Rabbits in the coastal sand dunes : weighed and counted = Konijnen in de kustduinen : geteld en gewogen

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GENERAL INTRODUCTION

1. THE MOTIVE OF THIS STUDY

Rabbits (Oryctolagus cuniculus (L.)) have lived in the coastal sand dunes of The Netherlands for centuries and have a large influence on the extent and structure of the dune vegetation. Man has always tried to control their numbers either to promote or to eradicate them (1.2). The arrival of myxomatosis in 1953 dramatically reduced rabbit numbers. The disease slowly became less virulent and some rabbits have developed resistance (1.3), with the effect that rabbit numbers have subsequently increased. This prompted the question: to what level will rabbit density increase and what will stop or slow down the increase? In ecological terms: will rabbit density grow until the carrying capacity of the dune habitat is reached, or will the density be held at a level below this limit by other processes?

The answer to this question is of interest to both nature manager and scientist. Carrying capacity is defined as the population size which the resources of the environment can just maintain (Begon, Harper & Townsend, 1986: 209). It is not a fixed value, but varies under the influence of climate, the actions of the rabbits themselves and through the actions of other herbivores and man. Important elements of carrying capacity are cover and food.

It is possible that in the natural situation predators keep the rabbit density below carrying capacity. In the past, 'duinmeiers' and their British counterparts the warreners, evidently believed that they could promote rabbit numbers by controlling predators, especially the fox. At the same time, however, 'duinmeiers' and warreners provided supplementary food to rabbits in winter (de Rijk, 1988; Sheail, 1971). They felt apparently that winter food supplies were the limiting factor, which, in ecological terms, means that the carrying capacity had been reached.

In 1976, when the University of Leiden started a research project on rabbits in the dunes, they invited Dr. H.V. Thompson, the then director of the Worplesdon Laboratories of the Pest Infestation Control Laboratory of the Ministry of Agriculture, Fisheries and Food, Great Britain, to visit the Meijendel dune system. He remarked that in this poor environment he would have expected food shortage to occur.

The main questions of this study

This study focuses on the factors which determine the size of the breeding population of rabbits, at the end of the winter. The main questions were: What determines the size of the breeding population? Do rabbit numbers increase to carrying capacity set by the food, or are they kept below this limit by e.g. intrinsic responses to density or by predation?

The numbers in summer are only partly set by the size of the breeding population. The number of young produced, and their survival in spring and summer, may depend on factors other than those which determine the size of the breeding population. Kluyver (1971), studying Great tits (Parus m.major), found that variations in reproductive success appeared to have no influence on the annual fluctuations in the size of the breeding population. This seems to be the case for rabbits also (Tittensor,1981). Factors that influence rabbit numbers in summer (myxomatosis, parasites, drying out of the vegetation, predators) are not included in this study.

When trying to answer the main questions, it proved necessary to develop a better understanding of what can be regarded as food of good quality for a rabbit, and of some aspects of rabbits' feeding behaviour and activity. These aspects are treated in separate chapters.

Field study

The study was mainly carried out in the 'Noord-Hollands Duinreservaat' (NHD), which is under the management of the Provincial Water Company of North-Holland (PWN), see fig.1 and 2.

Contents

The following section considers the dunes as a rabbit habitat, including the historical relationships between dunes, man and rabbit (1.2). Particular attention is paid to the region around Castricum, where the field study was conducted. The characteristics and spread of myxomatosis are discussed in section 1.3. From about 1950, more precise records on the numbers of rabbits caught or shot were kept by the management organisations of the dune reserves. These data have been used to establish recent developments in rabbit number (1.4). However, despite this large source of information, it turned out that the method of data collection was too crude to provide evidence on the factors which determine rabbit numbers.

A study on the seasonal changes in the condition of rabbits (ch.2) shows that the animals use their fat reserves during winter and that a severe winter can lead to mortality due to starvation. The problems of finding sufficient food are accentuated because the digestibility of the food available in wintertime decreases to a level below that needed for maintenance (ch.4). An analysis of diet quality is not straightforward: the quality of a particular meal should not be confused with that of the diet. These methodological aspects are first covered in chapter 3.

Chapter 5 presents the results of direct observations on the activity and numbers of a small population. Variation in the level of above ground activity during the year needs to be taken into account when assessing population size by sight counts, and when evaluating the effect of rabbit control. The conditions in winter that play a role in timing the start of the breeding season are analysed in chapter 6. Chapter 7 discusses the population dynamics of several populations of rabbits in the dunes to determine whether rabbit density in winter increase till the populations reach the limit set by the available food. In ch.7 it is also discussed whether a late start to the breeding season affects the total production of the population in that year. The second part of this chapter gives a general discussion on the population dynamics of rabbits in the coastal dunes.

