LUTRA

Journal of the Dutch Mammal Society
Volume 60 – Number 1 – June 2017

Arctic climate fugitives?

Hooray Hooray! A bowhead whale (*Balaena mysticetus*) was spotted off the Belgian and Dutch coasts during March and April 2017! It was probably the first bowhead whale ever recorded in the whole of the North Sea. Dozens of enthusiastic naturalists, including myself, hurried to the coast to observe this rare Arctic wanderer close to the beach. Some were lucky enough to catch a glimpse of the massive animal, or at least of its V-shaped blow, but many were disappointed, arriving a day too late. They shouldn't worry: the animal, or one of its conspecifics, might be back soon, in the coming months or years. Or perhaps they *do* need to worry? Our enthusiasm should also allow room for mindful uneasiness.

First of all, the possible way back home for this magnificent giant – and let's hope it *does* make it home - lies full of obstacles in the form of treacherous shores, areas with no suitable food, intense shipping, trash, lost fishing gear and killer whales (*Orcinus orca*), a predator from which it is relatively safe in ice-covered waters. But secondly, why did this animal venture this far south in the first place? It simply does not belong here. The Arctic lies thousands of kilometres further to the north. Its appearance in too southerly waters is not only an alarming signal for the species, but perhaps also for the whole ecosystem it lives in.

In the past we have often been confronted with wandering marine mammals not indigenous to the North Sea. These originate mostly from the nearby Atlantic Ocean, and we have embraced them as spectacular, once-in-a-life-time experiences and scientific opportunities. However, just a year before the appearance of the bowhead whale (the mammal with the longest life-span of all), another enigmatic species – and the inspiration for the medieval unicorn - popped up in our waters. In March 2016 a narwhal (*Monodon monoceros*) was observed in the River Scheldt in Belgian waters, having passed undetected through the Dutch part of the river. This unfortunate animal starved to death in unfamiliar waters without suitable prey, probably after a journey of many weeks or months. This was an exceptional find; it was not only the first record of this Arctic species for Belgium, and – if you wish – the second case for the Netherlands (although it was not actually observed there), it had also been almost 70 years since a narwhal had been recorded in the North Sea (Haelters et al., in press). We can only speculate if the unexpected appearances of the bowhead whale and the narwhal were related. However, in the last two years more Arctic species have been seen in unusual places: a solitary bowhead whale off the coast of the United Kingdom, France and Ireland (probably the same animal), beluga whales (*Delphinapterus leucas*) in Swedish, Northern Irish and English waters and a harp seal (*Pagophilus groenlandicus*) at the Dutch coast.

It is tempting to relate these observations to the universal, climate-driven, redistribution of life on earth (Pecl et al. 2017, Verboom 2014). In most cases, the redistribution of cold-water species is directed towards the poles. But for animals with a strong affinity for sea ice, which already live at the extreme north of our planet, there seems little alternative, even if travelling to warmer waters for these species appears counterintuitive. There has been a dramatic decline in sea ice in the Arctic since 1979 (IPCC 2013). The gradual melting of North Pole ice, predicted 30 years ago but apparently not taken seriously by everybody, has become a reality. Year after year, low ice coverage is recorded, both in summer and winter, with a long-term decrease that has become very pronounced in the last decades (Polyak et al. 2010). Record high temperatures in the north occur in rapid succession (Ricker et al. 2017).

Inevitably, a major change in sea ice dynamics will lead to a disruption in the functioning of the Arctic ecosystem, and it will probably influence the global climate. Rapid shifts in ice conditions are likely to have cascade effects through the food web of the Arctic (Hansen et al. 2002). There is concern about many species associated with sea ice, including narwhal and polar bear (*Ursus maritimus*; Evans et al. 2010). It is clear that polar bear depends on sea-ice, and killer whales are advancing north, well into narwhal habitats (Breed et al. 2017). The impact of climate changes on the bowhead whale is still unclear. This species might have had a distribution that extended further south in the 16th century – which was a relatively cold period, known as the Little Ice Age (Matthes 1939, Laidre et al. 2008). It might also take advantage of receding sea ice in spring to explore new feeding habitats (Heide-Jørgensen 2009) or might adapt to foraging in temperate shallow waters (de Boer et al. 2017).

Very knowledgeable people have calculated that limiting the increase in the global average temperature to 1.5 °C above pre-industrial levels would significantly reduce the risks and impacts of climate change (UN 2016). After that, things become tricky, and we lose some control. But have we not already lost control? We continue to deforest, we continue to massively burn fossil fuels and traffic jams are not getting shorter. Global trade - our need for raw materials and consumer goods – and our building and agriculture habits contribute to the process on a daily basis. Our short-term thinking and acting seem more destructive than ever. In the Arctic, disappearing sea ice opens doors for new shipping routes – *the Northwest Passage* – that will allow us to send or receive our goods faster and cheaper. And easier access to the Arctic creates opportunities for further exploration and exploitation of its natural resources.

So does the observation of a bowhead whale - possibly born long before climate change became an issue - and the stranding of a narwhal tell us the story of dwindling sea-ice? Can we consider them to be *climate fugitives*, wandering around, lost in an ice-free ocean? Frankly, at this moment, we cannot. *Statistically* such extremely rare records of marine mammals so far outside of their home ranges do not really demonstrate a change in their habitat: there are much better tools available for this. *Definite proof* is currently required whenever scientists send out warnings, especially when these warnings might entail the need for action. Moreover, the distribution of marine mammals is usually studied over relatively short timeframes, with little information about long-term natural change. In addition these changes may be confounded by continued exploitation or recovery from historical overexploitation. Seismic testing might also have an influence, as it profoundly alters the soundscape of the ocean environment and its inhabitants, some of which rely on that soundscape for their social interactions, feeding and receiving environmental information.

However, as ambassadors from the Arctic ecosystem, the southerly bowhead whale and narwhal do have a story to tell. They can help us in education about climate change, as they concern tangible and unexpected events that seem to indicate change. Fortunately climate education *is* slowly penetrating our schools. My five-year-old daughter recently surprised me with a request to use the bicycle instead of the car "*for the sake of penguins and polar bears*". We certainly will do so, "*but also for the sake of narwhal and bowhead whales*". Because while it is exciting to see such rare creatures close to our coasts, their arrival may be the portent of undesirable and perhaps irreversible changes.

Jan Haelters

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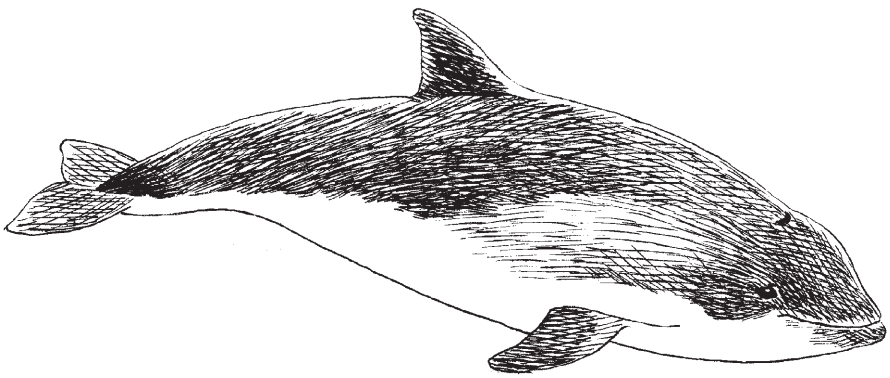

The semi-enclosed tidal bay Eastern Scheldt in the Netherlands: porpoise heaven or porpoise prison?

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Abstract: Harbour porpoises (*Phocoena phocoena*), the smallest of cetaceans, need to consume quantities of prey that amount to ca. 10% of their own body mass per day. They mostly feed on small fish, with the main prey species differing geographically. The $\delta^{13}C$ muscle signature of harbour porpoises sampled in the Eastern Scheldt, SW Netherlands, has indicated that animals tend to stay here for some time after they entered this semi-enclosed basin, and that they thus must feed on local prey. A relatively low primary production and low local fish biomass raises the question what there is for harbour porpoises to feed on in the Eastern Scheldt. This study reveals that there are no big differences between biological or stranding parameters of harbour porpoises found dead in the Eastern Scheldt compared with the adjacent North Sea (the "Voordelta"), but some differences in diet were found. Still, despite the low fish biomass in the Eastern Scheldt, no evidence of excessive harbour porpoise starvation was found. The main prey species for juvenile porpoises, both in the North Sea and in the Eastern Scheldt, were gobies. Gadoids were important prey for adults in both regions. Gadoid prey was supplemented by gobies and sandeels in the North Sea, and by squid and estuarine roundfish in the Eastern Scheldt. Our results demonstrate that harbour porpoises that stay in the Eastern Scheldt for a longer period of time may develop specialised feeding skills, to cope with the relatively poor prey base. Juveniles on the other hand, must settle for small and lean prey (gobies and small sepiolids) and may face competition from adults.

Keywords: Phocoena phocoena, stomach content analysis, prey composition, geographical differences, ecological trap.

Introduction

The harbour porpoise (*Phocoena phocoena)* is the most abundant, and also the smallest cetacean living in NW Europe. Cetaceans have a much higher energy metabolism than similarly sized land mammals, with the smallest species having the highest demands (Kanwisher & Sundnes 1965). Therefore, harbour porpoises need to feed at excessively high rates (Wisniewska et al. 2016) and must consume about 10% of their body mass of food per day to sustain themselves (Kastelein 1998).

Small and abundant fish species are the main prey of harbour porpoises (Santos & Pierce 2003). The prey spectrum, and hence the prey quality, varies geographically. For instance, harbour porpoises in the Kattegat and Skagerrak rely heavily on clupeids which have a high

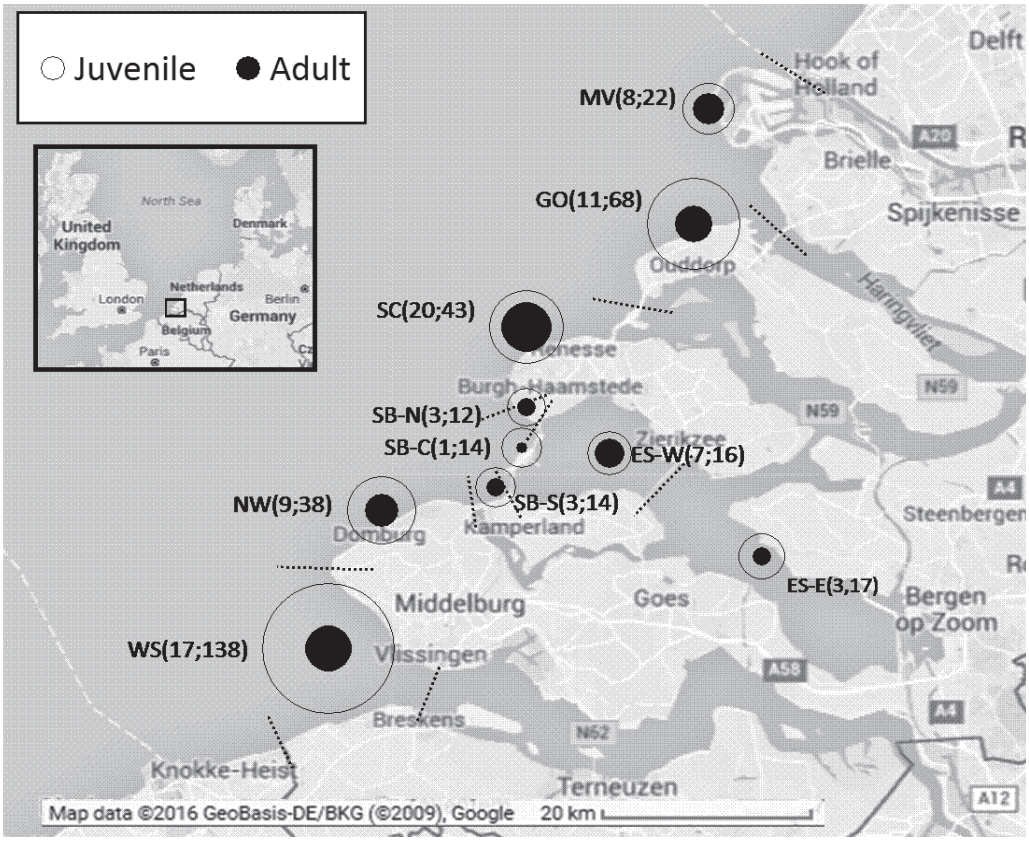

Figure 1. Study area. Stranded harbour porpoises (n-adults; n-juveniles 2006-2015) in geographically divided groups: MV = Maasvlakte, GO = Goeree, SC = Schouwen, SB-N = Storm surge Barrier-North, SB-C = Storm surge barrier-Central, SB-S = Storm surge barrier-South, NW = North-west Walcheren, WS = Western Scheldt estuary, ES-W = Eastern Scheldt-West, ES-E = Eastern Scheldt-East.

energy density, while porpoises in the eastern North Sea feed mainly on gobies and gadoids which are much leaner prey (Börjesson et al. 2003, Leopold & Meesters 2015).

Although harbour porpoises may move around a great deal in the open seas and oceans, and may thus encounter different prey in different seasons, porpoises living in a semi-enclosed tidal bay, the Eastern Scheldt (SW Netherlands), have been shown to have a distinct, local $\delta^{13}C$ muscle signature, indicating prolonged feeding on local prey (Jansen et al. 2013). Prolonged feeding in one place could be indicative either of good feeding conditions, or the impossibility to leave. Unless porpoises were born in the Eastern Scheldt, they must have entered the tidal bay from the outside, through openings in the storm surge barrier (Jansen et al. 2013). A relatively low fish biomass in the Eastern Scheldt, as compared to adjacent North Sea waters (Tulp 2015) in combination with long residence times of porpoises would suggest that the Eastern Scheldt is an ecological trap (Jansen et al. 2013).

Primary production within the Eastern Scheldt has been steadily decreasing since the onset of measurements and has halved between 1995 and 2010 (Smaal et al. 2013). This trend is reflected in higher trophic levels. With low nutrient concentrations and large stocks of grazing bivalves (Smaal et al. 2013), relatively low quantities of the local primary

production may be available to secondary producers and top predators, such as fish and harbour porpoises. Total fish biomass in the Eastern Scheldt is comparatively low and shows a decreasing trend, in contrast to the situation in the North Sea (Tulp 2015). In this study, we aim to find out if the diet of harbour porpoises in the Eastern Scheldt is different from that of their counterparts in the adjoining part of the North Sea, by comparing the stomach contents of stranded harbour porpoises, as well as prey fish densities in these two areas.

Methods

Study area

The Eastern Scheldt (SW Netherlands, figure 1) is a former open estuary. It was turned into a semi-enclosed tidal bay by the construction of a storm surge barrier, that was built from 1979-1986. This barrier has 62 openings, each 42 m wide, that allow water to flow through, albeit at a reduced rate. Two auxillary compartment dams, built further upstream from 1977-1987, have closed off the fresh water input through the rivers Scheldt and Rhine. The Eastern Scheldt now covers a surface of 350 km^2, including 118 km^2 of tidal flats, and it has a smaller tidal range, higher salinity and water transparancy, a longer water residence time and lower nutrient concentrations than the former open estuary (Nienhuis & Smaal 1994, Jansen et al. 2013, Smaal et al. 2013). The area is sub-divided in an Eastern and Western compartment, separated by a 5 km long bridge ('Zeelandbrug'), built on pillars that are 72.5-95 m apart. The openings in both the outer storm surge barrier and the inner bridge are large enough for harbour porpoises to pass through and porpoises can be found in the Eastern Scheldt on either side of the bridge.

Yearly total population counts (2009-2015, conducted between May and September) of harbour porpoises in the Eastern Scheldt suggest a population size of about 30-60 animals (rugvin.nl). Numbers in the North Sea are considerably larger; two aerial line transect surveys in August 2009 off the Dutch mainland coast (including the Voordelta) and in the Belgian sector of the North Sea have yielded estimated population sizes of 5795 (Scheidat et al. 2012) and 186 (Haelters et al. 2011), respectively, while subsequent surveys in July 2010, 2014 and 2015 off the Netherlands produced estimates 10,098, 18,778 and 11,674 animals, respectively (Geelhoed et al. 2015).

The stomach contents of stranded, dead harbour porpoises found in the Eastern Scheldt from 2006 to 2015 were compared with those of porpoises found along the shores of the North Sea, between Hook of Holland and the Belgian border, further referred to as North Sea, in the same period.

Available fish biomass and sizes of fish

Fish biomass data ($kg.ha^{-1}$ per fish species and length class) were obtained from standard annual demersal fish surveys of the Eastern Scheldt and the adjacent North Sea waters (Voordelta), 2006-2015 (data taken from Tulp (2015) and Dr Ingrid Tulp, Wageningen Marine Research, personal communication). In these years the surveys in the Voordelta were mostly done in the third week of October, while surveys in the Eastern Scheldt were done circa five weeks earlier, around mid-September. Fish growth between the two sampling periods was assessed for herring (*Clupea harengus*) and whiting (*Merlangius merlangus*), using daily fyke catches at Texel over the years 2006-2015 (waddenzeevismonitor.nl/monitoring.html; data courtesy Dr Henk van der Veer, NIOZ). We restricted the analysis of relative fish abundance to roundfish, as these comprise 97% of the prey mass taken by harbour porpoises in the Netherlands (Leopold & Meesters 2015). Biomass data for squid and other invertebrates were not available. Total lengths of fish, both found in the fish survey data and in the stomachs of the porpoises,

were assigned to 1 cm (below) length classes, with a length between e.g. 10.0 and 10.99 cm assigned to length class 10, etc.

Stranded harbour porpoises

A total of 505 dead stranded harbour porpoises were collected in our study area between 2006 and 2015 by members of the Dutch strandings network. The carcasses were transported to the Department of Pathobiology, Faculty of Veterinary Medicine, Utrecht University, for necropsy following the protocol of Kuiken & Garcia Hartmann (1991). Porpoise age was assessed as neonate (n=41; these were omitted from the analyses as these were still fully dependent on their lactating mothers), juvenile or adult. Non-neonates <130 cm were classed as juveniles and animals ≥130 cm as adults, unless gonad development showed otherwise. Over the years, 43 non-neonate porpoises were collected in the Eastern Scheldt and 421 along the coastline of the North Sea waters.

Age class, stranding date and location were recorded for each animal. Carcass freshness was scored using the Decomposition Condition Code (DCC; 1 (stranded (probably) alive) to 5 (very old, mummified carcass)) for each carcass. The Nutritional status (in terms of the Nutritional Condition Code, NCC; from 1 (very fat and muscular) to 6 (extremely emaciated); Kuiken & Garcia Hartmann 1991) of the collected porpoises and cause of death was established only for reasonably fresh specimen (DCC 1-3). Figure 1 depicts the geographical distribution of harbour porpoises strandings in the Eastern Scheldt and in the adjacent North Sea waters.

Stomach content analysis

Stomach contents of juvenile (North Sea: n=349; Eastern Scheldt: n=33) and adult (North Sea: n=72; Eastern Scheldt: n=10) animals were analysed separately, because diet is known to vary with porpoise age (or length; Leopold & Meesters 2015). Stomach contents were analysed using the methods as outlined in Leopold et al. (2015). In brief, stomach contents were washed and prey hard parts were collected under a dissecting microscope, identified to the lowest possible taxon, measured, their size corrected for wear and paired if possible. From these measurements, prey sizes and masses were estimated (Leopold et al. 2001). All prey species were assigned to one of the following prey groups; clupeids, sandeels, gobies, gadoids, other demersal roundfish, pelagic roundfish, estuarine roundfish, flatfish, squid, and other invertebrates (cf. Leopold & Meesters 2015). %FO (frequency of occurrence; stomachs containing a certain prey group, as a percentage of all stomachs), %N (number of prey; the number of individuals of one prey group, as a percentage of all prey found in all stomachs) and %M (mass of prey; the total reconstructed mass of one prey group, as a percentage of the total prey mass in all stomachs) were calculated for all prey groups. This was done separately for the North Sea and the Eastern Scheldt and separately for juveniles and adults, across all porpoises within each sample. As these three indices each provide a different representation of the diet, they were also combined in an index of relative importance IRI (cf. Pinkas et al. 1971) in which %M replaces % prey volume in the original IRI (cf. Carrassón et al. 1997):

$$IRI = (\%N + \%M)^* \%FO$$

The value of IRI is a rather meaningless figure, with the unit $\%^2$, and is only fit for comparing the relative contributions of different prey groups within a sample of predators. Therefore, we used the percentage IRI, which is a dimensionless number between 0 and 100:

$$\%IRI = (IRI_x/\Sigma(IRI_{a-z}))^*100,$$

being the IRI of prey group x divided by the sum of the IRIs of all (a…z) prey groups * 100 (cf. Carrassón et al. 1997).

