By first converting the data into a high-resolution grid and then reducing it to a lower resolution, we softened the harsh edges in population density between adjacent polygons.

The TOP10NL map of 2011 was used to calculate road density from primary and secondary roads. From this map, we selected all paved roads suitable for motorised traffic. We made a 250x250 metre grid and inserted the road dataset into this grid and then calculated the road length (in kilometres) within each grid cell.

The base maps of the parameters were merged using the union function. We deleted all grid cells with no land cover. In total, habitat suitability was analysed for 50,168 250x250 metre grid cells.

From the base map we identified all the grid cells with a human population of 25 people or more, a road density that exceeded 500 metres per square kilometre, had no water or were identified as urban areas (Schadt et al. 2002, Basille et al. 2009, Huck et al. 2010). Based on the resulting areas, we used the random point creator and buffered these points with a diameter of one kilometre. We then calculated the percentage of forest cover and percentage of coverage with agricultural lands within each circle. Lynx require at least 50% forest cover and can deal with a maximum of 10% agricultural lands (Schadt et al. 2002, Basille et al. 2009, Huck et al. 2010). We selected all circles that met these requirements and dissolved them with their neighbouring patches into bigger polygon patches. Lynx require territories of an average 100 km^2, with a minimum of about 60 km^2 for female lynx and more for male territories (Schadt et al. 2002, Molinari-Jobin et al. 2007, Schmidt et al. 2009). Territories can overlap across sexes. Of the areas that met all the parameters, we selected the patches that had the minimum size of 60 square kilometres.

Validation of the model is, unfortunately, not yet possible as there are no wild living lynxes in the Netherlands. Therefore, we made five extra maps to test the sensitivity of the habitat suitability models to changes in the most important factors; forest cover and road density. Whereas lynx normally require at least 50% forest cover, we also tested for 12.5%, 25% and 37.5%. In addition to the 500 m per square kilometre road density we also tested for 400 and 600 metres of road per square kilometre. As road density and human population density are known to strongly covariate (Glover & Simon 1975), we assumed this would also cover the effects of population density.

Results

The map resulting from the habitat suitability model (figure 2) shows that when all habitat demands are met, the Netherlands has five patches that can sustain at least one territory. The four smaller patches could not sustain a male territory and only one patch (in the Veluwe) could sustain a male territory next to several female territories. The total range of suitable lynx habitat amounts to 1054 square kilometres. However, these patches are not connected with each other.

The sensitivity analysis showed no signifi-

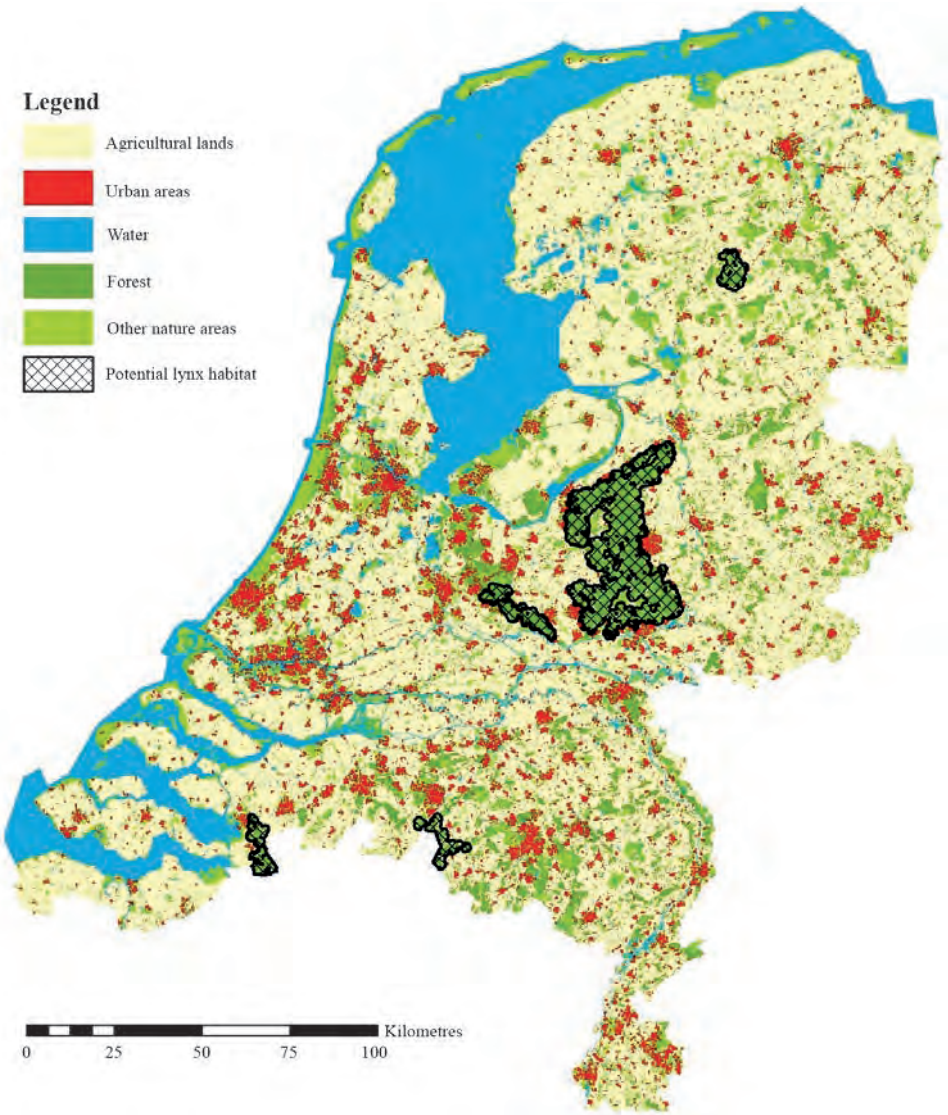

Figure 2. The maximum potential distribution of lynx in the Netherlands when taking all habitat demands into account (only grid cells with: road cover <500, human population >25, forest cover >50%). The total area with suitable area over the four patches is 1054 km^2. The four smaller patches cannot sustain a male territory, only the largest patch (the Veluwe) can sustain a male territory next to several female territories. *Map: G. Lelieveld, Vrije Universiteit / Alterra WUR.*

cant changes after changing the road density parameter. However, the sensitivity analysis did show that the minimum requirement of 50% forest cover over an area of at least 60 square kilometres was the most limiting factor for the suitability of habitat for lynx, as shown in figure 3. The maps show that the amount of suitable habitat for lynx increased from 1054 km^2 to 1575, 2275 and 4163 km^2 respectively, under the different selected criteria for forest cover.

