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 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^2 in 2019; www.cbs.nl), of which 7,680 km^2 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^2. 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	*n* 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 were we 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^2), 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.

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*.

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,

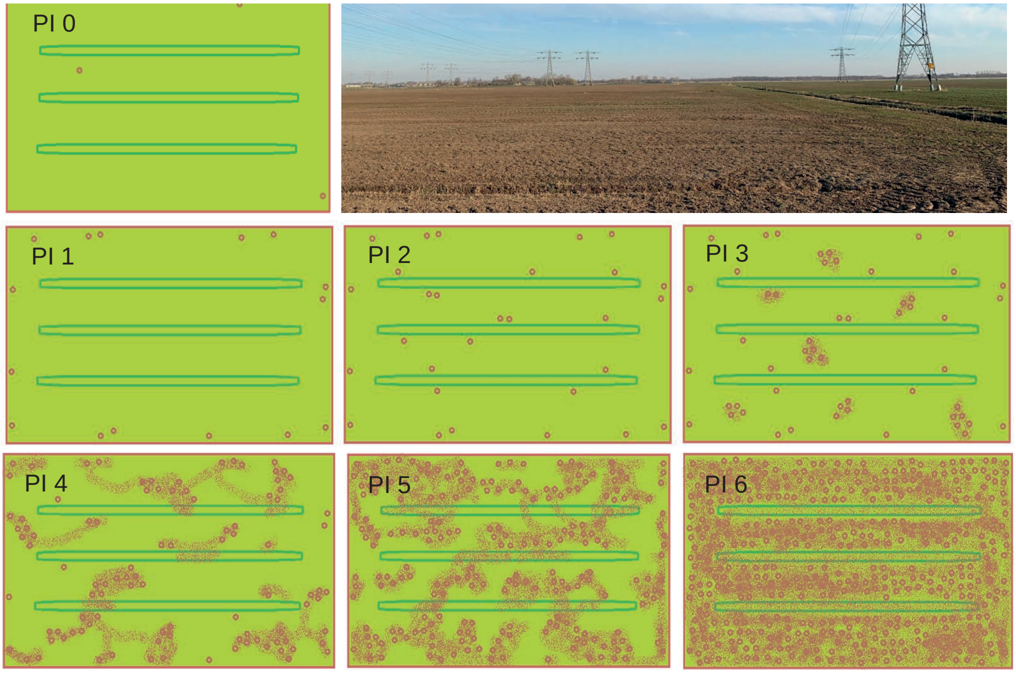

Figure 3. Visualization of the Parcel Index (PI) in seven classes. PI 0: none or hardly any vole activity; PI 1: clear vole activity in ditch edges, hardly any activity on the parcel; PI 2: clear vole activity in ditch edges and around surface drains, some burrows on the parcel, PI 3: as PI 2, with incipient 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

