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Mammalian prey in Laridae: increased predation pressure on mammal populations expected

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Abstract: The occurrence of mammalian prey in the diet of two species of large gulls, the herring gull (*Larus argentatus*) and the lesser black-backed gull (*Larus fuscus*), was investigated in order to quantify and compare the predation on mammals in coastal and inland colony sites. Specialised coastal nesting birds and a majority of individuals in an inland colony were found to feed on mammals frequently. The encountered mammalian prey included western hedgehogs (*Erinaceus europaeus*), shrews (Soricidae), voles (Cricetidae: Arvicolinae), mice (Muridae), moles (*Talpa europaea*), brown rats (*Rattus norvegicus*), rabbits (*Oryctolagus cuniculus*) and common brown hares (*Lepus europaeus*). Most mammalian prey may have been obtained on inland fields, during farming activities, some may have been captured within the colonies, and some were scavenged at roadsides. Many coastal mainland colonies of gulls have recently collapsed as a result of persistent predation by red foxes (*Vulpes vulpes*). In addition, gulls breeding along the coast in the Netherlands increasingly suffer from shortages of food (mostly marine fish and intertidal invertebrates) during chick-rearing in recent years. Inland breeding became more frequent and will further increase as a result of both factors, so that the gulls are expected to increasingly include mammals in their diet.

Keywords: predation, Laridae, mammalian prey, diet.

Introduction

Investigations into levels of predation of mammals would normally take the impact of raptors (Falconiformes), owls (Strigiformes), perhaps crows (Corvidae), and certainly other (predatory) mammals into account (e.g. Lambin et al. 2000, Sundell 2002, Trout & Tittensor 2008). The reason why other potential predators generally receive much less attention could be that the mammalian part of their diets is considered to be trivial or at least insignificant. Recent work on the ecology of omnivorous large gulls, Laridae, has repeatedly shown that mammalian predation can be significant in some areas and/or seasons (Cramp & Simmons 1983, Ewins et al. 1994, Solá et al. 1998). The food of coastal nesting herring gulls (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) in the Netherlands consists predominantly of tidal invertebrates and marine fish, but individuals from inland colonies can be completely terrestrial in their feeding habits (Spaans 1998a, Spaans 1998b). Camphuysen et al. (2006) showed that in one such case, a colony in Wormer- & Jisperveld (Noord-Holland), juvenile meadow birds and in particular various species of mammals were in fact highly important prey.

Gull populations in the Netherlands are in a state of flux, both with regard to breeding numbers and with respect to their breeding distribution. Until recently, herring gulls and lesser black-backed gulls were exclusively breeding in (large) colonies near the coast. In dune areas along the mainland North Sea coast, colonies of both species have suffered from persistent predation and disturbance by red foxes (*Vulpes vulpes*) since the mid-1980s and particularly in the 1990s, and many breeding areas were abandoned (Bouman et al. 1991, Spaans 1998a, Spaans 1988b). The gulls commenced nesting on buildings in towns up to 25 km from the coast and in other inland locations. Breeding colonisations further and deeper inland have occurred since (Hustings & Vergeer 2002, Poot 2008). On top of this: recent ecological studies suggest that coastal nesting lesser black-backed gulls are increasingly facing food shortages during chick-rearing and currently experience very low breeding success (Camphuysen et al. 2008a, Camphuysen et al. 2008b). The shortage of food is apparently worsened by a decline in fishing fleet size and novel (more sustainable) fishing techniques, so that further inland colonisations may be expected in the near future. With a significant proportion of mammalian prey in inland breeding gulls, this could lead to a forecast for an increasing predation pressure on mammalian populations.

This article evaluates our current understanding of the dietary preferences of coastal nesting and inland breeding large gulls with regard to mammalian prey on the basis of recent diet studies. Which mammal species are taken, where and how could they be captured and what levels of dietary specialization were found to date are questions underlying the analysis. From the analysis we will speculate on possible changes in predation pressure on certain mammal populations as a result of the ongoing colonisation of inland breeding habitats by large gulls.

Methods

Foraging distribution and behaviour were assessed during direct field observations (1986-2009), from an analysis of colour-ringed herring gulls (Camphuysen et al., in press-b, Camphuysen et al., unpublished data from 1986-2009), and from high resolution positional data obtained with GPS-loggers on individual lesser black-backed gulls (2008-2009). The diet was studied on the basis of food remains found in three breeding colonies (2005-2009):

Study area

Kelderhuispolder (Texel) – A well-established, mixed colony of herring and lesser black-backed gulls, studied since 2006, at the southern tip of Texel (Noord-Holland; 53°00'N, 04°43'E). Prior to egg-laying (mid-April) the colony was visited with increasing frequency along a preset trail through various study plots, leading through prime herring gull and lesser black-backed gull habitats. Nests were marked with a numbered wooden pole. Randomly chosen groups of nests were later fenced off with an enclosure, in order to monitor chicks until fledging. Food samples were collected from all marked territories from the pre-laying phase until and including the fledging period (April to August), 2006-2009. The nesting stage was characterised for each individual marked territory, using the following terms: Pre-laying, Laying, Incubation, Hatching, Chick care, Fledging, or Predated. To enlarge the number of food samples, colonies and associated club-sites were searched for prey remains at regular intervals of time. For these samples, breeding stages were termed in accordance with the breeding stage of the majority of the monitored (marked) nests.

Vliehors (Vlieland) – A well-established, mixed colony of the same two species, in a

dune valley of the Vliehors area (53°14'N, 04°55'E), studied irregularly since 2006 by SOVON. Food samples from marked territories of herring gulls were collected in 2006, stored in a similar way as described earlier, and analysed at NIOZ in 2008. The samples could in this case not be related to the breeding stage of the predators.

