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Tools

What is life without tools? For most of us, life may seem impossible without tools. Tool making and tool use is, without doubt, an indispensable part of human society, whether we live in the developed world or in more 'primitive' societies that still rely on hand tools for agriculture, hunting or gathering. Tools, although they differ in complexity, are used by all humans. In the animal world the use of tools is rare.

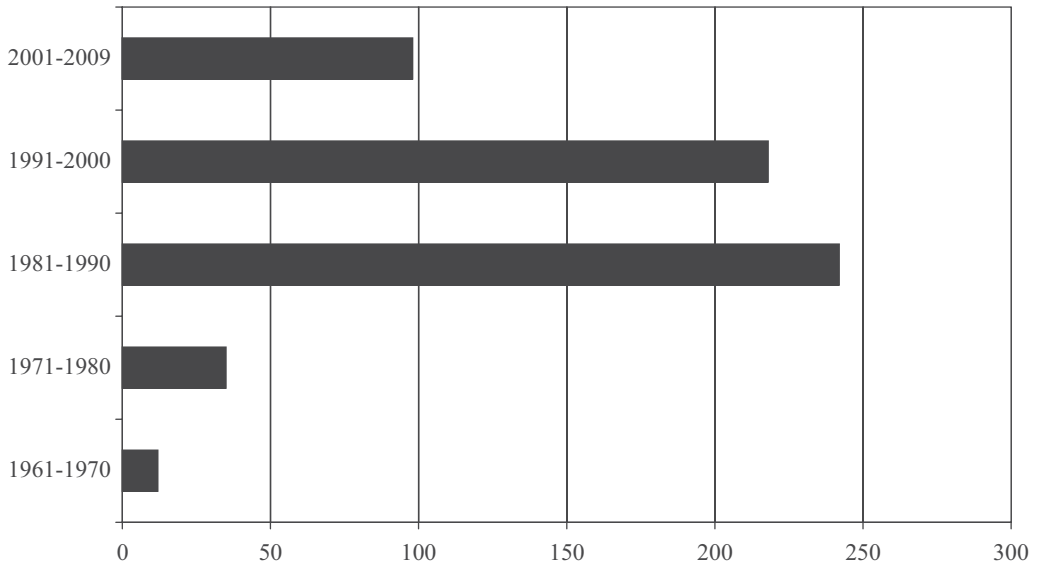
Primates are best known for their capability to recognise or design tools that may be of help in collecting food. In West Africa, for example, chimpanzees are known to use "fishing rods" to gather ants and termites, sticks to chase prey out of their dens, "shovels" to dig up roots and turnips and "hammers" to crack nuts. Remarkably, the animals also show the capacity to purposely adjust their tools to improve their performance. The type of tool and manner in which it is used may differ between different groups of the same species. For example, some chimpanzee groups use stone hammers to crack nuts and others use wooden ones. The choice of nut-cracking tool is not genetically determined, but depends on the "culture" of the clan. Furthermore, British primatologists discovered that animals that migrate to another colony may either adapt to the preferred method of nut cracking of the group they entered or introduce a new one.

Observations of primates using tools for other purposes than foraging are less frequent. One fascinating example is the use that gorillas in the Congo make of sticks to measure water depth, provide support or bridge muddy river banks during foraging in swampy areas. Another example is the use of tree leaves by orang-utans to produce alarm sounds when predators are nearby. It is assumed that the animals aim to mislead or frighten potential predators, as the low sounds made with the "trumpet" give the impression of originating from a larger animal.

But the use of tools is not limited to primates. Dolphins along the coast of West-Australia use sponges to catch fish. They select cup-shaped sponges, which they place upside down on their noses. The sponges allow them to root along the sea bottom and force their prey to leave their hiding places, without hurting their sensitive noses. As with chimpanzees, dolphins seem to teach their offspring the same trick, resulting in groups that show the "sponging" culture and groups that do not.

Mammals have also shown to be able to use man-made tools. Experiments with primates have shown that the animals purposely select the right tool for the right job. In addition to different primate species, dolphins and elephants have been shown to recognise themselves in a mirror and to use mirrors, when available, to check out body parts they normally cannot see.

To my knowledge Lutra has never presented research on the use of tools in mammals. Unfortunately, most tool-using species live outside of Europe and hence remain outside



Number of citations of articles published in Lutra.

the scope of Lutra. That does not imply that Lutra does not present remarkable and often unexpected findings, as proven by the papers in this issue on mammalian prey in Laridae (Camphuysen, De Boer, Bouten, Gronert & Shamoun-Baranes), long-term trends in hibernating bat numbers and species composition in a cave in Limburg (Grol & Voûte), and the use that water voles make of habitat refuges to avoid predation by mink (MacPherson & Bright). Secretly, however, I am still hoping for the discovery of red squirrels that use some sort of "nut crackers" or beavers that use "ropes" of plant material for strengthening their dams. And that, if such spectacular phenomena are discovered, it will be Lutra that presents the findings to the world!

Lutra itself is also a tool. It is an instrument to present new research results or interesting observations on mammals to the scientific world. The editorial board keeps looking for opportunities to improve procedures and the quality of the journal in order to better fulfill the journal's goal of being a scientific medium for mammalogists. Two recent improvements are worth mentioning. The first is that the peer review of submitted manuscripts has been changed into a "double blind" procedure, which means that the authors will not be known to the referees and vice versa. We believe with this change we can better guarantee objective and to-the-point judgements of manuscripts. The second is that, starting from Volume 54, Lutra will no longer publish articles in Dutch. English will be the only language used, since it is now the universal language of science. In practice this will not lead to significant changes, as the number of articles in Dutch has been very limited in the last decade – since 2001 only five out of ninety published full articles have been in Dutch, the last one in 2006. The Dutch summaries at the end of each article will remain.

The decision to publish only in English is strongly related to recently taken initiatives to have Lutra included in the *Web of Science* database. This database covers over 9,000 international and regional journals and book series in every area of the natural sciences, social sciences and arts and humanities. Inclusion in this database will not only give Lutra better exposure to people who use

the database to identify articles of interest, but also means that Lutra will be assigned an *impact factor*. The impact factor is a measure reflecting the average number of citations to articles published in scientific journals. It is frequently used as a proxy for the relative importance of a journal within its field, with journals with higher impact factors deemed to be more important than those with lower ones. With an impact factor Lutra can better measure itself against other journals. We believe this will be an important tool to inform potential authors about the quality of our journal and is likely to increase the number of high-quality manuscript submissions, as it is normally a prerequisite for academic authors to publish in journals with an impact factor. It is difficult to predict the impact factor that Lutra will be assigned. However, articles published in Lutra have been cited significantly more often since the 1980s (see graph). As there is always a delay of several years between the publication of an article and the moment when it is cited by other authors, the number of citations in the period 2001-2009 is likely to increase in the coming years and hopefully reaches similar or even higher levels than in the previous two decades. The inclusion of Lutra in the *Web of Science* will be decided in the summer of 2011, with the decision being based on an evaluation of the three most recent issues, starting from this one. The editorial board hopes that this initiative will act as a useful tool to improve the quality and reach of Lutra.

Edgar A. van der Grift

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, GPS, colour ringing.

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 1998b). 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 in Google Earth, 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 south tip of Texel as well as the frequent

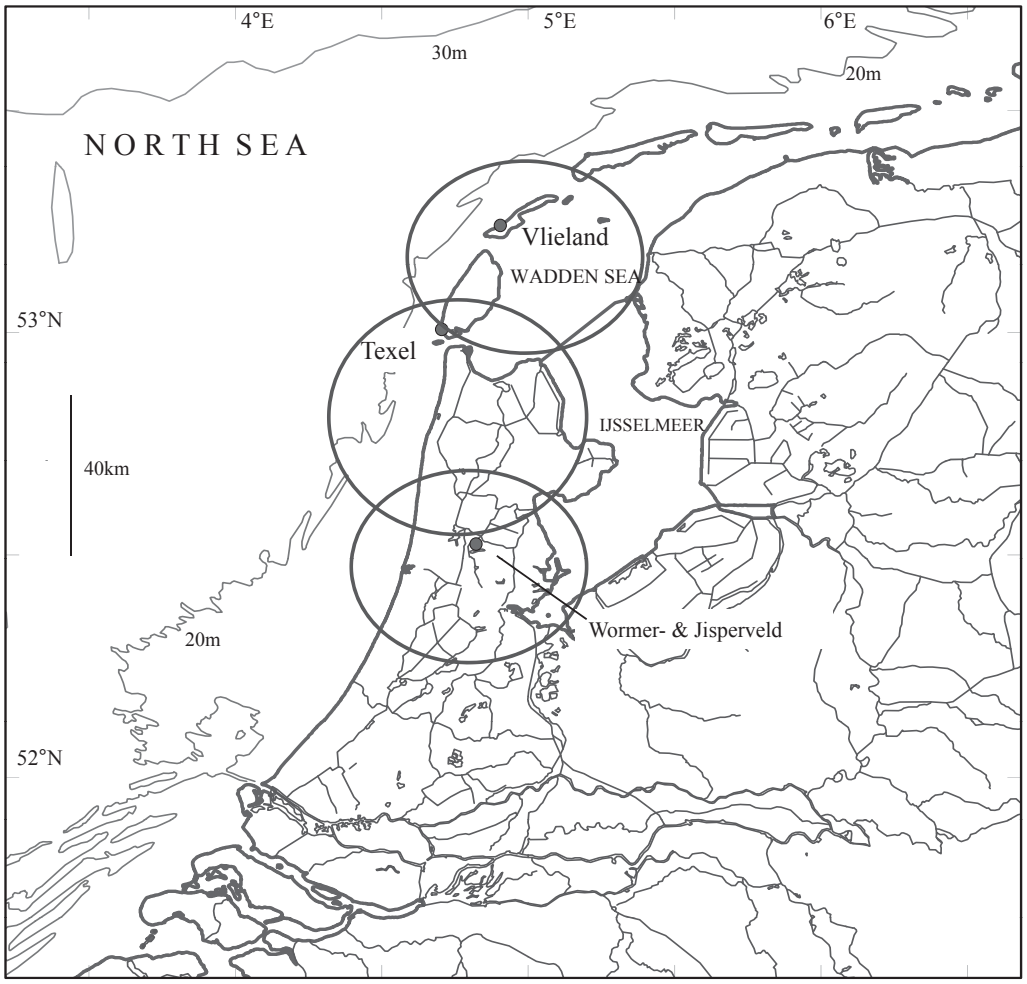

Figure 1. Presumed main foraging range based on colour-ring sightings of herring gulls and GPS positions of apparently foraging lesser black-backed gulls from Kelderhuispolder, Texel (central circle), based on Argos satellite tags) of herring gulls from Vlieland (top circle; for details, see: http://www.sovon.nl/default.asp?id=408), 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.