Statistical analysis

Differences in porpoise lengths between the North Sea and the Eastern Scheldt, for juveniles and adults separately, were assessed using the two-sample *t*-test allowing unequal variances. Harbour porpoises with known Decomposition Condition Codes (DCC) and Nutritional Condition Codes (NCC) were divided in the same regional/age groups and these data were also tested with a two-sample *t*-test allowing unequal variances. Before testing for differences in diet between the North Sea and the Eastern Scheldt, the possibility of latitudinal differences in diet was explored by regressing %M for each prey group per individual porpoise against the latitude of the stranding location (North Sea strandings only).

The total reconstructed biomass per prey group was calculated for each harbour porpoise. Initially, we considered eight groups of porpoises, based on age class (juveniles vs adult), season (summer (May-October) vs winter (November-April) and region (North Sea vs Eastern Scheldt) of stranding. Months with no porpoise strandings in one of the two regions were excluded from the analysis. For this reason, adults stranded in winter could not be analysed. Primer (Clarke & Gorley 2015) version 7.0.7 was used to perform a multivariate analysis. First the data was 4^{th} root transformed and the Bray-Curtis dissimilarity was calculated of each matrix. Differences in diet between groups were assessed using Permanova (Anderson 2001, McArdle & Anderson 2001), with variable region (North Sea vs Eastern Scheldt).

Table 1. Numbers and sizes (average with standard deviation, in cm) of herring (<16 cm) and whiting (<26 cm) in daily catches at Texel, 2006-2015 for September and October.

Month	Species	*n*	AVG	STD
September	Herring	158,834	6.66	0.95
October	Herring	46,630	8.72	1.67
September	Whiting	137	17.07	2.92
October	Whiting	407	19.14	2.92

Average fish length was calculated per prey group for fishes caught between 2006 and 2015 during the annual surveys both in the North Sea and the Eastern Scheldt. Differences in fish lengths between the two regions were assessed using two-sample *t*-tests allowing unequal variances. Significance level α=0.05 was used as a criterion for effect.

Results

Available prey

Prey fish biomass per surface area in the Eastern Scheldt was much lower than in the North Sea, across a wide variety of taxa (figure 2). Moreover, herring and whiting were found to be smaller in the Eastern Scheldt as compared to the North Sea, but this was probably due to fish growth between September, when the Eastern Scheldt was sampled, and October, when the North Sea was sampled. Average sizes of herring and whiting in the daily fyke catches at Texel showed similar differences between September and October (table 1).

Several within-group differences were found between the Eastern Scheldt and the North Sea. For instance, within the gobies, the comparatively large black goby (*Gobius niger*) comprised 12% of the biomass in the Eastern Scheldt (vs virtually zero in the North Sea). Within the gadoids, bib (*Trisopterus luscus*) made up 52% of the biomass in the Eastern Scheldt (vs 5% in the North Sea, while the reverse was true for whiting: 40% vs 89%). Within the clupeids, sprat (*Sprattus sprattus*) was virtually absent from the East-

Table 2. Causes of death for the animals sampled in the North Sea and Eastern Scheldt. Acute deaths include seal victims and fisheries bycatches; non-acute deaths include various diseases and emaciation.

Region	Unknown	Acute	Non-acute
North Sea	252 (60%)	87 (21%)	82 (19%)
Eastern Scheldt	25 (58%)	8 (19%)	10 (23%)

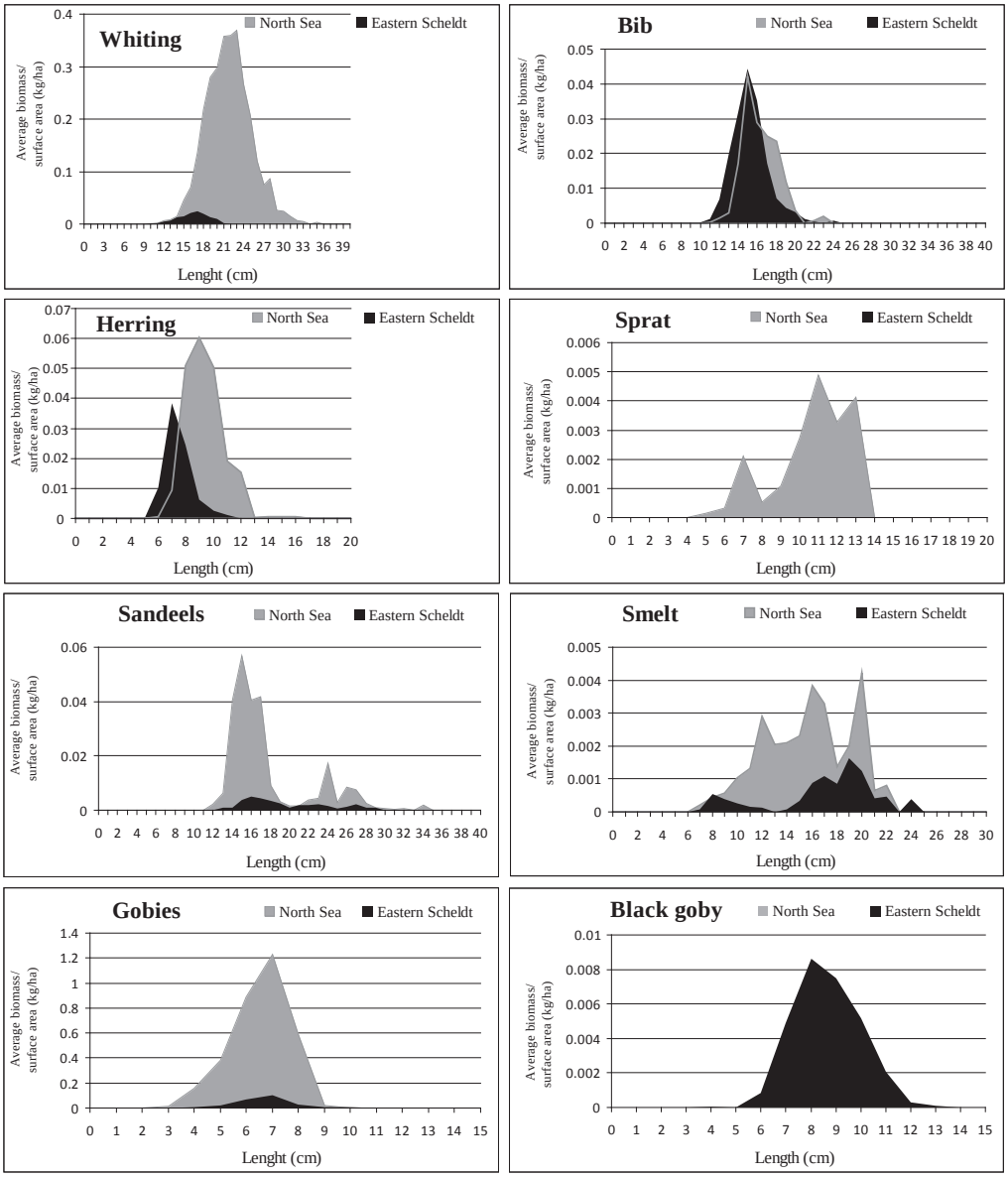

Figure 2. Average (2006-2015) fish biomass ($kg \cdot ha^{-1}$), for the most important prey species and prey groups, per cm (below) length class for the North Sea (grey) and the Eastern Scheldt (black). Note different scalings.

ern Scheldt samples while it made up 8.4% of clupeid biomass in the North Sea catches. In the group of estuarine roundfish, smelt (*Osmerus eperlanus*) contributed relatively less to the biomass in the Eastern Scheldt than in the North Sea, due to the dominance of sand smelts (*Atherina presbyter*) and pipefishes (Syngnathidae) in the Eastern Scheldt samples. However, as energy densities of different members within fish families are generally rather similar, this probably does not have large consequences for the porpoises.

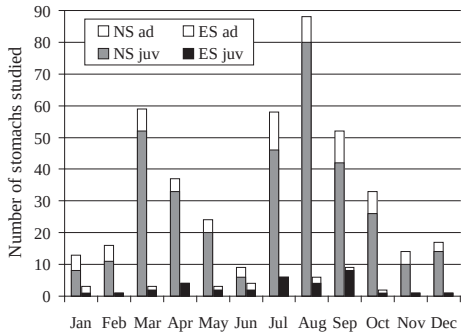

Figure 3. Seasonal distribution of harbour porpoise strandings for the North Sea (grey) and Eastern Scheldt (black), separately for adults (open) and juveniles (closed), total *n*=464 (2006-2015).

Seasonality in strandings

Overall, 464 porpoises were available for stomach content analyses, of which 421 came from the North Sea coastline. These show a bi-modal pattern in stranding time (figure 3), with peak numbers in spring (March/April) and summer (July through September). The temporal distribution of strandings in the Eastern Scheldt more or less follows that of the pattern found in the North Sea, but with only 43 porpoise carcasses collected from the Eastern Scheldt, a peak in spring strandings is not apparent.

Age, gender, condition, cause of death

Not all porpoises that stranded in the Eastern Scheldt or in the Voordelta could be collected and studied, therefore the characteristics of collected carcasses were compared to avoid bias due to incomplete sampling. Females comprised a minority among the stranded porpoises in both areas with 40.9% and 39.5% of the collected harbour porpoises, in the North Sea and the Eastern Scheldt, respectively. Most animals were juveniles: 83% among the North Sea strandings and 77% in the Eastern Scheldt. Animals classified as adults measured 145.5 ± 9.5 cm (*n*=63; range: 128-164 cm) in the North Sea and 146.7 ± 10.6 cm (*n*=10; range: 130-161 cm) in the Eastern Scheldt; for juveniles these figures were respectively 109.2 ± 10.6 cm (*n*=313; range: 81-138 cm) and 105.3 ± 10.8 cm (*n*=29; range: 85-127 cm) (*t*-tests: *P*>0.05 for both age classes). DCC and NCC did not differ significantly between the two regions (*t*-tests; *P*>0.05) and with an overall average DCC of 3.33, most carcasses were quite decomposed. This hampered establishing cause of death, which remained unknown in 277 (59.7%) cases. Among the porpoises for which a cause of death could be established, 56% of the animals had died from disease or starvation in the Eastern Scheldt (table 2). In the North Sea this percentage was 49%. From these comparisons we conclude that porpoises sampled in the two areas were similar, with only a slight difference in age composition (slightly more juveniles among the animals sampled in the North Sea).

Diet

Of the 464 examined stomachs, 369 contained prey remains and 95 were empty (20%). Among the animals found in the North Sea, 89 had empty stomachs (21%). In the Eastern Scheldt six out of 43 (14%) porpoises had empty stomachs. The probability of finding empty stomachs peaked in summer (July/August; figure 4).

Among the porpoises that were found with prey remains in their stomachs, both juveniles and adults showed a bi-modal pattern in strandings in the North Sea (figure 5). Peak numbers were found in early spring and in late summer/early autumn. Juveniles in the Eastern Scheldt showed a similar pattern. Numbers of adults with prey remains in their stomachs found in the Eastern Scheldt were too small to evaluate a temporal pattern.

No significant latitudinal trends in diet (%M per prey group) were found along the North Sea coastline, so this region will be treated as one, and compared to the Eastern Scheldt in

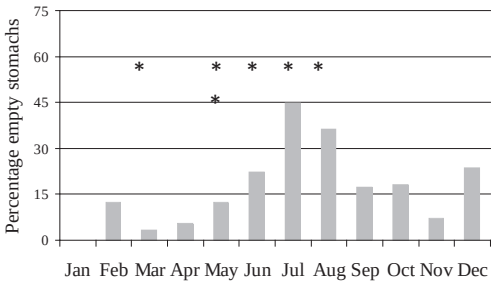

Figure 4. Percentage of empty stomachs among porpoises collected along the North Sea coastline (grey bars, *n*=89), and individual cases in the Eastern Scheldt (*, *n*=6).

the analyses. The %FO, %N and %M for all prey groups, for juveniles and adults in the North Sea and the Eastern Scheldt are given in tables 3, 4 and 5. Gobies dominated juvenile diets, in both summer and winter and in both the North Sea and the Eastern Scheldt, but particularly in the latter. In the North Sea, juvenile porpoises had eaten (in terms of prey mass) much more gadoids, clupeids and sandeels, while squid was far more important prey in the Eastern Scheldt. In terms of energy density of prey, North Sea juvenile porpoise diet (%M) included 24% (summer) to 33% (winter)

Table 3. Energy density, %FO, %N and %M for every prey group found in juveniles stranded during the summer (Jun-Oct) in the North Sea and the Eastern Scheldt. Relative energy densities of prey after Pedersen & Hislop (2001), MacLeod et al. (2007), Spitz et al. (2014), Leopold & Meesters (2015).

Juvenile summer		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (137)	%N (8913)	%M (33550)	%FO (18)	%N (5280)	%M (12599)
Gobies	low	65.69	87.78	22.75	77.78	96.27	58.37
Gadoids	low	34.31	3.25	49.14	38.89	0.30	4.77
Clupeids	high	5.11	0.11	0.19	11.11	0.15	0.54
Sandeels	high	22.63	4.23	12.81	22.22	0.09	0.45
Estuarine roundfish	high	8.76	1.44	11.13	33.33	1.04	4.09
Pelagic roundfish	high	0.00	0.00	0.00	0.00	0.00	0.00
Other demersal roundfish	low	1.46	0.02	0.04	5.56	0.02	0.04
Flatfish	low	0.73	0.01	0.17	5.56	0.06	0.08
Squid	low	33.58	2.55	2.38	50.00	2.05	31.66
Other invertebrates	low	18.98	0.61	1.40	5.56	0.02	0.00

Table 4. Energy density, %FO, %N and %M for every prey group found in juveniles stranded during the winter (Nov-Apr) in the North Sea and the Eastern Scheldt.

Juvenile winter		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (120)	%N (46,553)	%M (103,702)	%FO (10)	%N (2311)	%M (7622)
Gobies	low	85.00	93.13	34.58	90.00	94.81	72.98
Gadoids	low	35.83	0.86	23.63	30.00	0.65	17.69
Clupeids	high	49.17	1.62	13.00	30.00	0.26	3.07
Sandeels	high	40.00	2.12	10.14	60.00	1.47	3.89
Estuarine roundfish	high	35.00	0.95	8.28	20.00	0.22	0.61
Pelagic roundfish	high	15.83	0.22	1.99	20.00	1.04	1.09
Other demersal roundfish	low	3.33	0.06	0.49	0.00	0.00	0.00
Flatfish	low	5.00	0.10	0.33	0.00	0.00	0.00
Squid	low	21.67	0.55	7.41	20.00	1.17	0.51
Other invertebrates	low	30.83	0.39	0.13	40.00	0.39	0.16

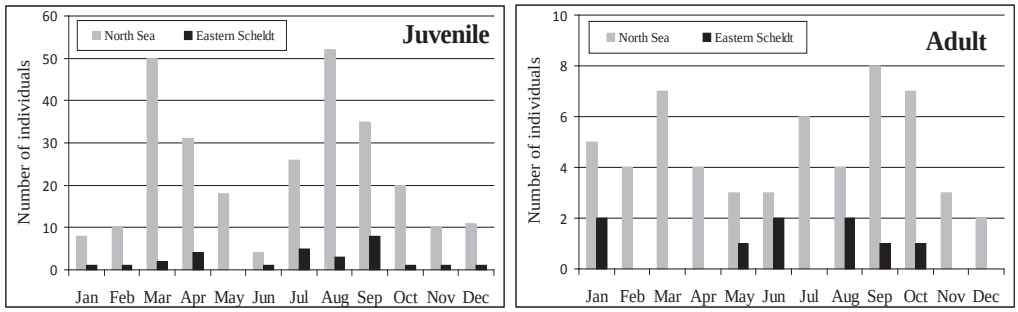

Figure 5. Stranded juvenile (left panel) and adult (right panel) harbour porpoises with prey remains in their stomach, from the North Sea (grey) and Eastern Scheldt (black).

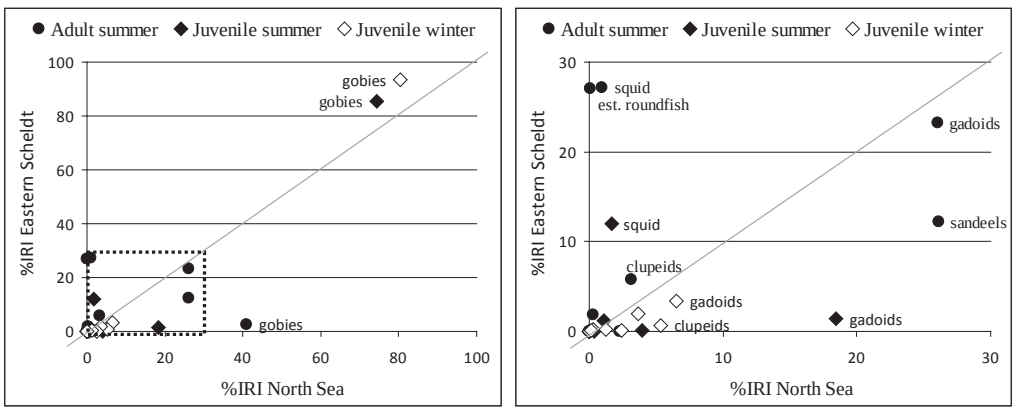

Figure 6. Left panel: percentage index of relative importance (%IRI) per prey group found in porpoises stranded in the North Sea against the %IRI per prey group found in porpoises stranded in the Eastern Scheldt. Right panel: zoomed in on 0-30%IRI.

Table 5. Energy density, %FO, %N and %M for every prey group found in adults stranded during the summer (May-Oct, except July) in the North Sea and the Eastern Scheldt.

Adult summer		North Sea			Eastern Scheldt		
Prey group	Energy density	%FO (25)	%N (3643)	%M (35961)	%FO (7)	%N (349)	%M (2165)
Gobies	low	48.00	68.21	13.21	42.86	4.01	0.61
Gadoids	low	48.00	3.71	48.04	57.14	4.01	25.90
Clupeids	high	20.00	4.09	10.89	28.57	1.15	13.78
Sandeels	high	68.00	20.29	16.36	28.57	6.30	25.32
Estuarine roundfish	high	8.00	0.27	0.50	28.57	44.41	25.39
Pelagic roundfish	high	20.00	0.69	10.17	0.00	0.00	0.00
Other demersal roundfish	low	4.00	0.03	0.14	0.00	0.00	0.00
Flatfish	low	4.00	0.03	0.01	0.00	0.00	0.00
Squid	low	36.00	1.92	0.61	42.86	38.11	8.58
Other invertebrates	low	36.00	0.77	0.07	57.14	2.01	0.42

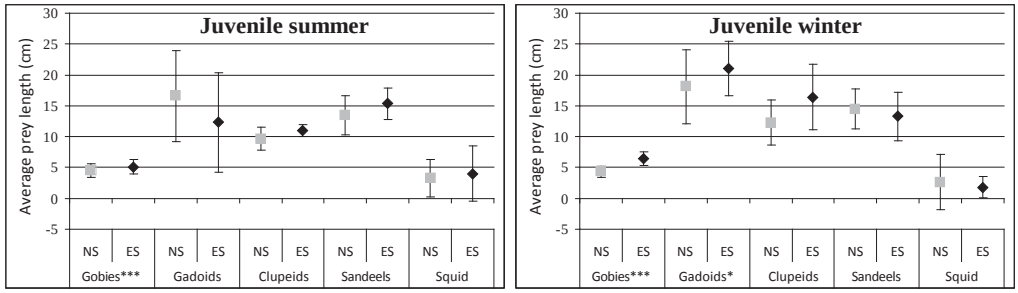

Figure 7. Average prey length (± standard deviation) for the main prey groups eaten by juveniles during the summer (left panel) and winter (right panel), for the North Sea (NS) and the Eastern Scheldt (ES). T-tests; * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

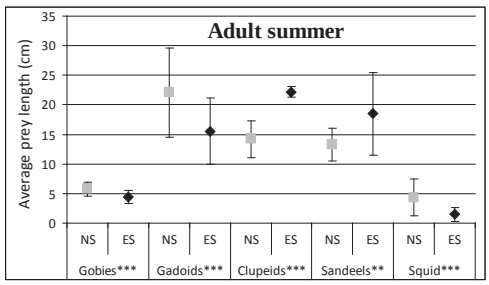

Figure 8. Average prey length (± standard deviation) for the main prey groups eaten by adults during the summer, both for the North Sea (NS) and the Eastern Scheldt (ES). T-tests; * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

high-energy prey, compared to only 5% and 9%, respectively in the Eastern Scheldt.

