THE RISE AND DISAPPEARANCE
OF
CONTINENTAL VOLE PLAGUE ZONES IN
THE NETHERLANDS

A. VAN WIJNGAARDEN
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I. INTRODUCTION, METHOD

The investigation into the causes of Continental vole (*Microtus arvalis* PALL.) plagues in the Betuwe showed that they were associated with very specific types of country, viz. what are known as back-swamp clay areas (van Wijngaarden, 1953, 1955a).

These areas are characterised by the presence of large tracts of very sparsely used pastures; the soil consists of very heavy clay and the drainage leaves a good deal to be desired. On the intermediate river ridge soils where the villages are located, orchards grow, and over which most of the roads run, voles never occur in plague density.

Hence it is highly probable that there are environmental factors that make it possible for a vole plague to occur in these well-defined areas, and that this is not the case elsewhere.

It might be possible to influence these environmental factors by specific methods of agriculture or other preventive measures, thereby abolishing the vole plagues that have existed here for centuries.

In order to conduct a more detailed study of these factors a list was made of all vole plague zones in the Netherlands so far as these were known. As many data as possible were assembled on the occurrence of the voles, the delimitation of the territory, the vegetation, form of cultivation, type of soil, drainage, etc.

In this investigation by „vole plague zone” is meant a territory in which the vole population periodically becomes so dense as to cause serious damage in pastures and hayfields.

Of course there are many places where voles also cause damage to orchards, vegetable gardens, and the like. In these cases, however, when the said crops do not directly border on a plague zone the population density is usually very low. No further notice is taken of such cases in this paper.

This investigation had its inception in an enquiry conducted in 1950 by the Plant Protection Service among its regional officers and the Government horticultural and agricultural extension officers and their assistants, as a result of the serious plague that occurred in 1949.

Use was also made of much data in the Annual Agricultural Reports (Staat van de Landbouw, etc. 1806–1856) and in the municipal records (a list of the records consulted will be found in van Wijngaarden, 1957a).
II. LITERATURE

The phenomenon of vole plagues being confined to certain types of country has long been known.

ALTUM (1867, in HEROLD, 1954) was struck by the fact that in Germany vole plagues only occurred where there were large adjacent areas of suitable habitats. Vole plagues never occurred in types of country intersected by hedgerows and wind-belts. This fact is confirmed by various writers referred to in HEROLD (1954).

They all explain this phenomenon by assuming that many more vole predators would live in hedgerow country than in open country, but we were unable to confirm this from the investigation carried out in the Betuwe. On the contrary, in this case the greatest number of raptorial birds were found to be concentrated in the vole plague zones. A similar impression was obtained of the predatory mammals, although no statistics are available concerning the population density of these animals (VAN WIJNGAARDEN, 1957 b).

HEROLD (1949) conducted an investigation into the vole fauna in the hedgerows in various districts of Germany. No voles were encountered therein, although great numbers of them existed in the treeless areas in the neighbourhood. His conclusion was that in addition to the predators it was chiefly micro-climatic causes that made the hedgerows impossible as a habitat for the Continental vole. LEIB and OLSCHOWY (1955) share the same view and describe the Continental vole as a „steppe animal”.

That hedgerows and the like are an unsuitable habitat for voles agrees with experiences in the Betuwe where during plague years the voles temporarily penetrated the willow plantations, for example, but completely disappeared from them again after the plague was over (VAN WIJNGAARDEN, 1953, 1955 a).

FRANK (1953 a) also indicated that in north-western Germany plague zones only occur in the alluvial „Marsch” areas. The other German plague zones are likewise very characteristic treeless, cultivated steppes. As causes of this phenomenon he (FRANK, 1954) quotes the fact that the surplus population may take up residence in a typical plague zone close to its birthplace, that there is no need for it to wander extensively in search of a suitable habitat, and the great losses which this would entail are thereby avoided. Moreover, he again refers to the supposed great dearth of predators in the plague zones and the absence of intraspecific competition.

The results of the investigation have already been provisionally published (VAN WIJNGAARDEN, 1955 b, 1956 a) and a part of the results were also published by FRANK (1956) after a visit to the Netherlands, together with the results of his investigation in the Oldenburg vole plague zones.
III. AREAS IN THE NETHERLANDS IN WHICH CONTINENTAL VOLE PLAGUES HAVE BEEN A REGULAR OCCURRENCE SINCE 1945

Listing the areas in the Netherlands in which vole plagues occur gave the following results (see Fig. 1).

From the province of Groningen voles are known to have been found in the pasture area on the boundary of the municipalities of Leek, Marum, Oldekerk and Groote-gast, although not in large numbers. Adjacent to the zone lying along the Hunze there is another plague centre north of the Zuidlaardermeer, i.e. the Kropswolde and Westerbroek pastures and the Onner polder.