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 neither ringed nor tagged and there is therefore no empirical data to assess their foraging range. The frequent occurrence of marine fish, the

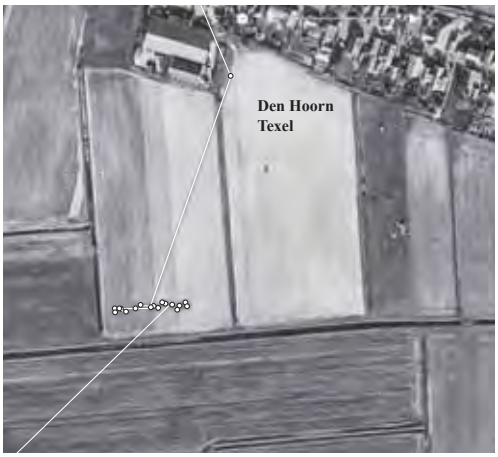

Figure 2. Foraging at (ploughed) agricultural land south of Den Hoorn, Texel of a lesser black-backed gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

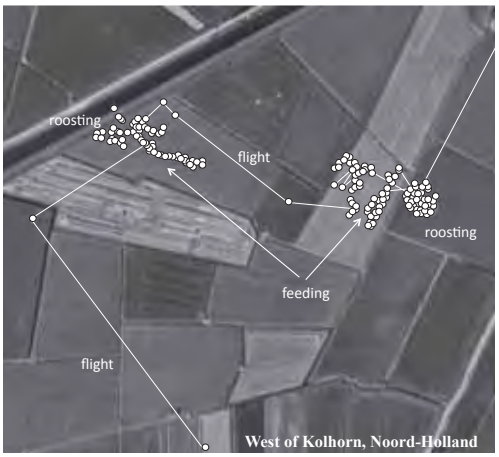

Figure 3. Foraging and roosting near Kolhorn, mainland Noord-Holland of a lesser black-legged gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads, white lines (not the arrows!) represent flights.

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), were 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

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

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 4) 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

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

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 indicative 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

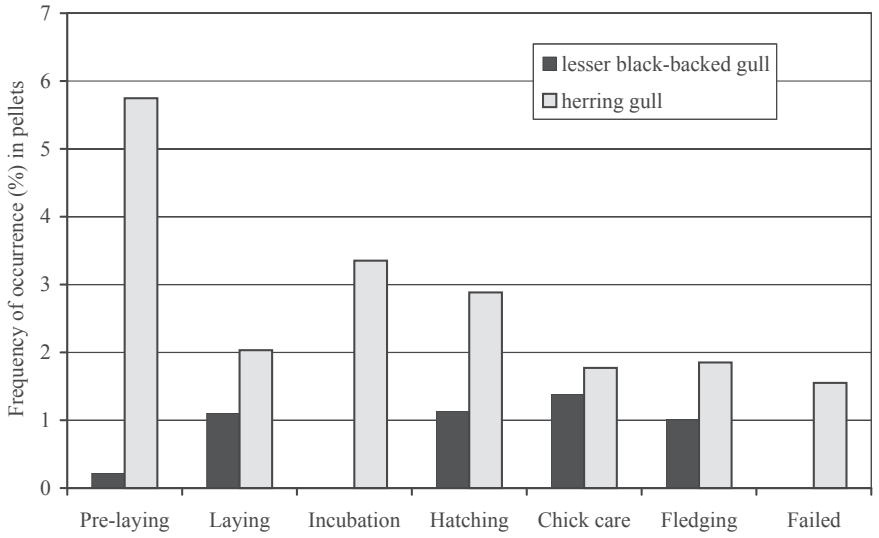

Figure 5. Frequency of occurrence (%) of mammalian prey through the breeding season in pellets and regurgitates collected from lesser black-backed gulls and herring gulls, Kelderhuispolder, Texel, 2006-2009.

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 4). 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 her-

ring 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.

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 prooidie-

ren 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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A preliminary investigation into whether grazing marsh is an effective refuge for water voles from predation

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Abstract: The water vole (*Arvicola amphibius*) has suffered a massive and rapid decline in the UK recently, due to habitat fragmentation and predation by American mink (*Neovison vison*). The spatial configuration of the habitat can mitigate the effects of predation on water vole colonies. In reed bed, mink predation rate declines with distance to a main channel. Over-winter mortality of water voles was monitored at an extensive grazing marsh site where mink were present to determine if this habitat provides a similar refuge from predation. Water vole mortality (74% by predation of which 71% by small mustelids) was significantly correlated with channel width and negatively correlated with distance to nearest scrub, suggesting that extensive grazing marsh can provide water vole with some refuge from predation.

Keywords: Arvicola amphibius, *Arvicola terrestris*, American mink, habitat refuge, wetland.

Introduction

The water vole (*Arvicola amphibius*) has suffered a massive and rapid decline in the UK in recent years (Strachan & Jefferies 1993, Jefferies 2003), attributed to the effects of habitat fragmentation and predation by introduced American mink (*Neovison vison*) (Barreto & Macdonald 1998, Barreto et al. 1998). It has been shown that the effects of mink predation on water vole colonies can be mitigated, in some circumstances, by the extent and configuration of habitat (Barreto et al. 1998). In pristine wetland in Belarus, Macdonald et al. (2002) reported that water vole abundance increased significantly with distance from the nearest river bank or lake shore, while the activity of American mink decreased. In the UK, Carter & Bright (2003) found that mink predation in extensive reed beds declined significantly with distance from water channels in excess of 10 m wide. One possible explanation was that mink and other terrestrial small mustelids are less active within reed beds and consequently less likely to encounter water voles there. Extensive grazing marsh with networks of ditches and channels of varying widths is another type of habitat that could potentially provide a partial refuge for water voles from predation by American mink. Habitat refuges offer a potentially sustainable, long term solution to water vole conservation and, by supporting source populations (Pulliam 1988), are likely to enhance the viability of water vole metapopulations in surrounding landscapes.

The objectives of the present study were to investigate over winter mortality of water voles at an extensive grazing marsh site where American mink were present, and to consider if any characteristics of this type of habitat reduce the level of mink predation on water voles.

Methods

The study was carried out at West Sedgemoor, Somerset, England (Ordnance Survey grid reference ST 361 238), a 584 hectare grazing marsh owned and managed by the Royal Society for the Protection of Birds.

Between October and November 2005 water voles were captured in live traps and capture locations recorded using a handheld GPS (Garmin Ltd., Romsey, Hampshire, UK) with a maximum error of ten meters. All animals heavier than 150 g were fitted with a radio collar (Biotrack, Dorset, UK) with a temperature-dependent mortality switch, which transmits an altered signal when an animal dies.

Radio collared water voles were located at twice weekly intervals from the commencement of trapping until February 2006 using hand-held Yagi antennae and Telonics radio receivers (Telonics, Mesa, Arizona, USA). Dead voles were retrieved and cause of mortality determined from a combination of field signs: tooth marks on collar and/or the corpse (Lyver 2000); predator hairs, scats or tracks in the immediate vicinity (Lawrence & Brown 1973); condition and location of the corpse. Predation was assigned to a small mustelid if the corpse was located within a water vole burrow which would be inaccessible to an avian or larger mammalian predator. Predation was only assigned to mink if there were mink scats or odour near a corpse, or canine punctures 9-11 mm apart on a water vole skull (Dunstone 1993).

To assess American mink activity at the site, mink rafts were placed approximately 1 km apart along main water courses within the reserve (Reynolds et al. 2004) and these were checked weekly. A systematic search was also carried out along smaller watercourses, tracks and linear features and all signs of mink activity were recorded.

Generalised linear models (McCullagh & Nelder 1983) were used to examine potential correlates of water vole survival. Explanatory variables considered were: site, distance from tree cover, distance from nearest scrub line, distance from 10 m channel, and width of channel along which each water vole's centre of activity was located. The binary response variable, whether an animal was predated or not, was offset by the number of weeks each vole was radio collared, since collars were not all first attached in the same week.

Results

A total of 39 animals were radio collared, of which 15 were captured less than 80 m from the main (>10 m wide) drainage channel, and the remainder were captured along small (≤5 m wide) ditches within the grazing marsh (table 1). Two animals absented within five days of being collared, so may have dispersed and were therefore removed from the dataset.

Predation accounted for nearly 74% of mortality; with confirmed small mustelid kills accounting for 71% of predation (table 2). Nine animals went missing after being monitored for several weeks, during which they remained at, or near, their original site of capture. It is unlikely that these adult voles would have dispersed out of radio receiver range (see Moorhouse et al. 2009) so it is most probable that they were also predated, but collars and any remains were not recovered. Following the protocol of Carter and Bright (2003), mortality was not assigned to American mink predation unless there was unequivocal evidence. In most cases in the present study the skull was absent or only partial remains were found, and scats were never found in the immediate vicinity, so there were no indisputable cases of mink predation. However the small mustelid category almost certainly includes at least some unverified mink kills. Signs of American mink were found at one of the mink rafts along the main channel and by a scrub line along a drove (track) nearby.

There was a significant difference in the minimum number of weeks alive between animals living less than 1500 m from a 10 m wide channel (9 ± 1.6) and those whose burrows were more than 1500 m from a 10 m wide channel (16 ± 1.5) (Mann-Whitney U test: Z=-2.205, n_1=15, n_2=22, P=0.027). In a generalised linear model, although the total deviance explained was relatively low,

Table 1. Width of channel and distances to main channel and scrub for each radio-tracked animal's home burrow/ centre of activity.

Animal	Channel width (m) on which home burrow located	Distance (m) to nearest 10 m wide channel	Distance (m) to nearest scrub
1	5.0	69.9	133
2	5.4	68.4	17.5
3	5.5	76.3	378
4	5.2	68.8	70
5	5.4	73.2	293
6	5.1	72.2	265
7	5.1	69.5	98
8	5.1	68.6	22.5
9	5.4	72.0	265
10	5.4	76.7	378
12	5.0	72.4	249
13	2.7	78.9	451
15	2.4	68.2	332
16	2.4	1700	383
17	2.4	1720	348
18	2.4	1630	434
19	2.4	1630	434
20	5.0	1320	742
21	2.4	1630	432
22	2.4	1640	396
23	2.4	1700	383
24	3.2	1570	485
25	5.0	1570	485
26	3.3	1600	442
27	2.4	1800	257
28	1.6	2300	126
29	1.6	2200	124
30	1.4	2200	117
31	1.3	2000	129
32	1.8	2100	84
33	5.0	1560	425
34	4.2	1630	425
35	4.2	1640	434
36	1.8	2200	117
37	3.2	1590	465
38	4.1	1390	662
39	1.4	1480	317

water vole mortality from predation was significantly correlated with channel width and negatively correlated with distance to nearest scrub (table 3). There were no significant interactions between either of the explanatory variables.

The predicted probability of mortality from predation for water voles in the present study

Table 2. Summary of water vole survival at West Sedgemoor (near = burrow <1500 m from main channel; far = burrow ≥1500 m from main channel).