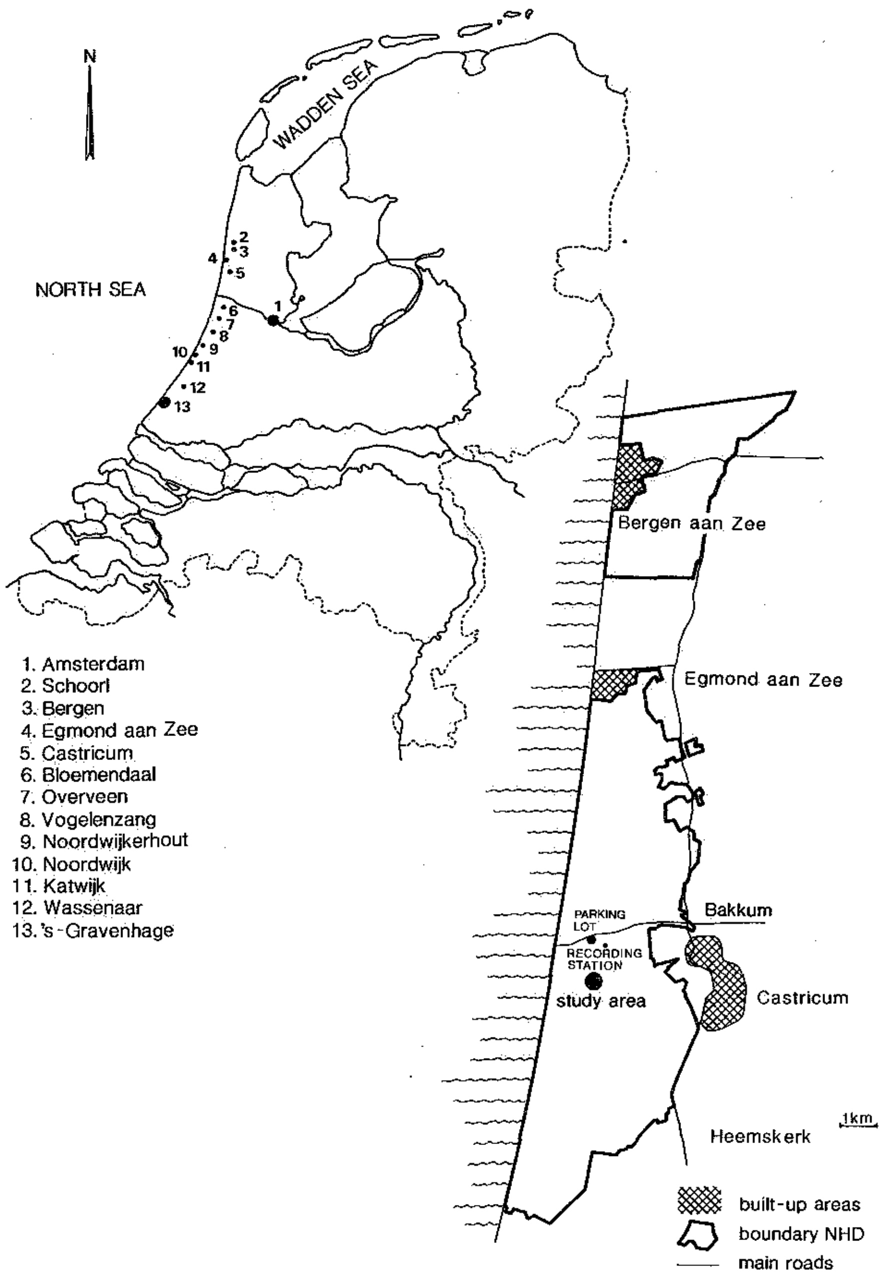


Fig 1 left: Map of The Netherlands with the towns and villages named in ch.1.2.
right: Outline of the Noord-Hollands Duinreservaat with location of the experimental study area, the parking lot where stops were found, and the the weather recording station of the PWN.

2.DUNES AS A RABBIT HABITAT

As said in 1.1, carrying capacity is influenced by the actions of the rabbits themselves, through modification of their habitat by burrowing and grazing. Rabbit grazing affects the food supply by changing the extent, structure and composition of the vegetation. The interactions of the rabbit with its habitat, in this case the coastal dunes is ilustrated below by data on burrows in the NHD, from the common history of the coastal dunes, man and rabbit, and by abstracts from studies on the influence of rabbits on dune vegetation cover.

BURROWS

In a study of land-use by rabbits in the Coto Doñana and the Camargue, Soriguer & Rogers (1981) describe the importance of a short distance between the warren and feeding grounds. According to Niethammer (1938) the maximum distance travelled for foraging is 600 m.

In the sandy soil of the coastal dunes rabbits can dig burrows easily, especially now most of the dunes are stabilized. Blowing dunes are not habitable by rabbits. Ranwell (1972) stated that "On larger dune systems with extensive areas of highly mobile dunes to seaward, rabbit density and grazing intensity was much reduced in these seaward parts". Pluis (1986) also found fewer burrow entrances in unstable sand.

In dunes, rabbits burrow almost everywhere, but they prefer slopes above valleys. In Meijendel Wanders (unpubl.) found no preference for particular vegetation types, and the placing of burrows under prickly shrubs and in the open dunes resembled the Chilean rather than the Spanish situation (Jaksic & Soriguer, 1981). This might indicate low predation pressure in the dunes. By venturing out into the open, rabbits obtain access to more food, but they make themselves more vulnerable to predation. The influences of predation and food on rabbit numbers in an experimental area in the open dunes is treated in ch.7.

During the years of the study there were many empty burrows. In September 1978 52% of the burrow entrances were estimated to be unused, with an average of 5.0 burrow entrances per rabbit. That Cooke & Hunt (1987) found burrow destruction a useful rabbit control measure indicates the importance of burrows to survival and growth of rabbit populations. At the height of the projects of dune stabilization, PWN and other dune managers used to combine the digging out of rabbits with burrow destruction. It is a pity that the effects were not systematically recorded.

Stops

Females prefer to drop their litters in extensions of existing burrows, but subordinate does make a seperate blind burrow: a so called breeding stop (Mykytowycz, 1959). In the main dunes hardly any stop was made. They were found in habitats where burrows were unavailable, i.e. in blowing sand dunes (Tinbergen,1970), on parking lots, on road verges and on playgrounds where the PWN prevented the establishment of permanent burrows (Mulder & Wallage-Drees, 1979). Foxes detected and dug out nests in burrows (Wood, 1980; own observation), but in the main dunes this was not common. Foxes living around the parking lots, however, learned how to open up stops to obtain the young. After 1978 stops were scarce (ch.7). To my mind this is another indication of the good quality of stabilized coastal dunes as a rabbit habitat.

HISTORY OF THE RABBIT IN THE COASTAL SAND DUNES

a. From introduction to 1795.

The land of origin

In the last glacial period rabbits were pushed back to a limited distribution comprising Spain and perhaps the south of France. The subsequent redistribution over Europe has been studied by van der Feen (1963), Rentenaar (1978) and Zeuner (1963). The following summarizes their findings.

The first description of the numbers of rabbits in Spain comes from the Phoenicians who founded their colonies there about 1100 B.C.. They describe a small mammal that looked like a hyrax (Procavia capensis, Pallas 1766). Hispania is probably the latin version of the Phoenician name for 'land of the hyrax'. The similarity of rabbits and hyraxes, and the fact that both species live in crevices and burrows, has also led to mistakes in early Bible translations. For example, the following lines are taken from the "King James Version' (1853 edition, which uses the old-english word coney for rabbit): Leviticus 11 (5): "And the coney, because he cheweth the cud, but divideth not the hoof; he is unclean unto you."
Proverbs 30 (26): "The conies are but a feeble folk, yet make their houses in the rocks."

The Romans also mention the presence of rabbits in Spain. They valued their meat, imported them to Italy and probably bred them there. The presence of rabbits in the south of France is first mentioned during that same period. It is not known whether these were descendents from imported animals from Spain, or whether they lived there before the Romans arrived. The composition of blood immunoglobulins indicates that the rabbits in the Dutch coastal dunes are more closely related to the ones in France than to those in Spain (W. van der Loo unpubl.).

How and when did the rabbit arrive in Holland?

Rabbits are mentioned rarely in early-mediaeval writings in France. They were exchanged as presents between noblemen and cloisters, for breeding and to release for the hunt. They are mentioned more frequently around 1400 and later. Rentenaar (1978) dates their first appearance in Holland to sometime after 1250; although de Rijk (1988) considers it probable that they arrived earlier. Rabbits were present on all the sandy soils in Holland by about 1400.
The subsequent history of rabbits in the coastal dunes is described by Boerboom (1958), Jelles (1968), Rentenaar (1978) and de Rijk (1988). A summary of their findings illustrates the common history of dunes and rabbits.