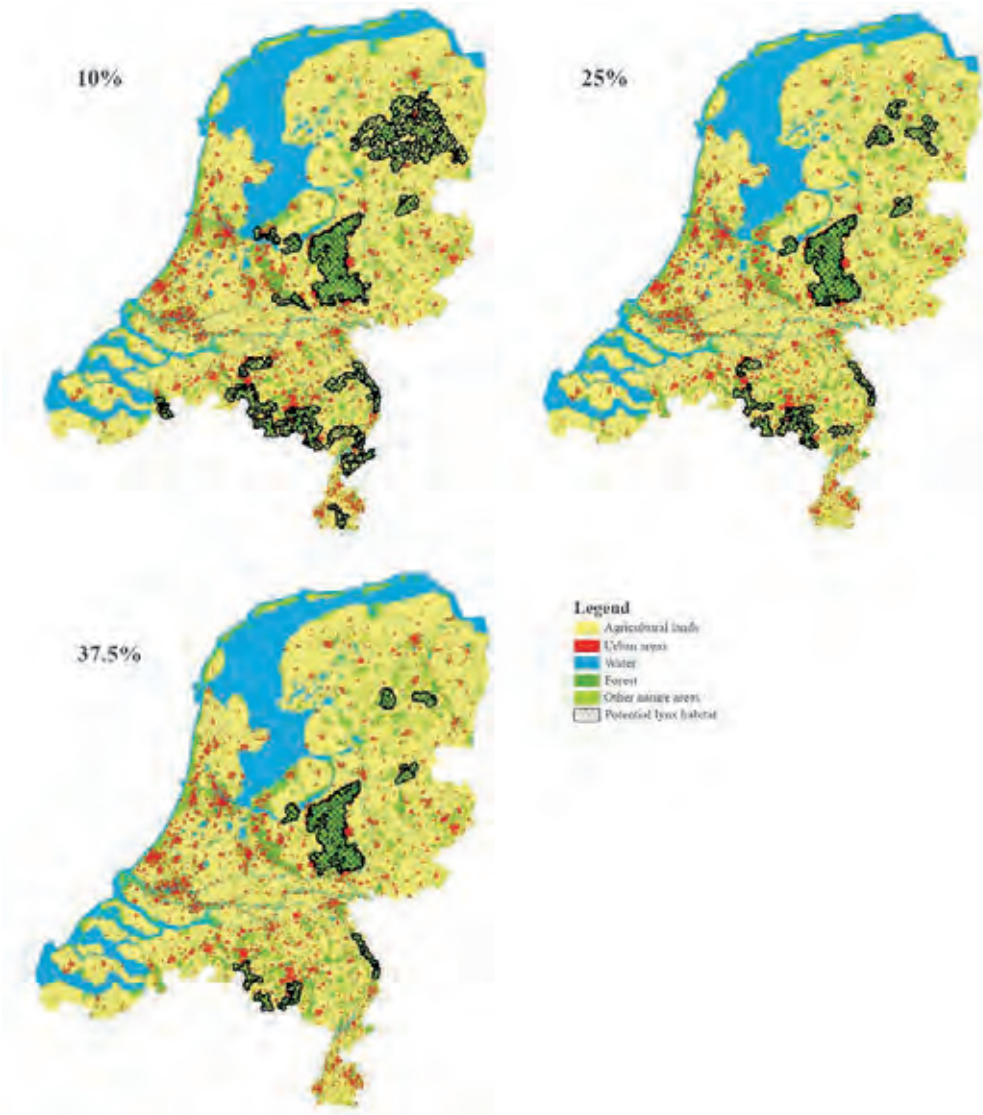

Figure 3. Output of the sensitivity analysis for the potential distribution of lynx assuming its tolerance to lower levels of forest cover (37.5%, 25% and 10% respectively) (with no maximum for cover of agriculture). *Maps: G. Lelieveld, Vrije Universiteit / Alterra WUR.*

Discussion

This study shows that habitat suitable for the lynx in the Netherlands is limited to a small number of isolated patches. This is in line with the assessment of Mulder (1992), although the results of this study more clearly and objectively show the most limiting factor: the low forest cover throughout the Dutch landscape, which would severely restrict the viability of a lynx population in the Netherlands. Because of this, the lynx would not be able to achieve a sustainable population in the Netherlands, unless the country's forests are actively reconnected. There has been policy on reconnecting nature areas in the Netherlands for 25 years, but it is

currently inadequate to support a viable lynx population. Limited forest cover might also be a constraint on the expansion of lynx populations elsewhere in Europe. The latest census (Kaczensky et al. 2013), which shows trends in the ten European lynx populations, reveals an increase in the lynx populations in Finland and the Jura Mountains, with the others remaining stable or even decreasing. It seems that legal protection by itself is not enough to restore lynx populations to their historic ranges (Breitenmoser 1998). As the lynx is highly averse to open areas, fragmented landscapes might prove a barrier to its dispersal. The lynx also finds it difficult to hunt in highly fragmented landscapes. Stahl et al. (2002) found that lynx were eight times less likely to attack sheep in meadows that were at least 250 meters away from forest than those immediately adjacent to forest cover. This strengthens the outcomes of the sensitivity analysis, which shows the lynx to be highly sensitive to changes in forest cover. This suggests that the restoration of large continuous forests in Europe might well prove to be an important factor in restoring European lynx populations.

In the habitat suitability analysis, several generalisations were necessarily made that might have influenced the results. First, the human population dataset was based on the number of people per neighbourhood, a more precise human population would have given more accurate outcomes. Also, all paved roads were given an equal weighting in this study, due to unavailability of data there was no correction for traffic intensity. In addition, minimum territory size for the lynx was based on the needs of females as male lynx territories usually cover several female territories. All these generalisations simplified reality for the purposes of modelling. To test whether these generalisations overly influence the model the model could be validated using lynx populations abroad, but most of the relevant data is difficult to access.

In this study, we solely focussed on ecological suitability of habitat for lynx. The European large carnivore census (Kaczensky et al. 2013) also featured the results of a questionnaire in which European experts were asked to identify the major threats facing large carnivores face in their countries. Almost all lynx experts ranked low acceptance and persecution as the biggest threats to the species (Kaczensky et al. 2013). The low acceptance of lynx might provide an extra limitation on its dispersal capacity. Molinari-Jobin (2003) argues that for lynx to spread across barriers and found a new (sub)population, a relatively strong stimulus is needed, such as strong demographic pressure that would drive emigration from the source population. "However", she states, "high local lynx abundance results generally in a hefty controversy, as local people do not accept peak lynx densities" (Molinari-Jobin 2003).

It is possible that individual lynx will show up in the Netherlands, as the fragmented lynx populations in Western Europe are slowly expanding (Kaczensky et al. 2013), although at the time of writing (March 2019) there have been no verified sightings of lynx in the Netherlands. This study has only focussed on potential suitable habitat within the Netherlands itself, although it is possible that the lynx may find suitable habitat patches in the border regions with Germany or Belgium. Due to limited access to the relevant data for Germany and Belgium, such an assessment was beyond the scope of this study.

Conclusions

This study assesses the viability of the lynx returning to the Netherlands. Our habitat suitability analysis shows that the Netherlands has only four suitable (and unconnected) habitat patches. The study also shows that the Eurasian lynx's strong preference for forest is the most limiting factor. This preference for forest might decrease over time through increased plasticity, although the amount of forest in the Netherlands is low

and highly fragmented. Therefore, we conclude that the fragmented forests of the Netherlands cannot sustain a viable lynx population at this moment.

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Samenvatting

Het huidige bosareaal in Nederland is onvoldoende voor vestiging van de lynx

In Europa heeft eeuwenlange overexploitatie en jacht van grote herbivoren en roofdieren geleid tot het uitsterven van grote zoogdieren zoals de lynx (*Lynx lynx*). Met de uitbreiding van het leefgebied van lynxen via rekolonisatie en herintroductieprogramma's is het mogelijk dat lynxen Nederland opnieuw koloniseren. Deze studie identificeert de belangrijkste voorspellers voor geschikt leefgebied voor lynxen in Nederland en de gebieden die voldoen aan deze ecologische vereisten. Het habitatgeschiktheidsmodel laat zien dat bosareaal de belangrijkste limiterende factor is voor potentieel leefgebied voor lynxen in Nederland. Het model laat zien dat slechts vier gebieden met geschikt leefgebied van voldoende grootte zijn om tenminste één vrouwelijke lynx te herbergen. Eén gebied, de Veluwe, heeft voldoende ruimte voor vier territoria van vrouwelijke lynxen met, overlappend, één territorium van een mannelijke lynx. De totale oppervlakte van geschikt leefgebied voor lynx in Nederland is 1054 vierkante kilometer; deze gebieden staan echter niet in verbinding met elkaar. Hoewel de afhankelijkheid van de soort voor bosareaal in de toekomst afneemt door toenemende plasticiteit van de soort, heeft Nederland een zeer beperkt areaal aan bos, dat bovendien gefragmenteerd is. Wij concluderen dat het gefragmenteerde bosareaal van Nederland op dit moment ongeschikt is voor een levensvatbare populatie van de lynx.

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Damage to dykes and levees in the Netherlands is extensive and increases with muskrat (*Ondatra zibethicus*) density

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Abstract: The muskrat (*Ondatra zibethicus*) is an invasive species in the Netherlands. Its burrowing habits are alleged to threaten the integrity of the extensive water control infrastructure, posing a public safety hazard in this densely populated, low-lying country. A national control program currently traps and kills tens of thousands of muskrats each year. The costs (annually about € 35M) as well as concerns raised by animal welfare groups have raised questions about whether the control program could be improved, and even whether it is necessary at all. To better quantify the extent of putative damage, 2634 km of dykes, levees and banks were inspected annually (2013-2016) for 'major', and 220 km for 'minor' damage. The study was co-organised with a large-scale experiment (reported elsewhere) manipulating muskrat control effort in 117 randomly-selected 5x5 km squares on the national reference grid. We estimated the mean density of major damage at 0.50 ± 0.05 s.e. and that of minor damage at 17.6 ± 3.8 s.e. per kilometer of bank/levee. For both major and minor damage, there is a significant and positive relationship with the average size of the muskrat catch in the same 5-km square over the previous six years. We also found that various types of standard bank protection structures were not effective as preventive measures against burrowing.

Keywords: Invasive Alien Species (IAS), pest-species, burrowing, dyke-failure.

Introduction

Due to the many waterways bordered by luxuriant vegetation, the presence of few predators and a mild climate, the Netherlands provides ideal habitat for the muskrat (*Ondatra zibethicus*), an invasive species in Europe. Muskrat numbers and distribution grew rapidly after its arrival in the Netherlands in 1941. A control programme was immediately started, because it was feared that muskrat burrows could compromise the integrity of

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Figure 1. Typical muskrat burrows. Above, left: projections of three typical forms. Adapted f*rom: COW 1984*. Above, right: burrow excavated from a bank, after filling with styrofoam. *Photo courtesy: M. Akkermans, STOWA*. Below, left: cross section. *From: COW 1984*. Below, right: excavated burrow in a levee. *Photo: H. van Hemert*.

dykes, and hence pose a serious public safety threat (Verkaik 1990, Barends 2002). The dike system in the Netherlands is extensive and essential to safety from flooding. There was also concern about other effects such as the occurence of sink holes in roads along waterways, as well as economic damage (Gaaff et al. 2007).