In contrast, adult diet (summer only) had a much higher energy density in the Eastern Scheldt than in the North Sea, as in the latter overall prey mass has relatively high contributions of both low-energy gobies and gadoids. Sandeels and estuarine roundfish (particularly sand smelt), and to a lesser extent, clupeids, together contributed much more to the overall prey mass in the Eastern Scheldt than in the North Sea, but note that sample sizes are small (7 animals from the Eastern Scheldt and 25 from the North Sea). Like for the juveniles, squid was a relatively important prey for adults in the Eastern Scheldt.

Within-group variation in prey found in individual porpoises was large, and the diets between the North Sea and the Eastern Scheldt did not differ significantly between any age or seasonal groups (table 6).

However, comparing the %IRI of North Sea and Eastern Scheldt diets (figure 6) shows that gobies are by far the most important prey for juveniles, in both regions. Gobies are also important to adults in the North Sea in summer, even though the total contribution to prey mass was not very large (table 5). Zooming in on the less important prey (figure 6, right panel), we find that gadoids are relatively important to juveniles in the North Sea (particularly in summer), while squids are more important in the Eastern Scheldt. Gadoids are almost equally important to adults in both regions, but North Sea adults had eaten comparatively many sandeels, while adults in the Eastern Scheldt relied more on squid and sand smelt.

Prey size

Juveniles tended to eat slightly larger gobies in the Eastern Scheldt, as compared to the North Sea (figure 7). Sizes of gadoids ingested by juveniles in the Eastern Scheldt in winter were larger than in the North Sea, whereas the difference in summer was not significant. Sizes of other prey did not differ significantly between the two regions, in any season.

Among adult porpoises, between-region prey sizes were different in all main prey groups

A harbour porpoise in the Eastern Scheldt with, in the background, the storm surge barrier. *Photo: W.J. Strietman.*

Table 6. Permanova table of results, on the data for all harbour porpoise stomachs with prey remains stranded in the devised seasons.

Age	Season	Variable	df	Pseudo-F	*P* (perm)	Unique perms
Juvenile	Summer	Region	154	1.0364	0.375	998
Juvenile	Winter	Region	129	0.59984	0.725	998
Adult	Summer	Region	31	1.6876	0.119	999

(only summer tested). Gobies, gadoids, and squids eaten in the Eastern Scheldt were smaller than in the North Sea, while energy-rich clupeids and sandeels were larger (figure 8).

Conclusion and discussion

The Eastern Scheldt has an impoverished fish fauna. Extensive surveys (2006-2015, Tulp 2015) showed that the biomass per surface area of the most import prey groups for harbour porpoises, i.e. gobies, gadoids, clupeids and sandeels in the Eastern Scheldt, were only 7.5%, 9.9%, 13.8% and 36.8%, respectively, of the biomass in the adjacent North Sea. Sprat was almost completely lacking from the Eastern Scheldt (figure 2). On the other hand, estuarine species like sand smelt and black goby were much more abundant in the Eastern Scheldt, and, based on prey remains found in the harbour porpoises, so were small sepiolids (squid). The latter, however, may also have been taken relatively often by porpoises in the Eastern Scheldt, for want of other prey.

Even though there is apparently less fish available in the Eastern Scheldt, the harbour porpoises that had stranded here did not differ from those found along the North Sea shorelines in terms of their average nutritional condition and length, gender and age ratios and causes of death. Porpoises in the Eastern Scheldt were thus remarkably similar to those sampled from the North Sea in these respects. It should be noted, however, that stomach contents of dead stranded animals were studied, which may present a biased view of the food intake of healthy animals. However, given that the porpoises in our two samples had largely the same characteristics, any bias would likely apply to both groups.

No differences were found in average reconstructed prey masses per stomach and the percentage empty stomachs between the

North Sea and the Eastern Scheldt. However, prey composition differed to some extent. Juvenile porpoises in the Eastern Scheldt took relatively less gadoids and clupeids than their conspecifics in the North Sea. In summer this was (partly?) compensated by a higher importance of squid in the diet. Overall, diet of juveniles in the Eastern Scheldt was dominated by small, lean prey, i.e. gobies and small squid. This resulted in a much leaner diet in the Eastern Scheldt, where most prey taken was both small and low in energy content.

In contrast, relatively few goby remains were found in stomachs of adult porpoises in the Eastern Scheldt. Sandeels were also rarely taken here, but this was compensated by a comparatively high importance of energy-rich sand smelts (estuarine roundfish). Like in juveniles, adults had also taken rather large quantities of squid in the Eastern Scheldt. With similar proportions of gadoids in the diets, adults in the Eastern Scheldt had a diet that was comparable to, or even of a higher quality (higher overall energy density of prey) than, the diet in the North Sea. Note, however, that numbers of adults available for study in the Eastern Scheldt were small. Tentative differences in diets of adults in the Eastern Scheldt as compared to diets in the North Sea may thus have been due to a low sample size, and more adults, particularly from the Eastern Scheldt need to be studied to resolve the question whether such differences are real.

We conclude that juvenile porpoises that find themselves in the Eastern Scheldt must survive here on a lean diet. With time, they may get a very good knowledge of local prey hotspots within the Eastern Scheldt and this may help them to cope with the available prey. Adults did not have an average diet that was inferior to that in the adjacent North Sea. A photo identification study in the Eastern Scheldt has shown that some individual porpoises survived here over a range of years, with one individual recorded over a period of eight years (Bakkers et al. 2016). Once settled in the Eastern Scheldt, harbour porpoises may become specialists, that can deal with the local feeding conditions. They take advantage of local specialties, like abundant small squid and sand smelts, while still being able to find enough gadoids to sustain themselves. The latter may seem remarkable, as gadoid abundance was found to be only 9.9% of that in the adjacent North Sea. Therefore, adult porpoises might be very good in catching these gadoids in the Eastern Scheldt, e.g. around artificial hard structures such as bridge piles, which are not sampled in the fishery surveys. Alternatively, a 90% reduction in gadoid presence has no effect on the abilities of porpoises to catch them, i.e. gadoids are just superabundant in the North Sea, from a porpoise perspective.

Juveniles may have less access to gadoid prey in the Eastern Scheldt, possibly because these fishes are too hard for them to catch, or because of competition with adult porpoises. Although juveniles in the Eastern Scheldt may thus face a prey base consisting mainly of small and lean prey, and possibly competition with adults, their average body condition did not differ from that of animals stranded along the North Sea coastline, suggesting that also the juveniles are able to cope with the prevailing conditions in the Eastern Scheldt.

Acknowledgements: This publication has been realised within the project "Eastern Scheldt Tidal Power", funded by the European Fund for Regional Development in the context of programme OP-Zuid and with a contribution of the Province of Zeeland. The underlying data were gathered in earlier projects commissioned by the Dutch Ministry of Economic Affairs under Grant BO-11-018.02-004. We would like to thank Jaap van der Hiele, the EHBZ / A Seal team and all other people who reported and collected stranded harbour porpoises around the Eastern Scheldt and along the North Sea coast. We thank the veterinary pathologists and all others at Utrecht University who helped conducting the autopsies during the last ten years. We thank Dr Henk van der Veer, NIOZ Royal Netherlands Institute for Sea Research for supplying herring and whiting fyke catch data and Dr Ingrid Tulp, Wageningen Marine Research, for making the

fisheries survey data available to us. And finally we like to thank Erik Meesters for help with the statistics and Ellen Besseling and two anonymous referees for reading and improving an earlier draft of this paper.

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Samenvatting

De Oosterschelde: een bruinviswalhalla of bruinvisgevangenis?

Bruinvissen (*Phocoena phocoena*) zijn de kleinste walvisachtigen. Vanwege hun geringe formaat en koude leefomgeving hebben ze circa 10% van hun eigen lichaamsgewicht aan voedsel per dag nodig om te overleven. Bruinvissen eten vooral kleine vissen, maar hun stapelvoedsel varieert per regio. In het Kattegat en Skagerrak eten ze bijvoorbeeld veel vette haringachtigen, terwijl bruinvissen in de Noordzee voornamelijk relatief magere grondels en kabeljauwachtigen eten. Van bruinvissen die de Oosterschelde binnen zwemmen via de openingen in de Oosterscheldekering is bekend dat zij langere tijd (weken, maanden of zelfs jaren) in de Oosterschelde blijven en dus overleven op het lokale prooiaanbod. De visstand in de Oosterschelde is echter ongeveer tien keer lager dan in de aangrenzende Noordzee, wat de vragen oproept waarom bruinvissen niet terug zwemmen naar de Noordzee, of ze wel voldoende te eten kunnen vinden in de Oosterschelde en wat hier de belangrijkste prooisoorten zijn. Daarom wordt in dit onderzoek gekeken wat het dieet van de bruinvissen in de Oosterschelde is, in vergelijking met het dieet van bruinvissen in de Voordelta (Hoek van Holland tot de Belgische kust).

Drie-en-veertig dode bruinvissen, gestrand tussen 2006 en 2015 in de Oosterschelde, zijn onderzocht, waarvan er 37 (28 juveniele en 9 volwassen dieren) visresten in hun maag hadden. Uit dezelfde periode zijn 421 (276 juveniele en 56 volwassen dieren met prooiresten) gestrande bruinvissen uit de Voordelta onderzocht. De bruinvissen uit de Oosterschelde en de Voordelta hadden een overeenkomstige leeftijdssamenstelling, geslachtverhouding, conditie en doodsoorzaken, maar vertoonden wel kleine verschillen in hun dieet. Ondanks de relatief lage visstand in de Oosterschelde is er geen bewijs gevonden van massale verhongering onder de gestrande bruinvissen in deze voormalige zeearm. Zowel in de Oosterschelde als in de Voordelta waren grondels en kabeljauwachtigen de belangrijkste prooien voor bruinvissen. Wel werden er verschillende soorten gegeten. In de Noordzee was wijting de favoriete kabeljauwachtige prooi; in de Oosterschelde waren dit bolken (steenbolk en/of dwergbolk). Sprot en zandspiering (vette vis) werden in de Oosterschelde nauwelijks gegeten, maar hier stonden wel een aantal estuariene soorten op het menu, zoals zwarte grondel en grote koornaarvis. Ook werden in de Oosterschelde relatief veel kleine inktvissen gegeten. Onze analyse laat zien dat bruinvissen die langere tijd in de Oosterschelde overleven hun dieet enigszins aanpassen om genoeg prooien van voldoende kwaliteit te kunnen vangen in deze relatief prooi-arme omgeving. Juveniele bruinvissen daarentegen, eten vooral magere en kleine prooien en zijn wellicht in competitie met volwassen bruinvissen.

Received: 18 December 2016
Accepted: 21 March 2017

Monitoring weasels (*Mustela nivalis*) with nest boxes

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Abstract: In November 2014 we placed ground-placed nest boxes for small mustelids, equipped with a track tube entrance, in a study area near Taarlo, Province of Drenthe, the Netherlands (6.62 E, 53.03 N) and checked these monthly until September 2016. Weasels (*Mustela nivalis*) used the boxes for resting and occasionally for catching rodents. The boxes were more frequently visited in summer and autumn than in winter and spring, probably as a result of seasonal fluctuations in the population caused by reproduction and mortality. It remains to be seen if annual population fluctuations can be reliably monitored.

Keywords: weasel, *Mustela nivalis*, monitoring, nest boxes, footprints, track tube, temperature logger.

Introduction

Because of their small size, sparse distribution, low abundance and obscure way of life, a systematic survey of weasels (*Mustela nivalis*) in the field, and monitoring in particular, are near-impossible without using destructive methods (McDonald & Harris 1999) or labour-intensive methods such as life traps. Tracks are difficult to find, let alone to identify reliably, and droppings can only be identified to species with help of DNA analysis. We initially sought to establish the presence of weasels in the study area with the help of track tubes (www.kleinemarters.nl). Between 1 March and 14 November 2014 we placed unbaited track tubes (40 cm pcv-tubes, diameter 8 cm) for a period of 14 days at 213 locations, but these resulted in only two weasels' tracks. We also experimented with a camera box or Mostela camera trap (van Maanen et al. 2015), but with little success. We therefore opted for a combination of methods: providing nest boxes (Criel 1988, 1990) and track tubes and the use of camera traps. This paper describes the efficacy of these non-lethal methods in monitoring weasel occurrence and behaviour.

Methods

Nest boxes made of wood or vertical slices of large pvc-tubes were placed on the ground, so that the inner space (20x20 cm) was accessible by two diagonal entrance holes with a diameter of 45 mm (www.zoogdierenwerkgroep.be). To enter the nest box weasels had to pass through a 40 cm long pvc-tube (diameter 8 cm). The bottom of the tube contained a platform with adhesion primer (paper is often eaten by snails) on which tracks can be traced. A flat sponge was added, soaked in a mixture of burnt bone-dust and oil, to improve the resolution of the track. To prevent the oil from leaking, the sponge compartment was surrounded by a rim of silicon-free sealant.

The nest boxes were placed in an area of 2.5x3 km near Taarlo in Drenthe (6.62 E, 53.03 N), with a mean distance of 285 m between the boxes (figure 1). We tried to position the boxes in a regular grid, but often landscape characteristics forced us to deviate from the predetermined grid. To increase the probabil-

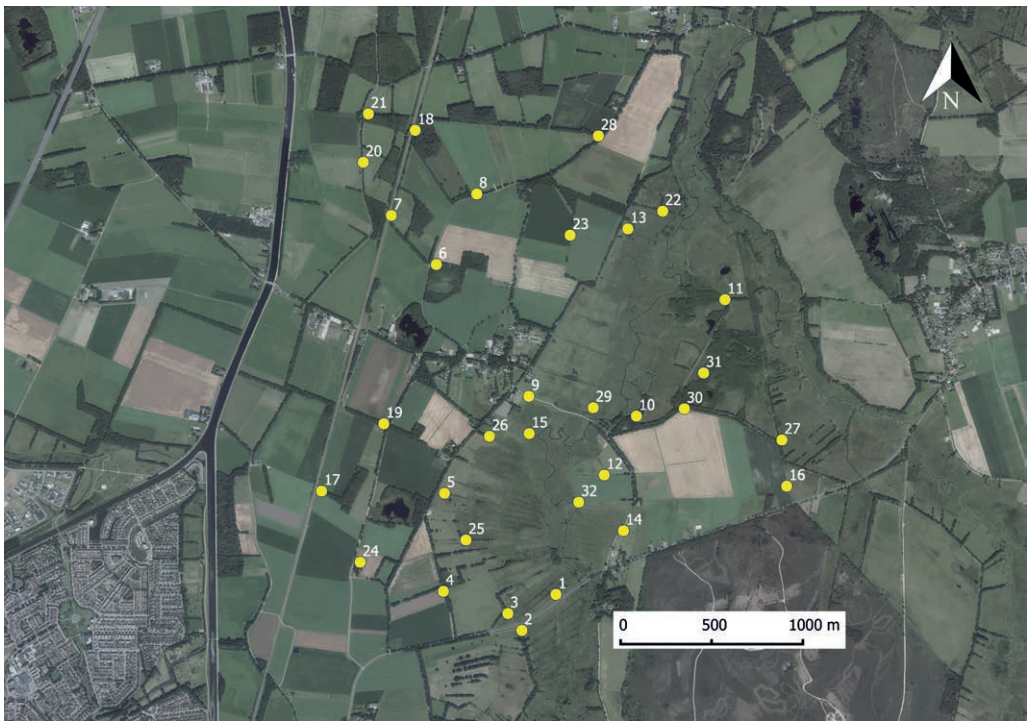

Figure 1. Distribution of nest boxes in the study area near Taarlo. Numbers correspond with numbers in figure 2 and in the text (Map data: PDOK).

ity of attracting weasels, we placed the boxes on line-shaped elements or on gradients in the terrain, such as hedgerows, ditches or edges of woodland (Šálek et al. 2010). Some boxes were placed in intensively used farmland outside the river valley. The boxes were well-hidden to avoid human detection or destruction. Despite the locations being carefully chosen, three boxes were lost during mechanised landscape maintenance. These were replaced as soon we became aware of their destruction.

A large part of the study area is covered by the river valley of the Drentsche Aa. For a long time this was an area of wet meadows, hedgerows and woodlots embedded in small-scale farmland with fields, heaths and small villages. From 1970 onwards the vicinity of the Drentsche Aa was drained, agriculture intensified and field sizes increased. Despite its protected status, the valley gradually became drier. At the end of the 20th century ditches

Figure 2. Weasel footprints on the platform of the track tube. Nest box no. 1, 22 August 2016. *Photo: Matthijs Smaal.*

were filled in order to counter drainage. Nowadays large sections of the river valley are very wet and partly changed into marshland. Slightly drier grasslands are mown once a year in August-October. A thorough description of

the area can be found in Spek et al. (2015). The river valley is surrounded by intensively used farmland with woodlots. Some of the boxes were located in the hedgerows that cross this landscape.

Boxes were checked monthly for tracks. The tracks were photographed, the platforms cleaned and, when necessary, coloration oil was added. Tracks of weasels look like very small cat tracks with pad widths of about 2 mm (figure 2). Tracks of mice and voles are more subtle and look like a flock of small points and dashes. Tracks of stoat (*Mustela erminea*) are generally larger and less clear than those of weasel because of their larger size and their feet being more hairy (the pad size of a stoat's hind foot, excluding nails, is 50% larger than that of weasels; see IJsseling & Scheygrond 1943: 352 and 355, although their figures do not distinguish between the sexes). We may have mistaken tracks of stoat for those of weasel, since the prints were not always crystal clear. Nine prints were confirmed as weasel by a photograph of the individual; by contrast we did not obtain any pictures of stoat. Not all the tracks recorded were of good enough quality to be identified. Individual pad prints of brown rats (*Rattus norvegicus*) can be very similar to those of weasels, although brown rats have longer toes. In this study we identified 122 tracks as belonging to weasels and 22 tracks that remained unspecified, which were omitted from the analysis. In nine cases (with a different nest box and/or different year) we confirmed our determination of weasels' presence with camera images.

In order not to disturb the animals we rarely opened the nest boxes to inspect the inside. In order to validate the use of boxes

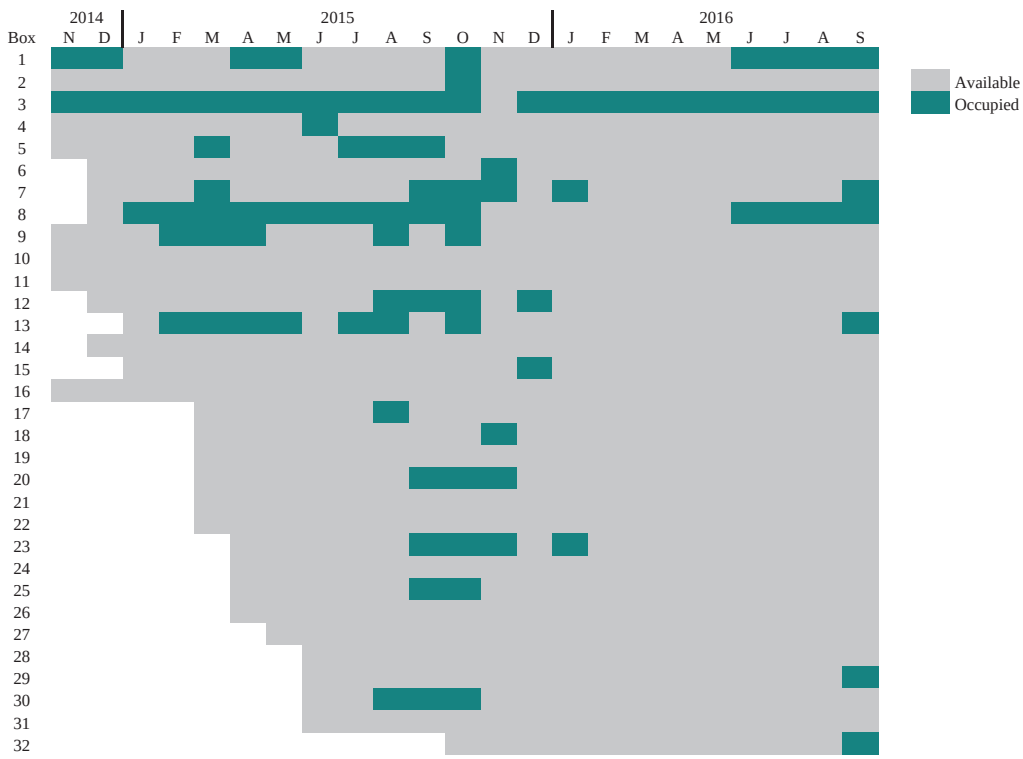

Figure 3. Availability and monthly use of nest boxes by weasels in the study area. Numbers refer to the map in figure 1.