The hunting of rabbits for sport by the nobility was never popular. Rabbits were caught primarily for profit. As Merula (1605) wrote, shooting rabbits provides more profit than pleasure. They were caught for their meat and fur, the fur being used to make coats. Parts of the dunes were leased as 'warandes' to so called 'duinmeiers'. This was comparable to the British way of establishing warrens, but the Dutch warandes were generally not walled or fenced in. At the same time, they were also used for hunting other game by the nobility. The duinmeiers tried to increase rabbit numbers by digging artificial burrows, providing hay in (cold) winters, controlling foxes, cats and polecats and leaving the does. They also had a responsibility for the upkeep of the dunes and in some cases were obliged to plant marram grass. Blowing sand is a threat to agriculture along the landward side of the dunes. The main method used to stabilize the dune sand has been to plant marram grass (Ammophila arenaria). The actions of the duinmeiers had one measurable result: around 1600 the fox was extinct in the province of Holland (Swaen, 1948).

Around 1500, rabbits were locally abundant and farmers adjacent to the inner edge of the dunes (Overveen, Bloemendaal and Bergen) requested the authorities to control them. The farmers themselves did not have the right to catch game on their lands. They even had to prevent their dogs and cats from catching rabbits, by cutting off part of a leg or the auricles respectively. Of course, poaching in the dunes was forbidden. The punishments for illegal hunting also became more severe with time. The only thing farmers could do to keep rabbits off their lands was to make and maintain a fence or deep ditch between their lands and the dunes. The maintenance of the fence was regulated in many places and the farmers had to pay for it. During the 17th century there is an increase in the number of references to fences. In some places, the duinmeiers had to take care that rabbit holes near the fence were destroyed. The rise in rent paid by duinmeiers in the 17th century, the fences and the increased severity of punishment for poaching indicate a growing economic importance for rabbits, and perhaps increases in numbers.

An early change in the relations between man and rabbits can be seen in 1661 when some farmers leased the right to parts of the dunes, and 'depopulated' them of rabbits (at Bergen, Tetteroode (Overveen), Vogelenzang, Noordwijk, Noordwijkerhout, Katwijk and Wassenaar). In 1756 the catching of rabbits on a farmer's own land was allowed in Bergen. However, the practice of leasing dunes for rabbit-keeping remained. De Rijk (1988) mentions rent payments from duinmeiers up to 1784. In 1747 the rabbit-fence near Castricum became buried under the blowing sand and had to be repaired at the expense of the farmers. At the same time, the inner dunes were planted with marram grass by subsidy from the government. Villagers had been obliged to plant marram grass in the inner dunes from before 1478 at least, but this duty was often taken over by the local authorities.

In the 16th and 17th century the authorities limited the rights of villagers to use the dunes for cattle grazing and other semi-agricultural purposes.

An interesting sign of the changing times was the permission by the 'Staten van Holland' in 1763 for the people whose lands bordered the southern dunes to catch rabbits and destroy their burrows in the inner dunes, and to keep the rabbits they caught. Also, controls on the state of the socalled 'depopulated' dunes were installed (Verster van Wulverhorst, 1840).

Commercial catching of rabbits was also practiced on sandy soils in the interior parts of the country, although it was nowhere as profitable as in the dunes. According to de Rijk (1988) this was due to the healthy seaside air, the temperate climate and the relief. Commercial trapping continued for the longest period (until 1940) on the islands in the Wadden Sea, where it comprised one of the few ways of making a living (Wallage 1982).

b. 1795–1985

In the turbulent period beginning in 1795, when the French army invaded Holland and many soldiers were encamped along the coast, rabbits were freely poached by soldiers and citizens alike. In some places they were almost eradicated (Boerboom, 1958). In 1814 the game laws were restored, though the group of people allowed to hunt increased. In these laws the rabbits were considered noxious. Commercial rabbit keeping was made impossible by the chaotic situation in 1795 and was not resumed thereafter. Kops (1798) showed in his stock-taking report on the state of the dunes that commercial rabbit catching no longer flourished at the end of the 18th century. There were places where the dunes could be considered 'depopulated'. New ideas about the economical use of the dunes were already in progress. The second part of Kops' report (1799) was a design for the fertilization of the dunes by farming and afforestation. This was considered too optimistic by some contemporary commentators, with some justification, as the first three farms achieved poor results. Nevertheless the idea caught hold and in the 19th century more farms were established. "Depopulation" was considered a first requisite for successful farming, and was also considered to be better for the establishment of forests. However, most farms failed before 1880, even before the drying out of the dunes by water catchment. Agriculture in the dunes declined. In the NHD in 1945 there were still 520 ha of arable land, in 1980 only 197 ha.

<u>Afforestation</u>
Afforestation used to be the task of the forester in the service of the nobility. Merula (1605) discusses explicitly the state of dune forests.

The depopulation of rabbits (1661) was followed by successful afforestation only in Bergen. The first concerted efforts to plant trees came at the end of the 18th century, after the reports by Kops. Later, in 1863, Dr. W.C.H. Staring, a firm promoter of afforestation, started experiments under commission from the government in the dunes from Schoorl to Schouwen. The establishment of forest was more successful than agriculture and continued until the 20th century, often as a way to procure employment, especially in autumn and winter. In most places it stopped by about 1950. Forestry has greatly changed the appearance of the dunes to the present time.

Water catchment

In the second part of the 19th century, the fresh groundwater in the sand dunes began to be exploited as a supply of drinking water for the cities and towns in the hinterland. The first company to do this was 'Gemeente Waterleidingen van Amsterdam' in 1853. For water extraction, parts of the dunes were bought or otherwise brought under the management of local governments, e.g. Meijendel by 'Duinwaterleiding van 's-Gravenhage' (DWL) in 1925 and the Noord-Hollands Duinreservaat (NHD) by the province of Noord-Holland in 1928. According to the decisions of the provincial council, the latter area was bought to fulfill four purposes:

a) to act as a natural sea-wall
b) to provide a water-catchment area
c) to form a nature monument
d) to provide an object for the procuring of employment.

The 'Provinciaal Waterleidingbedrijf Noord-Holland' (PWN), who became charged with the management of the NHD in 1934, has since worked at the integral stabilization of the dunes.

Around that time recreation in the dunes also increased and this necessitated a more active management policy.

After a while the water supply had to be supplemented by river water brought into the dunes. In the Noord-Hollands Duinreservaat this was implemented in 1957.

Rabbit control

The exploitation of the dunes has changed, and so has man's outlook on nature management. During the active agricultural exploitation of the 19th century, attemps were made to eradicate rabbits from the dunes. Outside the arable area, however, hunting for sport was the only active control measure against rabbits and this had little effect on the population density. Jelles (1968) illustrated increases in rabbit numbers after farmers left an area: in the part of the NHD called Bakkum depopulation was almost achieved in 1840, but in 1923/24, 9,400 rabbits were caught (over 600 ha).
The provincial authorities, who formed the management of the NHD, formulated rules to allow their own personnel to kill rabbits, in addition to hunting. In 1920 they employed the first rabbit catchers, who caught rabbits with ferrets and nets and by digging them out. According to Jelles (1968), rabbit numbers decreased, at least until 1941. The dunes were closed to citizens after this date when wartime bunkers

were erected and mines laid. Consequently rabbit numbers increased.