Wormer- & Jisperveld (Noord-Holland) – A colony of lesser black-backed gulls, situated in a nature area covering 18 km² (of which 0.7 km² is a protected area owned by Natuurmonumenten), between the towns De Rijp, Purmerend and Wormerveer (Noord-Holland; 52°31'N, 04°50'E). The area consists mainly of marshland, grassland and open fresh water channels and is situated at circa 15 km from the North Sea coast. Lesser black-backed gulls colonised the area in 2000 and the breeding population is rapidly increasing (Camphuysen et al. 2006). The site was visited and searched for regurgitated prey during three successive visits in 2005 (Camphuysen et al. 2006). All samples were taken during chick care from otherwise unmarked, non-monitored territories.

Foraging distribution and feeding habitats

Unique colour-ring combinations or codes were used to individually identify birds within and outside the colonies (for details see: Camphuysen 2008). Most ring-readings outside the colonies were made by amateur bird-watchers, whereas within colonies the presence of ringed individuals was monitored as part of this study. Sightings made during the breeding season (Apr-Aug) of colour-ringed adult birds around the natal colonies were used to assess the foraging range around the colony. Some herring gulls from Vlieland were fitted with Argos satellite transmitters in 2007 and 2008 (Ens et al. 2009). Results were downloaded from the internet to evaluate likely foraging areas in summer (http://www.sovon.nl/default.asp?id=408; accessed 30 March 2010).

For lesser black-backed gulls, where colour-ring data were considered less useful, because this species tends to forage and feed mostly at sea, the foraging range and feeding habitats were deduced from GPS tracking data obtained in two consecutive breeding seasons (2008-2009). Five (2008) and six (2009) breeding adults from the Kelderhuispolder colony were harnessed and fitted with a 17 g GPS-logger, designed and developed by the University of Amsterdam. Data were remotely downloaded from a base station erected within the colony and data-resolutions could be freely varied (via remote instructions) from one geographical position each three seconds at the highest rate to lower rates in order to save energy. Downloaded data were plotted on a Google Earth background, to obtain information on habitats and specific habitat-related activity patterns. Further details in Camphuysen et al. 2008b).

Food sampling, analysis and identification

During nest visits in the study colonies, territories were inspected for the presence of discarded prey items. Diets within most colonies were studied mainly from spontaneously regurgitated matter (pellets, large chunks of regurgitated matter, partly eaten food remains), from food boluses produced during handling of the birds, from chick-feeds sub-sampled within the territories and from stomach contents of animals found dead. Prey samples were individually bagged, numbered, and kept frozen for later analysis. It is clear that a complete picture of the diet of a seabird will not emerge from regurgitated materials only; the biases are well known (Barrett et al. 2007), and the frequencies of occurrence calculated are indices rather than absolute amounts of prey consumed. Comparisons were made only between comparable samples: pellets and (dried) regurgitated

Table 1. Samples (*n*) analysed in search of mammalian prey and number (*n*) and frequency (%) of mammalian prey found in food samples collected in colonies of lesser black-backed gulls (LBBG) in Wormer- & Jisperveld and at Texel (Kelderhuispolder), in colonies of herring gulls (HG) at Texel (Kelderhuispolder) and Vlieland.

Species	Location	Samples	Mammalian	Frequency (%)
LBBG	Wormer- & Jisperveld	161	72	44.7
	Kelderhuispolder, Texel	3546	32	0.9
HG	Kelderhuispolder, Texel	3003	82	2.7
	Vliehors, Vlieland	193	2	1.0
Total		6903	188	2.7

matter found at nest sites. The total number of food samples analysed, including 3707 samples for lesser black-backed gulls and 3196 for herring gulls are listed in table 1. Prey items were defrosted, sorted and analysed under an Olympus ZN51 binocular microscope (8-40x magnification) in order to find even minute prey items. Mammalian remains were usually identified with Husson (1962) or Kapteyn (1999), occasionally by using ordinary field guides. Dental aspects, specific bones or external characteristics (claws, spines, fur), and sometimes even intact mammals could be found in regurgitated prey remains.

Results

Foraging range and feeding habitats

Herring gulls colour ringed at Texel were during the breeding season mostly re-sighted within 40 km to the south of the colony (i.e. the northern part of Noord-Holland and the southern tip of Texel; figure 1). There was little evidence for frequent use of areas to the north of the breeding colony (i.e. most of Texel). The sightings were mostly confined to coastal sites, which is likely a reflection of observer effort rather than true distribution. The range of the species in the northern part of Noord-Holland is characterised by the frequent, albeit irregular occurrence of feeding frenzies in near shore waters, in the intertidal zone, on agricultural land, in cities, in sewage treatment centres and on various other locations. Few of these situations are suitable for consistent ring-reading.

Herring gulls nesting on Vlieland were mostly found foraging at breakwaters on the beach of Vlieland, on intertidal mudflats to the south and southeast of that island, on the northern half of Texel and along the Afsluitdijk, a long barrier separating the Wadden Sea from the IJsselmeer (figure 1). There was some evidence for terrestrial feeding from these satellite tracking data in mainland Noord-Holland (Balgzand-Amsterdam; analysed by Gallego (2008); raw data at http://www.sovon.nl/default.asp?id=408).

Colour-rings are a less suitable method to assess the foraging distribution of true seabirds, such as lesser black-backed gulls, but GPS logger data revealed that terrestrial feeding habitats are visited by most, and virtually exclusively by some specialist birds (Camphuysen et al. 2008b). The normal foraging range of birds from Texel carrying GPS loggers amounted to 40-80 km to the south and southwest of the breeding colony at Texel, but with a majority of the uploaded positions within 45 km, mostly to the SW of the colony (figure 1). Terrestrial feeders usually crossed the Marsdiep and entered mainland Noord-Holland through the Den Helder area, whereas return flights were mostly gliding flights along the dunes. Inland potential feeding areas were visited south to Hoorn (Noord-Holland) on regular feeding trips. Individual tracks of lesser black-backed gulls demonstrated the frequent use of coastal but also inland roosts in Noord-Holland and on the