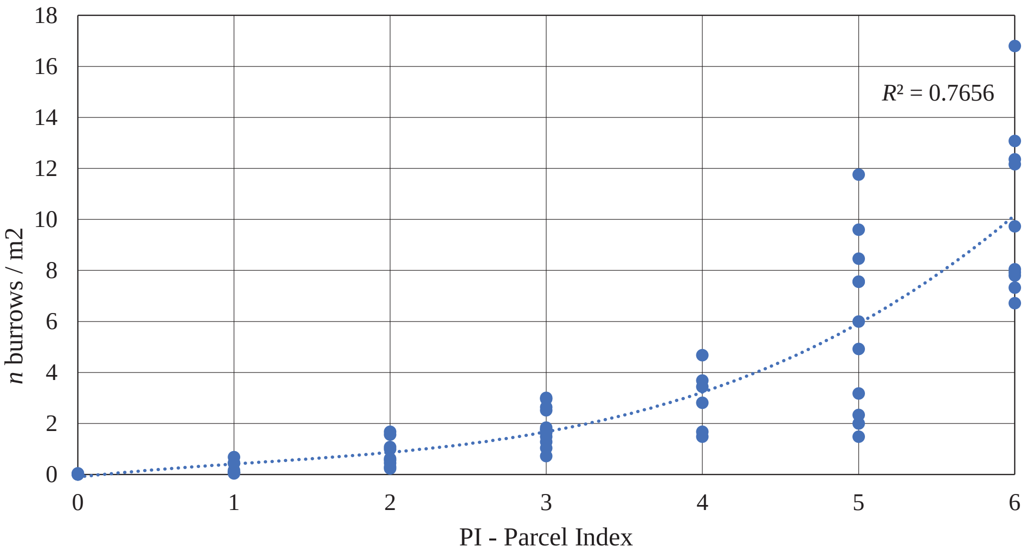

Figure 4. Mean burrow density per parcel as function of Parcel Index, measured on 61 parcels in Friesland in the period November 2019 – February 2020.

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 ViewScape model (provided by Wageningen UR; Meeuwsen & 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 (Meeuwsen & Jochem 2013). For drainage we used the digital map of

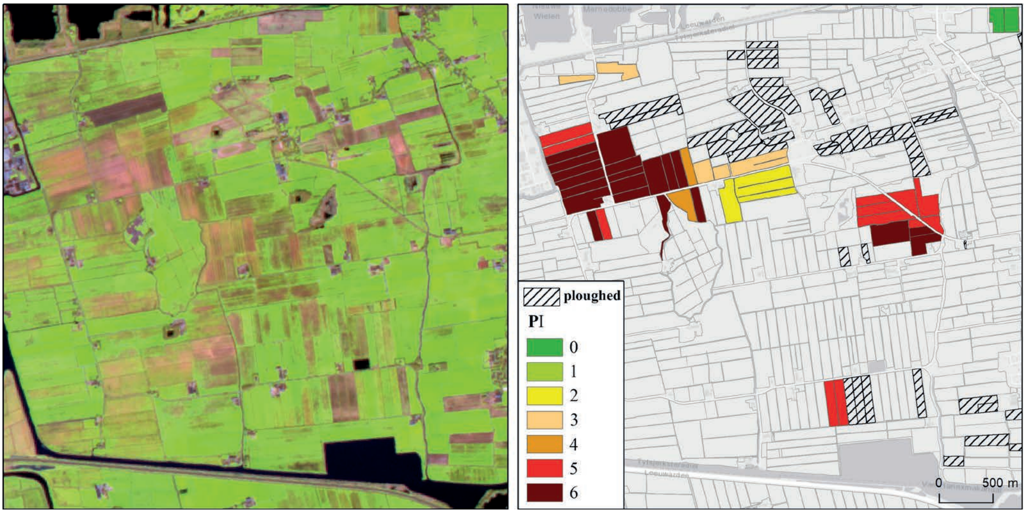

Figure 5. Part of a polder in Friesland with parcels with a high vole abundance. Left Sentinel-2 false colour image of 12 December 2019 and right the corresponding PI score of monitored parcels (fieldwork December 2019). PI not assessed in remainder of parcels.

Teunissen et al. (2012). Estimated drainage is defined as the difference in cm between surface level (AHN1 – elevation map – www.ahn.nl) 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 ~1 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),