Muskrats burrow to create shelter and sites for reproduction. Burrows vary in form from short, single tunnels to a network of lengthy tunnels interspersed with chambers. The entrance is usually submerged, presumably to reduce detection by predators. The outline and dimensions of typical burrows are presented in figure 1. Based on measures of five complete burrow systems (made by injecting liquid styrofoam and excavating the cast), burrow systems measure 2-6 m in width, extend 1.5-6 m into banks with nest chambers of 50 cm diameter, and entrances of 15-25 cm diameter (Akkermans 2014). The muskrats dig throughout the whole year as existing burrows are expanded to accommo-

date successive litters, and dispersing young animals establish their own burrow systems. Furthermore, muskrats may abandon established burrows and move to a new site if they are disturbed by predators, if the burrow is damaged by livestock or tillage, or if the water level changes and exposes or floods a burrow and upward digging is restricted.

The tunnels and displacement of soil that result from burrowing affect the hydraulic characteristics of dykes and levees. Even burrows that partially penetrate a levee can cause or contribute to an increase of seepage, internal erosion of embankment materials that may lead to 'piping' (due to shortening of seepage paths), perforation of impermeable components (revetments, clay covers), decreased dyke height due to collapsed burrows, direct seepage (by 'through-embankment' burrows), and decreased stability due to saturation of the levee. Over time, erosion may exacerbate the damage, eventually leading to a breach. Examples of levee breaches caused by animal burrowing can be found in Bayoumi & Meguid (2011) and in the International Levee Handbook (CIRIA 2013).

The need for muskrat control in the Netherlands to avoid such damage and risks has long been advocated (Ritzema-Bos 1917, Kluyver 1937, Thijsse 1937, van Koersveld 1953, Doude van Troostwijk 1976, Barends 2002), but systematically collected data on the extent of damage are lacking. This study aimed to quantify the damage attributable to muskrats, and to assess whether and how this is related to the number of muskrats in an area. To do so we measured the number of muskrat excavations found in randomly selected transects along waterways, and related it to the muskrat catch made in the same area over preceding years.

Animal welfare and some other organisations advocate the use of various bank protection measures (i.e. cladding or other hardened surfaces) as alternatives to muskrat control. These measures aim to make burrowing impossible or irrelevant (Spoorenberg 2007, Zandberg et al. 2011) and thus eliminate the need to capture and kill animals. We assessed the extent to which standard types of bank protection are effective in lowering structural damage by muskrat burrowing. Our main hypotheses are that the damage attributable to muskrat increases with the number of muskrats in an area (as estimated by the recent catch), and that some types of bank protection may be effective in preventing muskrat from burrowing.

Methods

Study area

The Netherlands (50°-54°N, 3°-8°E) is characterised by flat topography, with most of the country at an elevation between -10 and + 20 m Dutch Ordnance Level. Large areas are below sea level and about two-thirds of the country is protected by dikes against flooding. The low-lying western and northern parts of the country are characterised by peat and clay soils, while sandy soils predominate in the east and south. Most areas below sea level are anthropogenic, caused by peat extraction or achieved through land reclamation. Since the late 16th century, large polder areas have been created through elaborate drainage systems that include dikes, canals and pumping stations. The Netherlands has a dense human population of over 17 million on roughly 33,700 km^2. It has a mild maritime climate with average monthly temperatures ranging from 6°C in winter to 23°C in summer. Average annual precipitation is about 800 mm. Intensive agriculture dominates land use, occupying more than 55% of the country. Muskrats are found throughout the country, but over the past decades the catches have been especially high in low-lying peat and clay areas.

Data collection

This study formed part of an extensive investigation by the Dutch Water Authorities

('Waterschappen') into muskrats in the Netherlands. This study was integrated into a large-scale manipulative experiment (described in full by Bos et al. 2016) testing the effectiveness of trapping in reducing muskrat numbers. Briefly, the experiment took place nationwide from 2013-2016 in 117 5x5 km squares (of which the national reference grid contains a total of 2202), randomly selected from three 'strata' representing regions of historically high, medium and low muskrat catch. The experiment either increased or decreased trapping effort by 30%, or in control 5-km squares kept trapping effort at the level during the reference year preceding the start of the experiment. Effort is measured as hours of trapping time per kilometre of waterway per year. The experiment offered the opportunity to combine assessments of damage with a large set of other measures.

Burrow density and the incidence of damage was measured during the experiment with a program of inspection of banks and levees. Inspections took place annually during February and March, 2013 - 2016, and were carried out by two persons, one an experienced, professional muskrat trapper and the second a water infrastructure expert, both employed by the Dutch Water Authorities. Burrows are usually invisible from the surface, and have underwater entrances, and hence expertise and experience are required to be able to detect and score the extent of damage and to establish the cause.

Muskrat burrow entrances, eroded banks, slides of a slope/bank, depressions in the bank or levee, and bars in the waterway created by excavated soil were all classed as 'damage'. Each instance was judged by the inspectors as (a) certainly caused by muskrats, (b) possibly caused by muskrats, or (c) not due to muskrats, and further classified as 'major' or 'minor'. Damage was defined as 'major' if any of the following criteria were met: the volume of displaced soil exceeded 0.5 m^3, a depression in the bank or levee exceeded a surface area of 2 m^2 or a depth of 0.2 m, the length of the damaged or eroded bank exceeded 2 m, or the cost for repair exceeded € 2500. Damage not meeting any of the 'major' criteria was classified as 'minor'.

All instances of major damage were described, photographed, exact location noted, and given a unique identifier. The age at observation of the damage was judged (<3 months, 3-12 months, 1–2 years, >2 years) based on knowledge of the historical trapping record at that location, the morphology of the damage and the vegetation. For each instance of major damage the number of burrow entrances (*n*), the estimated cost of repair (euros), the surface area of settlements/sinks, and the volume of displaced soil were classified in three to five categories. In addition, the status (inhabited by muskrats or abandoned) and type of bank protection and soil type, was noted. The description was updated at each subsequent inspection. All these data were registered in a standardised way with a custom-designed application installed on a handheld device. Information from the previous year(s) was available to the observers.

Teams searched for major damage by walking along dikes and levees. The length of the banks and levees present in a 5-km square ranges from 0 up to 1560 km and 75 km, respectively, of which a portion (up to 44 km of banks and up to 20 km of levees, or 5-100%, depending on the total length in each 5-km square) was inspected. The inspected sections were chosen to be representative for each 5-km square with respect to vegetation, land use and water depth. To avoid edge effects the sections were located in the interior (middle 3 km x 3 km portion) of a 5-km square. The same sections, totalling 2634 km, were inspected annually.

Minor damages were located by carefully searching along the shoreline, including detailed examination by probing below the waterline. This was much more time-consuming than the search for major damage, because minor damage occurs more frequently and the inspection often required for

an observer to proceed in the water. Therefore, we selected 10 representative sub-sections for inspection and measurement of minor damage. Sub-sections averaged (mean ± se) 263 m ± 1.7 in length, were homogenous in bank type, and were positioned in the interior (middle 3 km x 3 km portion) of a 5-km square to avoid edge effects. Minor damages in each 5-km square were categorised into burrow entrances, eroded banks, slides of a slope/bank, depressions in the bank or levee (= settlements/sinks), and shallow bars in the waterway. Minor damages were counted per category per sub-section. The annual number of sub-sections inspected rose from 624 in 2013, to 853 in 2016 (average 774). A summary of the total length inspected of banks and levees is given in table 1.

The datasets generated during and/or analysed during the current study are available in the University of Groningen repository, DataverseNL https://hdl.handle.net/10411/EFR9TN

Table 1. Summary of the total length (km) of banks and levees present in the 117 experimental 5-km squares (divided into those assigned to the 39 control, 39 increased effort and 39 decreased effort treatments), and of the lengths inspected for major and minor damage. The same 2634 km of banks and levees were inspected annually for major damage over the years 2013-2016. The total length of sub-sections inspected for minor damage has varied somewhat between these years and the values for year 2016 are given in the table.

Object		Control	Decreased effort	Increased effort	Total
Banks	Present	16,406	14,142	15,084	45,632
	Major	685	719	701	2,105
	Minor	51	49	50	150
Levees	Present	595	412	526	1,544
	Major	150	164	215	529
	Minor	23	20	28	71
Total	Present	17,001	14,556	15,620	47,177
	Major	835	883	916	2,634
	Minor	73	70	77	220

Analysis

We summed for each 5-km square the number of major and minor damages that had been categorised as (possibly) caused by muskrats, including those repaired in previous years. The density (n km^{-1}) was obtained by dividing the number of major damages counted (n) by the total length inspected (km) per 5-km square. The density of minor damage was calculated by averaging the density (number of burrow entrances (n) divided by transect length in km) over all the transects in each 5-km square. The number of burrow entrances is the aspect of minor damage that was most prominent, least subjective, and easiest to interpret. We removed very short (<10 m) and long transects (>800 m) from the analysis, to increase consistency and robustness.

