On Original Species

While reading the proof sheets of this new issue of Lutra I became aware how all the articles in this issue are based on research that is quite original, in one way or another. ‘Original research’ has a very specific meaning in science and ironically Van Vuure’s article, which made me first think about originality, is not strictly original research, but more of a review. However, using linguistics as a basis for determining the historical occurrence of the wisent (or European bison) in various parts of the continent really is a novel and innovative approach towards the matter. But this article is about originality in more than one way. The question of which species are part of the original fauna of a country or region and those that are non-natives is currently a hot topic in nature conservation. There are numerous cases of introduced species outcompeting their indigenous cousins or otherwise causing problems. In many cases, exotic species have been introduced unintentionally when they hitched a ride with man, but there are many other examples where the introduction of some seemingly useful animal was intentional – though often misguided. But conservationists also need to watch their step. Canadian beavers are still present in parts of Europe, displacing European beavers. In Lutra 57-2 (2014), Van Vuure addressed the matter of the konik’s ancestry and in this issue he considers whether the (re?)introduced wisent is indeed indigenous to the Netherlands. We should remember that the original Dutch wisent would have been the steppe wisent (*Bison priscus*), the remains of which are regularly found in our coastal waters. Unfortunately, it’s been extinct for some 10,000 years.

There is no room for question that Reeves’ muntjac (*Muntiacus reevesi*) and Sika deer (*Cervus nippon*), are non-native species. Both are from Asia and neither ever trotted on European soil until their introduction here by man. One look at an adult male Reeves’ muntjac and one can see that they are original in at least one way: the males not only sport a handsome pair of short, curved antlers but also possess elongated upper canines which can be as long as 2.5 cm. This is definitely a novel and therefore original approach for a deer to fend off its competitors. That may be all well and good but it doesn’t make up for the effect they are having on our indigenous flora and fauna. Hollander’s article presents an up-to-date overview of the occurrence of both species in the Netherlands, and of current trade in, and possession of, them.

Elsewhere, Kleef and Wijsman present the results of their research which is original in the more traditional scientific sense. Their study explores a classic example of an adaptive response to fluctuations in food availability on interrelated trophic levels in the food chain. They found that Pine martens (*Martes martes*) change their hunting behaviour according to the availability of wood mice (*Apodemus sylvaticus*) as prey. Wood mice populations are, in their turn, strongly influenced by mast production of beech and common oak.

Pine martens are not the only species who live close to wood mice in the trophic pyramid. Wild boar (*Sus scrofa*) compete with wood mice and bank voles (*Myodes glareolus*) for acorns and, alongside mast production, their behaviour influences successful acorn germination. Wood mice display hoarding behaviour, stashing acorns for later consumption and tracking the fate of these hidden acorns, once again, required an original approach. Suselbeek's thesis, reviewed here by Lammertsma, describes the use of PIT-tags, usually a tool used by scientists to track all kinds of animals, to track the dispersal of acorns. Again one might say it's quite original.

Last in this list and first in this issue, there's an article by Thissen et al. on the distribution of the Pannonic root vole (*Microtus oeconomus mehelyi*) in Austria. Again in this case, there's no question regarding the status of the species. There's no doubt that it is part of the original fauna of Pannonia. In fact, the Pannonic root vole does one better: it's a local specialty, its range is restricted to a small part of Central Europe. Like the Dutch subspecies *Microtus oeconomus oeconomus*, it is an endemic subspecies; and its origin is in this region – and nowhere else. While the steppe wisent became extinct when the last ice age ended, the root vole clung on to existence and became an ice age relict. The preservation of the species through careful management therefore deserves our attention.

Eric Thomassen

The distribution of the Pannonic root vole (*Microtus oeconomus mehelyi* Ehik, 1928) in Austria

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Abstract: As part of a LIFE project about the Pannonic root vole (*Microtus oeconomus mehelyi*) in Slovakia we also have investigated its occurrence in the nearby Austrian part of its range. Reports of the vole go back to1897, when the presence of the species in Austria was first published. Apart from studying literature on the species' distribution, we have analysed owl pellet data and data of trapped specimens available from records at the Natural History Museum of Vienna (NMW) to illustrate the species' distribution in Austria up until 2010. For more recent years (2011-early 2015) we investigated its distribution in Austria by using snap and live-traps, and by analysing owl pellets. In this period we found the Pannonic root vole on the eastern and western side of the Neusiedler See. There are some indications that the root vole may have disappeared from the northern side of the lake due to habitat loss. We give recommendations for habitat management that can help conserve the species.

Keywords: *Microtus oeconomus*, *Microtus oeconomus mehelyi*, root vole, Austria, Neusiedler See, Seewinkel.

Introduction

The Pannonic root vole (*Microtus oeconomus mehelyi*) is a priority taxon of Annex II of the Habitats Directive and this subspecies is also listed on Annex IV of this directive. In consequence EU member states are obliged to inform the European Commission every six years about its conservation status. This publication has been written as part of the LIFE project "The conservation of root vole *Microtus oeconomus mehelyi*". The project provides a baseline study of the current status of the Pannonic root vole.

The root vole (*Microtus oeconomus*) has a continuous holarctic distribution from eastern Germany and northern Scandinavia, throughout all of Russia and Alaska and to north-western Canada. In addition there are isolated populations in southern Scandinavia, on Finnish islands in the Gulf of Bothnia, in the Netherlands, southern Hungary (Balaton and Kiskunság) and at the point where Austria, Hungary and Slovakia meet (Shenbrot & Krasnov 2005). These isolated populations have been described as separate subspecies; with populations in Austria, Hungary and Slovakia representing the Pannonic root vole (*Microtus oeconomus mehelyi* Ehik, 1928). Its known distribution, based on available literature and our own data, is presented in figure 1A. One record from near the river Drava in southern Hungary, published in the Hungarian Atlas of Mammals (Gubányi 2007), proved to be erroneous (A. Gubányi, personal communication). Pachinger (2003) published an isolated record in an owl pellet from eastern Slovakia.

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The recent situation in Hungary and Slovakia is relatively well-known. In southern Hungary the root vole is decreasing. It disappeared from Kiskunság in the 1960s (Demeter & Topál 1987), but is still present around Lake Balaton (e.g. Lanszki & Rozner 2007, Horváth et al. 2012, Purger 2014) and in the Hungarian part of the Neusiedler See and Hanság (Gubányi et al. 2002). Along the Danube it is present on Small Rye Island (Szigetköz / Malý Žitný Ostrov, Kleine Schüttinsel) and Great Rye Island (Žitný Ostrov, Große Schüttinsel) and at several localities just north and east of the larger island (Gubányi et al. 2009, Miklós et al. 2014). It was feared that it had disappeared from Great Rye Island because of hydrological changes caused by the Gabčíkovo hydroelectric power plant (Pachinger 1995). But Gubányi et al. (2009), in their review of the species' occurrence along the Hungarian/Slovakian Danube since 1902, and Miklós et al. (2011, 2014) have shown that the root vole is still present at several localities on Great Rye Island.

An overview of the distribution of the species in Austria was given by Spitzenberger & Bauer (2002) - based on earlier publications (Mojsisovics von Mojsvár 1897, Bauer 1953, 1960, Spitzenberger 1966, Hoi-Leitner 1989) and data from material at the Natural History Museum of Vienna (NMW). Since then presence of the root vole in Austria has been mentioned by Mühlböck (2003), for the Westliche Wörtenlacke, in the Seewinkel. For the national report under article 17 of the Habitats Directive, a survey with live-traps was carried out in the Seewinkel area in August 2011. In this survey the Pannonic root vole was only recorded at the Östliche Wörtenlacke (Ch. Walder, personal communication).

Given this, it was considered important to study more closely the current and recent status of the root vole in the Austrian part of the Neusiedler See area, including Seewinkel and Waasen / Hanság (figure 1B). In consequence, in the framework of the LIFE project, root vole experts from the Dutch Mammal Society (Dick Bekker, Rob Koelman, Wesley Overman and Johan Thissen) and Barbara Herzig and Katharina Spreitzer from the NMW joined forces to map the root vole on Austrian territory east and west of the Neusiedler See. The work focused on the east side, mainly the Seewinkel area, as analysis of owl pellets had demonstrated that the root vole is still present there while positive results for its presence in the western area were only very recently derived from owl pellets. This publication describes the history of the distribution in more detail and the current and recent status of the root vole in Austria.

The LIFE project "Conservation of root vole *Microtus oeconomus mehelyi*"

The general objective of the LIFE project "The conservation of root vole **Microtus oeconomus mehelyi*" (LIFE08/NAT/SK/000239, www.broz.sk/microtus/en) is to improve the recently unfavourable conservation status of the species in Slovakia, whose population is currently heavily fragmented and is potentially susceptible to extinction. In the project a strategic basis is developed for the successful recovery of this endangered subspecies, i.e. through habitat restoration or habitat improvement on specific sites important for the root vole.

The main threats to the root vole are habitat loss, fragmentation and degradation due to a changed water regime, the abandonment of traditional management of lowland meadows and reed beds and the genetic degradation of isolated populations. The main causes of these threats are large-scale land reclamation and drainage schemes, the ploughing of lowland meadows, the draining of wetlands and the overall intensification of agricultural production.

The most effective solution for conserving this rare species is therefore to reintroduce

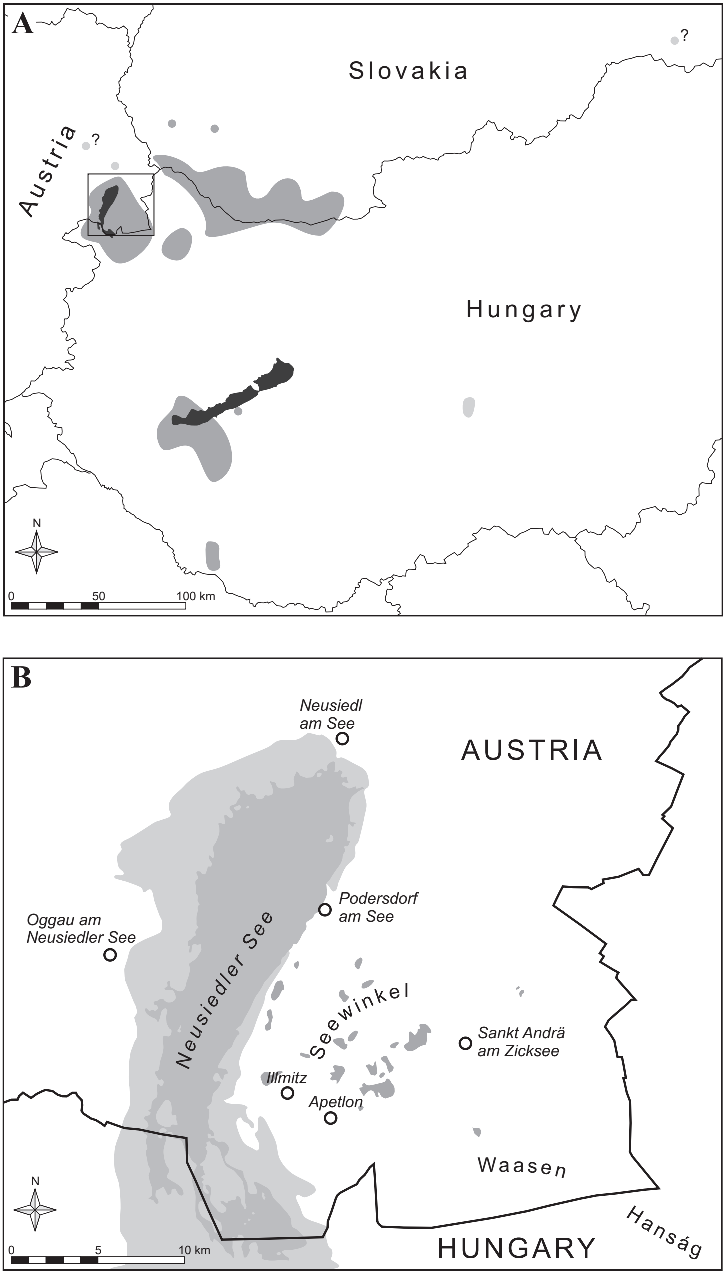


Figure 1. A. Distribution of *Microtus oeconomus mehelyi*. Compiled from published sources and own data: Slovakia – (Gubányi et al. 2009, Krištofík & Stollmann 2012, Pachinger 2003); Hungary – (Demeter & Topál 1987, Gubányi 2007, Gubányi et al. 2002, 2009, Purger 2014); Austria – (Spitzenberger & Bauer 2001 and own data). Presumably extant populations are shown in dark grey and reportedly extinct populations and questionable records (indicated by a question mark) are in light grey. The location of the study area is indicated by the black frame. B. Map of the study area. Water bodies and reed stands are shown as dark grey and light grey shading respectively.

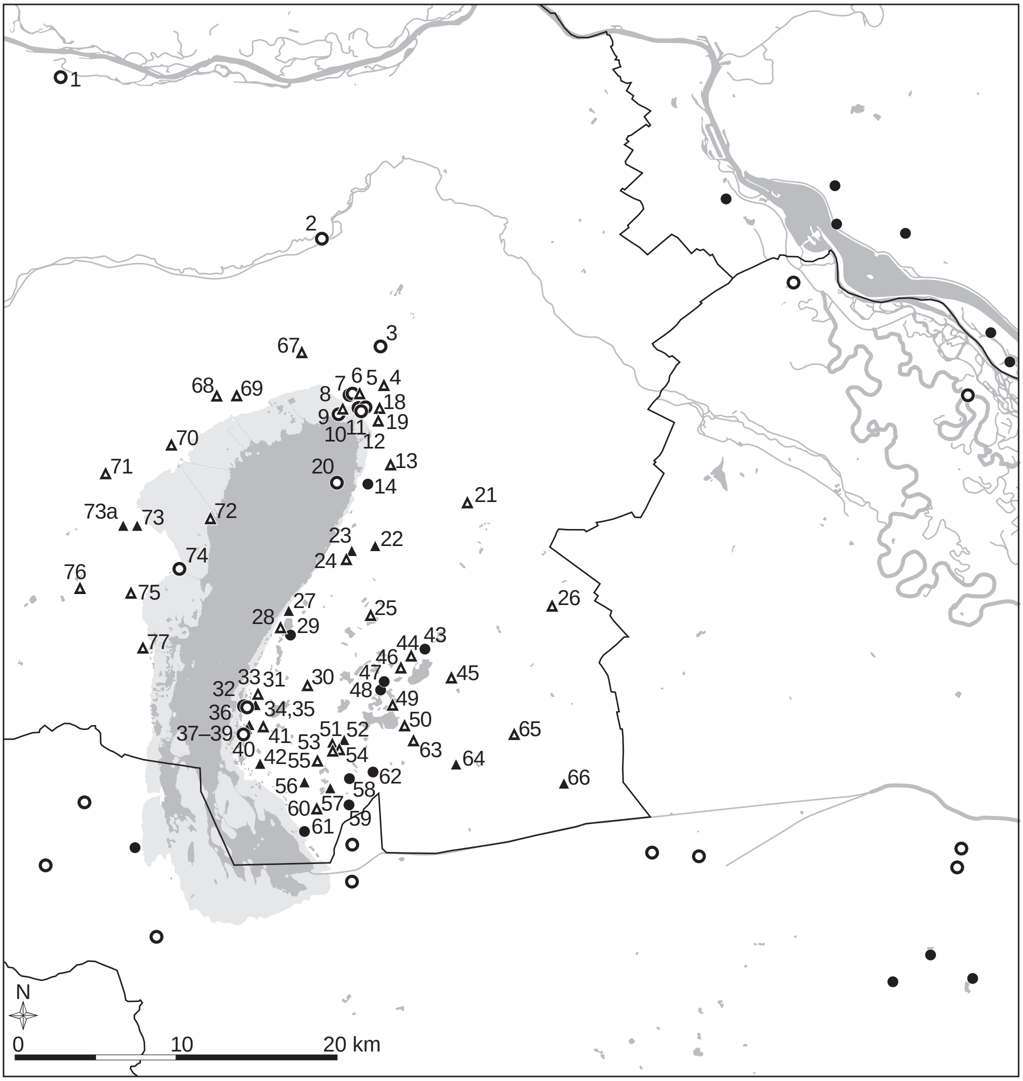


Figure 2. Records of *Microtus oeconomus mehelyi* from Austria. Direct records (trapped specimens, direct observations) are mapped as dots and records from owl or raptor pellets as triangles. Open symbols refer to records before the year 2000, filled symbols to records between 2000 and 2015. Extralimital records from Slovakia and Hungary have been extracted from Gubányi et al. (2002, 2009). Numbers refer to table 1 and the appendix.

traditional methods of agricultural production and to restore wetlands and bank vegetation in areas still inhabited by the root vole. The main objectives of the project are to restore a 33.5 km long stretch of the Čiližský brook and its adjacent wetlands, to restore 100 hectares of wet grasslands and 360 hectares of marshlands important for the target species and to cut 150 hectares of reed beds, all on Great Rye Island. There is also lack of scientific data and awareness, which are addressed by the LIFE project. Miklós et al. (2011, 2014), in their work for this LIFE project, have recently trapped the root vole at several local-

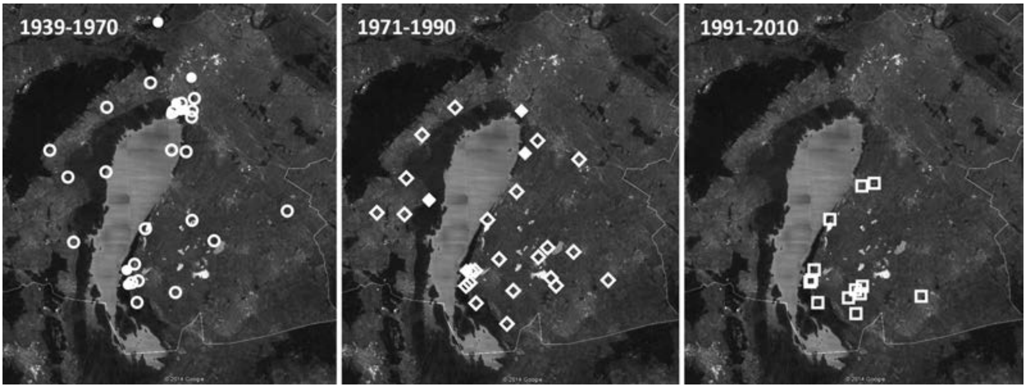


Figure 3. Records of *Microtus oeconomus mehelyi* in the Lake Neusiedl area from 1939 to 2010, divided into three periods: before 1971, 1971-1990 and 1991-2010. Filled symbols are trapping records, open symbols are records from owl pellets.

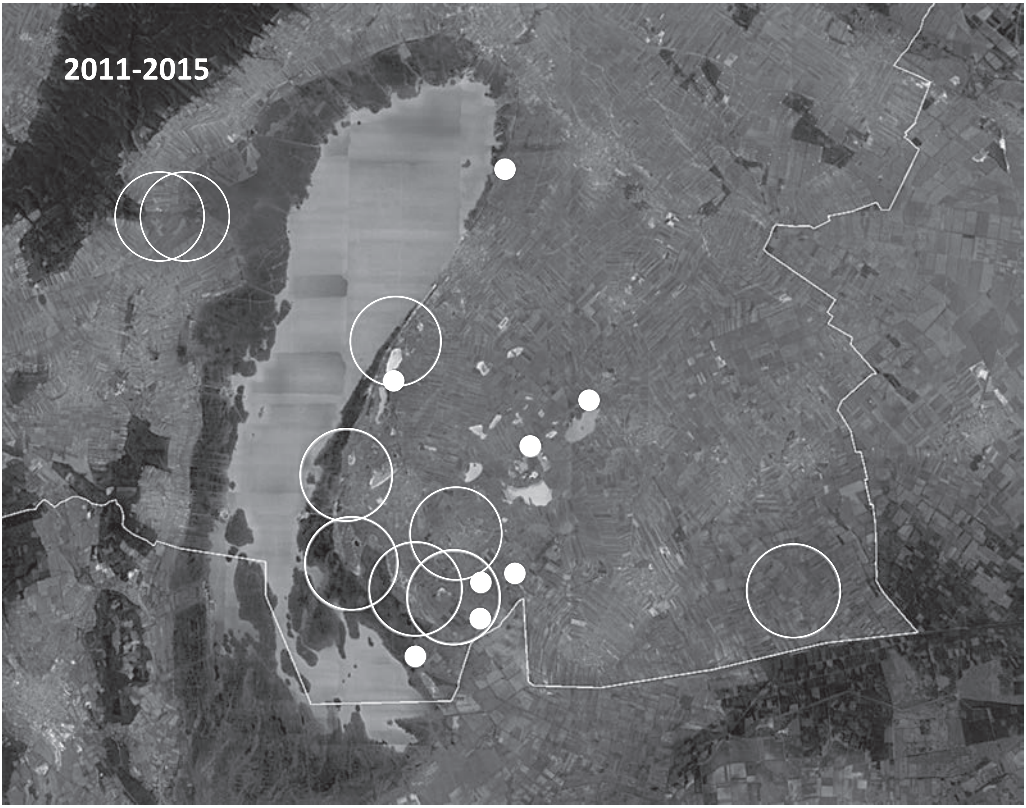


Figure 4. Recent proved distribution of *Microtus oeconomus mehelyi* (2011 to 2015). White dots show localities of successful trapping and circles (r= 2 km) are drawn around the localities where owl pellets that included remnants of *Microtus oeconomus mehelyi* were collected.

ities in the centre and the south of the Great Rye Island, including at Čiližský brook, and at many localities at the confluence of the Váh Danube and Nitra rivers, just east of the Great Rye Island.

Methods

The historical distribution (figure 2) of the root vole in Austria until 2010 was determined by using data from literature and from the mammal collection of the NMW. The NMW collection contains specimens from the years 1952 to 1964, 1969 and 1983 to 1986. Trapping in these years was done with commercial snap traps. In 2003 Mühlböck (2003, 2008) used live-traps (wooden box live-traps and wire cage traps; both from DeuFa GmbH, Neuburg, Germany) when studying small mammal communities on a pasture. All these collection localities are situated at the north and east side of the Neusiedler See. Records of the species from west of the lake were published by Hubálek et al. (1979) and Hoi-Leitner (1989) who both used snap trapping.