In the annual report of the PWN of 1940 a discussion was started on whether it would not be better to keep the control of rabbits in their own hands instead of leasing out hunting rights, because hunters were mostly interested in maintaining reasonable densities of game, densities which were fatal to young woods. In 1946, the PWN organised the hunting itself. Hunting was licensed for one day at a time. Game wardens were employed to care for the game and accom- pany the hunters. They also did the rabbit control. In 1955 and 1956, only 3% of the rabbit shoot was done by hunters (calculated from archives at the PWN). Rabbits were still not valued as 'game', just as in medieval times when the rabbits were leased to the 'duinmeiers'. As well as shooting, other methods of control like ferreting, digging and trapping were used, although the numbers taken by these techniques were not recorded. The game wardens also shot predators to protect songbirds, groundbreeders and game.

The return of the fox

Foxes were eradicated from the coastal dunes by the duinmeiers in the Middle Ages. Quite recently, foxes have returned to the dunes. According to Mulder (1982), the first individuals were seen in 1970 in the dunes near Heemskerk. From there they spread to the north and south, and built up in numbers. The increase levelled off after 1980. The first foxes were probably descendants from pets that were set free. In the dunes that are managed as nature reserves, they are not hunted or otherwise controlled, although heavy poaching occurs. One of the questions of this study is whether foxes have any impact on rabbit numbers (ch.7). Can the fox act as a regulating factor on rabbit populations, preventing them from reaching the densities observed before the onset of myxomatosis?

Nature management

In 1970, the policy of the PWN towards hunting changed. The provincial council decided that hunting was not compatible with nature conservation and abolished day-leases. It is now the task of the game wardens to control rabbits, feral cats, magpies and pheasants in the inner dunes from where they can cause damage to the agricultural lands.
In Meijendel today, shooting is seen solely as a tool for nature management, having regard to obligations by law (DWL, 1983).

From a national perspective the dunes are characterized by a high degree of abiotically determined dynamics. The policy behind the management of dune vegetation has now developed toward 'process management', which pays particular attention to the landscape-forming processes. This can be seen as the next stage after an active management policy aimed at maintaining the present diversity of ecosystems (dutch: patroonbeheer) (Sloet van Oldruitenborgh, 1982), such as sustained

mowing to conserve open vegetation in the inner dunes.
In process management the manager also takes active measures, e.g. initial mowing in order to start natural processes such as rabbit grazing (van der Vegte et al., 1985). To maintain the process they often use large herbivores, e.g. cows on 54 ha in the NHD in 1984. The argument is that large herbivores add dynamics to the system (PWN, 1985a & 1985b). Rabbits can halt succession, but cannot really push back scrub or forest (Oosterveld, 1983). Process management may also require active measures to start sand drifts on a limited scale (van der Meulen & Wanders, 1984).

The management goal of the PWN since 1985 has been: "The maintenance and promotion of the natural processes of soil genesis and development of the vegetation which form the basis of specific biocoenoses.
The management aims at:
- the promotion of the natural development of biocoenoses;
- the maintenance of the diversity of landscapes that has originated partly under human influences;
- the promotion of land use on the bordering land that secures the integrity of the present dunes and serves optimally the function for nature conservation."

INFLUENCE OF RABBIT ON VEGETATION COVER

Jelles (1968) and Rentenaar (1978) suppose that the presence of rabbits was both a result and cause of the paucity of the vegetation cover and vulnerability of the dunes to erosion, because of the simultaneous increase in rabbits and secondary dune formation.
The major relief forms in the dunes date from between 1400 and the 16th century (Jelgersma et al. 1970). Rentenaar (1978) considers there to be a relation between this and the increase of rabbits in the dunes at that time. In the 'Enqueste upt Stuck der Verpondinge' of 1494 and the 'Information idem' of 1514 a deterioration of agriculture and increase of rabbits is mentioned in villages that are today Bloemendaal, Overveen and Bergen. Maps from the period 1575-1680 show no trees in the actual sand dunes. In the description of the state of the dunes by Kops (1798) there seem to be fewer sand drifts than in the time of Merula (1605), but more than at present. Gevers (1826) still mentions daily shaping and disappearing of valleys.

Poor vegetation cover and sand drifts, however, can have several causes, that will be discussed here.

Primary dune formation

Even before the arrival of the rabbit, the dunes were liable to severe drifting. The primary formation of the Younger Dunes started in the 9th or 10th century (Klijn, 1981). The position of the coast line is determined by the sea level, tidal streams, direction of waves, depth and slope of the sea bottom, composition of the substrate, transport of sediment by rivers and even inland agricultural activities that influence the land level.

Activities of man

Zagwijn(1984) considers human interference with the vegetation to have been a contribution to the deterioration of the dunes before 1200. Jelgersma et al. (1970) attribute the extremely large scale erosion near Zandvoort in the 18th century to human activities. People gathered wood and winter feed for their animals, grazed cattle, cut sods for houses and fertilizer, and even cut marram grass (van Dieren, 1934). Red deer also lived in some of the dunes. In 1596 they had reached the unnaturally high density of 1 per 10 ha (Belonje, 1979). The hunting of red deer became less popular and with the decrease in interest the deer disappeared from the dunes (somewhere before 1650). The duinmeier, who actually leased a warande, took better care of the landscape than the people who used their old right to the 'wilderness'. The people living next to the dunes had a duty to plant marram grass, but in the foregoing we have seen that this was not practised sufficiently.

When the commercial exploitation of rabbits on the mainland came to an end around 1800, the 'Hoogheemraadschap Rijnland' and other local authorities forbade cattle grazing. Some private people planted marram grass. Even though all these

measures did not result in a sufficient improvement, it shows that it was realized that not just rabbits caused the deterioration of the dunes.
Grazing by cattle permits rabbits to extend their grazing areas (Edmondson, 1987; Oosterveld, 1983; Williams et al., 1974). The Jackrabbit, an American relative of our rabbit, is most abundant in areas moderately grazed by large grazers (Phillips, 1936).

Even actions meant to control rabbits sometimes had an opposite effect. Westhoff (1967) mentions erosion on the Boschplaat (Terschelling) as a result of the digging done by the shooting parties.

A main study on the formation of the dunes that puts the role of man in the forefront is the dissertation by van Dieren (1934) on the dunes of Terschelling. He showed that the shape of the dunes is the result of the combined operations of climate and vegetation. He came to the conclusion that the dunes had been heavily exploited and, consequently, carried an impoverished vegetation (heather with few other plant species). The number of plant species has increased since the dunes were artificially stabilized around 1870. This increased diversity is not considered beneficial because a number of typical dune plants have become rare or extinct (Visser, 1979). Van Dieren illustra- ted the importance of man by comparing the character of the original dune forms in the western part of the island, where fishing is the main livelihood, with the secondary forma- tions from the eastern part, where farming is most important (Van Dieren, 1932). Treading, burrowing or even atmospheric phenomena may soon start erosion in vulnerable areas.