We obtained from the Dutch Muskrat Control Program (which has maintained accurate records; see van Loon et al. 2017) and from Bos et al. (2016) the annual catch and effort expended in each 5-km square, and from these we calculated the cumulative catch (number of muskrats trapped per kilometer of waterway per year) for periods of 1-10 preceding years. The values for cumulative catch were log-transformed in order to meet assumptions of normality and homogeneity of variance. We also obtained for each experimental 5-km square the dominant soil type (clay, sandy-clay, peat and sand), and the type of treatment in the contemporaneous large-scale experiment.

To test whether the density of damage depended on experimental treatment and the history of the catch we competed linear mixed effect models using the package lme4 (Bates et al. 2015), in the R programming environment (R Core Team 2017). The model set (table 2) comprised a null model with only 5-km square as a random intercept, a model with year of measurement (2013-2016, coded from 1-4 and termed 'year') as predictor in addition to the random effect of 5-km square, mod-

Table 2. Ranking of the top 8 models competed to assess the density of major damages (n km^{-1}).
Year = year of measurement (2013-2016); catch = the (log_transformed) cumulative catch (log (n km^{-1})) in the 5-km square over the five or six years preceding each year; soil = dominant soiltype in the 5-km square; treatment = type of treatment in the contemporaneous large-scale experiment. The models are ranked according to AICc values. The first model (bold) is best supported by the data. K = number of free parameters; AICc = Aikake Information Criterion; delta AICc = difference in AICc value with best model; weight = AICc weight.

Model *	K	AICc	delta_ AICc	Weight
Year*(6y catch)	6	-26	0	0.90
Year*(6y catch) + soil	9	-22	5	0.08
Year*(5y catch)	6	-18	8	0.02
Year + (6y catch)	5	51	77	0
Year	4	102	128	0
Year * treatment	8	102	128	0
Year + treatment	6	105	131	0
null	2	210	237	0

* The null model contains only 5-km square as a random intercept. Each of the other models includes this random effect of 5-km square. The other models includeYear as predictor; Year + treatment as additive predictors; Year + treatment and the Year* treatment interaction; Year + cumulative catch over 1, 2, 3, 4, 5, 6, 7 and 10 preceding years as additive predictors; Year + cumulative catch over 1, 2, 3, 4, 5, 6, 7 and 10 preceding years as additive predictors and the year*catch interaction, either with or without soil class as a fixed factor.

els with year and treatment as predictors in addition to the random effect of 5-km square (additive: year + treatment and in interaction: year * treatment), and models with year and the (log-transformed) cumulative catch per km over 1, 2, 3, 4, 5, 6, 7 and 10 years respectively (additive: year + cum. catch and in interaction: year * cum. catch), with and without dominant soil type as additional fixed factor. The response variables 'density of major damage (n km^{-1})' and 'density of minor damage' (n km^{-1}), were log-transformed. The influence of individual data points on the final model predictions was assessed by calculating Cook's distance using the package Influence. ME (Nieuwenhuis et al. 2015).

The numbers of major damages (i.e. burrow systems) still inhabited by muskrats were tabulated in a contingency table with regard to age at observation and volume, hypothesising that the severity of damage would increase with age. Using a Chi-square test we tested the null hypothesis of independence of rows and columns.

The proportion of the number of entrances observed in different types of bank protection was compared to the proportion of length of sections inspected for these sections using a Chi-square test, to quantify the extent to which these types of bank protection could function as 'preventive measures'. To do so, the number of burrow entrances observed and the lengths of waterway inspected were averaged over the four years of study, and the expected number of burrow entrances was calculated by multiplying the overall mean density by the inspected length.

Results

A total of 1924 major damages classified as Muskrat-caused were detected during annual inspections of 2634 km of dikes and levees. Each year the total number of major damages attributable to muskrats increased by several hundred (mean 434 ± 44 s.e.) Most of these were new, but some had gone undetected in previous inspections. In 2016 (the last of the four annual inspections), the mean incidence of major damage was 0.50 km^{-1} ± 0.05 s.e. The majority of cases reflected major damages that were judged to be abandoned (83%), while 17% were still inhabited. About 10% of the cases were repaired annually. Most of the major damage was found in the low-lying 5-km squares in the north-east (province of Groningen), the delta of the river IJssel (province of Overijssel), and Zuid-Holland (fig-

Figure 2. Map of the 117 experimental 5-km squares, soil classes, and the density of major damage (n km^{-1}) observed in 2016.

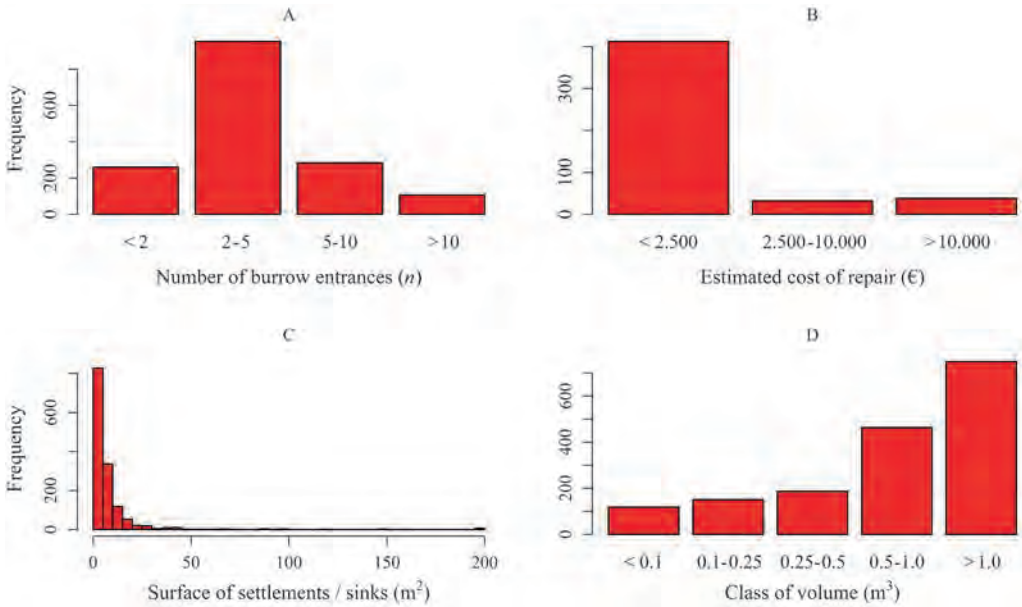

Figure 3. Histograms of the size of the major damages recorded. Panel A: number of entrances; Panel B: estimated costs of repair; Panel C: surface area of settlements and sinks; Panel D: estimated volume of soil displaced.

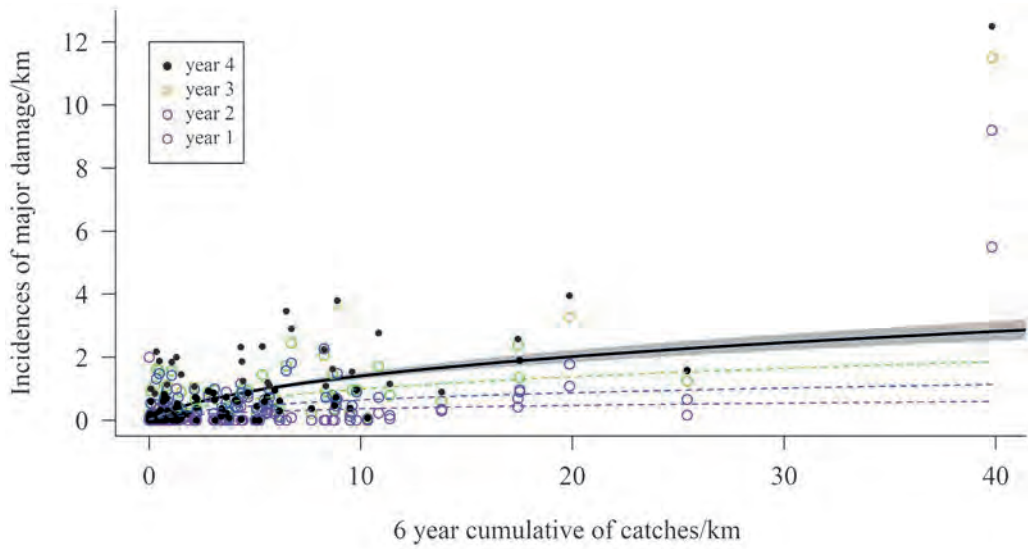

Figure 4. The relation between the density of muskrat-caused major damage in 2013-2016 (years 1-4, respectively) and the cumulative catch in the corresponding 5-km square during the preceding six years. Average inspected length per 5-km square was 22.5 km ± 0.89 s.e. The black line, log(y+1) = 0.035 + 0.35*log(x+1), represents the linear mixed regression model fitted for year 4 (2016), based on repeated observations (n=464) in 116 5-km squares. The grey shading is the 95% confidence interval for that year. Marginal R^2=0.38, conditional R^2=0.81.