	Near	Far	Total
Surviving	2	7	9
Predated *)	4 (4)	10 (6)	14 (10)
Other mortality	2	3	5
Missing	7	2	9
Total	15	22	37

*) in brackets: by small mustelids

increases as the width of channel on which their burrow/centre of activity is located increases (figure 1).

Discussion

The results of the present study suggest that some features of extensive grazing marsh have the potential to provide water voles with, at least a partial refuge from predation. There are a number of potential mechanisms for this effect. Spatial refugia can be areas which are not used at all by a particular predator because the habitat physically excludes or deters them (Gause et al. 1936, Atsatt & Odowd 1976). It is unlikely that this is the case for mink along small ditches in grazing marsh. In reed bed habitat, American mink are constrained to easily navigable channels (MacPherson 2010), probably because the interstitial habitat is energetically costly to move through. The terrestrial gait of American mink has been described as "scampering" (Dunstone 1993), and this is difficult to do amongst dense reed. The most efficient way for mink to traverse this type of habitat is by swimming underwater, as this has been estimated to be up to ten times less energy demanding than surface swimming (Williams 1983). This is only achievable in wider, deeper channels.In grazing marsh the flat, open terrain between channels and ditches is more easily navigable, however American mink show a strong avoidance of open areas (Gerell 1970, Dunstone 1993, Previtali et al. 1998, Yamaguchi et al. 2003) where they may be vulnerable to predation by foxes and dogs (Bonesi & Macdonald 2004). Mink escape by diving when attacked by predators and usually rest near deep water so as to have access to an escape route (Zabala et al. 2007b). Narrower ditches and channels may not provide sufficient depth of water for this to be effective. Habitat features that increases the risk to the predator, reducing the predator's activity, may provide prey with a spatial refuge (Brandt & Lambin 2007).

American mink foraging is usually restricted to the vicinity of den and suitable resting sites (Birks & Linn 1982). Therefore the distribution and availability of such sites is likely to be a significant factor in determining if and where mink forage in grazing marsh. This should be considered when assessing potential refuges for water voles in this type of habitat. It has been suggested that American mink use a small range of structures that allow for efficient foraging and ranging, and that lack or removal of these structures could render areas of abundant food effectively useless to mink (Zabala et al. 2007b).

Mink hunting behaviour is characterised by a fairly rigid suite of behaviours (Dunstone 1993). The most common is a detailed search-stalking behaviour in bramble thickets or areas of rank undergrowth. In more open areas American mink have been observed to move quickly along riverbanks stopping occasionally with raised heads to detect prey (Zuberogoitia et al. 2006). Dive rates are highly variable between individual mink (Hays et al. 2007) and diving as a hunting technique is thought to be related to high availability of a particular prey (Zuberogoitia et al. 2006). However it is unlikely that mink will hunt by pursuing its prey in vegetated waters with poor visibility and where mink cannot be fast enough. On smaller, undisturbed channels, submerged and emergent vegetation will provide water voles with refuges from predators (Barreto et al. 1998). It may also be the case that the observed refuge effect of narrow

Table 3. Generalised linear model examining water vole mortality from predation (n=37, of which $n_{predated}$=14) at West Sedgemoor (response variables in GENSTAT: binomial errors, logit link) offset by the number of weeks each animal was radio collared. Parameter estimates and s.e.s are in logits.

Explanatory variable	Parameter estimate	s.e.	Deviance	χ^2 probability
Constant	-26.236	0.418		
Nearest scrub	-0.00509	0.00108	12.35	<0.001
Channel width	2.007	0.111	16.24	<0.001
			Total deviance explained:	27.3%

ditches and channels results from the likelihood that they will be visited less frequently by mink, as they support a lower abundance and variety of prey species (Dunstone 1993).

Whilst there were no indisputable cases of American mink predation, more than 70% of predation on water voles during the course of the study was unequivocally attributable to small mustelid, which could include Western polecat (*Mustela putorius*), American mink, stoat (*Mustela erminea*) and weasel (*Mustela nivalis*). Polecats are not present but there was evidence of mink, weasel and stoat at the site.

Small mustelids, including American mink, frequently forage along linear features, and mature trees have been shown to be important as den sites for American mink (Halliwell & Macdonald 1996). This is why distance from track and nearest tree were also considered as potential explanatory variables. However, removal of these from the model did not significantly reduce the amount of deviance explained.

A limitation of using field signs to detect mink presence is that they provide no information on the age or sex of the animal(s). On a river system, Zabala et al. (2007a) found that female American mink preferred smaller streams than males, although the home range of females still included sections of the main (>10 m wide) river, usually at its junction with the tributary. It has also been shown that, in warm seasons, mink sometimes occupy marsh habitat some distance from stream banks (Sidorovich et al. 2001), so it may be that the partial refuge effect, observed here over winter, is seasonal. Further study is required to determine if this is the case.

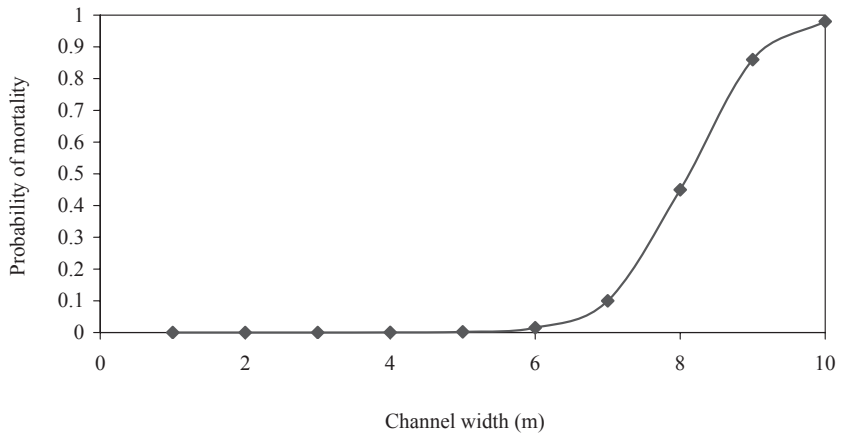

Figure 1. Predicted risk of water vole mortality from predation in relation to the width of channel on which a home burrow/centre of activity is located. Line represents the fitted relationship from a generalized linear model.

Conclusion

In conclusion, the rate of predation on water vole in the present study was observed to be lower on narrower ditches in grazing marsh than along the wide main channel. It is recommended that further research should be conducted to determine if this is the case throughout the year and at other similar sites, both with and without mink.

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Samenvatting

Een voorlopig onderzoek naar de betekenis van begraasd moerasland als effectief toevluchtsoord voor de woelrat tegen predatie

De woelrat (*Arvicola amphibius*) is recentelijk in het Verenigd Koninkrijk sterk en snel achteruitgegaan, met name door versnippering van het leefgebied en predatie door de Amerikaanse nerts (*Neovison vison*). De ruimtelijke structuur van het leefgebied zou deze predatie mogelijk kunnen verminderen. In rietlanden neemt de predatie af naarmate de afstand tot de hoofdwatering toeneemt. Om na te gaan of (extensieve) begrazing van rietland, waar naast de woelrat onder meer ook de Amerikaanse nerts voorkomt, een geschikte maatregel is om eerstgenoemde soort te beschermen, werd de mortaliteit van de woelrat gedurende de winter in zo'n begraasd gebied vastgesteld. Het blijkt dat de mortaliteit (74% door predatie en van deze predatie 71% door kleine marterachtigen) positief significant gecorreleerd is met de breedte van de meest nabije waterloop en negatief met de afstand tot het dichtstbijzijnde struikgewas. Dit suggereert dat begrazing van rietland metterdaad voor de woelrat enig soelaas kan bieden tegen predatie.

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Hibernating bats in the Schenkgroeve, an artificial limestone cave in south Limburg, the Netherlands

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Abstract: Between 1944 and 2010, sixty-one yearly winter bat surveys were carried out in the Schenkgroeve, a man-made, now abandoned, underground limestone excavation in Meerssen, in the south of the Province of Limburg, the Netherlands. This cave is divided into two separate parts, each with a different microclimate. The front part houses the majority of hibernating bats and is the focus of this paper. Over a period of 67 years, the numbers of hibernating bats of ten different species have changed considerably, although some general trends can be recognised. Because the census has had different objectives over the years, our evaluation of the census data is separated into three time periods: 1944-1959 (period A), 1960-1979 (period B) and 1980-2010 (period C). In period A bat banding was the main goal and this and other human disturbance led to a decline in numbers of lesser horseshoe bat (*Rhinolophus hipposideros*), Geoffroy's bat (*Myotis emarginatus*) and greater mouse-eared bat (*Myotis myotis*), while the number of other species such as Daubenton's bat (*Myotis daubentonii*), pond bat (*Myotis dasycneme*), whiskered/Brandt's bat (*Myotis mystacinus/brandtii*), Natterer's bat (*Myotis nattereri*) and brown/grey long-eared bat (*Plecotus auritus/austriacus*) remained more or less constant. In this period an average number of 70.3 bats per year were found, although between the years 1954 and 1959 the average was only 50.7 bats. In period B, when the main goal was to study the hibernation position of the bats in relation to climatic factors, the mean number of observed hibernating bats stayed at a low level of 62.8 bats per year. At the end of this period only Daubenton's bat showed a slight increase. In the beginning of 1980 an iron gate was installed. The number of Natterer's bats and Geoffroy's bats and, to a lesser extent, Daubenton's bats increased, while other species such as whiskered/Brandt's bats, pond bats and long-eared bats showed no significant changes in number. The average annual number of hibernating bats during period C increased to 198.0 bats. Between 1980 and 2010, the index of the number of bats hibernating in the Schenkgroeve increased almost seven fold. We discuss possible factors that may have influenced changes in the numbers of different species over the years. The reasons for the decline in bat numbers in periods A and B include the excessive banding of bats in period A and the effects of mushroom culture. Both are generally thought to have negatively affected bat numbers in the Schenkgroeve and other caves in Limburg. We can only speculate about the causes of the spectacular positive trends in more recent years, especially for Geoffroy's and Natterer's bat in period C, a phenomenon also observed in other hibernacula in Limburg. We recommend continuation of annually monitoring the bats hibernating in the Schenkgroeve, which is one of the most important hibernacula in Limburg and the Netherlands.

Keywords: bats, Schenkgroeve, limestone excavation, hibernation, winter quarters, bat counts, trends, banding, monitoring.

Introduction

The artificial limestone caves in the south of the Province of Limburg are very important hibernating quarters for bats in the Netherlands, and are nowadays used by at least ten species (Glas 1986, Weinreich 1992, Dijkstra et al. 2006, Verboom 2006). Most of these underground marl quarries are surveyed annually in winter as part of a national monitoring programme, which includes all known hibernation sites in the Netherlands. One of these caves is the Schenkgroeve, which is

located near the village of Meerssen in the south of the Province of Limburg and is generally considered one of the most important hibernation sites in Limburg, and in the Netherlands (Verboom 2006).