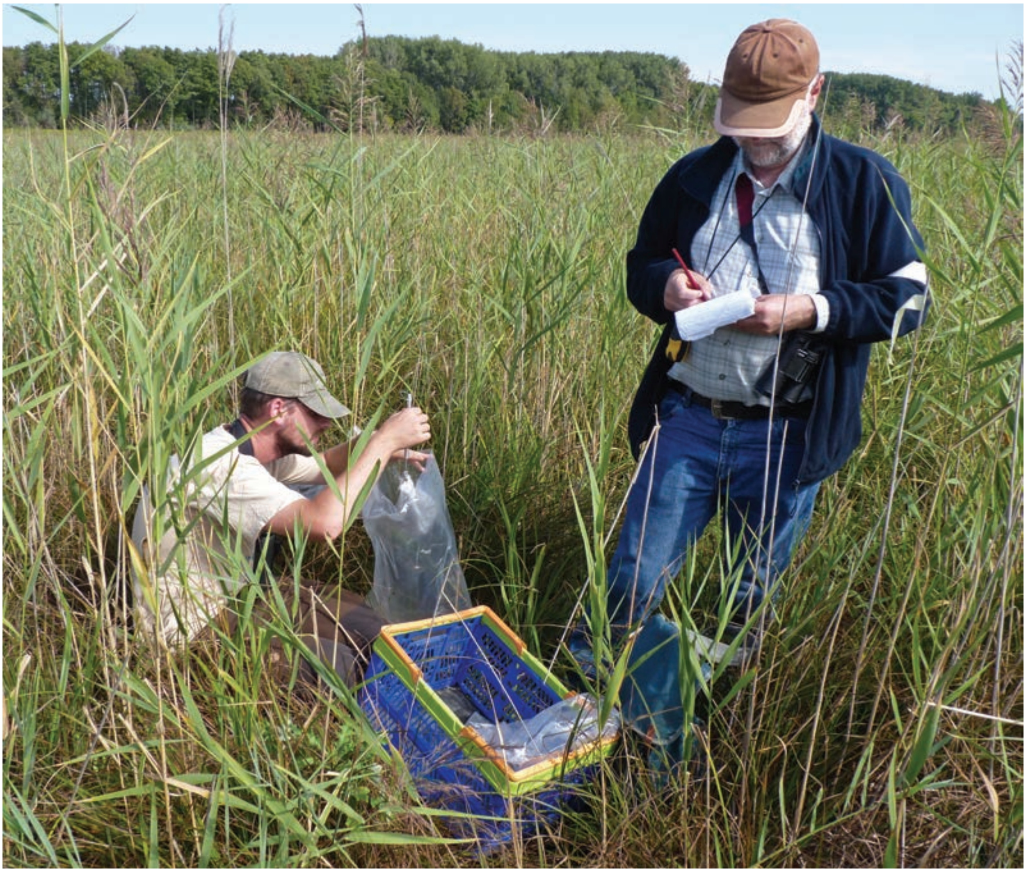
In the NMW collection also samples of owl pellets collected (in some years) between 1939 and 2015 from both sides of the lake were available. The majority of this material originated from the Seewinkel area in the east. These pellets were mainly from barn owl (*Tyto alba*) and to a lesser extent from short-eared owl (*Asio flammeus*), long-eared owl (*Asio otus*), little owl (*Athene noctua*) and falcons (*Falco* spp.).

From 2003 to 2014 Vinzenz Waba, a ranger at the Neusiedler See – Seewinkel National Park, collected a total of 97 samples of barn owl pellets that all originated from the southeastern side of the Neusiedler See. This area runs south from Podersdorf to Illmitz and Apetlon, covering about twelve square kilometres (figure 1B). Pellets were collected from 17 sites. Most samples (34) came from a locality known as Apetloner Hof, near the village of Apetlon, and there were twelve samples from the Hölle locality, at Illmitz. There were also six localities from which only one sample was collected. The barn owl has an overriding importance when collecting information about the presence of small mammals as, of all owls in Austria, it is the least specialised on any single prey type and its pellets thus show a wide prey spectrum. The amount of pellets per sample varied from one to a couple of hundred (conditions did not always permit exact counts).

Pannonic root vole (*Microtus oeconomus mehelyi*) in the Seewinkel area, Austria, 10 September 2011. *Photo: Rob Koelman*.

Prior to 2007 owl pellets were sorted out by several well trained people, using (remains from) calvaria and mandibles for identification. Since 2007 the owl pellets have been sorted out in the same way by K. Spreitzer. The remains of 285 samples of owl pellets are stored in the mammal collection of the NMW. While in another 19 cases only identification protocols but no remains of the small mammals were available.

To investigate the recent distribution (2011 to March 2015) of the root vole in the Neusiedler See area we also analysed owl pellets from the east and the west side of the lake. From



Wesley Overman and Johan Thissen, while weighing Pannonic root voles in an area with moist reed and sedge vegetation at Westliche Wörtenlacke, Seewinkel, Austria, 10 September 2011 (locality 48 in figure 2 and in the appendix). *Photo: Rob Koelman*.

2011 to 2015 only ten samples of owl pellets were collected in the west while by contrast 26 samples of pellets were received from the eastern side of the lake during this period. Five of the ten samples from the west were just single pellets of long-eared owl while the rest were barn-owl pellets. A study of the situation of the barn owl in eastern Austria in 2006-2009 (Donnerbaum & Frühauf 2010) had shown that barn owls were very rare on the western side of the Neusiedler See. In 2011 we received just one sample of barn owl pellets from the west. No other nesting or roosting sites of barn owls were located at that time and even special nest boxes mounted in the area in 2006-2009 had not (yet) been occupied. Currently, however, the situation of the barn owl seems to improve (A. Ranner, personal communication).

Altogether, 302 (1939-March 2015) samples of pellets from the area were investigated during this study, 133 of them contained the remains of one or more specimens of the root vole.

In addition, live trapping was done in the Seewinkel around Apetlon in the years 2011 and 2012. In September 2011 live trapping was done over 600 trap nights and in October 2012 over 280 trap nights. At every locality we had ten pairs of two Longworth live-traps during two nights in the field. The pairs of traps were 5-10 m apart. The live-traps were supplied with hay and baited with carrot and a commercial mix of rodent food. Living larvae of

Tenebrio molitor (mealworms) were added to reduce mortality of caught shrews. The traps were not pre-baited. Root voles caught in live-traps were marked by cutting hairs from the back with a scissor and a tissue sample was taken from an ear with a biopsy punch. In October 2012 we used snap traps baited with peanut butter, in an exercise that coincided with the collection of voucher specimens of other species, on the western and eastern side of the Neusiedler See (near Oggau and in Zitzmannsdorfer Wiesen - north of Podersdorf respectively). 180 snap traps were positioned in both these areas for one night.

Live trapping was restricted to biotopes which were considered to be appropriate for the root vole, based on our own experiences in the Netherlands, i.e. reedbeds with a well-developed understory of *Carex* vegetation and *Schoenetum*, while snap trapping also covered adjacent habitats

Results

Distribution

Results about the distribution presented here are divided into different time periods to illustrate the very uneven distribution of data - since most material was collected randomly. Only in recent years from 2011 till 2015 we were specifically looking for the root vole.

Before 1971
The first probable record of the root vole from present-day Austrian territory is from Fischamend, Lower Austria (locality 1 in figure 2 and appendix) (Mojsisovics von Mojsvár 1897). It is based on a note communicated to A. Mojsisovics von Mojsvár by August von Pelzeln, former curator of the ornithological and mammalogical collections of the NMW. The year of recording remains unknown. As August von Pelzeln died in 1891, that year is the *terminus ante quem* of the record. In the absence of voucher specimens or any other supporting documentation at the NMW, this record, which would also represent the earliest record of the Pannonic subspecies, was often regarded as questionable. However, in view of the present distribution of the species, further downstream along the Danube, and given that the Danube was not completely regulated in those days, the presence of the root vole near Fischamend seems plausible.

At least 60 years later, in 1951, Kurt Bauer (re)discovered the species in Austria at the Neusiedler See (Bauer 1953). Since then the root vole has been documented at several localities along the northern and eastern reed belt of the Neusiedler See (Bauer 1960, Spitzenberger 1966). It also has been documented for the area west of the lake by records from owl pellets from 1939 onwards (figure 3). Between 1958 and 1964 the species was found in two, most likely isolated localities: east of Bruck an der Leitha (locality 2 in figure 2 and appendix) and in the Teichwäldchen / Neusiedl am See (locality 3 in figure 2 and appendix). These isolated populations also corroborate the earlier presence of the species near Fischamend although this population is now considered to be extinct (Spitzenberger & Bauer 2002). These records prove the distribution of the root vole all around the lake during this period, including the western side and in adjacent areas in the east (Seewinkel and Waasen/Hanság) (figures 2 and 3).

1971-1990
During the second period 1971-1990 (figure 3) remains of root vole were found in several samples of owl pellets collected from around the Austrian part of the lake, as well as in the Seewinkel and the Waasen/Hanság. A few catches of root voles during this period indicate their presence to the west, north and east of the lake in 1977 (Hubálek et al. 1979) and 1985/86 (Hoi-Leitner 1989).

1991-2010
Remains from owl pellets from this period prove the presence of the root vole on the east-

Table 1. Results of small mammal trappings in 2011-2012 in the Neusiedler See area, Austria, aimed at finding root vole.

Nr in fig. 2 and Appendix.	Location name	Latitude	Longitude	Date	# Trap Nights L: live-traps s: snap traps	*M. oeconomus* (number of different individuals)	Other species Trapped (number of catches)
48	between Westliche and Östliche Wörtenlacke, Apetlon	47°46’43’’	16°52’21’’	Sept. 2011	40 L	9 (7m, 2f)	1 Na, 9 Sa
48	N of Westliche and Östliche Wörtenlacke, Apetlon	47°46’44’’	16°52’20’’	Sept. 2011	40 L	4 (2m, 2f)	3 Sa
	E Zicksee, St. Andrä /Zicksee	47°47’47’’	16°54’27’’	Sept. 2011	40 L	-	1 Na, 3 Sa, 2 Mg, 23 Aa, 1 Af
	Xixsee, Apetlon	47°45’44’’	16°50’25’’	Sept. 2011	40 L	-	2 Sa, 2 Sm, 19 Ma, 1 Mm, 3 Aa
59	S Apetloner Hof, Apetlon	47°42’44’’	16°50’38’’	Sept. 2011	40 L	1 m	1 Sa, 4 Aa
58	N Apetloner Hof, Apetlon	47°43’34’’	16°50’39’’	Sept. 2011	40 L	10 (9m, 1f)	2 Sa, 3 Ma, 3 Aa
	S Martentaulacke, Apetlon	47°43’54’’	16°50’54’’	Sept. 2011	40 L	-	2 Sm, 7 Mm
	N Martentaulacke, Apetlon	47°44’08’’	16°51’05’’	Sept. 2011	40 L	-	1 Sa, 10 Ma, 2 Mm, 1 Aa
43	N Zicksee, St.Andrä/Zicksee	47°47‘48“	16°54‘23“	Sept. 2011	40 L	1 f	1 Na, 1 Ma, 18 Aa, 2 Af
	Illmitz dam, Illmitz	47°45’13”	16° 44’46”	Sept. 2011	40 L	-	3 Ma, 24 Aa, 3 Af
	0.7 km NW Herrnsee, Illmitz	47°44’52”	16°45’35”	Sept. 2011	40 L	-	2 Mg, 17 Aa
29	NE Unterer Stinkersee, Illmitz	47°48’16”	16°47’33”	Sept. 2011	40 L	6 (4m, 2f)	1 Sa
	E Biologische Station, Illmitz	47°46’07”	16°45’51”	Sept. 2011	40 L	-	3 Aa
	W Biologische Station, Illmitz	47°46’09”	16°45’51”	Sept. 2011	40 L	-	6 Ma, 52 Aa
	0.6 km W Herrnsee, Illmitz	47°44’38”	16°45’47”	Sept. 2011	40 L	-	4 Sa, 1 Ma, 8 Ms, 32 Aa, 1 Mm
62	0.9 km NE Martentaulacke, Apetlon	47°43’47”	16°51’49”	Sept. 2011	- (dogs)	3 (1 m, 2f)	Note: no traps were placed
61	Neudegg, Apetlon	47°41‘49“	16°48‘29“	Oct. 2012	40 L	4 (2m, 2f)	1 Aa, 16 Mm
	Neudegg, Apetlon	47°41‘35“	16°48‘36“	Oct. 2012	40 L	-	3 Aa, 6 Asp
	Neudegg, Apetlon	47°41‘41“	16°48‘39“	Oct. 2012	40 L	-	7 Aa, 1 Ma, 8 Mm
	Zwikisch, Apetlon	47°42‘17“	16°48‘47“	Oct. 2012	40 L	-	5 Aa, 4 Asp, 2 Mm
	Zwikisch, Apetlon	47°42‘15“	16°48‘46“	Oct. 2012	40 L	-	3 Asp
	Zwikisch, Apetlon	47°42‘21“	16°49‘06“	Oct. 2012	40 L	-	6 Asp, 1 Sa
	0.8 km S Apetloner Hof, Apetlon	47°42‘50“	16°49‘37“	Oct. 2012	40 L	-	2 Aa, 2 Asp, 5 Ma
14	Viehhüter, Zitzmannsdorferwiesen, Neusiedl am See	47°53’26”	16°51’23”	Oct. 2012	180 s	1 m	10 Sa, 1 Cl, 9 Ma, 1 Asp, 1 Aa
	Steinriegel, Oggau am Neusiedler See	47°51‘50“	16°41‘40“	Oct. 2012	180 s	-	1 Sa, 7 Ma, 2 Asp, 4 Aa, 6 Mm

Species abbreviations: Aa – *Apodemus agrarius*, Af - *A.flavicollis*, As - *A. sylvaticus*, Asp. - *Apodemus* spp. (*A.flavicollis*, *A. sylvaticus*, *A. uralensis*), Cl – *Crocidura leucodon*, Ma – *Microtus arvalis* , Mg - *Myodes glareolus*, Ms – *Microtus subterraneus*, Mm – *Micromys minutus*, Na – *Neomys anomalus*, Sa – *Sorex araneus*

Table 2. Temporal steadiness (TS) and proportion of *Microtus oeconomus* (pMo) in owl pellets (Ta – *Tyto alba*, Ao – *Asio otus*) from localities re-sampled more than three times. Sample size is expressed as the minimum number of vertebrate prey items (MNVP). Samples were pooled by year for calculating TS and pMo. MNVP was calculated for every sample and these values were than pooled by year. For pMo and MNVP the mean and the range (in brackets) are given. TS was calculated as the number of years in which *M. oeconomus* was present, divided by all sampled years at a given locality. pMo was calculated as a percentage: 100 * Minimum number of *M. oeconomus* / MNVP. Only annual samples with MNVP ≥ 100 were used.

Locality	Years	Owl	TS	pMo	MNVP
56	10 (2003–2013)	Ta	1.00	1.04 (0.16–5.55)	555 (103–1420)
39	6 (2003–2010)	Ta	1.00	2.83 (0.72–4.52)	308 (242–421)
42	6 (1991–2013)	Ta	0.67	1.65 (0.00–6.83)	516 (269–1025)
19	5 (1951–1955)	Ta	0.80	0.65 (0.00–1.71)	544 (210–1301)
27	5 (1984–2011)	Ta	0.60	1.18 (0.00–4.11)	421 (114–973)
23	4 (2006–2009)	Ta	0.25	0.19 (0.00–0.76)	400 (285–557)
51	4 (1985–2014)	Ao	1.00	9.77 (0.68–14.52)	450 (146–1024)

ern side of the lake, in the Seewinkel and the Waasen/Hanság (figure 3) at this time. However we did not have a single sample of pellets from the western side of the lake from this period. Berg & Ille (2002) identified remains of root vole in owl pellets from Neusiedler See area between 1990 and 2000, but the precise original data are unfortunately not available any more. Trapping, in this case live trapping, of small mammals in this area was only done in 2001 and 2002 by Mühlböck (2003, 2008) just northeast of the Westliche Wörtenlacke (locality 47 in figure 2 and appendix). He trapped eleven individuals in 2001, and none in 2002.

2011- March 2015

In September 2011 we had 39 catches of root voles (31 different individuals) with Longworth live-traps (600 trap nights) at six out of 15 localities (figure 2, table 1). At locality 62, while we were putting out traps, the dogs of the Director of the National Park caught three root voles. As this already confirmed the presence of the species, we immediately removed the traps we had set out at this locality. In the course of the trapping with 180 snap traps to the east of the Neusiedler See during one night in October 2011 we caught a root vole in the Viehhüter reedbed in the Zitzmannsdorfer Wiesen, north of Podersdorf (locality 18 in figure 2 and appendix). In the course of the trapping with Longworth live-traps in October 2012 (280 trap nights) we caught four different root voles at one of seven localities.

The plan to trace root voles on the west side of the Neusiedler See by finding their remains in owl pellets could not be satisfactory carried out. From 2011 to March 2015 only 10 samples of owl pellets were obtained from this side of the lake. The single sample of pellets of a barn owl in 2011 from the western side did not contain any root vole remains. A further five samples from this area collected during this period were just single pellets produced by long-eared owls and none of them contained any remains of root voles. Finally, remains in two barn owl pellet collections from 2013 and another two from March 2015, proved the current presence of the root vole on the west side of the Neusiedler See.

The presently proven distribution of the species is shown in figure 4. In the east there is a good spatial correspondence between the records from the pellets and the results from trapping, with the exception of the record from the southeastern corner of the study area (locality 66 in figure 2 and appendix). In the summer of 2014 remains of a root vole were found in a pellet of a short-eared owl in the Sankt Andräer Wiesen. This is the only recent record from the Austrian part of the Waasen / Hanság area, although the species is known to occur in the Hungarian part of this area (Gubányi et al. 2002).

Temporal steadiness and proportion in pellets

Sufficient samples illustrating the steadiness of the root vole in a longer period were only available from the Seewinkel. Owl and raptor pellet samples containing root vole from the years 1939 to 2014 (n=85) document the presence of the species at 55 localities. On the basis of these samples we made the following calculation. The minimum number of vertebrate prey items (MNVP) in samples of pellets containing the remains of root voles ranged from 4 to 1999. The majority, 88% (n=75), of the analysed owl and raptor samples of pellets were from just two species of owls, barn owl (n=62) and long-eared owl (n=13). Other owl and raptor species in whose pellets the root vole was recorded are: short-eared owl, little owl and falcons. The root vole made up between 0.2% and 14.8% (mean = 2.4%) of the MNVP of barn owl and between 0.2% and 31.8% (mean = 9.4%) of the MNVP in samples of pellets of long-eared owl (only samples with MNVP ≥ 100).

Samples of pellets were collected from seven localities over four or more years (table 2). There were marked annual fluctuations in the proportion of root vole found in most of these samples, although the temporal steadiness was higher than 0.5 in six of the seven localities, indicating a more or less stable presence of the root vole in the area.

Habitat

In 2011 we caught root voles at moist to dry habitats around small water bodies and in 2012 in the reed belt of the Neusiedler See itself. In one case the traps were placed in a vast *Carex* field with *Lycopus* spp., *Juncus* spp., *Molinia caerulea* and *Lythrum salicaria*, but without reed *Phragmites australis*. At all other further localities we placed the traps at the edge of some reed areas. The reed was mainly mixed with *Carex* spp. with undergrowth of the following combinations:

- *Lycopus* spp., *Mentha aquatica, Epilobium* spp.
- *Lycopus* spp., *Althea officinalis, Sonchus* spp.
- *Potentilla anserina*
- *Lycopus* spp., *Symphytum* spp., *Typha angustifolia, Lysimachia vulgaris*
- *Agrostis stolonifera, Molinia caerulea, Sonchus* spp., *Mentha aquatica, Schoenus nigricans*

The three specimens caught by dogs (see above) were found in a slightly unusual habitat: a dry mowed part of a meadow with *Cladium* and reed.

Discussion

This study confirmed the recent distribution of the root vole in the Seewinkel area east of the Neusiedler See. Besides, we found proof of its occurrence west of the Neusiedler See. However, the number of samples of recent pellets from the west is insufficient to draw further conclusions about the root vole's overall distribution in this area. Nowadays there are only very few barn owls present there.

The only sample of barn owl pellets from the west in 2011 and a few pellets from long-eared owls in 2014 failed to show any sign of root voles, yet samples from the same area taken in 1986 always delivered positive results. Besides, we also failed to trap any root voles at a nearby location with 180 snap traps in one night in 2011. However, two barn owl pellet samples collected in 2013 and 2015 from a restricted area northwest of Oggau proved again the presence of the root vole there. Further localities will have to be investigated by trapping in the future.

The sites where root vole was formerly caught to the north of the lake, near the village Neusiedl am See, have completely changed. The reed belt is now mostly a built up area, offering insufficient habitat for root voles. The root voles in the second area, the Teichwäldchen, at the edge of the Parndorfer Platte, were already regarded extinct by Spitzenberger & Bauer (2002). In recent years this former small wetland has deteriorated due to water regulation.

The second area where the root vole's presence in Austria was confirmed, also the best surveyed area since the 1980s, is located east of the Neusiedler See. It comprises the Seewinkel and Waasen/Hanság areas, including the reedbelt in the Neudegg area south of Apetlon, on the eastern shore of the lake. Data indicate rather stable populations in these restricted areas. Most of the sites are in the Neusiedler See – Seewinkel National Park, thus putting a special responsibility on the park management.