Blow-out formation

As Watt (1937) put it: "their (rabbits') activities were not essential to the inception of blow-outs nor to their subsequent development, although they may assist both." Interestingly, he observed no correlation between number of rabbit burrows and blow-out formation.

Seventy percent of the area of the NHD is influenced by rabbits (burrowing, shallow scrapes, latrines), but the weight of material dispersed in that way is rather small (Jungerius 1986, 1987).

A study in an area where the manager allowed blow-outs to develop tended to the conclusion that blow-outs developed to a certain size depending on their place in the relief, after which they shrank again (Jungerius et al.,1981). However, to predict whether blow-outs stabilize or expand more research is needed (Noest,1987). When we know more about the circumstances under which the sand becomes 'active', we can take more precise management decisions and do not need to worry about every blow-out. Some managers even feel blow-outs should be encouraged (van der Meulen & Wanders,1984).

Recent studies on erosion in the dunes show that not only wind erosion but also water run-off is very important quantitatively. This occurs in humus rich soils, in circumstances different from those needed for wind erosion. Rabbit activity may increase water erosion because their pellets make the sand water-repellent (Pluis,1987).

vegetation composition

Rabbits do have a large influence on the structure and composition of vegetation, especially where they are abundant and the total production of the vegetation is low. Gillham (1955) studied the influence of rabbits on vegeta- tion on a wind-swept island off Pembrokeshire (Wales). She compared the development in rabbit-proof enclosures with that in rabbit-grazed vegetation and she came to the following conclusion: "The flora of the Pembrokeshire islands is the outcome of 'selective suppression' by wind and grazing, and comparison of grazed and ungrazed areas has shown that the latter is the more important of the modifying factors." Grazing leads to an increase in species number. The rabbits' grazing leads to greater diversity in vegeta- tion structure and plant species, provided that the grazing pressure is not too heavy (Zeevalking & Fresco,1977) and promotes higher diversity of other animal species (Mabelis, 1977). The rabbits' habit of making shallow scrapes also encourages annual plants (Burggraaf-van Nierop & van der Meijden,1984).

The drastic decrease in rabbit numbers after myxomatosis offered a unique opportunity to assess the effects that rabbits had on their environment. The sudden relief from grazing led to abundant flowering of the vegetation and in a few years to a decrease in plant species diversity (Boerboom,1958; Ranwell,1960; White,1961). The colour- rich annuals and rosette species suffered especially. Vegetation structure changed. The area covered by shrubs expanded (van Groenendaal et al., 1982; van Leeuwen & Westhoff, 1960; Salman & van der Meijden, 1985; Watt,1981). Evidently, rabbits had up till then eaten almost every seedling of Crataegus sp. The change in habitat affected other animals (de Bruyn, in press; Koning,1984) and the disappearance of rabbits had direct consequences for predator species (Hewson & Kolb,1973; Mörzer Bruyns,1958).

Interestingly, the change in vegetation that occurred after this decrease may still be keeping rabbit numbers lower than at pre-myxomatosis times. Not only that they are not able to push back the shrub once it has developed, but managers noticed that when the rabbit population recovered shrub expansion was not completely stopped. In many dune reserves they record a succession of the grassland vegetation, which they value negatively ('verruiging').

CONCLUSION

It might be concluded that low-density rabbit populations are not able to make the habitat more suitable for them- selves. The rabbit profited initially from the habitat created by the action of sea and man, and then at high population density maintained this suitable habitat. The size of the rabbit population itself is important for maintaining an optimum vegetation structure. At high density they make the habitat more suitable to themselves, whereas at low density long grass, scrub encroachment and the collapse of burrows make the habitat less suitable.

3.MYXOMATOSIS

History

Myxomatosis arrived in the coastal dunes of The Netherlands in September 1953 (van Koersveld, 1955). The disease probably mainly dispersed naturally from the north of France, where it was introduced deliberately in 1952. Dispersion, however, was frequently assisted by people, who took infected rabbits to other areas for the purpose of rabbit control. The introduction of myxomatosis into the British Isles was similarily deliberate.

Myxomatosis was first observed in 1896 by G.Sanarelli in Montevideo (Uruguay) in domestic rabbits (Oryctolagus cuniculus (L.)). The disease was infectious and highly lethal. Sanarelli described the disease and gave it its name after the mucinous tumours in the skin of the infected animals. The disease occurred sporadically in European rabbits maintained for various purposes in several places in South America. In 1930 there was an outbreak of the disease in California. Aragão discovered around 1940 the cause of the spontaneous outbreaks of myxomatosis in domestic rabbits in South America. Forty percent of wild caught Sylvilagus brasiliensis were easily infected with myxoma virus, whereas the remainder were resistant due to prior infection. So, Sylvilagus appeared to be the reservoir host for myxomatosis.

The disease was introduced into Australia in 1950 in a deliberate attempt to control (introduced) European rabbits. The disease is specific to Lagomorphs, although Lepus species are not very susceptible (Fenner & Ratcliffe, 1965). This made it a very promising agent for pest destruction. The preliminary laboratory experiments, designed to assess the dangers and potential of the disease when employed as a method of biological control, and practically all the early field studies, were conducted or sponsored by Australia's major governmental scientific organization, the Commonwealth Scientific and Industrial Research Organization (C.S.I.R.O.). In the field trials it became clear that myxomatosis was transmitted by biting and sucking insects, by mosquitoes in Australia and by the rabbit flea (Spilopsyllus cuniculi) in Europe. Consequently the disease spread easily from colony to colony, area to area.

In France, myxomatosis was introduced on 14 June 1952 by a private individual, dr. A. Delille, who was impressed by the results reached in Australia. He inoculated two rabbits with virus obtained from Switzerland and released them on his walled estate.

Myxomatosis is now almost co-extensive with the wild rabbit populations over the world with the notable exception of New Zealand.

Epidemiology
Myxomatosis is caused by a virus belonging to the poxvirus group. Transmission is mechanical. Infection may occur by direct contact with the tumours of an infected individual, but transfer of the virus by arthropod vectors is by far the most important mode of transmission. Known vectors include mosquitoes, biting flies, fleas, ticks, mites and lice. The only requirement for transmission appears to be the capacity of the same arthropod individual to bite two rabbits in succession. No research on myxomatosis has been done in The Netherlands, but a description of the development of immunity to the disease is provided by a summary of British research (see below), assuming that the flea is also the main vector in The Netherlands.