By far the most extensive vole plague zone in the Netherlands is in Friesland, although there are never extremely severe outbreaks in this province. This area comprises the entire district round the lakes, the so-called Lage Midden, and has a large offshoot from the south of the Ee to the Lauwerszee. Impoldering of storage channel areas has led to a considerable shrinkage of the plague zone during recent years, especially in Smallingerland. Vole plagues also occur in the polders on the island of Ameland.

There are no extensive plague zones in Drenthe. It is only in the extreme south-west that the low-lying parts of the municipalities of Nijeveen and Meppel adjoin the large plague zone in the top part of Overijssel. In 1949 considerable numbers of voles were reported from the pastureland strips along the various small rivulets ("diepjes"), e.g., the Peize pastures along the Peizerdiep, along the Gouw rivulet, and the Eelde pastures along the new Eelderdiepje. Mention was also made of the pastures along the Eener- and Oostervoortsdiepje and along the Hunze. At this period complaints concerning voles were also received from the Roderwolde and Lautingerwolde polders.

In Overijssel the vole plague zone in the north-west adjoins the zone in the province of Friesland. In the municipality of Oldemark very extensive grassland complexes are found in the Linde valley which until recently were used as communal pasture. Serious plagues were a regular occurrence in this district. Voles were found in the autumn of 1955 in coarse pastures along the Linde.

A very serious vole plague centre is also encountered in Kuinre, viz. the Kuinder polder. The tract between Blankenham and Blokzijl is also considerably infested both outside and inside the dyke. No voles were found here when I visited the district in the autumn of 1955. They were, however, present on the unexcavated strips of peat near Wetering and Nederland which are used as hayfields. A comparable situation is found in the entire district around Giethoorn and Wanneperveen. Here, too, vole centres are found on the unexcavated strips of peat and these cause outbreaks in the surrounding pastures, although not of a serious kind. The peat district bounded by the Meppel canal, Zwartewater, the Lichtmis canal and the Lichtmis-Zwolle motor road is also subject to vole plagues. They were most severe along the Meppel canal and at the back of the long, narrow plots that formerly began near Staphorst and Rouveen (in the direction of Hasselt). There is a very serious plague zone (municipal pastures of Genemuiden, Van Vleuten polder) on the other side of the Zwartewater, west of Genemuiden. The adjoining Kampereiland is subject to plagues, but these are never of such a serious kind.
The Mastenbroek polder is another traditional plague zone, particularly the northern part which again contains municipal pastures. Another very serious plague zone is encountered west and south of Kampen (Dronthen and Kamperveen polders). In the direction of the Veluwe (Zalkerbroek) the plague becomes less severe. There are a number of back swamps south of Zwolle (Windesheimer polder and Lierderbroek) where voles occur in the pastures during plague years, but they cause practically no damage. This is also the case here and there in the Yssel foreland (Olst). A curious plague centre (on low moor peat) is to be found near Vriezenveen. Here, too, we again find very long, narrow plots (de Boer, 1956). The North-East Polder has experienced a number of serious vole plagues.

In Guelderland a very serious plague zone is encountered in the Oosterwolde polder in the extreme north of the province. It adjoins the plague zone near Kampen. The Hattemerbroek polder and the Wapenvelder broekland more or less adjoin this whole area, although here the plagues are much less severe (Mesu, 1956). Towards the west a very narrow offshoot of the plague zone is to be found in the strip of pastureland along the Veluwemeer between Elburg and Harderwijk (municipal pastures). Still further west, where this pasture zone becomes rather wider again, voles are again found in the Putten and Nijkerk polder and the Arkmheen polder (Mörzer Bruïns, 1954). This zone again adjoins the Eem polder zone. Large numbers of voles already exist on the dyke sections of the new South-East Flevoland polder, particularly between Harderwijk and Lelystad and between Roggebotsluis and Elburg. Voles also occur in the Binnenveld between Veenendaal and Wageningen, although not in large numbers. Serious plague zones are again encountered between the big rivers in the so-called back-swamp areas. These back swamps rapidly increase in area towards the west and the vole plague becomes more serious in proportion. During the plague years we do not find many voles in the back swamps near Groesbeek (Duivense broek), Herwen and Aerdt, south of Elden, north-west of Elst, near Valburg and near Kesteren-Ochten. More serious are the plagues in the Ommerense Veld, the Maurikse Veld, the Lage Veld near Culemborg and Beesd and in the large back swamp between Gorkum and Waarderbos. Big outbreaks also occur in the Ooy polder near Nijmegen, in the Land of Maas and Waal, and in the Bommelerwaard. During serious plague years large numbers of voles are also encountered here and there in the forelands of the Rhine, IJssel, Maas and Waal.