Our trapping mainly took place in reedbeds with a developed understory of *Carex* vegetation and *Schoenetum*. In the 1950s the biotope selection of the root vole in the Neusiedler See – Seewinkel area was broader, including wet woods (alder and willow carrs) and *Molinietum* vegetations (Bauer 1953, 1960). In the 1980s Hoi-Leitner (1986) was unable to catch the root vole in woods and *Molinietum* vegetations, suggesting that increased competition from other voles, e.g. bank vole (*Myodes glareolus*) in woods as a reason for this. This process of displacement may have been enhanced by the planting of more wood samples and rows of trees in the region. A main competitor vole in reedbeds, the field vole (*Microtus agrestis*), is absent in the area, so the root vole could stand its ground in that habitat.

Conclusions and recommendations for management

Since the 1960s the distribution of *Microtus oeconomus mehelyi* decreased on the northern side of the Neusiedler See. The species might even be extinct there. The distribution on the west of the lake needs to be investigated thoroughly. On the east side of the lake catches of the Pannonic root vole were quite numerous, which indicates that the species still occurs in reasonably good numbers in this part.

The root vole needs moist meadows with sedges, *Lycopus* or reed with understory of sedges. These biotopes can be found around the lake and around small water bodies in the Seewinkel area and need to be conserved. This implies no, or less, mowing of those meadows and reed beds, removing cut reed and restricting year-round grazing on the shores of water bodies. These conservation strategies need to be implemented by the management of the Neusiedler See - Seewinkel National Park and the political institutions in Austria.

To preserve the ecological niche for the Pannonic root vole, we recommend stopping-up drainage systems and returning agricultural land into marsh areas so that the connectivity of these populations can be maintained. Core areas should be separated from each other no more than three km, with stepping stones and corridors in between (Bergers et al. 1998).

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References

Bauer, K. 1953. Zur Kenntnis von *Microtus oeconomus méhelyi* Ehik. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 82 (1/2): 69–94.

Bauer, K. 1960. Die Säugetiere des Neusiedlersee-Gebietes (Österreich). Bonner Zoologische Beiträge 11 (2–4): 141–344.

Berg, H.-M. & R. Ille 2002. Zur Situation der Schleiereule (*Tyto alba* Scop.) in Ostösterreich. Egretta 45 (1–2): 122–134.

Bergers, P.J.M., B. van den Boogaard, D.P.E.M. Frissen & W. Nieuwenhuizen 1998. De noordse woelmuis in het Deltagebied. Richtlijnen voor beheer en inrichting. IBN-rapport 365. IBN, Wageningen, the Netherlands.

Demeter, A. & G. Topál 1987. Mammals of the Kiskunság. In: S. Mahunka (ed.). The fauna of the Kiskunság National Park. Volume 2: 446–452. Akadémiai Kiadó, Budapest, Hungary.

Donnerbaum, K. & J. Frühauf 2010. Artenschutzprojekt Schleiereule Ostösterreich, Umsetzungsphase 2006-2009. BirdLife Österreich, Vienna, Austria.

Gubányi, A. 2007. Északi pocok *Microtus oeconomus* (Pallas, 1776). In: Z. Bihari, G. Csorba & M. Heltai (eds.). Magyarország emlőseinek atlasza: 164–165. Kossuth Kiadó, Budapest, Hungary.

Gubányi, A., S. Kalmár & F. Mészáros 2002. Insectivores and rodents from the Fertő–Hanság National Park and its surroundings. In: S. Mahunka (ed.). The fauna of the Fertő–Hanság National Park. Volume 2: 787–798. Hungarian Natural History Museum, Budapest, Hungary.

Gubányi, A., A. Dudich, A. Stollmann & M. Ambros 2009. Distribution and conservation management of the root vole (*Microtus oeconomus*) populations along the Danube in Central Europe (Rodentia: Arvicolinae). Lynx (n.s.) 40: 29–42.

Hoi-Leitner, M.K. 1989. Zur Veränderung der Säugetierfauna des Neusiedlersee-Gebiets im Verlauf der letzten drei Jahrzehnte. Bonner Zoologische Monographien 29: 1–104.

Horváth, G.F., B. Horváth, N. Sali & R. Herczeg 2012. Community-level response to different human disturbances and land use of small mammals in two marshland habitat patches in Hungary. Archives of Biological Sciences 64 (2): 613–628.

Hubálek, Z., W. Sixl, Z. Šebek, D. Stünzner, H. Troger & M. Valová 1979. Adiaspiromycosis of wild small mammals in Austria. Folia Parasitologica 26: 159–164.

Krištofík, J. & A. Stollmann 2012. Hraboš severský – *Microtus oeconomus*. In: J. Krištofík & Š. Danko (eds.). Cicave Slovenska: rozšírenie, bionómia a ochrana: 115–118. VEDA (vydavateľstvo Slovenskej akadémie vied), Bratislava, Slovakia.

Lanszki, J. & G. Rozner 2007. Kisemlősök vizsgálata, különös tekintettel az északi pocok (*Microtus oeconomus* ssp. *mehelyi* (Éhik, 1928)) elterjedésére a Balatoni Nagyberekben. Natura Somogyiensis 10: 365–372.

Miklós, P., D. Žiak, M. Ambros, A. Dudich, A. Stollmann & V. Hulejová Sládkovičová 2014. Records of Pannonian root vole (*Microtus oeconomus mehelyi*) in the south–western Slovakia in 2011. Folia faunistica Slovaca 19 (1): 57–63.

Miklós, P., D. Žiak, M. Ambros & A. Stollmann 2011. Nové nálezy hraboša severského panónskeho (*Microtus oeconomus mehelyi*) v oblasti Podunajskej roviny. Folia faunistica Slovaca 16 (1): 19–23.

Mojsisovics von Mojsvár, A. 1897. Das Thierleben der österreichisch-ungarischen Tiefebenen. Alfred Hölder, Wien, Austria.

Mühlböck, P. 2003. Kleinsäuger auf beweideten und unbeweideten Flächen im Nationalpark Neusiedlersee-Seewinkel (mit populationsbiologischen und ökologischen Beiträgen). Diplomarbeit. Universität Wien, Wien, Austria.

Mühlböck, P. 2008. Einfluss der Beweidung auf die

Kleinsäugerzönosen im Nationalpark Lake Neusiedl – Seewinkel (Burgenland, Österreich). Abhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich 37: 325–344.

Pachinger, K. 1995. Habitat a perspektívy prežitia hraboša severského panónskeho (*Microtus oeconomus méhelyi* Éhik, 1928) na Slovensku. In: P. Urban & D. Baláž (eds.). Výskum a ochrana cicavcov na Slovensku [1]: 37–40. Slovenská agentúra životného prostredia – centrum Banská Bystrica & Stredoslovenská pobočka Slovenskej zoologickej spoločnosti SAV Zvolen, Banská Bystrica, Slovakia.

Pachinger, K. 2003. Restitution der Pannonischen Nordischen Wühlmaus (*Microtus oeconomus mehelyi* Éhik, 1928) in der mittleren Donauregion – Methoden und Erkenntnisse. In: M. Stubbe & A. Stubbe (eds.). Methoden Feldökologischer Säugetierforschung. Volume 2: 373–380. Gesellschaft für Wildtier- und Jagdforschung e.V. and Institut für Zoologie / Arbeitsgruppe Tierökologie der Martin-Luther-Universität Halle-Wittenberg, Halle (Saale), Germany.

Purger, J.J. 2014. Survey of the small mammal fauna in north-western Somogy county (Hungary), based on barn owl *Tyto alba* (Scopoli, 1769) pellet analysis. Natura Somogyiensis 24: 293–304.

Shenbrot, G.I. & B.R. Krasnov 2005. An atlas of the geographic distribution of the arvicoline rodents of the world (Rodentia, Muridae, Arvicolinae). Pensoft, Sofia, Bulgaria.

Spitzenberger, F. 1966. Ein Beitrag zur Ökologie und Biologie von Neusiedler Feldmäusen (*Microtus arvalis*). Natur und Land 52 (1): 18–21.

Spitzenberger, F. & K. Bauer 2002. Sumpfwühlmaus, Nordische Wühlmaus *Microtus oeconomus* (Pallas, 1776). In: F. Spitzenberger (ed.). Die Säugetierfauna Österreichs: 456-461. Austria Medien Service, Graz, Austria.

Samenvatting

De verspreiding van de Pannonische noordse woelmuis (*Microtus oeconomus mehelyi* Ehik, 1928) in Oostenrijk

Als onderdeel van een LIFE project voor de Pannonische noordse woelmuis hebben we het voorkomen in Oostenrijk onderzocht. Deze ondersoort, met een beperkt areaal rond het drielandenpunt van Oostenrijk, Slowakije en Hongarije, is in 1897 voor het eerst voor Oostenrijk vermeld. Het voorkomen in de periode tot 2010 brachten we in beeld aan de hand van literatuur, braakbalpartijen en documentatie over verzamelde exemplaren, aanwezig in het Natuurhistorisch Museum in Wenen. In de periode 2011-2015 onderzochten we gericht het huidige voorkomen door analyse van braakbalpartijen en vangen met inloopvallen en klemmen. In deze recente periode werd de noordse woelmuis binnen Oostenrijk aangetroffen aan de oost- en westzijde van de Neusiedler See, terwijl de soort vroeger ook ten noorden van dit meer aanwezig was. Tenslotte geven we aanbevelingen voor het beheer van leefgebieden van de Pannonische noordse woelmuis.

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Appendix

List of root vole specimens and owl pellets used in this survey. The numbers correspond with those in figure 2.

Specimens: locality [coordinates, elevation], collecting date, number and sex (m, f, ind),
museums inventory number or field number, collector's name, citation.

Owl pellets: locality, collecting date, number of specimens (MNVP of the pellet sample), museum inventory number or protocol number, collector's name, citation.

Coordinates of collection localities of all owl pellets and of specimens caught before 2010 are given in degrees and minutes, thus marking the south-western corner of the minute quadrant in which the locality is located. For owl pellets we accepted this coordinate accuracy (to minutes) for the whole study period (i.e. to date), while for specimens caught during the period of 2011-2014 we used (more accurate) coordinates to the nearest second of the collecting locality.

Niederösterreich

Fischamend

1. Fischamend [c. 48°07'N, 16°36'E], no date [before 1891]: [no voucher known, see discussion in the main text for this questionable locality] (Mojsisovics von Mojsvár 1897)

Bruck an der Leitha

2. E Bruck an der Leitha [c. 48°01'N, 16°49'E], 8 Nov. 1964: 1 ind. (voucher in coll. Steiner; leg. H.M. Steiner) (Spitzenberger & Bauer 2001)

Burgenland

Neusiedl am See

3. Teichwäldchen [47°57'N, 16°52'E, 160 m], 3 Feb. 1958: 1m (NMW 17319; leg. F. Spitzenberger) (Spitzenberger & Bauer 2001)
4. Kalvarienberg [47°56'N, 16°52'E, 160 m], Apr. 1957: 2 ind. in *Asio* sp. pellets (22) (NMW 'pellet files' G1957-4, no vouchers; leg. K. Bauer)
5. barrack [47°56'N, 16°51'E, 125 m], May 1951: 5 ind. in *T. alba* pellets (255) (NMW 'pellet files' G1951-5, no vouchers; leg. K. Bauer)
6. Bahnwärter [47°56'N, 16°51'E, 117 m], 21–22 Aug. 1964: 2 ind., 9m, 18f (NMW 9977–9996, 10000–10006, 10008, 10009; leg. F. Spitzenberger) (Spitzenberger 1966)
7. siltation area at Bad Neusiedl train station [47°56'N, 16°50'E, 116 m], 27, 28 Jul. 1952: 1m, 2f (NMW 56169–56171; leg. K. Bauer), 30 Jul. 1952: 2m, 3f (NMW 56172–56176; leg. K. Bauer) [one specimen donated to Museum Wiesbaden], 10–11 Aug. 1952: 4m, 2f (NMW 56183–56188; leg. K. Bauer), 26–27 Aug. 1952: 1m, 2f (NMW 56189–56191; leg. K. Bauer), 29 Aug. 1952: 2f (NMW 56192, 56193; leg. K. Bauer), 7 Nov. 1952: 1m, 2f (NMW 56177–56179; leg. K. Bauer), 10 Nov. 1952: 1f (NMW 56180; leg. K. Bauer), 18 Jul. 1953: 1m (NMW 56181; leg. K. Bauer), 18 Nov. 1953: 1m (NMW 56182; leg. K. Bauer), 7 Apr. 1962: 1m (NMW 56198; leg. K. Bauer)
8. former Seemuseum [47°55'N, 16°50'E, 116 m], 4 Apr. 1951: 10 ind. in *T. alba* pellets (179) (NMW 'pellet files' G1951-1, no vouchers; leg. E. Pieler)
9. siltation area, behind the former Seemuseum (= near the former Vogelwarte) [47°55'N, 16°50', 116 m], Jun. 1952: 1 ind. (NMW 9341; leg. E. Sochurek), 30 Aug. 1952: 1m (NMW 62670; leg. K. Bauer), 31 Aug. 1952: 1m (NMW 56197; leg. K. Bauer), 7 Nov. 1952: 2f (NMW 62671, 62672; leg. K. Bauer), 30 May 1964: obs. (H.M. Steiner) (Spitzenberger 1966), 6 Jul. 1964: 1m (NMW 9915; leg. F. Spitzenberger), 18 Jul. 1964: obs. 1 ind., swimming (M. Dangel) (Spitzenberger 1966), 29–30 Jul. 1964: 1m, 6f (NMW 9929, 9930, 9933–9937; leg. F. Spitzenberger) (Spitzenberger 1966), 30 Oct. 1964: 1m, 1f (NMW 10033, 10034; leg. F. Spitzenberger) (Spitzenberger 1966)
10. siltation area, SW Kote 123 [47°56'N, 16°51'E, 116 m], 8–9 Aug. 1952: 1m, 3f (NMW 56199–56202; leg. K. Bauer), 16 Aug. 1952: 1m, 1f (NMW 56203, 56204; leg. K. Bauer), 16–17 Nov. 1952: 1m, 2f (NMW 56205–56207; leg. K. Bauer)
11. siltation area [47°56'N, 16°50'E, 120–123 m], 22 Sep. 1958: 1m (NMW 17320; leg. F. Spitzenberger), 26 Oct. 1961: 1 ind., 1m, 2f (NMW 7958–7961; leg. K. Bauer), 19 Jun. 1962 1m (NMW 17321; leg. F. Spitzenberger), 5 Nov. 1984: 2 ind. (NMW 54167, 54168; leg. M. Leitner), 16 May 1985: 1f (NMW 54169; leg. M. Leitner), 3 Jul. 1985: 3m,

2f (NMW 54170–54174; leg. M. Leitner), 6 Dec. 1985: 1m, 3f (NMW 54175–54178; leg. M. Leitner), 21 Dec. 1985: 3m, 1f (NMW 54179–54182; leg. M. Leitner),12 Jun. 1986: 1m (NMW 54166; leg. M. Leitner), 31 Jul. 1986: 2f (NMW 54183, 54184; leg. M. Leitner), 1 Aug. 1986: 3m (NMW 54185–54187; leg. M. Leitner), 3 Aug. 1986: 1m (NMW 54188; leg. M. Leitner)

12. siltation area, reed storage place [47°56'N, 16°51'E, 123 m], 4 Sep. 1952: 1m, 1f (NMW 56194–56195; leg. K. Bauer), 8 Sep. 1952: 1f (NMW 56196; leg. K. Bauer), 4–6 Jul. 1964: 3m, 7f (NMW 9870–9872, 9876, 9884, 9885, 9894, 9906, 9907, 9914; leg. F. Spitzenberger) (Spitzenberger 1966), 31 Jul. 1964: 1m, 1f (NMW 9943, 9947; leg. F. Spitzenberger) (Spitzenberger 1966), 30 Oct. 1964: 2m (NMW 10043, 10044; leg. F. Spitzenberger)
13. Ebendorf, Neusiedler Wiesen [47°53'N, 16°52'E, 118 m], 14 Apr. 1977: 1 ind. in owl pellets (20) (NMW G1977-69-4; leg. A. Triebl)
14. Zitzmannsdorfer Wiesen [47°52-53'N, 16°51-52'E, 117 m], May 1954: 1 ind. in *A. flammeus* pellets (32) (NMW 'pellet files' G1954-8, no vouchers; leg. K. Bauer), Mar. 1957: 1 ind. in *T. alba* pellets (26) (NMW 'pellet files' G1957-2, no vouchers; leg. K. Bauer), 20 May 1985: 1 ind. in *A. otus* pellets (140) (NMW G1985-27-2; leg. M. Leitner), 4 Jul. 1985: 1m (NMW 54164; leg. M. Leitner), Viehhüter 47°53'26,79"N, 16°51'23,627"E Oct. 2011: 1m (NMW SE11/55; leg. S. Engelberger, N. Hattinger & B. Herzig)
15. Not mapped: Neusiedl am See [c. 47°56'N, 16°51'E], Jun. 1952: 2 ind. (NMW 9339, 9340; leg. E. Sochurek), 11–14 Jul. 1969: 1m (NMW 15349; leg. [F.] Lukoschus)
16. Not mapped: "reed belt", 19 Oct. 1985: 1m (NMW 54165; leg. M. Leitner)
17. Not mapped: between Neusiedl am See and Weiden [c. 47°56'N, 16°51'E, 123 m], Dec. 1983 – Jan. 1984: 1f (NMW 62339; W. Grüner)

Weiden

18. Unger-Berg [47°55'N, 16°53'E, 150 m], Jun. 1951: 2 ind. in *T. alba* pellets (69) (NMW 'pellet files' G1951-9, no vouchers; leg. K. Bauer), [1951 ?]: 3 ind. in *T. alba* pellets (60) (NMW 'pellet files' G1951-7, no vouchers; leg. K. Bauer)
19. church [47°55'N, 16°52'E, 127 m], 27 Jun. 1951: 11 ind. in *T. alba* pellets (1017) (NMW 'pellet files' G1951-10, no vouchers; leg. K. Bauer), Sep. 1951: 3 ind. in *T. alba* pellets (284) (NMW 'pellet files' G1951-12, no vouchers; leg. F. Wolf), Summer 1952: 1 ind. in *T. alba* pellets (417) (NMW 'pellet files' G1952-2, no vouchers; leg. K. Bauer), Jul. 1955: 1 ind. in *T. alba* pellets (502) (NMW 'pellet files' G1954-4, no vouchers; leg. K. Bauer), 5 ind. in *T. alba* pellets (292) (NMW 'pellet files' G1955-10, no vouchers; leg. K. Bauer), Mar. 1957: 1 ind. in *T. alba* pellets (19) (NMW 'pellet files' G1957-1, no vouchers; leg. K. Bauer)
20. Podersdorfer (=Weidener) Schoppen [47°53'N, 16°50'E, 115 m], 18 Apr. 1951: 15 ind. in *A. flammeus* pellets (27) (NMW 'pellet files' G1951-3, no vouchers; leg. E. Pieler), 28 May 1951: 2 ind. in *A. flammeus* pellets (8) (NMW 'pellet files' G1951-6, no vouchers; leg. K. Bauer), 28 Jun. 1951: 2 ind. in *A. flammeus* pellets (4) (NMW 'pellet files' G1951-11, no vouchers; leg. K. Bauer), no date [before 1961]: obs. of nests (K. Bauer) (Bauer 1960: 302–303)

Mönchhof

21. church [47°52'N, 16°56'E, 131 m], 4 Jul. 1971: 1 ind. in *T. alba* pellets (303) (NMW G1972-20-10; leg. W. Walter)

Gols

22. equestrian stadium [47°51'N, 16°51'E, 120 m], 25 Feb. 2009: 1 ind. in *T. alba* pellets (307) (NMW G2009-14-6; leg. V. Waba)

Podersdorf

23. NE margin of the settlement [47°51'N, 16°50'E, 122 m], 14 Jun. 2005: 1 ind. in *T. alba* pellets (75) (NMW G2006-9-4; leg. V. Waba), 10 May 2006: 4 ind. in *T. alba* pellets (523) (NMW G2006-17-5; leg. V. Waba)
24. barn [47°51'N, 16°50'E, 120 m], Spring–Summer 1984: 6 ind. in *T. alba* pellets (509) (NMW G1985-4-6; leg. J. Steiner)
25. Podersdorfer Heide, N Birnbaumlacke [47°49'N, 16°51'E, 122 m], May 1956: 1 ind. in *A. flammeus* pellets (20) (NMW 'pellet files' G1956-7, no vouchers; leg. K. Bauer)

Halbturn

26. Albrechtsfeld [47°48'N, 17°00'E, 130 m], 7 Apr. 1963: 1 ind. in *A. otus* pellets (>517 [only mammals counted]) (HMS 63/1, in coll. Steiner?; leg. A. Howorka)