Table 3. Fixed effect sizes in the top model of the density of major damages (see table 2). The model includes a random effect of 5-km square. Marginal R^2=0.38, conditional R^2=0.81. Significance levels: *** =0.001, ** =0.01, * =0.05.

Fixed effects	Estimate	Std. Error	df	*t* value	Pr(>|*t*|)	Significance
Intercept	0.017	0.051	226	0.33	0.74	
Year	0.005	0.012	246	0.38	0.70	
Catch	0.042	0.035	226	1.22	0.22	
Year*catch	0.077	0.008	246	9.44	<2e-16	***

ure 2). These are the regions responsible for the majority of catches prior to and during the study period. Many 5-km squares in the Netherlands have little damage and regions without damage overlap to a large extent with areas where muskrat catches have been low or non-existent.

A summary description of major damage is provided in figure 3. The majority of major damages are characterised by multiple entrances (figure 3A), and had a repair cost less than € 2500 (figure 3B). The area of depressions or slumps associated with burrowing was in the majority of cases less than 10 m^2, but was occasionally estimated at 50 m^2 or even larger (figure 3C), while the volume of excavated soil was smaller than 1 m^3 in 58% of the cases (figure 3D).

The statistical model for the density of major damages best supported by the data includes the cumulative catch made over the preceding six years, the year of study, and a year by catch interaction (table 2). This model captures the great majority (0.90) of the model weight, and is 5 AIC units lower than the next best model. The top model is depicted graphically in figure 4, showing the cumulative muskrat catch (n km^{-1}, summed 2010-2015) in each 5-km square in relation to the density of major damage recorded in 2013 (year 1), 2014 (year 2), 2015 (year 3) and 2016 (year 4). Effect sizes are given in table 3.

The lines depicted in figure 4 are based on a linear mixed regression model with repeated observations in 116 5-km squares over four years (n=464). With regard to influential data, the Cook's distance for all datapoints was always lower than 0.2, but one 5-km square (identified as 2144 DEC) contributed three influential data points. Excluding it from the analysis did not alter the model ranking.

Table 4. The number of minor damages of all types distinguished recorded during the four years of inspections.

Type of damage	2013	2014	2015	2016
Burrow entrances	1729	2213	2595	3085
Eroded banks	288	548	468	870
Minor slides	354	370	351	442
Settlements/sinks	492	753	739	1084
Shallow bars	26	81	143	127
Inspected length (km)	161	203	217	218

Major damages estimated to be three months or more in age were larger than those found soon after presumed initiation (Chi-square test, P<0.001, n=274). Of damages younger than three months, 24% were in the smallest category (<0.1 m^2), and 22% in the largest (>1 m^2), while of those older than three months more than 60% are found in the largest category.

A total of approximately 16,750 minor damages were registered during the experiment, and are summarised in table 4. The majority of minor damage was in the form of burrow entrances (61%), followed by settlements/sink and eroded banks. The mean incidence of burrow entrances in 2016 was 17.6 km^{-1} ± 3.8 se, but in several 5-km squares densities >100 km^{-1} were observed. The cumulative number of minor damages recorded increased over the four-year period.

The model results for minor damage (den-

sity of burrow entrances) was very similar to that for major damage. The model involving year in interaction with the cumulative number of catches made over the past six years, was best supported by the data (see figure 5). The observed number of entrances per km increased with historical catch rate and over the course of the years.

Table 5 summarises the incidence of minor damage, as measured by the incidence of burrow entrances, in different types of standard bank protection. The density of entrances is not evenly distributed based on the length inspected (Chi-square=73.1, df=4, $P<0.001$), which means that there is an effect of the type of bank protection. Burrow entrances were found in each of the major types of bank protection inspected, except for 'sheet pile', where none were found at all.

Table 5. The number of burrow entrances (one aspect of minor damage) per type of standard bank protection recorded in subsections along waterways in the Netherlands. Data refer to the average numbers observed and average lengths of waterway inspected (with known type of bank protection*) over the four years of study. The number of burrow entrances expected (last column) was calculated by multiplying the overall mean density by the inspected length.

Bank protection	Mean inspected length (m)	Mean no burrow entrances observed	Burrow entrances expected
Sheet pile	3000	0	35
Rip-rap	5032	12	58
Hard revetment	2220	22	26
Braided tree branches or wood	9708	83	112
Natural bank/ slope (vegetated)	168,604	2064	1950
Total	188,563	2180	2180

* sheet piles are sections of sheet materials with interlocking edges; rip-rap refers to rock or other material used to armor the bank or slope against wave attack; hard revetments are sloping structures constructed with asphalt or concrete blocks to protect a bank or slope against erosion by waves.

Discussion

Assertions that muskrats would by their burrowing habits threaten the integrity of dikes and levees were made even before the 1941 arrival of this invasive species in the Netherlands (Ritzema-Bos 1917, Kluyver 1937, Thijsse 1937). The consequent apprehension for public safety was and remains the main reason for the ongoing extensive control program (van Koersveld 1953, Doude van Troostwijk 1976, Barends 2002), which currently costs about € 35 million annually. For the same reason, muskrats are subject to control in Flanders (Belgium) (Stuyck 2008, Vlaamse Milieumaatschappij 2010) and Lower Saxony (Germany) (Fritz & Röver 2015). This study provides the first systematically collected data on the extent of this damage, and supports these assertions. The information is highly relevant in relation to recent European legislation (EU regulation no 1143/2014) on the management of invasive alien species.

The overall average measured incidence of major damage is 0.50 km^{-1} ± 0.05 s.e., and of minor damage 17.6 km^{-1} ± 3.8 s.e. in year 4 of the study. This constitutes a substantial hazard in the Netherlands, given that more than 17,500 km of dikes and levees are present, and much of the country lies below sea level. The density measured in year 4 of the study likely provides the best estimate of the amount of damage present at any time, since it is a combination of the new damage from that year, older damage undiscovered in preceding years, and the known damage from the previous years. It is likely that the densities measured are underestimates. Muskrat burrows are difficult to detect because they are (by definition!) underground and have underwater entrances. Circumstances such as temporary water drawdowns (see figure 6) occasionally make more thorough inspections possible, and reveal burrow densities higher than the averages reported above.

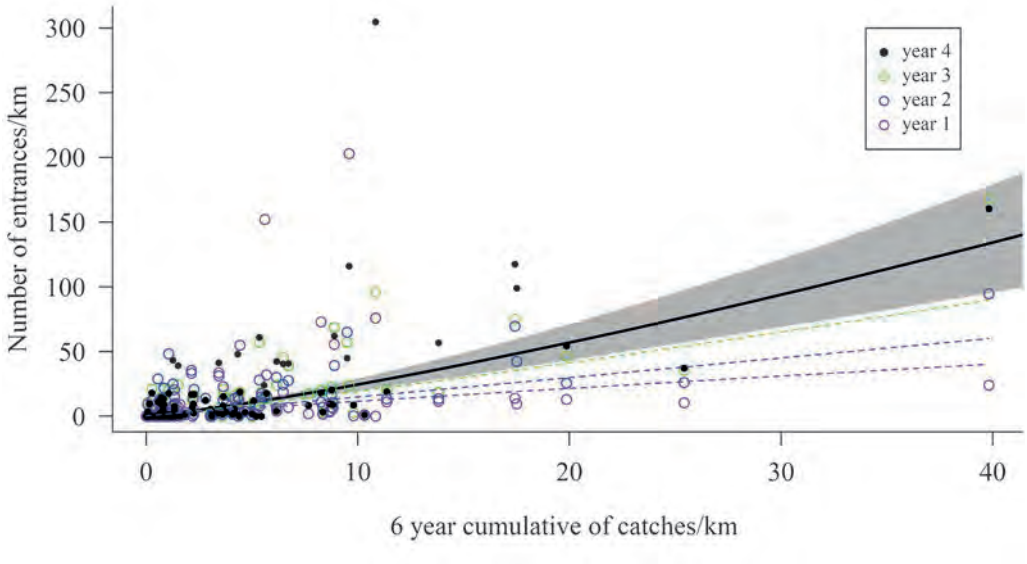

Figure 5. The relation between the density of muskrat burrow entrances (the most frequent type of minor damage) in 2013-2016 (years 1-4, respectively) and the cumulative catch in the corresponding 5-km square during the preceding six years. The black line, log(y+1) = 0.20 + 1.27*log (x+1), represents the linear mixed regression model fitted for year 4 (2016), based on repeated measures in 111 5-km squares. The grey shading is the 95% confidence interval for that year. Marginal R^2=0.45, conditional R^2=0.81. Average annual transect length was 263 m ± 1.7 s.e.