An extensive area of serious vole plagues is to be found in the Eem polder in the north of the province of Utrecht. Voles also occur in a small back swamp area behind Jutphaas. They are also sporadically reported in the peat district (Kockengen, Vinkeveen). They also occasionally occur in the forelands of the Rhine, in analogy to what we observed in other provinces. Slight vole plagues also occur in Utrecht between the foot of the Grebbeberg and Veenendaal, adjoining the Guelderland section of the Binnenveld.

In North Holland a serious plague zone is constituted by a small offshoot of the Eem polder complex near Huizen and Blaricum. Voles were also found very sporadically in the so-called Buitenveld near Assendelft, near Jisp, and in the Eilanden polder between the Beemster and the Schermer. Vole plagues occur in the Zeevang polder, particularly in fields which are only accessible by water, as well as on the island of Marken.

In South Holland voles were only sporadically found (1949) in pastureland. They occasionally occur, for example, in the area between Maassluis and Schipluiden along
the Bonenvliet and near the Bommeer, where there is even a patch of blue moor-grass land to be found. Reports were also received from Pijnacker, Nootdorp, Rijswijk, Warmond and Nieuwkoop. We find a more serious vole plague zone between Vianen and Gorcum, adjoining the Guelderland back-swamp area between Beesd and Culemborg.

In Zealand voles occurred in large numbers in 1949 in the pastures of various marshland areas. On Tholen they were found near St. Maartensdijk, on South Beveland in the Ierseke Moer, the Poel near Kruiningen, the district between 's Heer Arendskerke and 's Heer Abtskerke, and in the back swamps on the island of Walcheren near Aagtekerke, Meliskerke, Grijpskerke, Domburg and Zoutelande. Numerous voles were found in 1955 in the newly reclaimed Sloe polder and in the Schouwen polder.

One of the worst plague zones in the Netherlands is in the province of North Brabant in the Maas polders between the Maas and the 's-Hertogenbosch–Ravenstein railway line. It continues along the forelands of the Maas deep into Limburg, although the plagues are not so serious here. A separate territory lies west of 's-Hertogenbosch between Engelen and Vlijmen. A few other zones where the plagues are not so severe are found in the west of Brabant, viz. along the Mark in the Haagse, Hoevense and Ettense Beemden complex, and along the Donge in a number of polders between 's-Gravenmoer and Oosterhout. The back-swamp area in the centre of the Heusden and Altena district is likewise subject to vole plagues, as is also the Nieuwe Zwaluwse polder.

There are no real vole plague zones in Limburg. In extreme peak-years they do occur in the forelands of the Maas near Afferden and from Buggenum to Borgharen. A few voles are also occasionally found in meadows in the löss region.
IV. THE AUTOECOLOGY OF THE CONTINENTAL VOLE AND THE NORMAL DEVELOPMENT OF A PLAGUE

The mouse-like mammals of the Netherlands have scarcely ever been subjected to an autoecological survey. We know very little about the type of environment that satisfies the needs of the various species. The author’s own investigation (van Wijngaarden, 1953, 55a, 57b) showed that during minimum years voles are found almost exclusively in the coarse grass verges of roads and sides of ditches of plague zones. These constitute the vole’s optimum habitat in the Netherlands, i.e. its stations of survival.

The animals preferably establish the entrances to their runways in slopes, the slightest elevation being sufficient for this purpose. It is not easy for rainwater to penetrate this kind of runway. The coarse herbage found in numerous uncut and ungrazed verges of country roads and small polder-dykes is a second important point: it affords the animals cover and allows much of the rainwater to run off into the ditch without reaching the ground.

During the first year in which a plague develops the voles usually only live in these very favourable habitats. In the second year, when their numbers have considerably increased, patches of coarse grass in pastures and hayfields of a plague zone are also occupied. These patches owe their existence to the plats of cow-dung. If these plats are not spread the pasture dies at this spot and tussock-forming species of grass (Holcus lanatus, Deschampsia caespitosa) and thistles are able to establish themselves. These plants form dense tussocks or clumps which are systematically avoided by cattle. The intervening pasture is severely defoliated and eventually a miniature parkland is formed. It is these clumps, in fact, that enable voles to exist on grazing land as well (Frank, 1952; van Wijngaarden, 1956b).

During plague years voles also inhabit neglected pastures in their entirety, hayfields, willow plantations, and sometimes even orchards and arable land, but they entirely disappear again from all the latter habitats as soon as the plague is over. The vole has a narrow ecological range, but in the plague zones mass multiplication periodically forces it to make do with inferior, marginal habitats.

But throughout the country coarse grass verges and sides of ditches, and even neglected fields of grass are found where no plagues are actually encountered; here a few voles can only be captured with the greatest difficulty, and the population density remains very low, even when a vole plague is in progress elsewhere. This is shown, for example, from the population censuses we took at Hemmen in the Betuwe (van Wijngaarden, 1957b).