Illmitz

27. Hölle [47°49'N, 16°47'E, 118 m], Spring–Summer 1984: 10 ind. in *T. alba* pellets (973) (NMW G1985-5-7; leg. J. Steiner), 14 Mar. 2008: 17 ind. in *T. alba* pellets (397) (NMW G2009-2-9; leg. V. Waba), 4 Apr. 2008: 3 ind. in *T. alba* pellets (130) (NMW G2008-12-7; leg. V. Waba), 17 Apr. 2008: 1 ind. in *T. alba* pellets (43) (NMW G2008-7-6; leg. V. Waba), 15 Feb. 2011: 1 ind. in *T. alba* pellets (127) (NMW G2011-07-7; leg. V. Waba)
28. Oberstinker [Oberer Stinkersee], SW-Ufer [47°48'N, 16°47'E, 129 m], May 1957: 1 ind. in *A. flammeus* pellets (16) (NMW 'pellet files' G1957-6, no vouchers; leg. K. Bauer)
29. NE Unterer Stinkersee [47°47'22" N, 16°46'51" E], Sep. 2011: 6 ind. (this study)
30. Gemeindewald [47°47'N, 16°46'E, 117 m], 19 Oct. 1980: 7 ind. in *A. otus* pellets (219) (NMW G1984-22-2; leg. R. Triebel)
31. Albersee [47°46'N, 16°46'E, 117 m], Apr. 1964: 37 ind. in *A. flammeus* pellets (465) (NMW G1971-5-4; leg. ?)
32. Stationskanal [47°46'N, 16°45'E, 117 m], 5 Apr. 1964: 3m, 1f (NMW 11143–11146; leg. M. Ganso)
33. Seedamm at the Biologische Station [47°46'N, 16°45'E, 117 m], 3 Feb. 1985: 1 ind. in *A. otus* pellets (16) (NMW G1985-22-2; leg. M. Leitner), 11 Jul. 1985: 1m (NMW 54163; leg. M. Leitner)
34. Biologische Station [47°46'N, 16°45'E, 117 m], 2 May 1985: 15 ind. in *A. otus* pellets (25) (NMW G1985-33-2; leg. M. Leitner), 3 Mar. 2005: 7 ind. in *A. otus* pellets (262) (NMW G2005-11-3; leg. A. Grüll), 6 Apr. 2005: 26 ind. in *A. otus* pellets (1229) (NMW G2006-11-7; leg. A. Grüll), Jan.–Mar. 2013: 9 ind. in *T. alba* pellets (16) (NMW G2013-08-1; leg. V. Waba), 14 Jun. 2013: 9 ind. in *T. alba* pellets (149) (NMW G2013-04-7; leg. V. Waba)
35. woodlot E Biologische Station [47°46'N, 16°46'E, 117 m], 16 Mar. 1985: 2 ind. in *A. otus* pellets (31) (NMW G1985-20-2; leg. M. Leitner)
36. Seewäldchen Nord [47°45'N, 16°45'E, 117 m], Pferdekoppel, 31 Aug. 2007: 6 ind. in *T. alba* pellets (130) (NMW G2007-30-6; leg. V. Waba), 8 Sep. 2008: 3 ind. in *T. alba* pellets (159) (NMW G2008-16-9; leg. V. Waba)
37. Seewäldchen Süd [47°45'N, 16°45'E, 117 m], Seekoppel, 22 Apr. 2008: 8 ind. in *T. alba* pellets (457) (NMW G2009-04-8, NMW G2008-8-7; leg. V. Waba)
38. Illmitzer Wäldchen [47°45'N, 16°45'E, 118 m], 25 Mar. 1964: 5 ind. in *A. otus* pellets (71) (NMW G1978-2-4; leg. M. Ganso), 30 Nov. 1975: 2 ind. in *A. otus* pellets (50) (NMW G1975-13-4; leg. M. Staudinger)
39. paddock "Warmblutkoppel" [47°45'N, 16°45'E, 117 m], 28 Apr. 2003: 3 ind. in *T. alba* pellets (161) (NMW G2003-16-6; leg. V. Waba), 21 Jun. 2003: 7 ind. in *T. alba* pellets (264) (NMW G2003-21-10; leg. J. Waba), May 2005: 9 ind. in *T. alba* pellets (242) (NMW G2006-2-8; leg. V. Waba), 2 Jun. 2006: 1 ind. in *T. alba* pellets (114) (NMW G2006-4-6; leg. V. Waba), 26 Apr. 2006: 6 ind. in *T. alba* pellets (207) (NMW G2006-14-4; leg. V. Waba), 27 Apr. 2007: 9 ind. in *T. alba* pellets (273) (NMW G2007-12-8; leg. V. Waba), 24 Jun. 2008: 15 ind. in *T. alba* pellets (155) (NMW G2009-3-7; leg. V. Waba), 11 Jun. 2010: 2 ind. in *T. alba* pellets (278) (NMW G2010-04-11; leg. V. Waba)
40. Illmitzer Kanal, 2 km W Illmitz [47°45'N, 16°46'E, 115–117 m], 30 Mar. 1964: 1f (NMW 54309; M. Ganso), 20 Mar 1985: 3 ind. in *A. otus* and *T. alba* pellets (101) (NMW G1985-23-4; leg. M. Leitner), 1 May 1985: 7 ind. in *A. otus* pellets (101) (NMW G1985-30-3; leg. H. Hoi)
41. reed storage place [47°45'N, 16°45'E, 115 m], 5 Jan. 1964: 1 ind. in *T. alba* pellets (67) (NMW 'pellet files' G1964-4, no vouchers; leg. H. Freundl), 5 Jan. 1964: 2 ind. in *A. flammeus* pellets (77) (NMW G1971-9-6; leg. M. Ganso), 24 Mar. 1964: 6 ind. in *A. flammeus* pellets (72) (NMW 'pellet files' G1964-3, no vouchers; leg. H. Freundl)
42. Sandeck [47°44'N, 16°46'E, 119 m], 25 Mar. 1964: 6 ind. in *Asio* sp. pellets (10) (NMW G1991-11-1; leg. H.-H. Bergmann), 4 Feb. 1965: 6 ind. in *A. flammeus* pellets (262) (NMW G1966-1-4; leg. E. Freundl), Mar. 1965: 4 ind. in *Asio* sp. pellets (40) (NMW 'pellet files' G1976-65, no vouchers; leg. H.

Freundl), 21 Apr. 1965: 5 ind. in *Asio* sp. pellets (50) (NMW G1974-27-2; leg. ?), 1 May 1985: 71 ind. in *A. otus* pellets (327) (NMW G1985-29-4; leg. H. Hoi), 21 Mar. 1986: 70 ind. in *A. otus* pellets (220) (NMW G1986-10-3; leg. M. Leitner), 4 Jun. 1987: 2 ind. in *T. alba* pellets (4) (NMW G1987-3-2; leg. M. Leitner), Spring 2005: 3 ind. in *T. alba* pellets (4) (NMW G2005-2-2; leg. V. Waba), 26 Apr. 2006: 5 ind. in *T. alba* pellets (299) (NMW G2006-1-6; leg. V. Waba), 4 Mar. 2009: 9 ind. in *T. alba* pellets (621) (NMW G2009-12-10; leg. V. Waba), 29 May 2010: 1 ind. in *T. alba* pellets (94) (NMW G2010-05-8; leg. V. Waba), 20 Mar. 2013: 61 ind. in *T. alba* pellets (786) (NMW G2013-02-9, NMW G2013-01-11; leg. V. Waba), 31 May 2013: 9 ind. in *T. alba* pellets (233) (NMW G2013-06-11; leg. V. Waba)

Sankt Andrä am Zicksee

43. N Zicksee [47°47'47" N, 16°54'25" E], Sep. 2011: 1 ind. (this study)
44. Ziegelhof at the Zicksee [47°47'N, 16°53'E, 121 m], Dec. 1961: 2 ind. in *T. alba* pellets (75) (NMW G2003-12-5; leg. P. Schubert), 16 Apr. 1962: 46 ind. in *T. alba* pellets (1127) (NMW G1962-7-13; leg. M. Ganso)
45. premises "Fa. Bruck" [47°47'N, 16°56'E, 122 m], 11 Jan. 1985: 5 ind. in *T. alba* pellets (116) (NMW G1985-1-6; leg. M. Leitner), 21 Mar. 1986: 2 ind. in *T. alba* pellets (22) (NMW G1986-9-2; leg. M. Leitner)

Apetlon

46. S Auerlacke [47°47'N, 16°53'E, 121 m], 24 Aug. 1977: 1 ind. in owl (*Asio* sp.?) pellets (39) (NMW G1977-86-2; leg. J. Reid)
47. N Östliche Wörtenlacke [47°46'46"N 16°52'40"E], Aug 2011: 1 ind.(Ch, Walder), [47°46'46"N 16°52'45"E], Aug. 2011: 5 ind. (Ch. Walder)
48. between Westliche- and Östliche Wörtenlacke, N bank [47°46'46"N, 16°52'12"E, 118 m], 7–12 Aug. and 6–12 Sep. 2001: 11 ind.; one voucher 6.Sep. 2001: 1f (NMW 63438; leg. P. Mühlböck) (Mühlböck 2003, 2008), reedbed [47°46'43"N, 16°52'21"E], Sep. 2010: 9 ind. (this study), low vegetation [47°46'44" N, 16°52'20" E], Sep. 2010: 4 ind. (this study)
49. E Wörtenlacken [47°46'N, 16°52'E, 118 m], 15 May. 1985: 6 ind. in *A. otus* pellets (8) (NMW G1985-21-2; leg. M. Leitner)
50. Seewinkelhof [47°45'N, 16°53'E, 119 m], 30 Jun. 1971: 1 ind. in *Athene noctua* pellets (24) (NMW G1971-19-5; leg. W. Walter)
51. cemetery [47°44'N, 16°49'E, 120 m], 10 Jan. 1985: 5 ind. in *A. otus* pellets (226) (NMW G1985-3-3; leg. M. Leitner), 16 Mar. 1985: 13 ind. in *A. otus* pellets (162) (NMW G1985-17-3; leg. M. Leitner), 1 May 1985: 11 ind. in *A. otus* pellets (53) (NMW G1985-35-2; leg. M. Leitner), 20 Jun. 1985: 81 ind. in *A. otus* pellets (667) (NMW G1985-36-6; leg. M. Leitner), 21 Mar. 1986: 42 ind. in *A. otus* pellets (320) (NMW G1986-12-2; leg. M. Leitner), 10 May 1992: 45 ind. in *A. otus* pellets (310) (NMW G2003-34-3; leg. M. Ganso), 3 Jan. 2014: 1 ind. in *Asio* sp. pellets (99) (NMW G2014-01-3; leg. B. Herzig)
52. Rebschulgasse [47°44'N, 16°50'E, 120 m], 8 Jul. 2005: 3 ind. in *T. alba* pellets (164) (NMW G2006-7-7; leg. V. Waba), 6 Jun. 2006: 2 ind. in *T. alba* pellets (64) (NMW G2006-8-7; leg. V. Waba)
53. church [47°44'N, 16°49'E, 120 m], Jun. 1957: 11 ind. in *T. alba* pellets (922) (NMW 'pellet files' G1957-8, no vouchers; leg. K. Bauer)
54. Ried Neufeld [47°44'N, 16°50'E, 120 m], 15 Jun. 1992: 1 ind. in *A. flammeus* pellets (20) (NMW G1997-128-2; leg. V. Waba)
55. Apetlon-Rohrung [47°44'N, 16°49'E, 120 m], 7 Sep. 1992: 1 ind. in *A. flammeus* pellets (26) (NMW G1997-94-2; leg. V. Waba)
56. barn "Graurinderstall" [47°43'N, 16°48'E, 118 m], 11 Jun. 2013: 5 ind. in *T. alba* pellets (163) (NMW G2013-07-9; leg. V. Waba), 23 Sep. 2013: 5 ind. in *T. alba* pellets (159) (NMW G2013-09-9; leg. V. Waba)
56. Apetloner Hof [47°43'N, 16°49'E, 117 m], 9 Apr. 2003: 1 ind. in *T. alba* pellets (283) (NMW G2003-25-7; leg. [V. Waba]), Spring 2004: 31 ind. in *T. alba* pellets (534) (NMW G2005-3-11; leg. V. Waba), 16 Jul. 2004: 2 ind. in *T. alba* pellets (65) (NMW G2005-5-5; leg. V. Waba), 1 Jul. 2005: 1 ind. in *T. alba* pellets (59) (NMW G2006-5A-4; leg. V. Waba), 2 Jun. 2006: 1 ind. in *T. alba* pellets (234) (NMW G2006-6-7; leg. V. Waba), 11 May 2006: 2 ind. in *T. alba* pellets (38) (NMW G2006-

16-5; leg. V. Waba), 15 Jan. 2007: 1 ind. in *T. alba* pellets (106) (NMW G2007-16-5; leg. V. Waba), 2 May 2007: 1 ind. in *T. alba* pellets (90) (NMW G2007-10-6; leg. V. Waba), 27 Feb. 2008: 1 ind. in *T. alba* pellets (233) (NMW G2009-05-5; leg. V. Waba), 1 Jul. 2008: 1 ind. in *T. alba* pellets (108) (NMW G2008-5-7; leg. V. Waba), 1 Sep. 2009: 2 ind. in *T. alba* pellets (222) (NMW G2010-01-13; leg. V. Waba), 26 Nov. 2009: 2 ind. in *T. alba* pellets (689) (NMW G2010-02-11; leg. V. Waba), 4 Feb. 2011: 1 ind. in *T. alba* pellets (239) (NMW G2011-04-8; leg. V. Waba), 14 Apr. 2011: 3 ind. in *T. alba* pellets (221) (NMW G2011-03-7; leg. V. Waba), 2 Mar. 2012: 1 ind. in *T. alba* pellets (55) (NMW G2012-03-6; leg. V. Waba), 15 Mar. 2012: 1 ind. in *T. alba* pellets (124) (NMW G2012-02-6; leg. V. Waba), 7 May 2012: 1 ind. in *T. alba* pellets (321) (NMW G2012-04-9; leg. V. Waba), 31 May 2013: 1 ind. in *T. alba* pellets (103) (NMW G2013-05-9; leg. V. Waba)

58. N Apetloner Hof [47°43'34" N, 16°50'39"E], Sep. 2010: 10 ind. (this study)
59. S Apetloner Hof [47°44'44" N, 16°50'38" E], Sep. 2010: 1 ind. (this study)
60. Neudegg [47°42'N, 16°49'E, 116 m], 24 Mar. 1985: 1 ind. in *T. alba* pellets (11) (NMW G1985-25-3; leg. A. Grüll),
61. Neudegg 47°41'49" N, 16°48'29 "E, Oct. 2011: 2 m, 2 f (this study)
62. 0.9 km NE Martentaulacke [47°43'47"N, 16°59'49"E], Sep. 2010: 3 ind. (this study)

Pamhagen

63. Schwarzseelacke [47°44'N 16°53'E, 118 m], 31 Mar. 1981: 1 ind. in *Falco* sp. pellets (10) (NMW G1991-13-2; leg. A. Grüll)

Wallern

64. premises "Fa. Mosony" [47°43'N, 16°56'E, 120 m], Jun. 2005: 1 ind. in *T. alba* pellets (51) (NMW G2006-3-4; leg. V. Waba)

Tadten

65. Tadtener Meierhof [47°45'N, 16°59'E, 119 m], 19 Sep. 1984: 3 ind. in *T. alba* pellets (1011) (NMW G1984-11-8; leg. F. Reithner)
66. St. Andräer Wiesen [47°43'N, 17°03'E, 111 m], 8 Jun. 2014: 1 ind. in *A. flammeus* pellets (4) (NMW G2014-6-1; leg. H.-M. Berg)

Jois

67. forest strip E Jois [47°57'N, 16°48'E, 160 m], Apr 1957: 6 ind. in *Asio* sp. pellets (337) (NMW 'pellet files' G1957-3, no vouchers; leg. K. Bauer)

Breitenbrunn

68. church [47°56'N, 16°44'E, 136 m], 23 Sep. 1958: 2 ind. in *T. alba* pellets (344) (HMS 58/15, in coll. Steiner; leg. H.M. Steiner)
69. Hannesgraben [47°56'N, 16°45'E, 117 m], 22 Mar. 1983: 5 ind. in mainly *T. alba* pellets (72) (NMW G1984-9-9; leg. A. Grüll & R. Szesemsky)

Purbach

70. church [47°54'N, 16°41'E, 128 m], 26 Oct. 1984: 20 ind. in *T. alba* pellets (520) (NMW G1984-26-8; leg. M. Leitner)

Donnerskirchen

71. church [47°53'N, 16°38'E, 190 m], summer 1952: 12 ind. in *T. alba* pellets (392) (NMW 'pellet files' G1952-1, no vouchers; leg. K. Bauer)
72. Wulka estuary [47°52'N, 16°42'E, 120 m], 15 Oct. 1939: 3 ind. in *T. alba* pellets (19) (NMW G2003-11-2; leg. A. Seitz & R. Lugitsch)

Oggau

73. mill "Seemühle an der Wulka" [47°52'N, 16°40'E, 120 m], 7 Jan 1962: 98 ind. in *T. alba* pellets (947) (NMW G1985-24-8; leg. F. Sauerzopf), 20 Sep. 1986: 22 ind. in *T. alba* pellets (930) (NMW G1986-13-9; leg. A. Seitz & R. Lugitsch)`, 22 May 2013: 11 ind. in *T. alba* pellets (27) (NMW G2015-01; leg. J. Sommer), 20 Mar 2015: 3 ind. in *T. alba* pellets (211) (NMW G2015-03; leg. J. Sommer, A. Ranner, K. & A. Grafl, B. Herzig)

73a. yard "Seehof an der Wulka" [47°52'N, 16°39'E, 125 m], 22 May 2013: 5 ind. in *T. alba* pellets (26) (NMW G2015-02; leg. J. Sommer), 20 Mar 2015: 1 ind. in *T. alba* pellets (172) (NMW G2015-04; leg. J. Sommer, A. Ranner, K. & A. Grafl, B. Herzig)

74. reed belt near Oggau [c. 47°50'N, 16°42'E, 120 m], 2 Jun. 1977: 5m (no vouchers) (Hubálek et al. 1979; pers. comm. Z. Hubálek, May 2014)

75. church [47°50'N, 16°40'E, 130 m], 10 Jul. 1971: 7 ind. in *T. alba* pellets (202) (NMW G1973-2-9; leg. W. Walter)

Oslip

76. church [47°50'N, 16°37'E, 133 m], 26 Oct. 1984: 7 ind. in *T. alba* pellets (1994) (NMW G1984-27-12; leg. M. Leitner)

Rust

77. church "Fischerkirche" [47°48'N, 16°40'E, 123 m], Jul. 1955: 6 ind. in *T. alba* pellets (122) (NMW 'pellet files' G1955-1, no vouchers; leg. K. Bauer)
78. Not mapped: Rust, 1964: 2 ind. in *T. alba* pellets (68) (NMW G1991-5-5; leg. H. Langer)

Mast, mice and pine marten (*Martes martes*): the pine marten's reproductive response to wood mouse (*Apodemus sylvaticus*) fluctuations in the Netherlands

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Abstract: Mast production of beech (*Fagus sylvatica*) and common oak (*Quercus robur*) have been found to be synchronous, with annually alternating patterns of high and low production between 1993 and 2013. We found this to be the case in the Netherlands where the fluctuations in the Veluwe and the neighbouring central areas of the country were the same as in Drenthe, in the north of the country. Wood mice (*Apodemus sylvaticus*) show an immediate and high numerical winter response following an autumn of high mast production, and they are a main source of prey for pine marten. Our study, of a total of 372 litters of pine martens (*Martes martes*), found that pine martens responded to years of peak wood mouse abundance with significant larger litters, as a result of relatively higher numbers of litters with four and five kittens. Their litters were also born about one week later in years of low wood mouse numbers. The female pine marten seems to adapt different hunting behaviour during pre-weaning according to the density of wood mouse. In years of low wood mouse abundance the duration of females' hunting bouts are longer than in years of high wood mouse densities.

Keywords: pine marten, *Martes martes*, litter size, mast years, wood mouse dynamics.

Introduction

Fluctuations in mast production of deciduous trees seems to be coordinated in northwestern Europe (Övergaard 2007). In the central Netherlands the mast production of common oak (*Quercus robur*) and beech (*Fagus sylvatica*) dips every two or three years. This is followed by a decline in wood mouse (*Apodemus sylvaticus*) populations (Wijsman 2012). Interactions between mast production, small rodent abundance and the responses of their predators have been widely investigated (Ostfeld et al. 1996, McShea 2000, Zalewski 2004, Jensen et al. 2012, Selva et al. 2012, Wijsman 2012).

In a small country, such as the Netherlands, it can be assumed that fluctuations in mast production will follow a similar pattern nationwide. As such, this present paper investigates pine marten (*Martes martes*) data from the northern provinces of Friesland and Drenthe over the period 1993-2014. This data was collected by the first author and is combined with data from Wijsman (2012), the latter (from the central provinces) extended by three more seasons. The purpose of this study is to establish correlations and the strength of relations between wood mouse abundance (dependent on mast production) and the functional responses of pine marten, using a combined dataset of two geographically separate study areas in the Netherlands. On the supposition that low wood mouse abundance during the pine martens' lactating period might affect the female's hunting effort and possibly reduce the chances of kitten survival, the hunting response of lactating females at two levels of wood mouse abundance was also investigated.

Material and methods

Study area

Over the recent years the distribution of the pine marten in the Netherlands appears to have extended (Broekhuizen et al. 2015). Overall, however, the area mapped in Wijsman (2012) and the northern provinces are the core areas of Dutch pine marten presence (figure 1).

The study areas in the central part of the Netherlands are characterised by relatively poor and acidic sandy soils. Beech (*Fagus sylvatica*), common oaks (*Quercus robur*) and American oaks (*Quercus rubra*) are widespread, interspersed with coniferous plantations and heathland (Wijsman 2012). The northern study area the Drents-Friese Wold and its surroundings, on the border of Friesland and Groningen, consists of woodland that is about 60 years old on diluvial sands, again relatively poor in nutrients. Conifers abound, but deciduous trees, including beech and oak (*Quercus* sp.) also cover a considerable surface. These woodlands are widely spaced apart, separated by flat peat land and cultivated land (Kleef & Tydeman 2009).

Mast

Seed production of oaks and beeches in the Veluwe has been monitored by G.J. Spek of the *Vereniging Wildbeheer Veluwe* and in Drenthe by R.G. Bijlsma (figure 1). The Veluwe data cover the total mast production of beech and oak from 1990 to 2014, expressed in kilogrammes x 10^6 . Bijlsma's data are based on seed counts of beech and oak over the period 1993 to 2013, expressed in index classes of 1 to 5 for each species.

Figure 1. Core areas of pine marten presence in the Netherlands. A=Utrechtse Heuvelrug; B=Veluwe; C=Salland; D=Drenthe.

Wood mouse

Wood mouse abundance in Drenthe was sampled monthly by R.G. Bijlsma by counting active burrows in three plots of 10x10 m, data which was made available for the present study. Live trap sampling and nocturnal observations in the plots revealed bank voles (*Myodes glareolus*) to occur only occasionally. Accordingly these burrows are considered to be those of wood mice alone. Densities are expressed as the average number of active burrows per plot. We compare wood mouse abundance in winter to mast production from the preceding autumn.