Due to their outstanding importance for hibernating bats, many of the marl excavations in south Limburg have been included in four Natura 2000 sites. These areas have been designated as Special Areas of Conservation (SACs) primarily to protect three bat species, the pond bat (*Myotis dasycneme*), the greater mouse-eared bat (*M. myotis*) and Geoffroy's bat (*M. emarginatus*). The Schenkgroeve is part of the 'Geuldal' Natura 2000 site together with 20 other (parts of) underground marl quarries (see http://www.natura2000beheerplannen.nl/pages/geuldal.aspx).

Monitoring bat populations in their winter roosts is still recognised as one of the best available methods to gather reliable information on population trends. This information is needed to assess the status of bat species so that conservation measures (required under both national and European legislation) can be formulated. This paper provides such data for the Schenkgroeve, presenting the results of winter surveys of hibernating bats in this cave for a period of 67 years. It also provides an overview of the different methods and objectives of winter surveys over the years and their implications for the interpretation of results. General trends will be discussed in an attempt to understand the possible causes underlying the fluctuations in numbers.

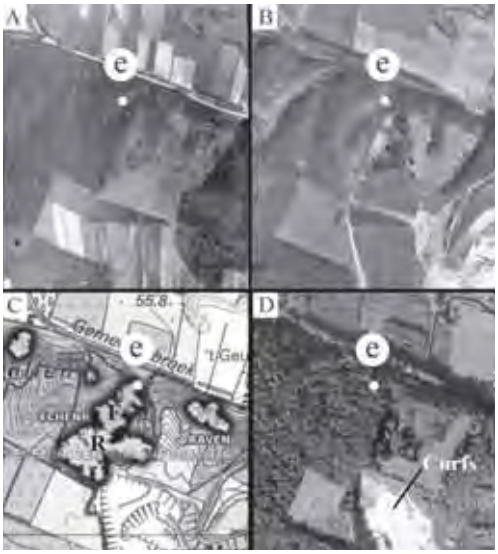

Figure 1. Location of the Schenkgroeve as shown in 1944 (A), 1961 (B) and today (C and D). F: front part of the cave; R: rear part of the cave; e = position of the entrance; 'Curfs' is the open marl pit named after the company. Courtesy of E. Stevenhagen (Stevenhagen Geo Informatica).

Material and methods

Description of the site

The entrance to Schenkgroeve is situated on the southern slope of the valley of the river Geul, south of the village of Meerssen (figure 1). Since 1976 it has been owned and managed by the *Limburgs Landschap Foundation*. The cave system (first explored in 1742) consists of a large number of corridors that have irregularly been excavated for limestone and now form a large labyrinth. The heights of the corridors vary from 2–4.5 m, with an average of 3 m (Stevenhagen 1997). In the 1950s, the Schenkgroeve was found to have a static cold climate, with the air being layered in winter (ter Horst & van Nieuwenhoven 1958). There is no reason to suspect any significant climate change since then. The air is almost totally saturated with water vapour which often condenses on hibernating bats (figure 2). Because the Schenkgroeve has only one entrance it is protected from the external environment and both humidity and temperature are buffered against rapid changes outside the cave.

The Schenkgroeve consists of two separate parts, a front section and a rear section (F and R in figure 1C). The two sections are divided by a limestone wall with an opening of approximately 1 m^2. This separation (S in figure 3) is not only a physical barrier between the two labyrinths, it also acts as climatic bar-

Figure 2. Natterer's bat in the Schenkgroeve covered with dew. *Photograph: Bernadette van Noort.*

Figure 3. Map of the front section of the Schenkgroeve in Meerssen (south Limburg). R = Rear part of the cave. S = Separation between front and rear section.Courtesy of E. Stevenhagen (Stevenhagen Geo Informatica).

rier: the temperature is higher in the rear section of the cave and there is less circulation of air (ter Horst & van Nieuwenhoven 1958). The use of explosives in a nearby quarry (Groeve Curfs, figure 1D) in the late 1940s and 1950s has left the western part of the rear section of the cave in an unstable and disorderly state. Most of the corridors here are covered with large fragments of marl that have fallen from the walls and ceiling. As a result of the unsafe conditions the rear part of the cave is rarely visited or inspected for hibernating bats. During the few visits that have taken place, only a few bats were recorded in this section. This data review does not cover the rear part of the Schenkgroeve, but we do not expect that this omission will reflect on the conclusions to be drawn in this paper.

By contrast, the corridors in the front part of the cave are tidy. On the west side, just before reaching the cave entrance, there is a small isolated system of corridors that once was connected to the main system (Bels 1952). In this paper it is considered part of the main system without further specification.

A section of the front part of the cave was intermittently used after the Second World War for growing mushrooms. These corridors were used between 1952 and 1954, but infections from mites and parasitic fungi and a lack of knowledge on how to solve this problem led this enterprise to be abandoned.

In this article we use the name Schenkgroeve, based on Bels (1952) and van Wijngaarden (1967), but the site is also referred to as 'Groeve Schenk' or 'Meerssener Groeve'. Walschot (2002) used the name 'Schenckgroeve', following official documents. Stevenhagen (1999) marks the cave as '77 (id E160)'.

Survey methods

Bat surveys in the Schenkgroeve have been carried out since 1944. In the early days of bat research in the Netherlands, hibernating bats were collected for banding in order to determine the number and diversity of the bat species in the caves. The migration and recovery of individuals that were sometimes

moved over long distances from the original banding location were studied, as well as changes in the population density, diversity and longevity of bats (Bels 1952). For these purposes, researchers collected as many bats as possible. The cave ceiling and walls were searched for bats which could be easily collected, while deep crevices, fissures and clefts were mostly overlooked, making the observations in those years very incomplete. The cave was inspected superficially mainly with kerosene lamps (e.g. Tilley®) and flashlights. Carbide lamps were occasionally used. Ir. D.C. van Schaïk, who acted as a guide, sometimes visited the caves prior to these bat collections to identify 'empty' corridors. This meant that only the most visible and obtainable bats were collected. A plan of the cave was not available at this time, so sections of the cave might have also been overlooked.

From 1960 onwards, the research objectives and survey methods changed. After 1960 bats were no longer handled and identification was done by visual appearance. In this period brighter flashlights and more powerful kerosene lamps were used. In 1980 the Schenkgroeve entrance was closed with a solid iron gate to prevent local people from entering the cave and disturbing the hibernating bats. From this time onwards more powerful flashlights were used to search for the bats. From 2005 on digital photography, bright (and durable) LED lights and binoculars were also used to identify bats.

Since the methods and the objectives changed over the years, data for the different time periods is not comparable and can not be used together to establish population sizes and trends. The data presented in this paper are therefore split into three different time periods: period A, from 1944 until 1959, representing the beginning of bat research in the Schenkgroeve (and other caves) by Bels, period B, from 1960 until 1979, and period C, from 1980 until 2009. The data used in this paper is drawn from the database of the Dutch Mammal Society, and was collected by researchers and by volunteers, including the authors. All the counts used in this paper were done in December and January, when hibernating populations are fairly constant (Daan 1973).

Trend analyses

Trends in bat populations are generally measured by one of three broad techniques: surveys of foraging areas, hibernacula counts or summer roost counts. Counts of hibernating bats may be suitable for species that are loyal to hibernacula (Daan 1980, Veith 1996). Trend analyses of these counts have been calculated using TRIM (Statistics Netherlands, The Hague / Heerlen, the Netherlands). Since systematic counts were only performed from 1980 onwards, we used 1980 as the starting date for the trend analyses. Population growth rates were calculated by $N_t = N_0 e^{rt}$, where 'N_t' represents the population size at time t, 'N_0' represents the initial population size (here 1980), 'e' stands for the base of the natural logarithm (approximately 2.71828), 't' represents the time period (here in years), and 'r' refers to the growth rate per year.

Bat censuses from 1944 till 2010

Period A: 1944 – 1959

In 1937 Bels started bat banding in the artificial limestone caves in southern Limburg. His research represented the beginning of ecological bat research in the Netherlands. During this period ten different bat species were found hibernating in the Schenkgroeve, including the rare barbastelle (*Barbastella barbastellus*) and the lesser horseshoe bat (*Rhinolophus hipposideros*), which was still rather common at that time (Bels 1952). While the barbastelle only occurred irregularly over the years and in very small numbers (one or two specimens) in the entrance section to the Schenkgroeve, a total number of 131 lesser horseshoe bats were banded with aluminium rings in

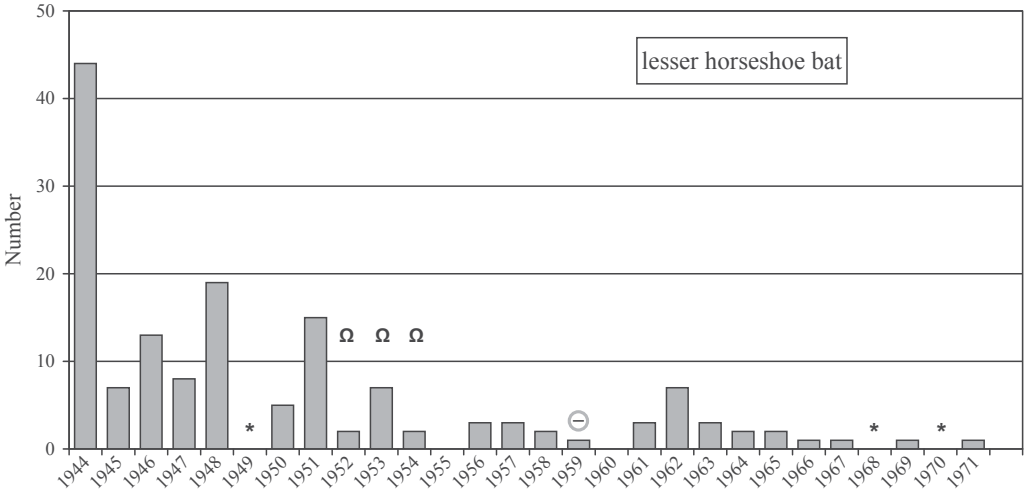

Figure 4. Number of hibernating lesser horseshoe bats in the Schenkgroeve. * = no census in that year. Ω = mushroom culture; ⊖ = end of bat banding.

this period. Between 1940 and 1950 the lesser horseshoe bat was the most numerous bat species hibernating in subterranean limestone quarries in the south of the Province of Limburg and in Belgium (Voûte & Glas 1992, van Vliet & Mostert 1997). Bels (1952) first visited the Schenkgroeve in 1944 and banded 44 lesser horseshoe bats. In the following years, the numbers counted and banded varied but, on average, decreased (figure 4). After 1951 the number of lesser horseshoe bats counted in the Schenkgroeve never exceeded seven specimens. Bels' banding studies in the marl quarries of Limburg indicated that the site fidelity, expressed as the percentage of bats recaptured in the following year, of hibernating lesser horseshoe bat (69.4%) was relatively low compared to other species (85.2-97.7%). As pointed out by de Wilde and van Nieuwenhoven (1954) this species shows a marked sensitivity to tactile stimuli and air currents, which makes the lesser horseshoe bat vulnerable to human disturbance. The last record of a hibernating lesser horseshoe bat in the Schenkgroeve was in 1971. Bat banding, as performed by Bels and others, is thought to have influenced the number of hibernating lesser horseshoe bats (Sluiter and Van Heerdt 1957) whose numbers also declined in other limestone caves in south Limburg (Voûte et al. 1980, Voûte & Glas 1992).