Hence the presence of suitable habitats in the plague zones does explain the presence of the voles, but not the periodic, mass occurrence of this species. Consequently there must be one or more other contributory factors in the plague zones.
V. THE ECOLOGICAL DETAILS OF THE PLAGUE ZONES

What exactly are the further ecological factors the specific plague centres have in common?

The type of soil can have no effect. Plagues occur on fen peat (Friesland, Zeevang polder), low moor peat (Vriezenveen), heavy clay (Betuwe) and sand (Veluwe border).

Frank (1954) also mentions widely different types of soil in the case of Germany, varying from dune sand on the Frisian Islands to pure low moor peat in the Emsland excavations.

Frank noticed as well that all plague zones are large, extensive plains without human habitation and practically bare of trees. This automatically calls to mind microclimatic factors, particularly as the vole is often described in the literature as a typical steppe animal (cf., e.g. Herold, 1949; Stein, 1955). But the largest Dutch “steppe”, i.e. the pastoral belt of Holland and Utrecht, is at the moment free from vole plagues.

Hence the only common feature of present-day vole plague zones is that they are all large, extensive plains of neglected or very sparsely used pastures and hayfields. In all cases they are difficult of access by road and poorly drained. The farms to which these fields are attached are often very far off (up to 10 miles distant), or the fields in question are only accessible by water. Consequently intensive use, the grazing of dairy cattle, manuring, trenching, etc. are very difficult. The pastures are often only used for fattening, grazing young cattle, or as hayfield.

Up till recently the areas concerned were often used as communal pastures and their management suffered accordingly (Drenthe pasturelands, the Markegronden near Oldemark, the municipal pastures of Genemuiden, the town pastures near Elburg and Harderwijk, the Gooise Meent, etc.).

The origin of this dispersed type of agriculture is easy to explain. Most vole zones were either unfit for human habitation in the past as a result of periodic floods or a high ground-water level, or a wrong method of settlement was adopted.

Examples of the first category are the Lage Midden of Friesland, the Mastenbroek polder, the Kampereiland, the Oosterwolde polder, the North Veluwe border, the back swamps in the river-clay area, etc.

Examples of the second group are to be found near Staphorst, Rouveen and Vriezenveen (de Boer, 1956). Here the plots occasionally have dimensions of \( 7 \times 4000 \) metres. Hence the fields furthest back are in this case very difficult to reach and become neglected.
VI. THE GRASSLAND VEGETATION OF THE PLAGUE ZONES

A good many additional ecological details may be inferred from the results of the recently published rough survey of the grassland vegetation of the Netherlands (De Boer, 1956). The writer has divided the vegetation of Dutch grasslands into a number of vegetation-survey-units. In certain areas groups of these units occur in specific ratios. These groups constitute the reference units of the vegetation cartogram compiled by the author. He gives a brief explanation and numerous details concerning the management, manuring, type of agriculture (pastures, meadows, leys), water level, etc. of each reference unit. If we now examine in what reference units vole plagues occur we find that it is only in units of which a high percentage of the grasslands present is poorly managed, where manuring is inadequate, where they are sparsely used or

<table>
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<th>Grassland vegetation-survey unit (according to De Boer, 1956)</th>
<th>Location of this vegetation survey unit</th>
<th>Degree of vole infestation in this area</th>
<th>% of moderate to insufficient grasslands</th>
<th>% of poor grasslands</th>
<th>% of humid grasslands</th>
<th>% of dry grasslands</th>
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In the remaining vegetation-survey units in which high percentages of good and very good grasslands are found vole plagues never occur.
cultivated as hayfields or hay pasture, or in which there is a high percentage of pastures with a subsoil of impermeable peat-layers (WIJNBERGEN, 1949). The vegetation cartogram does not show any single sizeable area in which poor grasslands are to be found but no vole plagues; the areas designated by the map as well-managed grasslands are equally free of vole plagues. A summary of the vegetation-survey units in which vole plagues occur is given in Table 1, and this again shows the close correlation that exists between the type of agriculture, the vegetation, and the occurrence of vole plagues.
VII. THE SIGNIFICANCE OF THE EXTENT OF THE PLAGUE ZONES

In addition to the presence of a sufficient number of stations of survival and coarse pastures there is, in my opinion, a third condition which a vole plague zone must satisfy. It was found that there has to be a certain area of such neglected plots of grassland, adjacent or substantially adjacent, for a plague to be able to break out. The minimum is about 1,000 hectares.

In „normal“ types of country, i.e. those of a variegated character the said condition is unfulfilled, consequently no plagues will occur and there will be no further appreciable rise in the population density during the second and third years of a cycle.