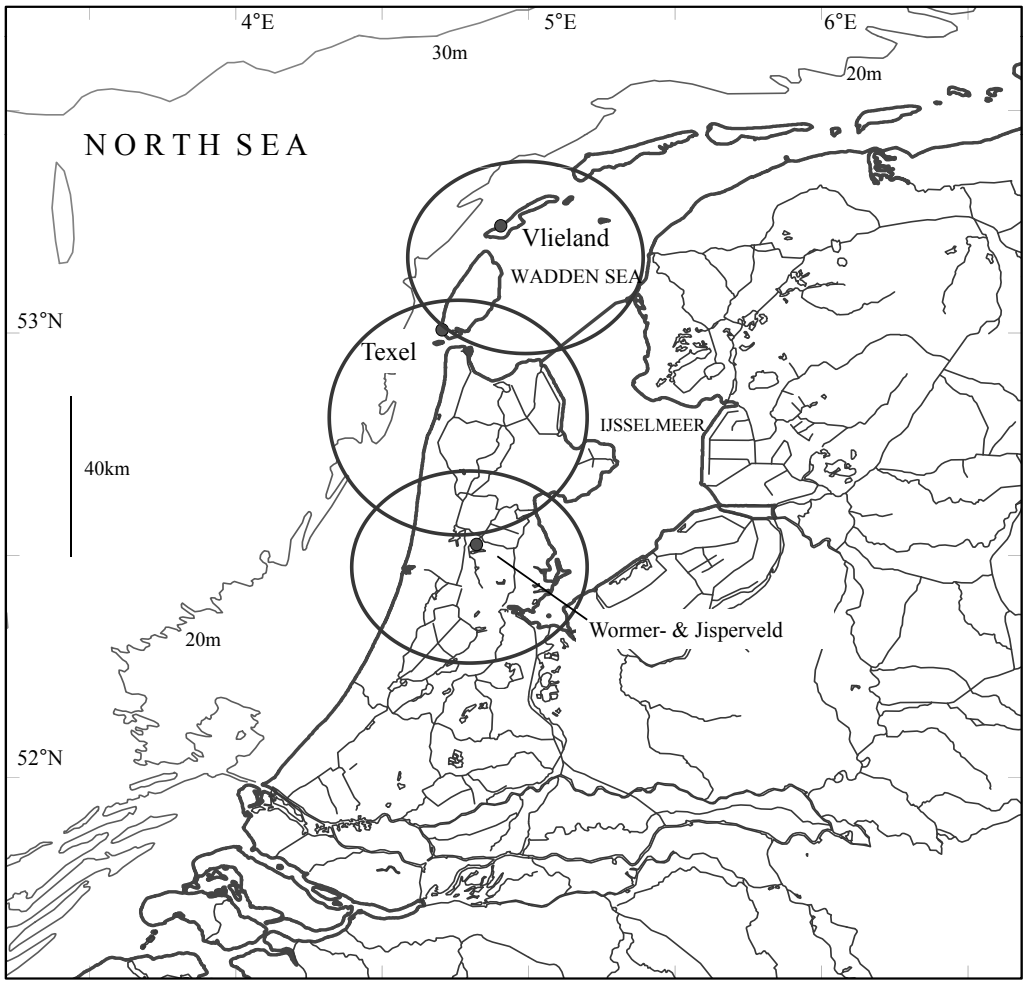

Figure 1. Presumed main foraging range based on colour-ring sightings of herring gulls and GPS positions of apparently foraging lesser black-backed gulls from Kelderhuispolder, Texel (central circle), based on Argos satellite tags) of herring gulls from Vlieland (top circle; for details, see: http://www.sovon.nl/default.asp?id=408), and expected foraging range based prey items (see text) of lesser black-backed gulls nesting in Wormer- & Jisperveld (lower circle). Colony locations are indicated by solid dots.

south tip of Texel as well as the frequent use of inland fields for roosting and foraging. Linear patterns in tracks over agricultural areas suggested that the animals were following either linear structures (in a deep ploughed field for example), or a machine working the fields, other plots represent roosts or the exploitation of other inland feeding opportunities (figures 2-4). The logger data confirmed suggestions that Texel birds frequently joined inland concentrations of large gulls roosting or foraging in the northern part of Noord-Holland. There was little evidence for frequent use of land areas to the north of the breeding colony (i.e. most of Texel), but some gulls, incidentally, foraged on the island.

Lesser black-backed gulls nesting within the Wormer- & Jisperveld colony were ringed nor tagged and there is therefore no empirical data to assess their foraging range. The fre-

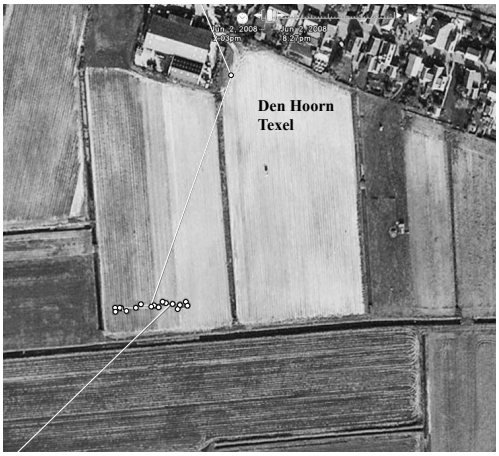

Figure 2. Foraging at (ploughed) agricultural land south of Den Hoorn, Texel of a lesser black-backed gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

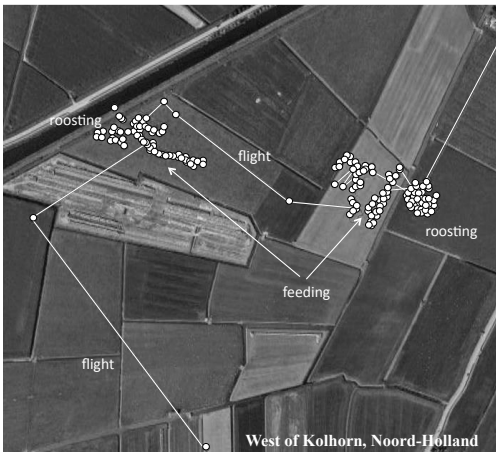

Figure 3. Foraging and roosting near Kolhorn, mainland Noord-Holland of a lesser black-legged gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads, white lines (not the arrows!) represent flights.

quent occurrence of marine fish, the simultaneous (and frequent) occurrence of freshwater fish species and the overwhelming abundance of terrestrial prey in the form of mammals and birds would indicate that, centred around the colony, a considerable inland area, and some parts of the North Sea and the IJsselmeer were within normal feeding range (figure 1).