Pine marten

Pine marten reproduction was assessed in

Table 1. Total mast production in the Veluwe (kg x 10^6), beech and oak mast production in Drenthe (index 0-10), wood mouse density (mean), pine marten litter size (mean) and date of birth (day number). Number of observations in brackets.

	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Total mast*	9.2	3.6	7.8	5.0	2.8	4.3	1.9	6.0		
Beech / oak mast*	10	2	7	6	3	3	3	6	0	6
Wood mouse	5.8	0	1.6	2.7	0	4.6	0	3.6	0	3.1
Litter size	2.92 (37)	2.43 (30)	2.44 (32)	2.88 (43)	2.60 (40)	2.98 (46)	2.74 (35)	2.86 (36)	2.52 (42)	2.97 (31)
Date of birth				96.3 (24)	104.5 (32)	99.1 (37)	103.9 (29)	95.3 (31)	104.4 (40)	95.5 (28)

* preceding year

terms of litter size and the timing of litter production between 2005 and 2014 for nests in the Veluwe and 2008-2014 for those in the Drents-Friese Wold and surrounding woodlands. A total of 372 litters have been studied. Kittens were counted and aged, at an early stage whenever possible, to exclude early mortalities.

The age of kittens was estimated from overall habitus paying attention to their colour, the development of fur and throat patch and whether or not the eyes were open. The date of birth was expressed numerically as Julian date, accounting for leap years.

From the den activity patterns of the lactating female the average number of hours outside the natal den during the kitten's preweaning age (< 7 weeks), was calculated using Kleef & Tydeman's methodology (2009) of taking temperature recordings inside the den. The differences between years of high (group A: 1999, 2001, 2003, 2005, 2007) and low wood mouse abundance (group B: 1998, 2000, 2002 and 2006) were compared.

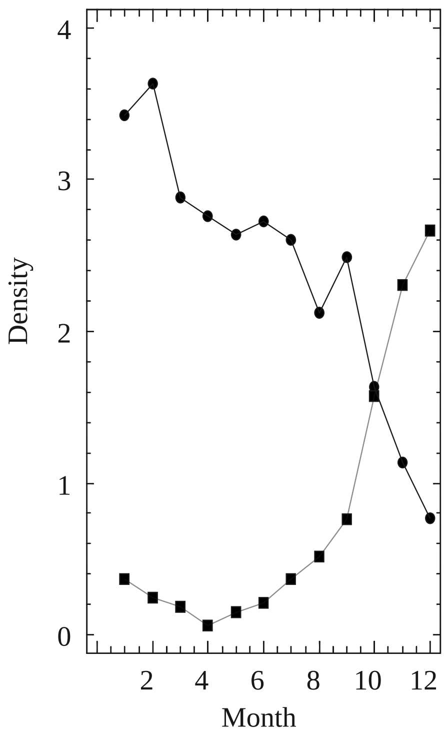

Figure 2. Seasonal variation of wood mouse density (mean) in 11 years of peak (circle) and 11 years of low density (square).

Statistical analyses

Relations between variables were tested by Pearson correlation and analysed by regression analysis when causality was suspected. Pearson correlation can be considered to be insensitive to non-normality and is to be preferred when using numeric variables (McDonald 2014).

The grouping of nominal variables was performed using Ward's method of cluster analysis and the results were subsequently tested for similarity using one-way analysis of variance (ANOVA) or two-sided *T*-tests when the

Table 2. Mean numbers and statistical differences for wood mouse density, pine marten litter size and date of birth in years of peak and low wood mouse density. Number of observations in brackets.

	Period	Peak	Low	*P*	Test
Wood mouse	1993-2014	2.21 (369)	0.78 (396)	0.0000	Mann-Whitney
Litter size	2005-2014	2.85 (225)	2.58 (147)	0.0054	ANOVA
Date of birth	2008-2014	96.7 (120)	104.3 (101)	0.0000	*T* - test

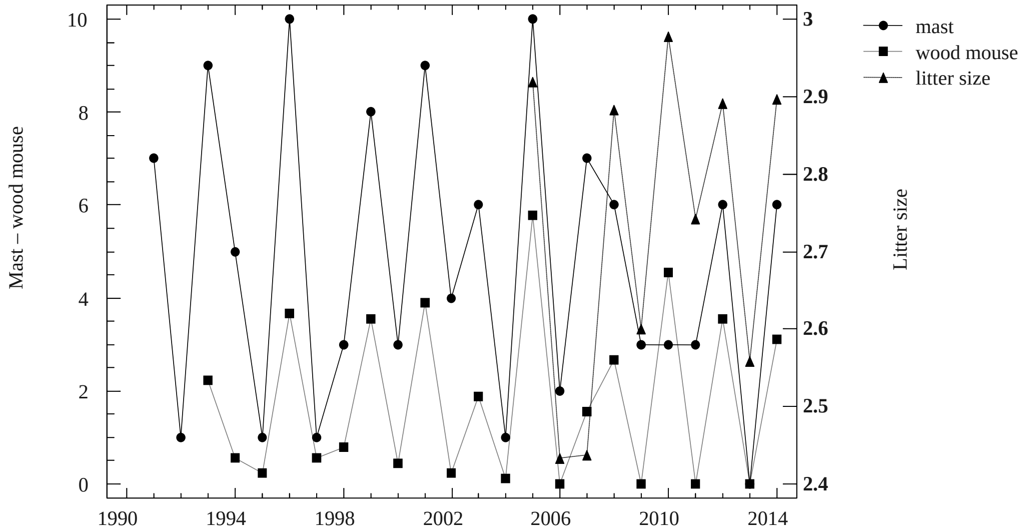

Figure 3. Beech/oak mast index (circle) in Drenthe, mean wood mouse density (square) and mean pine marten litter size (triangle) in the period 1991–2014. The mast index relates to the preceding year.

parametric conditions came close to normality and equality of variances. If far from these conditions a nonparametric Mann-Whitney signed rank test was used.

Results

The relationship between mast production and wood mouse abundance

Wood mouse densities increased throughout the year to reach a maximum number in winter and early spring. This increase was more pronounced in years of high numbers (see figure 2 and table 1). The abundance of wood mouse in late winter might be an important factor in the reproductive cycle of pine marten females because the blastocysts are on the verge of being implanted in the uterus wall. This process depends upon food availability and other factors such as photoperiod. According to Stubbe (1993, quoted in Stier 2012) the period of implantation ranges from mid-January to mid-March throughout the pine marten's geographical distribution. As such we chose to calculate annual densities of wood mouse for the period of January-March and compared these figures with the combined beech and oak mast production in Drenthe in the preceding autumn (see figure 3).

There was a significant correlation in beech and oak mast production in Veluwe and Drenthe (Pearson correlation R=0.6003, *P*=0.0051, resp. R=0.5725, *P*=0.0035). The total crop of beech and oak seeds was compared to the combined indices of beech and oak mast in the Drents-Friese Wold in order to look for spa-

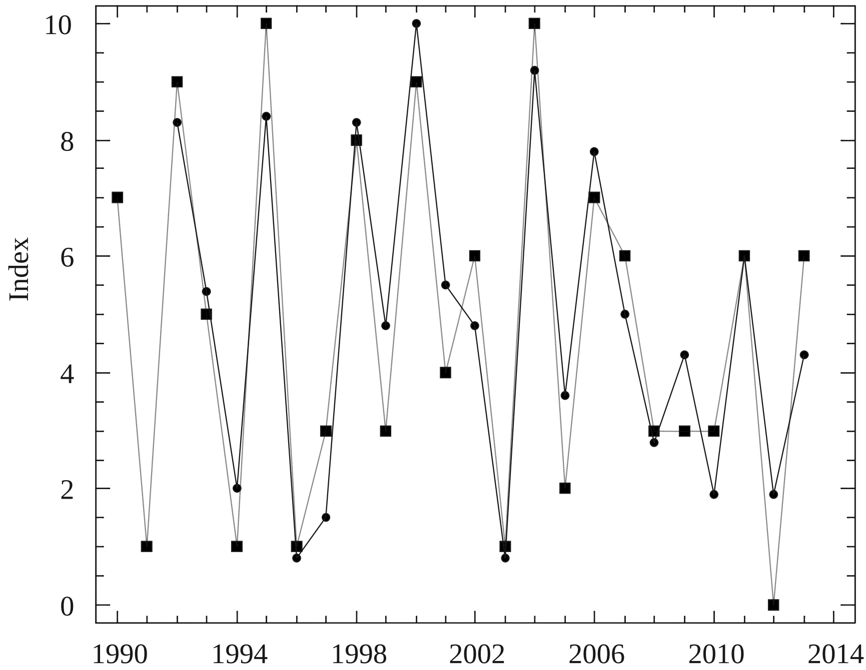

Figure 4. Total mast crop in the central area (circle) and beech/oak mast in the northern area of the Netherlands (square).

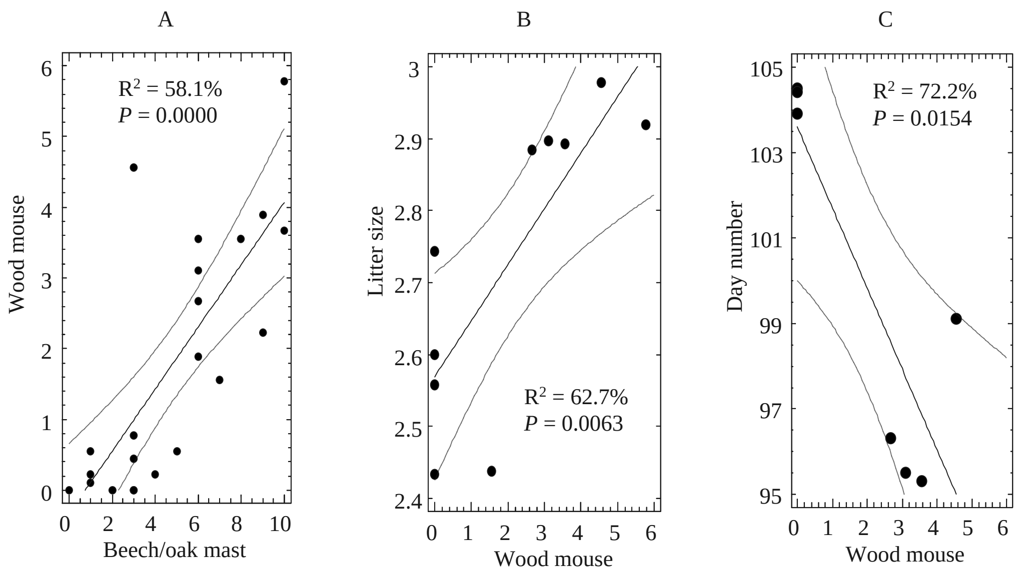

Figure 5. A: beech/oak mast (index) related to mean wood mouse density. B: mean wood mouse density related to mean pine marten litter size. C: mean wood mouse density related to pine marten mean date of birth, expressed as day numbers.

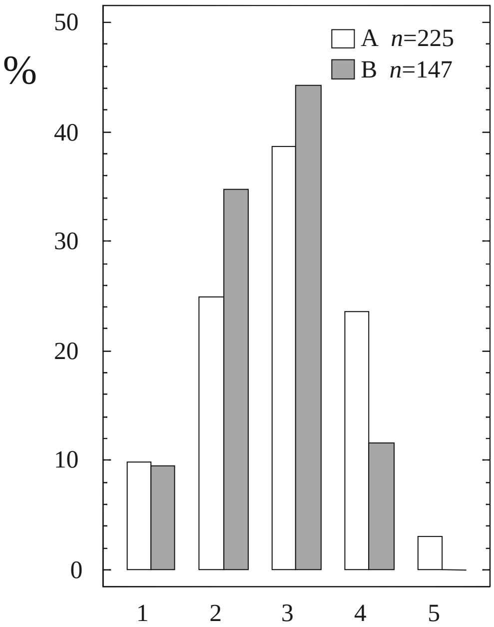

Figure 6. Relative distribution of pine marten litter size (%) in years of peak (A) and low (B) wood mouse density.

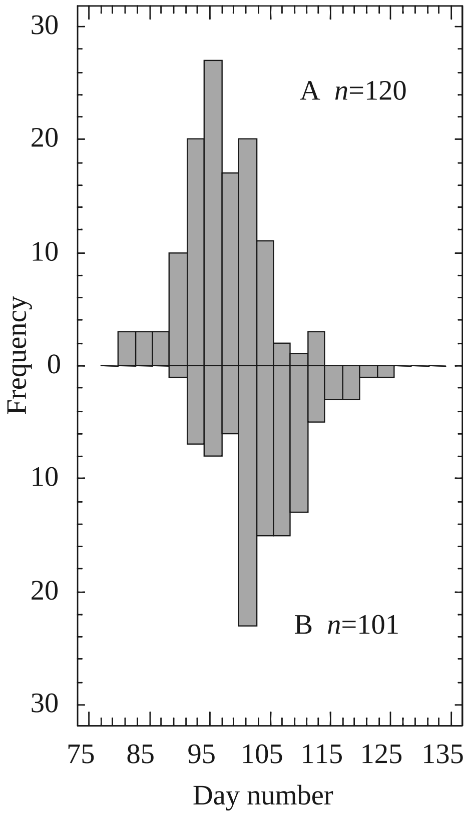

Figure 7. Frequency distribution of date of birth of pine marten litters (by day number) in years of peak (A) and low (B) wood mouse densities.

tial similarities in annual mast fluctuations. Masting in the two areas of the Netherlands was highly synchronised (Pearson correlation R=0.9259; P<0.0001) (see figure 4 and table 1).

The annual variations in masting and wood mouse abundance were also highly correlated (Pearson correlation R=0.7625; P<0.0001); 58% of the variation in wood mouse density was explained by mast variations (P<0.0001, figure 5A). Beech mast and oak mast were separately also significantly correlated with wood mouse numbers (Pearson correlation R=0.7931, P<0.0001 and R=0.5561, P=0.0072 respectively).

Wood mouse numbers and pine marten litter size

Apart from some minor deviations, wood mouse numbers showed a regular alternating pattern of high and low indices (figure 3). As such we grouped the years of high and low densities. The average index in wood mouse peak years (2.21 ± 0.10 SE) was almost three times higher than in low years (0.78 ± 0.07 SE), the difference being significant (Mann-Whitney, P<0.0001; table 2). The litter size of pine martens showed a similar pattern with larger litters in peak years of wood mouse (2.85 ± 0.07 SE) and smaller ones in years of low wood mouse abundance (2.58 ± 0.07 SE). Again, the difference is significant (ANOVA, P=0.0054; table 2). It was notable that litters of four and five kittens were more frequent in peak years of wood mouse (figure 6). Wood mouse abundance accounted for 63% of the variation in pine marten litter size (P=0.0063, figure 5B).

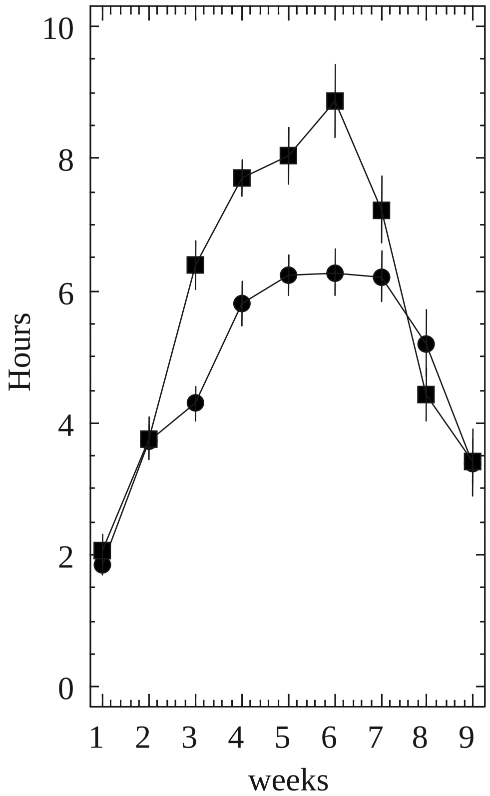

Figure 8. Time (hours) spent outside the natal den by the female pine marten related to the age (weeks) of the kittens in peak (circle) and low (square) wood mouse years.

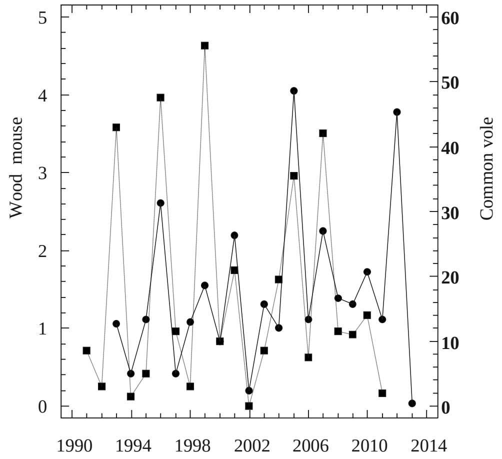

Figure 9. Mean densities of wood mouse (circle) and common vole (square) in the period 1991-2013.

The abundance of wood mouse and the date of birth of pine marten litters

The dates of birth of pine marten ranged between the second half of March and the first week of May, peaking in the second week of April. Birth dates in years of peak wood mouse numbers ranged from day 80 to day 112, but was later in years of low wood mouse numbers (days 91 to 125; figure 7). The average birth date in wood mouse peak years (day number 96.7 ± 0.55 SE) was about one week earlier than in years of low wood mouse numbers (day number 104.3 ± 0.68 SE) (*T*-test, *P*<0.0001, table 2). Wood mouse abundance accounted for 72% of the variation in these birth dates (*P*=0.0154, figure 5C).

The abundance of wood mouse and the activities of female pine martens

In years of low wood mouse densities the females' hunting time was on average one hour longer than in years of high wood mouse numbers (6.45 h ± 0.22 SE, resp. 4.99 h ± 0.14 SE) (*T*-test, *P*<0.0001). The time spent outside the den was strongly correlated with the kittens' age (*P*=0.0033; figure 8), increasing during lactation to about two and a half hours when the kittens reached 6 weeks of age, after which it declined towards the start of weaning.

Discussion and conclusions

Mast and mice

In a review of 15 studies on feeding ecology, Clevenger (1994) reported wood mice (*Apodemus* sp.), voles (*Microtus* sp.) and bank voles (*Myodes* sp.) to be the principal food of Eurasian pine martens. The representation of these species in the marten's diet varies with geographical region and prey density

(Jędrzejewski et al. 1993, Pucek et al. 1993, Helldin & Lindstrom 1995, Helldin 1999, Zalewski 2004, Rosellini et al. 2008). The densities of small rodents in winter and spring respond strongly to mast production (Jensen et al. 2012).

In the Netherlands bumper years of oak and beech are correlated but as oak trees are more common than beech trees, acorns account for the majority of the mast crop. The classic publication of the Białowieża Forest Group (Pucek et al. 1993) involves a 33-year long study of the population dynamics of small rodents. As there are no beech trees in Białowieża this may limit the relevance of this study to the Netherlands.

Data from Perdeck et al. (2000) and Hilton & Packham (2003) shows that the general biennial pattern of the fluctuation in beech mast production can be found in the Netherlands, England, Germany, Denmark and Sweden. A more or less synchronous production of beech mast production has also been observed over a wide area of northeastern Europe (Pucek et al. (1993) and the authors quoted by Perdeck et al. (2000)). In this light the correlation found in different parts of a small country such as the Netherlands is not surprising. Beech nuts are available as food for small mammals beyond the end of winter as witnessed by the many seedlings in May after a peak mast year (cf. Gurnell 1993).

The fluctuations in wood mouse numbers may be ascribed to fluctuations in mast production. Interestingly, although microtine species may occupy different habitats, their densities often show synchronous fluctuations. A study by Tkadlec et al. (2011) confirmed significant correlation in the annual fluctuations of common vole (*Microtus arvalis*) and wood mouse (figure 9, R=0,5966, *P*=0.0070). According to Zalewsky (2007), Elmeros et al. (2008) and Balestrieri (2011), bank voles are the more important prey item for pine martens. In general however the pine marten is an opportunistic feeder and can easily switch to different prey items according to the season, geographical range and abundance of prey (Jędrzejewski et al. 1993). Live trapping carried out around the 1st of March in 2013 (after a year of low mast production), caught 15 wood mice, while trapping the following year, at around the same time caught 115 wood mice, a factoral difference of 7.6 (Wijsman, unpublished results). Only a small fraction of the animals trapped in this study were voles. In another Dutch situation, the bank vole was also only occasionally found (Dijkstra 2013), indicating the wood mouse to be the main available prey item. In years with a high mast crop the wood mouse female produces about four litters with an average of five new born in each, which become reproductive after about 65 to 71 days (Bijlsma 2012). This high reproduction rate immediately after high autumn mast production results in peak wood mouse populations in winter and spring into the summer, producing a major food source that is easily available to the pine marten during a period that is of vital importance to successful reproduction.

Martens

Numerical responses of mustelids following cycles in microtine numbers have been documented in many studies (e.g. Erlinge 1981, Helldin 1999, Simon et al. 1999, Zalewski & Jędrzejewski 2006, Jensen et al. 2012). However these results do not always appear to be consistent and may sometimes reflect trap vulnerability more than actual numbers. Pine marten's longevity and territorial food behaviour result in a low potential increase rate and a slow numerical reaction to annual fluctuations in microtine numbers (Helldin & Lindstrom 1995, Helldin 1999). Our study has focused on the functional response of pine martens in terms of litter size, date of birth (Wijsman 2012), and the female's daily activity pattern. Pine martens in the Netherlands produce litters averaging 2.74 (this study). In years of peak abundance of wood mice more litters of 4-5 kittens were produced, increasing the average litter size compared to years of low wood mouse abundance, suggesting that reproduction might be influenced by food availability. Low populations of rodents result in smaller litters (Simon et al. 1999) possibly due to a higher mortality of embryos and nestlings (King et al. 2003 for the stoat, *Mustela erminea*, and Kirkpatrick 1988 (quoted by Frost & Krohn 1997) for the fisher, *Martes pennanti*). However, pine martens may compensate for there being fewer small rodents by switching to alternative prey, such as birds (Thompson & Colgan 1990, Jędrzejewski et al. 1993, Wijsman 2012). This might explain the small difference of litter sizes between years of peak and low wood mouse numbers. There is currently little data available on the survival and recruitment of young born pine martens in years with high and low mice numbers. Larger litters will only contribute to reproductive success if the kittens survive to be recruited into the population and to reach sexual maturity (Frost & Krohn 1997).