Besides the lesser horseshoe and barbastelle bats, seven to nine other species were found hibernating in the Schenkgroeve in this period: including greater mouse-eared bat, pond bat, Daubenton's bat (*Myotis daubentonii*), Geoffroy's bat, Natterer's bat (*M. nattereri*), whiskered bat (*M. mystacinus*) and/or Brandt's bat (*M. brandtii*) and brown long-eared bat (*Plecotus auritus*) and/or grey long-eared bat (*Plecotus austriacus*). Brandt's bat was only identified as a separate (closely related) 'sibling species' from whiskered bat in 1970 (Hanák 1970, Baagøe 1973), so there are no records of this species in period A. The identification of living whiskered bats, especially young individuals and females, is difficult, and can only reliably be done by using characters of the dentition and the shape of the penis (Hoogenboezem 1982, Schober & Grimmberger 1987, Dietz & von Helversen 2004), which would require handling. Since bats were not handled during the censuses after period A, we have no reliable data on the presence of Brandt's bat in the Schenkgroeve, and indicate the species as 'whiskered/

Table 1. Number of hibernating bats in the Schenkgroeve 1944-2010. h = lesser horseshoe bat; Bb = barbastelle bat; My = greater mouse-eared bat; da = pond bat; m = whiskered/Brandt's bat; d = Daubenton's bat; n = Natterer's bat; e = Geoffroy's bat; p = long-eared bat; i = species unknown. SUM = total number of bats; AVG = average, COUNT = number of years recorded.

Year	h	Bb	My	da	m	d	n	e	p	i	SUM	period
1944	44	2	18	19	35	7	16	37	7		185	A
1945	7		5	7	11	3	4	20	1		58	A
1946	13	1	16	10	16	2	5	15	4	1	83	A
1947	8		6	8	11	2	4	15	4		58	A
1948	19		4	7	22	4	8	30	4		98	A
1949												no census
1950	5		2				2	1			10	A
1951	15	1	9	21	26	6	6	13	5		102	A
1952	2		3	13	10	6	5	13			52	A
1953	7	2	5	13	24	12	23	11	8		105	A
1954	2	1	2	5	3	2	4	9	1		29	A
1955			4	10	10	8	8	10	3		53	A
1956	3		1	6	12	9	6	3	3		43	A
1957	3		2	13	17	5	8		2		50	A
1958	2		2	7	31	6	4	1	5		58	A
1959	1	1	2	12	25	10	11		8	1	71	A
1960		2		8	28	18	7	2	3		68	B
1961	3		1	11	24	8	2	1	4		54	B
1962	7	2	2	6	23	10	7	1	3		61	B
1963	3	2	3	7	12	10	7		5		49	B
1964	2	1	3	13	21	7	2		4		53	B
1965	2	2	7	19	21	18	4		5		78	B
1966	1		3	16	11	10	1		4		46	B
1967	1		4	12	25	12			4		58	B
1968												no census
1969	1	1	5	33	22	15	2	1	1		81	B
1970												no census
1971	1		1	9	26	28			1		66	B
1972												no census
1973		1	3	9	24	31		3		2	73	B
1974												no census
1975			2	5	17	28		2	4	2	60	B
1976				5	17	35	2	1		1	61	B
1977				4	16	25	1	3			49	B
1978				4	17	34	2	1	1	5	64	B
1979				9	19	41	2	2	1	10	84	B
1980				10	19	41	1	2	1	11	85	C
1981			1	8	22	43	2		1	12	89	C
1982			1	9	29	49	7	1	1	18	115	C
1983			1	11	19	71	7	2	2	18	131	C
1984			2	7	11	63	1		2	8	94	C
1985			1	9	18	45	2	2		13	90	C
1986			1	8	24	44	13		1	8	99	C
1987			1	8	32	58	10	1	2	7	119	C
1988			1	6	34	65	8	5	3	6	128	C
1989			2	5	24	74	10	5	1	10	131	C
1990			1	2	37	66	8	3	1	4	122	C
1991				2	23	53	10	4		5	97	C
1992				5	37	52	16	2		8	120	C
1993			1	9	30	99	20	6		7	172	C
1994				6	28	88	34	6	2	15	179	C
1995			1	9	28	44	46	13	2	5	148	C
1996				6	30	55	42	15	2	13	163	C
1997				1	31	53	44	11		13	153	C
1998				4	18	61	73	11	1	16	184	C
1999				5	31	65	82	16		3	202	C
2000				2	33	38	61	21	2	7	164	C
2001				4	23	46	48	31			152	C
2002				0	19	56	112	43	1	7	238	C
2003				3	30	57	90	44	1	6	231	C
2004				5	24	59	98	56	2	10	254	C
2005				18	30	79	151	70	2	8	358	C
2006				12	23	77	190	73	4	12	391	C
2007												no census
2008				14	32	73	277	93		9	498	C
2009			3	22	33	80	247	112	3	12	512	C
2010			2	12	27	60	291	116	1	11	520	C
	152	19	134	543	1375	2226	2154	959	133	304	7999	SUM
	6.6	1.5	3.4	9.1	22.9	37.1	37.8	19.2	2.8	8.4	131.1	AVG
1944-2010	23	13	40	60	60	60	57	50	48	36	61	COUNT

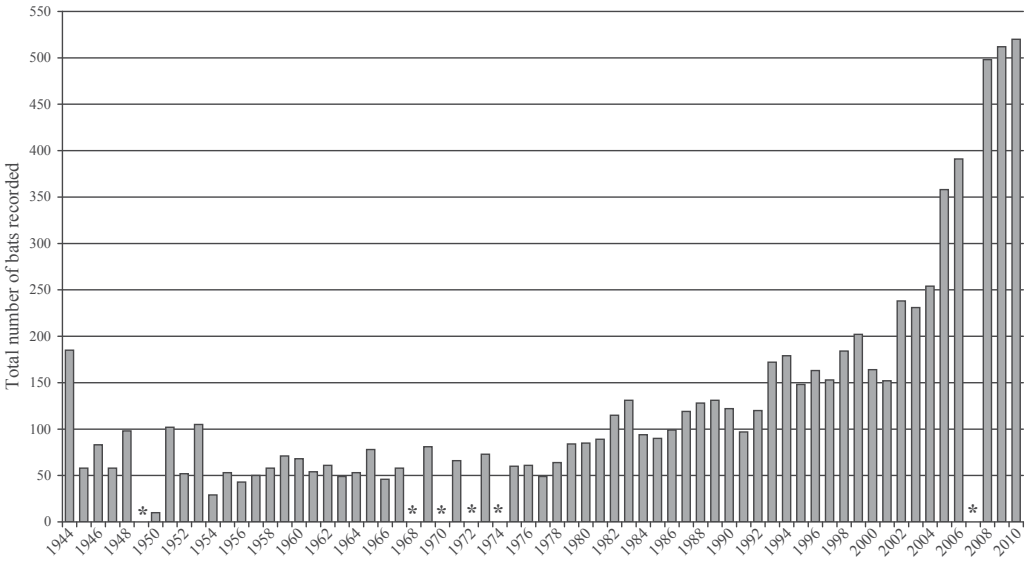

Figure 5. Total number of bats recorded in the Schenkgroeve 1944-2010. * = no census in that year.

Brandt's bat (*Myotis mystacinus/brandtii*)' in this paper. A similar situation applies for the brown long-eared bat and the grey long-eared bat, which are simply indicated here as 'long-eared bat (*Plecotus auritus/austriacus*)'.

The number of hibernating bats in nearly all limestone caves in south Limburg decreased rapidly during the 1940s and 1950s and then stabilised in the 1970s (Voûte et al. 1980). Sluiter and van Heerdt (1957) suggested increased economical exploitation (limestone exploration, mushroom culture and tourism) as a possible cause of the decline of the bat population in the caves between 1942 and 1957. Bat banding was also thought to have had a detrimental influence on the number of hibernating greater mouse-eared bats, Geoffroy's bats and lesser horseshoe bats, which showed overall declines of 80%, 85% and 81% respectively (Sluiter & van Heerdt 1957). In 1944 a total of 99 specimens of these three species were found, while in 1959 the number decreased to a total of three specimens (table 1). It is suggested that these three species are more sensitive to the disturbances described above than long-eared bats and other *Myotis* species. The hibernation periods of these three species end later than those of other species in the Schenkgroeve and disturbances during the winter months, which cause a loss of body weight, may have more serious consequences (van Nieuwenhoven 1956). Lesser horseshoe bat*s* and Geoffroy's bats typically hang free on walls and ceilings making them more vulnerable than species that hide in deep crevices. In the greater mouse-eared bats the decline in numbers might also be ascribed to ring-related mortality. These bats were quite often recaptured with seriously injured forearms as a consequence of them biting on their ring. For these reasons, the research group of the Zoologisch Laboratorium of the Utrecht University stopped banding these three bat species in 1955. From 1956 until 1958 banding was restricted to the pond bat, Daubenton's bat, whiskered/Brandt's bat and Natterer's bat. In 1959 it was decided to stop all banding activities in south Limburg (Daan 1980). From this year on bats were identified *in situ* without handling the individuals. In case of disagreement about the identification of the species, however, bats were still collected, and so were the banded specimens. Because of better lighting equipment bats that were

previously hardly visible, because they were situated deep in crevices, were now counted. If they could not be identified correctly they were noted as 'species unknown', resulting in a more systematic and complete count.

The number of hibernating bats in the Schenkgroeve declined from 185 in 1944 to 71 in 1959 with a record low in 1950 when only 10 specimens were found (table 1; figure 5). This low count followed a year (1949) when the cave was heavily polluted with smoke and was not visited. When the cave was used for mushroom culture in 1952 and 1954, only 52 and 29 bats were found (respectively), suggesting that this activity also had a negative influence on hibernating bats.

In period A, lesser horseshoe bats, Geoffroy's bats and greater mouse-eared bats showed a significant decline, whereas the number of pond bats, whiskered/Brandt's bats, Natterer's bats and long-eared bats remained more or less stable, their numbers averaging 10.8, 18.1, 7.6 and 4.2 respectively. The number of Daubenton's bats showed a slight increase in this period, averaging 5.9 bats per year. In period A an average of 70.3 bats per year were found. In the latter part of this period (1954 to 1959) this average declined to 50.7 bats per year. The most abundant species in the Schenkgroeve was the whiskered/Brandt's bat, which accounted for 24.0% of the bats found over these years, followed by Geoffroy's bat (16.9%), pond bat (14.3%), lesser horseshoe bat (12.4%) and Natterer's bat (10.8%). Daubentons bat and the greater mouse-eared bat were relatively scarce, accounting for 7.8% and 7.7% respectively (table 2).