Dietary composition

The dietary composition and the frequency of occurrence of mammalian prey was rather different between colonies (Texel and Vlieland as coastal colonies versus Wormer- & Jisperveld as an inland colony), and slightly different between species within colonies (Texel; tables 1-2). The food samples collected at the inland colony Wormer & Jisperveld, 44.7% of which with mammalian prey (*n*=161), are clearly different from those collected in colonies situated in coastal areas. Mammalian prey were fairly insignificant in herring gulls from Vlieland (1.0%, *n*=193) and in lesser black-backed gulls from Texel (0.9%, *n*=3546), but slightly more substantial in herring gulls from Texel (2.7%, *n*=3003).

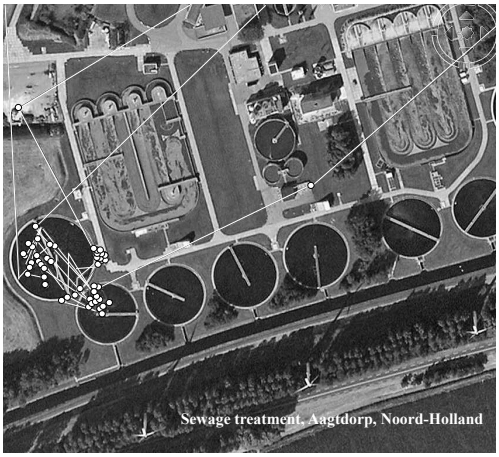

Figure 4. Foraging activity at a sewage treatment near Aagtdorp, Noord-Holland, of a lesser black-backed gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads, white lines represent flights.

Within colonies at Texel, high levels of individual specialisation on mammals could only be recognised in herring gulls. A total of 2399 herring gull pellets were collected at 225 individually marked nest sites. Mammalian prey were found at 25 sites (11.1% of the sites), whereas 72 pellets (3.0%) contained mamma-

Table 2. Frequency of occurrence (*n*, %) of main prey types in pellets and regurgitated matter, as the most readily available and common source of dietary information in all study colonies. Under 'fish' both marine and freshwater types are included. Some very rare groups (hydroids, sponges, barnacles, and unidentified Nematoda) were not listed in this table.

	Lesser black-backed gull				Herring gull			
	Kelderhuispolder		Wormer- & Jisperveld		Kelderhuispolder		Vlieland	
Group	*n*	%	*n*	%	*n*	%	*n*	%
Insects	631	17.8	6	3.7	250	8.3	13	6.7
Oligochaetes	140	3.9	31	19.3	33	1.1	1	0.5
Polychaetes	511	14.4			65	2.2	4	2.1
Echinoderms					19	0.6		
Gastropods	70	2.0	1	0.6	59	2.0	3	1.6
Bivalves	49	1.4			2108	70.2	126	65.3
Cephalopods	2	0.1			3	0.1		
Crustaceans	783	22.1	7	4.3	435	14.5	97	50.3
Fish	2812	79.3	32	19.9	650	21.6	54	28.0
Birds, non-Passerines	304	8.6	33	20.5	265	8.8	2	1.0
Birds, Passerines	17	0.5	3	1.9	29	1.0		
Mammals	32	0.9	72	44.7	82	2.7	2	1.0
Plants	451	12.7	4	2.5	304	10.1	5	2.6
Seaweeds	1	0.0			10	0.3	1	0.5
Human waste	209	5.9	7	4.3	477	15.9	3	1.6
Miscellaneous	149	4.2	3	1.9	398	13.3	28	14.5
Sample	3546		161		3003		193	

lian prey. At sites where mammalian prey were found at least once (n=25), an average (±SD) of 2.88 ± 5.2 pellets (max. 26 pellets at a single site) with mammal remains were picked up. Five herring gull sites with more than two pellets holding mammalian remains included:

- ZM120, a territory marked in 2007, 26 pellets containing mammalian remains; all rabbits (*Oryctolagus cuniculus*);
- ZM201, 2008, 10 pellets, rabbits (7), brown rats (*Rattus norvegicus*) (2), and unidentified mammals (1);
- ZM023, 2006, 4 pellets, rabbit (1), root vole (*Microtus oeconomus arenicola*) (2), and brown rat (1);
- ZM261, 2008, 4 pellets, rabbit (1), root vole (2), and house mouse (*Mus musculus*) (1) and with rabbit (1) and brown rat found in chick-feed samples;
- ZM035, 2006, 3 pellets, rabbits (2) and root vole (1).

In the same study (Texel, 2006-2009), 1039 pellets of lesser black-backed gulls were collected at 231 individually marked nest sites. Mammalian prey were found at eight sites (3.5% of the territories), whereas eleven of the pellets (1.1%) contained mammalian prey. At sites where mammalian prey were found at least once (*n*=8), an average (± SD) of 1.38 ± 0.7 pellets (max. 3) with mammal remains were picked up. The 'exceptional' lesser black-backed gull site with three pellets containing mammalian prey provided two species of voles (bank vole (*Myodes glareolus*) and root vole).

A brief description of prey items, the type of remains and the frequency of occurrence for each of the main groups of mammalian prey is provided below (tabulated in tables 3 and 4).

Hedgehogs

Western hedgehogs (*Erinaceus europaeus*) were found twice in pellets near two different

herring gull territories at Texel, both in 2008 (3 June and 25 July, Entry Dunes, Kelderhuispolder colony). The first sample contained a skull and teeth plus smaller fragments, the second pellet contained spines, bones, teeth and vertebrae. The remains were indicative for scavenged carcasses of mature hedgehogs, rather than for prey swallowed whole (e.g. hedgehog cubs). A scavenged carcass of a fully grown western hedgehog was found 14 May 2007 right in the middle of the colonies near a herring gull club site. This find was not included in the diet studies and it must have been an animal that was either found dead or killed by gulls within the colony, rather than transported through the air.

