

## Our fellow mammalians

Why do mammals fascinate us humans so much? Why do we seem to be more interested in these furry, hairy, mother milk-producing animals than in other organisms? First of all, I guess, because we ourselves belong to the class Mammalia. We feel connected and related.

The relation of humans to their mammalian relatives, though, is more than love and affection. From early mankind on, we have hunted other mammals. First of all, because they provided high-quality food, rich in proteins, minerals and vitamins. In addition, these animals provided our ancestors with skins and bones for clothing and tools. These hunters' relation to their prey was, however, complex and based on respect and admiration. Hunted animals figured, or were worshipped, in sagas and myths, and were depicted on rocks, the oldest forms of human art.

Some mammals posed a threat to humans, who were probably considered as competitors by sabre-toothed cats, hyenas and cave lions. Other mammals were considered as pests, preying on food stocks, and were scared off, kept away or killed. In other words, in those days, humans were self-evidently part of the food chain, as predators, as competitors, possibly even as prey, although, so far, there is no proof of the latter.

Later, when early humans started to settle and grow crops, our ancestors also discovered the

benefits of keeping mammals, for economic reasons, i.e. as food resources or as working animals. In the course of millennia, these, mainly hoofed, mammals were progressively domesticated. Over time, selective breeding altered these domesticated mammals into the present-day cows, sheep, goats and pigs that can be found all around us, and which are mostly very distinct from their wild ancestors.

Mammals were also kept for other purposes. Wolves became hunting dogs or served as guards to protect sheep and cattle, or humans. Cats were encouraged to guard the grain harvest from mice and rats. Dogs, cats and mammals such as rabbits and guinea pigs, became increasingly popular for their companionship. Nowadays, many homes have pet mammals, which are often treated by their owners as true friends or family members.

In terms of species diversity, domesticated mammals may not contribute much to the approximately 6400 presently known species of wild mammals (Connor et al. 2018). But when considering biomass, the figures tell a different story. Livestock, which mostly consists of cattle and pigs, completely dominates the mammalian world on earth today, with an estimated 60% of mammalian biomass! Less surprisingly, humans, with an estimated 36%, contribute more than one third (Bar-On et al. 2018).

For wild mammals, this leaves an astonish-

ing low estimate of just about 4% of the total mammalian biomass on earth, including humans, and not even 2% if we only count terrestrial mammals (Bar-On et al. 2018). And if humans are excluded from these calculations, domesticated mammals still outnumber their wild relatives by 14 times.

These figures justify a large exclamation mark, and it is no wonder that there are increasing concerns about what will happen to the world's biodiversity if 'business as usual' remains the norm. Just think about the space and potential mammal habitat these cows and pigs, not to mention the habitat needed to produce all the feed and fodder, take up, in a world that is already crowded by us, humans.

The aforementioned estimated 4% of wild mammal biomass still doesn't say much about the absolute numbers of individuals or species of mammals and how this figure compares to former times. In other words, what has happened to the earth's wild mammals ever since we, humans, entered the scene? Well, humans have probably played a key role in diminishing the number of species (Sandom et al. 2014). During what is called the Quaternary Megafauna Extinction, starting from 50,000 years ago, a relatively small population of no more than five million humans are largely held responsible for the loss of 178 species of the largest mammal species (weighing over 40 kg), mainly by hunting (Barnosky 2008). And if we look further back, at least 351 mammal species are thought to have become extinct since the beginning of the Late Pleistocene, some 126,000 years ago (Andermann et al. 2020). The most significant change came when humans made the transition from hunter-gatherers to farmers and keepers of livestock; even though hunting became less important by then, there was a rapidly growing demand for agricultural space. Over millennia, this caused an increased pressure on wild mammal habitat worldwide, which reduced the population trends and ranges of many spe-

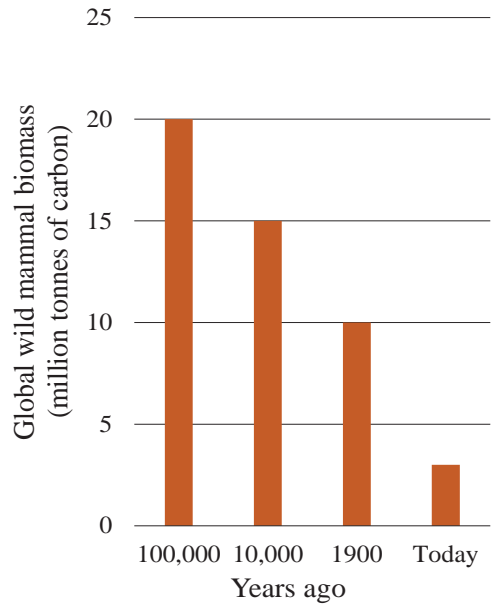


Figure 1. Global estimates of the wild terrestrial mammalian biomass over time since the rise of humanity. After Barnosky (2008), Smill (2011), Bar-On et al. (2018) and Ritchie (2021).

cies (now listed in IUCN and national Red Lists), including the smaller ones, and the loss of a number of these. In a study of the human impact on the diversity of mammals, Andermann et al. (2020) found that the current extinction rates of mammals are about 1700 times higher than those at the beginning of the Late Pleistocene. They calculated that at these rates, it would take only 810 years to extinguish the 351 mammal species that became extinct over the last 126,000 years.

Now if we look at the estimated amount of terrestrial mammalian biomass worldwide over the last 100,000 years (as reconstructed by Ritchie (2021), using various sources (Barnosky 2008, Smil 2011, Bar-On et al. 2018)), the picture is similarly dramatic (figure 1). Since the rise of humans, there has been an estimated decline of 85% of wild mammals. From what we know now, human activity was an important driver of the extinctions that took place thousands of years ago, and has been by far

the most significant cause in our more recent past, when the rate of mammal extinctions has become much faster than before.

Given these reflections of the past, the future of our fellow, wild, mammals seems gloomy, at least. This is also foreseen by Andermann et al. (2020) who predict a future extinction rate that, by 2100, will be much greater than what we see now. It's not all doom-mongering, however. The same authors, and others, also see options to turn the tide, to a certain degree, by increasing our conservation efforts (see also Leclère et al. 2020). So let's be optimistic, and keep our faith in maintaining what is left of the diversity of wild mammals, and the natural world in general, that still exists around us.

Speaking about diversity, this issue highlights a fair number of mammal species, including four voles. In cattle-grazed parts of the Netherlands, outbreaks of common voles (*Microtus arvalis*) used to be common but then for several decades, were almost unwitnessed. They recently seem to have returned. In an overview, Wymenga et al. analyze the circumstances in which these recent outbreaks have occurred and provide possible explanations for them. In contrast to the common vole, the root vole (*Alexandromys oeconomicus*) is a species in decline in the Netherlands. To get a clue about why, and what can be done in favour of the root vole, Paardenkooper & van Schie studied the habitat preferences in a wetland area of the endemic subspecies *arenicola*. Van Manen & Smaal unravel the activity of another vole, the bank vole (*Myodes glareolus*). Using camera traps they found out more about the voles' circadian and ultradian rhythms. The last vole in this issue, field vole (*Microtus agrestis*), was subject of an entirely different study. From owl pellets, Bekker extracted a field vole skull with an atypical dental pattern. In a short note, the author presents his ideas about the cause of this abnormality.

Two of this issue's papers highlight much larger

mammals. Van Mourik & de Jong studied phenotypic differences in antler development in red deer (*Cervus elaphus elaphus*) in two different, human-dominated, areas of the Veluwe. Heerebout presents a stranding of a sperm whale (*Physeter macrocephalus*) on a small island in Zeeland in the year 1429. This rarely reported event was 'unmasked' by a drawing in a local account.

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*Ben Verboom*



# Circadian and ultradian rhythms in free living bank voles (*Myodes glareolus*)

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**Abstract:** Data of 17,065 recordings in baited camera traps in the Netherlands revealed that bank voles (*Myodes glareolus*) expressed most activity between sunset and sunrise, with an exception for June-July. When corrected for the duration of respectively night and day the nocturnal bias was observed in all months, but was stronger when nights were longer. On top of the circadian rhythm, a rather distinct ultradian rhythm was superimposed, especially during the night. Activity peaked just after sunset in August-March, during sunset in April-May and before sunset in June-July, to be followed by a series of 1-4 distinct peaks and lows during the night. For full cycles (from peak to peak or low to low), mean duration was 224 minutes. Activity was highly synchronised between traps (individuals), areas separated by unsuitable habitat (populations) and years.

**Keywords:** bank vole, *Myodes glareolus*, activity, camera trap, circadian, ultradian, season, Struikrover.

## Introduction

From August 2018 through January 2020 activity patterns of mustelids were studied in various habitats in and near a river valley in the northern Netherlands. The study used camera traps in baited tubes. Apart from mustelids, many other mammal species were recorded. Bank voles (*Myodes glareolus*) appeared to be one of the most frequent visitors of the tubes. In this paper, we present an analysis of the camera trap recordings of bank voles that were made over the study period. The aim was to increase our insight into their daily activity patterns across the year.

## Methods

The camera traps were situated in a Struikrover\*, a pvc tube painted in camouflage

colours with a diameter of 20 cm, cut at an angle of 45° and covered by a lid at the other end. The longest length (along the bottom) amounts to 40 cm. The tube holds a trail camera in the back and bait at the other end. On top of the tube, just in front of the camera, is an opening with a diameter of 10 cm, covered by plexiglass. This opening provides the camera sensors with extra light, in order to avoid overexposure of pictures during sunny conditions. The camera lens is fitted with one of the lenses of a pair of reading glasses (for most camera types +3) in order to reduce the focal length to 35 cm. The cameras were set to make two or three pictures when triggered, followed by a one-minute pause. The Struikrovers were baited with a slightly opened sardine can. Bait was refreshed every 2-4 weeks.

The devices were placed in the half open landscape of the river valley of the Drentse Aa (6.64°E, 53.03°N; Province of Drenthe, the Netherlands). This area used to consist of wet meadows, hedgerows and woodlots, embedded in a small scale agricultural landscape

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Table 1. Number of locations where bank voles were observed during two-monthly periods, the number of records and the proportion (%) of records for the top three sites, and the rest.

	Dec-Jan	Feb-Mar	Apr-May	Jun-Jul	Aug-Sep	Oct-Nov
<i>n</i> locations	14	7	11	11	13	16
<i>n</i> observations	2811	2554	1153	1049	3009	6489
% 1	41.7	57.7	46.7	54.7	25.3	31.0
% 2	27.9	30.5	39.2	18.2	22.7	18.7
% 3	10.9	7.8	6.9	10.6	19.2	15.5
% others	19.6	4.1	7.2	16.5	32.8	34.8

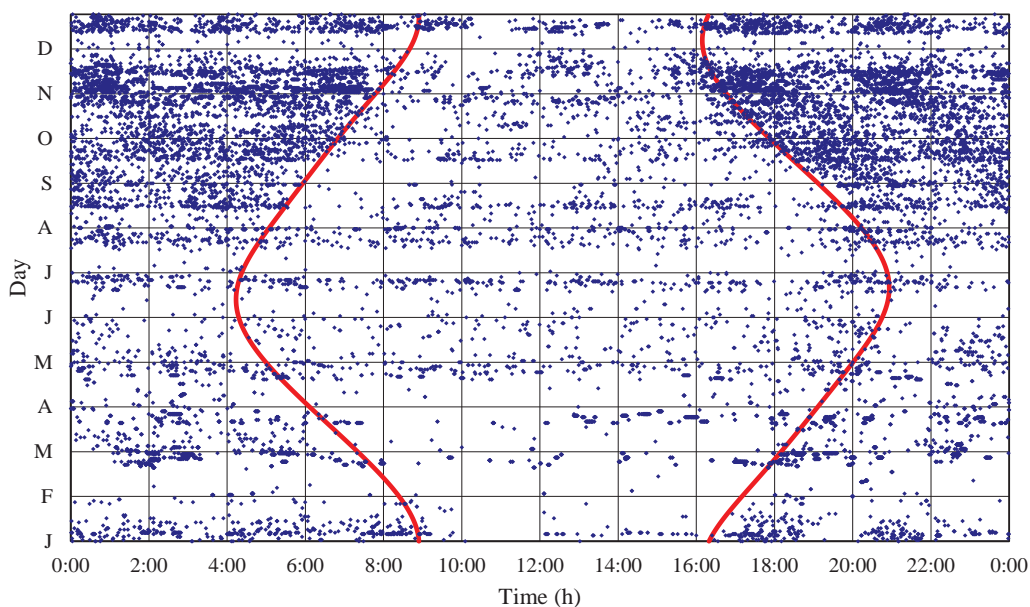


Figure 1. Monthly and diel distribution of bank vole observations via camera traps, relative to sunrise and sunset (red lines). Each dot represents one observation.

with fields, heaths and villages. From 1970 onwards the vicinity of the Drentsche Aa was drained, agriculture intensified and field sizes increased after land consolidation. Despite conservation measures, the river valley gradually desiccated. By the late 20th century ditches were filled in order to stop drainage, after which large sections of the river valley became very wet and partly changed into marshland. When possible, mowing takes place once a year in August-October (Spek et al. 2015). Several Struikrovers were deployed in other habitats like heaths and woodland. In most cases we placed the camera traps in lin-

ear vegetation elements or ecotones.

The data cover the period from 2 August 2018 through 19 January 2020. The Struikrovers were deployed at 42 locations and bait was refreshed 120 times (referred to as ‘sessions’). Across all two-monthly periods, bank voles were identified at least at seven locations. In some periods the data were strongly biased by records from, possibly, single individuals at a single site (table 1). The nearest neighbour distances between devices where bank voles were observed varied between 59 en 4386 m (mean=526 m, sd=829, *n*=35). The cameras were triggered 57,657 times, 17,065 of

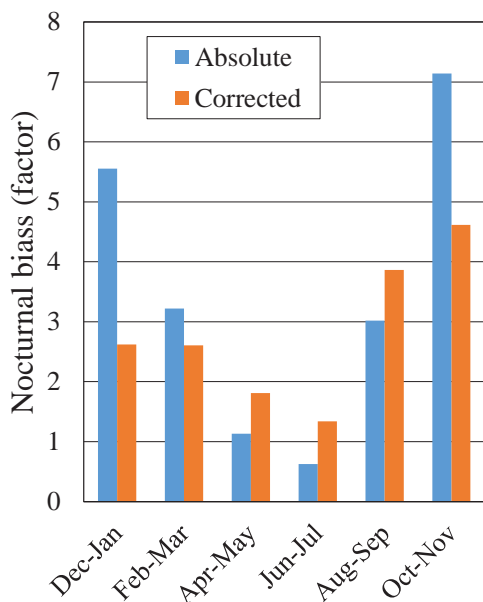


Figure 2. Intensity of nocturnal activity of bank voles, expressed as the proportion of observations between sunset and sunrise relative to the number observed between sunset and sunrise (1 = equal numbers during night and day; 2 = twice as many nocturnal observations etc.). Both the proportions in absolute numbers and in numbers corrected for the sum of day- and night-hours in the given periods are given. Based on data in table 1.

which referred to bank voles. All observations were registered in Central European winter time and related to local sunrise and sunset. Due to variable sample sizes, we used two-monthly periods: December-January, February-March, and so on. For the same reason we lumped data of different locations and years (see also Discussion). Calculations were made in Microsoft Excel.

It is possible that the sensitivity of the cameras was negatively influenced by high temperatures. This may have reduced the number of daytime observations during some very hot (>30°C) summer days. We assume this did not affect the general patterns as found in this study.

## Results

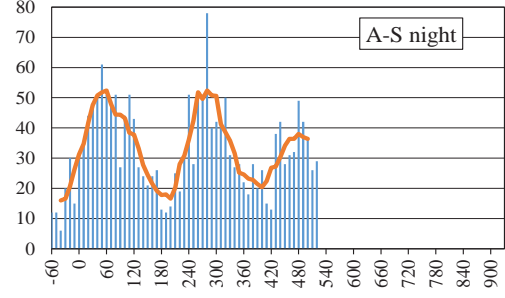
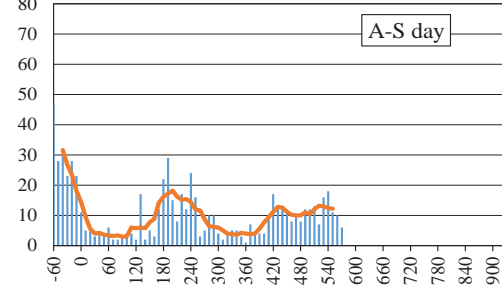
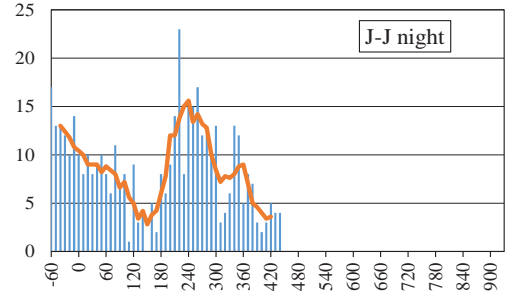
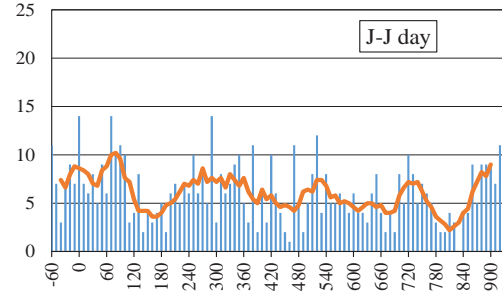
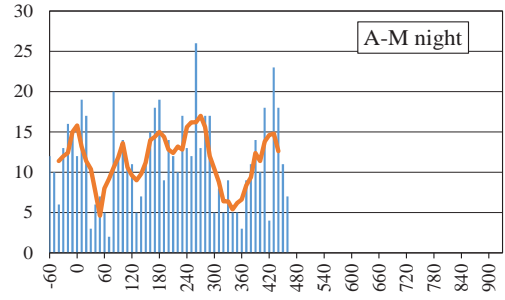
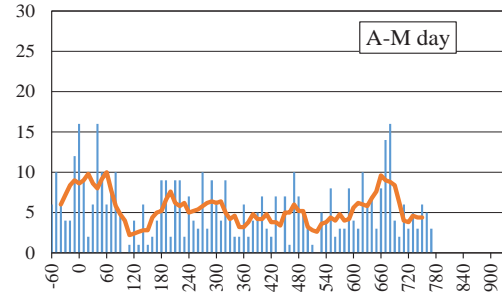
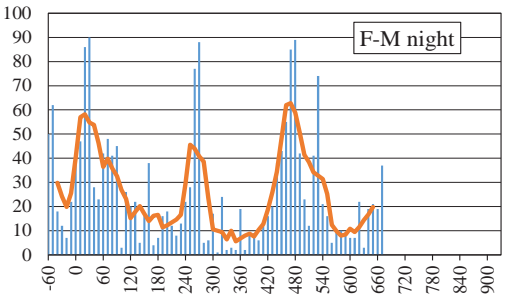
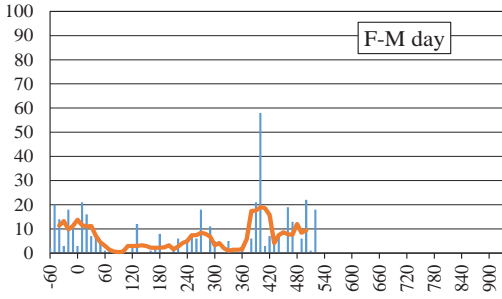
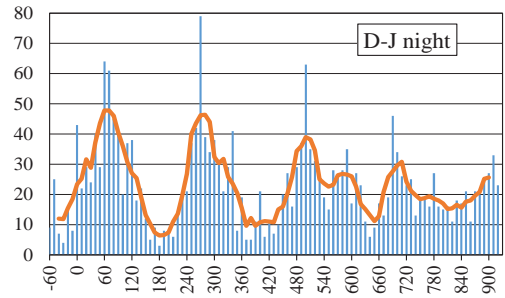
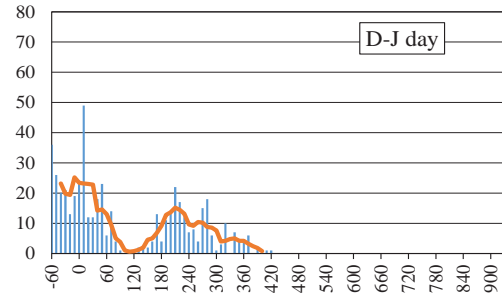
### Circadian rhythm

Throughout the year, bank voles were mainly nocturnal, especially during September-April and least so during May-August (figure 1). On average bank voles were 2.8 times more frequently observed between sunset and sunrise (night) than between sunrise and sunset (day). Nocturnal activity was most outspoken in October-November. In contrast, in June-July most observations were recorded during daytime (figure 2), which mainly derives from the lengthy period of daylight in summer. When corrected for available day- and night-hours, bank vole activity was always biased towards the night but three times more so in October-November than in June-July.

### Ultradian rhythm

On top of the circadian rhythm, a rather distinct ultradian rhythm was superimposed (figure 1), albeit with variable intensity across the year. An ultradian rhythm was especially evident during August-March (figure 3), with an activity peak just after sunset, normally within the hour, to be followed by a series of 2-4 distinct peaks and lows during the night. In April-July the activities started already about 1-2 hours before sunset and peaked at sunset during April-May and an hour before sunset in July and August. During April-May nocturnal activity was rather diffuse, but in June-July a distinct peak 4-5 hours after sunset was registered, fading away towards sunrise (figure 3). A diurnal activity peak at around 3-4 hours after sunrise was only evident in December-January and in August-September.

The mean interval between peaks and lows amounted to 115 minutes (sd=22.9, n=19) and between lows and peaks 109 minutes (sd=21.8, n=15), but the range was considerable. Cycles could theoretically be shortened by sunrise



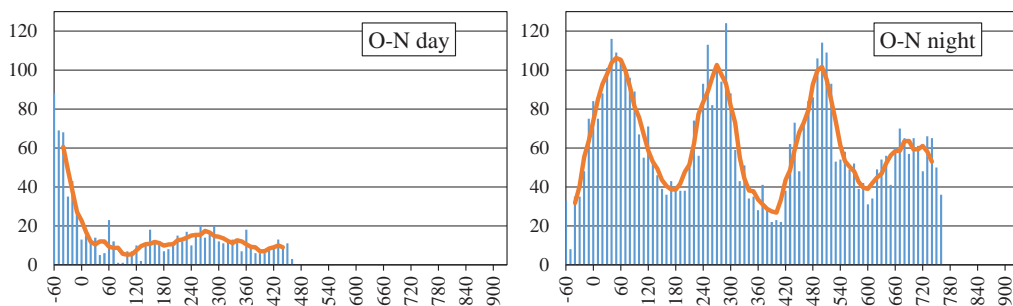


Figure 3. The number of bank voles recorded across the day per 10-minute periods relative to sunrise (left, one hour before sunrise to one hour before sunset) and sunset (right, one hour before sunset to one hour before sunrise), including running averages of five periods. Due to variable lengths of daylight periods and sample sizes, each time series is cut off at the shortest day or night.

or sunset, but cycles at the end of the day or end of the night were not shorter than other cycles. Since there may be some noise in the exact moment of a peak or a low (figure 3), we checked if very short cycles were followed by longer ones, but this was not clearly the case. The mean duration of full cycles (from peak to peak or low to low) was 224 minutes, ranging from 180-290 minutes ( $sd=27.7$ ,  $n=22$ ).

## Discussion

### Synchronized activity patterns between locations and years: a biased finding?

The activity patterns derived from the camera traps may have been biased given the fact that data of various locations have been lumped and sometimes more than 50% of the data in some months came from a single site. Generalising from meagre datasets may coincidentally produce synchronised activity patterns based on one or few individuals. The only validation possible came from October-November when a substantial number of locations provided data. The bank voles at these sites showed a highly synchronised activity pattern, in line with the finding reached for the entire dataset (figure 4). The autumn locations were sufficiently apart to exclude the possibility that the same individual was involved

(Johnsen et al. 2019). Even the activity pattern at a location 2.7 km apart from the others and separated from these by unsuitable habitat (open arable fields) was mostly in line with the pattern in general. We therefore presume that ultradian rhythms in bank vole activities are synchronised over large areas when conditions are more or less similar. Therefore it is probable that the rhythms are caused by an individual internal instead of a social mechanism, in agreement with Halle (2000).

Interestingly, for December-January the data originated from December 2018 and 2019 and January 2019 and 2020, i.e. covering two separate years. The patterns in both years were highly synchronised at sunset, but at the end of the night the pattern in 2018/2019 had developed a delay of an hour towards the end of the night (figure 5). This may indicate that the ultradian rhythm is not ruled by an endogenous clock alone and that environmental factors may influence the pattern to a certain extent.

### Circadian rhythm

The activity of bank voles is reported either as nocturnal (Bleicher et al. 2019), diurnal (Jędrzejewska & Jędrzejewski 1990) or variable according to season (Ylönen 1988). The choice of a predominantly diurnal or noctur-

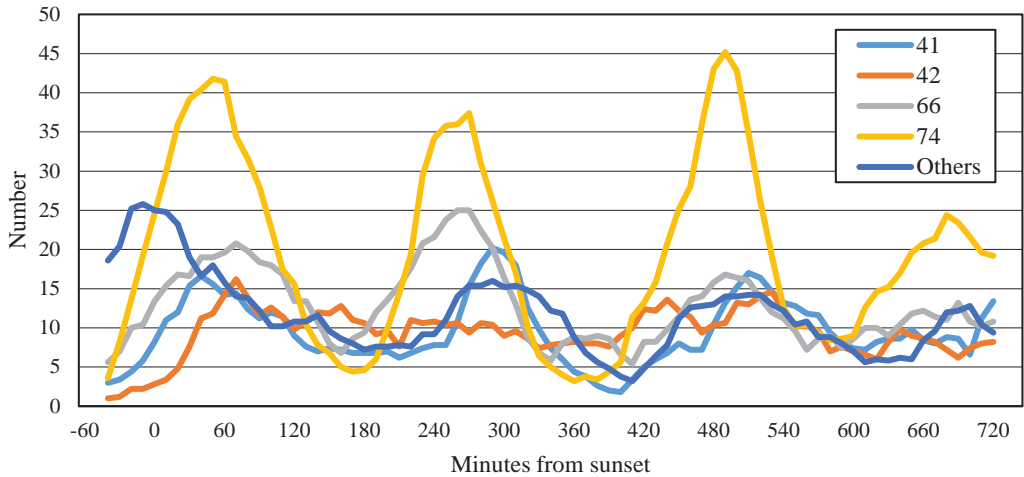


Figure 4. Number of registrations (moving averages per five ten-minute periods) of bank voles in the four most attended Struikrovers in October-November 2019. The category “Others” represents the summed observations in the other less attended Struikrovers. Nearest neighbour distances were 290 m (Struikrover 41), 371 m (42), 299 m (66) and 2750 m (74).