This is because voles are a marked territory-holding species that will fanatically defend its quarters against trespassers. Owing to this behaviour the surplus population is driven to seek a suitable habitat elsewhere, but settlement or attempts at settlement in inferior habitats in the neighbourhood will result in a vast mortality. This was found, for example, by Errington (1943) in the case of muskrats (Ondatra zibethica L.).

The result will be that in the scattered, favourable habitats the population will remain at a normal, i.e. very low level, and the surplus leaves and soon perishes in unsuitable habitats in the neighbourhood.

A countryside made up of diverse elements, i.e. pasture, roadside strips, arable land, orchards, tree-lined embankments, copses, etc., and where the area of habitats suitable for voles is a mere fraction of the total, will thus have an enormous buffering power against fluctuations in vole populations.

The situation is quite different in the vole plague zones. Here there are large adjacent areas of fairly suitable vole habitats; there is an almost complete absence of unsuitable habitats.

In minimum years i.e. those with a very low population density, the voles only live in the most favourable habitats of the zone such as the roadside strips, sides of ditches, etc.

The population increases in density and in the second year the inferior, marginal habitats are occupied, viz. coarse pastures, hayfields, etc.

At a certain point in the development of the cycle practically the entire area will be occupied by voles. As a result the surplus population in the centre will no longer be able to emigrate, being hemmed in on all sides by a countless number of defended territories. The animals are thus forced to establish themselves in situ, and there is a rapid increase in the population density, thus creating the conditions for a vole plague, which, in fact, are even abnormal for voles. Frank (1953) had indicated the possibility of the said phenomenon occurring, and we ourselves discovered the following additional facts which support this theory:

1. The larger a vole plague zone, the earlier the plague commences and the more severe it becomes (Van Wijngaarden, 1953).
2. In the centre of a plague zone the population density is fairly constant over wide areas and decreases rapidly on the margin. Obviously the degree to which the pastures are neglected also declines in this direction (the distance to the farms being less), but this is usually a very gradual process.
3. Mass multiplication also occurs when a vole population is sufficiently isolated in
some other way. An example of this was observed during the summer of 1956 on a small plot of land of three to four hectares near Diemen. On one side it was bounded by a factory wall and on the others by wide canals. Most of the land was covered with a very coarse, entirely neglected vegetation, the remainder being occupied by allotments. It was found that an abnormally high vole population existed in this very limited area, but that there were scarcely any voles in the neighbourhood.

4. The new polder-dyke from Harderwijk to Lelystad constituted an ideal vole habitat during the autumn of 1956. Nevertheless the animals had not occupied the entire dyke. On the landward side where the outbreak had occurred the population had become so dense as to assume plague proportions, but further out there was a rapid decline in the population density. We set 20 traps on this dyke at intervals of three kilometres and counted the numbers of holes per 20 square metres. The results are summarized in Table 2.

It can be seen from this table that the population density falls rapidly after the 6th kilometre post; the voles in the very thickly populated area do not migrate to the vacant section of the dyke. This must be caused by the animals defending their territories in the intermediate part that is less densely populated.

Table 2. The vole population on the Harderwijk-Lelystad dyke; autumn 1956

<table>
<thead>
<tr>
<th>KM</th>
<th>3</th>
<th>6</th>
<th>9</th>
<th>12</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>24</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of voles caught in 20 traps</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Number of holes per 20 sq.m.</td>
<td>75</td>
<td>6</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

1 In judging the numbers of holes found in the various trial sections it should be remembered that all this part of the dyke is inhabited by a thin population of long-tailed field-mouse (Apodemus sylvaticus L.).
VIII. THE CONTINENTAL VOLE PLAGUE ZONES IN THE NETHERLANDS PRIOR TO 1945

In chapter III we gave a survey of the areas where voles have occurred regularly in the pastures since the last war. But there is a great deal of further information to be found in the literature (RITZEMA Bos, 1879; HUSSON, 1956), in the Annual Agricultural Reports (1806–1956) and municipal records (1852–ca. 1910) which indicate that in the past the situation was considerably different from what it is to-day.

According to HUSSON (1956) serious plagues of mice formerly occurred in South Limburg (1410, 1686, 1742). The records are silent on this subject after 1800, so that we must assume that by this date the district was free from the phenomenon.

The period from 1800–1850

Vole plagues were reported in this period in the following areas:

Groningen: Oldambt, Westerwolde, the Peat Colonies.
Friesland: western and south-western parts.
Drenthe: occasional references, Zuiderveld being mentioned once: the reference is probably to vole plagues in the newly-developed peat colonies; FRANK (1953) found the same thing in the recent peat diggings in the Weser-Emms area.