Shrews

The common shrew (*Sorex araneus*) was the sole representative of this group and there was only a single occurrence of this species: Wormer- & Jisperveld, lesser black-backed gull, 23 June 2005 (complete regurgitated skeleton recovered). This prey item was found at a nest site of a bird that also took many waterfowl and meadow birds (mallard (*Anas platyrhynchos*): 2x); lapwing (*Vanellus vanellus*): 1x; black-tailed godwit (*Limosa limosa*): 11x; and redshank (*Tringa totanus*): 4x).

Moles

The mole (*Talpa europaea*) was a common prey of inland nesting lesser black-backed gulls (Wormer- & Jisperveld, 24 (33%) out of 72 samples containing any mammalian prey; 15% of all 161 prey samples analysed for that colony). Many of the pellets with remains of common moles contained some pitch-black fur and a subset of mole-bones, the humerus and jaws or skulls of which were used to assess the number of individuals taken. Single mole remains were spread over two individual pellets on at least two occasions. Moles were found only incidentally in the Kelderhuispolder colonies, with two prey remains of herring gulls (2 out of 86 samples with mammalian prey; table 5) and two further regurgitated parts of moles that could not be attributed to a particular gull species. Moles formed no more than a tiny fraction of prey types found in these coastal nesting gulls. Apart from the food samples collected, mummified remains of moles were found occasionally in and around the Texel colonies (moles do not occur naturally on the island); not attributed to a particular gull species.

The contents of most "mole-pellets" were such that apparently entire animals were swallowed prior to pellet production (most of the skeleton within single pellets). One pellet from Texel contained remains of a mole, marine fish and Coleoptera, representing a mix of marine and terrestrial feeding activities. Similarly, at least two pellets from Wormer- & Jisperveld contained remains of marine fish next to skeletal parts and fur of moles. GPS logger tracks of lesser black-backed gulls breeding at Texel confirmed that several individual foraging trips covered marine as well as terrestrial potential feeding grounds.

Voles

At least four species were found: water vole (*Arvicola amphibius*), bank vole, common vole (*Microtus arvalis*), and the endemic subspecies of the root vole. Water voles were only found in pellets produced by lesser black-backed gulls, including eight samples (5%, *n*=161 samples) from the inland colony Wormer- & Jisperveld (2005), and a single sample (0.02%, *n*=4162) from Texel (2007). Common voles were exclusively found in the Wormer- & Jisperveld colony, again being represented in eight different samples (5%, *n*=161). The endemic root vole was represented in food samples from both gull species, including positive identifications in two samples from Wormer- & Jisperveld (1.2%, *n*=161), ten samples from lesser black-backed gulls on Texel (0.2%, *n*=4162), and seven samples from herring gulls in that colony (0.2%, *n*=3904). One lesser black-backed gull pellet from Texel contained four lower jaws of root voles, but the other samples were all indica-

tive for no more than a single vole in each. The bank vole was only once positively identified in a pellet from a lesser black-backed gull at Texel (an intact individual regurgitated as chick-feed, but ignored by the offspring; 20 July 2007). Unidentified voles were found in 21 samples (13.1%) from lesser black-backed gulls in the Wormer- & Jisperveld colony and in 10 samples from Texel (0.2%), whereas only three pellets of herring gulls from Texel were found to contain unidentified voles (0.08%).

Mice

True mice (Muridae) were rarely encountered. A single wood mouse (*Apodemus sylvaticus*) was found in a pellet produced by a lesser black-backed gull at Texel during laying (10 May 2009), while the house mouse was recorded twice, both from herring gulls pellets produced during egg-laying in May 2007 and May 2008 at Texel. All three mice were swallowed whole and the pellet contained most of the skeleton, teeth, and fur.

Rats

Brown rats were found in herring gulls pellets collected at Texel in June 2006, June 2007, and May and June 2008 (laying, incubation, and chick-care), and in a single pellet produced by a lesser black-backed gull in the same colony (May 2008, pre-laying). Within the colony large parts of rats were found occasionally, as rejected prey remains, not clearly associated with territories. Within pellets, teeth and bones were used for identification, while (grey) fur and nails were frequently encountered. Three of the 'mammal specialist' herring gulls produced pellets with remains of rats, which is a high representation given the small number (five) of pellets with rats found in the colonies as a whole.

Hares and rabbits

Common brown hares (*Lepus europaeus*) were found frequently (5.6% of all samples, *n*=161), but exclusively, in the inland colony of lesser black-backed gulls at Wormer- & Jisperveld. In most cases, some remains (mostly hind legs) were retrieved, of a size and with a bone structure suggesting that mostly very young individuals were taken and transported into the colony. A single rabbit was retrieved in that same colony, but a mis-identification cannot fully be excluded in this case. Rabbits were common as prey for herring gulls in Kelderhuispolder (50 samples, 58% of all food samples of herring gulls with mammalian prey, 1.3% of all food samples), were occasionally found in food samples from lesser black-backed gulls in the same colony (15% of all samples with mammalian prey, 0.1% of all food samples) and rabbits were represented in the smaller sample of food samples collected at Vlieland (table 5). Two herring gulls at Texel had clearly specialised on rabbits (see above), and one produced at least 26 pellets with remains of rabbits in the course of one breeding season. This particular individual produced owl-like pellets, compact prey-remains, containing mostly fur and splintered bones. Young rabbits (bone structure) were clearly represented, but ageing was not always possible.

Unidentified mammals

Most unidentified mammals were small rodents (voles or mice) or shrews, given the small bones and short fine fur encountered in lesser black-backed gull pellets from Wormer- & Jisperveld (2x) and Kelderhuispolder (5x) and in pellets from herring gulls from the latter colony (9x). One herring gull pellet contained hairs of a large mammal (horse, deer?), while a single pellet found on Vlieland contained flesh and fur of an unknown mammal. Mice droppings (or at least droppings of small mammals) were found in five samples of herring gulls from Kelderhuispolder. While sample contamination might be expected in these cases (droppings from mammals scavenging regurgitated prey remains), it was the embedding of droppings within pellets that led us to believe that indeed the droppings were part of the regurgitated material.