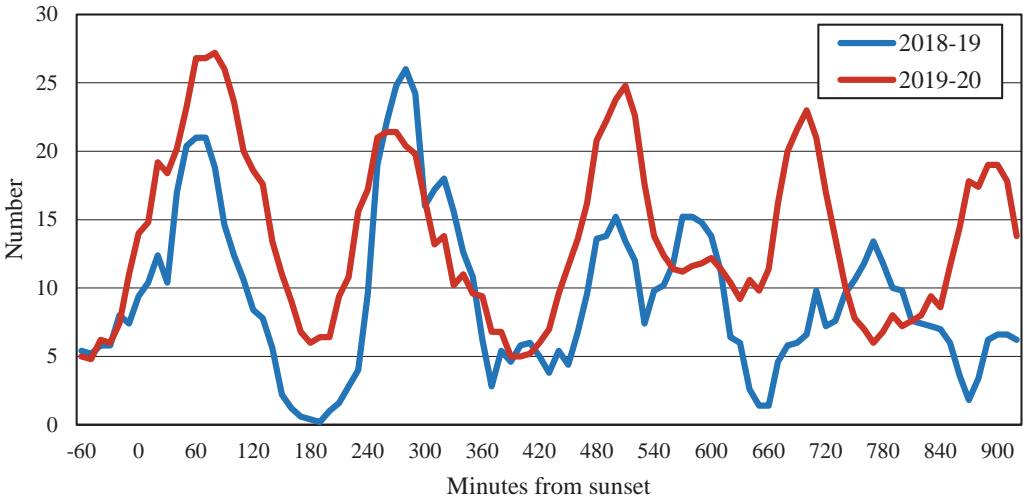


Figure 5. Number of registrations (moving averages per 5 ten-minute periods) of bank voles in December-January 2018-2019 and December-January 2019-2020 (different locations).

nal activity pattern is presumably a trade-off between energetic demands and the risk of predation. Foraging during the day could be more profitable due to better visibility of food items and higher ambient temperatures. In our study area, in the temperate climate zone, and under natural conditions, we more often encountered bank voles on foot under sunny conditions

than when overcast, especially in spring when ambient temperatures are still rather low.

At night prey species may be better detectable due to – on average – lower wind speed and higher air humidity. Our study via camera traps revealed the presence of a number of (partially nocturnal) predators, i.e. pine marten (*Martes martes*) (97% of the images trig-



Bank vole smelling the small opening of a sardine can in a Struikrover. Taarlo, 15 May 2018. Photo: Matthijs Smaal.

gered by night,  $n=32$ ), beech marten (*M. foina*) (96%,  $n=49$ ), red fox (*Vulpes vulpes*) (80%,  $n=5$ ), badger (*Meles meles* (75%,  $n=4$ ), Western polecat (*Mustela putorius*) (35%,  $n=17$ ), stoat (*M. erminea*) (33%,  $n=9$ ) and weasels (*M. nivalis*) (26%,  $n=277$ ). Numbers may be indicative of relative abundance. Aerial predators in the study area were represented by barn owl (*Tyto alba*) (nocturnal) and common buzzard (*Buteo buteo*) (diurnal), of which the latter has a local density of about one pair per 200 ha (van Manen, unpublished results). The barn owl is probably less common. The composition of the local predator guild suggests that the predation risk for bank voles may be highest during daytime due to the relative abundance of weasel and common buzzard. The predominantly nocturnal activity pattern of our bank voles may be a trade-off between two 'evils', of which nocturnal predators are the lesser. This is supported by an experimental study in Poland, where bank voles in semi-enclosures became more nocturnal in the presence of weasels (Jędrzejewska & Jędrzejewski 1990).

A nocturnal bias in activity was strongest during August–November and decreasing during December–July. This could be a result

of maximum food availability in autumn, decreasing food availability in the course of the winter, the increasing daylength in the course of spring and summer and an increase in food demand due to reproduction, or a combination of several or all of these factors.

### Ultradian Rhythm

Activity bouts in *Microtus* voles have been linked to a feeding pulse. In these species the duration of an above-ground activity bout takes about two hours. Activity cycles could depend on the time needed to digest meals, with on average longer cycles in larger species (Lehmann 1976, Daan & Slopsema 1978, Halle 2000). Relative to size, our bank voles had rather long activity bouts as compared to common voles of the same weight (Daan & Slopsema 1978). This difference might be related to differential diets.

As the observed ultradian rhythm was especially outspoken in periods when the voles were most nocturnal, a strongly synchronised ultradian rhythm might indicate high food availability. This is suggested by Grodzinski (1962), who found that activity patterns

faded when animals were offered only nutrient-poor food, but contrasts with Halle (2000) who states that ultradian rhythms were not affected by deprivation of food.

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## Samenvatting

### Activiteitritme van vrijlevende rosse woelmuizen

Tussen 2 augustus 2018 en 19 januari 2020 hebben we in en rond het beekdal van de Drentsche Aa op 42 locaties onderzoek gedaan naar het voorkomen van kleine zoogdieren met behulp van Struikrovers\*. Een Struikrover is een pvc-buis, met daarop een cameraval gemonteerd en een lek geprikt blikje sardine, dat als aas dient. Om een scherp beeld op 35 cm van de camera mogelijk te maken, werd een brillenglasje voor de lens gemonteerd. De locaties van de Struikrovers bestonden in enkele gevallen uit bos, maar meest uit houtwallen en slootranden in halfopen gebied. Het systeem was in hoge mate aantrekkelijk voor rosse woelmuizen (*Myodes glareolus*), die op 17.065 afzonderlijke momenten als bezoeker van een Struikrover werden geregistreerd. Ze bleken daarbij in de meeste maanden voornamelijk nachtactief, alleen in de periode juni-juli waren er meer registraties overdag dan 's nachts. Echter, wanneer werd gecorrigeerd voor het aantal beschikbare uren, bleek dat ook in juni-juli rosse woelmuizen 's nachts vaker werden geregistreerd dan overdag. In zijn algemeenheid vertoonden ze minder activiteit overdag naarmate de nachten langer waren. Naast een dag-nacht ritme hielden de muizen er ook een kortere activiteitscyclus op na, waarvan de gemiddelde duur 224 minuten bedroeg. Dit ritme bestond uit een serie van 1-4 cycli die begonnen rond zonsopkomst en zonsondergang. Het aantal cycli hing samen met de duur van de dag of nacht en nachtcycli waren meer uitgesproken dan overdag. De cycli verliepen synchroon tussen plekken die van elkaar waren gescheiden door voor rosse woelmuizen ongeschikt habitat en eveneens in dezelfde periodes in opeenvolgende jaren (december-januari 2018-2019 en 2019-2020).

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# Recurring outbreaks of common vole (*Microtus arvalis*) in grasslands in the low-lying parts of the Netherlands

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**Abstract:** In the past, outbreaks of common voles (*Microtus arvalis*) were a regular occurrence in agricultural grassland areas in the Netherlands, but they have been virtually absent in recent decades. However, after 2000 there have been three major outbreaks, in 2004-2005, 2014-2015 and in 2019-2020. To gain more insight into the distribution and underlying causes, this paper documents the occurrence of outbreaks in the Netherlands and maps the distribution during the recent outbreaks in the province of Friesland. In addition, a spatial analysis of damage reports of farmers during the outbreak in 2014-2015 has been carried out. The analysis shows that large outbreaks mainly occur in open landscapes on clay and peat soils that are drained intensively. The number of damage records is lower in case of pasture grazing. We conclude, that the intensive agricultural management of grasslands may not be the cause of outbreaks, but today's dairy farming practices with low water tables and less grazing of pasture, support outbreaks rather than dampening them.

**Keywords :** common vole, *Microtus arvalis*, vole outbreaks, land management, pest-species, water table.

## Introduction

In Europe, outbreaks of populations of common vole (*Microtus arvalis*) occur frequently (Jacob & Tkadlec 2010, Jacob et al. 2020). In recent years, this also has been the case in the low-lying parts of the Netherlands, which is remarkable since large-scale vole infestations seemed to be virtually absent here for almost half a century. Until the 1950s, outbreaks were fairly frequent in low-lying, open agricultural landscapes, notably in 'sparsely used pastures and hayfields' (van Wijngaarden 1957), but despite cyclic population fluctuations, only few local and regional outbreaks were reported in the period 1960-2003 (Dekker & Bekker 2008). In 2004-2005, however,

a severe vole outbreak covered the low-lying grasslands in the south-western part of the province of Friesland (van Apeldoorn 2005). Ten years later, in 2014-2015, an outbreak took place in the low parts of the Netherlands, with once again Friesland as the epicentre (Wymenga et al. 2016). Grasslands, dikes and road verges were eaten bare on a large scale. Vole-rich parcels could often be recognized from a distance by the many gulls, herons and birds of prey profiting from this food bonanza. In 2019-2020 there was another national outbreak and, again, the core area was situated in the low parts of Friesland.

The common vole is one of the most abundant vertebrate species in grasslands in agricultural landscapes in Europe (Jacob et al. 2014) and widespread in the Netherlands (Zekhuis 2016). Its occurrence is characterized by population fluctuations with

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a 2–4-year cycle and irregular outbreaks, often with large-scale agricultural damage (Jacob et al. 2014, Andreassen et al. 2021). The spatial distribution across agricultural landscapes is mainly determined by landscape structure, soil conditions and water tables. In general, their abundance increases with decreasing soil hardness and lower groundwater tables, avoiding overly sandy soils (Klemm 1964, cited in Blank et al. 2011), grasslands with a high groundwater table (0–20 cm below the soil surface; de Jonge & Dienske 1979) and regularly flooded grasslands (Jacob 2003, Wijnhoven et al. 2005, Beemster & Vulink 2013). The outbreak risk in eastern Germany was highest on fertile soils containing a high percentage of humus (Chernozem-soils) in areas with a high elevation (low groundwater table) and further increased in areas with a high soil air capacity (Blank et al. 2011). Also land use is a relevant factor as demonstrated by van Wijngaarden (1957). He concluded that ‘common vole plagues will have ceased to exist’ in the Netherlands due to, at that time, upcoming major changes in land use, from extensively used pastures and hayfields to increasing land use intensity as a result of improved drainage, and introduction of rotational grazing. In hindsight, his conclusions were drawn at the brink of large-scale changes in dairy farming in the Netherlands.

Delattre et al. (1996, 1999, 2009) showed how in France landscape structure and land use influence the spatial variation and amplitude of vole population fluctuations. In summary, they found a strong cyclicity and high amplitudes in open homogeneous grassland landscapes versus a weak cyclicity with low amplitudes in fragmented, most enclosed landscapes. Landscape fragmentation refers to the presence of landscape elements such as forest, woodland, hedges and wooded banks as well as grassland elements in arable landscapes, but also to the replacement of permanent grassland by arable farming. Predation is believed to be the main driver of these patterns (Delattre et al. 1999, Lambin et al.

2006, Giraudoux et al. 2013). According to this hypothesis, generalist predators, which find suitable habitat in fragmented, enclosed landscapes, dampen population fluctuations, while specialized vole predators in homogeneous landscapes, usually open areas of permanent grassland, enhance population cycles.

In their review about the mechanisms behind the cyclic population dynamics and irregular outbreaks of small rodents, Andreassen et al. (2021) make clear that the driving factors are still only partly understood, and several questions remain. With regard to changes in land use and landscape structure they wonder what possible pathways may affect small mammal population dynamics. In this light, the recent outbreaks in the Netherlands in drained polders below sea level, a situation not found elsewhere in Europe, are of interest. These polders consist largely of homogeneous and permanent grassland areas and as such provide optimal habitat for common voles, albeit in a much higher land use intensity than at the time of the study by van Wijngaarden (1957). The recent outbreaks raise the question of the reasons why this phenomenon has been virtually absent for a long time. In this paper we explore if large scale changes in management practice of dairy farming in the past decennia in the Netherlands are part of the explanation, and hypothesize that drainage and the absence of pasture grazing by dairy cows boost the occurrence of outbreaks in today’s intensively used grasslands.

## Methods

### Study area

Our study area includes grasslands in the low-lying parts of the Netherlands (50–54 °N, 3–8 °E), particularly in the province of Friesland where the field data were collected. About one-third of the land area of the Netherlands consists of grassland (9,830 km<sup>2</sup> in 2019; www.cbs.nl), of which 7,680 km<sup>2</sup> is permanent grassland

largely used for dairy farming. In the east and south of the Netherlands, grassland is interspersed with arable farming on sandy soils, in predominantly enclosed or semi-enclosed landscapes. In the north and west of the Netherlands, the vast majority of grasslands are found on peat and clay soils in open landscapes, mostly located in polders 0-6 m below sea level. In the past decades, dairy farming and associated land use have undergone a process of intensification and up-scaling aimed at maximizing production and reducing costs.

In Friesland 70% of agricultural land consists of permanent grassland, covering an area of 1,750 km<sup>2</sup>. A large part of these grasslands is found in flat and open polder areas, 0-2.6 m below sea level, on peat and clay soils in the western and central part of the province, bordered on the east side by an enclosed landscape on sandy soils. 75-100 years ago, the low-lying polders formed a floodplain-like landscape and polders were regularly flooded in winter. Nonetheless, this area was described by van Wijngaarden (1957) as the most extensive vole plague zone in the Netherlands in that time, although outbreaks there were 'never extremely severe'. As part of a large-scale governmental programme for land consolidation and land-use planning (van den Berg 2004, van der Molen & Wubbe 2020), these polders were optimally equipped for agricultural production, in particular for dairy farming, roughly in the period 1960-2000 and partly beyond. The most important interventions were drainage (up to 1.2 m below surface level), enlargement of parcel size by filling in ditches, improvement of land access, fertilisation (culminating in approx. 400 kg N/ha/yr in the 1980s, now reduced to about two-thirds of that amount) and introduction of frequent grassland renewal. Under these conditions, dairy farming changed markedly, with an increase in farm size and stocking density, later followed by a decrease in rotational grazing, with cows increasingly being fed in dairy barns rather than grazing on pasture. The result of this in 2021 is

a modern agricultural production landscape with a highly productive dairy farming. The downside of this development, in Friesland as well as in other parts of the Netherlands, is an unprecedented loss of biodiversity in agricultural landscapes (van Strien et al. 2016, Bouma et al. 2020, WNF 2020). Nowadays the majority of the grassland polders consist of species poor and monotonous grassland with small areas of maize. The previously characteristic biodiversity, in particular meadow birds, herbaceous meadows and invertebrate fauna, has largely disappeared.

### Data collection on population dynamics and spatial patterns

For this paper, we collected data in the framework of a study on the vole outbreak in 2014-2015, initiated by the regional water authority and provincial authorities in Friesland due to the perceived risk of damage to (earthen) dikes and the significant damage to dairy farming (Wymenga et al. 2016). In addition, we collected field data on indices of vole abundance from 2016-2020, particularly during the outbreak in 2019-2020.

We describe the multi-annual cyclic pattern of vole abundance in the Netherlands using long-term data (1960-2020) on the annual number of ringed nestlings of long-eared owl (*Asio otus*), barn owl (*Tyto alba*) and kestrel (*Falco tinnunculus*) in the Netherlands, provided by the Netherlands Institute for Ecology (NIOO-KNAW). The number of ringed individuals is a parameter for reproductive success because it is dependent on availability of chicks (ringing effort is not a limiting factor in this). In open areas these species forage predominantly on voles, and we assume that peaks in reproduction are caused by a high prey availability i.e., high vole abundance (cf. Daan & Dijkstra 1988, Bernard et al. 2010). To account for long-term population trends in these birds, the annual ringed numbers have been expressed as anomaly of the 5-yr run-

Table 1. Annual number of parcels and quadrats per quarter in which we measured burrow density ( $\#/m^2$ ) and number of parcels where we assessed the Parcel Index (PI) in Friesland in the period 2015-2020.

Year	Months	Period	<i>n</i> parcels	# quadrats	PI
2015	Jan-Mar	Jan-Mar	244	4879	-
2016	Oct	Oct-Dec	90	2060	-
2017	Mar	Jan-Mar	61	1550	-
2017	Nov-Dec	Oct-Dec	58	1435	-
2018	Sept	Jun-Sep	18	450	-
2018	Oct	Oct-Dec	8	200	-
2019	Sept	Jun-Sep	10	100	-
2019	Nov-Dec	Oct-Dec	52	1338	340
2020	Jan-Mar	Jan-Mar	11	275	966
2020	Oct	Oct-Dec	40	400	40



Figure 1. Grasslands in the Leechlân near Grou, largely eaten bare by common voles. In the foreground a 1x1 m plastic frame for monitoring burrow density. 1 September 2019. *Photo: E. Wymenga.*

ning mean. In addition, we obtained data on the number of fledglings (including nestlings which were not ringed) of barn owls in the province of Friesland over the period 2015-

2019 (data Kerkuilenwerkgroep Nederland, Johan de Jong), in order to correlate these to an index of vole abundance in Friesland over the same period (see hereafter).

Irregular peaks with extreme high densities of voles are generally considered as outbreaks, but there is no clear definition (Andreassen et al. 2020). During outbreaks, common voles reach densities of up to 1,000-2,000 individuals/ha (Jacob & Tkadlec 2010), about 2-3 orders of magnitude higher than in a typical peak year. In this study, we have no robust quantitative information on population densities for any year. However, outbreaks are known to cause widespread damage to crops and grasslands since time immemorial (Jacob & Tkadlec 2010), a phenomenon that does not go unnoticed. In this study we therefore distinguished outbreaks from lower 'normal' cyclical peaks by using reports of excessive agricultural damage by voles, mainly from grey literature or media publications (building further upon overviews by van Apeldoorn 2005 and Bekker & Dekker 2008). This approach does not exclude that we have missed local or regional outbreaks, but interviews with several farmers and researchers (>55 years old) from traditional outbreak zones in the Netherlands confirm our results. Outbreaks were scored as local (one or a few areas, 100s ha), regional (more areas, 1000s ha) or national (multiple areas spread across the Netherlands, 10,000s ha) based on the number of areas and the area over which severe damage to grasslands was reported.

To quantify the population fluctuations in recent years in Friesland, the core area in the Netherlands, we collected data on indices of the vole abundance with several methods during the last two outbreaks and partly also in intervening years (table 1). From February 2015 until March 2020 the relative abundance of voles was monitored by counting the number of burrows of voles on grassland parcels in Friesland. In 2015 we used a stratified sampling method, where parcels were randomly selected along three grids across the clay and peat soils in Friesland (details in Wymenga et al. 2016). A limited number of parcels ( $n=6$ ) on higher sandy soils were also sampled. In 2016-2020 four areas were selected where we



Figure 2. Grass clippings by common vole. The grass - in this case English ryegrass (*Lolium perenne*) - is pulled down into the burrow entrance. November 2019. Photo: Altenburg & Wymenga.

repeated our sampling; in these polder parcels were chosen randomly each year. For each parcel, the number of burrows was counted in 10 to 25 randomly selected quadrates of 1x1 m (=1 m<sup>2</sup>), at least 10 m apart (figure 1). The quadrates were selected by throwing a plastic frame in a chosen direction and the recording was made where the frame had landed.

In 2019 we introduced a semi-quantitative method, the so-called Parcel Index (PI), to assess the relative abundance of voles in large areas in a relatively short period of time. The PI is a qualitative assessment per parcel (varying in size, on average 3 ha,  $n=1346$ ) based on visible vole activity such as runways, burrows,

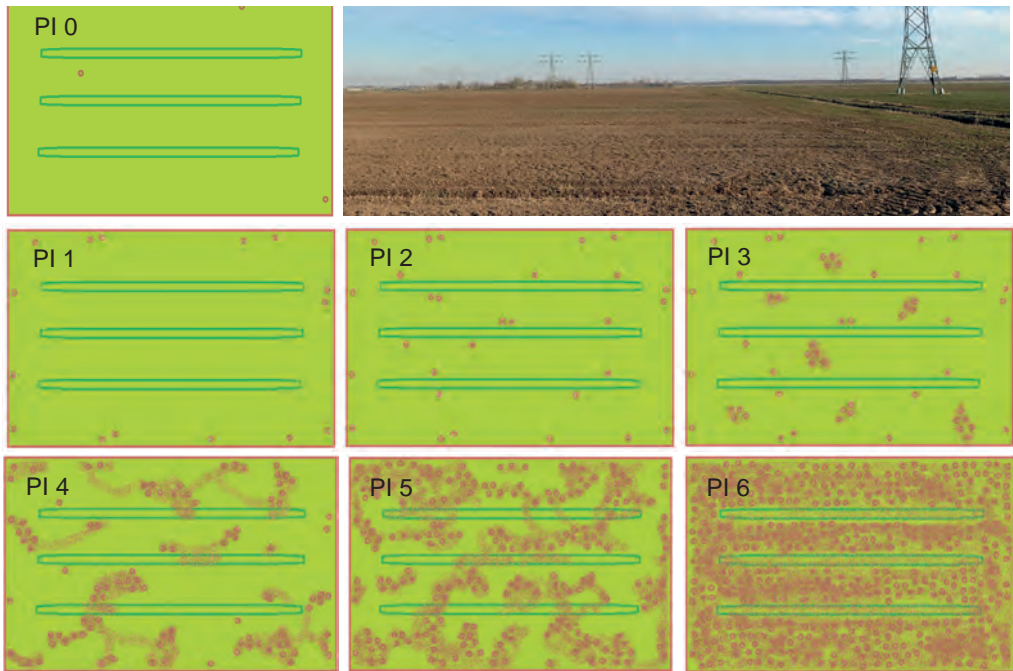


Figure 3. Visualization of the Parcel Index (PI) in seven classes. PI 0: none or hardly any vole activity; PI 1: clear vole activity in ditch edges, hardly any activity on the parcel; PI 2: clear vole activity in ditch edges and around surface drains, some burrows on the parcel; PI 3: as PI 2, with incipient clustering (bare spots, clusters of burrows) on the parcel; PI 4: clusters on the parcel grow together and are connected through above-ground tunnels, clusters cover less than half of the parcel; PI 5: as PI 4, clusters cover more than half the parcel; PI 6: very high burrow density, clusters of burrows all over the parcel, heavily grazed and partly bare (as on the photograph in the upper panel, March 2020, Suwâld, E. Wymenga).

clusters of burrows and grass clippings (figure 2). Through an iterative process of field testing and adjustment, seven classes were established, which were clearly distinguishable from each other in the field by the zonation and severity of vole activity on the parcels (figure 3). Figure 4 shows the relationship between mean burrow density and PI-class on 61 plots.

As a second step, we mapped the spatial distribution of the outbreaks. On national level we used vole damage records of farmers in 2004-2005 and 2014-2015. In these years, farmers were invited to report vole damage on the website of the regional farmer's association LTO. These reports, available on the level of postal zip codes, give an indication of the occurrence and extent of the outbreaks in those years. The 2014-2015 data are expected to be the most

complete due to the large media coverage of agricultural damage. Since farmers did not receive any monetary compensation in the end, much less damage was reported by farmers in subsequent years. The data for the later period (2016-2021) therefore do not provide a reliable picture and were not used.

For Friesland we also interpreted satellite images to map the outbreaks of 2004-2005, 2014-2015 and 2019-2020. We used Landsat-5 imagery for 2004-2005, Landsat-8 imagery for 2014-2015 and Sentinel 2 imagery for 2019-2020. On satellite images, a high vole abundance in grasslands becomes visible when vole activity (grazing and burrowing) leads to a reduced Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1976) and bare soil. This pattern is enhanced when grass

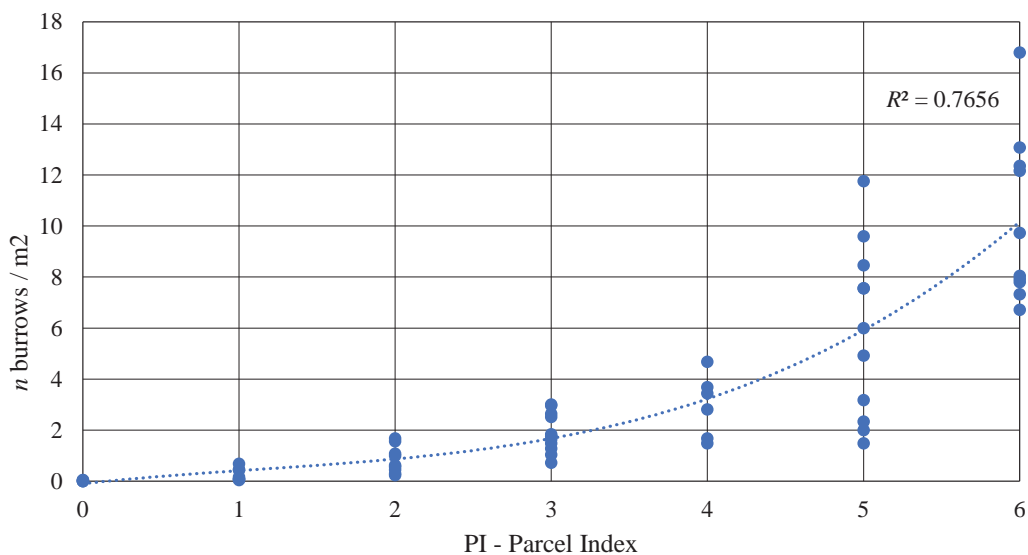


Figure 4. Mean burrow density per parcel as function of Parcel Index, measured on 61 parcels in Friesland in the period November 2019 – February 2020.

growth is delayed by drought or low temperatures. Next to vole activity, satellite images may also show severe drought or intensive grazing by geese, both of which also lead to a lower NDVI, but rarely to bare soils. To optimize visibility of vole-induced damage patterns, false colour composites were created, combining information from three different spectral bands (Short-wave infrared - Near infrared - Red) into one image (pixel resolution is 30 x 30 m for Landsat and 20 x 20 m for Sentinel). We tested in the field in 2019-2020 whether the visible patterns on the images indeed reflected vole-infested parcels, using PI. As a high PI score correlates with a high burrow density (figure 4), we assume that the pattern visible on the images is a good representation of the spatial distribution of the outbreaks. Note however, that the actual vole population density may have already passed its peak when bare soil is visible. Parcels with a high vole damage (PI 4-6) are typically visible on the satellite images by a pink and cloudy pattern. Parcels with more than 50% bare soil typically scored PI 5-6 (figure 5). We could not derive a clear quantitative NDVI or

bare soil criterion for assigning plots to a PI score, especially since heavily infested parcels quickly became overgrown with chickweed (*Stellaria media*). Therefore, the maximum extent of the outbreaks was drawn by eye on the basis of the false-colour composites, supported by maps showing the difference in NDVI per parcel in the month April between the outbreak year and the year prior to the outbreak (maps not shown in this paper).