The date of birth was also influenced by wood mouse numbers. In peak wood mouse years the date of birth was about a week earlier, indicating advanced implantation. Early implantation may relate to the female pine marten being in good physical condition in years of food abundance during the relevant photoperiod. While the photoperiod lasts for a timescale of several months, the pine marten's body condition determines implantation on a timescale of days. Early birth gives the kittens longer to grow and to gain experience after reaching independence before winter starts as has been found among badgers (Woodroffe 2009).

Food availability may affect the female's hunting success and her capacity to meet the energetic demands of lactation, especially in the pre-weaning period when the kittens are less than seven weeks old. In years of low wood mouse availability, the average time females spent outside the den during the pre-weaning period was about 28% longer than in years of high abundance (Kleef & Tydeman 2009), increasing to 41% by the time kittens were near weaning. However the total proportion of time spent outside the natal den appears to be equal among years of peak and low wood mouse densities (about 29%), indicating that extended hunting bouts force the female to hunt less frequently.

Longer hunting bouts may provide a sufficient success rate under low food conditions as the pine marten hunts over a larger radius of action. Changing her hunting behaviour in this way especially during pre-weaning only stresses the high demand of sufficient food supply during lactation (Zielinski 2000, Kruuk 2002). A small litter may then be helpful.

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References

Balestrieri, A., L. Remonti, A. Ruiz-González, M. Vergara, E. Capelli, B.J. Gómez-Moliner & C. Prigioni 2011. Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). Acta Theriologica 56: 199–207.

Bijlsma, R.G. 2012. Mijn roofvogels. Atlas Contact, Amsterdam, the Netherlands.

Broekhuizen, S., G.J.D.M. Müskens & H.J.W. Wijsman in press. Boommarter *Martes martes* (L., 1758). In: S. Broekhuizen, K.J. Canters, K. Spoelstra & J.B.M. Thissen (eds.). Atlas van de Zoogdieren van Nederland. Nationaal Natuurhistorisch Museum Naturalis, European Invertebrate Survey, Leiden, the Netherlands.

Clevenger, A.P. 1994. Feeding ecology of Eurasian pine martens and stone martens in Europe. In: S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell (eds.). Martens, sables and fishers: biology and conservation: 326-340. Cornell University Press, Ithaca, New York, USA.

Dijkstra, V. 2013. Over muizen en boommarters. Zoogdier 24 (3): 1-3.

Elmeros, M., M.M. Birch, A.B. Madsen, H.J. Baagøe & C. Pertoldi 2008. Skovmårens biologi og levevis i Danmark. Udredning om skovmårens økologi og forslag til fremtidig forskning og forvaltning. Faglig rapport fra DMU nr. 692. Danmarks Miljøundersøgelser, Aarhus Universitet, Denmark. [in Danish].

Erlinge, S. 1981. Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden. Oikos 36: 303-315.

Frost, H.C. & W.B. Krohn 1997. Factors affecting the reproductive success of captive female fishers. In: G. Proulx H.N. Bryant & P.M. Woodard (eds). Martes: taxonomy, ecology, techniques and management: 100-109. Provincial Museum of Alberta, Alberta, Canada.

Gurnell, J. 1993. Tree seed production and food conditions for rodents in an oak wood in southern England. Forestry 66 (3): 292-315.

Helldin, J.O. & E.R. Lindström 1995. Dietary and numerical responses of pine marten (*Martes martes*) to vole cycles in boreal Fennoscandia. In: I.D. Thompson (ed.). Proceedings of the International Union of Game Biologists. XXI Congress: 220-224. Halifax, Nova Scotia, Canada.

Helldin, J.O. 1999. Diet, body condition and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. Ecography 22 (3): 324-336.

Hilton G.M. & J.R. Packham 2003. Variation in the masting of common beech (*Fagus sylvatica* L.) in northern Europe over two centuries (1800-2001). Forestry 76: 319-328

Jensen, P.G., C.L. Demers, S.A. McNulty, W.J. Jakubas & M.M. Humphries 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. Journal of Wildlife Management 76 (3): 489-502

Jędrzejewski W., A. Zalewski & B. Jędrzejewska 1993. Foraging by pine marten *Martes martes* in relation to food resources in Białowieża National Park, Poland. Acta Theriologica 38 (4): 405-426.

King, C.M., P.C.L. White, D.C. Purdey & B. Lawrence 2003. Matching productivity to resource availability in a small predator, the stoat (*Mustela erminea*). Canadian Journal of Zoology 81 (4): 662-669.

Kleef, H.L. & P. Tydeman 2009. Natal den activity patterns of female pine martens (*Martes martes*) in the Netherlands. Lutra 52 (1): 3-14.

Kruuk, H. 2002. Hunter and hunted; relationships between carnivores and people. Cambridge University Press, Cambridge, UK.

McDonald, J.H. 2014. Handbook of Biological Statistics (3rd ed.). Sparky House Publishing, Baltimore, Maryland, USA.

McShea, W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81 (1): 228-238.

Ostfeld, R.S., C.G. Jones & J.O. Wolff 1996. Of mice and mast. Ecological connections in eastern deciduous forests. Bioscience 46 (5): 323-330.

Övergaard, R., P. Gemmel & M. Karlsson 2007. Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry 80: 555-565.

Perdeck, A.C., M.E. Visser & J.H. van Balen 2000. Great Tit *Parus major* survival and the beech-crop cycle. Ardea 88: 99-106.

Pucek, Z., W. Jędrzejewski, B. Jędrzejewska & M. Pucek 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop and predation. Acta Theriologica 38: 199-232.

Rosellini, S., I. Barja & A. Piñeiro 2008. The response of european pine marten (*Martes martes*) feeding to the changes of small mammal abundance. Polish Journal of Ecology 56 (3): 497-504.

Selås, V., E. Framstad & T.K. Spidsø 2002. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. Journal of Zoology 258 (4): 459-468.

Selva, N., K.A. Hobson, A. Cortés-Avizanda, A. Zalewski & J.A. Donázar 2012. Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PloS ONE 7 (12):

e51267. Doi: 10.1371/journal.pone.0051267.
Simon, N.P.P., F.E. Schwab, M.I. LeCoure & F.R. Phillips 1999. Fall and winter diet of martens (*Martes americana*) in central Labrador related to small mammal densities. Canadian Field-Naturalist 113: 678-680.
Stier, N. 2012. Zur Populationsökologie des Baummarders (*Martes martes* L., 1758) in Nordost-Deutschland. Wildtierforschung in Mecklenburg-Vorpommern, Band 1. Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz, Mecklenburg-Vorpommern, Schwerin, Germany.
Tkadlec, E., J. Suchomel, L. Purchart, M. Heroldová, L. Čepelka & M. Homolka 2011. Synchronous population fluctuations of forest and field voles: implications for population management. 8th European Vertebrate Pest Management Conference. Julius-Kühn-Archiv 432: 97-98.
Thompson, I.D. & P.W. Colgan 1990. Prey choice by marten during a decline in prey abundance. Oecologia 83: 443-451.
Wijsman, H.J.W. 2012 The effects of small rodent density fluctuations on the pine marten (*Martes martes*). Lutra 55: 29-40
Woodroffe, R. 2009. Body condition affects implantation date in the European badger, *Meles meles*. Journal of Zoology 236 (2): 183-188.
Zalewski, A. 2004. Geographical and seasonal variation in food habits and prey size of European pine martens. In: D.J. Harrison, A.K. Fuller & G. Proulx (eds). Martens and Fishers (*Martes*) in human-altered environments: an international perspective: 77-98. Springer-Verlag, New York, USA.
Zalewski, A. & W. Jędrzejewski 2006. Spatial organization and dynamics of the pine marten *Martes martes* population in Białowieża forest (E.Poland) compared with other European woodlands. Ecography 29: 31-43.
Zielinski, W.J. 2000. Weasel and Martens – Carnivores in Northern latitudes. In: S. Halle & N.C. Stenseth (eds). Activity patterns in small mammals: 95-118. Ecological Studies 141. Springer-Verlag, Berlin / Heidelberg, Germany.

Samenvatting

Mast in relatie tot muizen en de voortplantingsrespons van de boommarter (*Martes martes*) op aantalsfluctuaties van de bosmuis (*Apodemus sylvaticus*) in Nederland

De mastdynamiek van eik en beuk vertoont niet alleen onderling een parallel verloop maar ook regionaal verlopen de fluctuaties synchroon. Jaren met een hoge productie van mast werden gevolgd door een hoge dichtheid van bosmuizen in de daaropvolgende winter en voorjaar. Bij 372 boommarternesten werd in de periode 2005 tot 2014 het aantal jongen geteld en het tijdstip van de geboorte werd geschat. In jaren met hoge bosmuisdichheid werden er bij de boommarter meer jongen geboren dan in jaren met lage dichtheid. In de jaren met lage dichtheid vond de geboorte ongeveer een week later plaats en het boommartermoertje moest langer op jacht gedurende de zoogperiode.

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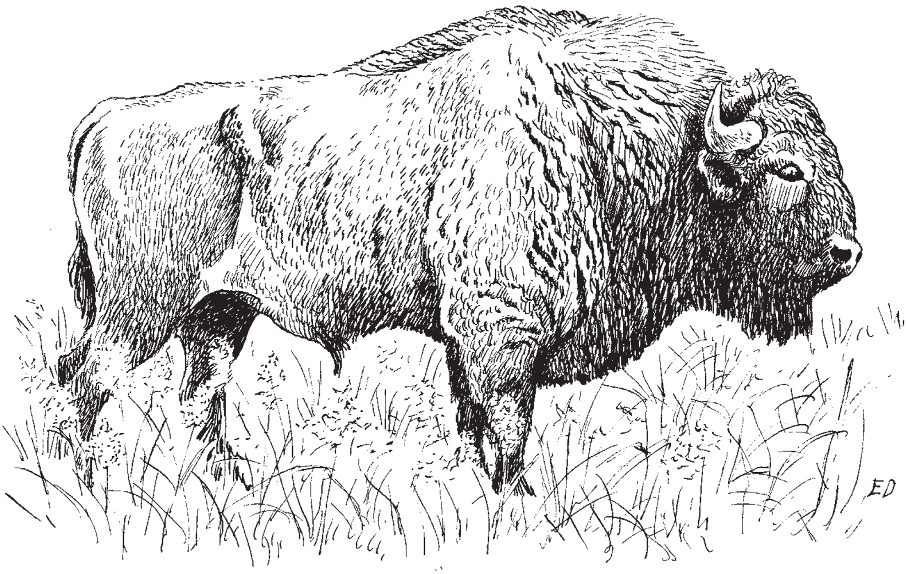
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Is the wisent (*Bison bonasus*) indigenous to the Netherlands and Belgium?

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Abstract: Some documents claim that the wisent (*Bison bonasus*) was present in north-western Europe during the Middle Ages. With the introduction of the wisent into Dutch nature management these claims are being repeated again. This article examines these claims and whether they tally. Bone finds would indisputably prove the former existence of the wisent in the Netherlands and Belgium. Records of bone finds show wisent did occur in north-western Europe in the Early Holocene, but no demonstrable wisent bones from the Middle and Late Holocene have been found in this area. The distribution of wisent bone finds in Europe shows that *Bison bonasus* mainly lived in central and eastern Europe. The spread of wisent toponyms in Germany also seems to reflect the preference of the wisent for a continental climate. This paper examines the written sources that make claims for the occurrence of the wisent in the Middle Ages in southern Sweden, England, Belgium and the Netherlands. It is clear that there are no reliable data. The claims partly arose due to name confusion with aurochs (*Bos primigenius*), partly through inaccurate interpretations of texts, and partly by people simply advancing unsubstantiated assertions. If the wisent occurred in the Netherlands and Belgium in the Middle and Late Holocene, it must have been just a rare vagrant, not a resident species.

Keywords: wisent, *Bison bonasus,* aurochs, *Bos primigenius*, archaeozoology, philology, occurrence, Belgium, the Netherlands.

Introduction

The wisent (or European bison, *Bison bonasus*) is increasingly playing a role in Dutch nature management. In 2007 some individuals were introduced into the Kraansvlak nature reserve near Zandvoort, in the Province of North Holland (Smit et al. 2008, Janssen 2015, and www.wisenten.nl) and there are currently plans to release wisents close to Kootwijk, in the Veluwe area (Kas 2014, Janssen 2015, and www.wisentopdeveluwe.nl). The rationale is that they are effective grazers, in need of conservation – as they are still an endangered species - and will attract tourists.

This introduction of the wisent is backed up by the proposition that this animal was unquestionably part of the Netherlands' native fauna during the Middle and Late Holocene. It is claimed that this animal was not only native to the Netherlands, but also that it lived in southern Sweden in the 11th century, in England during the 12th century and in the Ardennes (Belgium / Luxembourg) during the 14th century (for these claims see the websites referred to above, Pucek 1986 and Janssen 2015). In the Netherlands, *Bison bonasus* bones have been dredged up off of the North Sea coast (Drees & Post 2007) and it is claimed that even 'about 1000 years' ago, the animal was still present here (Smit et al. 2008, Janssen 2015). However very few supporting arguments have been put forward by the authors of the texts cited above and it is worth enquiring where these claims come from and whether they actually tally.

Method

To find out whether and when *Bison bonasus* occurred in the Netherlands and Belgium during the Holocene, I have searched written sources for mentions of wisent bones and of the occurrence of the wisent, and explored BoneInfo (http://archeologieinnederland.nl/bronnen-en-kaarten/boneinfo), the archaeozoological database.

Results

Bones

There are nearly no finds of wisent bone material from the Netherlands and Belgium from the Holocene, and in the Netherlands there are no finds from the Middle and Late Holocene (Zeiler & Kooistra 1998, Louwe Kooijmans 2012, BoneInfo)[1]. It is only from the transition period between the Late Pleistocene and Early Holocene that a number of bones (of which 14 metacarpi were investigated) were found in the Dutch part of the North Sea, which are all attributed to *Bison bonasus* (Drees & Post 2007). These belong to a small type of *Bison bonasus*, much smaller than the steppe bison (*Bison priscus*) which frequently occurred on the steppes of our regions during the last ice age. This *Bison bonasus*, which lived on the plains that are now covered by the North Sea, was significantly smaller than the today's wisent (Drees & Post 2007). Remains of *Bison bonasus* from the Early Holocene have also been found in Denmark (Degerbøl & Iversen 1945: Late Dryas) and Sweden (Ekström 1993: 8700 BP). As in the Netherlands, no more recent wisent bones have been found in these countries (Benecke 2005).

In Germany, wisent remains from the first centuries AD have been found in the former Roman town of Colonia Ulpia Traiana (nowadays: Xanten, about 20 km from the Dutch border) (Clason 1977, Krämer & Nolde 2012). However, since the Romans transported many large animals from afar for gladiatorial displays in their arenas (there was an arena in Colonia Ulpia Traiana) these wisents did not necessarily come from a local population.

Heinzelin et al. (1984) published the discovery of what they considered to be a fragment of a *Bison bonasus* bone found by the Scheldt river near Tournai (Belgium). This record was subsequently discussed by Van Alsté (1989). The bone fragment from the Scheldt river is the distal part of a humerus and was found in a fluvial deposit together with ceramic, leather and iron remnants from the Iron Age (650-450 BC) and the Gallo-Roman period (50-200 AD). In Belgium, no other *Bison bonasus* finds have been recorded (A. Ervynck, personal communication). The bone was determined on the basis of diagnostic features, set out by Stampfli (1963), but the method employed proved to be cumbersome (A. Gautier, personal communication). As such the determination that this was a wisent remains questionable.

There has been a long and ongoing debate about whether it is possible to distinguish wisent (*Bison bonasus*) from aurochs (*Bos primigenius*) on the basis of bones. Olsen (1960), whom Drees & Post (2007) relied on, compared the bones of *Bison bison* with those of domestic cattle *Bos taurus* and *Bos indicus*. Stampfli (1963) compared the bones of *Bison bonasus* and aurochs from a Swiss site from the third millennium BC and explained the ongoing discussion among specialists, concerning the determination of, in this case, that part of the humerus. Some (e.g. Wright 2013) consider it completely impossible to arrive at a decisive identification of a species on the basis of a single postcranial bone. Others (e.g. Stampfli 1963) argue this is possible, but is nevertheless difficult. Stampfli also mentions

[1] The Holocene can be roughly subdivided into Early Holocene (10,000-6,000 BC), Middle Holocene (6,000-1,000 BC) and Late Holocene (1,000 BC-today).

that a 'typical *Bison* structure' can quite often ('öfter') be seen in the bones of large domestic cattle. Wright (2013), in an extensive research on bone characteristics, concludes that only a substantial number of *complete* postcranial bones, and preferably the cranium itself, can give a definite answer. The close relationship between the two species, the age of the animal, intraspecies variation and sexual dimorphism can further confuse identification.

On Mesolithic and Neolithic sites in the Netherlands, many skull fragments, horn cores and horn sheaths of aurochs (*Bos primigenius*) have been found, and from 4400 BC also those of domestic cattle. Aurochs bones have been found both as catch in human settlements and as stray finds. Some of these bones have been determined to species on the basis of mtDNA. However no wisent skull fragment or other larger intact bones from the Middle or Late Holocene have been found in the Netherlands.

Written sources

The allegations that *Bison bonasus* lived for a very long time in England, southern Sweden and the Ardennes regularly circulated in the 20th century, and still do so. Pucek (1986) summarised them in a comprehensive treatise on various aspects of the wisent; in a paper that has been cited by many authors. It is striking that these allegations were factually debunked long ago, but are nevertheless still passed on as reliable data, without being checked. Because these claims are not supported by bone finds, their origin must lie in ancient texts, or in the imagination of the storyteller.

In the early 20th century, the historical zoologist Szalay (1915, 1917, 1938) occupied himself for decades with searching and interpreting ancient texts, which might provide evidence of the former occurrence of wisent, aurochs and other large mammals in Europe. A key aspect of this task was recognising the different names given to these animals. The different names given caused much confusion. Aurochs were given two different names '*urus*' and '*bubalus*'. In the Latin language, '*bubalus*' was the original name of the aurochs. When Julius Caesar conquered parts of Germania in 58-52 BC, the Germanic name of the aurochs ('ur') was latinised to '*urus*'. In the 19th and the early 20th centuries, many authors, not aware of the difference between the two bovine species, misinterpreted the term '*bubalus*' as a designation of the wisent. The Romans themselves called the wisent '*bison*', another word borrowed from the Germanic. This is the first name confusion which must be taken into account. The second has to do with the fact that, in the late Middle Ages, the original Germanic word 'ur' changed into 'auer' and later into 'auerochs'. Actually, 'auer(ochs)' was never used for the original aurochs (*Bos primigenius*), but only for the wisent (*Bison bonasus*) (Szalay 1938). During the 13th century, about the time the aurochs became extinct in German-speaking regions (apart from East Prussia), the name 'ur', which originally related to the aurochs, was passed on in an altered form ('auer(ochs')) to the wisent (figure 1). Until well into the 19th century, the wisent was called 'auer(ochs)' in Germany. From the late 19th century, when people started to realise that aurochs and wisent were two different species – after the explanatory study by Wrześniowski (1878) - the original name of the wisent was re-established.

The idea that the wisent was still extant in southern Sweden in the 11th century, comes from a text in a book by Adam von Bremen (Bremen & Laurent 1893) which outlines the history of northern Europe in the late 11th century. In this book it is claimed that '*uri bubali et elaces*' were captured in '*Sueonia*' (southern Sweden), and '*bisontes*' in '*Sclavonia et Ruzzia*' (regions in eastern Europe). Here '*uri bubali*' indicates aurochs, and '*elaces*' elk. Although Von Bremen situated wisents somewhere in eastern Europe, his description is so vague that it is of little value. In any case, he did not

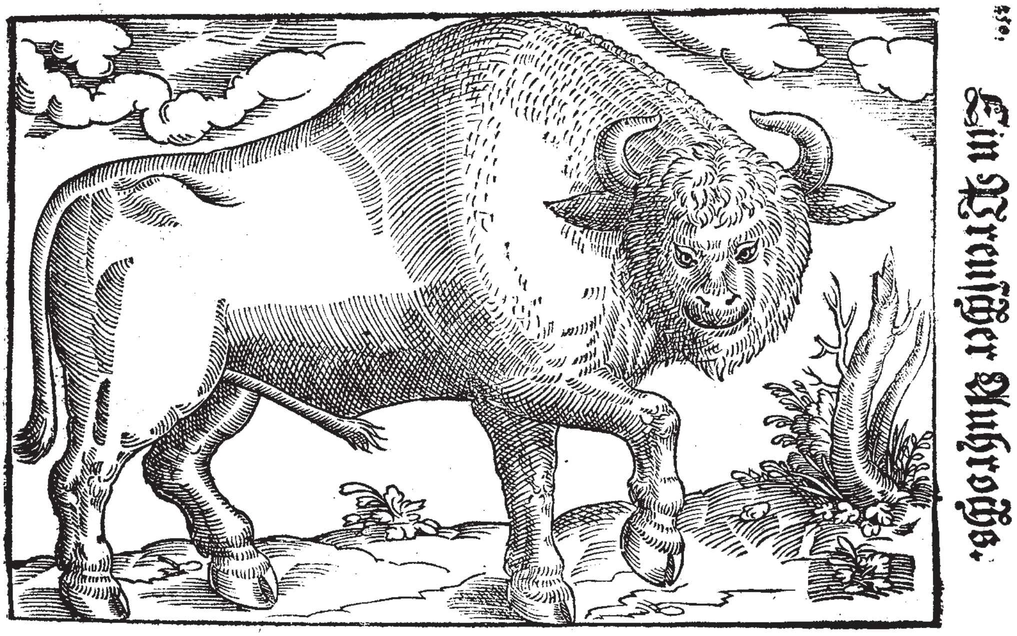

Figure 1. One of the earliest known illustrations of a wisent to appear in print. It depicts a wisent ('Ein Preuscher Auhrochs') in former East Prussia. From Hennenberger (1595).

mention wisents ('*bisontes*') in southern Sweden. Some authors, such as Genthe (1918), mistook Von Bremen's '*bubali'* as wisents, or misread the text, and mentioned wisents in southern Sweden in the 11th century.