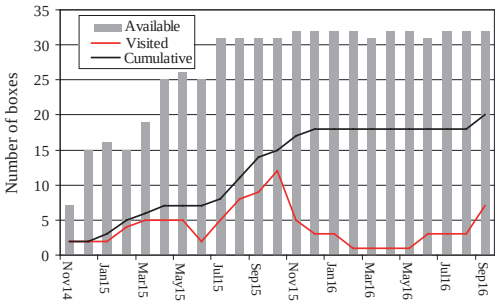

Figure 4. Available nest boxes and visits by weasels in the course of the study period (November 2014 - September 2015). 'Cumulative' is the number of individual boxes that were visited at least once.

by weasels, we mounted a temperature logger (Easylog USB-logger) inside nest box 3. The logger can store 35,000 measurements accurate to the nearest 0.1 °C. Initially we opted for an interval of 20 seconds between measurements, but later on changed this to every 1 or 2 minutes. When the logger was active, we checked the box more frequently to harmonise fluctuations of within-box temperature with visits of weasels, mice (Muridae) or voles (Cricetidae) and with fluctuations in ambient temperature. The logger was operational between 9 December 2015 and 23 February 2016 and between 17 April and 1 August 2016. During these periods 166,785 valid measurements were collected.

Results

Occupancy of boxes by weasels

It usually took several months before the nest boxes were visited by a weasel; 12 out of the 32 nest boxes were not visited at all. Three of the boxes were frequented by weasels 20, 28 and 29 days after they were put in place (i.e. weasel presence was recorded during the first check, so they were perhaps visited earlier than this). Duration of usage of a nest box (presumably by the same individual) ranged from one month to twelve months (figure 3).

Figure 5. Nest made out of fur and moss by a weasel. Nest box no. 3, 20 March 2015. *Photo: Matthijs Smaal.*

The number of boxes visited by weasels at any one time fluctuated considerably (3-38% per month). Box visits were more common in spring and summer 2015, with the maximum occupation in that year being reached in October. In November nest box occupancy declined and reached a minimum in February 2016, continuing until May. In June numbers started to increase again, and reached an annual high in September 2016. Overall occupancy was much lower in 2016 than in 2015 (figures 3 and 4).

Daily use of nest boxes by weasels

In general weasels left few, if any, traces inside the nest boxes. Only one box (no. 3) contained some sort of nest, made from moss and pieces of vole skin (figure 5), together with remains of at least 53 voles (106 incisors from the lower mandible, and many feet) (figure 6). This finding was made on 18 November 2015, after the nest box had been occupied for twelve consecutive months. We have no indication that nest boxes were used for reproduction.

Visits by weasels were registered via consid-

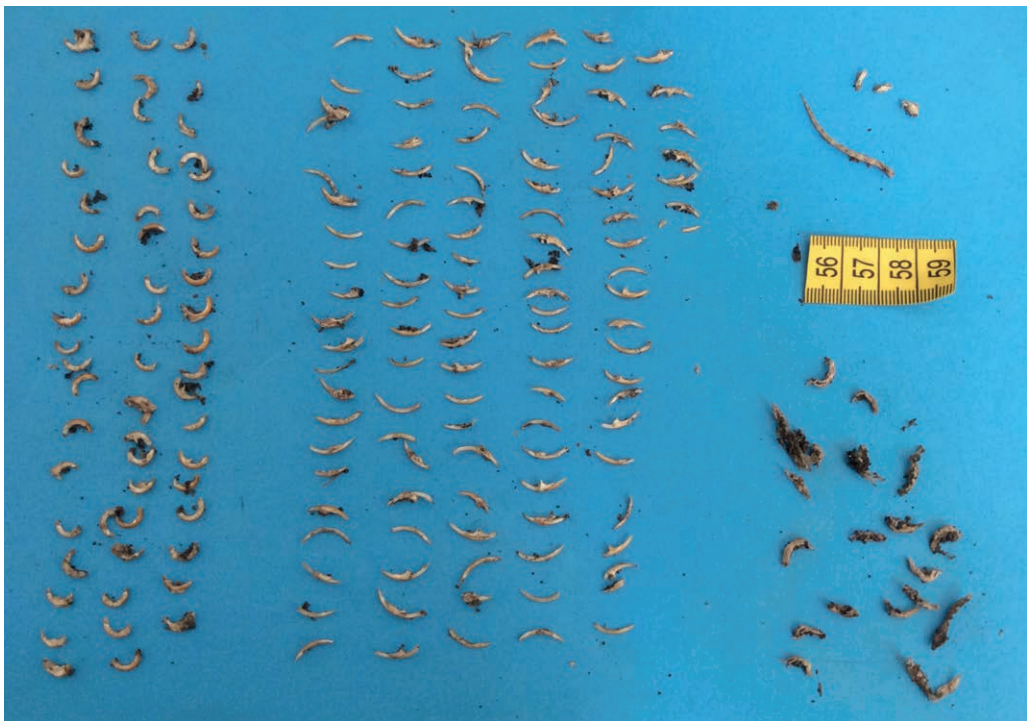

Figure 6. Incisors and feet of voles that were collected from nest box no. 3 after this box had been in use for 12 consecutive months. 22 November 2015. *Photo: Matthijs Smaal.*

erable rises in temperature in the box (+1.2-7.0 °C, mean 4.1 °C in consecutive measurements), probably caused by direct skin contact. All rises of this kind coincided with weasel visits.

When the animals prolonged their stay the temperature inside the box remained relatively high compared to the ambient temperature. After leaving the nest box temperature dropped in a typical curve (figure 7). Direct sunlight rarely changed the temperature in the nest box by more than 0.2 °C between measurements (occasionally up to 0.8 °C on hot days around noon). Apart from these outliers, short-lived fluctuations of 0.4-1.4 °C were recorded when weasels were absent, probably triggered by mice or voles. We cannot exclude the possibility that weasels produce a similar pattern when visiting the nest box for just a moment.

The data of the temperature logger showed that nest box no. 3 was visited intermittently, with visits varying considerably in duration. Temperature rises that were probably caused by a weasel occurred on three occasions in December 2015, twice (on the same day) in February 2016, four times in April and once in June. In December the visits lasted between six and a half and nine and a half hours. In all the other cases the visits lasted half an hour less (in April often for less than two minutes). These data show that visits became shorter towards spring. This difference was not correlated with temperature since temperatures in December 2015 were generally higher than in February and April 2016. There was no discernible pattern in the timing of visits across the day.

Other species visiting the nest boxes

The nest boxes we provided were suitable for animals up to the size of a stoat. A few tracks of brown rats were recorded in the track tubes

attached to the nest box, and several times they were photographed by camera traps near nest boxes. Tracks of mice, voles and shrews (wood mouse *Apodemus sylvaticus*, bank vole *Myodes glareolus*, field vole *Microtus agrestis*, Eurasian harvest mouse *Micromys minutis*, common shrew *Sorex araneus* and pygmy shrew *S. minutus* as evident from camera) were frequently recorded in the track tubes.

Discussion

Nest boxes were used by weasels as a temporary den, possibly also during hunting and in at least one case as a deposit to store prey. Weasels did not use the boxes to give birth or nurse a litter, possibly because the type we provided was too spacious and the entrances are sufficiently wide to allow stoats to enter. The presence of the larger and probably dominant stoat (King & Powell 2007) may affect occupancy rate of boxes by weasels, but the two species are known to coexist without much competition by using disparate habitats and by exploiting different food niches, with the weasel showing a more flexible and generalised habitat choice and a preference for voles (Aunapuu & Oksanen 2003). Moreover, although a stoat was photographed in the study area and DNA analysis of five mustelid droppings from the study area revealed that one out of five was of stoat (the rest Weasel; Elske Schut, Gendika BV): given the scarcity of field observations, stoats can be considered to be rare in the Drentsche Aa region.

The importance of voles as prey was illustrated by a pile of incisors of at least 53 voles found in one of the nest boxes, presumably the remains of a cache of a single weasel. Caching is well-known in weasels (e.g. Oksanen 1983, Rechstein 1993), a characteristic behaviour evolved under conditions of unpredictable food supply (King & Powell 2007). Weasel diets in Europe are typically dominated by small mammals (e.g. 46% and 61% of all prey; respectively Tapper 1979 and Brugge 1977), even so in more recent decades with declining food availability (see review in King & Powell 2007).

During nearly two years of research we recorded low numbers of weasels in boxes in spring, an increase in summer, a peak in autumn and low numbers in winter. This pattern is in line with expected population fluctuations due to reproduction between March and September (Deanesly 1944, Jędrzejewska 1987). We had, however, expected a more intensive use of nest boxes during winter, when weasels are known to search for drier places to rest (Zub et al. 2008).

Using nest boxes for monitoring small mustelids may seem a less elegant and more labour-intensive method than the use of track tubes or camera boxes. However, apart from production and placement in the field, which is time-consuming, checking 32 boxes takes less than a day and they are simple to manage as they stay at the same location. The permanence of location is an advantage, as weasels seem to take a long time to encounter (or get used to) nest boxes. In this regard, the advised time span for providing track tubes or camera boxes, i.e. 1-2 weeks (www.kleinemarters.nl), may be too short in areas where weasels are scarce. As weasels used the nest boxes for several purposes, the occupancy rate may increase over time. Whether recorded annual fluctuations reflect reality remains to be validated. To improve the efficacy, we plan to develop a nest box in which a camera can be placed as soon as the box is used. This will be especially useful to validate identifications of tracks, because, to date, we have been unable to unambiguously distinguish tracks of weasel and stoat (unlike Aunapuu & Oksanen 2003 and Norrdahl & Korpimäki 1995, who made species-specific identifications from tracks in snow).

Acknowledgements: We thank Rob Bijlsma, Dirk Criel, Jan Dekker, Jasja Dekker, Maurice la Haye, Tim Hofmeester, Hans Kleef, Frank van der Knaap, Monique de Lange, Guido Lek, Erwin van Maanen,

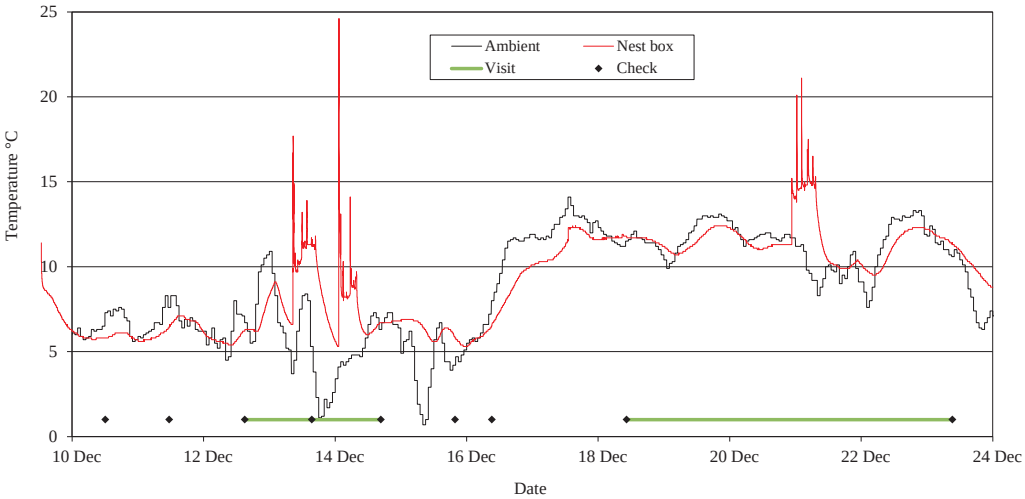

Figure 7. Temperature inside nest box no. 3 (measured with logger) and ambient temperature (hourly measurements at Eelde, 11 km north of the study area at a height of 1.5 m, source: KNMI) between 10 and 24 December 2015. According to tracks, weasel visited the nest box twice during this period. Track tubes were checked intermittently (dots).

Jeroen Mos, Aaldrik Pot, Johann Prescher, Jasper Schut, Peter van Stiphout and Karol Zub for discussing the merits and drawbacks of different methods and helping us to identify tracks. Staatsbosbeheer gave us permission to work in the protected river valley of the Drentsche Aa. Elske Schut of Gendika BV analysed the DNA of the five droppings. Special thanks to Rob Bijlsma who provided us with literature and improved the manuscript. We furthermore thank two anonymous reviewers for their constructive feedback and Nicholas Parrott (TextualHealing.eu) for editing the English.

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Samenvatting

Monitoren van wezels (*Mustela nivalis*) met behulp van nestkasten

Tussen november 2014 en september 2016 werd een monitoringonderzoek uitgevoerd naar wezels in een gebied van 750 ha bij Taarlo, Drenthe (6.62 E, 53.03 N). Twee-endertig op de grond geplaatste nestkasten voor kleine marterachtigen, voorzien van een sporenplank, werden maandelijks gecontroleerd. Om verstoring te voorkomen, werden de nestkasten zelf zelden geopend. De kasten waren min of meer regelmatig verspreid over het gebied geplaatst met een gemiddelde onderlinge afstand van 285 m, en waren steeds goed verstopt langs een houtwal, sloot of bosrand. In één van de nestkasten werden de frequentie en duur van wezelbezoeken vastgelegd met behulp van een temperatuurlogger. In de meeste gevallen duurde het enkele maanden totdat de nestkasten voor het eerst werden bezocht door wezels. Daarna vertoonde de bezettingsgraad sterke fluctuaties (3-38%), waarbij de bezetting hoger was in 2015 dan in 2016. Van de belopen nestkasten was er slechts één die een soort van nest bevatte, gemaakt van mos en muizenhuid. In deze kast lagen ook de snijtanden en voetjes van tenminste 53 woelmuizen, wat er waarschijnlijk op duidt dat de kast als tijdelijke opslagplaats voor prooi is gebruikt. Het is uit te sluiten dat de nestkasten gedurende de onderzoeksperiode zijn gebruikt om jongen in groot te brengen. Bezoeken van wezels aan de nestkast met temperatuurlogger kenmerkten zicht door sterke stijgingen en dalingen in de temperatuur. Dergelijke grote temperatuurschommelingen werden alleen vastgesteld wanneer op de sporenplank tevens prenten van wezels werden aangetroffen. Geringere veranderingen in temperatuur werden waarschijnlijk teweeg gebracht door bezoek van muizen of door veranderingen in de buitentemperatuur. Uit de data van de temperatuurlogger blijkt dat de wezel deze nestkast onregelmatig en op niet-vaste tijdstippen bezocht; de bezoekduur varieerde hierbij van minder dan 2 tot 493 minuten (n=10 bezoeken tussen 13 december 2015 en 20 juni 2016).

Received: 3 October 2016
Accepted: 30 March 2017

The social organisation of natural herds of koniks (*Equus caballus*): subordinate stallions, rule or exception?

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Abstract: This article describes the social organisation of herds of free-roaming koniks in the Netherlands and elsewhere in Europe, with a particular focus on the Oostvaardersplassen. Attention is directed to: 1. Herd size in relation to habitat conditions. 2. Composition of harems within those herds. 3. The role and relative number of subordinate stallions in those harems. On the basis of this information, the article subsequently describes the assumed situation regarding subordinate stallions at the Oostvaardersplassen and in other areas with large herds of free-roaming horses. Following this, the validity of this assumption is investigated for other konik grazing areas within the Netherlands, using field data that also include those from a repeated study about the Oostvaardersplassen. Finally, it is investigated whether the outcome also applies to feral horses (*Equus caballus*), Przewalski's horses (*Equus przewalskii*), zebras and African and Asiatic wild asses (*Equus spp.*) elsewhere in the world. The free-roaming koniks in Europe, in contrast to those elsewhere in the world, mostly live in nature areas that are rich in food and have an ample drinking water supply. In such areas, koniks appear to prefer to live in large groups. The ample food supply in the areas studied supports such large herds. In two other areas that were less rich in food, the harems opted to live separately. Large herds were also often found to break up into smaller herds in the wintertime, when food would become scarce. Exclusive home ranges with only one harem were found in certain areas with narrow road crossings or traversable dykes, or in long and narrow areas. Exclusive home ranges are different from true territories, as only the harems were defended, rather than the land itself. Thus, independent harems or groups can be formed not only as a result of food scarcity but also because of the type of terrain. Free-roaming koniks, in Europe, live in herds with a social organisation of harems and bachelor groups that is similar to elsewhere in the world among wild Equidae and feral horses. In Europe, however, this organisation can only be observed in nature areas with larger herds that live in an autonomously chosen social structure - thus, in areas with only limited human intervention. The presence of multiple harems, however, does mean that dominant stallions continually need to fend off the competition. This is why harems in such large herds often have a particular composition in which subordinate stallions also play an important role, in addition to the dominant stallion, both in tasks and numbers. Having subordinate stallions around offers advantages; they help to defend the harem and, thus, contribute to achieving the much-needed peace and quiet for mares and their foals. Subordinate stallions also help to prevent predation, and larger numbers of subordinate stallions are seen in situations of increased risk of predation. Subordinate stallions themselves, however, experience only few advantages in relation to their efforts. Thus, among the free-roaming koniks studied, there appeared to be no mutualism or altruism. Subordinate stallions and dominant stallions do appear to have different temperaments. Predation also seems to lead to the formation of large groups as well as to increased collaboration between stallions, although this is not - yet - the case in the Dutch situation. The occurrence of subordinate stallions, therefore, is the rule rather than the exception, and appears to be

related to herd size, the presence of rivalling stallions, predation and food supply.

Keywords: feral horse, social and spatial organisation, herd formation, dominant stallion, subordinate stallion, multi-stallion harem, Oostvaardersplassen, konik, free-roaming horse.

Introduction

There are bovines and horses in numerous nature areas in the Netherlands. In some cases, these are animals of the same gender and age that have been brought into the area for one season, but often they are free-roaming* animals living in natural herds, or a composition in between. Particularly the herds of free-roaming animals are provided with enough space to demonstrate their natural behaviour, such as in the case of the bovines and horses at the Oostvaardersplassen and various nature areas where large grazers are being managed by the FREE Nature organisation (the Dutch Foundation for Restoring European Ecosystems). Animals in those areas are often found to organise themselves into social herd structures. However, the degree to which this is natural behaviour and whether the behaviour is similar to that of the horse's original wild ancestor (*Equus caballus*) is unknown. The enormous herd of koniks at the Oostvaardersplassen, in particular, with its complex social organisation, is often viewed as the exception to the rule. Since 2008, this area has been home to a single large herd that, at the start of each summer season, contains around 900 animals over the age of one, as well as around 250 foals (Cornelissen et al. 2016). We set out to determine whether the Oostvaardersplassen are indeed an exception in this respect. This article describes both literature and field research into the social organisation of herds of free-roaming koniks, in the Netherlands and elsewhere in Europe, with a particular focus on the Oostvaardersplassen.

To obtain a greater insight into the importance of herds for Equidae in general, we focused our attention on: 1. Herd size in relation to habitat conditions. 2. The social organisation of herds, particularly the composition of the harems that are part of those herds. 3. The relative number of subordinate stallions and their role within those harems. On the basis of this information, we were then able to create an image of the assumed situation of subordinate stallions at the Oostvaardersplassen, as well as in other areas with large herds of free-roaming horses. Subsequently, we investigated whether this image also applied to other areas with herds of koniks in the Netherlands. To this end, we used field data that also included results from repeated research in the Oostvaardersplassen. Finally, we examined whether our results also apply to feral horses (*Equus caballus),* Przewalski's horses (*Equus przewalskii*), zebras and African and Asiatic wild asses (*Equus* spp.), elsewhere in the world.

* The koniks living in herds in nature areas in the Netherlands are sometimes characterised as *wild* horses. However, as long as herds are under human management, it would be more accurate to speak of *free-roaming* horses. Since these horses still have a known owner, they cannot be called *feral* horses like the mustangs and brumbies in North-America and Australia. In fact, in the Netherlands, only the Oostvaardersplassen contain herds of what could be considered *wild* horses, as human intervention there is limited to the culling of animals that would not have survived anyway.

Habitat conditions

Large herds have been observed to occur among all species of Equidae, ranging from hundreds of animals to over a thousand per herd (Berger 1986, Rubenstein 2011). Large herds often exist only temporarily, and mostly stay in locations with ample supplies of water

and high quality food (Rubenstein 2011). For those species that form harems, such as plains zebras (*Equus quagga*) and Mongolian wild asses (*Equus hemionus hemionus*), such herds were found to always consist of a conglomerate of harems and bachelor groups (Feh et al. 2001, Rubenstein 2011). Living in groups provides protection against predators (Rubenstein 2011), and this behaviour can still be seen in feral horses today — even though they have not been confronted with predators for generations (Rubenstein 2014). Living in groups not only reduces the individual risk of predation, it also means that a larger number of animals are available to keep watch, which increases the predator discovery rate, and, on balance, provides individual animals with more grazing time. In addition, herd formation offers protection in times of bad weather, and may help drive off bands of bachelor stallions (Rubenstein 2011). Bachelor or solitary stallions are adult males without a harem, who attempt to increase their chances of procreation by servicing or taking over mares from existing harems.