A second important finding of this study is the positive relation established between the muskrat catch and the extent of damage measured (Figures 4 and 5). Although the relationships differ in detail, the density of both major and minor damages rises with the muskrat catch recorded in preceding years, with a period of six years being most informative. Catches are interpreted as a proxy for population numbers, and population modelling by van Loon et al. (2017) corroborates that these measures are positively related. Van Loon et al. (2017) estimated the numbers of muskrat in exactly the same study plots - a posteriori - using a spatially explicit population dynamic model, while Bos & Gronouwe (2018) showed that the relation between damage and cumulative catch presented here also holds using the thus estimated population sizes of muskrat as an explanatory variable.

The study detected no effect of the experimental treatments on the level of damage, though the experimental treatments did alter the catch as predicted (Bos et al. unpublished data, 2016). Presumably this can be attributed to a time lag before the effects on damage are seen, because several years are required until burrows collapse and cause major damage that is visible on the surface. Historical and experimental data (Bos et al. 2019, van Loon et al. 2017) show that the muskrat catch increases strongly in the absence of control, which in combination with the catch-damage relationship quantified here shows that the incidence of damage would also rise.

Our conclusions about the effectiveness of standard bank protection measures are based on hundreds of sub-sections distributed throughout the country. The majority of these were visited repeatedly. Two types of standard bank protection measures, 'sheet pile' and 'rip-rap' clearly had lower incidence of minor damages than expected based on the overall incidence, but frequent burrowing was nonetheless observed in almost all types of bank protection structures. The data thus indicate

Figure 6. Outer slope of the levee along the Veendiep canal, during a drawdown of the water level to facilitate inspection. Several burrow entrances can be seen. March 2012. *Photo: M. Rothengatter*.

these are not effective measures against burrowing, perhaps unsurprising as these measures were designed to protect against erosion rather than against burrowing. In fact, such measures may even complicate matters by camouflaging developing burrow systems. Better knowledge of muskrat burrowing habits might help in this regard. In particular, the maximum depth below the water surface where burrowing takes place, is not yet sufficiently known to design bank protection measures properly. We therefore recommend a study of the burrowing capacity of muskrats.

When evaluating the need for and usefulness of muskrat control, knowledge on the relation between numbers and serious damage is one of the criteria that needs to be considered (Lammertsma & Niewold 2005). Other criteria include the evidence that muskrat density is causally related to control (Bos et al. 2019, van Loon et al. 2017), ethical considerations (Warren 2007, Zandberg et al. 2011) and a lack of feasible alternative methods to maintain safety from flooding. It is recommended to carefully study the feasibility of alternative methods to prevent damage for any given landscape, and provide a cost-benefit analysis (Bos & Gronouwe 2018, Reyns et al. 2018). The relationships between trapping effort and catch, and between catch and damage (this study) underlie such analysis of the most economical long-term management strategy. The options for muskrat control range from 'no control' to 'eradication'. The costs include those of the control program, and of the ongoing inspection and repair of banks and levees. Both are proportional to the numbers of muskrat present. Ceasing control eliminates the cost of the trapping program, but would require substantial investment in bank protection, and would require inspection, as well as repair and maintenance costs. The complete removal (sensu Robertson et al.

2017) of muskrats would require sustained up-front investment in the trapping program, but would lower the costs of control and repair later. The quantitative relationships established here and in van Loon et al. (2017), and Bos et al. (unpublished data), will allow the best course of action to be decided.

Conclusions

There is a significant and positive relation between the burrowing damage observed and historical catches of muskrat. This is valid for minor and major damages distinguished in this study.

Many 5-km squares in the Netherlands have little damage, but on average 0.50 ± 0.05 s.e. incidences of major damage (above the tresholds defined by us) were found per km in 2016. Minor damage occured much more often, with 17.6 burrow entrances / km ± 3.8 s.e. on average.

The average size of major damages is in the order of 1 m^3 of displaced soil, habitations with 2 to 5 entrances and an average surface of 10 m^2.

Muskrat do not avoid banks that are characterised by standard protection measures, such as hard revetments and rip-rap, which have not especially been designed as preventive measures against burrowing.

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Samenvatting

Graafschade door muskusratten in oevers en kades

In Nederland worden muskusratten intensief bestreden. De bestrijding is een middel om de (water-) veiligheid te waarborgen, door graverij in dijken, waterkeringen en andere infrastructuur te voorkomen. Tot in het vorige decennium was het echter een onbeantwoorde vraag of de hoeveelheid schade wel gerelateerd is aan de aanwezige aantallen muskusratten. Tussen 2013 en 2016 zijn daarom de omvang en aantallen van schades, die zijn toe te wijzen aan graverij door muskusratten, systematisch gekwantificeerd in 117 representatieve 5 km x 5 km hokken. Voor de registratie zijn in deze 5-km hokken vaste tracés op oevers en waterkeringen geselecteerd en is gedurende vier jaren de schade door graverij geïnventariseerd. Ieder jaar zijn 2634 km oevers en keringen geïnspecteerd om schadegevallen boven een bepaalde drempel van omvang of verwachte reparatiekosten te tellen en te beschrijven (de grote schades). Om ook niet zichtbare en de

wat kleinere schades goed in beeld te brengen zijn systematisch korte transecten (gemiddeld 263 m lang) 'afgetrapt', o.a. op de aanwezigheid van pijpjes die in de oever of de waterkering zijn gegraven. Over een totale lengte van 220 km is aldus op deze transecten het aantal kleine schadegevallen vastgesteld (kleine schades). De schade-inventarisatie werd georganiseerd in samenhang met een grootschalig, landsdekkend veldexperiment, waarbij is gevarieerd met de bestrijdingsintensiteit en waarover elders wordt gerapporteerd. Voor alle 5-km hokken is informatie beschikbaar over een groot aantal parameters, waaronder bodemtype en aantallen vangsten. De van buiten zichtbare omvang van de schades door muskusratten is veelal gering. De geschatte orde van grootte per geval fluctueert rond 1 m^3 vergraven grond, met meestal 2-5 ingangen onder water op het moment van ontdekking. Meerdere schades bij elkaar of op de verkeerde plek kunnen echter een reëel gevaar voor de veiligheid vormen. De grootste aantallen schades worden in laag Nederland aangetroffen. Dichtheden van grote schades variëren tussen 0 en 12 per km, maar liggen gemiddeld op 0,50 ± 0,05 s.e. gevallen per km. Schades beneden de gestelde drempel van omvang of risico komen veel meer voor, gemiddeld ca. 17,6 ± 3,8 holen per km. Voor zowel de grote als de kleine schades is er een relevant en statistisch significant positief verband aangetoond tussen het aantal schades en het aantal muskusratten dat in de voorgaande zes jaren was gevangen. De resultaten voor kleine schades laten zien dat graverij toch optreedt als de oever beschermd is met harde bekleding en stortsteen. Bij een kadeconstructie met een stalen damwand is evenwel geen schade aangetroffen. De in deze studie verzamelde informatie is waardevol, omdat het één van de essentiële bouwstenen is om een goede afweging te kunnen maken over nut en noodzaak van bestrijding van muskusratten.

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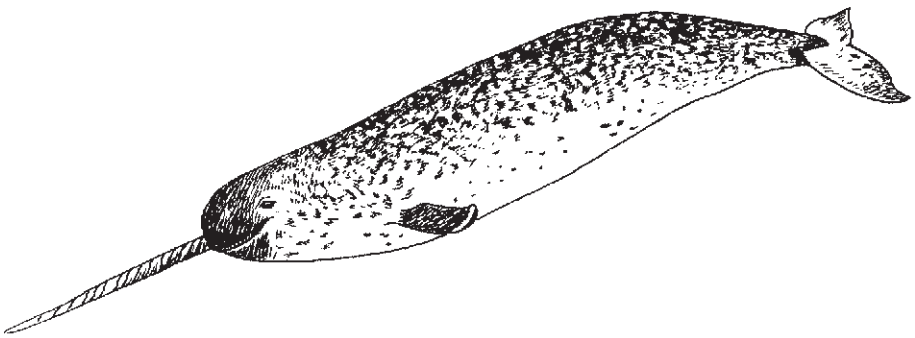

De zee-eenhoorn in kaart gebracht

De zee-eenhoorn in kaart gebracht. Zee-eenhoorns in woord en beeld in de middeleeuwen en vroegmoderne tijd

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Op 10 januari 2019 promoveerde de tandarts-orthodontist en kunsthistorica aan de universiteit van Leiden op een opmerkelijk, en lijvig, proefschrift over de zee-eenhoorn.