Finally, we collected spatial data on soil, landscape openness, drainage and land use in the Netherlands. We used a digital soil map (de Vries et al. 2003), scale 1:50,000, to distinguish between main soil types (sand, peat and clay soils). To account for the openness of the landscape we used the digital data of the ViewScope model (provided by Wageningen UR; Meeuwssen & Jochem 2013). Openness of the landscape is defined in this model as the landscape overlooked which is not blocked by a rising object or a too prominent slope in the terrain, with a resolution of 25 m for terrain and landscape data and 100 m resolution for the assessment points (Meeuwssen & Jochem 2013). For drainage we used the digital map of



Figure 5. Part of a polder in Friesland with parcels with a high vole abundance. Left Sentinel-2 false colour image of 12 December 2019 and right the corresponding PI score of monitored parcels (fieldwork December 2019). PI not assessed in remainder of parcels.

Teunissen et al. (2012). Estimated drainage is defined as the difference in cm between surface level (AHN1 – elevation map – [www.ahn.nl](http://www.ahn.nl)) and the surface water level maintained by pumping on polder level, as published by the relevant water authority. For land use, in particular grazing on pasture, we used the data of van der Schans & Keuper (2013), based on a sample of 500 dairy farms in the Netherlands. These data indicate for each farm in the sample whether or not grazing on pasture of dairy cattle is practised.

## Analysis

We used the spatial data on soil, landscape openness, drainage and land use (pasture grazing) in the Netherlands as factors and analyzed their impact on the spatial distribution of vole damage reports of farmers in 2014-2015 in a multiple regression model (GLM). Since the vole damage reports by farmers correspond well to parcels with visible vole damage in Friesland (Wymenga et al. 2016), we assume that they also represent the outbreak distribution on a national level.

To link the spatial data, we used a grid of hexagons with a cell size of  $\sim 1 \text{ km}^2$  and superimposed this in GIS on the maps of soil type, landscape openness, drainage, grazing of pasture and the number of damage reports. The value of each of these factors was then determined per hexagon. Damage reports were available at postal zip code level and in GIS as the number of records per hexagon. For the statistical analysis these were converted to presence or absence data because it could not be determined with certainty how many farmers within a zip code area had reported damage (i.e., multiple farmers or, for example, multiple parcels per farmer). In the full model we tested the relevance of soil type, openness of the landscape and drainage as separate factors and their interactions. Pasture grazing was not included in the full model, due to the limited set of data (too many missing values). The relevance of pasture grazing therefore was tested in separate models for peat and clay soils, limited to the hexagons for which data on openness, drainage and grazing was available. To present the results in this paper in histograms, data were divided into classes: soil (three classes), openness (twelve classes),

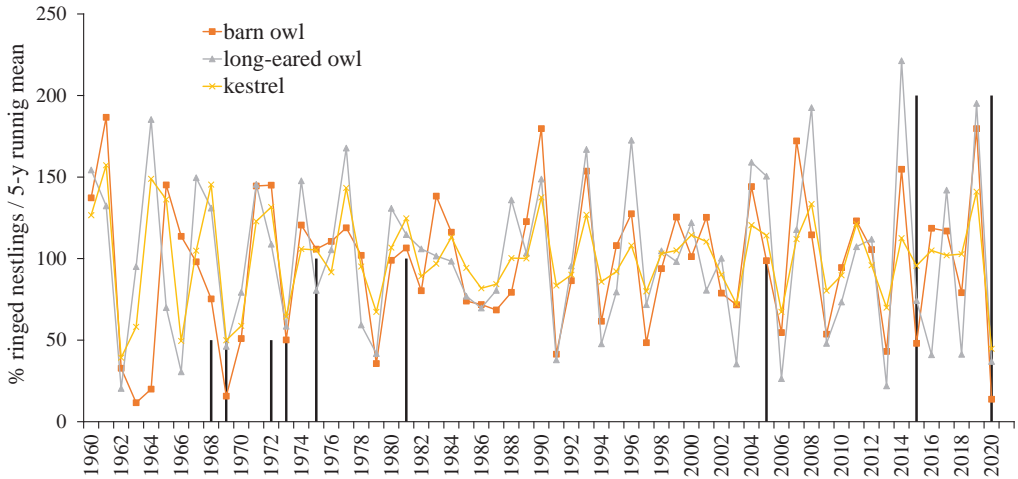


Figure 6. Annual variation in the number of ringed nestlings of long-eared owl, barn owl and kestrel in the Netherlands in the period 1960-2020. Data are expressed as the fraction of the five-year running mean, to reduce long-term trends. Source: Bird migration station, NIOO Heteren. Vertical lines represent reported outbreaks in grassland areas in the Netherlands, scored as local (short), regional (mediate) and national outbreak (long).

drainage (six classes) and grazing (two classes). For each class, the number of hexagons with damage reports and the total number of hexagons was determined, resulting in a percentage of damage reports per class.

## Statistics

The data were analyzed in R (R-core statistics, R Core team 2013) with multiple logistic regressions. We performed backward selection to select the final model. *P*-values were determined on the basis of Wald tests. The analyses were done with the 'raw' data (no distinction in classes).

## Results

### Cyclic fluctuations and outbreaks in the period 1960-2020

The annual number of ringed nestlings of vole-eating birds in the Netherlands shows a cyclical pattern with a peak in reproduction about every three (range two-four) years (fig-

ure 6): the barn owl had 18 peaks over the past 60 years, the long-eared owl 20 and the kestrel 18. Peak years of these bird species mostly coincide but not always. This may be due to severe winters (for example 1963: very low number of barn owls) or to regional differences in vole peaks and the place where most birds were ringed. Fluctuations in burrow densities in Friesland during 2015-2020 are consistent with this cyclical pattern, including the two recent outbreaks (table 2). In Friesland, the reproduction of the barn owl is highly correlated to vole abundance as measured by burrow densities (Pearson  $R=0.75$ ,  $n=5$ , figure 7).

Recent outbreaks occurred in 2004-2005, 2014-2015 and 2019-2020, at intervals of ten and five years respectively. In 2007-2008 high densities of common voles were established in Polder Mastenbroek, province of Overijssel, but these were not classified as an outbreak by Gerritsen (2016). From 1960 to 2003, no large-scale national outbreaks were reported. Local and regional outbreaks in grassland areas were described in 1968 and 1972 (Polder Mastenbroek, >1,000 ha; Gerritsen & Lok 1986), 1967 and 1971 (Gendringse Broeklanden near

Table 2. Burrow density (#/m<sup>2</sup>, mean, maximum and sd) per quarter in polders on peat and clay soils in the low parts of Friesland in the period 2015-2020 (sampling locations in Wymenga et al. 2016). Quarters which have not been monitored are not included in the table.

Year	Abstract:	<i>n</i> parcels	Mean	Max	Stdev
2015	Jan-Mar	238	4.81	17.20	3.61
2016	Oct-Dec	90	0.69	5.40	1.19
2017	Jan-Mar	61	0.69	5.40	1.19
2017	Oct-Dec	58	0.98	4.72	1.07
2018	Jul-Sept	18	0.60	2.48	0.78
2018	Oct-Dec	8	1.09	2.32	0.84
2019	Jul-Sept	10	5.85	10.00	2.50
2019	Oct-Dec	52	3.39	16.80	3.87
2020	Jan-Mar	11	3.89	12.16	4.55
2020	Oct-Dec	40	0.19	0.90	0.26

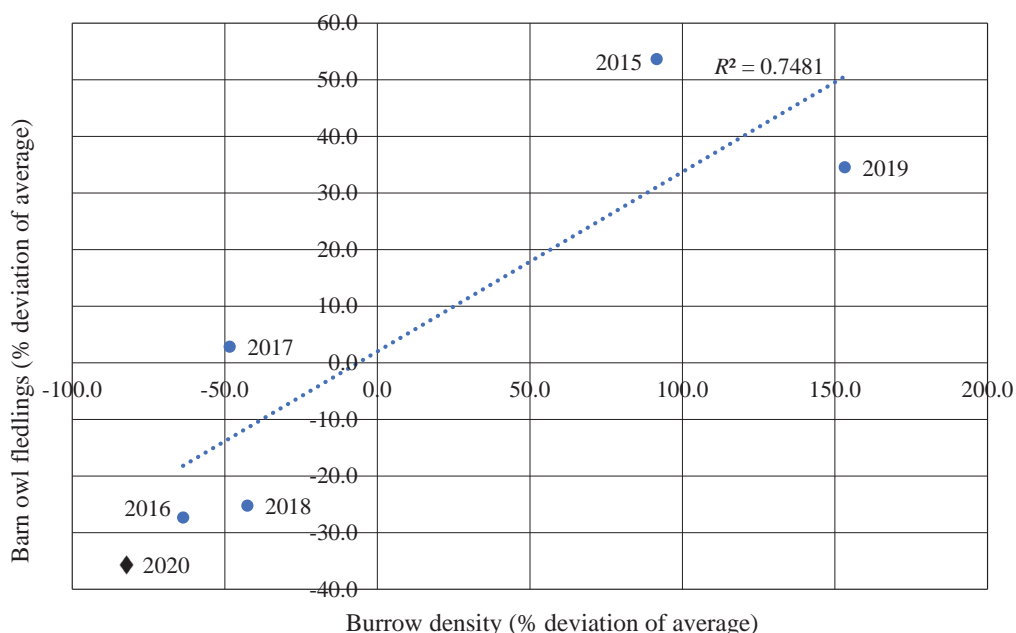


Figure 7. Number of fledglings of barn owl in Friesland as a function of vole abundance, as measured by burrow densities. The number of fledglings is expressed as the percentage annual anomaly of the average over the period 2015-2019. For 2020 this number was estimated based on incomplete data due to the COVID 2 pandemic, and not included in the linear regression. Corresponding burrow densities are also expressed as the percentage annual anomaly of the average over the same period.

the river Rhine, 100s ha; de Bruijn 1979), in 1974 and 1980 (Alblasserwaard and surroundings, resp. 8,000 and 11,000 ha; Jonkers & van Wijngaarden 1975, Jonkers 1981). Outside grassland areas, vole outbreaks were

reported in newly established polders following embankment, like in 1971 in the former estuary Lauwersmeer (Timmerman 1971), and on fallow fields in 1992 in the province of Groningen (1000s ha; Koks & van Scharen-

burg 1997). All outbreaks took place in ‘regular’ peak years as derived from figure 6. Note however, that peak years in different areas may occur in successive years, as for instance in 1967-1968 and 1971-1972 and during the recent outbreaks, when high densities of voles were found throughout the winter, until March the following year, and locally beyond.

To check whether our reconstruction corresponds to the experiences and memories from the field, we interviewed five farmers and researchers (all >55 years old) with long-term relevant field experience in traditional outbreak zones in the Netherlands. Apart from the reported outbreaks, they unanimously stress they have no recollection of (large) outbreaks in the period 1960-2003; although it is noted that there were sometimes years with high densities but no excessive outbreaks.

### **Spatial distribution of recent outbreaks**

The spatial distribution of vole damage reports in the Netherlands in 2014-2015 is shown in figure 8. Vole damage was mainly reported by farmers in open landscapes on peat and clay soils, especially on peat soils with a drainage of more than 60-80 cm below surface level (figure 9). The same pattern emerges from the spatial extent of the three recent outbreaks in Friesland (figure 10), and is reflected in the burrow densities measured: during our field work in Friesland in 2015 we found five burrows/m<sup>2</sup> on average on peat and clay soils, while on sandy soils the density was significantly lower (0.4 burrows/m<sup>2</sup>; Univariate Anova:  $F_{5,234}=5.1$ ,  $P < 0.001$ ; details in Wymenga et al. 2016). Supplemented by information from van Apeldoorn (2005) and Wymenga et al. (2016), the distribution of recent outbreaks can be summarized as follows:

*2004-2005:* outbreak in the open and central part of Friesland on grasslands on peat soils, over an area of c. 6,600 ha, extending on peat soils into the province of Groningen. Elsewhere, very localized in grasslands on

peat and clay soils in the centre of the Netherlands (van Apeldoorn 2005).

*2014-2015:* large scale outbreak in Friesland, on peat and clay soils, on a much larger scale (ca. 60,000 ha) than in 2004-2005, and also with a much greater extent than the vole plague zone reported by van Wijngaarden (1957). Also extending into the province of Groningen. Elsewhere in the Netherlands, exceptional vole damage in grasslands was reported in peat and clay areas in the centre, mostly in areas where also in the past outbreaks have been reported, like in Polder Mastenbroek, Eemland, the Alblasserwaard and Vijfheerenlanden (Wymenga et al. 2016).

*2019-2020:* in Friesland, the outbreak covered much the same area as the previous outbreak, but over a smaller surface area (about 37,546 ha). During the outbreak many farmers flooded their grasslands, in an attempt to mitigate damage. Elsewhere in the Netherlands, vole damage in grassland areas was reported in the north (province of Groningen), in ‘traditional’ outbreak areas such as the Alblasserwaard, Vijfheerenlanden and Krimpenerwaard and further east in other areas along the rivers Rhine, Lek and Waal, particularly the Betuwe.

### **Analysis of distribution in relation to landscape and land use**

The spatial analysis demonstrates, that most damage is reported in open, well drained areas on peat and clay soils (figure 9). The spatial patterns as presented were tested in a multiple logistic regression, in a full model for soil type, openness and drainage, and separate models for grazing, openness and drainage on peat and clay soils. In the full model, all of the individual factors as well as their interactions contributed significantly to the model (table 3). For both peat and clay soils also grazing of pasture seems relevant, with less recorded damage in grazed pastures (figure 11). Pasture grazing as individual factor is however only

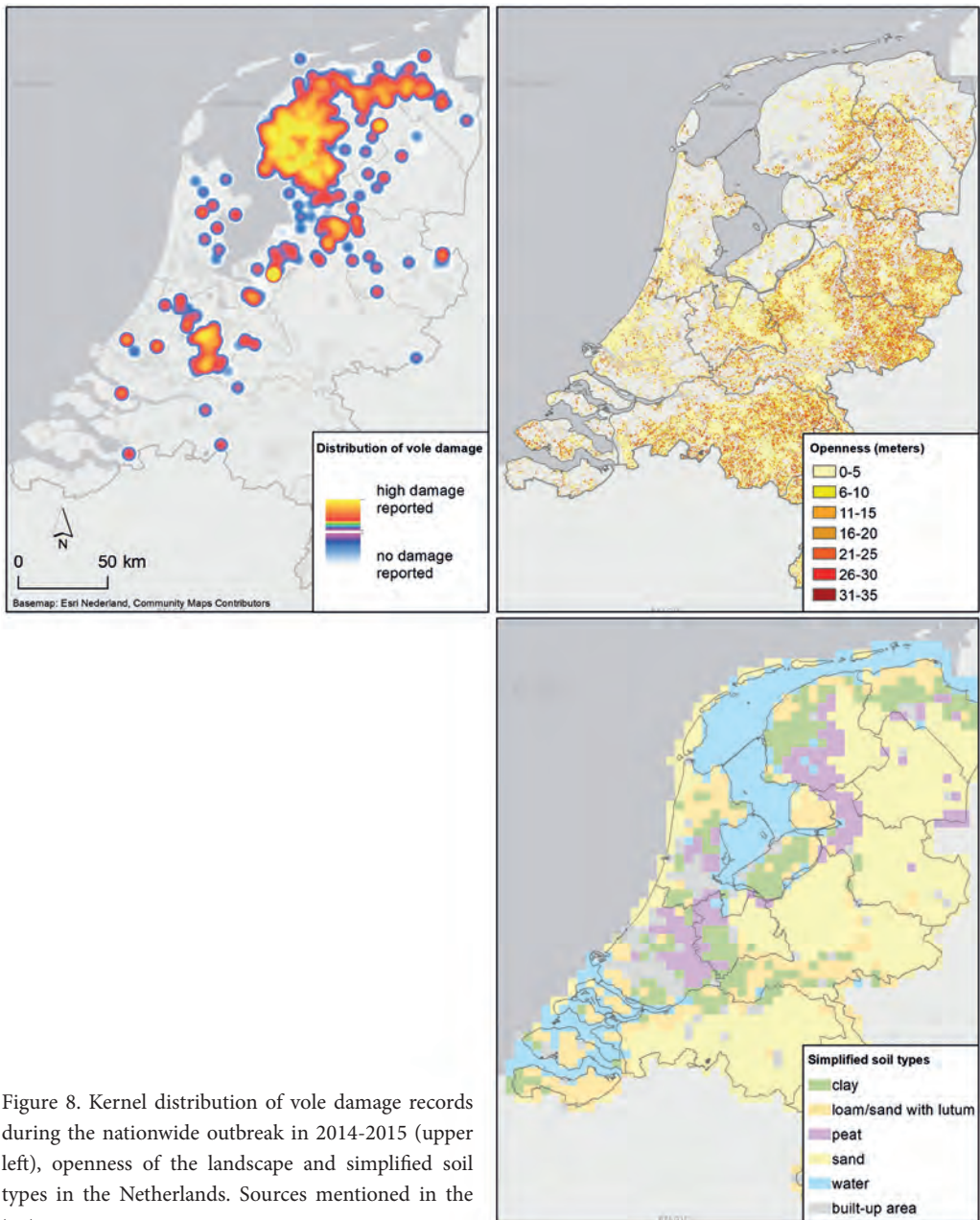


Figure 8. Kernel distribution of vole damage records during the nationwide outbreak in 2014-2015 (upper left), openness of the landscape and simplified soil types in the Netherlands. Sources mentioned in the text.

significant in the regression models for peat. In the clay model openness and drainage produce the best fit, and grazing is not significant nor the interaction of drainage x openness x grazing (table 3).

## Discussion

Van Wijngaarden (1957) provided an overview of the 'vole plague zones' in the Netherlands around 1950, and these appear to be largely the same areas where outbreaks occurred in

Table 3. Summary results of multiple logistic regression models. Dependent variable is ‘vole damage’ (yes or no). Explanatory variables and their interactions are tested for three models: 1. Overall model with soil types together ( $n=16,421$  observations). 2. Model with only peat soils ( $n=309$ ). 3. Model with only clay soils ( $n=286$ ).  $P$ -values for significant factors:  $P<0.001$  \*\*\*,  $P<0.01$  \*\*,  $P<0.05$  \*

Full model		
Overall model - with factors soil x openness x drainage, grazing not included	Peat model – with factors openness x drainage x grazing of pasture	Clay model - with factors openness x drainage x grazing of pasture
Final model	Final model	Final model
Soil type ***	Openness of landscape ***	Openness of landscape ***
Openness of landscape ***	Drainage ***	Drainage *
Drainage ***	Grazing of pasture ***	
Soil type x drainage **		
Soil type x openness of landscape *		
Drainage x openness of landscape ***		
Soil type x drainage x openness ***		

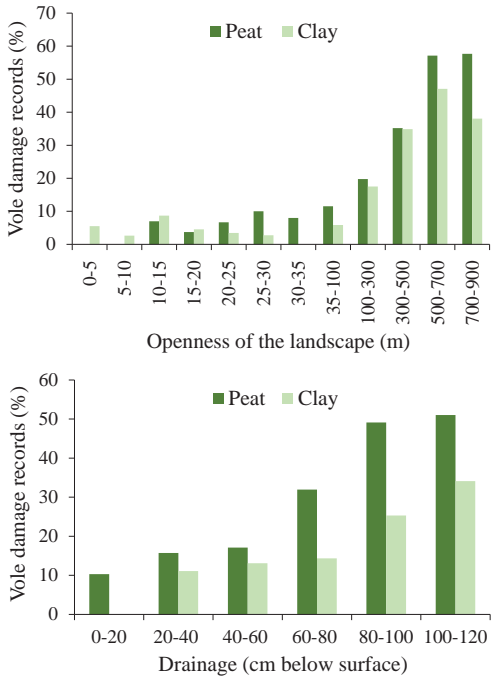


Figure 9. Percentage distribution of vole damage records by farmers for openness of the landscape and drainage on peat and clay soils in the Netherlands. The percentage of hexagons with damage records is given per class (for each class ‘damage’ and ‘no damage’ = 100%).

the period 2004-2020: grassland areas with dairy farming on peat (and partly clay) soils in central Friesland, NW Overijssel (notably Polder Mastenbroek) and in Eemland, on clay and peat soils all along the rivers Waal, Rhine and Lek, particularly in the Alblasserwaard and the adjacent Vijfheerenlanden. The spatial patterns found, with outbreaks in open landscapes on relatively dry and soft soils, are consistent with earlier studies in temperate Europe (cf. Delattre et al. 1996, 1999, 2009, Blank et al. 2011). Van Wijngaarden (1957), however, predicted that the outbreaks would cease to exist as a result of scaling-up and intensification of land use. As we made plausible in this paper, indeed outbreaks in these areas were virtually absent for decades, but after about half a century, returned.

With the forecast of van Wijngaarden in mind, the return of outbreaks of common voles to Dutch grasslands areas, which are among the most intensively used grasslands in the world, seems rather paradoxical (cf. Jobsen 1988). Biodiversity in this agricultural production landscape is under such pressure that there hardly seems to be any room left for natural dynamic processes such as vole outbreaks. We may however interpret the devel-

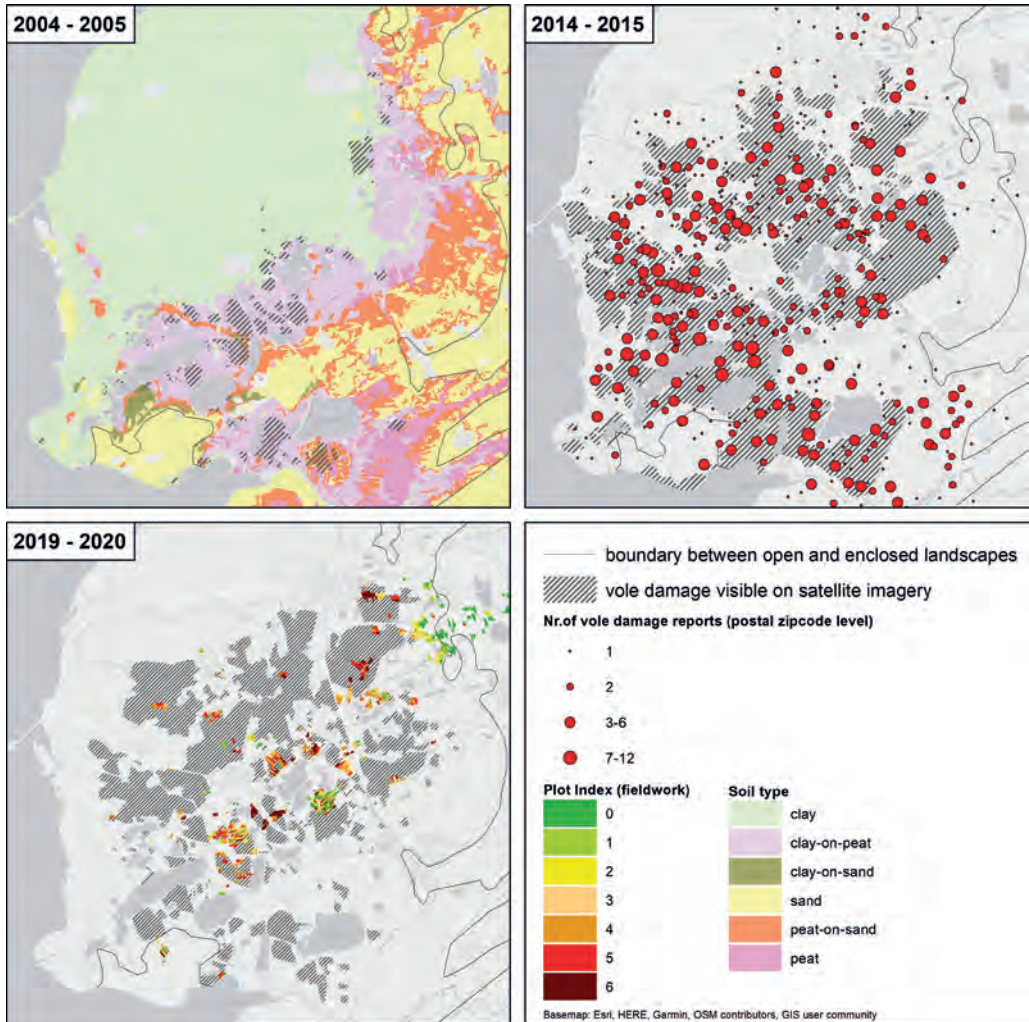


Figure 10. Maximal extent of visible vole damage (bare soil, low NDVI) on satellite images in 2004-2005, 2014-2015 and 2019-2020. For 2014-2015 we also show the distribution of damage reports of farmers (on the level of postal addresses, size of dot varies with number of reports), and for 2019-2020 in colour the plots PI. The black line on the east side of the maps represents the 0 m (Dutch Ordnance Level) altitude, coinciding with a landscape changes from 'open' to 'enclosed' landscape.

opments using the same mechanisms identified by van Wijngaarden (1957). While we will not address underlying processes such as predation and other factors here (cf. Andreassen et al. 2021), we discuss the role of large-scale land-use changes, particularly rotational grazing and improved drainage in the disappearance and reappearance of recent outbreaks.