The degree of herd formation among plains zebras in Africa depends on the size of the bachelor bands trying to take over or service the mares. In such cases, stallions from various harems have been observed to collaborate, in order to chase larger groups of bachelor stallions away (Rubenstein 2011, Rubenstein 2014). Studies on plains zebras and Mongolian wild asses (Bahloul 2001, Feh et al. 2001, Rubenstein 2011) have shown food availability not to affect herd formation, although having an ample food supply nearby is one of the characteristics of the locations in which herds are staying. Most wild Equidae and feral horses outside Europe live in oligotrophic ecosystems with a short growth season (Berger 1986), and in lower densities than those in more nutrient-rich European nature areas that, in addition, have a mild climate and usually an ample drinking water supply. In the Netherlands, most konik herds also roam nutrient-rich soils, such as floodplains and reclaimed marine clay areas that have a relatively long growth season (nine months), as well. The ample food supply and resulting lack of food competition means these areas are able to sustain large herd sizes, without herds needing to break up. However, as yet unclear is the precise mechanism that causes these Equidae to live in large groups.

Social organisation: herds and harems

Wild Equidae live in herds of various social structures, which largely depend on the characteristics of their habitat (see previous section). For example, in predator-poor, semi-desert areas, the stallions of feral donkeys (*Equus africanus)* and onagers (*Equus hemionus*) in low-predation, semi-dessert areas in Israel and India, and Grévy's zebras (*Equus grevyi*) in Africa, have territories that they defend against congeners, and bands of mares travel along these territories looking for food and water (Feh et al. 2001, Rubenstein 2011, 2014, Ransom & Kaczensky 2016). The strongest stallions have the best territories and therefore are most frequently visited by mares.

In regions with moderate precipitation levels, the Equidae generally live in harems, such as the plains zebras in Africa (Rubenstein 2011), the Camargue horses in France (Duncan 1992), the feral horses in North America, New Zealand and Australia (Ransom & Kaczensky 2016), and the Przewalski's horses in Mongolia (Wit et al. 2006). Such harems typically consist of a dominant stallion and multiple mares with young offspring. Dominant stallions can be described as stallions in charge of their harem, who have the first choice of which mares to service. This is why, often, most of the foals in a harem are sired by the dominant stallion. The members of a harem stick together, and dominant stallions defend their harem against rivals. Mares prefer a steady harem with a dominant stallion, to ensure they can graze in peace and stay in a good physical condition (Rubenstein 2011,

2014). Young animals usually leave the harem when they become sexually mature, forming bachelor groups or temporary groups of adolescents (Berger 1986, 1987, Rubenstein 2011, Ransom & Kaczensky 2016). Harem home ranges usually overlap; however, in certain circumstances, harems can be territorial, such as is described about Shackleford Island (Rubenstein 1981, 2014). On this island, food and water are widely spread and the sea forms a natural boundary, which means stallions only need to defend the land side of their territory. The island has also been observed to contain groups of varying compositions (Rubenstein 1981), which is rare in feral horses elsewhere.

Mongolian wild asses in Turkmenistan and Mongolia show both types of behaviour (Feh et al. 2001). In areas of predation by wolves, harems are the norm, and groups consisting of only female animals and their young are rare, whereas the latter is found more often in regions where wolves are hardly seen (Feh et al. 2001). Mongolian wild asses, therefore, also appear to adjust their social organisation to habitat conditions.

Subordinate stallions

A phenomenon related to the social organisation of Equidae herds that has not yet been described for Europe is that of subordinate stallions. These adult stallions are harem members, who are subordinate to the dominant stallion. The main role of these subordinate stallions is that of defending the harem against other stallions. Subordinate stallions are often found in harems of feral horses in North America, New Zealand and Australia (Berger 1986, Linklater 1998, Ransom & Kaczensky 2016).

Although the dominant stallion usually sires the foals, subordinate stallions were also found to have sired foals, on occasion. These subordinate stallions not only do the hard work, they are able to reproduce as well, and, thus, also benefit from their position within the herd. However, these benefits seem relatively limited. In herds of feral horses in New Zealand, subordinate stallions and bachelor stallions were found to have about equal access to mares in the harems (Linklater 1998). Populations of feral horses were also found to include harems with two dominant stallions, in addition to those with subordinate stallions. In such cases, the dominant stallions were seen to work together to defend their harem (Rubenstein 2011, Ransom & Kaczensky 2016). Often, such collaborations are already formed when they are still within the bachelor groups. Their relationship is one of equals, with both stallions participating in procreation and neither being subordinate to the other.

The literature does describe collaborations between dominant stallions from different harems in herds of wild Equidae, but there is no mention of harems with subordinate stallions. For example, no subordinate stallions have been observed in herds of wild Przewalski's horses in the Hustain Nuruu National Park in Mongolia (Feh et al. 2001). Feh et al. (2001) do describe harems of Mongolian wild asses with more than one stallion, but not whether there are any subordinate stallions. It can be deduced from their article that these stallions concern both youngsters and more mature stallions. Bahloul (2001) also mentions the occurrence of steady groups of Mongolian wild asses with one or two stallions, which may point to the presence of subordinate stallions.

Oostvaardersplassen

The herd of koniks at the Oostvaardersplassen is the only truly wild herd of horses in Europe of which the social organisation is not subject to human interference. The Oostvaardersplassen population basically consists of one large herd roaming the area. This large herd is subdivided into numerous harems containing many subordinate stallions. Bachelor groups, older solitary bachelor stallions and temporary associations of young males and females are an integral part of this herd (Nieuwdorp 1998).

It is expected that the structure of this herd is not unique, but that the nutrient-rich environment in the Netherlands would in fact be able to support other large herds of horses with harems that contain substantial numbers of subordinate stallions. It is assumed that the presence of multiple harems within one herd means that dominant stallions continually need to fend off the competition. Subordinate stallions are a godsend, in those circumstances; they help to defend the harem and thus contribute to achieving the needed rest for mares and their foals.

This article investigates whether both these assumptions are correct, and, if so, whether they provide more insight into the social organisation of free-roaming herds of koniks in the Netherlands.

Method

Over the past 25 years, nature conservation organisations FREE Nature and ARK Nature have acquired a large amount of knowledge about free-roaming herds of koniks and how these are managed in various nature areas, both in the Netherlands and abroad. Since 1991, the ancestry of each individual animal is recorded in the herd database of FREE Nature, as well as the current and past roaming areas, the harem or bachelor group the animals belong to, and their position within the herd (dominant or subordinate stallion) and any changes in that position. In addition to field observations, ancestry research into the DNA of many animals has identified the dam as well as the sire of the animals, and in rare cases even revealed a foster mother. As DNA research has not been done for all animals, a foal's sire is sometimes unknown.

We used data from this database for the year 2013 for a more in-depth analysis, because of the relatively large size of the konik herds in that year, which resulted in a rather large amount of data available for analysis and interpretation. In 2013, around 400 koniks of FREE Nature were roaming 15 nature areas. From the information in the database, we determined the number of subordinate stallions per harem, as well as the ancestry of the foals that were born in the following year. In addition, the data helped to determine gender ratios within FREE Nature herds, as well as the herds' annual reproduction level. We approached the herd managers of FREE Nature and enquired about the occurrence of multiple, equally dominant stallions within a harem, and whether harems and bachelor groups would roam together or had separate territories and displayed territorial behaviour.

In order to compare the information with that on the Oostvaardersplassen, we looked at whether areas with large herds of koniks from FREE Nature had a different social organisation than areas with smaller herds. The larger the herd in a particular territory, the larger the number of outside competitors for harem stallions to fend off. If this fact would affect the number of subordinate stallions, then smaller herds were expected to have fewer subordinate stallions than larger herds. The line between small and large herds was drawn, more or less arbitrarily, at 25 koniks. Of the small herds, in 2013, there were eleven areas containing one harem each; larger herds were found in seven areas, mostly containing multiple harems per area (26 harems in total). We calculated the average number of subordinate stallions per harem, for both types of areas.

The co-author conducted a study, between February and June 1998, into the social organisation of herds of koniks at the Oostvaardersplassen (Nieuwdorp 1998). In the autumn of 2014, we returned to the Oostvaardersplassen to investigate whether the social organisation of 1998 was still in place, 16 years later. To this end, during one day in 2014, we counted the adult stallions in the harems of a part of the herd. On that day, we counted over 500 horses of the total herd of around 1150; a 40% sample of the total number of koniks at the Oostvaardersplassen at the time. The other koniks could not be counted because they

Fighting konik stallions. Oostvaardersplassen, 29 November 2014. *Photo: Leo Linnartz.*

were in one large group, in a location that was difficult to access. Of the 58 harems in the counted part of the herd, we documented the size of the harems and the number of adult stallions within them. In addition, we observed where the harems were located in relation to the rest of the counted herd. We also saw stallions that did not belong to any harems, but we did not count those.

Rubenstein (2011) also - and elaborately - includes ethological aspects in describing the systematics of Equidae species and subspecies. As these aspects were also explicitly included in our study, we follow Rubenstein's opinions about systematics and scientific nomenclature.

Results

The herds of FREE Nature

Predominantly in a single herd

The FREE Nature herds of free-roaming koniks, generally, consist of single, large groups per area, all year round. In 2013, this was the situation in 12 of the 15 FREE Nature areas. In Groenlanden (one of the areas, near the Dutch city of Nimwegen), one harem roams separately from the large herd. This separate harem has its own territory, which is mainly located in the sub-area 'Oude Waal', which is connected to the rest of the area by a traversable dyke. During high tide, the Waal River forces this harem to move to Groenlanden, on the land side of the dyke, but the harem remains separate from the other harems in Groenlanden.

Two other areas do not contain a single large group, and they each have two harems with one dominant stallion each. In both areas, the dominant stallions have subdivided the area into two exclusive home ranges separated by a clear boundary. In one case, this is a narrow road crossing that divides the area into two parts. The other case concerns a long and narrow nature area with a limited contact zone separating both home ranges. In this last area, once during a dry summer, there was no more drinking water in one home range, forcing the local harem to travel to the other harem's home range to drink — after drinking, they would quickly leave 'enemy territory', each time, and return to their side of the

contact zone. Immediately after the rains had replenished the drinking water supply, the two home ranges returned to being occupied exclusively by their original harem.

Social groups within herds

The FREE Nature herds of free-roaming koniks in the Netherlands have a social organisation consisting of harems and bachelor groups. In 2013, there were 37 harems divided over 15 territories. In nine of these territories, there was also a band of stallions. In six of those, the bachelor groups roamed separately from the harems, whereas in the other three, they moved together with the herd.

FREE Nature area managers, on occasion, have observed groups of adolescents containing a young mare and some young stallions, but such groups are usually only temporary and a prelude to the formation of a new harem. Sometimes, sexually mature daughters remain in the harem into which they were born, but are serviced only by unrelated stallions. Illustrative in this respect is the following observation: 'This morning, there was some unrest in the herd. A closer look revealed that a yearling filly was outside the herd. She was being chased by the dominant stallion of her birth harem and then went over to another harem. Once there, she was serviced by a yearling colt. The dominant stallion of that harem stood by without interfering. Afterwards, the filly returned to her birth harem and peace was restored.' Some days later, she moved to the other harem, permanently.

In 2013, on four separate occasions, this occurred with a stallion from outside the harem. On one occasion, the dominant stallion did service his own daughter. Sometimes sons of dominant stallions service such daughters. This behaviour was not observed in 2013, but it did occur in 2014. Furthermore, not all adult mares within a harem allow the dominant stallion to service them. Of the 70 foals studied in the spring of 2014, 83% had been sired by the dominant stallion and another 9% by a stallion from outside the harem. The remaining 9% had been sired by adult stallions from within the harem. In two cases (3%), this concerned an adult son of the dominant stallion.

Subordinate stallions

In FREE Nature's herds of free-roaming koniks, similar numbers of colts and fillies are born (the gender ratio was 0.93 in 2013, with 53 colts against 57 fillies). In the herds in total, however, the gender ratio is less balanced, varying from 0.73 (1 January 2013) to 0.62 (on 31 December 2013).

In 2013, 46% of all FREE Nature harems contained more than one adult stallion, but only one dominant stallion per harem. The other stallions were found to be subordinate stallions, in a subservient, supportive role. Usually, there would only be one subordinate stallion, but in 8% of cases there were two or three. In territories with fewer than 25 horses in total, 18% of the harems have a subordinate stallion, whereas in those with more than 25 horses per area, this is 58%. Moreover, in the latter category, harems more often have more than one subordinate stallion (20% in large herds, against 0% in small herds).

Harems with more than one dominant stallion are rare in FREE Nature herds. Only one such case is known, in the Rug nature reserve, near Roosteren, along the Meuse in the province of Limburg, but this situation was not present in the year 2013. Both of those stallions originated from the same bachelor group. Another known case is that of a three-year-old stallion and a four-year-old stallion from the same bachelor group, who together succeeded in conquering a harem. Surprisingly enough, the youngest of the two went on to become the dominant stallion, and the older, subordinate stallion has not serviced any mares in years.

The herd at the Oostvaardersplassen

At the Oostvaardersplassen, which is a nature area rich in food, around 1150 koniks live in

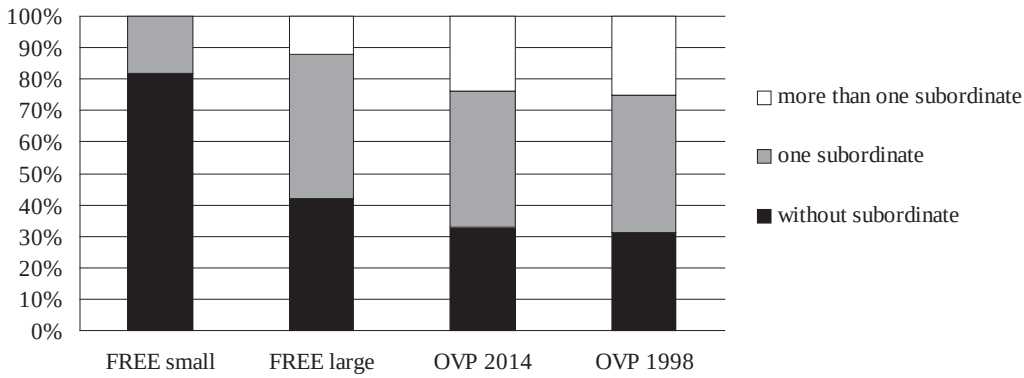

Figure 1. Percentage of subordinate stallions in harems of koniks; in areas (1) with a small FREE Nature herd (summer 2013, *n*=11) and (2) a large FREE Nature herd (summer 2013, *n*=26), and at the Oostvaardersplassen (3) in the autumn of 2014 (*n*=58) and (4) the spring of 1998 (*n*=32).

one large herd, in a more or less balanced gender ratio, on 24 km^2 of short and tall grasslands with patches of young forest. This equals a population density of around 48 horses per km^2. In 1998, the herd was much smaller, 391 horses, and consisted of 32 harems, each with one dominant stallion and 3.6 mares, on average. In 2014, there were 58 harems in the part of the herd that we counted.

Subordinate stallions

Similar to the FREE Nature herds, the harems at the Oostvaardersplassen also contain many subordinate stallions. In both 1998 and 2014, 67% of harems had at least one subordinate stallion. In both years, 25% had more than one subordinate, with a maximum of six adult stallions in one harem in 2014 (in 1998, the maximum was eight). Harems with only one adult stallion, thus, are in the minority, and were found to roam along the edge of the herd more often than those with multiple stallions.

Figure 1 shows that subordinates are found in over half of all harems — in large FREE Nature herds and those at the Oostvaardersplassen. In FREE Nature areas with small herds of koniks (fewer than 25 individuals per herd), subordinates were observed in 18% of harems.

Subordinate stallions not only occur regularly in konik harems, they also constitute a sizeable share of the herd. Of the 509 horses counted in the harems at the Oostvaardersplassen in 2014, 11% were dominant stallions and 12% were subordinate stallions. The harems studied, on average, each consisted of nine horses, which were dominant and subordinate stallions, mares and those too young to live outside their harem of birth. Only few bachelor groups were seen, and they were always found to consist of young stallions only. In addition, solitary stallions were observed, as well.

During the study of 1998, dominant stallions made up 11% of horses living in harems and 16% were subordinate stallions (figure 2). The harems consisted of an average of nine animals per harem, including two foals. Of all male animals older than one year, nearly half were either dominant stallions or subordinate stallions in a harem; here, also, there were more subordinate stallions than dominant ones, with 19% and 28%, respectively (of those over the age of one). Nineteen per cent of young stallions (between one and three years old) were in a harem, and only 9% were in a bachelor group. The remaining stallions (25%) were living a solitary life. Harems, on average, had three adult mares for every two adult stallions. The gender ratio of the entire herd was 1.01 (167 stallions against 165 mares).

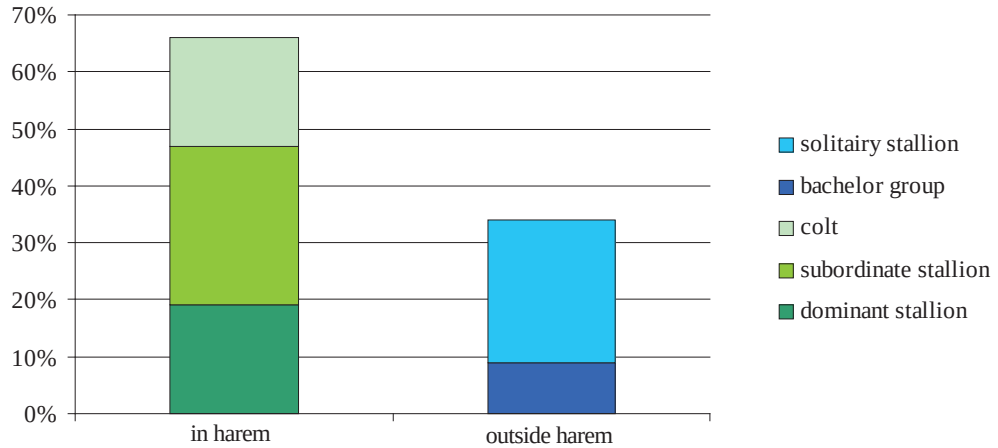

Figure 2. The number of stallions over the age of one, at the Oostvaardersplassen in 1998, outside and in harems, distributed over the various social categories.

Discussion

Habitat conditions

Exclusive home ranges are rare among feral horses, who mostly live in overlapping home ranges (Berger 1986, Linklater 2000). They are also rare among the FREE Nature koniks. A narrow connection between two nature areas does invite the forming of two exclusive home ranges. Two nature areas in which home ranges were exclusive, indeed had such a narrow part (see above) separating them. The third case concerned a long and narrow nature area. In the three areas, the contact zone between the exclusive home ranges was only small, which also made the ranges easier to defend. Moreover, these nature areas all had an ample supply of food and water, and primary needs are usually no impediment to the forming of an exclusive home range. This is similar to the situation on Canada's Shackleford Island (Rubenstein 1981), where three exclusive home ranges are located on the narrow part of the island, which has an amply supply of food and water and boundaries between the home ranges are relatively short. On Shackleford Island, the sea takes care of the 'defence' of the other boundaries, whereas the areas with herd from FREE Nature have cattle grids around them. However, in these three cases, the areas were not really territories, as instead of the boundary, the harem was actively defended (Linklater 2000). Therefore the herds of FREE Nature also have no territories but exclusive home ranges that result from spatial conditions and are not characteristic of feral horses (Linklater 2000).

In most of FREE Nature areas with large herds of koniks, all animals roam together as one group that consists of several harems, bachelor groups with young stallions and solitary stallions. This behaviour is not out of necessity, as food and water are plentiful throughout these areas (contra Linklater 2000). Such large herds of horses have also been observed elsewhere (e.g. Berger 1986).

In the small FREE Nature areas, bachelor groups often do live separately from the harem, as the dominant stallion has plenty of time to fend off the other, mostly young, stallions. Dominant stallions in these areas regularly go over to the bachelor group to posture and fight; confrontations that are always won by the dominant stallion, thus confirming his dominance. In places with multiple harems, a dominant stallion cannot abandon his harem for long periods of time because of the dominant stallions of other harems nearby. In such cases, a bachelor group will stay on the edge

Part of a large koniks herd at the Oostvaardersplassen, showing several harems. *Photo: Leo Linnartz.*

of the herd. This type of behaviour was also observed at the Oostvaardersplassen in 1998 and 2014.

The fierceness of the dominant stallions of harems as well as the season also partly determine whether bachelor groups are tolerated nearby. When mares are in heat, harem stallions are fiercer, and the young stallions of the bachelor group will stay at a greater distance from the harem, whereas older stallions of a bachelor group will in fact move closer to the harem's mares.

In contrast to plains zebras, dominant konik stallions do not work together to fend off bachelor groups. The konik stallions in such groups are mostly inexperienced and usually do not collaborate, which means there is no need for the dominant stallions to work together.