The original strain of myxomatosis from South America (strain I) causes mortality of nearly 100%. There is a well-defined sequence of appearance and subsequent multiplication of the virus in different organs. Symptomatology, and viral titres in all sites, reach maximum on the eighth and ninth days, and death usually occurs on the tenth day. Nestlings and malnourished rabbits show negligible symptoms, but they die as quickly as healthy individuals (Houlihan & Derrick, 1945). The cause of death in myxomatosis is obscure. Death can not be attributed to the growth of virus in a vital organ (Fenner & Ratcliffe, 1965).
Rabbits dying of acute myxomatosis (in the laboratory) usually eat well until shortly before death. Animals which survive the acute disease may die through other concurrent infections (infestation with Graphidium strigosum or snuffles due to Pasteurella).

Influences on mortality rate
When more attenuated virus strains became available, it became possible to investigate the factors that influenced mortality. Mortality is not selective with respect to age groups. Marshall (1959) studied the influence of ambient temperatures, and concluded that mortality was higher at lower temperatures. Differences in environmental temperature were probably responsible for the seasonal differences in mortality notes by Mykytowycz (1956).

Seasonal differences in occurrence of myxomatosis
In our temperature climate, mortality from myxomatosis peaks in September. This occurs because of an abundance of fleas in autumn that coincides with peak numbers of non-resistant (juvenile) rabbits in the population. The infection can be maintained for at least 300 days (Knorr, 1983). Fleas stay on the rabbits or remain in the rabbit burrows throughout the winter months (Williams & Parer, 1971).

Immunological response
The response of the rabbit population to infection with myxoma virus is affected by the genetic resistance of the host and the virulence of the virus. Both actively and passively acquired immunity influence the epidemiological pattern of viral infections.

In long-lived animals, active immunity governs the pattern of spread of the disease through the herd. However, the importance of active immunity in wild rabbits is limited because of their short life-span. Even so, recovery from myxomatosis, caused by any one of the myxoma virus strains that have been examined to date, confers almost complete cross-protection against re-infection by any of the other strains (Fenner & Ratcliffe,1965). Passive immunity, i.e. maternal transfer of antibodies to offspring, plays a role. It does not protect the young completely, but may enable them to live through an initial virus-attack, and thus acquire active immunity.

Evolution of the virus and resistance in the rabbit

The virus that was originally released in Australia and France was highly lethal (strain I). Soon after the introduction, and spread of this virulent virus through the populations of wild European rabbits in Australia and Europe, attenuated viral strains started to appear. In both continents there is now a wide spectrum of virus strains which vary greatly in virulence. Several hundred strains obtained from the field in Australia and Europe have been tested and classified into one of five 'grades' of virulence depending upon the mean survival time of inoculated rabbits. Several factors interact to determine which virus strain will be dominant in the rabbit population.

Where the main vector is the rabbit flea, one would expect that this would lead to selection for the most lethal strain. Infective fleas on rabbits which are dying from acute myxomatosis leave more frequently compared to those on rabbits which die only after a prolonged illness or which recover.

Selection for innate resistance also gives an advantage to more virulent strains. Fenner and Ratcliffe (1965) ascertained that variation in host response after inoculation with a small dose of virus from an attenuated strain, was due primarily to differences in innate resistance in the rabbits. These differences were presumably determined by genetic factors. Resistant rabbits have a longer survival time after infection. More virulent strains will affect rabbits even if they possess some genetic resistance (Ross & Sanders, 1984). On the other hand, weaker strains allow the illness to persist for a longer time, with a greater chance for infections to be contagious. The mean percentage of infective fleas is inversely related to the survival time of the host (Mead-Briggs & Vaughan, 1975).

In England, a moderate strain, grade III, is now dominant in the field (Mead-Briggs & Vaughan, 1975; Ross & Tittensor, 1981). This is probably also the case in The Netherlands.

The co-evolution of virus and rabbit might be expected to result in outbreaks of myxomatosis continuing to occur at irregular intervals in wild populations.

Recently, van der Loo et al. (1987) observed a systematic shortage of rabbits with a certain genotypic combination of immunoglobulin (Ig). They calculated that 9% extra mortality was correlated with this particular combination of Ig allotypes, and suggested that this combination was associated with lower resistance to myxomatosis than other combinations.

4. ANALYSIS OF LONG-TERM TRENDS FROM GAME BAGS

THE 'CATCH PER UNIT EFFORT' METHOD

From about 1950, yearly reports are available giving the number of rabbits obtained from three dune reserves, namely: Meijendel, Kennemerduinen and Noord-Hollands Duinreservaat (see fig.2). The policy towards rabbit management differs between these areas, and therefore, they are treated separately below. The data have been used to try to determine long-term trends in rabbit population density. The underlying assumption is that the size of the game bag has a positive relation to population size. This is the 'catch per unit effort' method, i.e. for the same effort (e.g. time spent) the number of animals obtained is related to the population density. Several conditions must apply for this method to be valid (Caughley, 1977), e.g. with relation to the situation involving catching rabbits:

1. Conditions of catching must be standardized (weather, time of the day, visibility of the terrain).
2. Catching efficiency should be standardized (e.g. professional versus amateur hunters).
3. Equipment must be standardized (shooting in daytime is not comparable to shooting atnight with a spotlicht, or to shooting with the help of drivers, or to ferreting or using snap-traps).
4. The catching of one animal should not interfere with the catching of another. There is an effect of 'time saturation'.The hunter can shoot only so many animals before the survivors are out of range. This is comparable to the 'handling time' needed by predators catching prey (Holling,1959). This means that above a certain density the number of animals shot per time unit remains constant and does not increase with further increases in density.
5. Animals must not learn to avoid capture.

When these five conditions are met, the regression of absolute density on catch per unit effort is linear through the origin (Ricker, 1940).

The bag data used to determine increases and decreases in rabbit numbers were not originally gathered with the intention of using them for such an analysis. Therefore, the usefulness of the data has first to be considered. With regard to the above mentioned conditions:

1. We may assume that conditions of catching did not differ much between years.
2. Catching efficiency should not have changed much, unless the overall method changed (e.g. night-shooting vs. daytime-shooting). Unfortunately, the method used was not always recorded.
3. The same applies to equipment.
4. The relationship is unlikely to be linear. As population density increases, a point is reached where the 'time saturation' per rabbit determines the maximum that can be shot per unit of time. However, at high rabbit densities the management usually puts in extra effort (e.g. time of the game wardens) into control, so that total numbers

caught will tend to keep a positive relationship with density.

5. The areas managed were large in relation to the number of wardens, and they did not return to the same site until after they considered that sufficient time had elapsed for the increased alertness of the rabbits to wear off (at least in the NHD and the Kennemerduinen).

Most important for the usefulness of the method is that the hunting effort stayed the same over the years.