### Rotational grazing as a constraint for the development of outbreaks

Several local long-term studies demonstrate the negative impact of grazing on the occurrence and abundance of common voles (Beemster & Vulink 2013, Lagendijk et al. 2018) and field voles (*Microtus agrestis*) (Evans et al. 2006). Trampling disturbs bur-

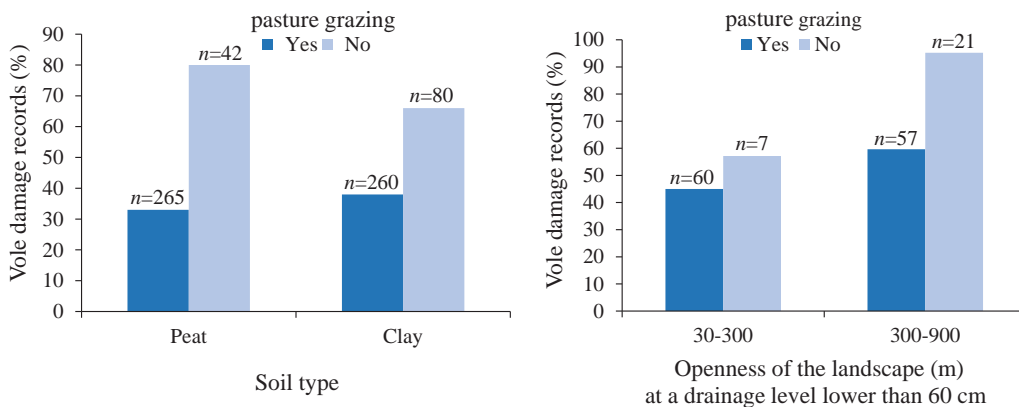


Figure 11. Percentage distribution of vole damage records by farmers for grazing on dairy farms, resp. presented for open and enclosed landscapes and on peat and clay soils in the Netherlands. The percentage of hexagons with damage records is given per class (for each class ‘damage’ and ‘no damage’ = 100%).

row formation and persistence and, probably more important, grazing results in shorter vegetations. The lack of cover in short-grazed grasslands may lead to a higher perception of risk of predation (Jacob & Brown 2000), resulting in lower fitness and reproduction (Dehn et al. 2017). The present study also suggests an impact of grazing. Our analysis shows that damage is less frequently reported on farms with rotational grazing. Interviews with farmers at the locations where the vole outbreak started early in 2015, showed that this was consistently the case on ungrazed parcels with relatively long grass (Wymenga et al. 2016). On clay the effect of grazing was less pronounced, probably explained by the stiffness of clay through which these grasslands are less vulnerable to vole damage than peat grasslands.

Pasture grazing on dairy farms in the Netherlands has changed considerably in the past decades. Between 1950 and 1984 (introduction of production quota for dairy farms in the European Economic Community) the livestock population in the Netherlands grew by 65% from 1.52 to 2.5 million cows (www.cbs.nl), after which it steadily declined to 1.5 million cows in 2020. Until the turn of the millennium, grazing by dairy cattle was mainly practised from the second half of

April to September, and until the 1990s, a large proportion of dairy cattle also grazed at night (40%, Subnel et al. 1994). Cattle grazing included the field margins, which may act as locations where after outbreaks remaining common vole populations reside, called ‘stations of survival’ by van Wijngaarden (1957). The long-term and large-scale increase in grazing pressure in the second half of the former century must have been unfavourable to common voles, and may have acted as a major constraint on the development of outbreaks, in line with the prediction by van Wijngaarden (1957). Later, this pattern changed markedly as dairy cattle was increasingly stabled year-round (Keuper et al. 2011). In the southwestern part of the province of Friesland for example grazing by dairy cattle decreased from almost 100% in the period up to 2000 to 50-70% in 2013 (www.cbs.nl). This decrease in intensive rotational grazing coincides with the return of outbreaks.

### Improved drainage as support for outbreaks

In this study, damage reports were most frequently reported by farmers on soils with a drainage of 80-120 cm and least with a drain-

age of <60 cm. This is consistent with current knowledge (Wijnhoven et al. 2013, de Jonge & Dianske 1979, Jacob et al. 2014), that common voles thrive on relatively dry soils. Brüger et al. (2010) found an average depth of nests of common voles of 22 cm and a maximum burrow depth of common voles of 30 cm, which means that drainage of >80 cm ensures relatively dry conditions to voles and promotes survival. This is illustrated by Wymenga et al. (2016), who determined the actual presence of common voles on 41 parcels from 1-5 December 2015, using the so-called Vole Sign Index (VSI, Lambin et al. 2000), after excessive rainfall in November (129 mm of rainfall against an average of 80 mm; <https://www.weerstation-leeuwarden.nl>). On parcels with a high water table (drainage of 0-20 and 20-60 cm below surface level), both with water-saturated soils after the rainy period, hardly any presence of voles was measured, while well-drained parcels (water table of 80-120 cm below surface level) had a high presence of voles.

In the Netherlands, peat and clay soils are normally drained to 40-120 cm below ground level. The basis for this water management model was laid down during land consolidations programs in the 1980s-90s. The lowest water levels (80-120 cm below surface level) are maintained in polders in Friesland, significantly lower than elsewhere in peat and clay regions in the Netherlands. This may explain why grasslands on peat and clay soils in Friesland seems to be more sensitive to vole outbreaks than other areas. In the period investigated by van Wijngaarden (from the first dykings to 1956), these grasslands were regularly flooded in winter. Outbreaks were not uncommon around 1850 but no severe outbreaks were recorded. Van Wijngaarden describes his impression that the severity of outbreaks increased in the first half of the former century, associated with improved pumping methods (steam pumps), while declining in later years owing to the increasing intensity with which pastures were being farmed. The further improvement of drainage (and decline

of pasture grazing, see above) in the past decades may explain why the current Frisian outbreak zone is much larger than given by van Wijngaarden (1957).

Without intensive drainage, low-lying polders would have a high groundwater level and outbreaks or high densities of common voles would be extinguished in autumn and winter, considering the net rainfall surplus in the Netherlands from October to March. The same process might occur in the event of heavy showers in summer and autumn, but intensive drainage prevents this. Currently, even new drainage techniques are being considered to reduce greenhouse gas emissions from drained peatlands in the Netherlands. This 'subsoil irrigation' involves water supply to grasslands during drought and draining during wet conditions (van den Akker et al. 2012), levelling of the variations in phreatic groundwater levels caused by rainfall or droughts. We assume this will further optimize the grassland habitat for common voles.

### **Outbreak dynamics in a stressed landscape**

Outbreaks lead to severe agricultural damage through loss of fodder (quality and quantity) and costs for grassland renewal (Jacob et al. 2014). In 2014-2015, the damage in the Netherlands was estimated by the regional farmers' organisation LTO at 73 million euros (de Boer 2015). Building on their experiences in 2004-2005 and 2014-2015 many farmers in Friesland, and partly elsewhere in the Netherlands, flooded their grasslands in 2019-2020 to mitigate damage (van Assen et al. 2020), a technique used in this region by farmers already in the 19<sup>th</sup> century (archives regional media; [www.archiefleeuwardercourant.nl](http://www.archiefleeuwardercourant.nl)). Low-lying polders were sometimes inundated entirely but usually grassland parcels were irrigated using pumping machinery. Based on our observations and interviews with dozens of farmers during our fieldwork from Novem-



Figure 12. Detail of a crack in the topsoil of peat in the Koufunderige (19 July 2019), a polder area in Friesland and also an important outbreak area during the three recent outbreaks. *Photo: Niek Bosma.*

ber 2019 to March 2020, and additional information from the Frisian water authorities (personal communication N. Bosma), we estimate that ca. 5000 ha was flooded or irrigated with pumps, which is < 10% of the area infested by voles. At the farm level, these measures were effective as grass growth on flooded parcels regained quickly (as measured by NDVI; van Assen et al. 2020), but the effect on the spread and intensity of the outbreak has been local at best, especially in case farmers took collective action. The successive outbreaks did, however, contribute to farmers' increasing awareness of the vulnerability of the current landscape to outbreaks due to low water tables.

Andreassen et al. (2021) state in their review, that irregular outbreaks of small rodents including common voles seem to be primarily linked to stochastic weather events. The inten-

sive agricultural management of grasslands may therefore not be the cause of outbreaks, but this paper shows that today's dairy farming practices support outbreaks rather than dampening them. The impact of outbreaks is not limited to the outbreak years themselves. For example, the recent vole outbreaks boosted the predator community (Kleefstra et al. 2015, Wijnandts 2015), amongst others resulting in an extreme poor breeding success of meadow-breeding waders such as black-tailed godwit, lapwing and oystercatcher in Friesland in the years following an outbreak due to high predation (cf. Loonstra et al. 2020, Hooijmeijer et al. 2020). In addition, on intensively drained peatlands in Friesland, the combination of drought (summer 2018, spring 2020), manure injection (pushed into the soil) and remaining old burrowing systems led to 30-80 cm deep cracks in the soil, causing severe soil dehydra-

tion (own field observations; figure 12).

The outbreaks and cascading effects on agriculture, soils and biodiversity stimulated the public debate on water levels and desirable measures. To support further debate we need a good understanding of the above processes, and we therefore strongly recommend further research on this, preferably in an experimental setting. Important questions to focus on, are: 1. Whether and how grazing can be used as a management tool in the years prior to outbreaks. 2. The role of 'stations of survival' (refuge habitat patches; Jobsen 1988), such as road verges, dikes, field margins and small pieces of fallow land, in the current intensively used agricultural landscape. Finally, cyclic fluctuations and irregular outbreaks are a fact and a well-established and important ecological phenomenon (Jacob et al. 2014). There is however reason to consider mitigating the effects because of the serious public and economic consequences. One conclusion that may be drawn is that there is reason to act against the low water tables that are currently being maintained in peat and clay areas in the Netherlands, Friesland in particular.

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respectively. A special thanks goes to the farmers and researchers we could consult on the occurrence of vole outbreaks in their working area in past decades. Their willingness to share stories and memories with us was most welcome: Piet Keestra, Klaas Kooistra, Joris Könning and colleagues, Gerrit Gerritsen and Ale de Vries. Ron Ydenberg, Johan Thissen and two anonymous referees provided this article with valuable comments. Finally, we would like to thank Niek Bosma of Wetterskip Fryslân for the entertaining discussions about voles and their whereabouts, which were a real stimulus to complete this paper.

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## Samenvatting

### Terugkerende uitbraken van veldmuizen in graslanden in Friesland en overige delen van laag-Nederland

In het verleden kwamen uitbraken van veldmuizen (*Microtus arvalis*) regelmatig voor in graslandgebieden in Nederland, maar de laatste decennia zijn ze vrijwel afwezig. Na 2000 zijn er echter drie grote uitbraken geweest, in 2004-2005, 2014-2015 en in 2019-2020. Om meer inzicht te krijgen in de verspreiding en onderliggende oorzaken, wordt in dit artikel het voorkomen van uitbraken in Nederland nader belicht, en is de verspreiding tijdens de recente uitbraken in Friesland in kaart gebracht. Daarnaast is een ruimtelijke analyse uitgevoerd van schademeldingen van boeren in Nederland tijdens de uitbraak in 2014-2015. Uit de analyse blijkt dat grote uitbraken vooral voorkomen in open landschappen op klei- en veengronden die intensief worden ontwaterd. Het aantal schaderegistraties is lager in geval van beweiding. We concluderen, dat het intensieve agrarische beheer van grasland mogelijk niet de oorzaak is van uitbraken, maar dat de praktijk van de gangbare melkveehouderij met lage grondwaterstanden en geen of beperkte beweiding uitbraken eerder ondersteunen dan temperen.

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# Spatiotemporal variations in antler development among two neighbouring, yet isolated, red deer populations

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**Abstract:** Whereas wildlife occurring in fragmented landscapes is frequently the subject of genetic investigation, there has been relatively little attention for associated spatiotemporal variations in phenotypic traits. For example, many studies have reported the genetic variation and structure of present day red deer (*Cervus elaphus elaphus*) – showing both hybridization with other *Cervus* species and fragmentation – but the consequences for phenotypic traits, even when as conspicuous and elastic as antler size, have not been considered. To examine fine-scale differences in a phenotypic trait in large wildlife species inhabiting fragmented landscapes, we analyzed the antlers of red deer from two neighbouring populations occurring in the Netherlands. To test for area and drought effects, we quantified antler mass, burr circumference and the number of tines from antler series shed in the years 2011 to 2020 by 25 stags of the population at the Hoge Veluwe Estate ( $n=20$ ) and the relict population at Planken Wambuis ( $n=5$ ). We found that red deer from the Hoge Veluwe have significantly heavier and larger antlers with more tines (average mass: 3.0 kg; average burr circumference: 23.0 cm, average number of tines: ten) than deer from the neighbouring relict population from Planken Wambuis (2.3 kg, 21.5 cm and eight tines, respectively). Despite the provision of drinking water and pasture management within the Hoge Veluwe, antler development appeared to be significantly diminished by the summer drought of 2018, but only in mature stags (males aged seven years and older). We thus found, on the one hand, a naturally induced variation in a phenotypic trait, despite wildlife management aimed at relaxing natural stressors. On the other hand, the considerable phenotypic variation detected at a small spatial scale illustrated strong anthropogenic influence: it appears that wildlife populations in fragmented landscapes are not only affected genetically, but also phenotypically. We conclude that in fragmented landscapes, deer antlers – and perhaps phenotypic traits of wildlife in general – are strongly shaped by anthropogenic influences, but that naturally induced variation is not completely erased.

*Keywords:* red deer, antler, phenotype, fragmentation, translocation, drought, wildlife management.

## Introduction

Compared to genetic variations, phenotypic variations of wildlife within fragmented landscapes have rarely been investigated. In (north-)western Europe, for example, a multitude of studies has shown that fragmenta-

tion, translocation and hybridization have been, and are, altering the genetic variation of large free-ranging mammals (e.g. Hartl et al. 2003, Coster & Kovach 2012, Goedbloed et al. 2012, de Jong et al. 2020). Yet, the question of the effects of these human influences on phenotypic variation has hardly been addressed

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(but see Otto 2018; and specifically for birds, e.g., Bosse et al. 2017, Strubbe et al. 2020, Benham & Bowie 2021).

Anthropogenic impact on phenotypic variations is likely to be complex, and the diversity of human influences implies it may both enhance and diminish phenotypic variations (Chiyo et al. 2015, Fulgione et al. 2016). In addition, the impact will be conditional on the observed spatial and temporal scales. Translocations may be local and initially increase phenotypic variation; however, in the long run translocations and subsequent gene flow may homogenize phenotypic traits (Gippoliti et al. 2021). In western Europe, translocations and fragmentation have resulted in a genetic mosaic, as is the case with red deer (*Cervus elaphus*) populations in the Netherlands (de Jong et al. 2020). This has possibly led to differences in a conspicuous phenotypic trait, namely the size and form of antlers. Turning to other European wildlife, wild boars' (*Sus scrofa*) hybridization with domesticated pigs has not only altered their coat patterns (aberrant, spotted, hybrids) but, more fundamentally, has possibly increased their litter sizes (Fulgione et al. 2016).

Within the *Cervus* genus, there are considerable variations in body size, coat patterns and antler form – which is mostly present at large spatial scales, but also within Europe and even within countries (Geist 1987, 1998). Landscape openness may be an important driver of this variation. Crown formation at the tip of red deer antlers (a trait developed during the Middle Pleistocene) makes the European form distinct from the Asian (maral) and north-American (wapiti) lineages (Lister 1984). Within European red deer, there are possibly small differences in crown shape, and other antler traits. Hence, given impacts of translocation and fragmentation (both common occurrences for red deer over past centuries), it is likely that phenotypic variations of red deer have been distorted. More specifically, this may have enhanced the spatial diversification of the forms of red

deers' antlers, as well as, potentially, new forms, due to hybridization of deer with distinct phenotypes. Meanwhile, the gene flow between connected populations with different ancestries could potentially homogenize phenotypic variations within the species as a whole (de Jong et al. 2020). In the fragmented forest and heathland area of the Veluwe, the Netherlands, some wildlife managers claim that neighbouring red deer populations show clear differences in antler shape and size, and the timing of breeding (J. Leidekker, personal communication) - despite small spatial scales (populations only few kilometres apart). However, to date, these phenotypical variations have not been quantitatively examined.

The natural environment could cause variations in the phenotypic traits of red deer (see Charmantier 2014), as an adaptation to conditions (ecotypes), e.g., camouflage and thermoregulation (Foote et al. 2016), or have a social function (Geist 1987). On the other hand, phenotypic variations may not be an adaptation, but a constraint imposed by the environment. For example, inadequate nutrition, in particular, may limit organismal development. In addition to genetic factors (Peters et al. 2021), the antler size of deer is strongly determined by nutrition (Brown 1990, Torres-Porras et al. 2009, Dryden 2016). Food and water availability varies both spatially (e.g., river floodplains vs. hill lands) and temporally (productive vs. unproductive seasons for plants). As stag antlers grow and are discarded annually they make for an excellent indicator of temporal variations in resource availability (Brown 1990, Dryden 2016).

The increase in the frequency and intensity of droughts in western Europe is particularly influential on the primary production of an ecosystem and overall water availability. Despite the attention given to climate change and the subsequent increase in drought frequency and severity (European Commission 2009), there has been little attention paid to the possible effects of such changes on the phenotypes of large herbivores. One study

found that red deer in the Iberian peninsula produced smaller antlers in years of drought (Azorit et al. 2002, Torres-Porras et al. 2009). In the Veluwe area, wildlife management techniques, such as fertilizing grazing lawns and the provision of drinking pools and salt licks may buffer the effects of extreme environmental variations, such as droughts. Nevertheless, it is not clear if wildlife management can completely mask adverse environmental resources and conditions (a topic worthy of further investigation).

Given the diverse set of both diversifying and homogenizing factors – of both natural and anthropogenic origin – we were interested in whether spatiotemporal variations in antler development exists in red deer of the Veluwe.

In this study we test for the effects of location and drought on antler development among red deer in the Veluwe. These considerations lead us to ask the following questions:

1. Are there differences in antler development between red deer from the Hoge Veluwe Estate and the relict population of Planken Wambuis?
2. What is the effect of drought on antler development among the red deer population in the Hoge Veluwe Estate?

Using deer antlers as a case study, we aim to increase understanding of phenotypic variations in wildlife that occurs in fragmented, yet spatially proximate, landscapes.

## Methods

### Approach and study area

We made use of the antler collections of the Hoge Veluwe National Park and the Planken Wambuis Nature Reserve. In Hoge Veluwe, game wardens actively search for shed antlers and, for many stags, almost complete series of antlers are available. At Planken Wambuis antler collection is more *ad hoc*, and there are only a few intact series of antlers from consec-

utive years available. In both areas, game wardens individually recognize stags and their antlers, which enabled accurate identification, and aging, of shed antlers.

Although adjacent, Hoge Veluwe and Planken Wambuis and their deer populations are separated by a road and fences. Moreover, the two areas differ in many ways and the deer populations have contrasting demographic histories. Whereas the red deer of Hoge Veluwe all stem from founders introduced from other European countries (Pelzers 1991), it is thought that the red deer of Planken Wambuis are, at least partially, autochthonous (Beijer 1897a, 1897b, Schuitemaker 1944, de Jong 2020). Deer densities are higher in Planken Wambuis (5 ind/km<sup>2</sup>) than in Hoge Veluwe (3 ind/km<sup>2</sup>) (Leidekker & Ouden 2018, Faunabeheerenheid Gelderland 2019).

### Data collection

Three parameters were used as indicators for antler development: mass, burr circumference and the number of tines (figure 1). These parameters were chosen because of their use in related studies (Fennessy et al. 1992, Torres-Porras et al. 2009) and the number of parameters was restricted to three for the sake of feasibility.

We measured antler parameters in June 2021 on a total of 240 antlers of red deer stored at local facilities in the Hoge Veluwe National Park and at Planken Wambuis. Antler series (multiple years of one individual) were selectively sampled, focusing on the completeness of the series, the inclusion of antlers from 2019 and 2020, and quality of the antlers (preferring a low level of gnawing). Mass was measured with an analogue measuring scale with an accuracy of 50 grams. Burr circumference was measured with a string around the burr, which was then placed along a ruler, resulting in an accuracy of 5 mm. All externalities above the burr, were regarded as tines. Whenever one



Figure 1. Anatomy of the red deer antler (left side).

or more beams were missing, the tines were not counted for that antler, as it cannot be predicted with certainty whether that beam might have formed a single or multiple tines.

### Data processing

The final database contained entries on 198 red deer antlers from Hoge Veluwe and 42 red deer antlers from Planken Wambuis (each side of an antler counting as a separate entry), with the year of formation ranging from 2011 to 2019 (shedding: 2012 to 2020). Entries with an estimated loss of mass of more than 5% due to damage, were excluded from all data processing. Entries for the deer ‘Hubertus’, were only included in the correlation test. This is because, in contrast to other deer in the study area, this individual was unafraid of humans, and therefore had an advantage over the other deer in foraging. The absolute and relative mass growth were computed for each antler, relative to the preceding antler of the same individual and same side (left/right).

The antlers developed for the rut of 2018 were regarded as been developed under conditions of drought. The year 2018 is widely regarded as a year of exceptional drought with below average rainfall (582 mm rainfall in

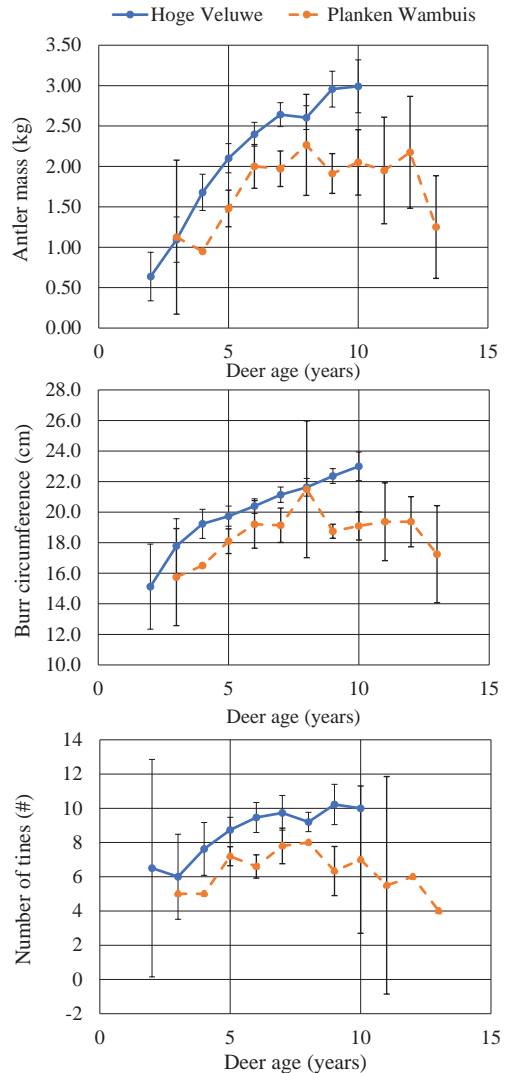


Figure 2. Top: the effect of age on the mass of antlers of red deer from Hoge Veluwe and Planken Wambuis. Error bars display a 95% confidence interval around the estimated mean. Middle: the effect of age on burr circumference of antlers of red deer from Hoge Veluwe and Planken Wambuis. Bottom: the effect of age on the number of tines of antlers of red deer from Hoge Veluwe and Planken Wambuis.

2018, opposed to an average of 880 mm over the other years in the decade - meteorological measuring station in De Bilt, Netherlands) (KNMI 2021), combined with above average

temperatures and number of sun hours, causing higher evapotranspiration (den Ouden 2018, Sluijter 2018).

Statistical analyses were run in IBM SPSS Statistics v28.0.0.0 (190). To test the differences in antler development between Hoge Veluwe and Planken Wambuis, we conducted an univariate General Linear Model (GLM) with the three measured parameters as dependent factors, area as a fixed factor and age as a random factor.

Strong mutual correlations between the three measured parameters made it possible to exclude burr circumference and number of tines in the further tests on the effects of drought and yearly developmental growth (see appendix 1-3). Hence, we were confident in only using mass as an indicator. This indicator was preferable over the other two variables as it had the largest range in data and the lowest relative measuring error. We modelled antler growth in both areas by conducting a linear regression analysis. Mass was entered as the dependent variable, and age and  $(age)^2$  as independent variables, yielding a 2<sup>nd</sup> degree function describing antler growth with age. To test for the effect of drought on the annual change in antler mass (both absolute and relative) of red deer from Hoge Veluwe, we conducted another univariate GLM, using the drought of 2018 as the fixed (binary) factor. In addition, we conducted Mann-Whitney-U tests on the absolute and relative mass change, comparing antlers from the same age class in dry and normal circumstances.

## Results

### Spatial variation in antler mass

Red deer antler mass could be explained by area and age (GLM; area:  $df=1$ ,  $F=26.095$ ,  $P<0.001$ ; age:  $df=11$ ,  $F=9.600$ ,  $P=0.002$ ; no interaction effect:  $F=2.008$ ,  $P=0.056$ ). Stags from Planken Wambuis typically reached their peak antler mass at the age of eight, with

a value of approx. 2.3 kg. In the Hoge Veluwe, stags reached their peak mass at the age of ten (or possibly older), with a value of approx. 3 kg. In Planken Wambuis, antler mass began to decrease among stags older than eight years (Figure 2a). Antler mass differed between the two areas at all ages, with higher masses among the Hoge Veluwe population. By age ten, when Hoge Veluwe stags reached their peak antler mass, the difference in mass amounts to 50%: in Planken Wambuis antler mass of ten year old stags was typically 2 kg, compared to 3 kg for stags from Hoge Veluwe (figure 2a).