In the FREE Nature herds of koniks, there is little competition over food. Adult mares foal every year, and up to an advanced age, and there are hardly any winter deaths. This means an average annual 30% increase in the herd (2008–2014 period). The fact that the large herd of over 1000 koniks at the Oostvaardersplassen breaks up into several sub-groups in winter, when food is scarce, is an indication that the available food supply does play a role. An example, in this respect, is what occurred when a FREE Nature harem with a dominant stallion and one subordinate stallion was moved from food-rich Leeuwense Waard along the Waal River to the arid dunes of Oranjezon. In this area, which is low in food, the group rather quickly split up into two harems. There was not enough food for them to roam the area as one group, and the threat of rivals had ceased to exist. The dominant stallion and the subordinate stallion each took part of the harem for themselves and proceeded to avoid each other, although their territories did overlap.

The fact that food availability does play a role in herds splitting up does not explain the opposite; why they roam together in one group in times of abundance. Stallions and mares have different individual interests in group formation (Linklater & Cameron 2000). For dominant stallions, being far away from any rivals is appealing, whereas mares and their foals are vulnerable to predation and benefit from living in a large herd. This benefit disappears if, in winter, a dwindling food supply becomes a problem, and large herds are forced to break up into smaller ones. Thus, food availability does appear to be a limiting factor to the formation of large herds. Whenever the food supply is ample, large conglomerations of groups are formed. Plains zebras also form

large groups in such situations, with the largest herds being formed in locations where the competition from bachelor stallions is strong (Rubenstein 2011).

Another advantage of such large conglomerations which has not been mentioned before is that it enables the horses to dominate over other grazers. Whenever a large herd of koniks suddenly arrives in a certain area, free-roaming bovines or red deer (*Cervus elaphus*) move away. This happens not only at the Oostvaardersplassen, where around 1000 koniks live in a single herd, but also in FREE Nature areas with large herds. This provides the horses with access to the best grazing areas. Foraging opportunities and food supply therefore also determine whether free-roaming horses benefit from forming large herds.

Social organisation

In contrast to the herd at the Oostvaardersplassen, the FREE Nature herds are affected by human interference. At regular intervals, FREE Nature reduces the number of animals within a herd by rounding them up and removing a number of them. The social organisation of the herd is taken into account, as much as possible, by preferably removing complete harems or bachelor groups. Sometimes, young animals who are getting ready to leave the harem are removed as well. This practice appears successful, as the FREE Nature herds of more than 25 animals showed little difference with those at the Oostvaardersplassen, in both 1998 and 2014, in terms of harem composition and the occurrence of bachelor groups. However, there were fewer harems with more than one subordinate stallion in relatively large herds. In an entirely natural herd with an ample food supply, the age and gender ratios may be expected to be similar to those at the Oostvaardersplassen. In addition, there seems to be a gradient; a gradual increase in the number of subordinate stallions in growing herds, while there are hardly any subordinate stallions in small herds. The large herd at the Oostvaardersplassen was found to contain not only more harems with a subordinate stallion, but also, and particularly, a larger number of harems with more than one subordinate stallion.

Notable is the skewed gender ratio in the FREE Nature herds (0.73 and 0.62 versus 1.01 at the Oostvaardersplassen). This is primarily caused by human intervention. At birth, the gender ratio is far less skewed (range of 0.72–1.08, average 0.89, over the 2010–2014 period, with a total of 275 fillies and 246 colts). Moreover, the number of natural deaths among mares was observed to be higher than among stallions (13 and 3, respectively), whereas among the animals that were removed, stallions dominated (112 stallions versus 91 mares). Area managers are more inclined to remove a number of young stallions rather than an entire harem when a herd needs thinning to prevent the area from becoming overpopulated. In addition, bachelor groups are not always possible in smaller areas, when the dominant stallion will not tolerate them, or because the band avoids fighting the dominant stallion by moving out of the area, which means that area managers then need to capture and return them.

The social organisation of the large herd of koniks at the Oostvaardersplassen appeared not to have changed much in 16 years. This despite the fact that: 1. Numerous adult animals of the 1998 herd would no longer have been alive in 2014. 2. The herd nearly tripled in size since 1998, and 3. The conditions in the area had become more difficult, as the grazer population reached the area's carrying capacity already many years before. This indicates that the social organisation, as seen in 1998, is stable and typical for this area.

The situation of 1998, at the Oostvaardersplassen, shows that close to 20% of the stallions are dominant stallions and that harems also have a similar number of young stallions. Only 9% of stallions live in a bachelor group.

The others are subordinate stallions (28%) or solitary stallions (25%) that live among the herd. The same can be seen within the FREE Nature herds, despite the skewed gender ratio. Only a small number of stallions managed to become dominant stallions; some were too young and lived in a harem or bachelor group where they were learning how to fight, thus increasing their chances of one day conquering a harem for themselves; others were solitary or subordinate stallions. Wild horses that live in New Zealand and North America show a similar picture (Linklater 1998, Berger 1986), despite the fact that those animals do not live in large herds and do have overlapping territories.

Some of the harems with multiple stallions at the Oostvaardersplassen may have two stallions in equal position who came from the bachelor group at the same time and, together, conquered the mares (Rubenstein 2011, Ransom & Kaczensky 2016). The FREE Nature herds, however, hardly show any of such coalitions. In general, the stallions have clearly distinct roles; the subordinate stallion fights off any intruders and the dominant stallion stays with his mares. This division of roles is also often seen at the Oostvaardersplassen, and in 1998 no harems were observed with stallions in equal position (Nieuwdorp 1998). Most of the harems' additional stallions counted in 2014 would have been in a subordinate position. The horses benefit from a clear division of roles, as this keeps the number of conflicts to a minimum - which in turn benefits the mares, as it increases their opportunities for nursing their foals, and thus also reduces foal mortality.

Subordinate stallions compared

Subordinate stallions are common in the large FREE Nature herds and at the Oostvaardersplassen (figure 1), with 58% to 69% of harems having one or more subordinate stallions. This is a higher percentage than reported for herds elsewhere (by up to 50% (Linklater 2000)). The maximum number of subordinate stallions per harem is also higher at the Oostvaardersplassen than in harems elsewhere, with a maximum of eight at the Oostvaardersplassen versus four elsewhere (Linklater 2000). In nature areas with large herds of koniks, there is a large degree of rivalry between adult stallions. Particularly in the period after foals are born and mares come in heat again, stallions fight frequently and barely allow themselves time to eat. Bachelor stallions will attempt to service a mare in heat, or to conquer her to start a harem for themselves. And then there are the dominant stallions of other harems, who try to conquer a mare to add to their own harem. This applies not only to rivalling harem stallions, but also to solitary, adult stallions and the more mature stallions in a bachelor band. In such cases, having one or more subordinate stallions in the harem is to the advantage of the dominant stallion, as they help him protect the harem.

The fact that there are fewer or no competing stallions in the smaller FREE Nature herds may be the reason why those herds have fewer subordinate stallions than the larger FREE Nature herds. And this would also explain why the enormous herd at the Oostvaardersplassen, relatively speaking, has the highest number of subordinate stallions. At the Oostvaardersplassen, the harems with only one stallion are positioned more often along the edge of the herd, compared to those that have subordinate stallions. This seems to confirm that rivalry between stallions is a particularly strong driving force behind the phenomenon of subordinate stallions. Studies of feral horses in North America also point to this fact; there are hardly any subordinate stallions among the low numbers of stallions on certain islands (Linklater & Cameron 2000, Ransom & Kaczensky 2016), whereas subordinate stallions are a common occurrence in herds with the usual 1:1 ratio between stallions and mares (Ransom & Kaczensky 2016).

Furthermore, in Latvia, subordinate stal-

lions appear to also help defend the harem against wolves. Following confrontations with such predators, harems were often found to have more subordinate stallions than they did before (J. van der Veen, personal communication). Bachelor plains zebras also have been observed to roam together in groups more often when the risk of predation increases (Rubenstein 2011). Mongolian wild asses regularly form large conglomerations of harems and bachelor groups, with stallions from various harems working together to fend off wolves (Feh et al. 2001). This may also explain the higher survival rate of foals in such large groups, compared to those in independent harems (Feh et al. 2001). Thus, dominant stallions appear to tolerate subordinate stallions more readily when doing so is to their advantage; a larger number of mares in a harem is likely to provide more offspring and, when the risk of predation is increased, the foal survival rate is higher with subordinates around.

Subordinate stallions may originate from various places; sometimes they are the sons of the dominant stallion. These sons often leave the harem again, at a certain point, to start their own harem. This also depends on a stallion's temperament. Most subordinate stallions, however, arrive from outside the harem, such as from a bachelor group. An unrelated subordinate stallion would be able to service the daughters of the dominant stallion, which saves them having to go outside the harem to be serviced by a stallion other than their farther. DNA data have shown this to happen on occasion, but not often. In 2013, for example, no such case was found, with subordinate stallions only having serviced adult mares in the harem, and not the dominant stallion's daughters. Research among mustangs in North America showed that, here too, the dominant stallion's daughters were hardly ever serviced by subordinate stallions or their father; they were mostly serviced by stallions from outside the harem (Berger 1986).

The possibilities for subordinate stallions to sire offspring within the harem are limited; in 2013, only four in 70 foals (6%) born in FREE Nature herds were found to have been sired by a subordinate stallion, while six were sired by stallions from outside the harem and two by sons of the dominant stallion. Subordinate stallions may have the opportunity to take over all or part of a harem, but this does not happen very often. Moreover, there is also a fair bit of aggression between the dominant stallion and subordinate stallions (also see Linklater & Cameron 2000). All things considered, their role as the subordinate stallion appears to have only few advantages for them. As is the case for feral horses in New Zealand, the free-roaming koniks also show no signs of mutualism or altruism (Linklater & Cameron 2000). Horses are typically social animals and it seems that subordinate stallions choose to join a harem and resign themselves to play the subordinate role, when and if the dominant stallion allows them to do so.

Furthermore, subordinate stallions and dominant stallions are also radically different in temperament. Subordinate stallions are fighters and hard workers, whereas dominant stallions are calm and caring. When subordinate stallions have the opportunity to act as dominant stallion, they are usually not very good at it. Their position is often taken over by a dominant stallion coming from outside, and they revert back to their subordinate role or are even chased off by the incoming dominant stallion.

In practice, there are large differences in temperament between dominant stallions as well (personal observations, T. de Bode & R. Meissner, personal communication). Some act very aggressively towards rivals, while others appear very caring towards the mares and foals. Ultimately, the mares choose their dominant stallion. If a stallion is not to their liking, he will not become the harem's dominant stallion (R. Meissner, personal communication). There have even been cases reported of mares themselves changing harem after the arrival of a new dominant stallion (T. de Bode, personal communication).

Conclusions

In contrast to elsewhere in the world, the free-roaming koniks in Europe mostly live in nature areas that are rich in food and have an ample supply of drinking water. Koniks appear to prefer living in large groups, which is accommodated by the ample, high quality food supply in the investigated areas. In two areas that were less rich in food, the harems opted to roam independently, and in winter, when food is scarce, large herds were also found to break up into smaller groups.

Exclusive home ranges containing a single harem were found in certain areas with narrow road crossings or dykes, or in long and narrow areas, but these are relatively rare. These home ranges are different from true territories, as only the harems were defended, rather than the land itself. Thus, independent harems or groups can be formed not only as a result of food scarcity but also because of the type of terrain.

Free-roaming koniks, in Europe, live in herds with a social organisation of harems and bachelor groups that is similar to elsewhere in the world among wild Equidae and feral horses. This contributes to the notion that past domestication is unlikely to have influenced the type of social organisation (Linklater 2000). In Europe, however, this organisation can only be observed in nature areas with larger herds that live in an autonomously chosen social structure — thus, in areas where there is only limited human intervention.

Having rivalling harem stallions and bachelor stallions looming nearby, however, is an inherent aspect of large herds. This is why harems in such large herds often have a particular composition that also includes subordinate stallions who play an important role, in addition to the dominant stallion, both qualitatively, in tasks, and quantitatively, in numbers. Such subordinate stallions also help to defend the harem against predation, and their numbers increase with the risk of predation. Subordinate stallions themselves, however, experience only few advantages in relation to their efforts. They hardly service any mares in the harem, and, if the dominant stallion should die, they do not often appear successful in holding on to the harem for themselves. Thus, among the free-roaming koniks studied, there appeared to be no mutualism or altruism. Subordinate stallions that join a harem were found to have a different temperament or develop in a different way, compared to dominant stallions.

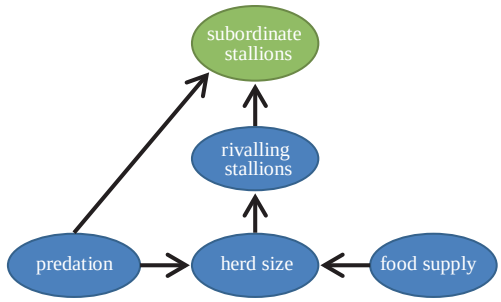

Figure 3. Predation and food supply determine herd size; herd size has an effect on the degree of rivalry between stallions; this rivalry, together with predation, in turn affects the number of subordinate stallions within harems.

In addition, predation also appears to lead to the formation of large groups as well as to more collaboration between stallions, although this is not (yet) the case in the Dutch situation. Subordinate stallions, therefore, are the rule rather than the exception, and their occurrence depends on herd size, the presence of rivalling stallions, predation and food supply (figure 3).

Acknowledgements: We thank the managers of the various FREE Nature herds for providing the data and for the many years they spent recording the data in their joint database on the herds' social organisation. We also thank Roeland Vermeulen, Wouter Helmer and Hettie Meertens for their input and constructive comments. Special thanks go to René Meissner and Tanja de Bode, who provided important contributions to this article, with their clear observations of the konik

herds of ARK and FREE Nature. We furthermore thank two anonymous reviewers and editors Kees Canters, Jan Piet Bekker and Eric Thomassen for their constructive comments. Last but not least we thank Annemieke Righart for the English translation of our paper.

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Samenvatting

De sociale structuur in natuurlijke kuddes koniks (*Equus caballus*): secondanten, regel of uitzondering?

Dit artikel beschrijft de sociale structuur van kuddes vrijlevende koniks in Nederland en elders in Europa met bijzondere aandacht voor de Oostvaardersplassen. Daarbij richt onze aandacht zich op: 1. De grootte van kuddes in relatie tot de leefomstandigheden. 2. De samenstelling van de harems als onderdelen van die kuddes. 3. De relatieve aantallen en de rol van secondanten in die harems. Op basis van deze informatie schetsen wij vervolgens een beeld van de gedachte situatie rond secondanten in de Oostvaardersplassen en andere gebieden met grotere kuddes vrijlevende paarden. Daarna onderzoeken we de geldigheid van dit beeld voor andere gebieden in Nederland waar kuddes koniks grazen. Dat doen

we aan de hand van verzamelde veldgegevens waarbij ook de uitkomsten van een herhaling van het onderzoek in de Oostvaardersplassen worden betrokken. Tenslotte gaan we na of de verkregen uitkomsten ook van toepassing zijn op verwilderde paarden (*Equus caballus*), przewalskipaarden (*Equus przewalskii*) en zebra's, ezels en halfezels (*Equus* spp.) elders in de wereld.

Anders dan elders op de wereld leven vrijlevende koniks in Europa veelal in voedselrijke natuurgebieden met een ruime beschikbaarheid van water. Koniks blijken daar een voorkeur te hebben om in grote groepen te leven. Het goede voedselaanbod in de onderzochte terreinen ondersteunt het leven in grote kuddes. In een tweetal minder voedselrijke gebieden kozen de harems ervoor om ieder apart te leven. Ook als in de winter het voedsel schaars wordt, breken grote kuddes vaak op in kleinere.

In een aantal terreinen met een smalle weg- of dijkovergang of met een smalle, langgerekte vorm was er sprake van exclusieve leefgebieden van op zijn minst één van de harems. Dit waren geen territoria, omdat niet het leefgebied zelf, maar de harem werd verdedigd. Naast voedselschaarste kunnen dus ook terreinomstandigheden leiden tot het leven in gescheiden groepen.

Vrijlevende koniks in Europa leven in kuddes met een sociale structuur met harems en hengstengroepen die overeenkomt met de structuur zoals die wereldwijd voorkomt bij wilde paardachtigen en vrijlevende paarden. In Europa is deze structuur echter alleen waar te nemen in natuurgebieden met grotere kuddes in zelfgekozen sociale verbanden. Dus in gebieden waar menselijk ingrijpen beperkt is.

De aanwezigheid van meerdere harems maakt het echter wel noodzakelijk dat leidhengsten voortdurend concurrentie op afstand moeten houden. Harems in deze grote groepen kennen mede daarom vaak een aangepaste haremsamenstelling, waarbij naast een leidhengst ook secondanten een belangrijke rol spelen, zowel in taken als in aantallen. Onder dergelijke omstandigheden biedt de aanwezigheid van secondanten voordelen: ze helpen mee de harem te verdedigen en zorgen daarmee voor de broodnodige rust voor merries en hun veulens. Ook helpen secondanten mee om predatie te voorkomen en zijn er meer secondanten in situaties met predatiedruk. Secondanten hebben zelf echter weinig voordeel bij hun inzet. Er is bij de onderzochte vrijlevende koniks dus geen sprake van mutualisme of wederkerig altruïsme. Secondanten blijken wel een ander karakter te hebben dan leidhengsten.

Predatie blijkt ook te leiden tot het vormen van grote groepen en tot meer samenwerking tussen hengsten, maar dat doet zich in Nederlandse situatie (nog) niet voor. Het voorkomen van secondanten is dus eerder regel dan uitzondering en lijkt een relatie te hebben met, kuddegrootte, rivaliserende hengsten, predatie en voedselaanbod.

Received: 19 October 2016
Accepted: 27 April 2017

Chris Smeenk, 1942-2017

Op 23 maart 2017 overleed Chris (Christiaan) Smeenk op 74-jarige leeftijd. Hij werd op 6 juli 1942 geboren in de gemeente Oost- en West-Souburg, nu deel van Vlissingen, als eerste van drie kinderen in een domineesgezin. In 1945 verhuisde het gezin naar Breda en in 1950 werd vader Smeenk beroepen naar Almelo, waar bij Chris op de lagere school, mede door toedoen van zijn onderwijzer A.W. van der Kooij, belangstelling voor de natuur werd gewekt.

Chris en zijn broer Hans ontwikkelden zich toen ze op het Christelijk Lyceum Almelo zaten tot enthousiaste vogelaars. Zondagsochtends trokken ze er samen op uit, maar zorgden wel steeds op tijd in de kerk aanwezig te zijn. Chris' zus Everdien was te jong om daar bij aan te sluiten, maar werd later zelf een verdienstelijk amateurornithologe en vlinderbeschermster. De broers ontwikkelden ook beiden een grote affiniteit tot het orgelspel; Chris was heel trots op zijn antieke kabinetorgel. Hij verzorgde veel toelichtingen bij orgelconcerten in Den Haag voor de stichting Musica Antica da Camara.

Na het behalen van het einddiploma gymnasium-α ging Chris in 1961 biologie studeren, eerst in Utrecht, later in Leiden. Als α-man verliep zijn studie via de MO-opleiding. Voous (1995) vermeldt dat Chris na het behalen van het MO-diploma op 10 januari 1969 zowel het kandidaatsexamen als het doctoraalexamen aflegde. Het eerste met het judicium 'na aarzeling' (Chris had het als α-man moeilijk met exacte vakken), het tweede met 'cum laude'. Hier had hij zelf zijn vakken kunnen kiezen.

Tijdens zijn studie in Leiden ontmoette Chris zijn studiegenote Nellie Enserink, met wie hij in 1971 trouwde en die daarna niet meer van zijn zijde is geweken.

Hoewel Chris tijdens zijn studie ook een botanisch onderzoek deed (Wieffering & Smeenk 1971), lag Chris' hart bij de ornithologie. In de zomer van 1968 ving hij op Terschelling als eerste in Nederland een Noordse nachtegaal (*Luscinia luscinia)* (Smeenk 1969a). Tijdens zijn studie deed hij ook een onderzoek naar de verschillen in de voedselkeuze van bos- en ransuil, onder supervisie van Prof. K.H. Voous. Bij dit onderzoek onderzocht Chris ook de legselgrootte van de bosuil (Smeenk 1969b). Voor controle van zijn determinaties van de inhoud van de door hem verzamelde braakballen bezocht hij de collectie van 's Rijksmuseum van Natuurlijke Historie (RMNH). Hier kwam hij in contact met pater A.M. Husson S.C.J., toenmalig conservator zoogdieren. Husson had in 1962 zijn determinatietabel voor schedelresten in braakballen van uilen gepubliceerd (Husson 1962), maar hij raadde Chris aan ook contact op te nemen met Bauke Hoekstra, die inmiddels ook veel kennis van determinatieken-

merken van de muizenschedels had verkregen. Bauke was toen al medewerker van het RMNH 'buiten bezwaar van 's Rijks schatkist'. Via Bauke kwam Chris al vroeg in contact met de zoogdierkunde en de Vereniging voor Zoogdierkunde en Zoogdierbescherming (VZZ), waarvan Bauke toen al jarenlang lid was.