Table 2. Relative abundance of different species in the Schenkgroeve in percentages over the years 1944–1959 (period A), 1960-1979 (period B) and 1980-2009 (period C).

	1944-1959	1960-1979	1980-2008
lesser horseshoe bat	12.4	2.1	0.0
barbastelle	0.8	1.1	0.0
greater mouse-eared bat	7.7	3.4	0.3
pond bat	14.3	16.9	3.7
whiskered/Brandt's bat	24.0	32.1	13.5
Daubenton's bat	7.8	32.8	30.5
Natterer's bat	10.8	3.9	33.7
Geoffroy"s bat	16.9	1.7	12.9
long-eared bat	5.2	4.0	0.6
species unknown	0.2	2.0	4.7

Period B: 1960 – 1979

This period was a time of more intensive and systematic searching for bats, partly due to an awareness of a serious decline in bat numbers over previous years. Despite this, bat numbers in the Schenkgroeve remained at a similar level, with an average of 62.8 bats per year. The average (and relative) number of whiskered/Brandt's bats increased in this period, to an average of 20.2 per year, as did the number of Daubenton's bats which increased to an average of 20.6 bats per year. Together the two species accounted for almost two-thirds of bats found in the Schenkgroeve, whereas the lesser horseshoe bat and Geoffroy's bat contributed only 2% of the total number count. Only 21 lesser horseshoe bats and 17 Geoffroy's bats were recorded in period B, with averages of 2.3 and 1.7 bats respectively per year. There was no significant change in the average numbers of long-eared bats and barbastelle bats. The average number of pond bats in period A was identical to that in period B (10.6 bats/year). In contrast to period A when no unidentified bats were found, 2.0% of the bats could not be identified in period B (table 2), probably due to an increase in search effort.

Period C: 1980 – 2010

As a result of the rapid decline in numbers of most bat species found hibernating in the 1950s, 1960s and 1970s, which was especially pronounced in the limestone caves in Lim-

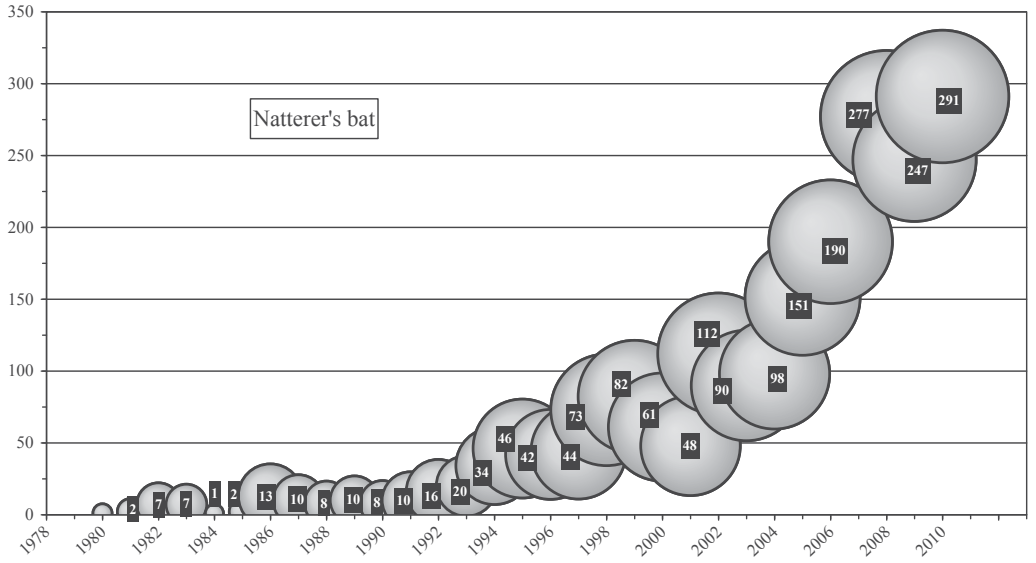

Figure 6. Number of Natterer's bats in the period 1980-2010. The diameter of the circle represents the number of Natterer's bats in relation to the total number of bats found in that year.

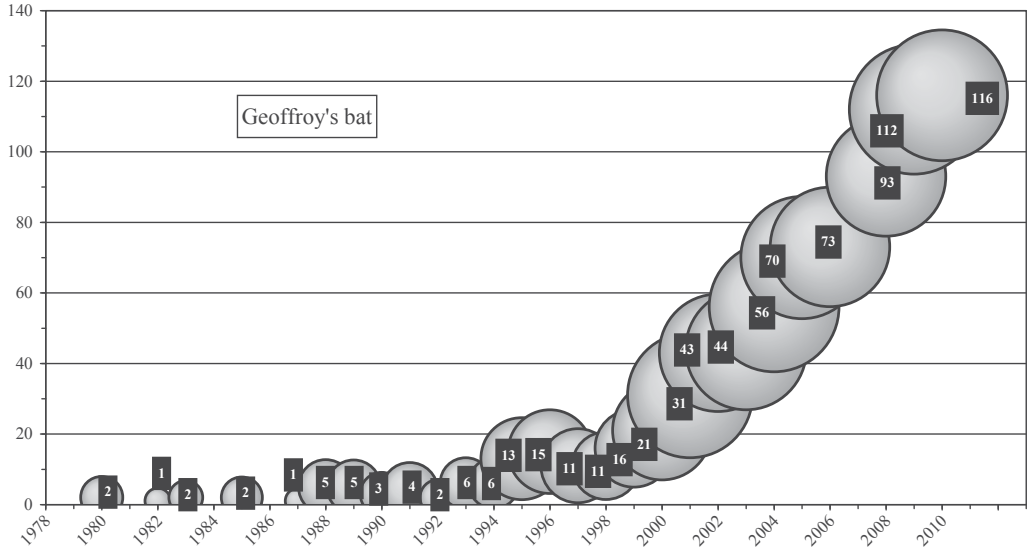

Figure 7. Number of Geoffroy's bats in the period 1980-2010. The diameter of the circle represents the number of Geoffroy's bats in relation to the total number of bats found in that year.

burg (Daan 1980), all bats became legally protected in the Netherlands in 1973, making it illegal to catch or kill bats. Efforts were made to reduce disturbance to the bats hibernating in the Schenkgroeve, including installing a locked iron grille that allowed bats to enter

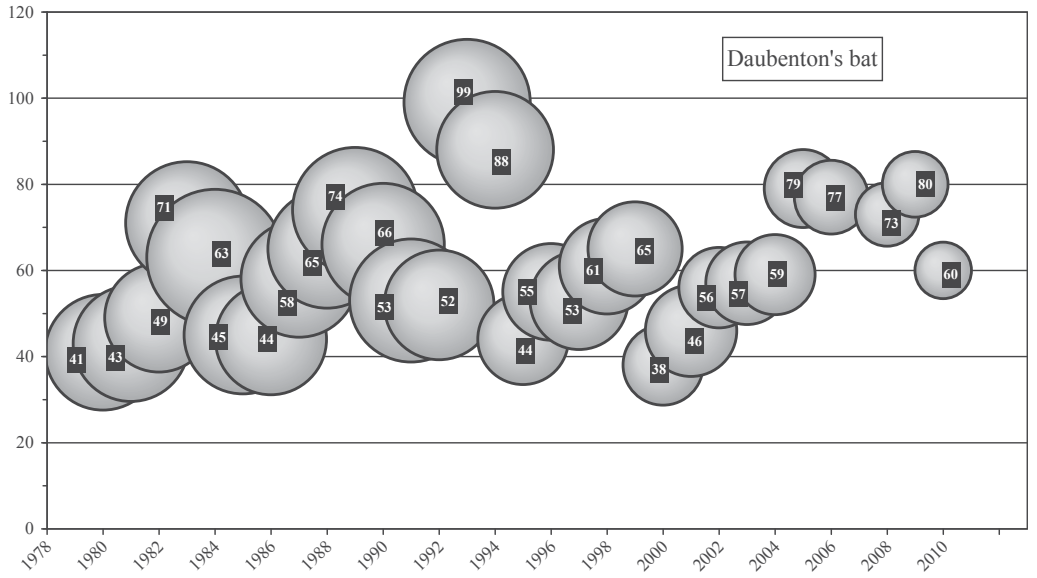

Figure 8. Number of Daubenton's bats in the period 1980–2010. The diameter of the circle represents the number of Daubenton's bats in relation to the total number of bats found in that year.

and leave, but prevented unauthorised access by humans.

From the early 1980s on, bat numbers in the Schenkgroeve started to increase. In 1980 85 bats were recorded and this figure increased by around 50% by the mid 1990s and then tripled by 2004. Since then the increase has been much stronger: recent counts have resulted in more than 500 bats.

The average annual number of bats recorded from 1980 to 2010 was 198.0, a remarkable growth in comparison to period A (average 70.3) and period B (62.8). The significant increase in numbers in period C is largely due to an increase in two species: Natterer's bat and Geoffroy's bat. The number of Natterer's bats grew from less than 10 specimens per year in the early 1980s to 200-300 in recent years (table 1; figure 6). It is now the most abundant species in the Schenkgroeve. An increase of Natterer's bats has also been observed in other limestone caves and hibernacula in south Limburg (Weinreich & Oude Voshaar 1987, Dijkstra et al. 2006, Verboom 2006).

In period C the number of hibernating Geoffroy's bats also showed a strong increase, from only a few specimens in the 1980s and early 1990s to well over a hundred in 2009 and 2010 (table 1; figure 7). Natterer's and Geoffroy's bats together now represent over 70% of bats in the Schenkgroeve.

The numbers of both Daubenton's bats and whiskered/Brandt's bats have, on average, increased slightly in period C, although counts of both species have shown much variation over the years (table 1; figures 8 and 9). Although Daubenton's bat was the second most common bat over the whole period C (33.7%), its relative abundance in the Schenkgroeve decreased in this period (from 48% in 1980 to less than 20% after 2005) and in comparison with both earlier periods. The same also applies for the whiskered/Brandt's bat.

Pond bats were recorded in low numbers (1-11) through most of period C (table 1). However, from 2005 onwards their numbers increased. The highest number of pond bats (22) was found in 2009.