Similarly, burr circumference could be explained by area and age (GLM; area:  $df=1$ ,  $F=31.810$ ,  $P<0.001$ ; age:  $df=11$ ,  $F=7.340$ ,  $P=0.003$ ; no interaction effect:  $F=1.408$ ,  $P=0.204$ ). At all ages, Hoge Veluwe deer had a greater burr circumference than the deer from Planken Wambuis. Peak circumferences were reached at the ages ten or higher at Hoge Veluwe and at eight years at Planken Wambuis, with approximate values of 23.0 cm and 21.5 cm, respectively. At Planken Wambuis, a decrease in circumference was seen after eight years and, more notably so, after twelve (figure 2b).

Lastly, the number of tines could also be explained by area and age (GLM; area:  $df=1$ ,  $F=44.035$ ,  $P<0.001$ ; age:  $df=11$ ,  $F=4.328$ ,  $P=0.014$ ; no interaction effect:  $F=0.997$ ,  $P=0.438$ ). Deer from Hoge Veluwe typically formed antlers with more tines than similarly aged deer from Planken Wambuis. Deer from Hoge Veluwe had the most tines (10) at the age of 9-10 years and the most tines found on a stag from Planken Wambuis was eight, on an eight year old individual. (figure 2c).

The effect of age on antler mass in both areas could be explained by linear regression analysis with a quadratic function (Hoge Veluwe:  $P<0.001$  and  $F=146.501$ ; Planken Wambuis:  $P<0.001$  and  $F=16.686$ ). For Hoge Veluwe, the relationship was numerically expressed as  $Mass = -0.667 + 0.734*Age + -0.038*Age^2$  (coefficients yielded resp.  $t=-2.448$ ,  $P=0.015$ ;  $t=8.016$ ,  $P<0.001$ ;  $t=-5.180$ ,  $P<0.001$ ). The

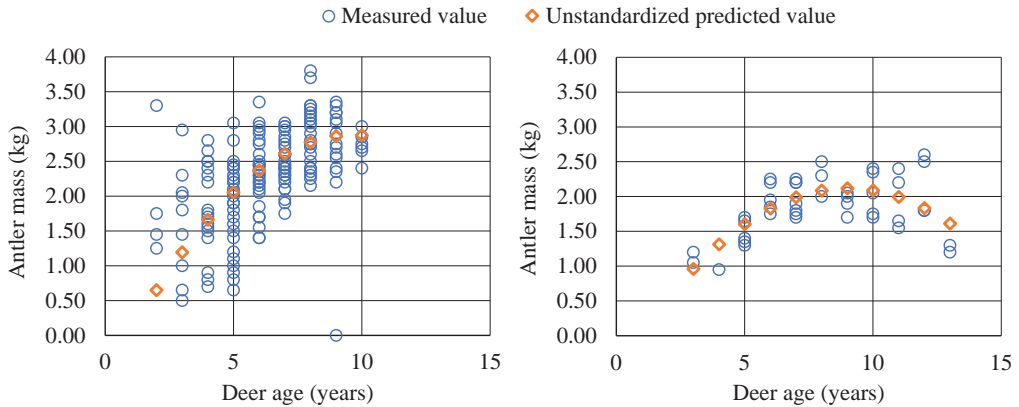


Figure 3. The effect of age on the antler mass of red deer in Hoge Veluwe (left) and Planken Wambuis (right). Non-standardized predicted values were obtained from linear regression models predicting the following relations: for Hoge Veluwe:  $Mass = -.667 + 0.734 * Age + -0.038 * Age^2$ ; and for Planken Wambuis:  $Mass = -0.482 + 0.577 * Age + -0.032 * Age^2$ .

model predicted maximum antler mass at age ten, with value of 2.871 kg (figure 3). For Planken Wambuis, the relationship can be numerically expressed as  $Mass = -0.482 + 0.577 * Age + -0.032 * Age^2$  (coefficients yielded resp.  $t = -1.158$ ,  $P = 0.254$ ;  $t = 5.354$ ,  $P < 0.001$ ;  $t = -4.924$ ,  $P < 0.001$ ). The model predicted maximum antler mass at age nine, with a value of 2.121 kg (figure 3). From this it follows that red deer from Hoge Veluwe typically achieve a higher maximum antler mass than those from Planken Wambuis.

### The effects of drought on antler mass change

For deer from the Hoge Veluwe, absolute antler mass change was not related to age (figure 4) (GLM;  $df = 7$ ,  $F = 3.317$ ,  $P = 0.123$ ) and relative antler mass change decreased with age (figure 4) (GLM;  $df = 7$ ,  $F = 15.449$ ,  $P = 0.005$ ). Antler growth rates were higher among younger than older individuals: in juvenile males, antlers typically increased by 175% compared to the previous year; in stags, this change was typically 120%. Notably, at the age of eight both absolute and relative antler mass change showed relatively low increases under normal

circumstances (figure 4).

Outcomes of statistical tests on the effect of the 2018 drought on antler development were equivocal. Relative antler development was not affected by the drought (GLM; drought:  $df = 1$ ,  $F = 3.500$ ,  $P = 0.123$ ; drought\*age:  $df = 4$ ,  $F = 1.330$ ,  $P = 0.264$ ). In contrast, absolute antler mass was affected by the interaction between drought\*age, with the main effect of drought being close to significance (GLM; drought:  $df = 1$ ,  $F = 5.646$ ,  $P = 0.072$ ; drought\*age:  $df = 4$ ,  $F = 3.449$ ,  $P = 0.011$ ). Under normal rainfall conditions red deer stags aged seven and older typically increased their antler mass by 300 to 500 grams, in the dry year the antler mass of most stags did not grow or even decreased (estimated average growth of 0 gram or lower). Once again, notably, at age eight relatively low values for mass change were observed under normal circumstances (figure 4).

Mann-Whitney-U tests corroborated the observed patterns for the effect of drought on mass change (both absolute and relative). In five and six year old deer no effect of drought was observed on absolute nor relative mass change (5-abs:  $z = -0.892$ ,  $P = 0.205$ ; 5-rel:  $z = -0.183$ ,  $P = 0.462$ ; 6-abs:  $z = -0.300$ ,  $P = 0.401$ ; 6-rel:  $z = -0.634$ ,  $P = 0.279$ ) Similarly, deer of eight years old, which had relatively low mass

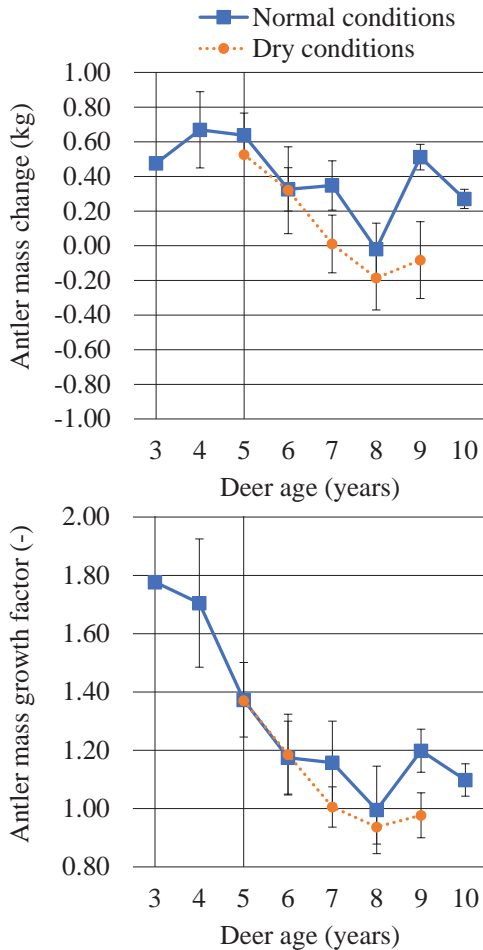


Figure 4. Absolute (top) and relative (bottom) mass change of red deer antlers from Hoge Veluwe, plotted against deer age. Mass change is calculated relative to the preceding year. Antlers developed during the drought of 2018 are regarded as having developed in ‘dry conditions’ (582 mm annual rainfall), opposed to antlers formed in the other years between 2011 and 2020, which are regarded to have developed under ‘normal conditions’ (880 mm average annual rainfall). Error bars display 95% confidence intervals around the estimated means. Raw data plots are included in appendix 3a and 3b.

change values under normal precipitation conditions, experienced no discernible effects from the drought on antler mass change (abs:  $z=0.956$ ,  $P=0.175$ ; rel:  $z=-1.198$ ,  $P=0.126$ ). For

deer of seven and nine years old, there was a significant effect of drought on both relative and absolute mass change, indicating lower mass change values in the year of the drought (7-abs:  $z=-2.354$ ,  $P=0.008$ ; 7-rel:  $z=-2.382$ ,  $P=0.008$ ; 9-abs:  $z=-3.214$ ,  $P<0.001$ ; 9-rel:  $z=-3.188$ ,  $P<0.001$ ).

## Discussion

To investigate fine-scale spatiotemporal variations in the development of antlers of red deer occurring in a fragmented landscape, we measured mass, burr circumference and the number of tines of antler series of red deer originating from 2012 to 2020, from two neighbouring populations in the Netherlands that have contrasting demographic and management history. Diverse anthropogenic influences may have caused diversification (due to e.g., translocations and isolation due to fragmentation) but also homogenization (due to e.g., connectivity measures and wildlife management interventions) of antler development. We found strong differences in antler development between the relict population of Planken Wambuis and the neighbouring population from the enclosed Hoge Veluwe Estate: antlers in the estate population were up to 50% larger. Furthermore, the results showed an inhibiting effect of the 2018 summer drought on antler development, though only in mature stags (i.e., stags of seven years and older). We thus found spatiotemporal fine-scale variations in a phenotypic trait, which – as we argue below – is caused by a combination of natural and anthropogenic influences.

### Explanations for the observed fine-scale variations in antler development

The observed phenotypic differences between the two adjacent red deer populations are most likely explained by anthropogenic activities. We suspect the differences in antler phe-



Figure 5. Series of seven subsequent antlers from a red deer stag from Hoge Veluwe.

notypes are best explained by the contrasting genetic ancestry of the two populations (autochthonous relicts vs. an imported estate population) (Schuitemaker 1944, Beijer 1987a, 1987b). Furthermore, landscape and habitat fragmentation have led to long-term isolation of large mammals occurring in the Netherlands. This was already known to prevent genetic heterogenization among red deer (de Jong et al. 2020), and with our findings can now also be regarded to have led to ‘phenotypic fragmentation’.

It is unlikely that the physical environments of the two samples was significantly different, given that the areas are directly adjacent, contain similar soil and vegetation types and are both open for recreation during daytime. There are two possible anthropogenic explanations for the observed differences. First, differences exist in wildlife management. Whilst the approaches at the two sites are largely similar (water ponds, salt licks, fertilised grazing lawns, etc.), Hoge Veluwe provides more intense management. Moreover, in Hoge Veluwe deer are kept at lower densities (approx. 3 ind/km<sup>2</sup>) than in Planken Wambuis (approx. 5 ind/km<sup>2</sup>) (Leidekker & Ouden 2018, Faunabeheerenheid Gelderland

2019). Alternatively, observed differences in antler weight may have a genetic cause; the two populations have different genetic ancestry, with Hoge Veluwe having a higher proportion of allochthonous genetic variations due to importing red deer from other European populations (de Jong et al. 2020).

With single antler weights of 2 to 3 kg, the antler sizes of red deer from the Veluwe are small in comparison to other European populations. Although in ‘harsh’ environments, such as the Isle of Rhum, Scotland, antler weights barely reach 1 kg (Kruuk et al. 2002), in many parts of Europe single antler weights of 5 kg and higher are common (Geist 1987, p. 251; Geist 1998, table A7). High antler weights are related to supplementary feeding or management, but also to fertile soils. A few decades ago, when supplementary feeding was still widespread practice in the Veluwe area antler weights there reached 5 kg (van den Hoorn 1996, p. 179).

Despite the effect of location on the level of antler development (more developed antlers at Hoge Veluwe), the relation between age and development remained largely unaffected. Maximum antler mass was reached by stags at similar ages (age ten at Hoge Veluwe and age

eight at Planken Wambuis; figure 3). Our findings on the age-mass relation were in line with expectations based on other studies (e.g. Clements et al. 2010). Thus, although sizes differ, the general antler development at the individual level are similar in the two areas (figure 3, with an example series of antlers in figure 5).

### **Explanations for the observed variation in antler development induced by drought**

Antler development of red deer stags in the Netherlands generally concludes in mid-July, indicated by the stags shedding the velvet from their antlers, although scientific sources on this are lacking (Vodnansky 2009). The most severe circumstances of the drought of 2018 developed over the course of July, once antler development had almost finished. Nonetheless, the months of May and June saw below average precipitation and above average evapotranspiration, and after these months a potential precipitation deficit of approx. 175 mm had been recorded (national average). Throughout July this deficit rapidly increased to a value of approx. 300 mm, which then decreased slightly, ending up at approx. 280 mm by the end of September (Sluijter et al. 2018). The local potential precipitation deficit for Hoge Veluwe followed a similar pattern to the national average, with a deficit of approximately 180 mm, 300 mm and 260 mm at the 1<sup>st</sup> of July, August and September, respectively (appendix 4) (KNMI 2018). So while the precipitation deficit worsened the most dramatically over the course of July, about 60% of the deficit had been established by the end of June. This implies that, though not at maximum severity, the deer did in fact experience conditions of drought during antler development stages in 2018.

The findings on the effects of the 2018 drought showed the impact that natural circumstances can have on animals, despite active management. Our results are in line

with conclusions from similar studies on Iberian red deer, for which less developed antlers in males exposed to conditions of drought have also been reported (Torres-Porras et al. 2009). The physiological explanation for the observed relation could be an overall (near) catabolic status – in energy or protein – leaving little opportunity for production including antler development. Alternatively, deer could have experienced a shortage of specific minerals required for antler development, in particular calcium and phosphorus. From an ecological perspective, there are several potential explanations: (i) during droughts, deer have more energy expenditure due to higher thermoregulatory costs; (ii) during droughts, deer have lower nutrient intake, because weather conditions and thermoregulation (including more passive behaviour) limit their foraging activity (Bugalho & Milne 2003); (iii) during droughts, deer have lower nutrient intake, because droughts cause a deterioration of forage quality and abundance.

Regarding explanation (i), within the study area, close forest stands provide sheltered microclimates, which reduce the need for active thermoregulation, e.g., through sweating and panting (Parker & Robbins 1984, Thompson et al. 2021). In addition, in the study area, red deer are already tuned to daytime avoidance, adopting a crepuscular activity pattern (Ensing et al. 2014). Regarding explanation (ii), irrespective of droughts, red deer in the study area are always limited in their foraging activity, because of their aforementioned pattern of avoiding daylight activity. At first, explanation (iii) appears unlikely, given the availability of fertilized grazing lawns and lick stones. However, the grazing lawns only provide part of the deer's diet, and most of the provided lick stones only contain sodium and chlorine (thus, lacking, *inter alia*, the calcium and phosphorus used in antler construction). During the drought, game wardens observed that, in comparison to other years, the deer were in relatively poor

overall condition (Ruseler, personal communication). Also, in the year of the drought, wardens observed that deer started rutting later than usual, which may be a consequence of an overall lower body condition. Thus, we think that lower nutrient availability is the most likely underlying cause of the reduced antler development during the drought year.

The absence of an inhibiting effect of drought in deer younger than seven years old differed from other studies. A 2001 study by Torchhammer et al. showed that drought affected the body mass of young deer more severely than the body mass of older animals. In fact, inhibited growth in a deer's first year (due to e.g., drought) can reduce antler development in subsequent years (Forchhammer et al. 2001, Torres-Porras 2009). Although our study did not take body mass into account, these observations seem to conflict with our findings, as antler mass positively generally correlates with body mass.

We consider it intriguing that the antler development of juvenile deer was unaffected by the drought, as this contradicts our expectations. Since juvenile individuals experience the largest yearly increases in antler growth, this would suggest they require relatively more nutrients than older deer. However, adult deer with maximum antler development do require the absolute maximum amount of resources for antler growth, which could explain why they appeared to be more affected by the drought. On the other hand, this is contradicted by the timing of antler development in stags of different age. With increasing age, antler development starts earlier in the year, while the end date remains constant (Clements et al. 2018). Given that the drought occurred in late spring and early summer (i.e. the final stages of antler development), individuals of all ages experienced the same negative impacts due to the drought. From this it follows that the older stags had a relatively shorter time of negative impact on their antler development due to the drought. This suggests that antler development in younger stags

would be more susceptible to the effects of drought, due to a relatively longer period of dry circumstances.

To clarify these differences in the susceptibility of deer of different ages to drought, future studies could include relative antler mass in comparison to body mass and evaluate how this ratio develops with age and responds to drought. Furthermore, the mobilization of calcium and phosphorus from the skeleton for antler growth at different ages could be included, as this may determine the underlying mechanisms for the different responses to drought (and possibly other environmental factors).

Furthermore, the absence of a significant effect of drought on eight year old deer is difficult to explain (since deer of the ages of seven and nine *were* affected). Considering the small sample sizes, there is a possibility for a type II error (i.e., a false negative: the effect was also present in eight year old stags, but not found). Future research should aim to obtain larger sample sizes (especially in drought years), and preferably test for multiple times of drought at multiple locations.

## **General implications of the phenotypic variations**

Whereas the impacts of anthropogenic activities on genetics have received much attention (Hartl et al. 2003, Coster & Kovach 2012, Goedbloed et al. 2012, de Jong et al. 2020), there has been less research on their influence on phenotypes (but see Crispo et al. 2010, Fulgione et al. 2016, Thompson et al. 2019). Our study shows that humans not only induce genetic variations among large mammalian wildlife, but also phenotypic variations. Antlers are a clear 'phenotypic showcase'; almost literally showing that the morphology of wildlife can be shaped by humans. Across the species range, vertebrates may have striking intra-specific phenotypic variations (Kingdon 1990) and there are certainly many sub-

tle or invisible phenotypic traits as well. All these traits are potentially subject to anthropogenic alterations. Studies have addressed concerns about the mixing of subspecies and races due to anthropogenic wildlife translocations, which could have consequences on the adaptive capacity of species (Gippoliti et al. 2018, Thompson et al. 2019, Gippoliti et al. 2021). Additionally, selective hunting focused on individuals with impressive phenotypical features, causes populations in general to have less impressive features - e.g., current day elephants typically have smaller tusks than half a century ago, due to hunting focused on animals with large tusks (Chiyo 2015). In the Hoge Veluwe, the contrary occurs: to assert negative selection on poor body condition, hunting is directed towards animals with a low body condition (J. Leidekker, personal communication).

Furthermore, if the drought of 2018 was a manifestation of climate change, then climate change affects antler development, and thus animal phenotypes. In any case, our findings show that natural disturbances are not easily mitigated by wildlife management interventions. In the study area, red deer are helped to overcome scarcity by the installation of water pools, the provision of lick blocks (although mostly salt), and mowing and the fertilization of meadows. While anthropogenic effects can be strong, as addressed earlier, it becomes apparent that natural fluctuations in phenotypic traits are still present.

## Conclusions

In this study, we have investigated the effects of spatial and temporal variations in environmental circumstances on the antler development of red deer in an area of mostly heathland in the Netherlands. After doing measurements on 240 antlers from two sites in the Dutch Veluwe region and conducting statistical tests, we conclude firstly, that red deer from the relict population in Planken Wam-

buis grow less developed antlers than those from the population from the Hoge Veluwe Estate; and secondly, that antler development by red deer of more than seven years old from Hoge Veluwe was inhibited by drought. The former shows that in human-dominated landscapes antler development is steered by a combination of natural and anthropogenic forces.

Whilst it was known the red deer populations in Hoge Veluwe and Planken Wambuis were genetically differentiated because of their long-term isolation, our study found how the latter has also led to 'phenotypic fragmentation'. Thus, anthropogenic actions can shape what an animal looks like. The results emphasise the impact that fragmentation and population isolation can have on wildlife.

The drought of 2018 was found to have an inhibiting effect on antler development in the Hoge Veluwe Estate, and thus influenced the phenotypes of this large wild mammal. This indicates that droughts can impact red deer antler development, despite mitigating wildlife management interventions. Furthermore, if the summer drought of 2018 was a manifestation of climate change, then our study showed that climate change affects the exterior of mammals (i.e., their appearance). Furthermore, our results indicate that natural disturbances are not easily or fully compensated for by management interventions. With the presence of water pools, salt licks, and meadow management, the deer at Hoge Veluwe still experienced an inhibiting effect on antler development as a result of the summer drought. Despite the earlier mentioned strength of anthropogenic impacts, a complete 'eradication' of natural influence on animal phenotype therefore appears difficult. With droughts expected to become more frequent and severe due to climate change, wildlife managers should re-evaluate their management actions and anticipate the possible consequences of climate change on animal phenotypes (and, possibly, related animal performance).

Future research should ideally consider multiple years of drought rather than one, and test for drought at multiple locations rather than one. A possible interaction effect of location and drought could then also be included. Furthermore, the relation between deer age and susceptibility to droughts could be explored in more detail, as the unexpected differences between adult and juvenile antler development under conditions of drought would make for an interesting study.

**Acknowledgements:** We are thankful for the opportunity to conduct measurements on the red deer antlers from the private collections of the Hoge Veluwe National Park and the Planken Wambuis Nature Reserve. Furthermore, we are grateful for the time that Jakob Leidekker, Henk Ruseler and Han ten Seldam took to have insightful conversations and to share their knowledge on antler development by, and the management of, the red deer populations of the Veluwe area. Thanks also to two anonymous reviewers for their helpful comments to improve the manuscript and to Nicholas Parrott (TextualHealing.eu) for his English language editing.

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## Samenvatting

### Effect van herkomst en droogte op geweivorming door edelherten van Planken Wambuis en Hoge Veluwe

Hoewel de invloeden van mens en omgeving op de genetica van zoogdieren in West-Europa uitgebreid bestudeerd zijn, is er weinig aandacht geschonken in onderzoek aan mogelijke effecten op de fenotypes. Het doel van deze studie is om meer kennis te vergaren over de relaties tussen fenotypische variatie, en variatie (op kleine schaal in tijd en plaats) van omgevingsvariabelen. De focus van deze studie ligt op de geweivorming van edelherten (*Cervus elaphus elaphus*) in West-Europa, als duidelijk fenotypisch kenmerk. Onze resultaten zijn gebaseerd op gemeten variabelen (massa, omtrek boven de roos, en aantal enden) aan in totaal 240 edelhertgeweien, gevormd tussen 2011 en 2020, uit twee natuurgebieden in de Veluwe. Verder presenteren wij hier de gevonden effecten van de zomerdroogte van 2018 op de geweivorming van edelherten in Nationaal Park Hoge Veluwe. Allereerst is er kwantitatief bewezen dat de geweien van edelherten op de Hoge Veluwe (gem. massa: 3.0 kg; gem. omtrek: 23.0 cm, gem. aantal enden: 10) verder ontwikkeld zijn dan van de herten op Planken Wambuis (2.3 kg, 21.5 cm, 8 enden, respectievelijk). De genotypische verschillen tussen de populaties van de twee gebieden waren reeds bekend, als resultaat van decennialange isolatie door de landschapsversnippering in Nederland. Maar uit onze resultaten blijkt nu ook, dat het gefragmenteerde, antropogene landschap direct beïnvloedt hoe geweien van edelherten eruit zien, en daarmee tot een zekere “fenotypische fragmentatie” leidt. Dit zal zich hoogstwaarschijnlijk niet beperken tot de zichtbare fenotypische kenmerken, maar zal ook invloed hebben op de onzichtbare kenmerken. Ten tweede tonen onze uitkomsten aan dat de zomerdroogte van 2018, over het algemeen, de geweiontwikkeling van edelherten boven de 6 jaar oud heeft geremd. De onderzochte geweien, die zich had-

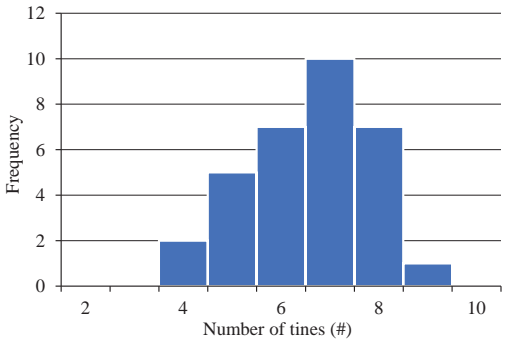
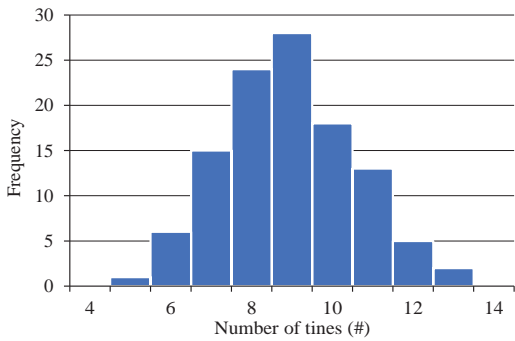
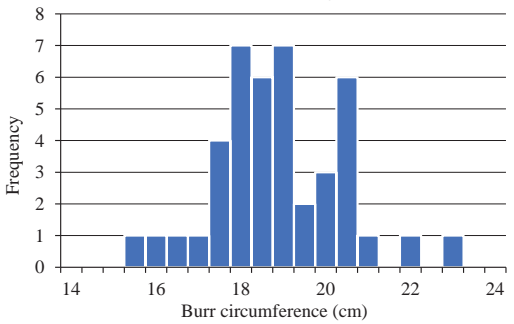
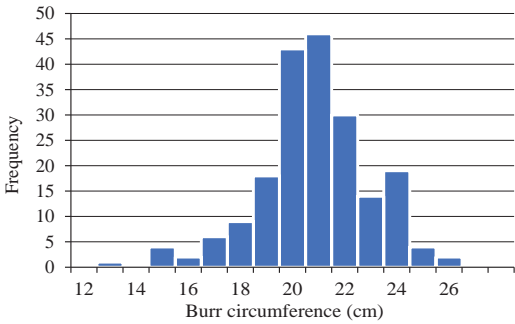
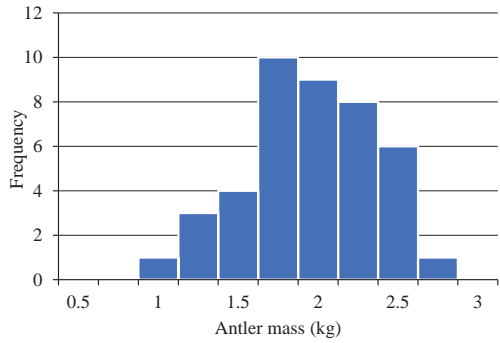
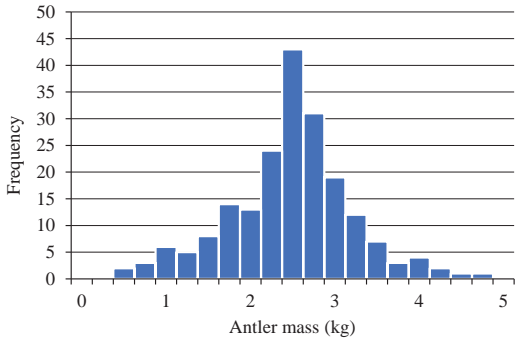
den ontwikkeld tijdens deze tijd van droogte, vertoonden een relatief lagere groei t.o.v. het voorgaande jaar, dan geweien die ontwikkeld waren in jaren met gemiddelde neerslagcijfers. De droogte heeft deze invloed kunnen uitoeffenen, ondanks de aanwezigheid van meerdere proactieve (natuur)beheermaatregelen. Hoewel de invloed van de mens op de natuur significant is, blijkt hieruit dat de invloed van de omgeving op fenotypische ontwikkeling niet

gemakkelijk gecompenseerd wordt door antropogene interventies. Indien de zomerdroogte van 2018 verklaard kan worden als een gevolg van klimaatverandering, betekent dit dat klimaatverandering directe impact heeft (of kan hebben) op het uiterlijk van wilde dieren in West-Europa.