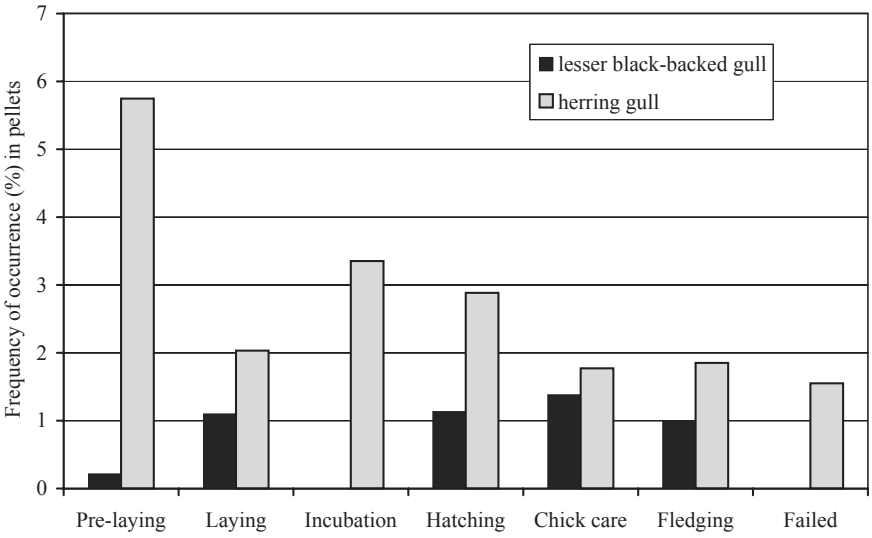

Figure 5. Frequency of occurrence (%) of mammalian prey through the breeding season in pellets and regurgitates collected from lesser black-backed gulls and herring gulls, Kelderhuispolder, Texel, 2006-2009.

Mammalian prey and breeding phase

For the Kelderhuispolder colonies, prey samples could be arranged according to breeding stage. The predators, herring gulls and lesser black-backed gulls, produced an almost perfect mirror image in frequency of occurrence of mammalian prey (figure 5), with high frequencies prior to egg laying in herring gulls, but rather few mammals in food samples in lesser black-backed gulls in that period. Relatively high frequencies of mammalian prey were found during incubation and hatching in herring gulls, whereas lesser black-backed gulls did not produce a single pellet with mammals during egg-laying and had relatively high frequencies during chick-care (hatching – fledging).

Discussion

The importance of mammalian prey

The food samples provide information on the prey species and also to some extent on the age composition of mammalian prey. The underlying data are evidently biased, because swallowed whole preys are more likely to be retrieved from pellets (compact assemblages of indigestible remains) than for example fleshy bits scavenged from a road-kill. By using frequencies of occurrence and a similar methodological approach between colonies and different predator species, apparent patterns in the utilisation of mammalian prey can still be evaluated, even though actual levels of predation may be incorrect (likely too low).

The proportion of mammals in prey samples obtained in different colonies was strikingly different. The colony in Wormer- & Jisperveld, where 45% of the collected prey samples were found to contain mammalian prey, is situated at circa 15 km from the North Sea coast. Lesser black-backed gulls colonised the area in 2000 and the breeding population is rapidly increasing (Camphuysen et al. 2006). Assuming a 40 km foraging range around the breeding locality, a large part of agricultural land in Noord-Holland is within reach as a potential feeding area. The large numbers of meadow birds, moles and voles indicate that the birds forage frequently on land, possibly in the immediate surroundings of the colony. The

presence of marine fish and freshwater fish, however, shows that other habitats, including the open sea, are exploited as well.

For gulls nesting in coastal colonies, the level of utilisation of inland foraging opportunities was until now much less clear. In an earlier study, Spaans (1971) demonstrated the abundant use of (uncovered) refuse dump sites in the provinces of Friesland and Drenthe by herring gulls nesting at Terschelling, but found little evidence for other abundant terrestrial prey items, apart from insects. Mole, wood mouse, and voles (*Microtus arvalis*, *M. agrestis* and *M. oeconomus arenicola*) were listed as rare, incidental prey species on Terschelling, while juvenile rabbits were frequently encountered in years that rabbits were abundant on the island. From the study of Spaans (1971) it was unclear whether mammalian prey was locally obtained or flown in from the mainland. New data, including information derived from colour-ringed individuals and in particular the GPS logger data have demonstrated that some individuals from coastal colonies do in fact forage deep inland, at least occasionally. The data obtained at Texel, where the mole does not naturally occur, provide further evidence that at least some of the mammalian prey is flown into the colonies from abroad (in this case most likely from the Noord-Holland mainland). GPS logger data (lesser black-backed gulls from Texel) and Argos satellite tracking data (both gull species from Vlieland) seemingly confirm (further analysis is required) that individual birds are highly faithful to particular foraging sites or feeding habitats. Mammalian prey in coastal breeding lesser black backed gulls is currently rather rare, while it is slightly more frequent in herring gulls from Texel. The herring gulls from Vlieland (note small sample size) were near-completely focused on intertidal, marine prey. Incidental studies elsewhere in Europe confirmed that inland nesting large gulls prey on mammals to a greater extent than coastal nesting individuals (Stevens 1943).

Where and how would mammalian prey be obtained?