De resultaten van Chris' onderzoek naar de voedselkeuze van bos- en ransuil (Smeenk 1972) waren voor professor Voous reden Chris voor te dragen voor het uitvoeren van het vergelijkend onderzoek naar de ecologische relaties bij vijf roofvogelsoorten in het Tsavo Park in Kenya (1970-1973), waarop hij in 1974 bij professor Voous aan de VU-Amsterdam promoveerde (Smeenk 1974). Bij dit onderzoek kwam Chris' aanleg voor talen goed van pas. Al tijdens zijn studietijd in Leiden leerde hij IJslands omdat hij met drie studiegenoten naar IJsland zou gaan (met IJsland bleef hij zich de rest van zijn leven verbonden voelen). Voordat hij naar Kenya ging leerde hij Swahili. Toen hij tijdens zijn laatste ziekbed een verpleegster uit Tanzania trof, sprak hij met haar Swahili.

Van 1974 tot 1976 werkte hij als wildbeheerder in het Pandam Wildlife Park in Nigeria. In 1976 werd Chris bij het RMNH aangesteld als conservator zoogdieren, als opvolger van A.M. Husson. Ondanks zijn nieuwe aandachtsveld zag hij toch kans om samen met Nellie een aantal observaties aan Afrikaanse roofvogels te publiceren (Smeenk & Smeenk-Enserink 1977, 1983).

Bij het RMNH groeide zijn belangstelling voor de VZZ, de huidige Zoogdiervereniging. Hij trof er A.C. (Dolf) van Bruggen, die toen in het bestuur van de VZZ zat en tevens hoofdredacteur van Lutra was. Het etiketteren en verzenden van Lutra was toen nog een hele klus, waarbij veel VZZ-leden uit Leiden werden ingeschakeld. Al in 1979 nam Chris de ledenadministratie van de VZZ voor zijn rekening en in 1981 nam hij de eindredactie van Lutra over van Van Bruggen, die in 1973 de redactie van het blad had overgenomen van A. Scheygrond. Chris bleef dit werk 17 jaar lang doen, tot 1998, toen hij hierin werd afgelost door Sim Broekhuizen. Chris streefde ernaar van Lutra een echt wetenschappelijk tijdschrift te maken en sinds 1983 verscheen het als een gebonden uitgave met een stevige blauwe kaft. Zijn indringende voorstellen voor verbetering van de ingezonden artikelen werden niet steeds door alle auteurs direct gewaardeerd, hoewel het uiteindelijke resultaat in het algemeen tot tevredenheid stemde. Hoewel hij zijn mederedacteuren wel op de hoogte hield van de ontwikkelingen bij en rond Lutra, deed Chris het redactiewerk vrijwel alleen. Ook verzorgde hij voor Lutra tal van boekbesprekingen (vermeld in een toegevoegde lijst). Voor zijn inzet voor de VZZ, in het bijzonder voor het vele werk voor Lutra, ontving hij in 1992 de Dr. A. Scheygrondprijs.

Met zijn grote redactionele vaardigheid was Chris een ideale eindredacteur van de eerste Atlas van de Nederlandse zoogdieren (Broekhuizen et al. 1992), temeer daar hij bij het museum beschikte over vrijwel alle publicaties over zoogdieren in Nederland, ook in de 'grijze' literatuur van allerlei club- en verenigingsblaadjes (al was soms iets niet te vinden). Daar was hij zeer trots op. Wel koos de redactie van de atlas ervoor zijn kritisch commentaar op de manuscripten door een andere redacteur aan de auteurs te laten overbrengen, waar Chris ruimhartig mee instemde.

Chris had een grote belangstelling voor de historie. Zo schreef hij samen met Bauke Hoekstra een mooi en gedegen historisch overzicht van de zoogdierfaunistiek in Nederland (Hoekstra & Smeenk 1992). Hij spitte graag en vaak in de archieven om oude opgaven 'van het stof der eeuwen te ontdoen', zoals hij het zelf uitdrukte. Voorbeelden hiervan zijn de studie naar afbeeldingen van vogels op 17de-eeuwse tegels naar gravures van Adriaan Collaert (Holthuis et al. 1971), een oude vermelding van de bosvleermuis in Groningen (Smeenk 1982a), het overzicht van oude potvisstrandingen (Sliggers & Smeenk 1992), de butskop van 1958 (Smeenk 1991d), de bespre-

Chris Smeenk bij de apencollectie in Naturalis, mei 2008. *Foto: Dolph Cantrijn.*
Chris Smeenk at the primate collection at Naturalis Biodiversity Center, May 2008. Photo: Dolph Cantrijn.

king van tekeningen van zoogdieren in Brazilië op tekeningen uit de 17de eeuw (Boeseman et al. 1990), van illustraties van vleermuizen in oude wetenschappelijke werken (Smeenk 1991c), van de herkomst van een deel van de zoogdierencollectie van Von Henrici (Cranbrook et al. 2007) en van het werk van de 19de-eeuwse dierenschilder Joseph Wolf (Smeenk 2001, 2002).

Als conservator bij het RMNH ontwikkelde Chris een brede kennis van veel zoogdiersoorten. De diersystematiek en taxonomie hadden zijn speciale belangstelling. Zo verdiepte hij zich in de systematiek van onder meer het sikahert (Groves & Smeenk 1978), de zeehonden (Smeenk 1982b), de Japanse bosmuis (Smeenk et al. 1982), de Sikkim woelmuis (Kaneko & Smeenk 1996), de Japanse slaapmuis (Smeenk & Kaneko 2000), de Afrikaanse potto (Smeenk et al. 2006), de Afrikaanse wilde ezel (Groves & Smeenk 2007), de Australische oostelijke koeskoes (Smeenk 2009) de Nesomyinae van Madagaskar (Carleton et al. 2014) en de Zuidoost-Aziatische gladneusvleermuis (*Vespertillio oreias*) (Csorba et al. 2016). Ook herzag en bewerkte hij de veldgids *Säugetiere Afrikas und Madagaskars (*Haltenorth & Diller 1977) tot Elseviers gids van de Afrikaanse zoogdieren (1979).

Chris bleef zich zijn hele verdere leven verbonden voelen met Afrika, wat onder meer wordt geïllustreerd door zijn medeweking aan een checklist van de vogels in het oostelijke Tsavo park in Kenya (Lack et al. 1980). Zijn laatste arbeid betrof een atlas van walvisachtigen in de Rode Zee (Notarbartolo di Sciara et al. (eds), in press). Dat deze atlas inhoudelijk af was gaf Chris in zijn laatste weken veel voldoening en het is spijtig dat hij de verschijning van deze atlas niet meer heeft kunnen meemaken.

Chris' voorganger Husson maakte in de periode 1968-1976 samen met zijn Amsterdamse collegae P.J.H. (Peter) van Bree en W.L.

Chris Smeenk met een gekleurde plaat van de snaveldolfijn (*Steno bredanensis*) in het Teylers Museum in Haarlem, 11 juli 2014, ter voorbereiding van zijn bijdrage over deze soort in de Atlas van de Nederlandse Zoogdieren (2016). Foto: H. Voogd, Teylers Museum.
Chris Smeenk studying a coloured plate of rough-toothed dolphin (Steno bredanensis) *at Teylers Museum in Haarlem, 11 July 2014, to prepare his chapter on this species in the Atlas of the Mammals of the Netherlands (2016). Photo: H. Voogd, Teylers Museum.*

(Wim) van Utrecht overzichten van de op de Nederlandse kust aangespoelde walvisachtigen, waarbij ze voortbouwden op het werk van de bekende Nederlandse walviskenner A.B. van Deinse, biologieleraar aan het Erasmiaans Gymnasium te Rotterdam. Toen Husson in 1976 met pensioen ging nam Chris ook hierin zijn taak over. Het overzicht van de strandingen in 1976 en 1977 (van Bree & Smeenk 1978) was de eerste van een rij overzichten die verscheen in Lutra (van Bree & Smeenk 1980, Smeenk 1986, 1989, 1992, 1995, 2003, Camphuysen et al. 2008). Hierna werden de strandingsgegevens opgenomen in het digitale bestand van www.walvisstrandingen.nl, wat niet wegnam dat Chris doorging met het melden van bijzondere strandingen in periodieken voor een breder publiek. Het hoogtepunt van de strandingsoverzichten was voor Chris het deel over het voorkomen van Cetacea in de Nederlandse wateren in de Atlas van de Nederlandse zoogdieren van 2016, dat hij samen met Kees Camphuysen verzorgde, waarbij hij met een fijne stofkam op ultieme wijze door alle waarnemingen is gegaan (Broekhuizen et al. (red.) 2016): een geweldige prestatie die een uniek overzicht heeft opgeleverd.

Zijn eerste betrokkenheid bij de strandingsoverzichten was ook het begin van een intense belangstelling voor de Cetacea. De gestrande dieren – vooral bruinvissen- werden lange tijd meestal door Chris zelf opgehaald, soms

bij erbarmelijke weersomstandigheden. Vaak werd hij vergezeld door Marjan Addink, een samenwerking die resulteerde in een aantal publicaties.

Chris werd een internationaal erkende specialist in deze soortengroep en was een van de initiatiefnemers van de European Cetacean Society. Hij was bijzonder geïnteresseerd in de strandingen van potvissen ("de Noordzee is een potvisval") en hij analyseerde de veranderingen in de patronen van de strandingen van tuimelaar, gewone dolfijn en witsnuitdolfijn (Bakker & Smeenk 1987, 1990, Kinze et al. 1996, 1997), bruinvis (Addink & Smeenk 1999, Evans et al. 1987, Smeenk 1987a, 1988, Addink & Smeenk 1989, 2000, Evans et al. 1989, Smeenk & Addink 1990, Addink et al. 1995, Addink & Smeenk 1997, 2000) en potvis (Smeenk & Addink 1992, Smeenk 1997, 1999, Pierce et al. 2007). Hij besteedde ook aandacht aan bijzondere waarnemingen: noordkaperbeenderen (Kompanje & Smeenk 1996), de 'Arabische dolfijn' (Smeenk & Addink 1996), de dolfijn van Cuvier (Waerebeek et al. 1997) en de snaveldolfijn (Addink & Smeenk 2001).

Het onderzoek van de gestrande dieren dat hij organiseerde stelde hem en anderen in de gelegenheid om gegevens te verzamelen over onder meer de voortplanting, de maaginhoud (Smeenk & Gaemers 1987, Santos et al. 2001, 2002, Jansen et al. 2010), het voorkomen van pathogenen en ecto- en endoparasieten (Fransen & Smeenk 1991, Jauniaux et al. 1998), ook in oud materiaal (Holthuis et al. 1998), de belasting met gechloreerde koolwaterstoffen (PCB's e.d.) (Addink et al. 1993, van Scheppingen et al. 1996, Pierce et al. 2008) en de dood van bruinvissen als bijvangst van visserij (García Hartmann et al. 2004). Bij veel andere publicaties bood hij essentiële hulp, ook zonder dat hij co-auteur was.

De breedte van Chris' belangstelling voor en kennis van de Cetacea en zijn taalvaardigheid leidden ertoe dat hij herhaaldelijk werd gevraagd een bijdrage aan handboeken te leveren: Handbook of Marine Mammals (Reeves et al. 1999a, 1999b), Swift as a Shadow. Extinct and Endangered Animals (van den Hoek Ostende et al. 1999), Mammals of the British Isles, 4th edition (Harris & Yalden (eds) 2008), Encyclopedia of Marine Mammals Second Edition (Rudolph & Smeenk 2009) en, niet te vergeten, de Atlas van de Nederlandse zoogdieren (Broekhuizen et al. (red.) 2016) en tot slot het al gememoreerde Cetacea of the Red Sea (Notarbartolo di Sciara et al. (eds), in press).

Naast zijn intensieve belangstelling voor de walvisachtigen had Chris ook een speciale belangstelling voor vleermuizen. Voorlichting over deze groep vond hij belangrijk voor de bescherming ervan (Smeenk 1987b, 1991a, 1991b). Dat resulteerde niet alleen in een beschermende wetgeving die tot op de huidige dag uniek is te noemen vanwege zijn robuustheid, maar later ook in het boek 'Vleermuizen' (Voûte & Smeenk (eds) 1991), met daarin ook een hoofdstuk van zijn hand over de oorsprong en ontwikkeling van vleermuizen (Smeenk 1991c).

Om het belang van de natuur – en in het bijzonder van zoogdieren – en de bescherming daarvan onder de aandacht van een breder publiek te brengen, leverde Chris ook regelmatig bijdragen aan populair-wetenschappelijke tijdschriften en andere op een breed publiek gerichte media (zie de apart opgenomen lijst). Ook was hij in de jaren 1980 lid van de Natuurwetenschappelijke Commissie van de Natuurbeschermingsraad.

Na zijn pensioen raakte de verhouding tussen Chris en Naturalis getroebleerd, waar Chris veel verdriet van heeft gehad. Alleen de bibliotheek bleef voor hem toegankelijk. Hij bleef echter tot het laatst aan het werk. Een aantal zaken die hij nog onder handen had, zoals de typelijst van de zoogdieren in Naturalis, een uitgebreid artikel over potvisstrandingen en een boek over de Natuurkundige Commissie voor Nederlands-Indië, waarvan het in 2020 tweehonderd jaar geleden zal zijn dat deze commissie werd ingesteld, zullen hopelijk niet onuitgegeven blijven.

Chris verzorgde een in memoriam voor

zowel A.M. Husson (Holthuis & Smeenk 1988), A. Scheygrond (Smeenk 1996) als voor L.B. Holthuis (Smeenk 2010), voor wie hij een grote sympathie had. Het voelt vreemd nu een in memoriam te schrijven voor Chris Smeenk zelf, in het besef dat we veel facetten van zijn leven onbenoemd laten en ons hebben beperkt tot een (ruime) keuze uit zijn voornamelijk zoogdierkundig werk.

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Chris Smeenk, 1942-2017. On 23 March 2017, Chris Smeenk passed away, at the age of 74. For more than 40 years, Chris was a prominent member of the mammal community. As a boy, and later, in his study years at Leiden University, Chris developed an interest in ornithology. After performing studies on

owls, his PhD study at VU Amsterdam was on birds of prey in Kenya, which he successfully completed in 1974. Chris' professional introduction into (the world of) mammals was in 1976, with his employment as curator of mammals at the Leiden Natural History Museum. From then on, Chris became increasingly involved in the Dutch Society for the Study and Protection of Mammals (now called the Dutch Mammal Society). From 1981 to 1998, Chris was managing editor of Lutra. His aim during these years was to turn Lutra into a scientific journal of mammalogy. In 1992 he was awarded the Dr A. Scheygrond Award in recognition of his great achievements for the Mammal Society and especially for Lutra. Chris was involved in an impressive list of scientific papers, mainly on the systematics and taxonomy of a range of mammals. Over the years, he developed a growing interest in Cetacea, and, to a lesser degree, in bats. From 1978 to 2008 Chris, alone or with colleagues, published lists of cetaceans stranded on the Dutch coasts, in Lutra. Chris had a special interest in sperm whale strandings, and analysed stranding patterns and trends of several other species as well. Chris was acknowledged as an internationally renowned specialist on cetaceans, and was one of the founders of the European Cetacean Society. Chris, who fluently spoke several languages, including Icelandic and Swahili, was involved in several international handbooks on (marine) mammals, and two Dutch mammal atlases, both as an author and an editor. One of his more recent achievements was the excellent part on cetaceans in the latest Dutch Mammal Atlas (Broekhuizen et al. 2016), which he wrote together with Kees Camphuysen. He was also one of the authors and editors of the atlas of cetaceans of the Red Sea, which will be published later in 2017.

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First record of Geoffroy's bat (*Myotis emarginatus*) in the province of Zeeland, the Netherlands

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First observation

On 23 December 2016, during the annual winter census of hibernating bats in Haamstede, province of Zeeland, a Geoffroy's bat (*Myotis emarginatus*) was encountered. The specimen had chosen a horizontal niche in a relatively dry casemate in the forest around the castle of Haamstede (figure 1). The medium-sized bat showed several characteristics that are typical for the species: a rhomboid outline, a warm yellow-brown coloured fur and relatively small feet and long ears, which drop down almost perpendicularly; the ears' lateral margins showed an almost rectangular notch (see left ear in figure 1).

The winter census in Haamstede was first accomplished in 1982-1983 and 1983-1984 by Gerhard Glas and Gerard Slob and has since 1985-1986 been repeated every year (Bekker & Mostert 1995) up till now. This is the first observation of Geoffroy's bat in Haamstede as well as in the province of Zeeland.

Figure 1. Geoffroy's bat (*Myotis emarginatus*) in a hibernaculum in a casemate in Haamstede, province of Zeeland, the Netherlands. *Photo: Kees Mostert*.

Hibernation ecology

Geoffroy's bat is considered a thermophilic bat species (Vergoossen & Buys 1997). During hibernation, Bezem et al. (1964) found a preference of this bat species for limestone quarries in small excavations in the ceilings, where the ascending warmer air can accumulate, resulting in higher temperatures at these hibernation sites. In natural cave systems these bats hibernate in the warmer parts at temperatures between 5 °C and 9 °C (Gaisler 1970). In Vlaanderen, Geoffroy's bat is predominantly found in hibernacula in the fortresses of Antwerp (Lefevre & Verkem 2003). For some of these fortresses with hibernating Geoffroy's bats, Jooris & Goossens (1980) mention temperatures between 8 °C and 11 °C.

Former distribution

The distribution of Geoffroy's bat in Europe is concentrated in southern and central Europe and reaches its northern border in Oirschot (province of Noord-Brabant, the Netherlands), Hönnetal (Nordrhein-Westfalen, Germany) and further to the east in Olsztyn (Silesia, Poland) (Topál 2001). Glas (1986) mentions for the Netherlands a northern limitation along the line Roermond-Tilburg-Antwerpen and, further on for Belgium, a northern-western limitation along the line Antwerpen-Kortrijk.

Winter censuses in southern Limburg (the Netherlands) started in 1937 and since that time Geoffroy's bats have been found regularly in limestone quarries (Bels 1942, 1952). In 1983 a nursery colony was discovered in the loft of an abbey near Echt, in the central part of Limburg (Vergoossen & Buys 1992). In the first decade of this century a new nursery colony was found in the loft of a nearby monastery (Dekker & Regelink 2010), and later, in the years 2012, 2013, 2015 also in cattle barns (Dekker & Janssen 2016) in this part of Limburg. In 2003 a single specimen was discovered in a church loft in the municipality of Valkenswaard in the southeastern part of the adjacent province of Noord-Brabant (Rienks & Twisk 2003). In 2008 other summer observations of single Geoffroys' bats (discovered during church loft visits, mist netting, autonomous bat recordings and tracking down of animals with radio-transmitters) were done in this part of Noord-Brabant, resulting in Bergeijk as the northwesternmost known location of the species (Regelink & Dekker 2009).

Besides the provinces of Noord-Brabant (southeastern part) and Limburg (southern half), extralimital discoveries of Geoffroy's bat in the Netherlands were reported from the provinces of Groningen and Noord-Holland. In the province of Groningen a Geoffroy's bat was collected in 1954. It is now in the collection of Naturalis Biodiversity Center, Leiden (RMNH.MAM .29135 20/2/1954 leg. G.F.Wilmink).

In the province of Noord-Holland two specimens were collected in September 1953 in the Kennemerduinen, and stored in the collection of the Zoological Museum Amsterdam (nowadays relocated in Naturalis Biodiversity Center, Leiden, ZMA.MAM.1967 25/9/1953 Velzen, NH). In the same province a single specimen was reported in January 1954 in the fortress Hinderdam in Nederhorst den Berg (observation of S. Braaksma and J. Th. de Smidt) (Van Wijngaarden et al. 1971). Glas (1986) noted that this observation could not be validated because evidence was missing.

The collected specimens from the provinces of Groningen and Noord-Holland were checked again (for reasons of preparing regional atlases) and were confirmed.