The idea that the wisent occurred in England in the 12th century goes back to a text by Genthe (1918). He wrote that 'probably in the 12th century there was evidence of wisents in England' but produced no further proof of this. According to Szalay (1938) he got this from a passage about the occurrence of aurochs and wisent in Europe in an article by Struckmann (1882). Struckmann was also misled by the name confusion and claimed (among other things) that the aurochs 'became extinct in England only in the 12th century', although he did not provide any evidence for this. As mentioned before, Genthe also misinterpreted Von Bremen's description.

Similarly, the existence of the wisent in the Ardennes in the 14th century, cannot be found in any reliable written source (Szalay 1938). The '*bubalus*', or aurochs, was mentioned in a narrative of a hunt in the surroundings of Aachen in the 9th century, but there are no more mentions of them since then. How the claim on the occurrence of the wisent in the Ardennes in the 14th century came about, can be explained as follows. Szalay (1917) stated that there is no mention of aurochs or wisent in the entire French hunting literature and hunting poetry from the 12th to the 16th centuries. As an example he cited the renowned hunting book by Gaston Phoebus (from around 1388), where all the big hunting game of France (which then included the Ardennes), was described (Phoebus 1931). From Szalay's statement in 1917, Genthe (1918) concluded that 'around 1400' the wisent no longer existed in France, because Phoebus did not mention it. From Genthe's assertion, Sztolcman (1924) then concluded that 'the wisent disappeared in France in the 14th century'. Pucek (1986) adopted Genthe's and Sztolcman's view and concluded that the wisent became extinct 'in north-east France (Ardennes, Vosges)' by the end of the 14th century.

What still remains unexplained is the origin of the statement that the wisent still occurred in the Netherlands 'about 1000 years' ago. There are no bone finds to confirm this and the occurrence of this animal is not mentioned in any ancient texts. The explanation probably lies in the mention of the only Dutch wisent toponym 'wisenthurst' ('wisent hurst') dated back to 1145 AD and found near Gendringen on the Dutch-German border (Gysseling 1960, de Vries 1962, van Vuure 1984, Philippa et al. 2009). In different texts, this name was also written as 'wesenthorst', 'wezenhorst' and 'wisenhurs'. A wisent toponym may indicate the previous occurrence of the wisent there, irrespective of whether this animal was rare or common. It may indicate the former regular occurrence of this animal, but it could also mean that people immortalised a one-off encounter with an exceptional and rare animal species. Some years ago, a (still) unknown author, presumably not realising the meaning of a toponym, understood the year of the mention of this toponym as indicating the time of occurrence of the wisent there, and for convenience made 'about 1000 years' ago from it. However, toponyms may exist for centuries before being mentioned in documents.

Bone finds elsewhere in Europe

Unlike in Belgium and the Netherlands, a relatively large number of *Bison bonasus* bones have been found in central and eastern Europe. Nevertheless, judging by the number of bones in relation to those of red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) or roe deer (*Capreolus capreolus*), this animal must have occurred there in relatively low densities. As more wisent bone finds become known in Europe, the image of its distribution area is becoming increasingly clear. Benecke (2005) brought the bone finds of the wisent together in a map, which was further supplemented by Kuemmerle et al. (2012) with finds in eastern Europe derived from Heptner et al. (1961) (figure 2). This map shows that the wisent hardly occurred in western and southern Europe. Although wisents lived in the steppes and forest steppes of southern Russia, they were not present in the vast steppes east of Volgograd (Heptner et al. 1989) where one would expect them to have lived in large numbers. The wisent probably descends from a steppe dweller such as the steppe bison (*Bison priscus*) and is closely related to another steppe dweller, the American bison (*Bison bison*). Even the so-called forest bison (*Bison bison athabascae*), which can still be found in central Canada, does not actually like forests as such, but usually lives in extensive grass and sedge marshes within the surrounding forests (Carbyn et al. 1993).

At present the (natural) food and habitat choice of the wisent is not fully known, and discussions about this are still going on (Kowalczyk et al. 2011, Kerley et al. 2012, Bocherens et al. 2015).

Discussion

In theory, the lack of reliable bone material of *Bison bonasus* in the Netherlands and Belgium, from the Middle and Late Holocene, does not mean that the animal did not occur here: absence of evidence is not evidence of absence. But given that archaeological research in these countries is long and well established, that the conditions for finding bones are often excellent, and that many bones of the wisent have been found in central and eastern Europe, one can tentatively draw the conclusion that this animal was not a resident species in the Netherlands and Belgium during the Middle and Late Holocene. Only bones (of an apparently small subspecies) of *Bison bonasus* from the Late Pleistocene / Early Holocene have ever been found in the Dutch portion of the North Sea. If the wisent regularly occurred in the Netherlands and Belgium during the Middle and Late-

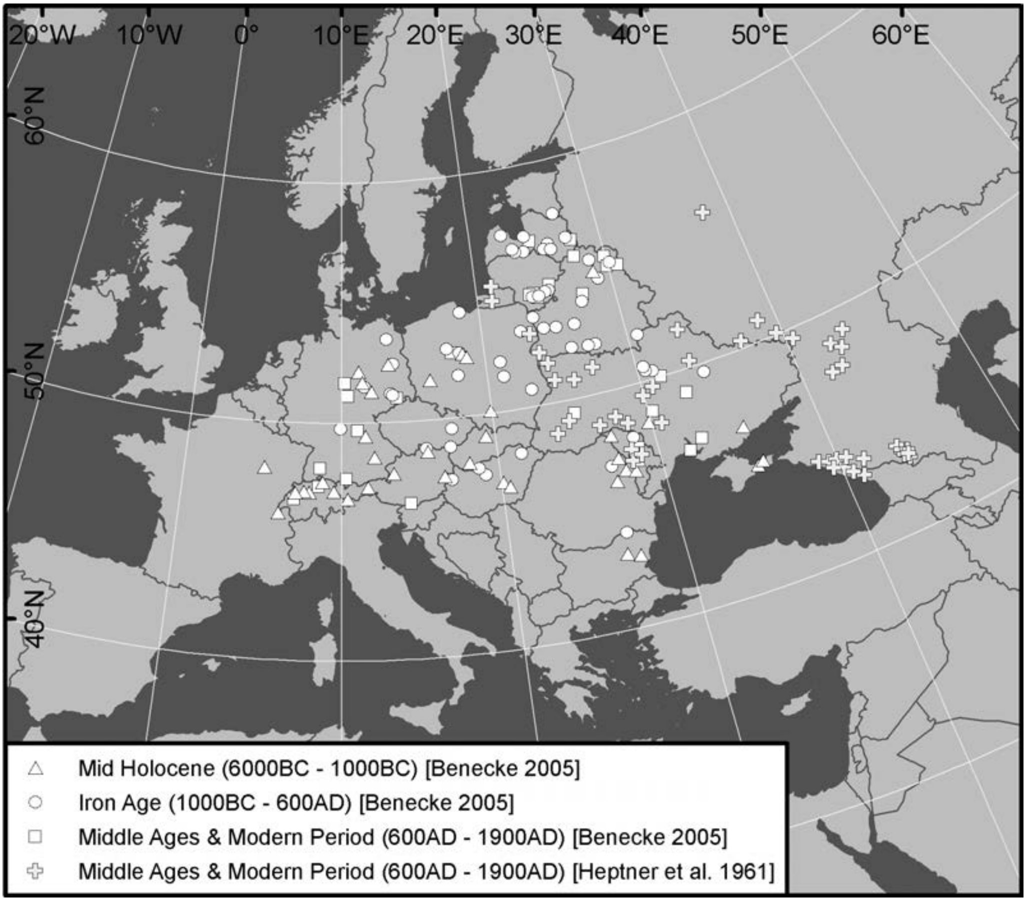

Figure 2. Distribution of bone finds of the wisent (*Bison bonasus*) in Europe from the Middle and Late Holocene (source: Kuemmerle et al. (2012); with permission of the author and publisher) © 2011 Blackwell Publishing Ltd.

Holocene, some of its bones should have been found here. The knowledge to correctly determine wisent bones, the financial resources to carry out archaeological excavations and the find conditions for bones in western Europe are certainly not any less or worse than in central and eastern Europe.

It is also noteworthy that Szalay (1915), on the basis of wisent toponyms, concluded that wisents probably only occurred very occasionally, at best, in western Europe. In England and Belgium no certain wisent toponyms have been found. In France, only one reasonably certain wisent toponym, 'wisinthovua' ('wisent river meadow') has been found, in NE Alsace, in the northeast of the country. Whereas wisent toponyms are hardly found in western Europe, they are more commonly found in Germany. Here there is a certain gradient in toponym density. In the northern half of the country only about five toponyms have been found, in contrast with about 25 in the southern half (Szalay 1915). Whether this also points to a preference for a continental climate remains questionable.

If wisent did occur in the Netherlands and Belgium during the Middle and Late Holocene, this was only because it occasionally crossed the 'German' border. We can assume that it was extremely rare in Belgium and the Netherlands. Possibly only wandering bulls showed up; wisent bulls are renowned for covering large distances, of up to 350 km (Krasińska & Krasiński 2007). For one reason or another the wisent did not thrive in north-western Europe. During the Early Holocene, the North and the Baltic seas were dry - there was a different, more continental climate, a different vegetation and a different composition of animal species.

The climate in the range of the wisent, as shown in the map by Kuemmerle et al. (2012), is continental by nature, with warm summers and cold winters. The wisent's possible dislike of a maritime climate maybe explains why it did not occur much in north-western Europe, although there are other possible reasons (habitat fragmentation by the formation of islands in southern Scandinavia, food availability or competition with other animal species). This question is one for future exploration.

Conclusions

Research has been done into the validity of the claim of whether the wisent (*Bison bonasus*) is indigenous to the Netherlands and Belgium. Here I have examined the allegations that the wisent was present up until the Middle Ages in north-western Europe, including the Netherlands and Belgium, by using archaeozoological records of bone finds and (alleged) mentions of the wisent in written sources. In the Netherlands and Belgium, there are no (reliable) bone finds of the wisent from the Middle and Late Holocene, and the mentions in written sources turn out to be misinterpreted and / or unfounded. Only one single wisent toponym might indicate a presence of the wisent in the east of the Netherlands at this time. From bone finds of the wisent in Europe it can be concluded that the wisent's range was mainly in central and eastern Europe.

It should be concluded that while the wisent may have occurred regularly in the Netherlands and Belgium during the Early Holocene, after that time it was no longer a resident species there. Given the finds of wisent bones elsewhere in Europe, the wisent rather seems to have been, at most, a rare vagrant in the Netherlands and Belgium.

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References

Benecke, N. 2005. The holocene distribution of European bison – the archaeozoological record. Munibe (Antropologia – Arkeologia) 57: 421-428.

Bocherens, H., E. Hofman-Kamińska, D.G. Drucker, U. Schmölcke & R. Kowalczyk 2015. European bison as a refugee species? Evidence from isotopic data on Early Holocene bison and other large herbivores in Northern Europe. PLoS ONE 10 (2): e0115090. Doi:10.1371/journal.pone.0115090.

Carbyn, L.N., S.M. Oosenbrug & D.W. Anions 1993. Wolves, bison....and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Circumpolar Research Series nr 4. University of Alberta, Edmonton, Canada.

Clason, A.T. 1977. Jacht en veeteelt van prehistorie tot middeleeuwen. Fibula-Van Dishoeck, Haarlem, the Netherlands.

Degerbøl, M. & J. Iversen 1945. The bison in Denmark. Danmarks Geologiske Undersøgelse (Raekke 2) 73: 1-62.

de Vries, J. 1962. Woordenboek der Noord- en Zuidnederlandse plaatsnamen. Het Spectrum, Utrecht, the Netherlands.

Drees, M. & K. Post 2007. *Bison bonasus* from the North Sea, the Netherlands. Cranium 24 (2): 48-51.

Ekström, J. 1993. The Late Quaternary History of the Urus (*Bos primigenius* Bojanus 1827) in Sweden. Lundqua Thesis 29. Lund University, Lund, Sweden.

Genthe, F. 1918. Die Geschichte des Wisents in Europa. Bialowies in deutscher Verwaltung 3: 119-140.

Gysseling, M. 1960. Toponymisch woordenboek van België, Nederland, Noord-Frankrijk en West-Duitsland (vóór 1226). Deel II. Belgisch Interuniversitair Centrum voor Neerlandistiek, Brussel, Belgium.

Heinzelin, J. de, J. de Coninck, A. Gautier, E. Gilot & J. Heim 1984. La Vallée de l'Escaut à Pont-A-Chin. Annales de la Société Géologique de Belgique 107: 89-101.

Hennenberger, C. 1595. Erclerũg der Preussischen grössern Landtaffel oder Mappen. Gedruckt zu Königsperg in Preussen / Bey Georgen Osterbergern.

Heptner, V.G., A.A. Nasimovich & A.G. Bannikov 1961. Mammals of the Soviet Union. Volume I: Artiodactyla and Perissodactyla. Amerind Publishing, New Delhi, India. [in Russian]

Heptner, V.G., A.A. Nasimovich & A.G. Bannikov 1989. Mammals of the Soviet Union. Volume I: Ungulates. E.J. Brill. Leiden, the Netherlands.

Janssen, C. 2015. De wisent. De Volkskrant, 14 maart 2015: 48-49.

Kas, J. 2014. De Veluwe wordt beetje wilder. Amersfoortse Courant. Regio-Amersfoort, July 24: 4.

Kerley, G.I.H., R. Kowalczyk & J.P.G.M. Cromsigt 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35: 519-529.

Kowalczyk, R., P. Taberlet, E. Coissac, A. Valentini, C. Miquel, T. Kamiński & J.M. Wójcik 2011. Influence of management practises on large herbivore diet – Case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261: 821-828.

Krämer, J. & N. Nolde 2012. Die Befunde und Funde von Insula 15 in der Colonia Ulpia Traiana. Xantener Berichte 24: 57-197. Verlag Philipp von Zabern, Darmstadt/Mainz, Germany.

Krasińska, M. & Z.A. Krasiński 2007. European Bison – The Nature Monograph. Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.

Kuemmerle, T., T. Hickler, J. Olofsson, G. Schurgers & V.C. Radeloff 2012. Reconstructing range dynamics and range fragmentation of European bison for the last 8000 years. Diversity and Distributions 18: 47-59.

Louwe Kooijmans, L.P. 2012. Holland op zijn wildst? De Vera-hypothese getoetst aan de prehistorie. De Levende Natuur 113 (2): 62-66.

Olsen, S.J. 1960. Post-cranial skeletal characters of *Bison* and *Bos*. Papers of the Peabody Museum of Archaeology and Ethnology 35 (4). Harvard University, Cambridge, MA, USA.

Philippa, M., F. Debrabandere, A. Quak, T. Schoonheim & N. van der Sijs (eds.) 2009. Etymologisch woordenboek van het Nederlands. Deel 4: S-Z. Amsterdam University Press. Amsterdam, the Netherlands.

Phoebus, G. 1931. Le livre de la chasse. Maîtres de la vénerie: vol. 2. E. Nourry, Paris, France.

Pucek, Z. 1986. *Bison bonasus* (Linnaeus, 1758) – Wisent. In: J. Niethammer & F. Krapp (eds.). Handbuch der Säugetiere Europas. Band 2/II, Paarhufer: 278-315. Aula-Verlag, Wiesbaden, Germany.

Smit, C., J. Dekker & J. Cromsigt 2008. Ruimte voor de wisent in de lage landen. De Levende Natuur 109 (1): 32-33.

Stampfli, H. 1963. Wisent, *Bison bonasus* (Linné), 1758, Ur, *Bos primigenius* Bojanus, 1827, und Hausrind, *Bos taurus* (Linné), 1758. In: J. Boessneck, J.-P. Jéquier & H.R. Stampfli (eds.). Seeberg, Burgäschisee-Süd. Teil 3: Die Tierreste. Acta Bernensia II. Verlag Stämpfli & Cie, Bern, Switzerland.

Struckmann, C. 1882. Über die Veränderungen in der geographischen Verbreitung der höheren wildlebenden Tiere im mittleren Europa und speziell in Deutschland seit der älteren Quartärzeit bis zur Gegenwart. Zeitschrift für wissenschaftliche Geographie 3: 173-183.

Szalay, A.B. 1915. Der Wisent in Ortsnamen. Zoologische Annalen 7 (1): 1-80.

Szalay, A.B. 1917. Wisente im Zwinger. Zoologischer Beobachter LVIII: 144-150.

Szalay, A.B. 1938. Hundert irrige Wisentbelege. Verlag J. Neumann, Neudamm, Germany.

Sztolcman, J. 1924. Matériaux pour l'histoire naturelle et pour l'historique du Bison d'Europe (*Bison bonasus* Linné). Annales Zoologici Musei Polonici Historiae Naturalis. Tom II, Zeszyt 3-4: 49-136.

van Alsté, H. 1989. Wisenten in Nederland, feit of fictie? Een onderzoek naar het inheemse karakter van de wisent (*Bison bonasus*) in Nederland. Verslag nr. 1052. Landbouwuniversiteit Wageningen, the Netherlands.

van Vuure, T. 1984. Een wisenttoponiem in Nederland. Huid en Haar 3 (1): 1-4.

von Bremen, A. & J.C.M. Laurent 1893. Adam's von Bremen Hamburgische Kirchengeschichte. Dyk, Leipzig, Germany.

Wright, E. 2013. The history of the European aurochs (*Bos primigenius*) from the Middle Pleistocene to its extinction: an archaeological investigation of its evolution, morphological variability and response to human exploitation. PhD thesis. Department of Archaeology, University of Sheffield, UK.

Wrześniowski, A. 1878. Studien zur Geschichte des polnischen Tur. Zeitschrift für Wissenschaftliche Zoologie 30, Supplement 45: 493-555.

Zeiler, J.T. & L.I. Kooistra 1998. Parklandschap of oerbos? Interpretatie van het prehistorische landschap op basis van dieren- en plantenresten. Lutra 40 (2): 65-76.

Samenvatting

Is de wisent (*Bison bonasus*) inheems in Nederland en België?

Diverse bronnen behandelen het (mogelijke) voorkomen van de wisent (*Bison bonasus*) in de Middeleeuwen in Noordwest-Europa, te weten Zuid-Zweden, Engeland, België en Nederland. Botvondsten zouden onmiskenbaar wijzen op de vroegere aanwezigheid van *Bison bonasus* in Nederland en België. De motivering voor de introductie van de wisent in het kader van het natuurbeheer in Nederland is onder meer op deze gegevens gebaseerd. In dit artikel wordt nagegaan waar de vermelde beweringen vandaan komen en of ze feitelijk kloppen.

Wat de vermelde botvondsten betreft, blijkt dat er in het Vroeg-Holoceen nog wel wisenten in Noordwest-Europa voorkwamen, maar dat daar later, uit het Midden- en Laat-Holoceen, geen aantoonbare wisentbotten gevonden zijn. Uit de verspreiding van botvondsten van de wisent elders in Europa blijkt dat *Bison bonasus* vooral in Centraal- en Oost-Europa leefde. Ook de verspreiding van wisenttoponiemen in Duitsland lijkt een voorkeur van de wisent voor een continentaal klimaat te weerspiegelen.

In geschreven bronnen is nagegaan of er gegevens te vinden zijn over het voorkomen van de wisent tot in de Middeleeuwen in Zuid-Zweden, Engeland, Nederland en België. Gebleken is dat er dienaangaande geen betrouwbare gegevens te vinden zijn. De onderzochte beweringen zijn deels tot stand gekomen door naamsverwarring met de oeros (*Bos primigenius*), deels door verkeerde interpretatie van teksten, en deels door het doen van ongefundeerde beweringen.

Als de wisent in het Midden- en Laat-Holoceen al in Nederland en België voorkwam, dan moet hij hooguit een zeldzame dwaalgast zijn geweest en zeker geen standwild.

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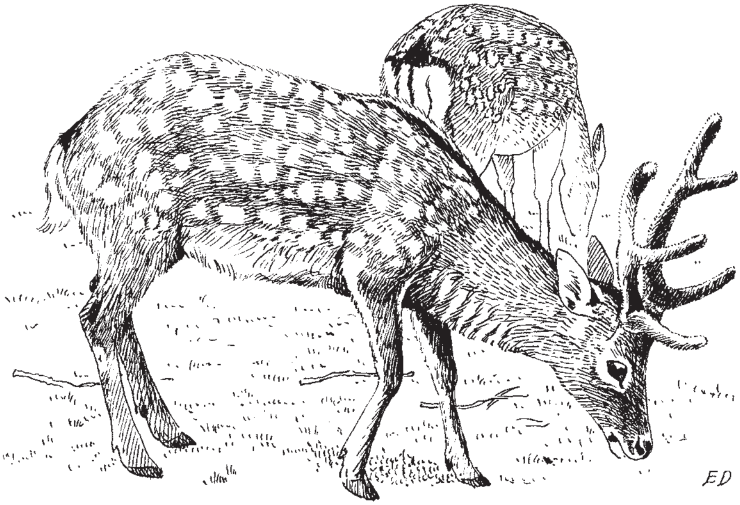

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Reeves' muntjac (*Muntiacus reevesi*) and sika deer (*Cervus nippon*) in the Netherlands

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Keywords: Reeves' muntjac, sika deer, distribution, exotic mammals.