One can often only speculate as to where and how these prey were obtained. One important question would be: are they actively hunted, or is mammalian prey mostly taken by scavengers utilising carcasses found during foraging. In fact, 1. the prey may have been dead when utilised (scavenging behaviour), 2. it may have been sick or otherwise immobilised or slow and therefore more readily available, 3. the prey may have been made available through farming activities (aerial or ground pursuit behaviour), 4. the prey could be captured alive by hunting gulls (active pursuit), or 5. mammalian prey was stolen from or found as leftovers from other predators (for example from raptors or crows; Barnard & Thompson 1985). Very few actual field observations exist, except for the frequent occurrence of scavenging gulls along roads (road-kill utilisation). Most actively foraging gulls in agricultural areas (including meadows) are birds trampling for worms, birds competing for prey behind machines working these areas, or birds searching for prey while walking in recently worked or fertilised fields. It is difficult, certainly in the absence of direct observations, to speculate about the actual origin of the retrieved mammalian prey items. Herring and lesser black-backed gulls are powerful animals, known to attack and kill surprisingly large prey at times (e.g. Camphuysen et al., in press-a).

Some prey were available in the immediate surroundings of the breeding site, other prey may require more travel to obtain. Rabbits as prey at Texel tended to fluctuate with their presence (from sightings) within the colony area, although exact data were not kept. While scavenging at road kills around the colony did occur, most rabbits found at the territory of the specialised gulls were expected to be targeted within the dune area, possibly even within the colony. Common brown hares at Wormer- & Jisperveld are abundant

within the nature area and these could also be considered local prey. The fact that most rabbits at Texel and most hares at the mainland colony were seemingly rather young animals might indicate that these were often actually captured prey rather than carcass finds.

Western hedgehogs are plentifully available as carcasses along roadsides (Texel and Vlieland included), but being nocturnal, they are difficult to hunt and kill for gulls. One partly eaten carcass of an adult hedgehog found within the colony at Texel would suggest, however, that these animals are occasionally killed.

With respect to the presence of species in the immediate surroundings or even within the study colonies, it is clear that the strong representation of root voles at Texel and at Wormer- & Jisperveld is in accordance with their endemic occurrence in either area. Voles, shrews and mice attract immediate attention of gulls standing in colonies when they briefly rush from one covered place to another over the open after disturbance (C.J. Camphuysen, unpublished data). This behavioural response (alertness) is so immediate, that active chases of gulls towards these smaller mammals could be expected as soon as they leave cover for whatever reason. These animals could just as well be captured within colonies, in the immediate surroundings of breeding places, or in distant feeding areas. Only species composition within each of these areas could be indicative for the possible origin of certain prey. Unfortunately, the resolution of data on the occurrence and distribution of mammals within the Netherlands is not very high (Broekhuizen et al. 1992) and for that reason, within the context of this article, we did not further explore this issue. Interesting, however, is the recovery of water vole remains at Texel, where this species is not known to occur (Broekhuizen et al. 1992). Bank voles, also not reported from Texel by these authors and represented in at least one food sample from lesser black-backed gulls on the island, do in fact occur also on the island.

Moles at Texel (or Vlieland for that matter) could also only originate from the mainland so that these prey items must have been flown in from distant feeding areas. Moles in the Wormer- & Jisperveld area could just as well have been local prey. How does a gull capture moles, however? It is not entirely unlikely that gulls would monitor active mole runs and respond when moles push up the turf during one of their frequent checks of the run. There are some accounts of moles swallowed alive at least by herring gulls although this might not be without risk for the predator (Lyster 1972). Quin (1969) reported a fledgling lesser black-backed gull that regurgitated an intact, fresh mole. Jansen (2007) described a form of symbiosis between moles and gulls, where herring gulls were seen to associate with moles pushing up turf, because the escaping response of earthworms triggered by the activity of the mole would make these worms an easy prey for the gulls. Possibly the mole would be targeted as soon as it became visible under these conditions. Alternatively, moles could be captured swiftly when they become uncovered during ploughing or other activities by farmers on their land.

Forecasting an increase in utilisation of mammalian prey

The populations of herring and lesser black-backed gulls have increased spectacularly in the Netherlands in the second half of the 20th century, following phases of plundering, protection, persecution, and again (partial) protection during the 19th and 20th centuries (Spaans 1998a, Spaans 1998b, Spaans 2007). Mainland coastal colonies, however, became under pressure in the mid-1980s when red foxes re-colonised the dune areas (Bouman et al. 1991, Spaans 1998a, Spaans 1998b). Many mainland colonies collapsed and inland breeding became more frequent. Recently the coastal colonies are facing food shortages because less fishery offal is produced

(Camphuysen et al. 2008b). This combination of food shortage and predation pressure most likely will lead to further shifting from marine foraging habitats towards terrestrial areas. Given the importance of mammalian prey in these areas, increased predation pressure and a stronger impact on mammal populations could then be expected.

Conclusions and implications

Evidence is provided that mammalian prey is a significant food resource for gulls nesting inland and for some specialised gulls in coastal colonies. Mammalian predation has usually been interpreted as being a compensatory mortality factor, removing only the doomed surplus (Trout & Tittensor 2008). However, the number of mammals taken by gulls can be substantial (represented in up to 45% of all prey samples within some colonies). For a number of reasons mentioned earlier, the tendency of gulls to forage on inland locations will likely increase and as a result, predation pressure on various mammal species will be higher. In case of predation by gulls, however, for which scavenging is a common technique and where active hunts may be the exception rather than the rule, predatory levels are unlikely to quickly pose a major threat to mammal populations.

Avoiding predators spatially or selecting safer habitats does improve survival prospects of potential prey animals. However, in the case of a new predator arriving on the scene (as with introduced alien predators), prey populations might lack the behavioural traits to escape predation efficiently. Fey et al. (2006) provided evidence for a microhabitat shift of native prey animals (voles) caused by an alien predator, the American mink (*Neovison vison*) and similar shifts are likely to occur when large gulls increase substantially as potential predators. As generalist predators, gulls may be expected to switch to alternative prey when more usual resources decline below a certain threshold or when they enter new habitats. At the same time, they are likely to respond swiftly to population oscillations of mammalian prey (rodent outbreaks for example; Ruiz & Simeone 2001) and may even have a stabilising effect on vole or mice population dynamics (Andersson & Erlinge 1977, Hanski et al. 1991, Sundell 2002).