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## Appendices:



Appendix 1. Histograms of measured red deer antler parameters, from top to bottom: mass, burr circumference and number of tines. Left column: measurements of antlers from Hoge Veluwe; right column; measurements of antlers from Planken Wambuis.

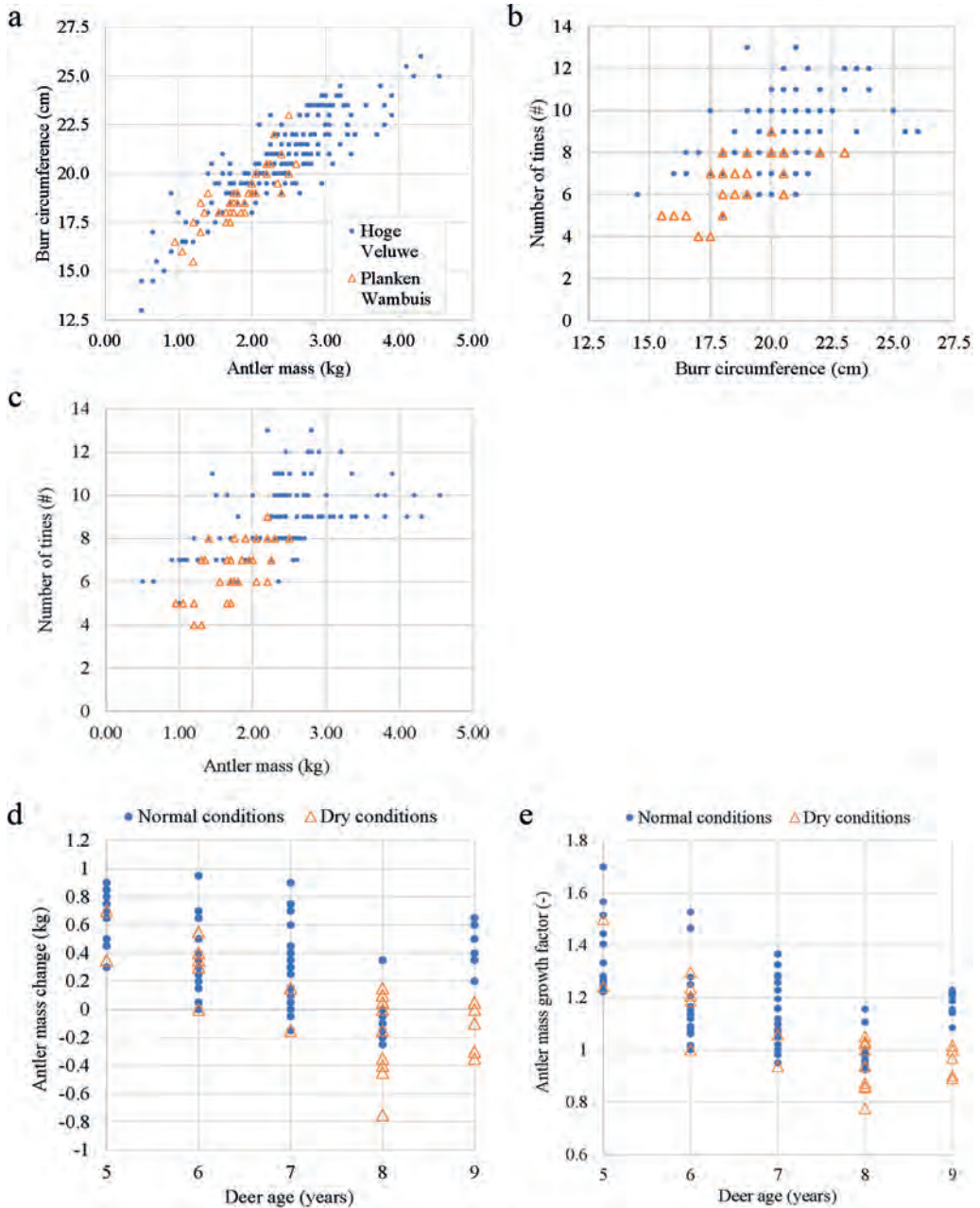
Appendix 2. Output of Pearson correlation tests conducted on the following measured antler parameters: antler mass, burr circumference and number of tines. Top: Hoge Veluwe. Bottom: Planken Wambuis.

		Antler mass	Burr circumference	Number of tines
Mass	Pearson correlation	--		
	<i>n</i>	198		
Burr circumference	Pearson correlation	0.872**	--	
	Sign. (2-tailed)	<0.001		
	<i>n</i>	198	198	
Number of tines	Pearson correlation	0.504**	0.467**	--
	Sign. (2-tailed)	<0.001	<0.001	
	<i>n</i>	112	112	112

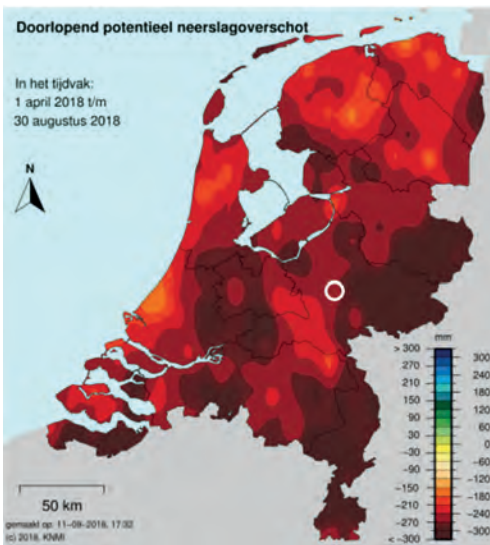
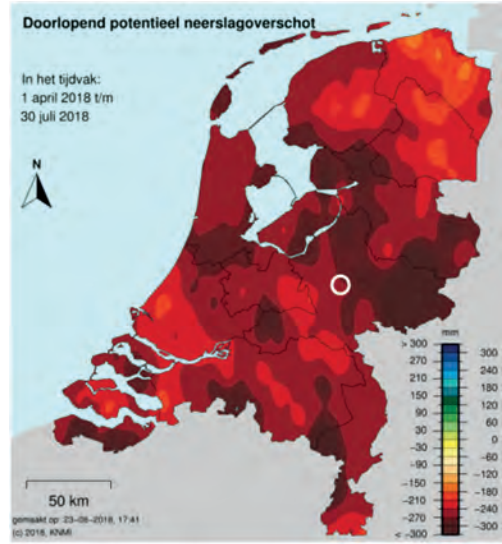
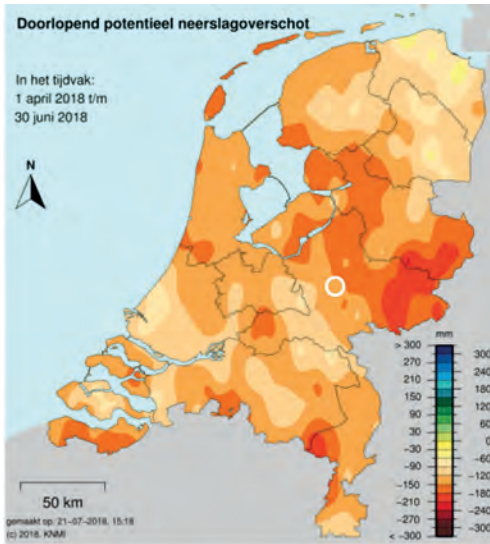
  

		Abstract:	Burr circumference	Number of tines
Mass	Pearson correlation	--		
	<i>n</i>	42		
Burr circumference	Pearson correlation	0.848**	--	
	Sign. (2-tailed)	<0.001		
	<i>n</i>	42	42	
Number of tines	Pearson correlation	0.624**	0.633**	--
	Sign. (2-tailed)	<0.001	<0.001	
	<i>n</i>	32	32	32

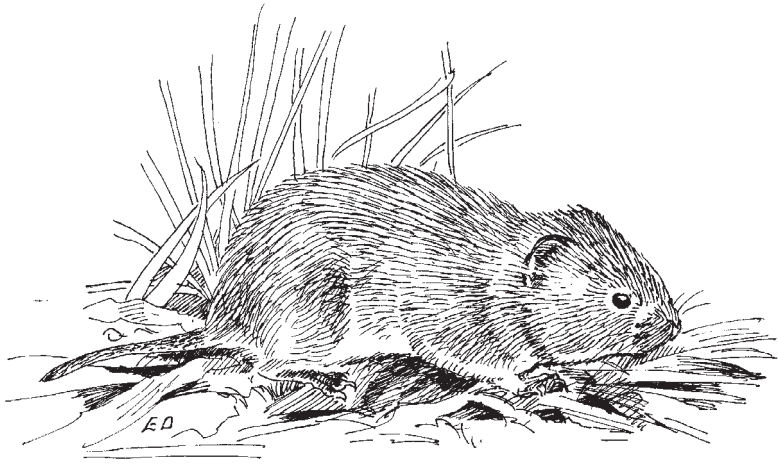
\*\* Correlation is significant at the 0.01 level (2-tailed).



Appendix 3. a-c: Plots of burr circumference v. antler mass (a), of the number of tines v. burr circumference (b), and of burr circumference v. antler mass (c) of the sampled red deer antlers from Hoge Veluwe and Planken Wambuis. d and e: Plots of absolute antler mass change v. deer age (d) and of antler mass growth factor v. deer age (e) for sampled antlers from Hoge Veluwe. Mass change is calculated relative to the preceding year. Antlers developed during the drought of 2018 are regarded as formed under 'dry conditions' (582 mm annual rainfall), opposed to antlers formed in the other years between 2011 and 2020, which are plotted as having developed in 'normal conditions' (880 mm average annual rainfall).



Appendix 4. Continuous potential rainfall deficit in the Netherlands on 30 June (upper left), 30 July (upper right) and 30 August (bottom). The white circle indicates the location of the Hoge Veluwe National Park. Taken from KNMI (2018), <https://www.knmi.nl/nederland-nu/klimatologie/geografische-overzichten/archief-neerslagoverschot>, altered by R. van Mourik.



# The habitat preference of root voles in Nieuwkoopse Plassen, the Netherlands

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**Abstract:** The root vole (*Alexandromys oeconomicus arenicola*) is one of the species for which Nieuwkoopse Plassen & De Haeck (Provinces of Zuid-Holland and Utrecht, the Netherlands) has been designated as a Natura 2000 site. This subspecies is endemic to the Netherlands and can only be found in five regions in the country. The decline of root vole populations is mainly due to the loss of suitable habitat and to competition with other vole species, especially the field vole (*Microtus agrestis*), the common vole (*Microtus arvalis*) and bank vole (*Myodes glareolus*). The main research questions were: what is the relation between vegetation type, type of land management and location within the field on the abundance of root voles in Nieuwkoopse Plassen & De Haeck? It was expected that root voles would prefer extensively managed reed vegetations and rough wet grasslands and that root voles prefer sites close to the edge, as opposed to the centre of fields. It was found that lowland hay meadows, a habitat type that has almost completely disappeared in recent years, and helophytes vegetation are important vegetation types for root voles. Fen woodlots and grasslands dominated by velvet grass (*Holcus lanatus*) or ryegrass (*Lolium perenne*) were found to have the lowest abundance of root voles. Winter mown vegetation where clippings were burnt held higher numbers of root voles, whereas hayfields that were mowed in mid June and grazed for some time before and after mowing were not good for root voles. Within the fields root voles preferred locations close to the edge over central locations.

**Keywords:** root vole, *Alexandromys oeconomicus Arenicola*, land management, vegetation, habitat preference.

## Introduction

In order to protect endangered habitat types and wild flora and fauna in Europe the Member States of the European Union introduced the Habitats Directive in 1992. This obliged Member States throughout Europe to designate Natura 2000 sites to ensure the survival of Europe's most valuable and threatened species and habitats. In the Netherlands each Natura 2000 area has a Designation Order that specifies the conservation objectives, derived from the Habitats Directive (Minis-

try of Agriculture, Nature and Food Quality 2006).

One of these Natura 2000 sites is the Nieuwkoopse Plassen & De Haeck (hereafter Nieuwkoopse Plassen). This area is located in the provinces of Zuid-Holland and Utrecht and measures 2028 ha (figure 1). The Nieuwkoopse Plassen is a fen marsh, featuring different stages of fen succession and is characterized by nine habitat types and contains eight valuable or threatened species. Some of these habitats, such as transition mires and quaking bogs, are very rare and vulnerable, and provide an important habitat for rare flora and fauna.

One of the conservation objectives for the

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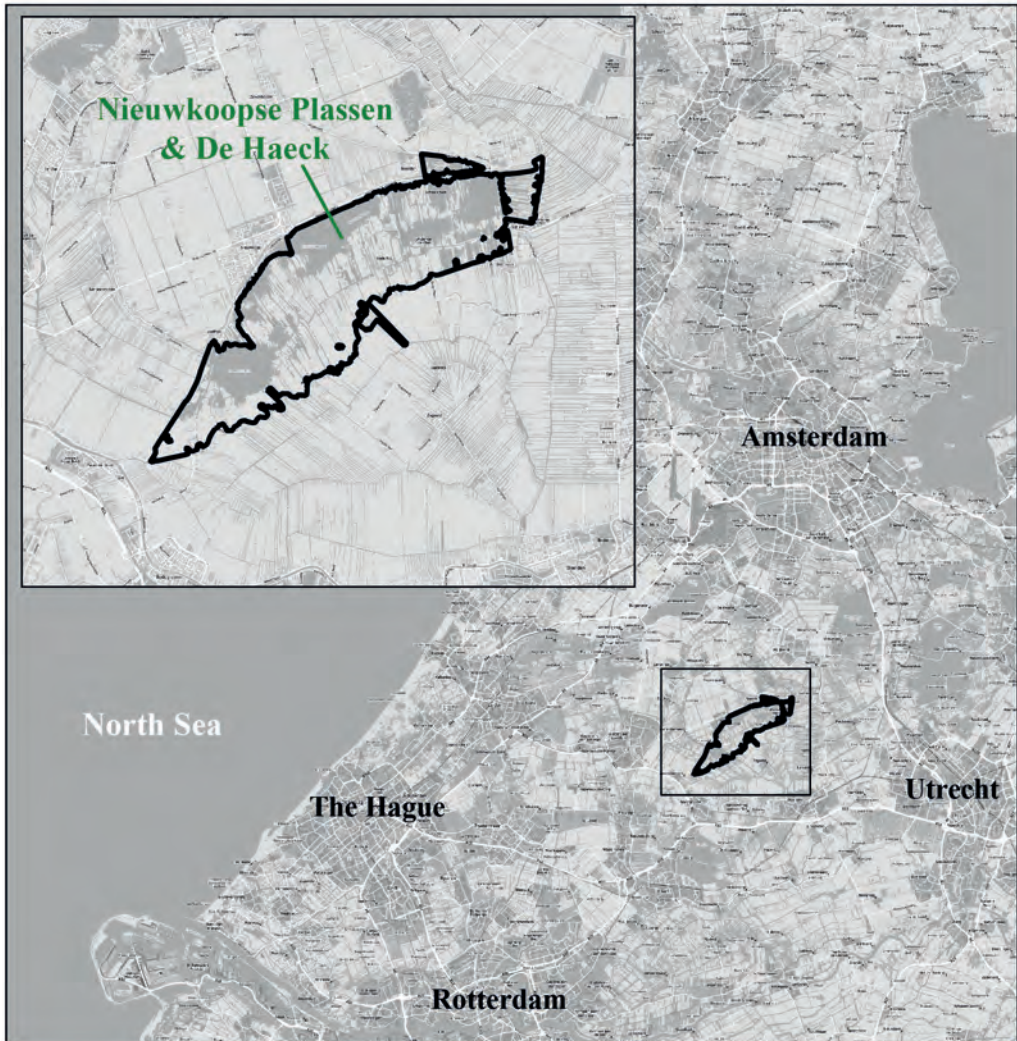


Figure 1. Location of the Natura 2000 site of the Nieuwkoopse Plassen & De Haeck, between Rotterdam and Amsterdam, the Netherlands.

Nieuwkoopse Plassen is the preservation of the size and quality of the habitat in order to preserve the population of the root vole (*Alexandromys oeconomicus arenicola*) (Provincie Zuid-Holland 2015). This sub-species of the root vole is endemic to the Netherlands and can only be found in five regions: Texel, the Frisian lake district, the northern part of Noord-Holland, Nieuwkoopse Plassen and the Delta region in the southwest. As this sub-species is endemic, the Netherlands has a big

responsibility to protect it. Since 1950 the root vole in the Netherlands has declined by 35% (van Norren et al. 2020). This decline is mainly due to the disappearance of suitable habitat, a lack of dynamic water level management (Bergers & Nieuwenhuizen 2000) and competition with other voles, mainly the field vole (*Microtus agrestis*), the common vole (*Microtus arvalis*) and the bank vole (*Myodes glareolus*) (Drees 2003, La Haye et al. 2004, Mostert & Bekker 2019). In areas where root voles com-

pete with these other species, they are almost exclusively found in reed and grass vegetation at the waterside (La Haye et al. 2001). Management measures such as mowing, grazing and sod cutting can cause a decline in the root vole population (Bergers et al. 1998a), even though they also have some benefits for the survival of the root vole population as they prevent the encroachment of shrubs. Yet, at the same time short vegetation enhances predation risk. Grazing can lead to the trampling of their burrows and nests (Jacob 2008).

Further research into the habitat preference and dispersal of root voles in areas with competing vole species has showed that root voles prefer wet nutrient-poor grasslands, reeds and thickets (Bergers et al. 1998b). Research on root voles in the province of Noord-Holland, showed that species rich reed lands and wet extensive managed grasslands had the highest abundance of root voles (Nijhof & Van Apeldoorn 2001). This is in line with the diet of root voles, which mainly consists of young shoots of reed, sedge and grass (Tast 1982). In 2016 research was done on the habitat preferences of root voles in the Nieuwkoopse Plassen. This research showed that root voles have a preference for winter mown reed lands and extensively grazed grassland with common rush (*Juncus effusus*) (Zielman 2016, Van Schie & Zielman 2019).

The main research questions for this research were: what is the relation between the abundance of root voles in fields in the Nieuwkoopse Plassen and: 1. Vegetation type. 2. Type of land management. 3. Location in the field? In addition, we analyzed whether the potential living area for the root voles in the Nieuwkoopse Plassen has increased or decreased and whether the number of root voles caught has increased or decreased over the course of the years.

The first hypothesis was that root voles would prefer reed vegetation and wet, structure rich grasslands. Secondly it was expected that extensive land management would be preferred over intensively managed land.

Thirdly it was expected that root voles prefer sites close to the edge, as opposed to the centre, of a field, because they prefer wetter conditions than other vole species so this is their preferred habitat when competing voles are present. Lastly it was expected that the potential suitable habitat for the root voles would have increased between 2009 and 2019 due to a change towards less intensive management, creating more suitable places for them to hibernate during winter.

This study started in 2010. Results of the period 2010-2016 have already been published (see van Schie & van Veen 2012, van Schie & Zielman 2019), but in one more year (2018) field data were collected and, more importantly, the vegetation was mapped again in 2019. The recent vegetation map allowed a better analysis of the relation between vegetation and the abundance of root voles.

## Materials and methods

### Data gathering

Data on the abundance of root voles in the Nieuwkoopse Plassen were collected every year between 2010 and 2016 and again in 2018. The animals were caught with Longworth live-traps placed in transects about hundred metres long. Approximately every ten metres a pair of traps was placed. After two days in the field when the bait and the trapping mechanism were blocked, the traps were activated for four days and checked twice a day for voles. Whenever a root vole was trapped it was taken out and, when a vole was caught for the first time, a small piece of fur was cut near the tail. This allowed us to ensure that each individual was only counted once in the data analysis, and to exclude recaptures. The captured root voles were attributed to the trap transects, as it was not specified in which exact trap the voles were caught.

Vegetation was mapped according to a standardized protocol (BIJ12 2016). These vegetation

Table 1. Table showing the number of transects that were monitored in each year, with a total of 259 transects combined in which root voles were caught in 126.

Year	Total number of transects	Number (and %) of transects with root voles
2010	45	38 (84)
2011	39	22 (56)
2012	31	13 (42)
2013	19	16 (84)
2014	23	9 (39)
2015	41	15 (37)
2016	25	8 (32)
2018	36	5 (14)
Total	259	126 (49)

maps are a digital visualisation of where different vegetation types can be found within a nature area. For this analysis vegetation maps from 2009 and 2019 were available (Damm & Van 't Veer 2010, Langbroek et al. 2019). It was decided to link capture data between 2010 and 2014 to the 2009 vegetation map and data from 2015, 2016 and 2018 to the vegetation map of 2019, under the assumption that these maps would show most similarity with the existing vegetation in the corresponding years.

The management regime that was used on the different fields in the Nieuwkoopse Plas-sen was mapped every year. To determine what management regime should be linked to which root vole trapping year we checked in which season the trapping was performed. The root vole catches were linked to the management regime that was in use before the catching moment, in either the same year or previous year.

### Data analyses

To determine to what vegetation and / or management type a recorded root vole should be attributed, a buffer of five metres was put

around the transects using QGIS (QGIS development team 2021). This buffer was made because it was possible that there was more than one type of vegetation or management per transect. A buffer of five metres was chosen to exclude surface area on the other side of ditches and to avoid overlap between transects located near the edge and in the centre of fields. The buffer was thereafter used to calculate the number of Root Voles per transect per Vegetation type or Management (RVVM) (equation 1).

Here  $N$  represents the number of unique root voles captured per transect over the four days, with the surface area measured in square metres. No set surface area can be given as this differed per transect, as due to unevenness in the fields not all transects were exactly one hundred metres long.

### Statistical analyses

As normality was proven, a One-Way-ANOVA was used to test the relationship between land management type and the number of root voles. If a difference was found a post-hoc Tukey test was run. To test the relation between vegetation type and the number of root voles a Kruskal-Wallis test was used, as in this case normality was not proven, and when a difference was found a post hoc LSD test was run. To check whether more root voles were found close to the edge or at the centre of fields a  $t$ -test was used, as normality was proven. To test whether the number of root voles caught changed over the course of the years a linear model was used. For all these tests the independent variables were vegetation type, management type, location in the field or the years and the dependent variable was the number of root voles per transect. The statistical analyses were performed using R statistics (R Core Team 2013).