The number of rabbits obtained were recorded in annual reports, often summarized per calender year. Such data are not the best measure, however, for understanding population processes. It would have been better to have summarized numbers from one breeding season to the next. Sometimes data per month were available in the archives. In the NHD the number of game wardens employed slowly decreased, whereas in Meijendel the number of people allowed to catch rabbits varied between years. The effort spent on rabbit control is a decision of management policy, and is influenced by considerations of dune management and of keeping good external relations. These considerations are sometimes mentioned in annual reports, but it is rarely recorded how much time was spent in taking the total catch. This is the largest drawback of these data.

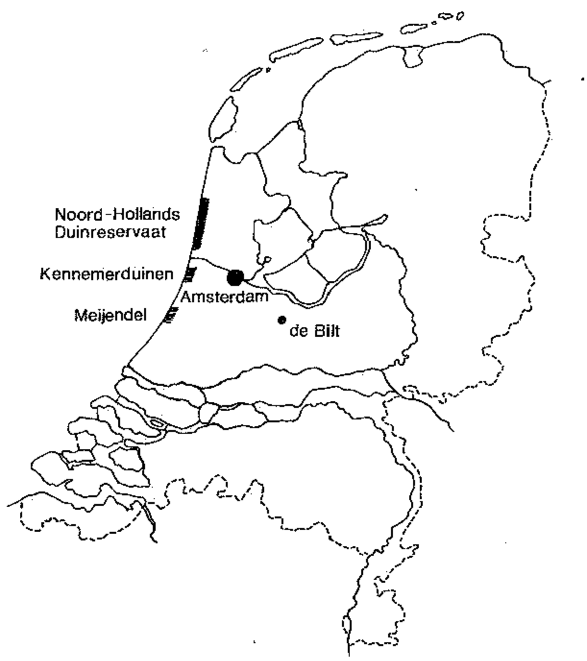


Fig.2 Map of The Netherlands with three dune reserves

THE DATA SETS

(a) Meijendel (2,000 ha).

This reserve is managed by the water supply company of 's-Gravenhage, 'Duinwaterleiding van 's Gravenhage (DWL)'. The royal hunting department has a hunting right on an area of 1400 ha. They do not give information about numbers of game obtained. (An assessment by DWL-personnel amounts to 2,000 rabbits per year). In this part of the reserve rabbits are also controlled by the DWL. A separate body, the Hoogheemraadschap Rijnland is in charge of the strip of dunes bordering the sea. This area has been left out of the following calculations. Thanks to the efforts of Mr. J.J. Maat, chief dune warden, data on the yearly bag are available from 1964 (fig. 3:a). For interpretation, it should be realized that rabbits that could not be sold (too lean, with myxomatosis, or too damaged) were usually left in the dunes and were not counted. In particular, the percentage with myxomatosis can not be assumed to have been the same between years. Since 1975 counts are available per month. Rabbits were shot, ferreted, and before 1970 they were also trapped. Lower numbers since 1970 may be due to the countrywide prohibition of the gin trap. Catching and shooting was done by personnel working for the water company, initially during their spare time, but nowadays as part of their job requirements.

The participants varied between years. From 1961 to 1980, the general number of participants decreased from 12 to 10. The time spent controlling rabbits depended on their own policy and so the 'catch effort' varied between years. Also, the market price probably influenced catch effort.

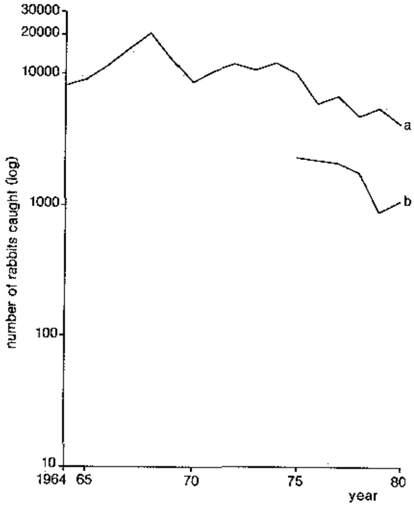
In 1981 nature conservation considerations led to the area under rabbit control being reduced to a quarter. Consequently, the data since 1981 can not be compared directly with earlier samples, and therefore, have not been included in the analysis.

The validity of the yearly data has been studied by comparing a series obtained by two persons who used only one method (ferreting) in October, November and December (fig. 3:b) with the yearly totals(fig.3:a). It is assumed that these data were obtained with a more constant 'catch effort'. The two data sets show different annual fluctuations, especially in 1978-79. January and February 1979 were severe and in many areas rabbit density in autumn was lower than in de preceding years (own study, see ch.7). It is strange that in Meijendel the total catch in 1979 was higher than in 1978. This questions whether the total catch per year has a direct relation to the population size of rabbits in that year.

(b) Kennemerduinen (1200 ha)
Until 1976 the rabbit hunt followed a regular pattern. Weekly night-shooting was conducted by the director, Mr.E.C.M. Roderkerk, supplemented with rabits shot by game wardens and some private hunters. Fig. 4:a shows the annual totals shot (from the annual reports). For 1963-1976, the available per month and a summary of the numbers for Oct.+Nov.+Dec. is given in Fig. 4:b. These data were collected with an approximately constant catch effort. However, they show similar variation and the same fluctuations as the total catch. Management policy changed in 1976, and data from after 1975 are not presented here.

(c) Noord-Hollands Duinreservaat (NHD) (4765 ha).
As described in 1.2 the managing company of the NHD, the Provincial Water Company of North Holland (PWN, has gradually loosened the tie between rabbit control and hunting rights, and taken the former into its own hands. Rabbits were shot mostly by game wardens in its service. Until 1970, some rabbits were shot for sport (12% of the total in 1956, no data for the other years). Some gin trapping was also carried out up to 1970 (279, 231 and 159 rabbits in 1967, '68 and '69 respectively). These figures are not included in the yearly totals. Rabbits that had no value for sale were nevertheless included in the count. Also, rabbits found dead with myxomatosis (150 in 1954, 5634 in 1955, 203 in 1956) were collected , because the management thought myxomatose rabbits were an awkward sight for the public; they were included in the total count.
Fig. 5:a gives these total counts. The increase in numbers between 1948 and 1954 was due to more efficient control methods (Doude van Troostwijk, 1964). The high number in 1955 contains many rabbits found dead. Only after 1955 was the rabbit population density mirrored in the total catch. The length of the hunting season varied yearly. It usually started in mid-August, but could be advanced to July e.g. when rabbits caused damage to agriculture. The close of the season varied from the end of December to April, depending on the rabbits' damage to young trees. From 1964 to 1980 the number of game wardens employed decreased from 13 to 6, and in 1970 their assignment changed. Annual reports did not provide enough information to correct for the variation in effort. Total catches have been calculated for the Oct.+Nov.+Dec. period from 1965 to 1980 (fig. 5:b). They show that the catch in the autumn hunt has about the same variation between years and showed same fluctuations as the yearly game bag. The effect of differences in length of the hunting season between years seems to be small.