Overijssel: north-western part.
Guelderland: the district south of the Zuider Zee, the Betuwe.
Utrecht: only the name of the province is mentioned.
North Holland: the district west of the Haarlemmermeer, the Sloten, Osdorp, Middelveld and Aker polders, Weesperkarspel, Waterland, near Schermerhorn, Groot-Schermer, Limmen, and the district between Hoorn and Enkhuizen.

South Holland: the Westland (Maasland), Delfland, Schieland, Rijnland, Krimpenerwaard, Rozenburg, IJsselmonde, Voorne-Putten, Hoekse Waard and the Beyerlanden.
Zealand: Tholen.
North Brabant: Land of Heusden and Altena, the Langstraat, Steenbergen, around Breda.
Limburg: nothing was reported from this province.

The period from 1850 to 1900

The following data were assembled on the vole plagues in this period:

Groningen: severe plagues are reported from the Oldambt, Westerwolde, Westerkwartier (slight), Bellingwolde, the Dollard polders and the Peat Colonies.
Friesland: plagues only appear to occur in the north-eastern part and in the centre of the province.
Drenthe: a number of voles are reported here and there in the various municipalities, probably in the peat excavation areas.
Overijssel: the districts around Staphorst, Rouveen and Kampen are mentioned, but plagues were of infrequent occurrence.
Guelderland: severe plagues were regularly experienced in all back-swamp clay
areas between the big rivers and in the Guelderland valley near Renswoude.

Utrecht: the district along the Kromme Rijn, the Vecht district, the Eem polder, and the entire western part of the province were mentioned. Voles were reported near Winkel in the north, in the pasture area in the centre of the province, the Zeevang polder, Waterland, and the area east and west of the Zaan.

North Holland: in this period a vast vole plague zone is met with in the district north of the Rhine, the entire centre of the province, Delfland, the Krimpenerwaard, the Alblasserwaard, Putten and Beyerland. The outbreaks were sometimes very severe in this area.

South Holland: plagues were recorded in Schouwen, Tholen and South Beveland. Plague zones were found in the Land of Heusden and Altena and in the north-western part of the province.

Zealand: no data was found for this province.

The period from 1900 to 1945

The following plague zones were found for this period:

Groningen: there is an almost complete absence of information on the occurrence of vole plagues (1933: Meeden, Blijham, Oldekerk).

Friesland: the situation remains substantially unchanged in this province. Severe plagues occurred in the drained pasture lands in particular (e.g. the Deelen: drained in 1920, plague in 1921).

Drenthe: we have no information from this province.

Overijssel: a number of plagues are reported from the Kampereiland and the Mastenbroek polder. In the North-East polder a number of plagues immediately after the reclamation.

Guelderland: a number of plagues were reported from the Oosterwolde polder. There is little change in the situation in the area between the big rivers.

Utrecht: only a few plagues are mentioned in this province, among others near Abcoude and Veenendaal and in the south-western part of the province.

North Holland: there are hardly any further genuine vole plagues. We only discovered a few reports of voles. A number of plagues swept the Wieringermeer after the reclamation, and plagues also occurred on the Enclosing Dam.

South Holland: here also only a few plagues are reported from the centre of the mainland.

North Brabant: the plagues are decreasing in intensity in the Land of Heusden and Altena and in the north-west of the province. Serious vole plagues are beginning to manifest themselves in the Maas polders now the Beers spillway has been closed.

Limburg: we have not found any reports of vole plagues in Limburg during this period.
IX. THE ECOLOGICAL FACTORS GOVERNING THE DISAPPEARANCE OR RISE OF VOLE PLAGUE ZONES

Chapters III and VII show that four groups of vole plague zones may be distinguished.

We will now deal with these groups in turn and discuss the conditions that led to the rise or disappearance of the vole plague zones in these areas. They are shown diagrammatically in Van Wijngaarden (1957a).

a. Districts in which vole plagues are a „traditional“ feature.

A good example of this group is the Betuwe; the Frisian plague zone also belongs here in part.

It is obvious that the first plagues in the Netherlands did not arise until after the first dykings. We were unable, however, to trace these very first plagues in the records anterior to 1800.

Vole plagues are found in the above-mentioned areas during the whole of the period investigated by us, i.e. from 1806 to 1956 inclusive. Our impression is that it was particularly after 1850 that the vole plagues greatly increased in severity in both districts. In our view this is to be associated with the improved pumping methods that were gradually introduced (steam pumps). But of late years the plagues have become much less severe. This is no doubt owing to the increasing intensity with which pastures are being farmed, spraying with herbicides, the introduction of rotational grazing, and improved drainage. (In the Betuwe, for example, the Linge Regulation has been in force since 1954).

b. Districts in which plagues did not formerly occur but do so at present

North-east Overyssel, the Eem polder and the Maas polders near Oss may be included in this group. The first two areas were very frequently subject to floods. The records of Kampen repeatedly state that the driven-up waters of the Zuyder Zee flooded the whole district. It was only when these floods ceased to occur for a number of years in succession that a vole plague was able to develop. Hence after the completion of the Enclosing Dam in 1932 vole plagues began to be a regular occurrence.