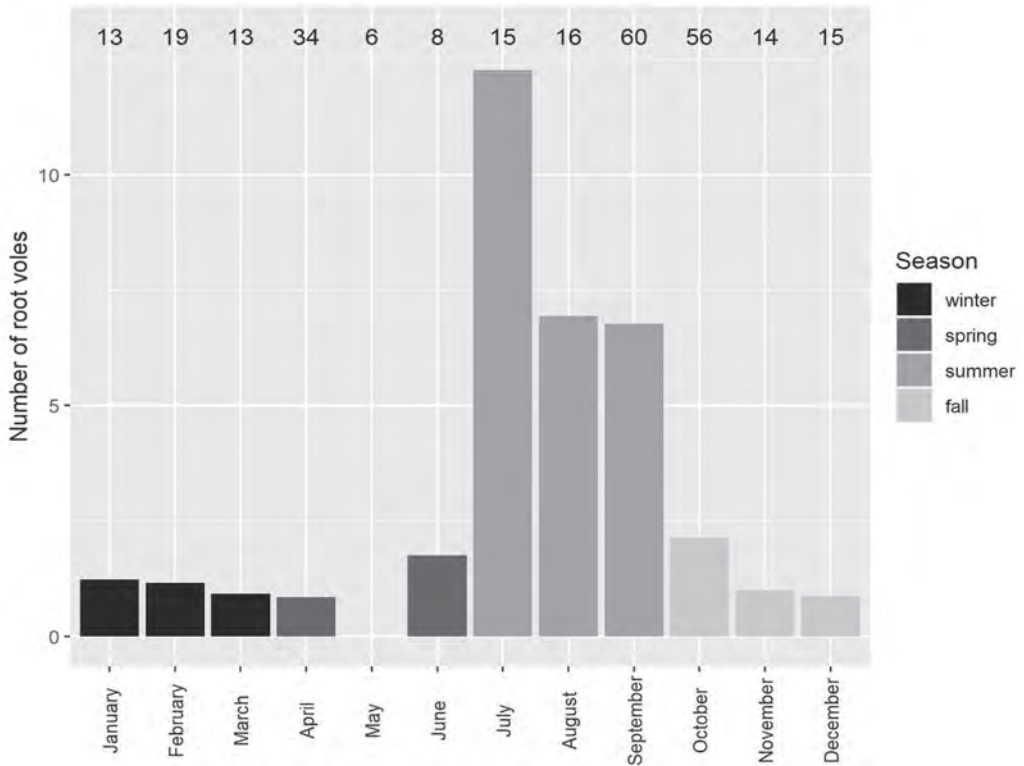


Figure 2. Graph showing the mean number of root voles (y-axis) and the month of the year in which they were caught (x-axis).

### Temporal analyses

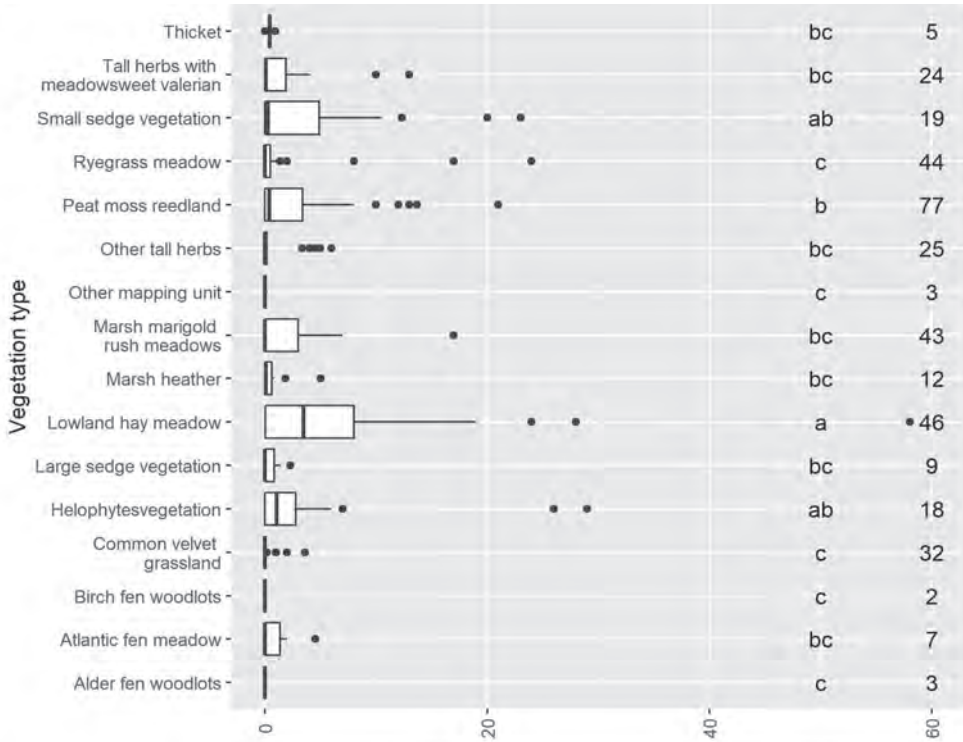
After the statistical analyses, the results were processed to perform temporal analyses. First, both the vegetation type and management type were divided into groups according to the outcome of the statistical analyses. Afterwards a score was given to each group, where a higher score means a more suitable area for root voles. These scores are based on the significant differences between the vegetation types and management types. For vegetation, a score between one and five was used and for management a score between one and three. Four maps in total were made according to these scores, two maps for vegetation and two maps for management type according to the mappings of 2009 and 2019. We then analyzed whether the potential habitat increased or decreased between 2009 and

2019 as a result of changes in vegetation type and management regime.

### Results

Root voles were surveyed in a total 259 transects between 2010 and 2016 and in 2018. The lowest number of transects was in 2013 (19) and the most transects were laid out in 2010. Root voles were caught in 126 transects in total (table 1). The transects were not all monitored in the same months each year, but all months have at least six transects. The transects were most frequently monitored in September and October (60 and 56 transects respectively; see figure 2). This figure also shows that the summer months (July-September) had the highest mean number of root voles. It was therefore decided to run all the analyses twice, once

A



B

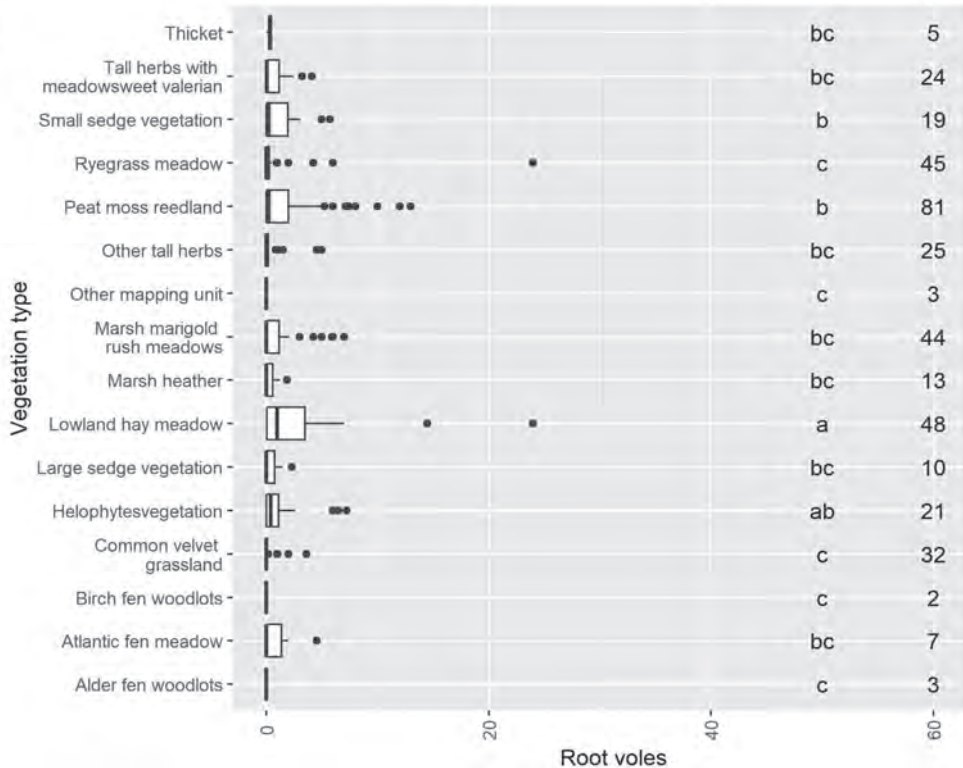


Table 2. Total area of habitat suitable for root voles (by category) according to the vegetation maps of 2009 and 2019. c is low suitability, a high.

Score	Year	Area (ha)	Percentage	Score	Year	Area (ha)	Percentage
1 (c)	2009	452.57	38.13	1	2019	602.54	49.08
2 (cb)	2009	413.63	34.85	2	2019	496.56	40.44
3 (b)	2009	113.85	9.59	3	2019	84.56	6.89
4 (ab)	2009	66.83	5.63	4	2019	44.11	3.59
5 (a)	2009	139.94	11.79	5	2019	0	0
Total	2009	1186.82	100	Total	2019	1227.76	100

with the normal data and one with corrected data. For the corrected data the number of root voles caught in the summer months was divided by four, as in the summer months on average, about four times the number of root voles were caught.

### Vegetation

A Kruskal-Wallis test showed that there was a relationship between vegetation and the number of root voles. This was found for the uncorrected data ( $X^2_{(17)} = 52.57; P < 0.001$ ) and the corrected data ( $X^2_{(17)} = 42.631; P < 0.001$ ). The *post-hoc* analysis for the uncorrected data showed that lowland hay meadow was the vegetation type where most root voles can be found, closely followed by helophytes vegetation and small sedge vegetation. It also showed that grasslands dominated by velvet grass or ryegrass, birch and alder woodlots were least likely to be suitable for root voles (figure 3). The corrected data showed a differ-

Figure 3. Boxplot A shows the uncorrected data with the mean, standard deviation and outliers for root voles found per vegetation type, where the number of root voles is measured by the root voles caught per transect. The letters show the vegetation types by category. The numbers behind the letters show the frequency in which vegetation type were found in at least part of a transect. Boxplot B shows the corrected data. Here the numbers changed, as with the corrected data the transects were separated by the month and there was some overlap between locations.

ence for small sedge vegetation, for the corrected data it no longer belongs to group a but to group b (see below for explanation).

After the statistical analyses, the vegetation scores were assigned to different groups. Figure 3 shows letters, which form the different groups. Group a (just the lowland hay meadows), which had the highest abundance of root voles was assigned a score of 5 and group c had the lowest number of root voles and was assigned a score of 1. It was found that between 2009 and 2019 score 5 habitats, where most root voles resided, disappeared from the Nieuwkoopse Plassen and scores 3 and 4 also decreased (table 2).

### Land management

A One-Way-ANOVA, on both the uncorrected and corrected data ( $F_{(12)} = 2.095, P = 0.018$  and  $F_{(12)} = 2.242, P = 0.010$  respectively) showed that the types of management had a significant effect on the number of root voles present. The *post-hoc* analysis showed that areas that were mowed in the winter, after which the mown vegetation was burnt, had a higher number of root voles than areas that were mown once a year, which had the fewest root voles (figure 4). The corrected data showed a somewhat different picture, here the main difference was between ‘conventional farming’ and ‘meadows, which were mowed around June 15 and grazed for some time before and after mowing’. These meadows were assigned to group b and areas where encroaching trees

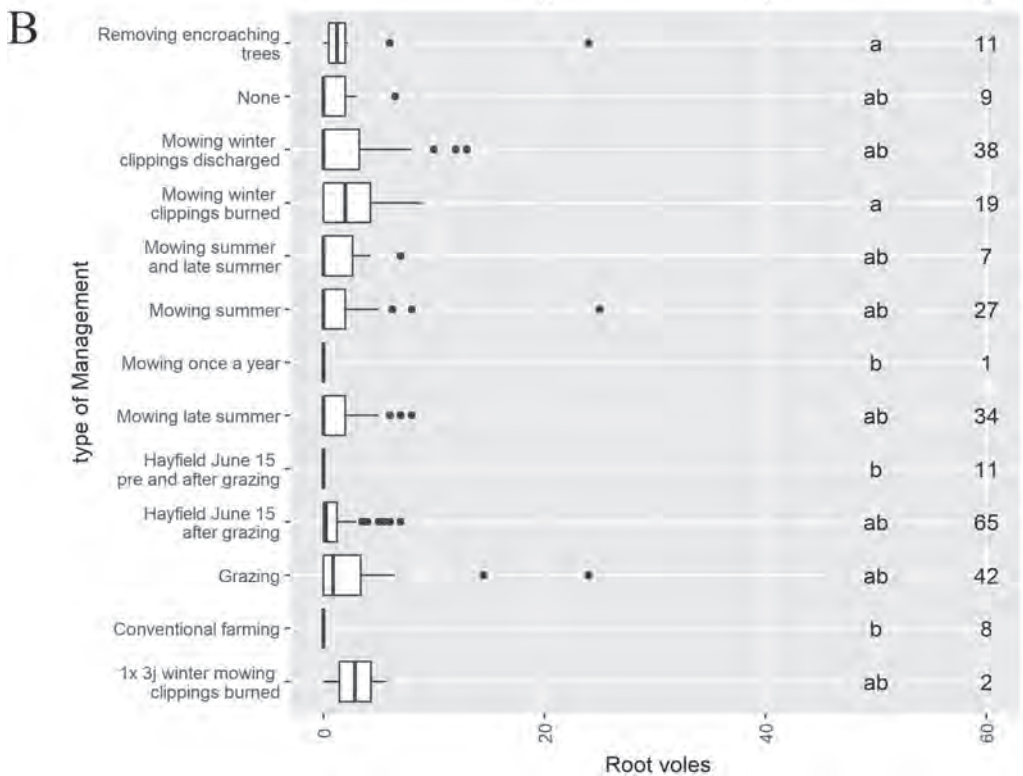
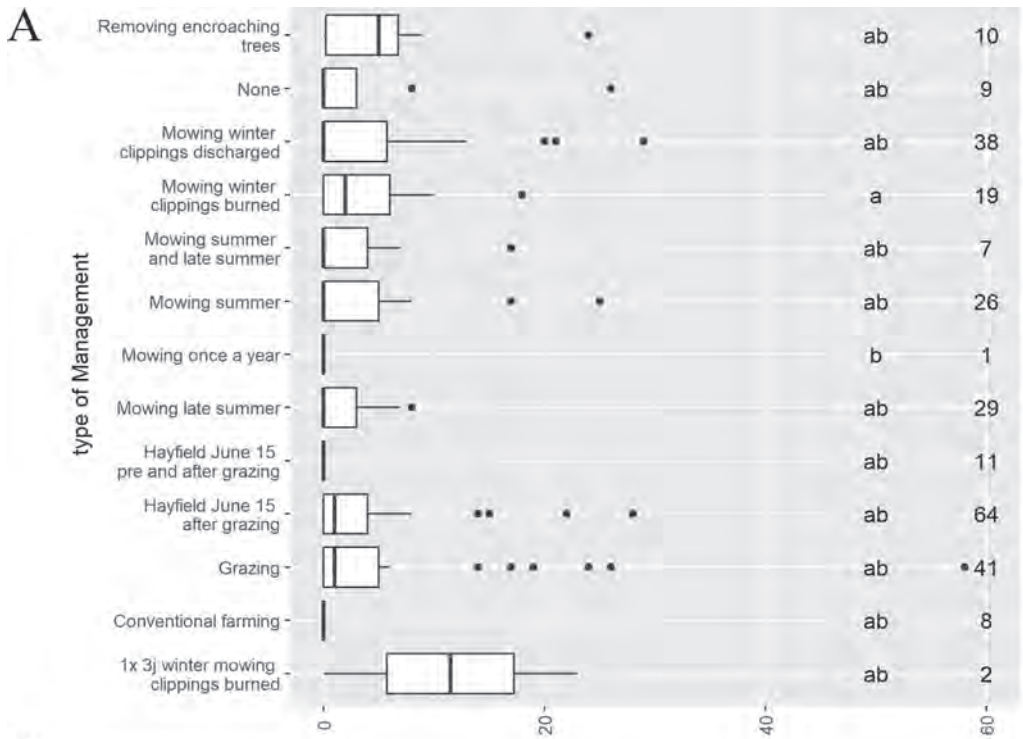


Table 3. Total area of land (by category of suitability for root voles) under different types of management. b is low suitability, a high.

Score	Year	Area (ha)	Percentage	Score	Year	Area (ha)	Percentage
1 (b)	2009	36.09	6.05	1	2019	40.12	8.18
2 (ab)	2009	312.46	52.41	2	2019	437.01	89.07
3 (a)	2009	247.69	41.54	3	2019	13.52	2.76
Total	2009	596.24	100	Total	2019	490.65	100

had been removed were assigned to group a.

A small adaptation was made after the statistical analyses of land management to assign land to different categories. Land on which trees had been removed was allocated to group a, as this category of land had a higher mean average of root voles than winter mown grasslands, which was already allocated to group a. Land that was mowed once a year, land that was managed with no maximum grazing density and no restrictions on management was put into group b together with the hay meadows with grazing before and after mowing, because no root voles were found on land managed according to these strategies. Group a was given a score of 3, group ab was given a score of 2 and group b was given a score of 1. Here score 1 represents the least attractive option for to root voles and a score of 3 the most attractive. We found that between 2009 and 2019 almost all the areas with a score of 3 disappeared (table 3).

### Location of the transect in the field

Transects were almost equally divided between being near the edge of a field ( $n=129$ ) or in the

Figure 4. Boxplot A shows the uncorrected data with the mean, standard deviation and outliers for root voles found in each type of land management per transect. The letters show the different types of management regime by category. The numbers next to the letters show the number of times that these management types occurred within a transect. Boxplot B shows the corrected data.

centre ( $n=127$ ). After performing t-tests on the uncorrected and corrected data it was found that root voles prefer sites close to the edge, as opposed to the centre of fields in habitats where there were competing voles ( $t=3.024$ ,  $P=0.003$  and  $t=2.551$ ,  $P=0.011$  respectively).

### Root vole abundance

As it was found that the potentially best habitats for root voles, both in terms of vegetation and land management had declined, or even disappeared entirely between 2010 and 2018 we also tested to see if the number of root voles caught also had declined in this period. Using a linear model, we found that the number of root voles caught declined for both the uncorrected data ( $R^2=0.039$ ,  $P=0.015$ ) and the corrected data ( $R^2=0.040$ ,  $P<0.001$ ) (figure 5).

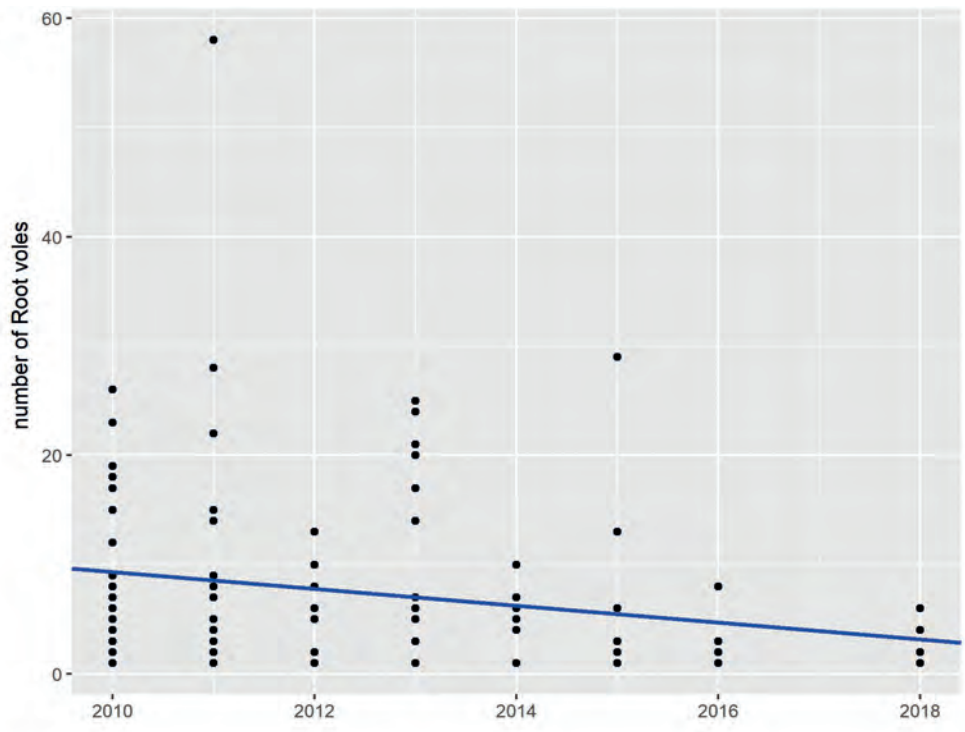
## Discussion

In the interpretation of the results it needs to be born in mind that in this study the field vole, a major competitor of the root vole, was not recorded in the Nieuwkoopse Plassen. In areas where the field vole is present the root vole can be limited to fewer vegetation types because of competition (Bergers et al. 1998, La Haye et al. 2001).

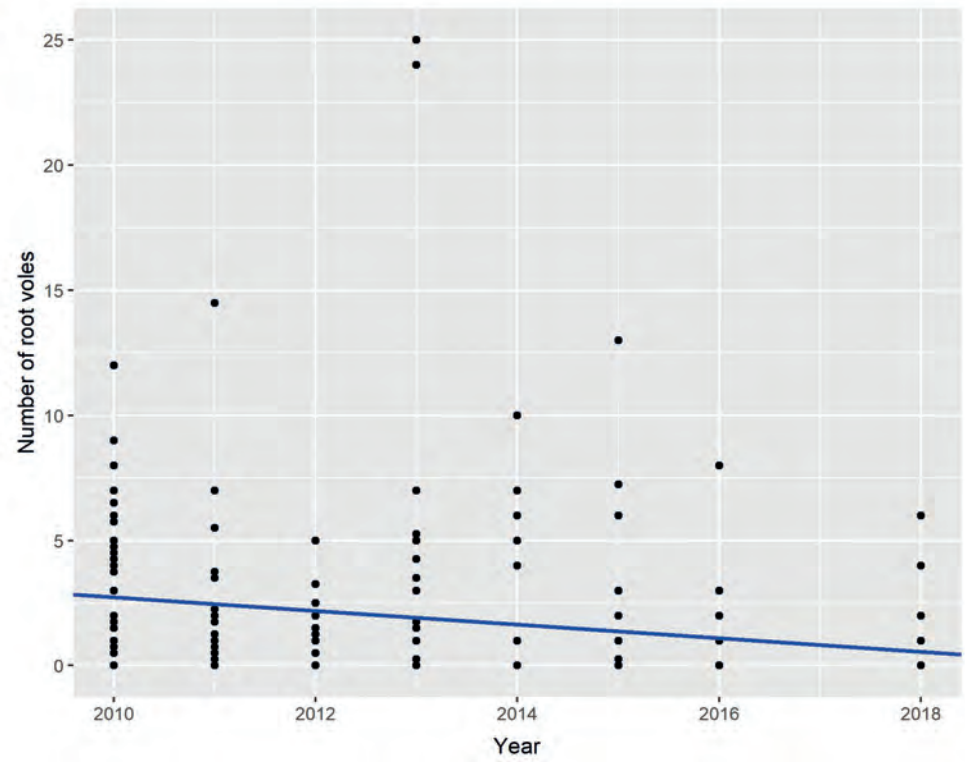
### Vegetation

The vegetation analyses showed that lowland

A



B



hay meadows are the best vegetation type for root voles in the Nieuwkoopse Plassen. These meadows mainly consisted of meadow foxtail (*Alopecurus pratensis*) and false oat-grass (*Arrhenatherum elatius*). This is a vegetation type that occurs mostly on (semi)wet and nutrient rich soils. Previous research also showed that root voles prefer wet areas, but in those studies the wet areas were nutrient poor (Bergers et al. 1998b, Nijhof & van Apeldoorn 2001). However, two of the five regions of the Netherlands where root voles can be found (the Delta region and Texel) are generally nutrient rich. This difference in nutrient richness might not be that important because young shoots of sedge and grasses, which root voles eat, can be found in both nutrient rich and nutrient poorer soils. Another important factor for the root voles is structural variation in the vegetation (BIJ12 2017). This is something that lowland hay meadows can have when plant species, such as common rush and rough bluegrass (*Poa trivialis*), are present but without these plants the meadows can lack structural variety. The presence of common rush has been shown to be an important factor for root voles in previous research (Zielman 2016, van Schie & Zielman 2019). In addition, lowland hay meadows are known to be quite wet and can even temporarily flood. Root voles prefer wet or even temporarily flooded meadows, although flooding rarely occurs in the Nieuwkoopse Plassen. It was not a surprise that helophytes vegetation was the second-most preferred vegetation. This is a wet and structure rich vegetation in which other vole species, that could be competitors with the root voles, usually do not live. It was also no surprise that fen woodlots scored badly, as very little food is available

Figure 5. Graph A shows the uncorrected data with the transects in which root voles were captured. Each point represents one transect with the corresponding number of root voles. There is no data for 2017, as no transects were laid out that year. Graph B shows the corrected data.

there and the opportunity to make burrows is almost non-existent.

## Land management

The analysis for the best management strategy showed that mowing in winter and then burning the mown vegetation yielded the highest number of root voles per transect. Burning mown vegetation might sound counter-productive in terms of creating a suitable habitat but it reduces the competition with other vole species, mainly because root voles live in burrows and are thus mostly safe from fire. Another reason why this management strategy might be good is because a smaller machine can be used for the mowing and no machine has to be used to remove the mown vegetation as these are burned. Using a smaller machine might mean that the burrows of root voles have a higher chance of remaining intact due to there being less disturbance.

It was also not surprising that hayfields which were mowed around June 15 with pre and post grazing for some time were bad for root voles. This management strategy means that there are three disturbances every year, the first of which is grazing in spring, after which the area is mowed around June 15<sup>th</sup> and then grazed again. This also means that the vegetation is short all the time. Short vegetation in turn increases the risk of predation, not just upon root voles, but on voles in general (Jacob 2008). The same goes for conventional farming in the Nieuwkoopse Plassen, in which farmers are mostly free to manage their land as they like, providing that they comply with general laws and regulations. This means in practice that the land is used intensively and due to this the vegetation is usually short and lacks structural variety.

A management strategy that could possibly have a positive effect on the root vole population is dynamic water level management. By manipulating the water level, the area can be left wetter for a longer period in spring, which

would dislodge the field vole. Another added benefit is that small islands can be formed when the water level is gradually lowered. As root voles are better able to swim than other voles, they can settle in these areas earlier than other vole species (Vandenbosch et al. 2009). Root voles are also better adapted against cold than other vole species and hence thrive better close to water. Van Wijngaarden & Zimmermann (1965) described that the ideal habitat of the root vole is the place where water meets land.

### **The location of root vole in fields**

More root voles were caught along the edge of fields than in the centres. The edges of fields are usually wetter or might even contain a water ditch, which suits the root voles, and would be more nutrient rich, especially in peat moss areas, which usually means more available food. The edges in agricultural areas are also richer in structure, but not necessarily richer in nutrients. Moreover, both the management and vegetation is, in most cases, different near the edge of a field than in the centre. This difference is mainly that 5-10% of the reeds near the edge are not mowed, to allow animals to find shelter to get through the winter, which can also serve as a shelter or foraging area shortly after mowing.