Introduction

Both Reeves' muntjac (*Muntiacus reevesi*) and sika deer (*Cervus nippon*) are non-indigenous to the Netherlands. In other European countries these two deer species pose risks to both biodiversity and ecosystems and also generate economic damage. Sika deer has been found to interbreed with endemic red deer (*Cervus elaphus*) in Germany and England (Lammertsma et al. 2012). In areas with a high abundance of muntjacs, the species has been responsible for the decline of woodland plants like bluebells (*Hyacinthoides* sp.) (Smith-Jones 2004, The Deer Initiative 2008) and oxlip (*Primula elatior*) (Tabor 1997). By changing forest structures, the habitat of woodland butterflies and birds like the nightingale (*Luscinia megarhynchos*) may be destructed, resulting in a local decline of these species (Cooke & Farrel 2001). In high abundances, muntjacs have been found to repress roe deer (*Capreolus capreolus*) as a result of food competition (Chapman et al. 1994, Smith-Jones 2004).

Sika deer

The first observations of sika deer in the Netherlands in the wild date from 2005 (Dutch National Databank Flora and Fauna, www.ndff.nl); since 2008 the species has been observed more frequently. From 2008 onwards, two specimens have been living on several estates in Het Gooi, between 's-Graveland and Hilversum (Province of Utrecht) (figure 1). Most of the observations concern a single individual, but there are some reports of a male and a female together. Reproduction in the wild has not yet been documented in the Netherlands. Since the species was first observed in the wild, its distribution in the Netherlands did not change. The possibility of sika deer entering the Netherlands from Germany, where 1500 sika deer lived in seven established populations in 2005, is expected to be low (Lammertsma et al. 2012). The nearest population in Sauerland (Nordrhein-Westfalen) is located over 200 km from the Dutch border. So far, there has been no documented expansion of the species in the Netherlands. In the first three months of 2015, three sightings were reported of an escaped sika deer in the Biesbosch, in the southwest of the Netherlands.

Reeves' muntjac

The first confirmed sightings of Reeves' muntjac in the Netherlands date from the period

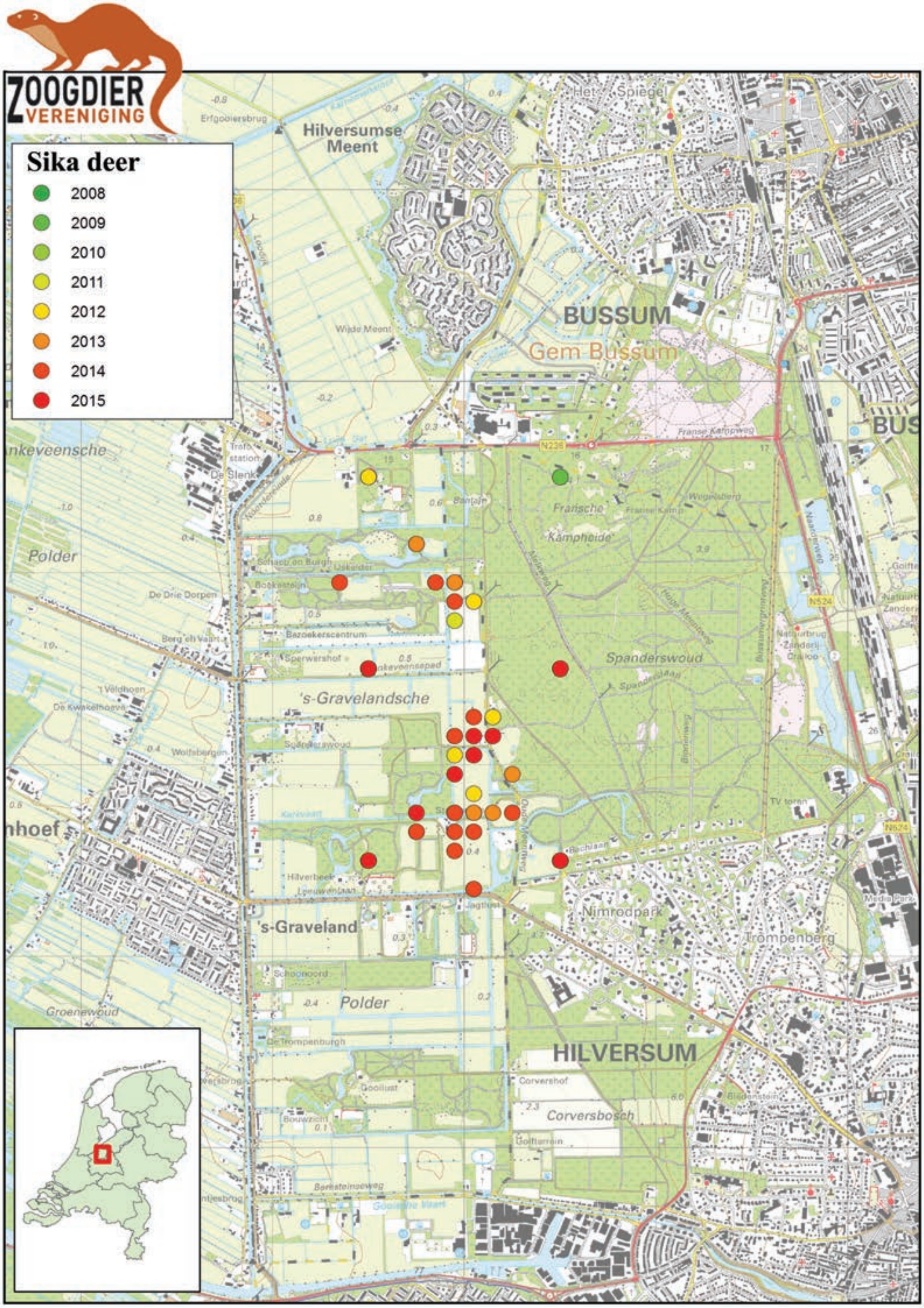

Figure 1. Observations of sika deer in the period 2008-2014 in country estates between 's-Graveland and Hilversum, Het Gooi (Province of Utrecht) (source: Dutch National Databank Flora and Fauna, www.ndff.nl).

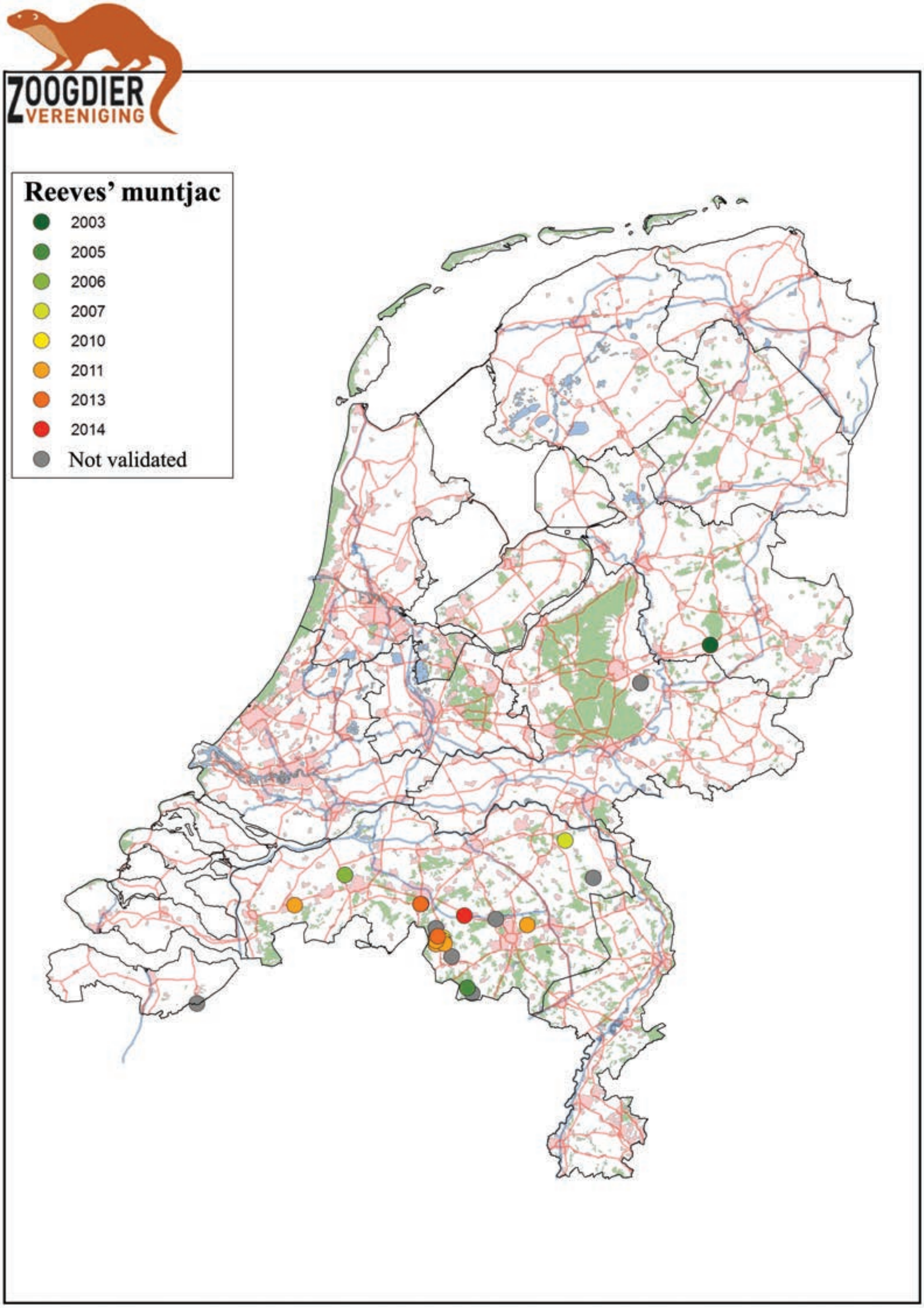

Figure 2. Observations of Reeves' muntjacs in the period 1997-2012 in the Netherlands (source: Dutch National Databank Flora and Fauna, www.ndff.nl).

1997-1998, when the species was reported from the Veluwe (Province of Gelderland) and from east of the river IJssel (Achterhoek, Province of Overijssel). Currently small numbers of Reeves' muntjac are still present at the Veluwe, but from other parts of the Netherlands only very few observations have been reported (figure 2). In 2013 and 2014, only three sightings have been documented from the Veluwe: one in the northern part near Nunspeet and two in the eastern part near Voorst. It is thought that these animals were released by private owners or escaped from animal parks. The number of observations since 2010 was smaller than in the period 2000-2005.

In the Province of Noord-Brabant, the situation is completely different (figure 2). The first muntjacs have been reported here in 2005 and since then, their numbers have been growing. Most observations come from the country estate De Utrecht and surrounding areas (south of Tilburg) and concerned single animals. A first case of a mother and a fawn was reported in 2013, near Goirle. It appeared that the fawn was born in the wild, but there were no indications that mating happened in the wild (Koelman 2014). Other observations in Noord-Brabant concern only single individuals at various locations. Only in the Maashorst, in eastern Noord-Brabant, multiple sightings were recorded: one in 2006 and one in October 2014.

Late 2013/early 2014, a muntjac was observed on several days at several locations near the Belgium border at the village of Heikant in Zeeuws-Vlaanderen (Province of Zeeland).

The increasing number of muntjac observations in the southern part of the Province of Noord-Brabant is possibly related to the growing number of animals in Belgium (Hollander 2014); while only few observations were made here until 2012, the number increased to 12 in 2013 and to 24 in 2014. Most of these observations are concentrated east of Antwerp, but some come from the country estate De Utrecht near the Belgian border.

On 7 October 2014, a young male muntjac fell victim to a car accident at country estate Baest near Oirschot (Province of Noord-Brabant) (figure 3). Traffic victims may be a first indication for higher abundances (Chapman et al. 1994). When the abundance is low, the number of traffic victims is limited due to the muntjac's secretive way of living. The species may therefore remain unnoticed for a long time.

Trade and possession

Muntjacs and sika deer are both kept in small numbers in the Netherlands in zoos, animal parks and by private people. Since 2000 the trade and possession of muntjacs is forbidden in the Netherlands and zoos need a licence for keeping these animals (Hollander 2013). Monitoring of websites providing trade of exotic mammals shows that sika deer were offered at least six times in the Netherlands in 2014, comprising a total of 13 individuals. Muntjacs are not offered on Dutch websites, while in Belgium several individuals were offered on websites in 2014 in at least three occasions. In Germany a *Muntiacus reevesi micrurus* (a Taiwanese subspecies) was offered. This subspecies is currently not known to be kept as a pet animal in the Netherlands. Muntjacs may also be intentionally released in the wild for hunting purposes in Belgium and the Province of Noord-Brabant. Both sika deer and muntjac are frequently being imported from the United Kingdom and Germany into Belgium (Baiwy et al. 2013).

On the first of February 2015 a so-called Positive List has come into effect in the Netherlands. This list restricts the possession of some, explicitly mentioned, exotic animals (Ministerie van Economische Zaken 2015). As from 1 April 2015, ten (sub-)species of muntjac are listed as prohibited to be kept. Sika deer is not mentioned on the Positive List, either 'positive' (allowed) or 'negative' (prohibited).

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References

Baiwy, E., V. Schockert & E. Branquart 2013. Risk analysis of the sika deer, *Cervus nippon* (Linnaeus 1758). Risk analysis report of non-native organisms in Belgium. Cellule interdépartementale sur les Espèces invasives (CiEi), DGO3, SPW / Editions, Gembloux / Université de Liège, Liège, Belgium.

Chapman, N., K. Claydon, M. Claydon & S. Harris 1994. Muntjac in Britain: Is there a need for a management strategy? Deer 9 (4): 226-236.

Cooke, A.S. & L. Farrel 2001. Impact of muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. Forestry 74 (3): 241-250.

Hollander, H. 2013. Risico-analyse muntjak (*Muntiacus reevesi*). Rapport 2013.09. Zoogdiervereniging, Nijmegen, the Netherlands.

Hollander, H. 2014. Vormt de muntjak een risico? Zoogdier 25 (1): 1-3.

Koelman, R.M. 2014. Surveillance Muntjak Goirle. Onderzoek naar het voorkomen van de muntjak (*Muntiacus reevesi*) in Park Boschkens in Goirle. Rapport 2013.39. Zoogdiervereniging, Nijmegen, the Netherlands.

Lammertsma, D.R., G.W.T.A. Groot Bruinderink & A.J. Griffioen 2012. Risk assessment of Sika deer *Cervus nippon* in the Netherlands. Report 2295. Alterra, Wageningen, the Netherlands.

Ministerie van Economische Zaken 2015. Invoering huisdierenlijst zoogdiersoorten. Brief aan de Tweede Kamer der Staten Generaal. DGA-DAD / 14203274. Ministerie van Economische Zaken, Den Haag, the Netherlands.

Smith-Jones, C. 2004. Muntjac. Managing an alien species. The Cromwell Press, Trowbridge, Wiltshire, UK.

Tabor, R.C.C. 1997. The effects of Muntjac deer, *Muntiacus reevesi*, and Fallow deer, *Dama dama*, on the Oxlip, *Primula elatior*. Deer 11 (1): 14-19.

The Deer Initiative 2008. Muntjac Deer. Species Ecology. England & Wales best practice guides. The Deer Initiative, Chirk, UK. URL: http://www.thedeerinitiative.co.uk/uploads/guides/167.pdf.

Samenvatting

Muntjak en sikahert in Nederland

Muntjak (*Muntiacus reevesi*) en sikahert (*Cervus nippon*) zijn hertensoorten die niet van nature in Nederland voorkomen. Beide soorten kunnen de biodiversiteit negatief beïnvloeden, zoals in andere Europese landen reeds is gebleken. Het sikahert kan kruisen met het inheemse edelhert. Muntjaks kunnen schade toebrengen aan zeldzame bosplanten en door overbegrazing de vegetatiestructuur zodanig veranderen, dat effecten optreden op diverse insecten- en vogelsoorten. Daarnaast kan bij hoge dichtheden het ree worden verdrongen. Dit artikel bespreekt de status van beide soorten in Nederland. Het sikahert komt vanaf 2008 voor in ‘s Graveland (maximaal twee individuen). Sinds begin 2015 wordt een dier regelmatig gezien in de Biesbosch. Het voorkomen van de muntjak in Nederland is sinds 1998 bekend van met name de Veluwe (recent niet meer) en Noord-Brabant (in toenemende mate) en enkele andere locaties. Van beide soorten is (nog) niet bekend dat zij zich voortplanten in Nederland. Muntjak en sikahert worden beide in kleine aantallen gehouden door particulieren, in hertenparkjes en in dierentuinen. Sinds 2000 is de handel in muntjaks verboden in Nederland. De zogenoemde Positieflijst, die 1 april 2015 in werking trad, verbiedt het houden van tien (onder)soorten van muntjak; sikahert staat niet op deze lijst.

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Figure 3. This Reeves' muntjac fell victim to a car accident near country estate Baest near Oirschot (Province of Noord-Brabant). *Photo: M. van Roessel.*

Of mice and oaks

Of mice and oaks. Conditional outcomes in a seed-dispersal mutualism.
L Suselbeek 2014. PhD thesis. Wageningen University, Wageningen, the Netherlands.

Most of Lutra's readers will know Passive Integrated Transponder (PIT) tags, so-called chips, for monitoring pets and other animals or to study population dynamics. Suselbeek (2014) applies this technique on seeds of oak (*Quercus robur*) in order to track the dispersal of seeds and study the fate of seeds dispersed by scatter-hoarding rodents. This thesis focuses on seed-dispersal interactions between wood mice (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*) and wild boar (*Sus scrofa*). Based on his results the use of PIT tags on acorns is a suitable, novel method to track the dispersal of acorns without rodents being able to remove the tags. Tags buried up to 30 cm were retrieved and used to show whether acorns were hoarded in larders or scattered.

After this first success an attempt was made to unravel the complex interactions between acorn production, survival and dispersal of acorns, hoarding behaviour of mice and competition with wild boar. This is not an easy task due to the large number of variables involved. Oak produces alternating rich and poor mast years. Hoarding and feeding behaviour of mice also varies as does population density. Wood mice and bank voles may function as mutualists of oak when scatter hoarding, or function as seed predators when larder hoarding or when recovering and eating acorn caches. Hoarding patterns of mice can vary between individuals and between populations, and the depredation rate of acorns may vary with mice density. Wild boar population dynamics is influenced by acorn production (Groot Bruinderink et al. 1994). In autumn, and in winters of rich mast years, mast is the main constituent of the diet of wild boar. Body weight and condition induces the reproductive capacity in the succeeding spring of (sub)adults and they influence mortality of juveniles. Body weight and condition varies depending on acorn supplies and the availability of alternative forage such as broad-leaved grasses or seeds of beech (*Fagus sylvaticus;* also a stochastic mast producer). Numbers of wild boar can therefore show large stochastic fluctuations over the years and numbers vary between areas depending on the spatial distribution of resources. Depredation rates of acorns therefore depend on wild boar population density.

The results obtained by Suselbeek show that there is a large variation in hoarding patterns depending on acorn abundance. A field study was conducted in twelve sites, six in areas with a long history of wild boar presence and six without wild boar presence in the area. The study showed that intra- and interspecific competition for seeds between mice and wild boar increases seed-dispersal distance and seed spacing patterns, thereby increasing seed germination. Successful seed germination was most likely when acorn abundance was high and rodent abundance was high, regardless of wild boar presence. Seed germination was also relatively high with low acorn and mice abundance and wild boar absent. Although it is hypothesised in Suselbeek's thesis that patterns of hoarding are flexible and that they depend on the community of species and their abundances, effects of wild boar in shaping the mutualism between mice and oak was only marginally tested and detected in a controlled experiment. Probably this is due to the setup of experiments in an controlled environment with small outdoor arenas using six month old piglets from a semi-wild population in a 7 ha fenced natural area (Natuurpark Lelystad). Throughout the experiment the boar were fed which might have influenced wild boar foraging strategies. The diet of free ranging wild boar varies between years, seasons or even days and the diet of piglets differs from adults (Groot Bruinderink et al. 1994, Baubet et al. 2003, Groot Bruinderink et al. 2009). Feeding behaviour of free ranging wild boar in a natural situation therefore might show different results.

The thesis highlights the necessity to study the complex interactions induced by stochastic fluctuations in seed production and population dynamics of wild boar and mice. In order to understand ecosystem functioning further studies focusing on the network of species involved are needed. Groot Bruinderink et al. (2009) also suggested that studies on free ranging wild boar are necessary to get more grip on the effect on the ecosystem of fluctuating numbers of wild boar. To assess the impact of wild boar on the successful germination of acorns will however need to incorporate even more variables. Wild boar do not only compete with mice as predators of seeds, but also impact the survival of oak by their rooting activity. Also beech as another mast producer plays a significant role on the habitat use, diet and condition of wild boar as does the distribution of resources. Long term field studies are therefore needed incorporating a large numbers of variables.

References

Baubet, E., Y. Ropert-Coudert & S. Brandt 2003. Seasonal and annual variations in earthworm consumption by wild boar. Wildlife Research 30: 179-186.

Groot Bruinderink, G.W.T.A., E. Hazebroek & H. van der Voet 1994. Diet and condition of wild boar, *Sus scrofa scrofa*, without supplemental feeding. Journal of Zoology (London) 233: 631-648.

Groot Bruinderink, G.W.T.A., D.R. Lammertsma, G.A.J.M. Jagers op Akkerhuis, W. Ozinga, A.H.P. Stumpel, J.M. Baveco & R.W. de Waal 2009. Ex ante evaluatie van maatwerk beheer van wilde zwijnen. Rapport 1944. Alterra, Wageningen.

Suselbeek, L. 2014. Of Mice and Oaks. Conditional outcomes in a seed-dispersal mutualism. PhD thesis. Wageningen University, Wageningen, the Netherlands.

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