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Samenvatting

Zoogdieren als meeuwenvoedsel: een toenemende predatiedruk op zoogdierpopulaties kan worden verwacht

Eventuele predatiedruk op zoogdieren wordt meestal in de eerste plaats verondersteld te worden veroorzaakt door roofvogels, uilen, misschien kraaien en in elk geval door andere zoogdieren (roofdieren). Redenen voor het buiten beschouwing laten van predatie door bijvoorbeeld grote meeuwen worden vermoedelijk gevonden in de veronderstelling dat dit op een verwaarloosbare schaal voorkomt. Recent onderzoek aan de ecologie van zilvermeeuwen (*Larus argentatus*) en kleine mantelmeeuwen (*Larus fuscus*) heeft aangetoond dat in sommige vestigingen in het binnenland heel andere prooidieren worden gevonden dan in de grote kolonies langs de kust. Onder de prooiresten in een kolonie kleine mantelmeeuwen in het binnenland werden zelfs bijzonder veel zoogdieren aangetroffen. In dit artikel wordt de voedselkeuze van meeuwen in drie kolonies langs de kust (zilvermeeuwen en kleine mantelmeeuwen op Texel, zilvermeeuwen op Vlieland) vergeleken met de prooidieren die gevonden werden in een kolonie dieper in het binnenland (kleine mantelmeeuwen in het Wormer- & Jisperveld). Onder de aangetroffen zoogdierresten bevonden zich egels (*Erinaceus europaeus*), spitsmuizen (Soricidae), woelmuizen (Cricetidae: Arvicolinae), ware muizen (Muridae), mollen (*Talpa europaea*), bruine ratten (*Rattus norvegicus*), hazen (*Lepus europaeus*) en konijnen (*Oryctolagus cuniculus*). Met behulp van kleurringen, satellietzenders en GPS-loggers werd het foerageergebied van de vogels in de kolonies langs de kust in kaart gebracht. Daaruit bleek dat Texelse vogels grote delen van de kop van Noord-Holland bestreken en Vlielandse vogels de noordelijke helft van Texel, het Vlielandse strand en wadplaten ten zuiden en zuidoosten van Vlieland. Van de meeuwen in het Wormer- en Jisperveld werden geen waarnemingen van het eigenlijke foerageergebied gedaan, maar de prooiresten lieten zien dat daaronder de Noordzee (zeevis), gebieden met zoetwater (zoetwatervis), stedelijke gebieden (menselijk afval) en vooral weilanden (weidevogels, waterwild, en zoogdieren) gerekend moesten worden. De GPS-loggers gaven gedetailleerde informatie over het ruimtelijk gebruik in Noord-Holland en zij toonden het bezoek van rustplaatsen en foerageeractiviteit in landbouwgebied onomstotelijk aan. Op Texel werden enkele gespecialiseerde (zilver-)meeuwen aangetroffen waarvan er één zich geheel op (jonge) konijnen had toegelegd. Mollen waren een opvallend vaak voorkomende prooi in het Wormer- en Jisperveld, terwijl de incidentele aanvoer van mollen op Texel (waar die soort niet natuurlijk voorkomt) op aanvoer door de lucht wees en aanvullend bewijs vormde voor de aanvoer van prooien uit het vasteland van Noord-Holland. Endemische Noordse woelmuizen (*Microtus oeconomus arenicola*) waren veel voorkomende prooien op Texel en in het Wormer- en Jisperveld. Het foerageren achter landbouwmachines maakt dat de meeuwen vermoedelijk kunnen profiteren van vers gedode of onvrijwillig blootgelegde zoogdiertjes op boerenland. Het is ook mogelijk dat er actief op kleine zoogdieren wordt gejaagd, al zijn daarvan maar weinig directe waarnemingen bekend. Tevens zal er geprofiteerd worden van verkeersslachtoffers langs de weg, zoals egels, hazen, konijnen en ratten, zodat ook grotere soorten 'met gemak' als prooi kunnen dienen. Beide meeuwensoorten zijn in de loop van de vorige eeuw sterk in aantal toegenomen. Recentelijk is het bestand zilvermeeuwen sterk teruggelopen, nadat open vuilstortplaatsen werden gesloten of werden overdekt. De huidige, gestabiliseerde populatie lijkt zich op natuurlijke prooien,

vooral in de getijzone, te hebben geconcentreerd. Kleine mantelmeeuwen krijgen nu echter in toenemende mate te maken met voedseltekorten als gevolg van veranderingen in de kustvisserij. Deze soort zal zich daarom net als de zilvermeeuw in de toekomst sterker op het binnenland gaan concentreren en de eerste bewijzen daarvoor zijn al voorhanden. Bij het wegvallen van traditioneel voedsel en bij de toenemende neiging om voedselbronnen in het binnenland aan te boren zullen zoogdieren in de nabije toekomst dus ook veel meer met meeuwen als predatoren te maken krijgen. Gezien de diversiteit van de prooidieren, het opportunistische foerageergedrag van de meeuwen en het vermoeden dat vooral verzwakte, erg jonge of reeds dode zoogdieren gepakt worden, zal deze verhoogde predatiedruk, in elk geval op korte termijn, naar verwachting geen enkel probleem voor de zoogdierpopulaties op leveren.

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Table 3. Mammalian prey of lesser black-backed gulls at Wormer- & Jisperveld and in Kelderhuispolder at Texel (shown are total number of prey samples with each species represented).

Species	Wormer- & Jisperveld	Kelderhuispolder
Common shrew	1	
Mole	24	2
Water vole	8	1
Bank vole		1
Common vole	8	
Root vole	2	10
Microtus spp.	21	10
Wood mouse		1
Brown rat		1
Common brown hare	9	
Rabbit	1	5
unidentified mammal	2	5

Table 4. Mammalian prey of herring gulls in Kelderhuispolder at Texel and at Vliehors, Vlieland (shown are total number of prey samples with species represented).

Species	Kelderhuispolder	Vliehors
Western hedgehog	2	
Mole	2	
Root vole	7	
Microtus spp.	3	
House mouse	2	
Brown rat	5	
Rabbit	50	1
mice droppings	5	
unidentified mammal	10	1