### **Changes in habitat availability**

There were big changes in the potentially suitable habitat between 2009 and 2019, both regarding the land management type and the vegetation type. The group of vegetation types with the highest abundance of root voles (lowland hay meadows) was completely gone in 2019 (table 2) and for land management the categories with the highest abundance decreased by almost 90% in the same period (table 3). The lowland hay meadows disappeared to a change in management. In the

last couple of years of the survey more fields in the Nieuwkoopse Plassen were mowed or grazed, which was done to allow more opportunities for the endangered habitat types and plant species that are, like root voles, protected by the Habitats Directive. More focus on other conservation objectives also contributed to the decrease in suitable habitat: burning mown vegetation no longer takes place in the Nieuwkoopse Plassen because it has a large negative effect on almost all the other red list and target species.

### **Conclusions**

The two most important vegetation types for root voles are lowland hay meadows and helophytes vegetation. Fen woodlots and grasslands dominated by velvet grass and ryegrass were found to be the least populated vegetation types in the Nieuwkoopse Plassen. Vegetation that was mowed in winter, and then burnt seemed to be positive for root voles. On the other hand, hayfields that were grazed for some time in spring and summer and mown around June 15 were not good for root voles. Root voles prefer locations close to the edge of fields over locations in the centre. Between 2009 and 2019 the potential suitable habitat for root voles in the Nieuwkoopse Plassen decreased substantially. We conclude that the combination of burning mowed vegetation and leaving vegetation at the edge of fields after mowing provides optimal habitats for root voles.

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## Samenvatting

### Habitatvoorkeur van de Noordse woelmuis in de Nieuwkoopse Plassen

De Noordse woelmuis (*Aleandromys oeconomus arenicola*) is één van de habitatrichtlijnsorten voor het Natura 2000-gebied

de Nieuwkoopse Plassen & De Haeck. De ondersoort *arenicola* is een ondersoort van de Noordse woelmuis die alleen in Nederland voorkomt en in maar vijf regio's, wat de bescherming van dit type van de Noordse woelmuis extra belangrijk maakt. De achteruitgang van de Noordse woelmuis is vooral te wijten aan het verdwijnen van geschikt leefgebied en aan concurrentie met andere woelmuizen, met name de aardmuis, veldmuis en rosse woelmuis. De onderzoeksvraag was: wat is de relatie tussen vegetatietype, type beheer en locatie op het perceel met het voorkomen van de Noordse woelmuis in de Nieuwkoopse Plassen & De Haeck? De verwachting was dat Noordse woelmuizen een voorkeur hebben voor extensief beheerde helofytenvegetaties en ruige, natte graslanden. Ten tweede was

de verwachting dat Noordse woelmuizen de locaties langs de oevers van een perceel prefererden ten opzichte van het midden van een perceel, omdat de oevers natter zijn. Uit de analyse bleek dat vossenstaart-, glanshaverhooilanden en helofytenvegetaties het belangrijkste waren. Ook bleek dat er in broekbossen, witbolgraslanden en raaigrasweiden de minste Noordse woelmuizen werden gevonden. Het beste beheertype voor de Noordse woelmuizen was het maaien van de vegetatie in de winter, waarna het maaisel werd verbrand. Beheer waarbij gemaaid wordt rond 15 juni en begrazing daarvoor en daarna was het minst geschikte beheertype.

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# An abnormal enamel pattern of the first lower molar ( $M_1$ ) in a field vole (*Microtus agrestis*) from the province of Zeeland, the Netherlands

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**Abstract:** In barn owl (*Tyto alba*) pellets, a skull from a field vole (*Microtus agrestis*) was found with an abnormal dental pattern. The enamel ridge of the first right lower molar displayed a 'capital M' outline. The rim of the root was thin (as in a regular  $M_1$  molar), without irregularities or thickenings. Other morphs described in field voles and even the 22 morphotypes of other European and Asian arvicoline species within the genera *Alexandromys* and *Microtus* do not bear any resemblance to this specimen. The very rare abnormality in this field vole can be described as the 'syndrome of the unilateral missing lingual re-entrant angles of the anterior cap complex of  $M_1$ '. It is hypothesized that the form wasn't caused by an infection, abnormal growth after an accident or tumour growth but most probably by an epigenetic condition.

**Keywords:** field vole, *Microtus agrestis*, lower first molar  $M_1$ , re-entrant angle, anterior cap complex, province of Zeeland, the Netherlands.

Amidst some 2000 skull and mandibles of field voles (*Microtus agrestis*) extracted from barn owl (*Tyto alba*) pellets from different places in the province of Zeeland, the Netherlands, one specimen immediately attracted attention. The first right lower molar ( $M_1$ ) of this specimen displayed an abnormal shape: a molar without a single closed triangle and with a buccal enamel ridge forming a 'capital-M' outline (figure 1). Both middle upper molars ( $M^2$ ) of NHG26739 show the characteristic postero-internal lobe ('*agrestis*-Schlinge') for field voles. The enamel pattern of  $M_1$  of the left mandible shows a 'normal' morph (see figure 4a). The skull measurements are within the range provided by Krapp

& Niethammer (1982), indicating this is compatible with a (sub)adult specimen.

The specimen originates from a pellet sample collected June 1999 in Poortvliet (Tholen); both mandibles and the cranium are preserved with the number NHG26739 and have been added to the collection of the Koninklijk Zeeuwsch Genootschap der Wetenschappen (KZWG, Royal Zeeland Scientific Society), located in the Zeeuws Museum in Middelburg, in the province of Zeeland.

The description of the elements of the occlusal surface of  $M_1$  in this short note follows the nomenclature of Van der Meulen & Zagwijn (1974) (figure 2). Surface elements in addition to those presented in figure 2 are extended with a novel numeration.

The occlusal surface of the first right lower



Figure 1. Occlusal view of the right lower molar row of field vole NHG26739. Red arrow: first molar ( $M_1$ ).

molar of specimen NHG26739 shows two dentine fields: the posterior loop (PL) and the anteroconid complex in which the anterior cap (AC1) is broadly linked with T1, T2 and T3. Two salient angles are present on the lingual side: LSA1 on the posterior loop and LSA2 on the basis of the anteroconid complex. On the lingual side only one re-entrant angle is present (LRA1). On the buccal side four salient angles are present: BSA1 is part of the posterior loop, while BSA2 and BSA3 originate from the anteroconid complex and BSA4 is the buccal-side bended tip of the anterior cap. All three buccal re-entrant angles, BRA1, BRA2 and BRA3, are part of the anteroconid complex with BSA2, BRA2 and BSA3 together forming the 'capital M'.

Furthermore, specimen NHG26739 shows

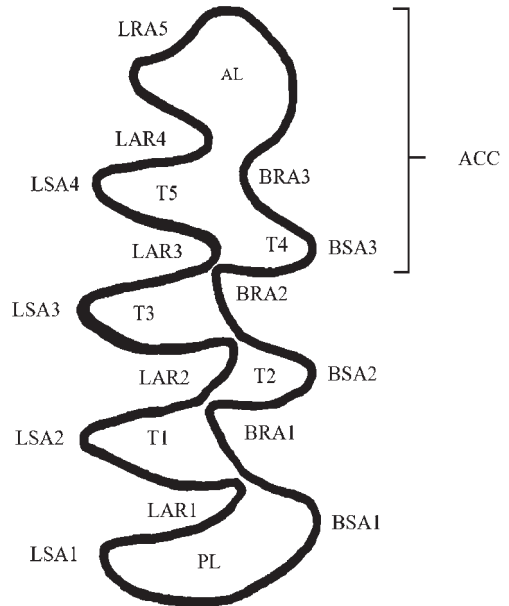


Figure 2. Elements of the occlusal surface of the right  $M_1$  in *Microtus* (and *Alexandromys*) species (after van der Meulen & Zagwijn 1974). PL: posterior loop, AL: anterior loop, ACC: anteroconid complex, T1-T5: triangular loops of the occlusal surface, LSA2-LSA4: lingual salient angles (the lingual side of PL can be regarded as LSA1), LRA1-LRA5: lingual re-entrant angles, BRA1-BRA4: buccal re-entrant angles, BSA1-BSA5: buccal salient angles.

some peculiarities:

- The lingual occlusal enamel rim of  $M_1$  is slightly thickened (figure 3b);
- From the lingual view only one groove of the re-entrant angle is present (figure 3g);
- From the buccal view three grooves of re-entrant angles are present (figure 3h);
- The rim of the root is thin (as in a regular  $M_1$  molar) and exhibits no signs of irregularities or thickenings (figure 3d);
- The alveolus of  $M_1$  is slightly broadened and lacks the presence of ribs on the lingual side, which are normally present for the collagen attachment between molars and the alveolus (figure 3j).
- The occlusal length of  $M_1$  right is slightly shorter than  $M_1$  left, 2.50 mm as opposed to 2.90 mm.

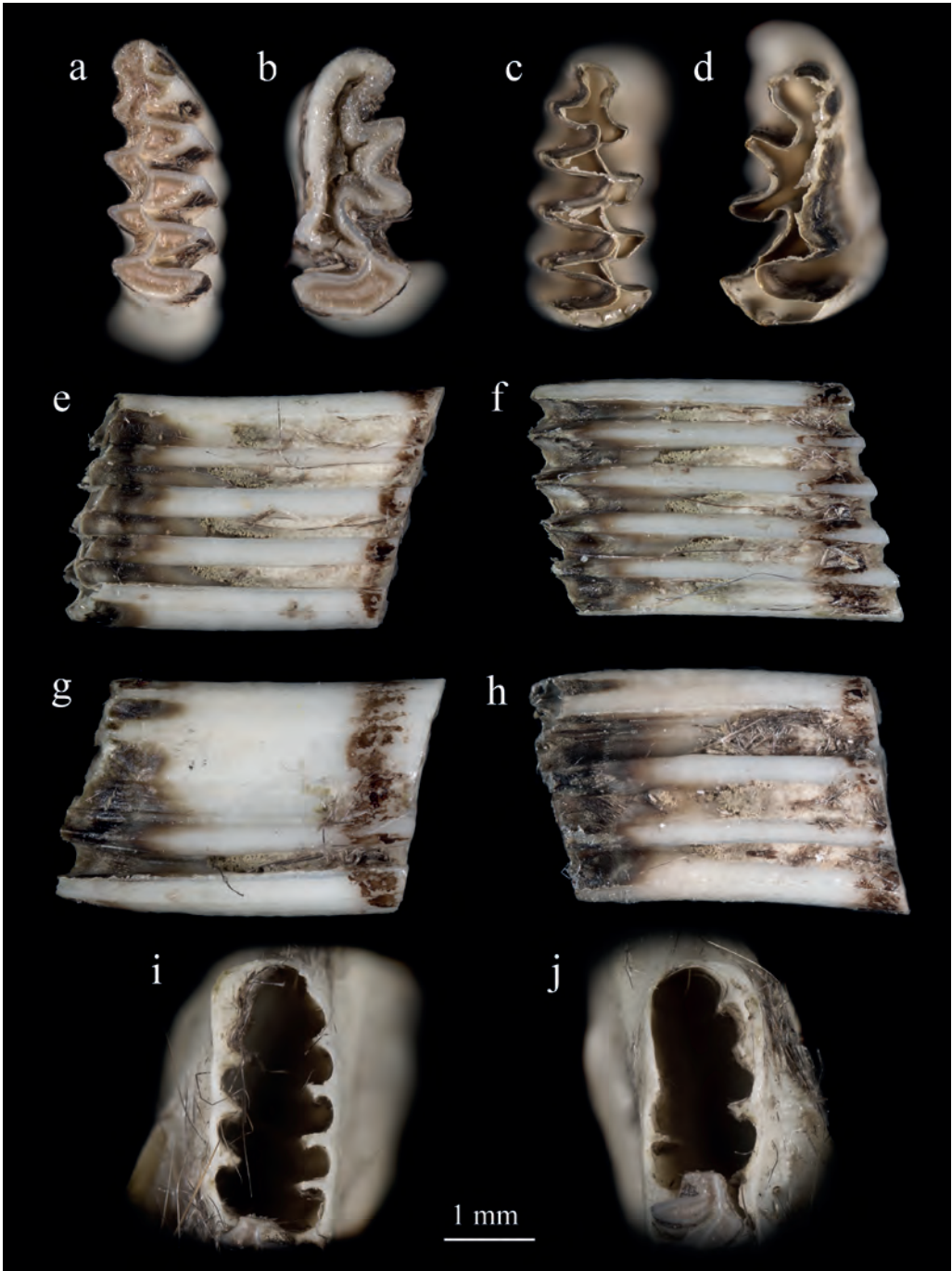


Figure 3. Views of the left (a, c, e, f, and i) and right (b, d, g, h and j) first molar ( $M_1$ ) including its alveoli of field vole NHG26739. Top row: occlusal views (left), views at the rim of the root (right); second row: lingual and buccal views of left  $M_1$ ; third row: lingual and buccal views of right  $M_1$ ; fourth row: alveolar views. Photos (focus-stacked images): Ben Verboom.

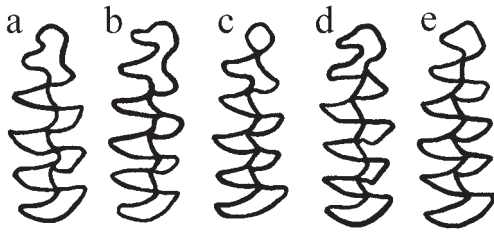


Figure 4. Schematic impression of morphs of the right first lower molar  $M_1$  of the field vole, after Kapischke et al. (2009). a: 'normal'; b: 'oeconomus+'; c: 'maskii'; d: 'oeconomus++'; e: 'arvalis/agrestis++'.

- The measurements of the right and left lower molar row were 5.90 and 5.50 mm respectively.

The most common pattern of the enamel ridge of  $M_1$  in field voles is a posterior crescent loop, an anterior loop with three lobes between five alternating triangles, three lingual and two buccal, here further described as 'normal' (figure 4a). As early as 1905 Rörig & Börner and, later on, many other authors (e.g. Zimmermann 1956, Reichstein & Reise 1965, Reichstein 1966 and Reinwald 1967) described other morphs of the molar pattern in field voles from different German federal states. Other morphs of  $M_1$  in field voles from Russia (Ognev 1950) and Italy (Locatelli & Paolucci 1995) have also been described. Recently Kapischke (1992), Jentzsch (2006) and Kapischke et al. (2009) described more different morphs of this molar: 'maskii', 'oeconomus+', 'oeconomus++' and 'arvalis/agrestis++' (figure 4b-e). The description of these morphs starts with the variations with five closed triangles and characterized as: a. 'Normal': with anterior and posterior loop. b. 'Oeconomus +': an additional salient angle on the lingual side, mimicking the characteristic 'knight-form' (similar to the knight symbol in chess). c. 'Maskii': with a constricted and separated apical knob on the anterior loop. Patterns with six closed triangles consist of: d. 'Oeconomus ++': the enamel pattern as in b) with a buccal at a constricted salient angle. Morphs, that have been described as

'arvalis/agrestis ++' have seven closed dental triangles, shown in e). Frequencies of these morphs in field voles vary across Europe; for instance in two German federal states (Bavaria and Saxony-Anhalt) the frequencies for 'normal' molars are about 69%, and about 25% for 'oeconomus +', with the other morphs accounting for less than 5%.

Angermann (1974) depicted 'maskii' (as in figure 4c) and 'oeconomus', the latter with two closed triangles on the lingual buccal sides. The 'oeconomus' morph should be presented with the cranium in a ventral view to rule out confusion with those of root voles (*M. oeconomus*); therefore this morph is not presented here.

Recently Synyavska & Peskov (2020) described 22 morphotypes of European and Asian arvicoline species within the genus *Alexandromys* and *Microtus* with depictions of the anteroconide complexes. In those depicted morphotypes two or three lingual salient angles of the anteroconide complexes are present, making four or five of these angles on the whole lingual side of the  $M_1$ . None of the described morphs in figure 4 show any similarity to the occlusal pattern of the right first lower molar of specimen NHG26739.

Bilateral asymmetry of the morphotype dental pattern has been observed in various studies. In a study of morphotype dental patterns in the narrow-headed vole (*M. gregalis*), within-individual differences among right and left molars, when present, suggests that bilateral asymmetry of the morphotype dental pattern could be regarded as an inherent characteristic of an individual (Markova et al. 2013). Polly et al. (2011), investigating contralateral  $M_1$ s from the same individual using Procrustes distance, a form of nearest-neighbour matching, found that 15 out of 24 (63%) *M. agrestis* did not match. Kapischke et al. (2009) found 'oeconomus+-morph' in field voles to be symmetrically present on both sides in most cases and just occasionally on one side only.

In the narrow-headed vole, age differences in morphotype dental patterns of specimens

of one month and older were non-significant and negligible compared to among-individual variation (Markova et al. 2013). It seems safe to assume that morphotype dental patterns in field voles older than one month remain the same and specimen NHG26739, estimated to be a (sub)adult individual, has at least had its differences in the first lower molar patterns since its first month of its life.

The buccal and lingual views as well as the aspect of the right alveolus of  $M_1$  (see figure 3g, h and j) shows smooth molar sides and no signs of overgrowths of enamel, dentin or cementum, characteristic for odontomas (Boyd 1961) or complex odontomas (Nelson & Thompson 2010). Based on these observations the origin of this abnormal molar seems unlikely to be a (post)-infectious dental condition, an abnormal growth after an accident or of neoplastic origin. The unilaterality of the abnormality and the exclusion of other causes make an epigenetic condition most probable.

Changes towards increased complexity of the first lower molars in field voles start from the mesial part of the tooth, this is the anterior cap complex (Kapischke et al. 2009). All the variations of the described morphs of the enamel pattern in field voles in the first lower molar are expressed by the number of constrictions, resulting from salient angles originating from the lingual or buccal enamel ridges. Changes occurring in a more distal region of the molar, mostly show reductions in complexity (Kapischke et al. 2009). Several authors refer to the different frequencies of the numbers of triangles in these different morphs, depending on the longitudes. The findings of Reichstein & Reise (1965) suggest that there may be some general vegetational factors since field voles have some dental variations that are simpler (less complex) in north western Germany and Denmark than in other parts of Germany. Guthrie (1971) suggests the higher frequency of field voles that have simpler teeth in somewhat the same area as common voles, might be explained by increasing competition between these species.

A reduction of two salient angles just on the lingual side in the anterior cap complex of the (right)  $M_1$  is not in line with the stepwise changes of morphs. In specimen NHG26739, this pattern is present on the right buccal side of  $M_1$ ; however, there is no formation of angles on the lingual side of this molar. The abnormal enamel pattern of the first lower molar ( $M_1$ ) in specimen NHG26739 does not belong to the regular variations of field voles, nor of other European and Asian species of the genus *Alexandromys* and *Microtus*. Therefore the deviation described here, has to be considered as a very rare abnormality. The proposed description for the abnormal enamel pattern in this field vole is the 'syndrome of the unilateral missing lingual re-entrant angles of the anterior cap complex of  $M_1$ '.

**Acknowledgements:** Special thanks are rewarded to Piet Stols, who collected the barn owl pellets from Poortvliet (Tholen). Ben Verboom took the photographs of the different views of the molars and mandibles. The author wishes to thank the anonymous reviewers for their helpful comments and suggestions for improvement on a previous version of the manuscript. Nicholas Parrott kindly helped improving the English.

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## Samenvatting

### Een afwijkend emailpatroon van de eerste onderkies ( $M_1$ ) bij een aardmuis uit de provincie Zeeland

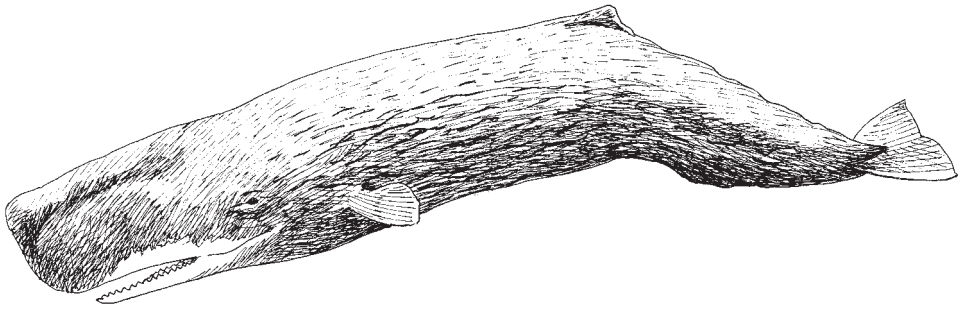
In overblijfselen van een aardmuis (*Microtus agrestis*) (specimen NHG26739) afkomstig uit braakballen van een kerkuil (*Tyto alba*) werd een opvallende afwijking vastgesteld. De emailrand van de voorste kies in de onderkaak heeft aan de wangzijde de vorm van een hoofdletter 'M'. De rand van de wortel is dun, zonder onregelmatigheden of verdikkingen, wat er op wijst dat deze kies niet kan worden omschreven als een element na een infectie, abnormale groei na een ongeval of een van de kies afkomstige tumor. Het "normale" patroon van de voorste kies in de onderkaak van de aardmuis kenmerkt zich door een achterste halvemaanvormige lus aan de achterzijde, een lus met drie lobben aan de voorzijde en daartussen vijf driehoeken, afwisselend drie aan de tongzijde en twee aan de wangzijde. Dit "normale" patroon, de andere bekende patronen ('morphs') van de aardmuis en zelfs de 22 verschillende morphotypes van andere soorten behorende tot de geslachten *Alexandromys* en *Microtus* uit Europa of Azië vertonen geen enkele gelijkenis met specimen NHG26739.

De zeer zeldzame afwijking van de onderste eerste molaar in deze aardmuis kan worden omschreven als het 'syndroom van de unilateraal, ontbrekende, inspringende hoeken aan de tongzijde van het voorste kapcomplex'. De

afwijking is hoogst waarschijnlijk veroorzaakt door een epigenetische verandering.

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# A sperm whale (*Physeter macrocephalus*) washed ashore at Biervliet in 1429

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Figure 1. Map with the location of the former isle of Biervliet (arrow) after the storm surge of 1404.

Around 15 February 1429 (proleptic Gregorian date 24<sup>th</sup> February) a male sperm whale (*Physeter macrocephalus*) was washed ashore on the island of Biervliet (figure 1), just inside the mouth of the Westerschelde (Western Scheldt) in the province of Zeeland, the Netherlands. A pile work for sea defense was hit and damaged. Due to later land reclamations, the stranding locality (51.329 N, 3.690 E) is today situated inland.

The sperm whale is documented by a drawing, clearly depicting the diagnostic features of the species, in the annual account of the town of Biervliet for 1428-1429 (figure 2), which also reported on the repair of the damaged

pile work<sup>1</sup>, and the expenses paid for the men, sent from Doornik (Tournai) to slaughter the whale<sup>2</sup>. At that time Doornik was not a part of the county of Flanders, but a domain of the French Crown (nowadays in the province of Hainaut, part of Walloon,) and therefore it is believed that the whale could have been claimed by the French king. No more detailed information about this stranding, such as total length and other body dimensions or oil yield were provided by the account. This re-discovery of the sperm whale stranding is the first well-documented and dated sperm whale stranding from the 15<sup>th</sup> Century and

<sup>1</sup> Algemeen Rijksarchief Brussel, Rekenkamer inv no 32076 fol 14 v.

<sup>2</sup> Algemeen Rijksarchief Brussel, Rekenkamer inv no 32076 fol 15 v.

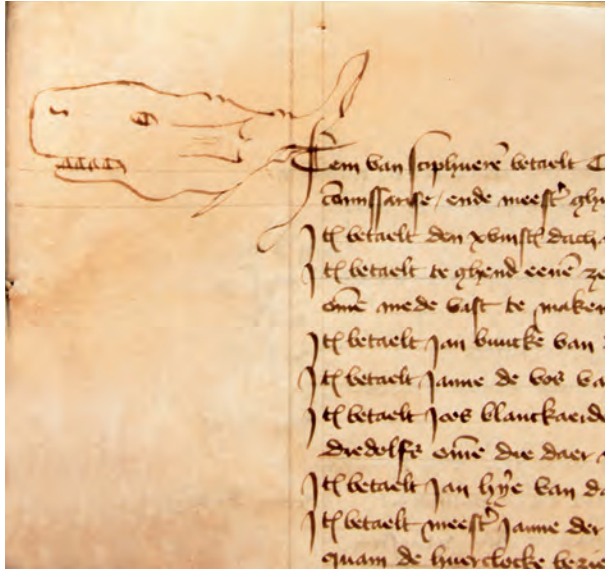


Figure 2. Drawing in the margin of the annual account of the town of Biervliet for 1428-1429.

the earliest reported stranded sperm whale for the Province of Zeeland. The date of the stranding falls into the main known stranding season for sperm whales in the North Sea and provides an addition to the overview of stranded sperm whales around the North Sea (Smeenk & Evans 2018). An integral transcription and retranslation of the relevant medieval text is provided elsewhere (Heerebout, in press).

**Acknowledgements:** Mr. Jan van Loo, studying the archives of Biervliet, informed me about the drawing of the sperm whale and Mr. Rinus Willemsen was kind enough to transcribe the relevant parts of the 15<sup>th</sup> Century handwriting.

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## Samenvatting

### Een potvisstranding bij Biervliet in 1429

De stadsrekening van Biervliet (Zeeuws-Vlaanderen) over 1428-1429 begint met een marginale, natuurgetrouwe tekening van een potvis. In februari 1429 spoelde aan de noord-oostelijke hoek van het eiland van Biervliet een potvis aan tegen een paalhoofd en dat raakte beschadigd. Het herstel van het paalhoofd werd extra vergoed, zo ook de personen die het dier opmaten en het slachtten. Deze vermelding is een aanvulling van het recente overzicht van gestrande potvissen langs de Vlaamse (Zeeuwse) kust en rond de Noordzee (Smeek & Evans 2018).

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