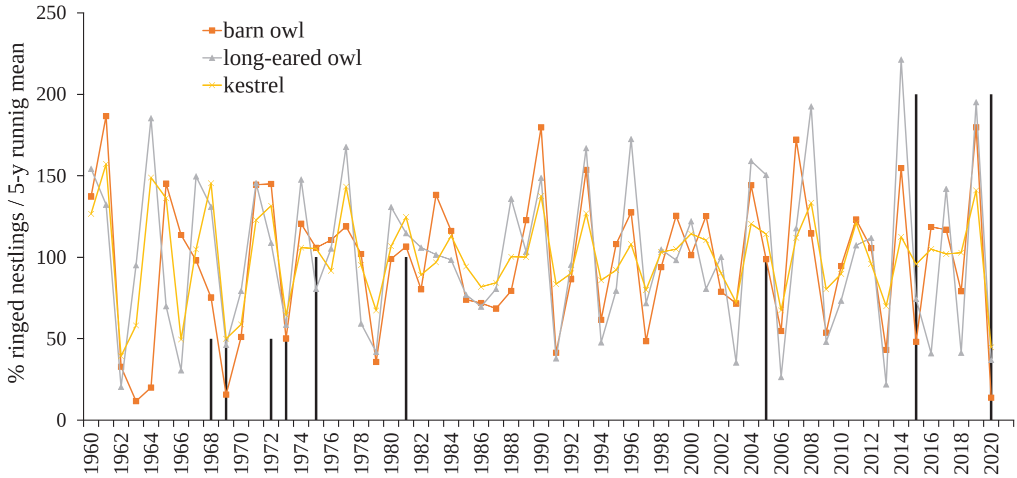

Figure 6. Annual variation in the number of ringed nestlings of long-eared owl, barn owl and kestrel in the Netherlands in the period 1960-2020. Data are expressed as the fraction of the five-year running mean, to reduce long-term trends. Source: Bird migration station, NIOO Heteren. Vertical lines represent 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 (figure 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^2, 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:	*n* 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

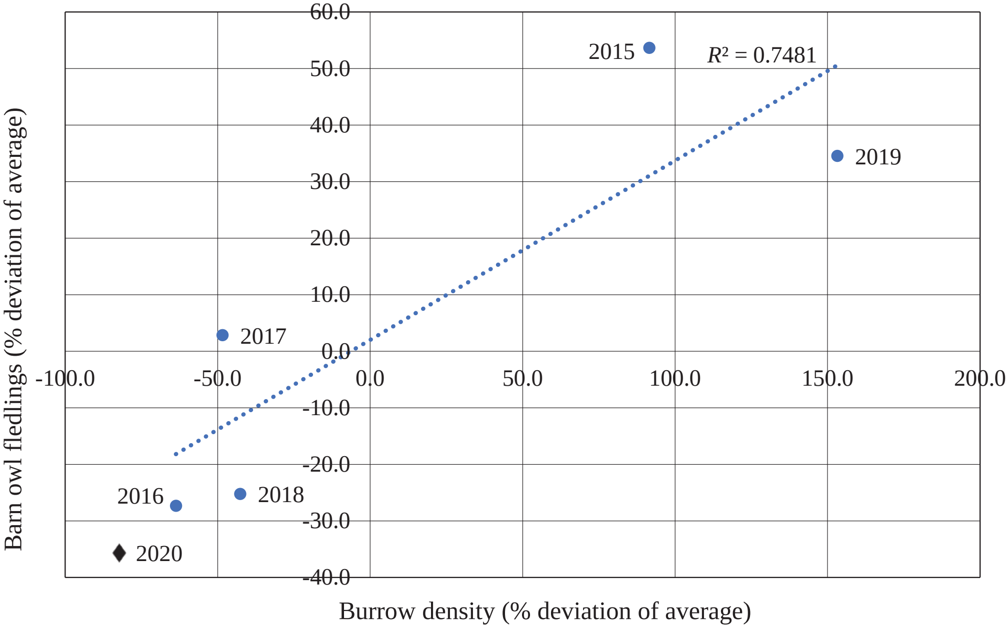

Figure 7. Number of fledglings of barn owl in Friesland as a function of vole abundance, as measured by burrow densities. The number of fledglings is expressed as the percentage annual anomaly of the average over the period 2015-2019. For 2020 this number was estimated based on incomplete data due to 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 Scharenburg 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^2 on average on peat and clay soils, while on sandy soils the density was significantly lower (0.4 burrows/m^2; 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