The Maas polders constitute a similar case. Here the plagues did not properly set in until after the Beerse Maas was closed in 1940.

c. Districts in which vole plagues occurred formerly, but no longer occur at present.

A comparison of Figs. 1 and 2 shows that large areas of the Netherlands are to be included in this category, viz. the whole of north and north-east Groningen, a part of North Holland, the whole pasture area of South Holland and Utrecht, the South Holland islands and the Krimpenerwaard.

In Groningen one of the causes of the disappearance of vole plagues is no doubt the decrease in the surface area of grassland (cf. Figs. 1 and 2). The same is true of the South Holland islands. There has, however, been practically no reduction in the grassland acreage on the mainland of South Holland, in North Holland, and in Utrecht.

We can see from De Boer's grassland map (1956) that the latter areas are at pre-
sent occupied by good to very good pastures, indicating very good management and very intensive use. Over practically the whole area pastures alternate with hayfields, ration grazing is employed, bent-grass and thistles are cut out, all non-graminae are suppressed with hormonal sprays, and trenches and sides of ditches are kept in good order. These preventive measures result in a completely uniform, close sward and make large areas of pasture land completely unsuitable as a vole habitat.

There is no doubt that entirely different conditions formerly prevailed in these areas, as is shown, for example, by the rapid decrease in the acreage of blue moor-grass land in recent decades. Thus since the introduction of intensive grassland farming the vole plagues have come to an end.

d. Districts in which no vole plagues occurred formerly, but did so later, and are now disappearing again.

This group includes the Zuyder Zee polders (Wieringermeer and the North-east Polder), the Enclosing Dam, the South-east Flevoland dykes, the Schouwen polder subsequent to the large flood 1st February 1953, and the Quarles polder in the South Sloe.

After their reclamation all these polders underwent a period of lying fallow, followed by very sparse cultivation (the Wieringermeer even underwent two such periods).

All these areas have had to contend with a number of very severe vole plagues which disappeared, however, after ten years or more when the entire polder had been brought under cultivation and very intensive farming was begun in all parts. The plagues disappeared on the dykes as well, apparently because the adjacent land in course of reclamation now has a sufficient buffering effect. On the Enclosing Dam the vole population is kept at a low level by intensive sheep-grazing.

In some of this new polders the plague developed along different lines than in the "traditional" plague zones. Frequently the primary habitats were formed by the heaps of excavated earth lying alongside ditches and canals and overgrown with weeds. From these, leys, lucerne fields, winter cereals and the like became infected, in other words this is the same interplay of forces as elsewhere exists between roadside verges and coarse pastures.

To sum up, we may conclude, therefore, that in the Netherlands vole plagues occur in all regions where more land has been enclosed by dykes than can be immediately used on an intensive scale. The periods of dispersed use of the land may be very long, as in the case of the back-swamp areas between the big rivers, or only a few decades (e.g. the Ysselmeer polders) and it is precisely during this period that the vole plagues occur.
X. POSSIBILITIES OF PREVENTING VOLE PLAGUES

We have seen from the above that three conditions must be satisfied for a vole plague to occur, viz.:

a. There must be a sufficient number of coarse, unclipped and fairly untrodden grass verges to serve as stations of survival.

b. There must be neglected pastures with numerous coarse tussocks of grass, and hayfields, in order to absorb the surplus population during the second year of the cycle.

c. There must be a certain area of adjacent pastures and hayfields in order to make possible a very high population density.

In order to put a stop to the plagues one of these three factors can now be eliminated. The removal of all coarse vegetation from dykes and road verges is a very strenuous task that must be carried out at regular intervals. Moreover it causes disfigurement of entire countrysides when the wild flora are destroyed on a large scale.

The last two factors provide many more possible starting-points. It was found in 1955 that a great improvement could be effected with comparatively little trouble.

The Back-Swamp Areas Committee at Tiel has recently done a great deal of intensive work in order to improve the back-swamp areas. One method adopted in their attempts to bring about improvements is the granting of subsidies to farmers who are willing to carry out normal maintenance work on their land, viz. spreading manure, fertilizing, cleaning trenches and sides of ditches, haymaking in good time, rotational and if possible ration grazing, etc.