No more than one or two mouse-eared bats per year were recorded in period C in the Schenkgroeve, with the exception of 2010

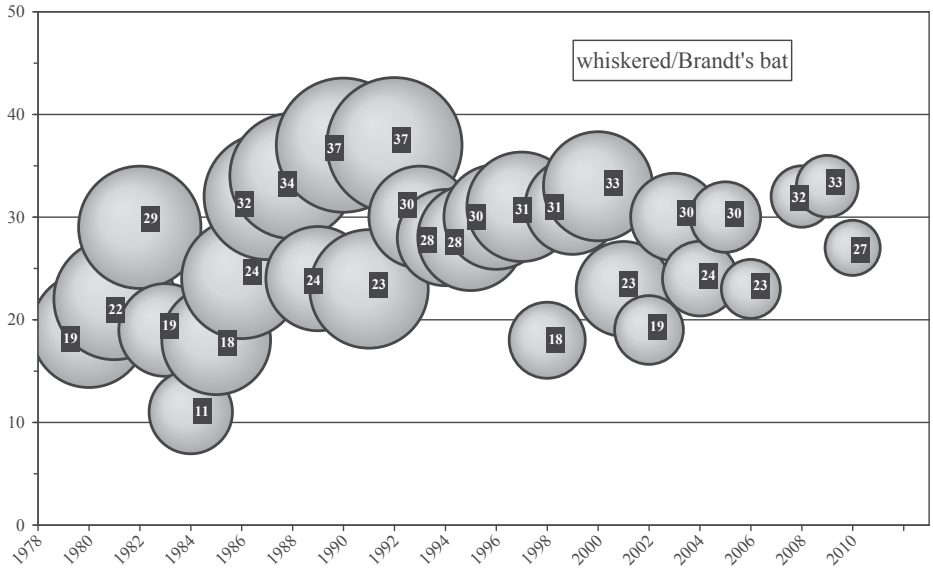

Figure 9. Number of whiskered/Brandt's bats in the period 1980-2010. The diameter of the circle represents the number of whiskered bats in relation to the total number of bats found in that year.

when three specimens were found; between 1995 and 2008 the species was not recorded at all (table 1). The decline of this species has also been observed by Weinreich and Oude Voshaar (1987) and is probably due to climatic changes and changes in foraging habitats.

Trend analyses

The 30 years of census data of hibernating bats in the Schenkgroeve between 1980 and 2010 may give an indication of the relative population growth of different bat species. If we take the number of hibernating bats in 1980 as a standard index of 100 we can see that between 1980 and 1992 this index stabilised at approximately 100, while between 1993 and 2001 it increased to a level of 200 (figure 10). From 2001 onwards the index increased to 612 in 2010, meaning that the total number of bats in period C has increased by 512%.

Trends were calculated for five species, Daubenton's bat, whiskered/Brandt's bat, pond bat, Natterer's bat and Geoffroy's bat. The numbers of the other species were insufficient to give a reliable figure of the trend. These trends do provide an indication of the potential development of species in the future. The numbers of Daubenton's bats have increased to an index figure of 146, meaning a growth of 46% (2.3% per year) in the period since 1980 (figure 11). The index of the whiskered/Brandt's bats is 140, which is lower than that found by Dijkstra et al. (2006) and Verboom (2006) who observed increases in the caves in south Limburg of 2.2 and 2.5 times for whiskered/Brandt's bats from 1986-2004 and from 1986-2005 respectively. The index for the pond bat showed a negative trend towards 50 in 2004, indicating a decline in hibernating pond bats in the Schenkgroeve. From 2004 until 2008, however, this figure increased to 220 in 2009 and 120 in 2010 (figure 11). In period C the growth rate for the pond bat has been 2.8% per year, although it has fluctuated sharply. The data for Natterer's bat and Geoffroy's bat are presented in figure 12. The spectacular increases of both species have resulted in indices of 291,000 and 5,800 respectively, which correspond to annual growth rates of 20.9% and 14.2%.

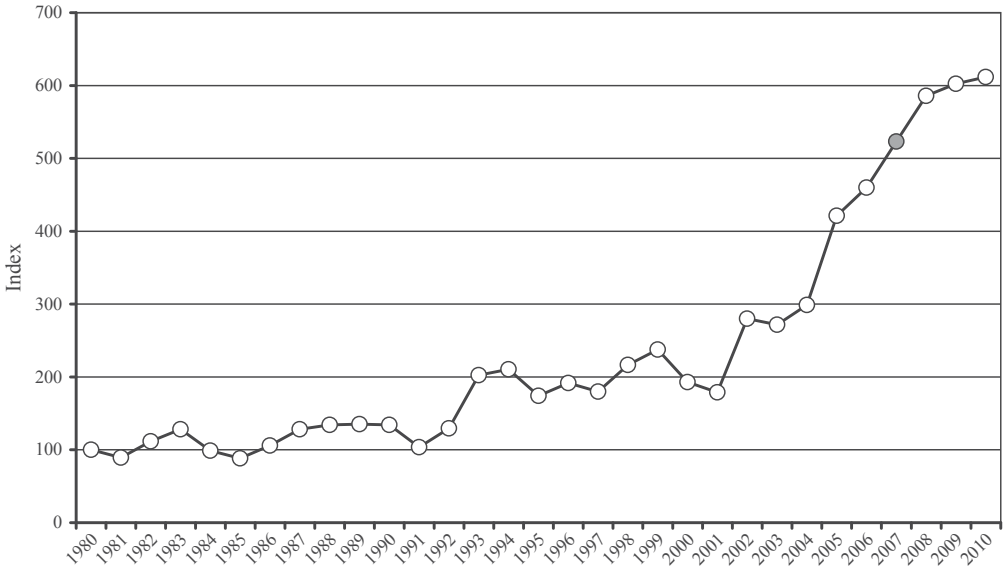

Figure 10. Index of bat numbers in the Schenkgroeve 1980-2010. Index 1980 = 100. In 2007 there was no census, therefore the index is the calculated mean of the index of 2006 and 2008.

Possible factors influencing fluctuations in bat numbers

Period A (1944 – 1959)

Since bats in this period were only collected for bat banding activities to determine the population dynamics, migration and the recovery of bats in the same cave, search efficiency in these censuses was very low. We may assume that actual bat numbers in this period were considerably higher than the counts suggest. Furthermore, in 1952-1954, when mushroom culture took place, several corridors could not be inspected. It is thought that mushroom culture has a negative influence on the number of hibernating bats (Sluiter & van Heerdt 1957). It is not known whether this is due to the smell and fermentation of the horse dung on which the mushrooms grow, to the frequent presence of workers and the installation of physical barriers with plastic curtains and illumination or to an increase in temperature in the cave.

After bats were collected an aluminium ring was fixed around the bats' right underarm, and they were released in the same cave. Banding was thought to have strong negative effects on the welfare of bats and on bat populations by causing prolonged disturbance, hampered agility and (fatal) infections (Daan 1980). Adult mortality among banded bats might have been as high as 82% per year (Daan 1980). Given an annual birth rate of one young per year, the average mortality (including juvenile mortality) in a population should be no more than 33% for the population to sustain itself (Sluiter et al. 1971). The effect of forearm bands on insectivorous bats varies between species and according to band type, band size and metal type. An assessment of injuries to the forearms of 17 species of microchiropteran bats marked for ecological studies showed serious injuries in 16 of the 17 species, while survival rates for three species were estimated at between 0.19 and 0.75 (Baker et al. 2001). In a study of three species of horseshoe bat in northern Bulgaria, 7.6% showed slight and 6.4% showed severe injuries due to forearm bands (Dietz et al. 2006).

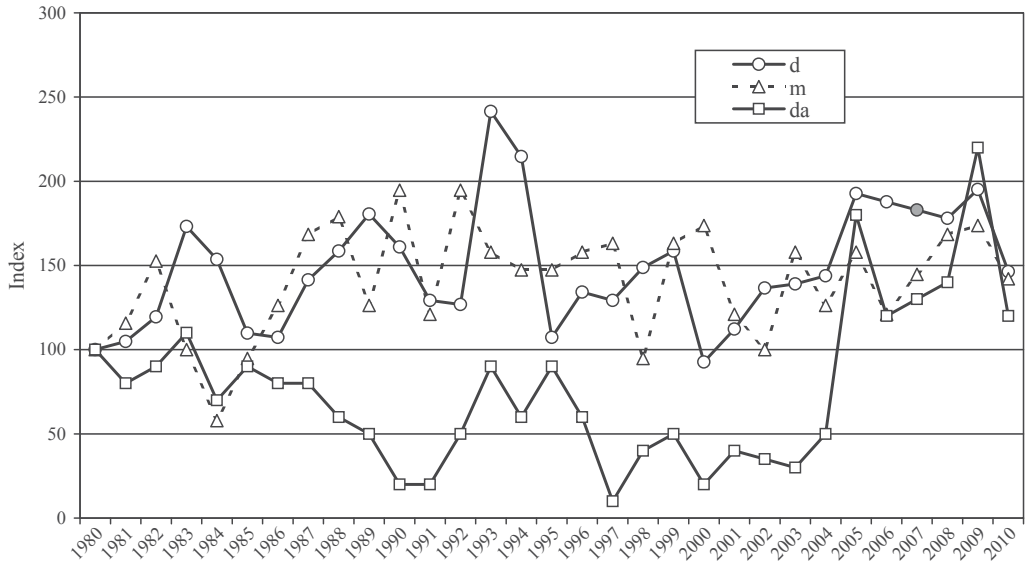

Figure 11. Indices of Daubenton's bat (d), whiskered/Brandt's bat (m) and pond bat (da) in the Schenkgroeve 1980-2010. Index 1980 = 100. In 2007 there was no census, therefore the index is the calculated mean of the index of 2006 and 2008.

The banding of lesser horseshoe bats in period A was thought to have contributed to the significant decrease in numbers found hibernating in the caves of south Limburg, including in the Schenkgroeve (Daan et al. 1982). Banding may also have negatively affected other species, especially greater mouse-eared bat and Geoffroy's bat. The populations of whiskered/Brandt's bat, Daubenton's bat, Natterer's bat, pond bat and long-eared bats showed no significant changes in this period.

Period B (1960-1979)

The observed decrease in the numbers of several species during the years of bat banding motivated researchers to intensify their searching efforts in order to obtain information on the status of different bat species. Despite this renewed effort, populations did not show a recovery in period B, with the possible exception of Daubenton's bat at the end of period B. The greater mouse-eared bat, which was still relatively common in the beginning of period A, with up to 18 observed specimens, showed a further decline in period B. It is possible that the disappearance of a large nursery colony of 300-400 pregnant females after the gradual collapse of their corridors in the nearby Sint Pietersberg cave in the mid 1950s attributed to the decline of this species in Limburg (Vergoossen & van der Coelen 1986). Only one specimen, banded in the Schenkgroeve on the 29th of December 1946, was recaptured, on the 5th of June 1948 in Dilsen, Belgium, 18 km away. The decline in roosts and summer colonies of the greater mouse-eared bats in the surrounding areas of Germany, Belgium and northern France could possibly explain the disappearance of this species in the Schenkgroeve (Racey 1992).