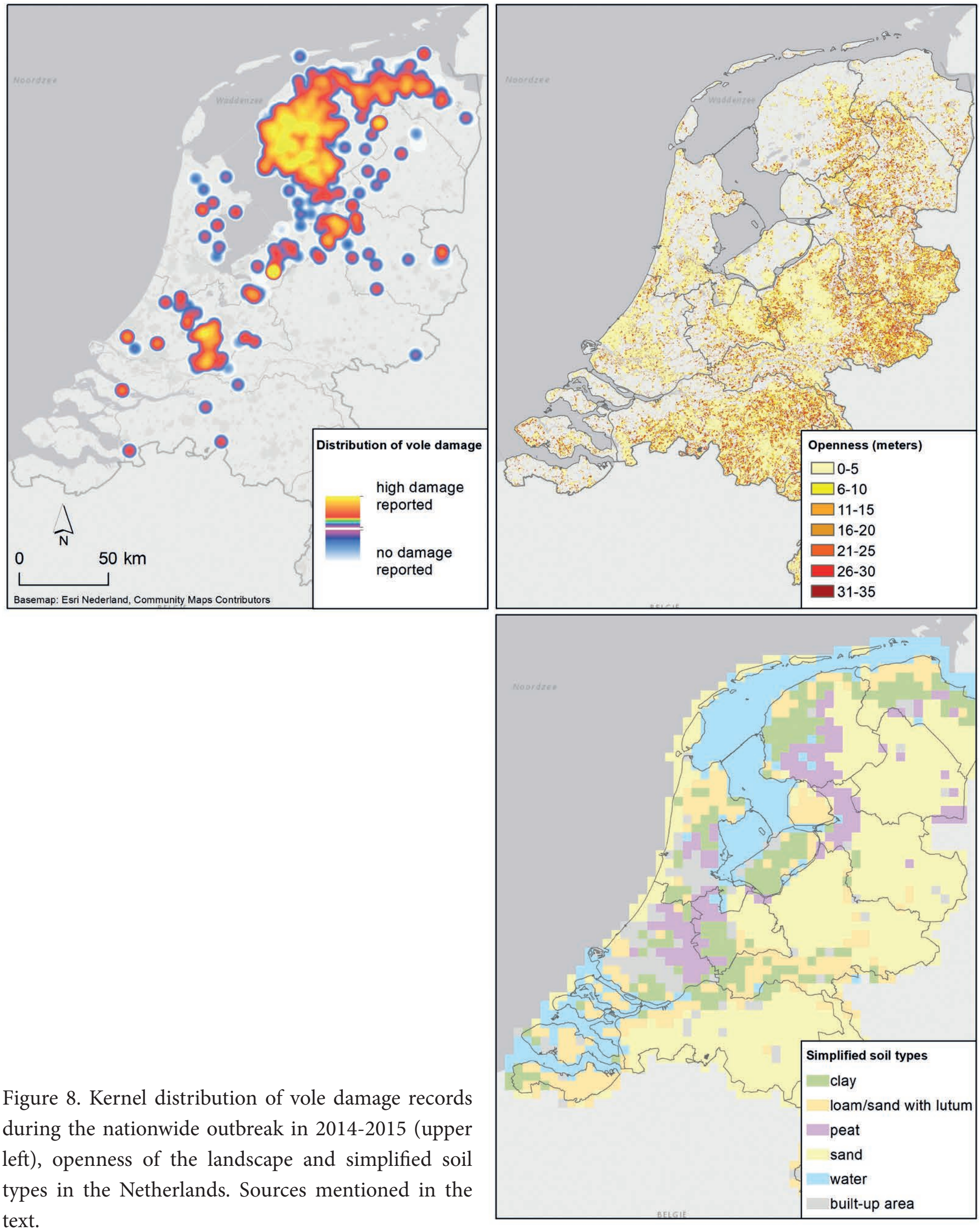

Figure 8. Kernel distribution of vole damage records during the nationwide outbreak in 2014-2015 (upper left), openness of the landscape and simplified soil types in the Netherlands. Sources mentioned in the text.