Population developments

Glas (1986) estimated the total population of Geoffroy's bats in limestone quarries in southern Limburg in the early period of bat banding (starting in 1937) at more than 600 individuals. Daan (1980) noticed a sharp decline in numbers of hibernating individuals in these quarries in the 1940s and 1950s. After that period the total numbers showed a steady decline until the 1960s, while the numbers during the winter censuses in the 1970s and 1980s up until 1987 varied between 50 and 70 individuals (Glas & Voûte 1992). After these years of stabilisation the total numbers of hibernating Geoffroy's bats from 1986 onwards showed a steady increase: winter census data showed an eighteenfold increase compared to 2006 (Verboom 2006, Dekker & Regelink 2010), while total numbers in nursery colonies peaked at over 1000 individuals in 2015 and 930 in 2016, including colonies directly across the border in Germany (Dekker & Janssen 2016). In recent years, these colonies have shown a lot of dynamics, moving and separating from sites in two large groups

and several smaller groups (Dekker et al. 2014).

As seen from the Geoffroy's bat hibernation site in Haamstede in Zeeland, the nearest hibernation sites and nursery colonies in the Netherlands are located in the municipality of Echt (Dekker & Regelink 2016), at a distance of 166 km. In May 2008 Regelink & Dekker (2009) reported an observation of Geoffroy's bat in the municipality of Bergeijk, province of Noord-Brabant, 113 km from the hibernation site in Haamstede (figure 2).

During the late 1990s in Vlaanderen (Belgium), which comprises the provinces of West-Vlaanderen, Oost-Vlaanderen, Antwerpen, Vlaams-Brabant and Limburg, a total of ten nursery colonies of Geoffroy's bat were known, spread out over all of these provinces and with an approximate total of 400 to 500 individuals (Lefevre & Verkem 2003). After repeated visits to these nursery colonies, numbers in the provinces of Antwerpen, Vlaams-Brabant and Limburg alone were determined at a combined total of 412 specimens in 2010, 478 in 2011 and ca. 560 in 2012 (Dekeukeleire & Janssen 2012). The nursery colony nearest to the hibernation site in Haamstede is in the municipality of Sint-Amands (96 individuals in 2015), at a distance of 79 km (personal communication Daan Dekeukeleire). The nearest hibernation sites are located in the fortresses around Antwerpen, at a distance of 65-80 km in a southeastern direction (Boers 2012). In summer and early autumn, when several species of bats (including Geoffroy's bat) show swarming behaviour, the fortresses around Antwerpen were surveyed with mist nets. In 2013 one specimen was caught in Kapellen (Willems et al. 2016), 65 km southeast of Haamstede (figure 2).

Figure 2. Location of a newly discovered Geoffroy's bat (*Myotis emarginatus*) hibernation site in Haamstede (province of Zeeland) (indicated by arrow) and the locations of the hibernation sites (▪), nursery colonies (*) and mistnet/hand catches (o) in the Netherlands and Belgium nearest to Haamstede. (+) indicates the location of a radio-transmittered specimen in the Netherlands, close to the Belgium border.

Discussion

The Geoffroy's bat in Haamstede described here is the first documented observation for the Netherlands just outside its regular distribution area after the decline of the species, which took place until the 1960s. Considering the distance from Haamstede to the nearest edges of its range, it is plausible that the hibernating Geoffroy's bat in Haamstede originates from a nursery colony in the municipality of Sint-Amands (Belgium), although evidence is missing.

Červený (1999) describes Geoffroy's bat as a predominantly sedentary species, which shows limited movements of usually less than 40 km. Bels (1952), who studied banded individuals, found a longest migration distance of 106 km for Geoffroy's bat. Like Geoffroy's bat, the greater mouse-eared bat (*Myotis myotis*) does not migrate over long distances. Stutz (1999) characterised the greater mouse-eared bat as an occasional migrant with longest recorded movements of 390 km. Since both species of bats also share the same southern distribution in the Netherlands, it is interesting to note that several verifiable reports of mouse-eared bat are available from the central, more northern regions in the Netherlands (Verheggen 2016).

The Geoffroy's bats collected in the city of Groningen in the province of Groningen

(1954: 1 specimen) and in the Kennemerduinen in the province of Noord-Holland (1953: 2 specimens) as well as the Geoffroy's bat in Haamstede could indicate a wider (more northerly) distribution of Geoffroy's bat in the Netherlands than assumed up to now, as Dekker & Regelink (2010) suggested. However, the near future will show whether the reported Geoffroy's bat in Haamstede was an incidental vagrant. Or that it is the result of a changing climate, or of more favourable local circumstances in Vlaanderen (Belgium), gradually influencing favourable adjacent areas in a north-western direction.

Through this report, we call upon surveyors to pay extra attention to the possible presence of Geoffroy's bat during the annual winter and regular church attic censuses and during mist net inventories, including those performed well outside the species' currently known distribution.

Acknowledgements: We would like to thank Jeroen Willemsen and Jan Alewijn Dijkhuizen for their help during the bat hibernation census. Han van der Meer and his successor André Hannewijk, rangers working for Natuurmonumenten, facilitated the entry to bunkers that are closed to the public. Peter Twisk kindly provided details of the survey in the southeastern part of Noord-Brabant (the Netherlands), as did René Janssen, Daan Dekeukeleire and Kris Boers for the most recent outcomes of the counts in colonies and hibernation sites situated in Vlaanderen (Belgium). We also thank Guido Keijl for his help finding the old records in the collection of Naturalis Biodiversity Center in Leiden. Finally we thank the two anonymous reviewers for their constructive comments.

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Samenvatting

De eerste waarneming van de ingekorven vleermuis (*Myotis emarginatus*) in de provincie Zeeland

Op 23 december 2016 werd tijdens de jaarlijkse wintertelling in Haamstede (provincie Zeeland) een overwinterende ingekorven vleermuis aangetroffen in een relatief droge bunker. Het betreft de eerste gedocumenteerde melding in Nederland buiten Limburg en aangrenzend zuidoostelijke Brabant sinds

de jaren 1950. De populaties in Limburg bevinden zich op een afstand van 166 km van de huidige, dichtstbijzijnde vindplaats in Nederland. De meest noordelijke bekende zomerverblijfplaats in Vlaanderen (België) bevindt zich in de omgeving van Antwerpen, op 65 km ten zuidoosten van de winterverblijfplaats te Haamstede. Oude meldingen (waarvan er twee verifieerbaar zijn) van ingekorven vleermuizen in de Kennemerduinen in september 1953 en een vondst in Groningen in 1954 (Naturalis Biodiversity Center, Leiden) kunnen er op wijzen dat de soort tot in de eerste helft van de vorige eeuw een ruimere verspreiding in Nederland heeft gekend. De nabije toekomst zal uitwijzen of deze waarneming in Haamstede betrekking heeft op een incidentele zwerver of dat het om een voorbode gaat van een verdere uitbreiding van het leefgebied. De klimaatopwarming en de gunstige aantalsontwikkelingen in Limburg en Vlaanderen zullen eventuele uitbreiding van deze zuidelijk georienteerde soort zeker gunstig beïnvloeden. Wij hopen door middel van deze melding extra aandacht te vestigen op de mogelijke aanwezigheid van de ingekorven vleermuis tijdens de wintertellingen alsmede tijdens kerkzoldertellingen buiten het huidige bekende verspreidingsgebied.

Received: 25 January 2017
Accepted: 2 April 2017

Remarkable mandibular fracture healing in an early Holocene bottlenose dolphin (*Tursiops truncatus*)

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Abstract: The Natural History Museum Rotterdam (the Netherlands) holds a large osteological collection of fossil and recent cetaceans. A right mandible of a bottlenose dolphin (*Tursiops truncatus*) shows signs of perfect healing of a severe traumatic fracture. Its size, colour, state of preservation and the collection site (Southern North Sea bed) point to an estimated age of ca. 8000-7000 years BP (early Holocene). We describe this remarkable fossil mandible and hypothesise about possible causes of the injury.

Keywords: bottlenose dolphin, *Tursiops truncatus*, injury, North Sea, Holocene, fossil.

Introduction

The bottlenose dolphin (*Tursiops truncatus*) is, nowadays, a rare visitor of the Dutch coastal waters and, on a larger scale, of the entire North Sea (Camphuysen & Peet 2006, Aaris-Sørensen et al. 2010). However, during the warmer periods of the early Holocene the bottlenose dolphin was a common species of the Dutch marine mammal fauna (Post 2005), which is supported by an abundant collection of skeletal remains of early Holocene bottlenose dolphins kept in the Natural History Museum of Rotterdam, the Netherlands (NMR) (287 specimens including 25 mandibles). All specimens were collected from the North Sea bed by commercial trawlers.

One of the isolated mandibles kept in this collection (coll. no. NMR 9991-12149) shows signs of perfect healing of a severe traumatic fracture. The dolphin endured a complete fracture of the right mandible, but somehow managed to survive the serious accident. This article describes the remarkable fossil mandible and hypothesises about possible causes of the injury.

Material

NMR 12149 is an almost complete right mandible of an adult bottlenose dolphin dredged by a commercial trawler in the Southern North Sea in 2005. Apart from some missing fragments of the apex and alveolar bone tissue, the mandible is fairly well preserved. Nine alveoli are still recognisable, and two mental foramina can be observed. The total length of the bone is 418 mm, the length of the precoronoid crest is 196 mm and the distance between the two mental foramina is 56 mm. The height of the mandible at the fracture line measured 84 mm and the height at the symphyseal surface is 35 mm. The greatest height of the mandibular fossa is 92 mm and the length of the mandibular foramen at least 144 mm. The breadth of one of the middle tooth alveoli measures 11 mm. These measurements point clearly to an adult bottlenose dolphin, excluding other common dolphins of the Holocene of the North Sea like the common dolphin (*Delphinus delphis*) and dolphins of the genus *Lagenorhynchus*. Size, color, state of preservation and site (Southern North Sea bed) indicate an estimated age of ca. 8000-7000 years BP (early Holocene) (table 1).

Table 1. Published 14C dates of fossils of bottlenose dolphin (*Tursiops truncatus*) from the North Sea. GrA: University of Groningen; UtC: University of Utrecht

Fossil	Site	Code	Age
Mandible, No 3920	Smiths Knoll	GrA 25851	8135 +/- 45 BP
Mandible, NMR 2273	Smiths Knoll	GrA 25850	7390 +/- 50 BP
Vertebra, No 2683	Brown Bank	UtC 7885	7270 +/- 60 BP

Description

On the buccal side of the mandible – from the location of the precoronoid crest downwards, a large healed fracture line extends vertically over the complete ramus of the mandible. On both sides of the healed fracture, the bone tissue is marginally swollen and rounded, and shows an uneven surface.

A small V-shaped scar is located in the middle of the fracture itself. About 4 cm towards posterior another, smaller, straight scar is visible. This scar is covered partly with secondary bone growth. On the lingual side of the mandible the fracture line can also be observed over the complete surface of the inside of the mandibular ramus. If viewed dorsally and ventrally it becomes clear that the main body of the mandible was broken in two fully separated parts. During the subsequent healing process the two bone surfaces fused again, however not in the same plane because the posterior part shifted laterally over 5-7 mm (figure 1).

Discussion

Possible causes of the fracture

The fracture of the NMR 12149 mandible is clearly not the result of a secondary disease or a pathological condition (pathological fracture), but is obviously caused by a sudden traumatic impact. Fractures of mandibles (and other bones) of extant odontocetes can hypothetically result from: 1. Collision with a vessel. 2. A traumatic blow by a snout or tail of another cetacean. 3. A high jump from the water surface with the dolphin landing on a drifting object or other cetacean. 4. An attack by a large shark.

(1) For the early Holocene (the timeframe in which the bottlenose dolphin of the described mandible supposedly lived), motorised human activity (on the seas) did not exist and can be disregarded as the potential cause.

(2) The possibility that the trauma was indeed caused by a lateral blow from the snout or tail of a larger odontocete (such as a killer whale – *Orcinus orca*), or another bottlenose dolphin of the pod to which the dolphin belonged, is real. Documentation of aggressive non-predatory interactions between sympatric odontocete species exists (Shane 1995, Orr & Harwood 1998, Wedekin et al. 2004, Scott et al. 2005). Bottlenose dolphins establish and maintain dominance within the pod by biting, chasing and smacking their tails on the water. Male dolphins are observed to be more aggressive than females. The aggressive behaviour is mostly limited to raking and scathing one another with their teeth, resulting in tooth rake marks that cause superficial lacerations which heal as white scars (Scott et al. 2005). The patterns of tooth rake presence and prevalence likely result from offensive sexual coercion of adult females by adult males and intra-sexual male competition (Scott et al. 2005). Male bottlenose dolphins are known to fight and kill rivals and offspring. It has also been observed that they participate in non-predatory aggressive interactions with smaller harbour porpoises (*Phocoena phocoena*) and even commit interspecies infanticide (Patterson et al. 1998). Bottlenose dolphins have been observed to 'sandwich' a porpoise between two dolphins,

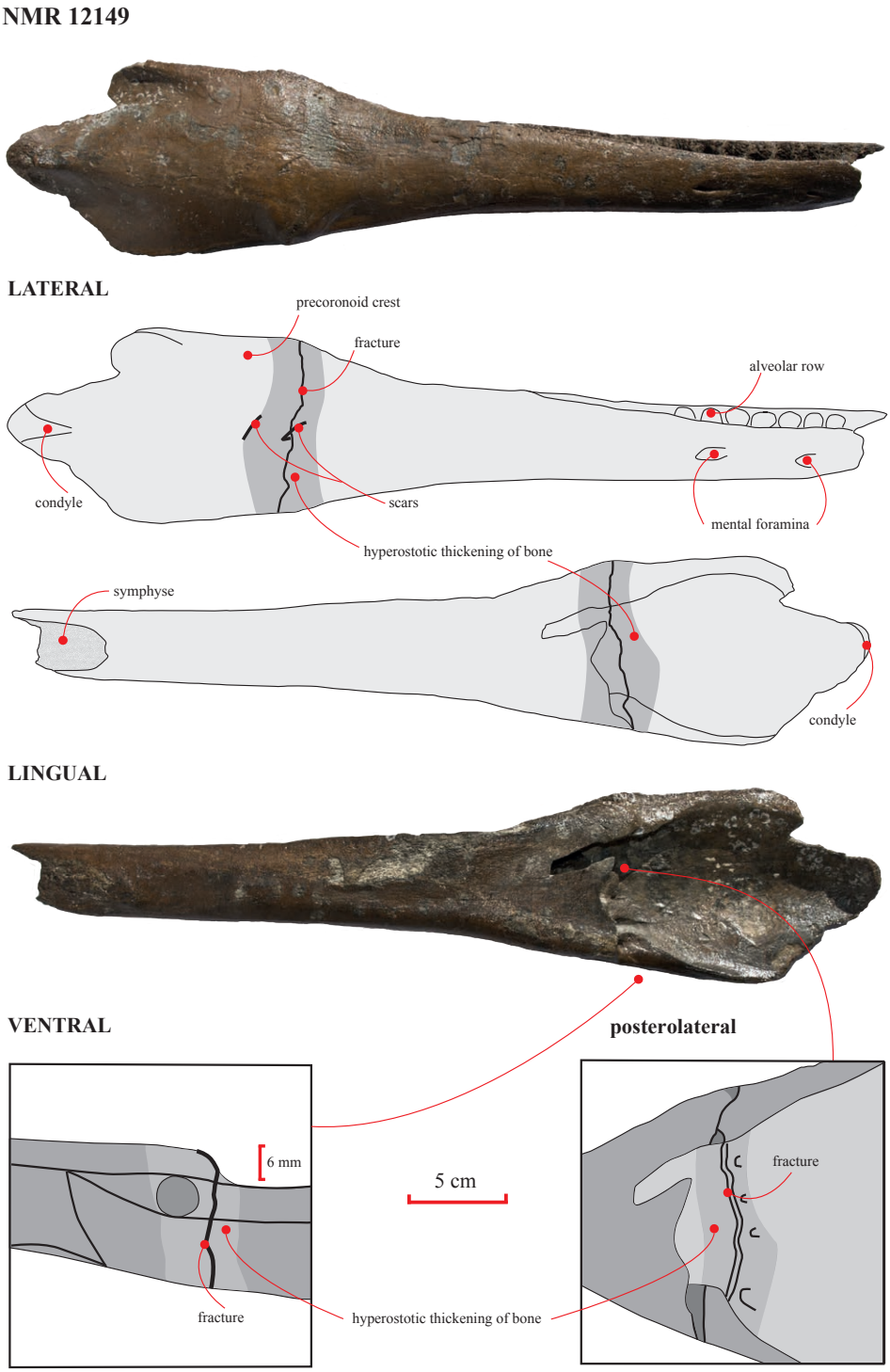

Figure 1. Mandible of bottlenose dolphin (*Tursiops truncatus*) NMR 9991-12149.

but also to drown, toss and ram smaller cetaceans. Between 1991 and 2011, at least 137 harbour porpoises died as the result of attacks by bottlenose dolphins in Cardigan Bay, Wales, United Kingdom (Cotter et al. 2012).

(3) Bottlenose dolphins have been observed to jump as high as six metres (20 feet) above the water surface and to land on their bellies or sides. If the dolphin of the described mandible jumped out of the water and landed on a floating object or another dolphin, the fractured mandible could have been the painful result of the acrobatic action.

(4) The least likely possibility is an attack by a large shark. Although not frequently observed, large sharks have been known to prey on dolphins, and fatal attacks by large white sharks (*Carcharodon carcharias*) and tiger sharks (*Galeocerdo cuvier*) on fully grown bottlenose dolphins have occasionally been observed (Heithaus 2001, Celona et al. 2006, Fallows et al. 2013). However, the two small superficial scars on the surface of the fracture were not involved in the initial healing process of the fracture, making it totally unlikely that they were part of the same trauma. One of the scars is on the surface of the healed fracture. Hypothetically they could have been caused by a second injury or even post mortal scavenging, in any case after the fracture had healed. We conclude that the scars are most likely unrelated to the initial trauma.

Survival

Depending on the hunting environment and available prey, most dolphins use raptorial feeding strategies, suction feeding strategies, and/or a combination of both methods (Hocking et al. 2017). The bottlenose dolphin survived despite the obvious fact that the completely fractured mandible must have caused the dolphin substantial discomfort with eating and hearing. However the masseter muscle, if not fully severed, may have covered the fracture and kept the fractured jaw parts in position. The jaw fat in the mandible may also have been disrupted, causing disturbance of sound passing to the inner ear through the sound conducting tissue of the jaw fat. However as this tissue is solid but also flexible, it may have served as an inner splint for the fractured bone. Therefore two possible scenarios for the survival of the dolphin may be envisioned:

a. The animal was still able to eat in its normal way because of the support of the fractured bone by the massive masseter muscle and the inner jaw fat.
b. The animal managed to survive by suction feeding only with minimal movements of beak and tissues. In this way it could collect the basic energy necessary for the long healing process. Suction feeding (catching and swallowing of prey – fish and/or squid – by oral pressure without active mandible movements and oral processing) is noted in most extant odontocetes. Some families depend for their food intake almost exclusively on suction feeding (e.g. beaked whales - Ziphiidae, sperm whales - Physeteridae), others (like the dolphins - Delphinidae) combine various feeding methods subject to the available prey (Werth 2006). Sperm whales use for the process only the most posterior part of the mouth and their short tongue as a piston and are reported to survive and live with a healed and grotesquely curved mandible (Werth 2004). It is observed that bottlenose dolphins and porpoises are able to eat by suction feeding (Ito et al. 2002).

Conclusion

It appears most likely that the traumatic fracture of the mandible in the described specimen was caused by sexual coercion of an adult female by adult males, or by intra-sexual male competition. The fact that the mandible healed proves that (bottlenose) dolphins with a completely fractured mandible are able to survive until the injury has completely healed.

Acknowledgements: Henry van der Es (Natuurhistorisch Museum Rotterdam, the Netherlands) guided access to specimens under his care, Sander Schouten (Natuurhistorisch Museum Rotterdam, the Netherlands) joined useful discussions on shark bite marks on cetacean bones, and Mark Broch ('s-Gravenhage, the Netherlands) assisted with matters of language. Two anonymous reviewers provided helpful comments on an earlier draft of the manuscript. All deserve our thanks.

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Samenvatting

Een opmerkelijke, herstelde, onderkaakfractuur van een tuimelaar uit het vroeg-Holoceen

Het Natuurhistorisch museum Rotterdam beheert een uitgebreide collectie skeletmateriaal van fossiele en recente Cetacea. Een van de collectiestukken, een rechter onderkaak van een tuimelaar (*Tursiops truncatus*) laat een

perfect geheelde, ernstige traumatische fractuur zien. De kleur en fossilisatiegraad van het fossiel en de vindplaats (Zuidelijke Noordzee) wijzen in de richting van een leeftijd van circa 8000-7000 jaar oud (vroeg Holoceen). Ondanks het feit dat de onderkaak compleet gebroken was, heeft de tuimelaar kunnen overleven en kon de fractuur perfect genezen. In dit artikel beschrijven wij deze opmerkelijke onderkaak en geven onze hypothese over de mogelijke oorzaak van de fractuur.

Received: 17 May 2017
Accepted: 8 June 2017