In period B, the lesser horseshoe bat became almost extinct in the Netherlands. It is believed that banding in the previous years was partly responsible for this (Sluiter and van Heerdt 1957). Other factors that may have played a role are climatic changes, the disturbance of summer and winter quarters, the removal of many linear vegetations and the

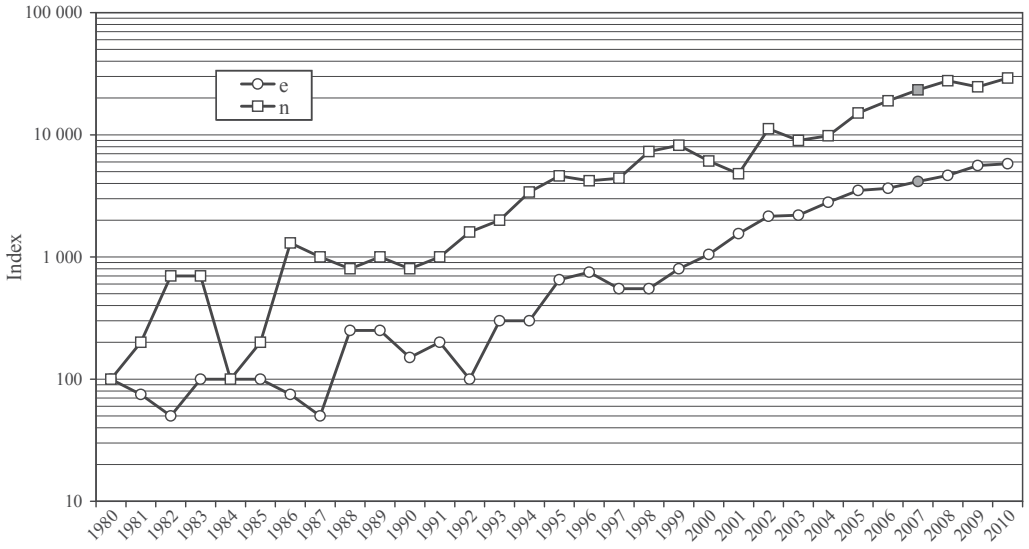

Figure 12. Indices (log scale) of Geoffroy's bat (e) and Natterer's bat (n) in the Schenkgroeve 1980-2010. Index 1980 = 100. In 2007 there was no census, therefore the index is the calculated mean of the index of 2006 and 2008.

intensive use of insecticides (Vliet & Mostert 1997). The numbers of Daubenton's bats in the Schenkgroeve remained stable and even increased slightly at the end of this period. It is suggested that their main food source, aquatic insects, suffered less from the use of insecticides than insects that mainly live over land (Daan et al. 1982).

Period C (1980 – 2010)

It is difficult to be certain that the installation of an iron gate in 1980 had a positive effect on the numbers of bats hibernating in the Schenkgroeve. Some species increased in number, others remained stable. The disappearance of the lesser horseshoe bat from the Schenkgroeve and the extinction of the species from Limburg and the Netherlands may be due to southern Limburg being located at the periphery of the range of this species. In spite of increased protective measures, the lesser horseshoe bat has severely declined in much of its former range, including neighbouring Germany and Belgium. Several causes for its decline have been suggested, including the destruction of their roosts, pesticide contamination, changes in the structure of its habitat and competition with other species (e.g. Stebbings 1988, Arlettaz et al. 2000). However, it is believed that habitat destruction and the effects of pesticides are the main causes of the population decline (Bontadina et al. 2000).

Over the years numbers of greater mouse-eared bat have remained very low in the Schenkgroeve. However in limestone caves in south Limburg as a whole increasing numbers have been found after 2005. Numbers have almost tripled between 1995 and 2005 (Dijkstra et al. 2006, Verboom 2006).

Trend analyses show that numbers of both Geoffroy's bat and Natterer's bat in the Schenkgroeve have increased more rapidly than the numbers in the caves in Limburg and in Limburg as a whole (Dijkstra et al. 2006, Verboom 2006). The range of Geoffroy's bat in the Netherlands is restricted to the Province of Limburg and the numbers recorded in winter quarters exceed those found in the summer period, so it is likely that at least some of these hibernating animals come from else-

where, such as Belgium, where several nursery colonies are known to exist (Verkem et al. 2003, Verboom 2006). Yet, on the other hand, there seems to have been an increase in summer populations (Vergoossen et al. 2009). The causes of the rise the numbers in winter quarters are currently unknown. Possibly, climate change has had a positive influence, because this species is often found in the warmer parts of the caves and is also known to be thermophilous in summer, preferring warm attics.

The annual census of the Schenkgroeve is of high value in helping us to understand fluctuations in bat numbers and being able to place these in a broader (regional) perspective. In addition, the Agreement on the Conservation of Bats in Europe has encouraged consistent monitoring methodologies on a pan-European scale for a range of species (Stebbings 1988). Natura 2000 sites require the monitoring and assessment of the conservation status of habitats and species in Natura 2000 sites on a regular basis, to evaluate the achievements that have been made and to get a better insight in the possible effects of measures. The Dutch government is obliged to report every six years to the European Commission on the achievements made in Natura 2000 sites. Since the Schenkgroeve is currently one of the most important caves for hibernating bats in the Geuldal Natura 2000 site, a continuation of the annual census is highly recommended.

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Samenvatting

Overwinterende vleermuizen in de Schenkgroeve (Meerssen, Limburg) van 1944 tot en met 2010

De Schenkgroeve, een ondergrondse mergelgroeve bij Meerssen, Zuid-Limburg, geldt als een van de belangrijkste winterverblijven voor vleermuizen in Limburg en Nederland. De groeve maakt onderdeel uit van het Natura 2000-gebied 'Geuldal'. Van 1944 tot en met 2010 werden hier 61 jaarlijkse wintertellingen van vleermuizen uitgevoerd. De Schenkgroeve kent twee gedeelten. Het voorste gedeelte huisvest het overgrote deel van de overwinterende vleermuizen. Het achterste deel wordt hier buiten beschouwing gelaten; uit de (onder meer vanwege veiligheidsoverwegingen) spaarzame bezoeken bleek dat hier weinig vleermuizen overwinteren. In een periode van 67 jaar vertoonde het aantal overwinterende vleermuizen van tien verschillende soorten aanzienlijke fluctuaties. Enkele algemene trends kunnen worden herkend. Doordat doelstellingen en methodieken in de loop der jaren wisselden, is met het oog op een evaluatie van de inventarisaties een onderverdeling gemaakt in drie perioden, 1944-1959 (periode A), 1960-1979 (periode B) en 1980-2010 (periode C). In periode A was het hoofddoel het ringen van vleermuizen. De sterke aantalsafname van enkele soorten in deze periode in de Schenkgroeve en andere groeven in Limburg wordt deels toegeschreven aan de verstoringen en verwondingen als gevolg van het ringonderzoek. Ook de champignoncultuur in de jaren 1952-1954 heeft mogelijk een negatieve inlvoed gehad. Met name de kleine hoefijzerneus (*Rhinolophus hipposideros*), de ingekorven vleermuis (*Myotis emarginatus*) en de vale vleermuis (*Myotis myotis*) hebben waarschijnlijk onder het intensieve ringonderzoek geleden; aantallen van de watervleermuis (*Myotis daubentonii*), de meervleermuis (*Myotis dasycneme*), de baardvleermuizen (*Myotis mystacinus*/*brandtii*), de franjestaart (*Myotis nattereri*) en de grootoorvleermuizen (*Plecotus auritus/austriacus*) bleven min of meer constant. In periode A werden gemiddeld 70,3 vleermuizen per jaar gevonden in de Schenkgroeve. In periode B was het belangrijkste doel het vaststellen van de relatie tussen de hangpositie van de overwinterende vleermuizen en klimatologische factoren. Het gemiddelde aantal overwinterende vleermuizen per jaar bleef ongeveer gelijk aan dat van voorgaande jaren. Aan het einde van deze periode vertoonde alleen de watervleermuis een toename. In 1980, het begin van periode C, werd een ijzeren hek geplaatst. Vanaf 1980 nam met name het aantal overwinterende franjestaarten en ingekorven vleermuizen in de Schenkgroeve aanzienlijk toe, een ontwikkeling die ook elders in Limburgse groeven wordt waargenomen. Ook het aantal watervleermuizen vertoonde een stijging. Baardvleermuizen, meervleermuis en grootorvleermuizen lieten geen significante aantalsveranderingen zien. Het gemiddelde aantal vleermuizen in periode C nam toe tot 198,0 vleermuizen per jaar, hetgeen volgens een indexberekening overeen-

komt met een zevenvoudige toename tussen 1980 en 2010. Het monitoren van populaties is een belangrijk instrument voor natuurbeschermers. De gegevens kunnen inzicht verschaffen in de factoren die ten grondslag liggen aan de populatie-ontwikkelingen en bieden de mogelijkheid beheersmaatregelen te formuleren. Bovendien is Nederland verplicht om regelmatig (elke zes jaar) een rapportage te sturen aan de Europese Commissie over de staat van instandhouding van de soorten en habitattypen in Natura 2000-gebieden. Aangezien de Schenkgroeve geldt als een van de belangrijkste groeven voor overwinterende vleermuizen binnen het Geuldal, is het van belang om juist hier de jaarlijkse monitoring te continueren.

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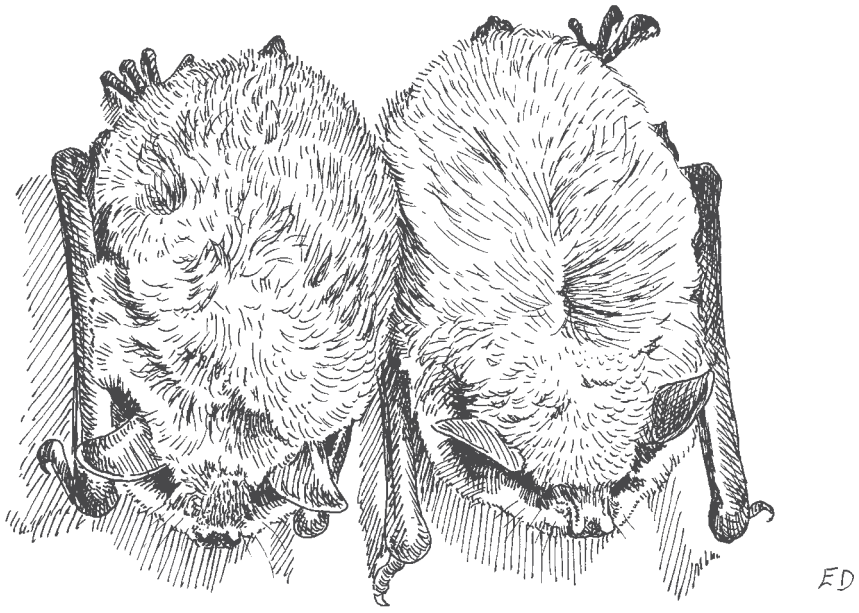
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