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 ***		

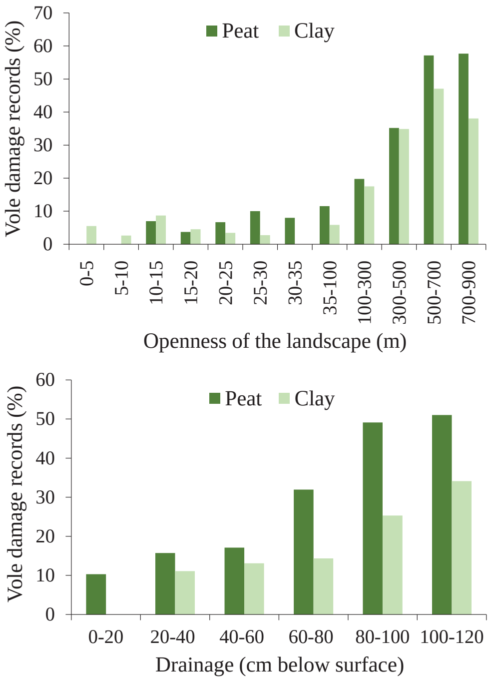

Figure 9. Percentage distribution of vole damage records by farmers for openness of the landscape and drainage on peat and clay soils in the Netherlands. The percentage of hexagons with damage records is given per class (for each class 'damage' and 'no damage' = 100%).