De eenhoorn is vooral een mythologisch schepsel. Er wordt in historische beschrijvingen onderscheid gemaakt tussen de (land-) eenhoorn en de zee-eenhoorn. Het bestaan van de land-eenhoorn wordt vanaf de zestiende eeuw, vooral door het ontbreken van fysiek bewijs, toenemend betwijfeld. Wat de land-eenhoorn vooral onderscheidde van een paard was de gedraaide hoorn op het voorhoofd van het fabeldier. Aan deze hoorn werden bijzondere (geneeskrachtige) eigenschappen toegeschreven. Waarnemingen en beschrijvingen van zee-eenhoorns (narwal – *Monodon monoceros*) verlegden de aandacht van de land-eenhoorn naar de zee-eenhoorn, zeker nadat de tanden van narwals als fysiek bewijs voor het bestaan van de zee-eenhoorn konden worden verzameld. Er werd een medisch belang aan de 'hoorn' van de zee-eenhoorn verbonden. Veel auteurs verklaren daarmee de 'plotse' aandacht voor de zee-eenhoorn en het tanen van de aandacht voor de land-eenhoorn.

Zijlstra-Mondt acht het aannemelijk dat narwaltanden via handelsroutes vanuit het noorden Europa hebben bereikt. Al in het jaar 793 blijken er handelscontacten te hebben bestaan tussen Noormannen en het Europese continent en het Verenigd Koninkrijk. Het vroegste bewijs voor de vondst van narwaltanden is te vinden in het werk van de IJslandse geschiedschrijver Arngrímur Jónsson (1568-1648) die een zeereis uit 1126 beschrijft en de daarbij plaatsgevonden schipbreuk op de westkust van IJsland. Op IJsland, zo beschrijft Jónsson, was een *Lükatiorn*, een lijkenmoeras. Vele skeletten van verdronken zeelieden werden er gevonden, maar ook de kostbare '*Dentes balenarum*', voorzien van Rune-tekens, zeer waarschijnlijk handelswaar. Daar de eenhoorn-horens dus echt bestonden werd de vraag naar deze rariteit groot en veel tanden vonden hun weg naar de rariteitenkabinetten en vorstelijke schatkamers. In de collectie van het Rijksmuseum in Amsterdam bevinden zich drie met rune-tekens voorziene narwaltanden, afkomstig uit het bezit van de Duitse keizer Hendrik IV (1050-1106). Een werkelijk vroege en accurate waarneming en beschrijving van de narwal, door Zijlstra-Mondt geciteerd, is van de Dominicaan Vincent de Beauvais (ca. 1190-1264): '*De Monoceros is een zeemonster dat op zijn voorhoofd een zeer grote hoorn heeft waarmee hij tegemoetkomende schepen kan doorboren en een massa mensen kan vernietigen. Maar de goedheid van de schepper jegens het menselijk geslacht heeft hierin voorzien, want omdat het dier geschapen is als een traag dier, kunnen de schepen aan hem ontsnappen zodra hij is waargenomen.*'

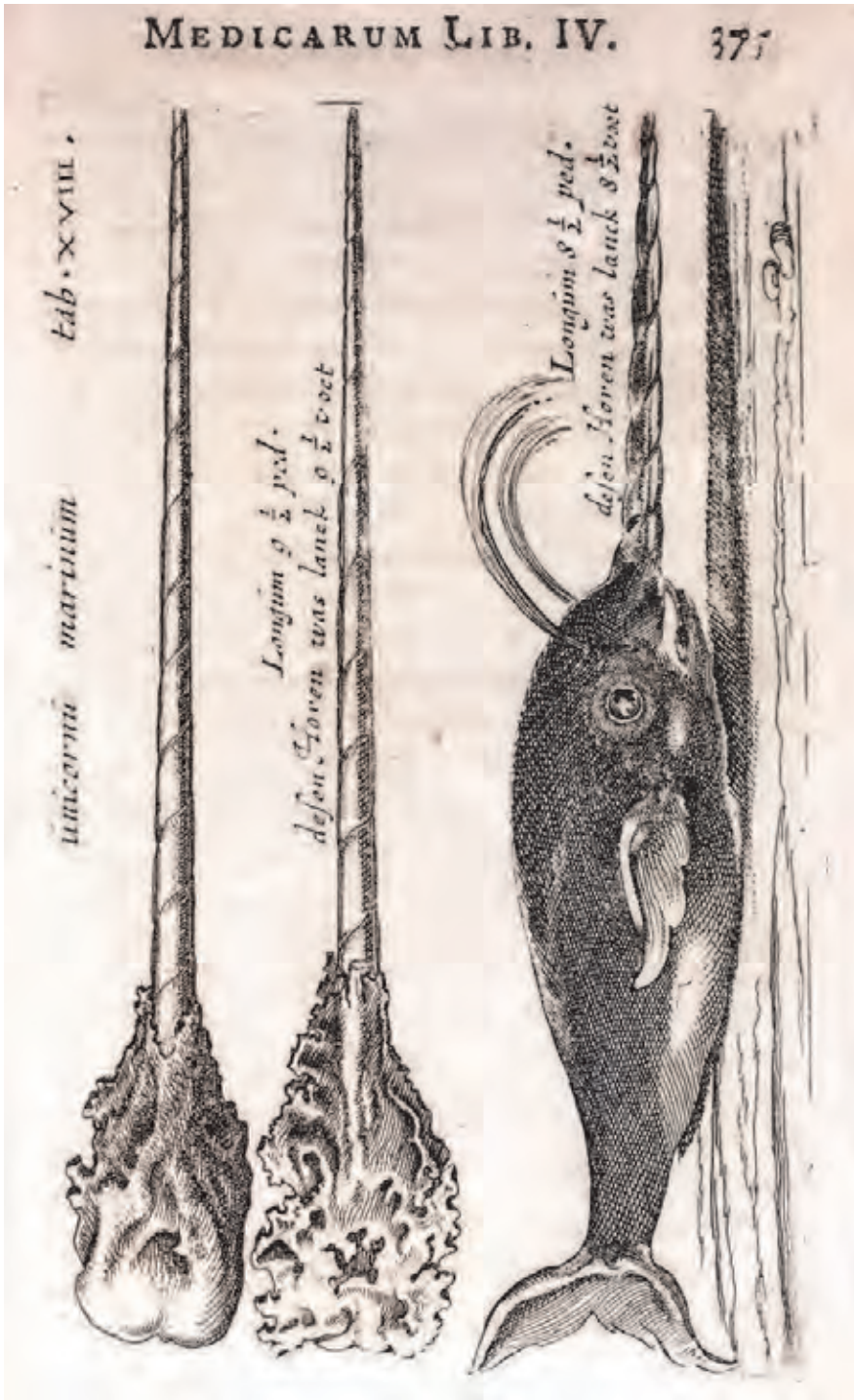
Een vraag die Zijlstra-Mondt zich stelde was of, met de aandacht voor de zee-eenhoorn, de symboliek van de land-eenhoorn werd overgedragen. Het proefschrift voorziet vooral in deze lacune. Het is een uitputtende opsomming van bronnen en afbeeldingen in cartografische bronnen en voorstellingen op kunstwerken van zee-eenhoorns, vooral vanaf de zestiende eeuw. Zij benadert het motief van de zee-eenhoorn in vroegmoderne werken in chronologische volgorde. Hierdoor

is de dissertatie een waar standaardwerk voor eenieder die zich in het mythische schepsel wil verdiepen. Daarnaast is de tekst ook nog eens zeer toegankelijk en op sommige plaatsen meeslepend geschreven. Ik moet professioneel veel dissertaties lezen en dat is niet altijd een onverdeeld genoegen, maar het werk van Zijlstra-Mondt vormt hierop een welkome uitzondering. Ik zal na lezing van het werk niet meer onbevangen langs het paleis op de Dam in Amsterdam kunnen lopen zonder op te kijken naar de '*Amsterdamsche Stede Maeght*' die omringd blijkt door vier zee-eenhoorns.

De mythologische zee-eenhoorn vindt zijn basis dus in de 'echte' zee-eenhoorn: de narwal. Cetologen en de in walvisachtigen geïnteresseerde lezers van *Lutra* zullen vooral over de historische informatie over deze enigmatische dolfijnensoort willen lezen in relatie tot het mythologische fantasiedier. Zij komen in het boek aan hun trekken.