The fields treated in this way stand out even at a distance on account of their fresh green colour amid the yellow plain of dead grasses and thistles that determines the aspect of the "normal" back-swamp grasslands. The fields treated according to the methods of the so-called grassland improvement scheme now constitute an excellent subject of study. During the summer of 1955 (a maximum year in the Betuwe) the vole population was counted in these and adjoining fields (statistics in VAN WIJNGAARDEN, 1956b). It was found that even when there was a dense population living in the adjacent pastures the voles did not succeed in establishing themselves in the properly maintained pastures.

If a certain percentage of the pastures were now to be improved in a specific back-swamp clay area there is no doubt that a vole plague would be out of the question. The necessary preventive measures can be introduced without a great deal of difficulty, being entirely in line with developments in modern grassland management. Moreover the output of the fields is frequently more than doubled as a result of taking these measures.

The results obtained in the areas described in chapter IX under c also show that this method will be attended with success. Serious vole plagues were formerly experienced in these areas, but at present they no longer occur since the management of the pasture has been intensified.

Instead of trying to effect a gradual reduction in the intensity of the vole plagues by propagating and introducing modern methods, the problem can, of course, also be definitely solved at once, viz. by means of reallocation.
This step will be all the more effective if farms are transferred to the reallocation area and at the same time sufficient space is reserved for wind-belts and the planting of trees and shrubs by farmhouses and roads.

It should be emphasized that there is no need to disturb copses, or any blue moor-grass reserves that may still exist. Such areas will even help to increase the buffering power of the new countryside formed since they are, in fact, unsuitable vole habitats.

In many vole plague zones the following reallocations have either already been applied for, are being carried out, or have recently been completed:

Vriezenveen, Staphorst, the Dronthen polder, Oosterwolde, the Putten and Nijkerk polder, the Zeevang polder, the back-swamp clay areas near Ingen and Maurik, Tielerwaard, Maas and Waal, the Maas polders, Duivense broek, etc.

It may be concluded from the above that the problem of vole plagues in the Netherlands will be solved when the methods indicated earlier are applied. Thus in a few decades the possibility of extreme fluctuations in the population density of the Continental vole in the Netherlands, a phenomenon of such great interest to biologists, will have ceased to exist.
SUMMARY

1. As is known from the literature, and as was also clearly shown from our investigation of the Continental vole population of the Betuwe, vole plagues only occur in certain well-defined zones.

2. A list was made of the zones where such plagues occur in the Netherlands and their ecological details were assembled.

3. Voles have a narrow ecological range. In minimum years they only live in optimum habitats, viz. in roadside verges, sides of ditches, and the like, where there is an incline, coarse vegetation and cover. As the plague develops further marginal habitats such as hayfields and coarse pastures are occupied, and subsequently even willow plantations, orchards and arable land. It is not only necessary for suitable habitats to be present, but also essential that they should adjoin each other over a given area. The animals on the border of such a type of country defend their territories, thus preventing the surplus population from emigrating from the centre. These animals are consequently obliged to settle down on the spot, and this causes a high population density: the vole plague.

In a countryside with a mixed vegetation the surplus population leaves suitable habitats for less suitable ones where it perishes. The total population remains at a normal, i.e. very low level.

4. The geographical distribution of the vole plague zones was formerly quite different from what it is to-day, as was shown by an examination of the records.

5. In certain areas the plagues have disappeared as a result of more intensive methods of agriculture. In others which have recently been reclaimed or protected against periodic floods, but are still sparsely used, fresh plague zones have arisen.

6. It follows from what has been said above that by intensifying the management of pasture in a given zone large areas can be made inhabitable for voles; this makes it impossible for a plague to occur. In the summer of 1955 it was found that this could be carried out already on a small scale.

Reallotment definitely puts an end to the plagues as it is always attended by a more intensive cultivation of the farmlands.

7. Nature reserves, wind-belts, copses, willow plantations and other areas of this type should be spared as much as possible for the purpose of vole control as they enhance the buffering power of the countryside in question.
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Vole plague zones in the Netherlands about 1950
(The acreage under grass is copied from the grassland map by 'T HART AND DE VRIES, 1949.)

Considerable numbers of voles periodically present in the pastures

Serious vole plagues

Voles periodically present at scattered places in the pastures

Permanent grassland

This map belongs to Verslagen van Landbouwkundige Onderzoekingen NF 6135. "The rise and disappearance of continental vole plague zones in the Netherlands" by Dr. A. VAN WUNGAARDEN
Vole plague zones in the Netherlands about 1850
(The acreage under grass is copied from the
1:50000 Topographical Map surveyed in 1837-1859)

- Considerable numbers of voles periodically present in the pastures
- Serious vole plagues
- Voles periodically present at scattered places in the pastures
- Permanent grassland

This map belongs to "Verzameling van Landbouwenkundige Documenten" Nr 8215
"The rise and disappearance of continental vole plague zones in the Netherlands" by Dr. A. VAN WUNGAARDEN