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-

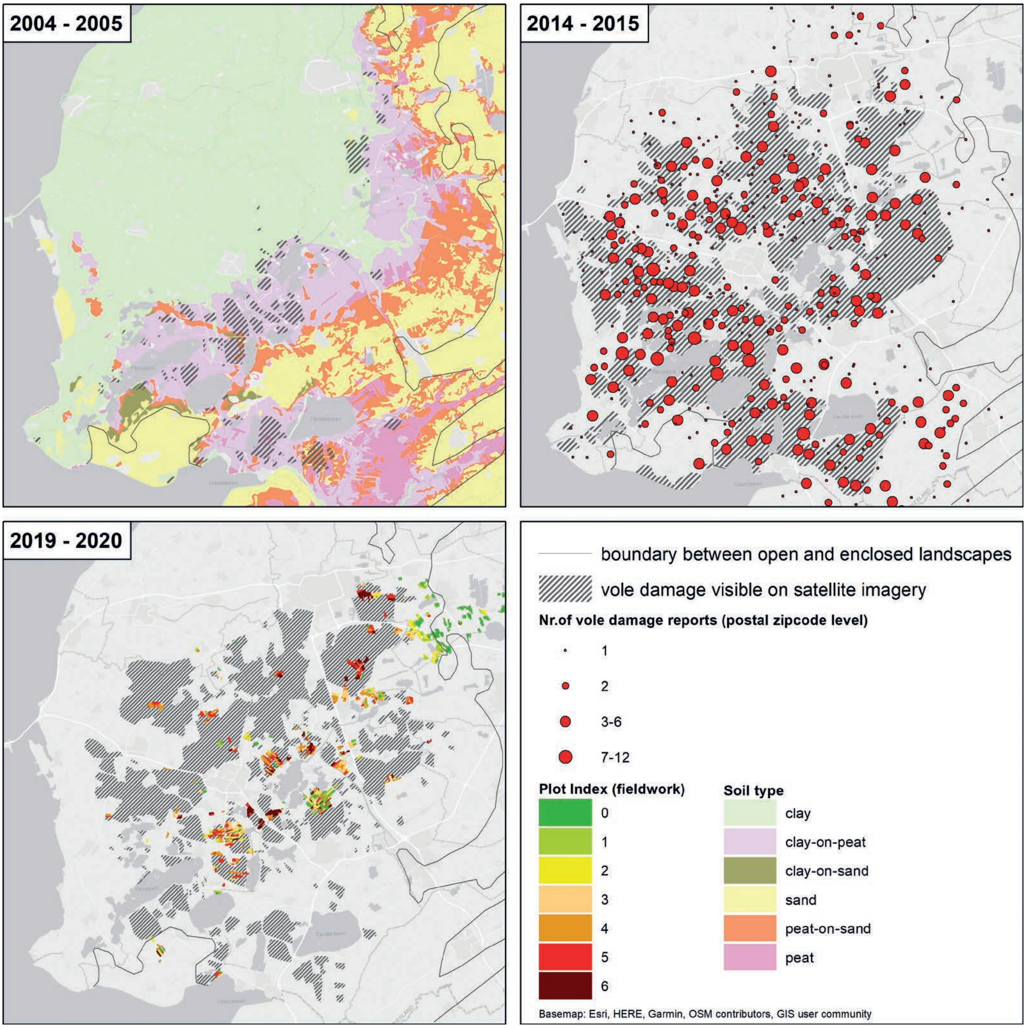

Figure 10. Maximal extent of visible vole damage (bare soil, low NDVI) on satellite images in 2004-2005, 2014-2015 and 2019-2020. For 2014-2015 we also show the distribution of damage reports of farmers (on the level of postal addresses, size of dot varies with number of reports), and for 2019-2020 in 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-

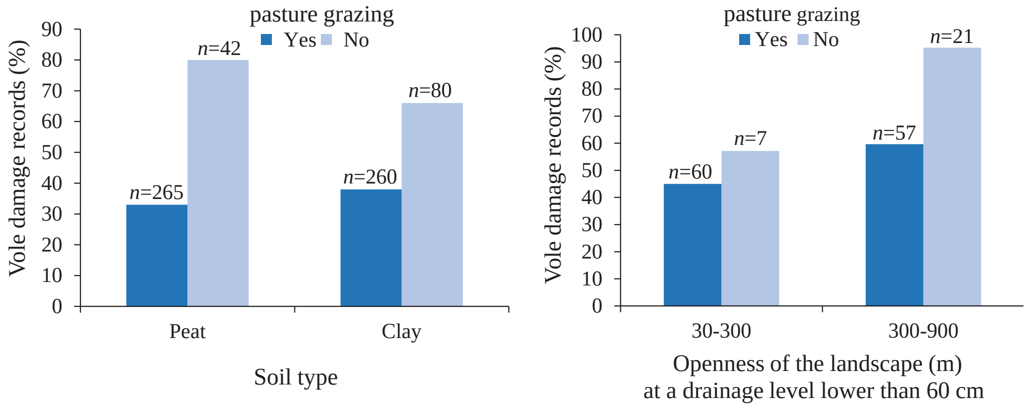

Figure 11. Percentage distribution of vole damage records by farmers for grazing on dairy farms, resp. presented for open and enclosed landscapes and on peat and clay soils in the Netherlands. The percentage of hexagons with damage records is given per class (for each class 'damage' and 'no damage' = 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 drainage of <60 cm. This is consistent with current knowledge (Wijnhoven et al. 2013, de Jonge & Dienske 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 19e century (archives regional media; 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 Koufurderige (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 intensive 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 dehydration (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.

Acknowledgements: This paper is written as a synthesis of our work on common voles from 2015-2020, especially in the province of Friesland. The basis for this work was carried out in 2015, made possible by funding from and cooperation with various organisations and their researchers, as well as the enthusiastic efforts of numerous field workers (for acknowledgements see Wymenga et al. 2016). For the fieldwork and reporting in the following years, special thanks go to Japke van Assen, Yde van der Heide, Hedwig de Jong, Ruth Koffeman, Inge Kok, Mark Koopmans, Margriet van der Zwam-Krijn and Teun Smink. We would especially like to thank all farmers and other landowners who kindly gave us permission to enter their fields. For the analysis in this paper we received data on fledglings of barn owls from Johan de Jong (Kerkuilenwerkgroep Nederland), of ringed birds from the NIOO-KNAW, and background digital data on openness of the landscape and grazing from Wageningen University & Research and CLM Onderzoek en Advies BV 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 Köning 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.

Received: 3 May 2021
Accepted: 31 August 2021