Ik ken de zeventiende-eeuwse medische literatuur goed, dus was blij verrast met het feit dat Zijlstra-Mondt ook hieruit heeft geput. In de tweede (en latere) druk(ken) van het boek *Observationes Medicae* (1652-1739) schrijft de Amsterdamse arts en burgemeester Nicolaes Tulp (1593-1674) (vooral bekend van het schilderij 'De anatomische les' van Rembrandt) in het een-na-laatste hoofdstuk over de '*Unicornus marinum*' (Zijlstra-Mondt schrijft hier foutief over '*Unicornus marinus*'). Als praktiserend arts schrijft Tulp in dit hoofdstuk over de veronderstelde geneeskrachtige werking van vermalen 'horen' van de narwal. Zijlstra-Mondt schrijft in haar dissertatie hierover (p. 84): '*Aan de hoorn van het dier schrijft hij dezelfde eigenschappen toe als Plinius.*' Dit is opmerkelijk omdat Plinius nergens over narwaltanden schrijft. Plinius schrijft wel dat 'horens' alleen aan viervoetige dieren voorkomen en heeft het over de geneeskrachtige werking van vermalen horens van de land-eenhoorn. Tulp verwijt Plinius juist dat hij de tanden ('horens') van narwal en walrus in deze negeert. Volgens Tulp zouden de 'horens' van deze dieren dezelfde krachten moeten hebben als die van viervoetige dieren om 'kwade venijnen' te bestrijden en 'zweet af te drijven'. Hij haalde vervolgens de Deense arts Caspar Bartholin (1585-1629) ('*At negat Casparus Bartholinus…*') (Zijlstra-Mondt schrijft (p. 142), incorrect, dat Tulp in zijn boek naar de zoon van Caspar Bartholin, Thomas Bartholin (1616-1680) verwijst) aan die *niet* in geneeskracht van de 'horens' in het algemeen en in die van de narwal in het bijzonder gelooft. Tulp zelf geloofde er uiteindelijk, alles afwegende, ook niet in en spreekt zijn schaamte uit over het bedrog. In de Nederlandse vertaling van de *Observationes Medicae*, *Geneeskundige waarnemingen* (1740) schrijft hij: '*In welk beuzelagtig verdigstel ik waarlyk niet langer kan door de vingeren zien, maar ik schaam my dat de wereld zoo lang bedrogen is, in een middel, van de menschen onzer eeuw, eer door gedragen, dan door ondervinding of uitkomst bevonden, gelyk te zien is by Hieronumus Mercurialis, Ambrosius Paree, en andere voorname mannen onzer Konst.*' Verderop in haar boek (p. 142) komt Zijlstra-Mondt nogmaals terug op het boek van Tulp, alwaar zij een iets gedegener, maar niet foutloze, analyse geeft.

Ter illustratie van het uiterlijk van de narwal geeft Tulp een, met name anatomische, beschrijving van een op 2 juni 1648 (Zijlstra-Mondt schrijft foutief 4 juni 1648) op het Schotse eiland May dood gevonden mannelijke narwal. Deze narwal, zo beschrijft Tulp, was 18 voet lang (Zijlstra-Mondt schrijft foutief over 22 voet), twaalf voet breed en had een 'kop als een karper' (*capute cyprino*). Het lijk werd door een scheepschirurgijn ontleed en beschreven. Uit deze beschrijving heeft Nicolaes Tulp de gegeven informatie betrokken. De anatomische beschrijving is terdege en accuraat. Zo wordt beschreven dat de tand in de rechter bovenkaakhelft zat en in de linker bovenkaak niets van een tand zichtbaar was. Ook andere anatomische details worden correct weergegeven. Zo wordt geschreven dat de staartvinnen aan de zijkanten van het einde van de wervelkolom zaten. Bij het hoofdstuk



Figuur 1. Tabula XVIII '*Unicornus marinum*' uit *Observationes medicae*, Editio sexta, 1739, Georgium Wishoff, Leiden. Collectie E.J.O. Kompanje.

geeft Tulp een gravure waarop de schedel van de ontlede Schotse narwal bezien vanaf boven en vanaf onder is weergegeven. Deze afbeeldingen zijn redelijk accuraat en laten zien dat de tand rechts vanuit het rostrum ontspringt en de twee neusgaten boven op de schedel liggen en zij tonen de grilligheid van het bot. Verder is er op de plaat ook een afbeelding van een levende narwal op het strand. Deze is echter verre van accuraat. Het is meer een bruinvis met borst- en verticale staartvin als van een vis en een uit de bovenkaak ontspruitende tand die er anders uitziet dan de tand aan de afgebeelde schedel. Uit twee neusgaten die relatief gezien ver uiteen liggen spuit water (of condens) als was de narwal nog levend (figuur 1). Zijlstra-Mondt schrijft dat de chirurg deze afbeelding op May heeft gemaakt: '*De narwal werd ontleed en getekend door een chirurg… Op de tekening zijn zowel het anatomisch preparaat als het intacte dier afgebeeld*.' Dit is opmerkelijk. De tekening van deze narwal komt namelijk in het geheel niet overeen met de beschrijving van de chirurg. Het is daarom aannemelijk dat Tulp alleen tekeningen van de schedel van de door de chirurg ontlede Schotse narwal tot zijn beschikking had en de afbeelding van het gestrande dier een fantasie-afbeelding is en dat deze niet gerelateerd is aan de Schotse narwal. Tulp schrijft hier namelijk zelf ook over dat dit de afbeelding is van Thorlac, de bisschop van Scalonia Hola op IJsland die de afbeelding aan de Franse ambassadeur La Tuilerie in Denemarken had gestuurd, en die vervolgens in Parijs is uitgegeven. Hij schrijft verder dat deze afbeelding redelijk overeenkwam met de narwal van May, maar dat bij deze, door de verrotting, de twee spuitgaten niet meer zichtbaar waren.

Zijlstra-Mondt noemt, uiteraard, de beschrijving en afbeelding uit het boek van Tulp, maar is hier verre van kritisch. Zij neemt aan dat de afbeelding van de (levende) narwal op het strand door de chirurg is gemaakt naar de werkelijkheid. Dit is, zoals gezegd, niet correct. Schedel en afbeelding van het intacte dier zijn van twee verschillende narwals. Zij had dit kunnen weten want Tulp schrijft hierover in de tekst en bovendien staat in de gravure dat de tand van de Schotse narwal 9½ voet lang en de tand van IJslandse narwal 8½ voet lang was. Zij geeft in haar dissertatie (figuur III.3) de gravure uit het boek van Tulp weer. Echter dit is een bewerkte afbeelding daar de twee neusgaten met de water- / condensstralen ontbreken (vergelijk figuur 1 bij deze recensie).

Verderop in haar dissertatie beschrijft zij de kopergravure uit het boek van Tulp opnieuw. Zij had deze aangetroffen in het traktaat *Les Observations plusiers singularitez & Choses Memorables* van de Franse wetenschapper Pierre Belon (1518-1564). Het boek was uit 1555. Zijlstra-Mondt beschrijft dat Belon, niet onverwacht, alleen de land-eenhoorn beschrijft en niets over de narwal schrijft. De plaat is waarschijnlijk door een eigenaar na 1652 uit het boek van Tulp verwijderd en ingevoegd in zijn exemplaar van het traktaat van Belon. Zij beschrijft dat zij in twee andere exemplaren van het traktaat, niet onverwacht, de plaat niet aantrof. Vervolgens verliest zij zich in een bijna onnavolgbare en onwaarschijnlijke conclusie dat de plaat door de gravure uit het boek van Tulp later los verkrijgbaar was en opnieuw werd gebruikt en dat deze '*…alsnog deel ging uitmaken van Belons beschrijvingen, echter nog steeds zonder beschrijving*' (p. 119). Zijlstra-Mondt geeft in een figuur in haar boek (figuur III-24) de in het traktaat gevonden plaat van Tulp weer. De zin hiervan ontgaat mij volkomen en is ook historisch gezien van geen enkel belang. Iemand heeft een uitgescheurde plaat uit het ene boek in een ander boek uit zijn bibliotheek ingevoegd. Iets wat veelvuldig voorkomt in boeken uit deze tijd. Niet vermeldenswaardig in een historisch overzicht.

Op oude afbeeldingen van gestrande walvissen en dolfijnen wordt vaak een straal water of condenspluim weergegeven vanuit de spuitgaten. Veelal twee stralen vanuit beide neusgaten die eindigen in het ene spuitgat. In figuur II.2 geeft Zijlstra-Mondt de afbeelding van de *Vipera maris* uit *De Natura Rerum*

(1290) van Thomas de Cantimpré weer. Zij ziet in de twee licht gekromde lijnen boven de kop 'twee rechtopstaande hoorns'. Aannemelijker lijkt mij dat dit twee waterstralen zijn vanuit het spuitgat van de walvis.

De dissertatie van Zijlstra-Mondt is een aanwinst over de 'zee-eenhoorn' literatuur vanwege een uitputtende opsomming van afbeeldingen en beschrijvingen in boeken, cartografische bronnen en voorstellingen uit kunstwerken. De tekst is zeer toegankelijk geschreven met een gedegen bronverwijzing. Echter, haar biologische duiding over de narwal laat helaas her en der te wensen over en is op sommige punten, voor zover ik dat kan beoordelen vanuit mijn medische / medisch-historische en zoölogische expertise, onlogisch, onjuist, onvolledig en onkritisch. Een bron die ik goed ken, het boek van Nicolaes Tulp, bleek slordig en onjuist geciteerd en verkeerd geanalyseerd. Ik maak mij daarom zorgen over de zorgvuldigheid van andere bronanalyses in het boek. Hoe zuiver zijn deze?

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