Predation by fox
Despite the increase in fox numbers between 1970 and 1980, no effect was seen on rabbit numbers in the game bag.


30000
20000
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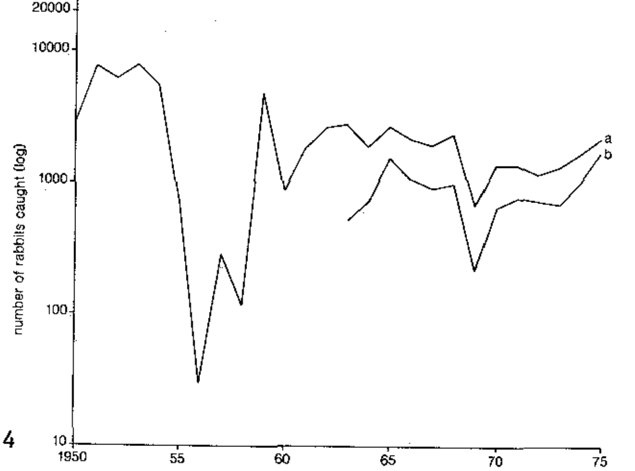
number of rabbits caught (log)
a
b
1964
65
70
75
80
year

Fig.3


30000
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number of rabbits caught (log)
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1950
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year

Fig.4

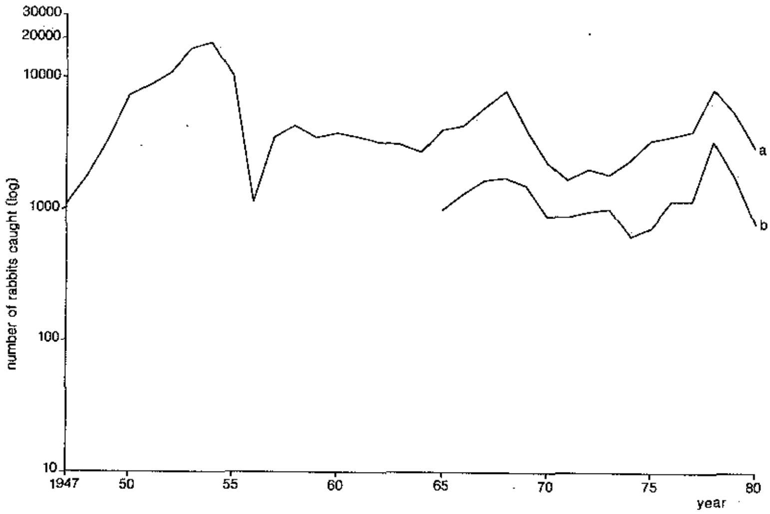

Fig.5

Fig.3 Yearly catch of rabbits at Meijendel (ordinate in log-scale)
a. Total numbers shot, ferreted and trapped
b. Numbers ferreted by two employees, Oct.+Nov.+Dec. 1975 and 1977-1980

Fig.4 Yearly catch of rabbits at Kennemerduinen (ordinate in log-scale)
a. Total numbers shot 1950-1975
b. Numbers shot by Roderkerk 1963-1975

Fig.5 Yearly catch of rabbits at Noord-Hollands Duinreservaat (ordinate in log-scale)
a. Total catch 1947-1980
b. Catch Oct.+Nov.+Dec. 1965-1980

Catch-effort

For the years 1977-79, PWN measured the catch-effort per manhour to compare the efficiency of different hunting methods. Numbers killed show similar annual fluctuations to the total catch (table 1), but were more pronounced. It seems that hunting pressure increased with lower population density.

Table 1

Rabbit catch per manhour
shooting at daytime

year	catch/hour
1977	0.57
1978	1.01
1979	0.39

This was also shown by data from the field study: the game bag of September 1979 contained 85% juveniles, while the warrens on the study site and supposedly the population in the dune reserve contained 39% juveniles. Evidently, hunting kills disproportionally more (inexperienced) juveniles.
When an increase in the percentage of adults in the game bag occurs, as in November and December 1979, this should indicate a heavier hunting pressure (table 2). It might be concluded that there is a direct relationship between catch size and rabbit density, but that this relationship is obscured by changes in management policy, and by the (unconscious) aim of the game wardens to reach about the same catch every year.

Table 2

percentage of juveniles in the game bag NHD
n=total catch per month

	September		October		November		December	
	n	%	n	%	n	%	n	%
1978	93	88	45	82	72	65	95	76
1979	171	85	64	88	29	46	79	55
1980	103	87	48	79	102	73	84	69

Number of juveniles in December,
1978 vs. 1979 : $X^2 = 7.85$, $p < 0.05$
1979 vs. 1980 : $X^2 = 3,35$, n.s.

RELATIONSHIP BETWEEN RABBIT DENSITY AND WEATHER

When the total catch on the three reserves is compared (a in figs.3,4 & 5), we see that the fluctuations in numbers are not synchronised, except for the influence of myxomatosis in 1956. The series from 1964-'80 have no significant correlation with each other. Synchronous fluctuations would suggest that one or more common factors, operating over large areas, influence rabbit density, e.g. the weather. Since the series are not synchronous, the data suggest that weather is not important.

The influence of weather might be revealed by a different approach. Spittler (1976) was able to predict the number of hares on account of the quantity and distribution of rainfall. I analysed the data with regard to the influence of different weather conditions. The following factors were used for the combined period of January, February and March: average temperature, number of days with more than 1 mm rain and number of snowdays. Number of snowdays and temperature proved to be highly correlated (r=-0.86,n=16,9 <0.005). Temperature and rainfall were not significantly correlated with any of the series of number of rabbits caught. However, when looking at the coldest winter, 1979 (average temperature in Jan. & Feb. -2.1 ^{o}C), and the next coldest, 1970 (average temperature in Jan. & Feb. 2.3 ^{o}C), there is a fall in the bags from the NHD, and also in the total bag at Meijendel in 1970 (fig.3:a), but not in the Kennemerduinen. Moreover, the fall in numbers killed in the NHD since 1970 could also be a result of changes in the rabbit control policy.

One cannot draw conclusions on the influence of the weather from these data. Its operation on rabbit density might not be revealed because of the influence of changes in management and human behaviour on these data.

POACHING

To get reliable data on the numbers of rabbits poached is almost impossible. Th. Bakker has recently studied the extent of poaching by inhabitants of Egmond aan Zee by interviewing poachers and game wardens (Bakker & Wallage, in prep.). The data appear to be reliable.
Egmond aan Zee borders the NHD, and catching rabbits has always been an important way to tide-over the seasons. The poachers involved all grew up within the neighboorhood. According to them, there were more rabbits in the dunes before myxomatosis arrived than at present. Like the game wardens they start catching rabbits in August and kill most from October to December.
From the interviews Bakker draws the conclusion that the total kill by people from this neighboorhood is between 10,000 and 20,000 rabbits/year, mainly from the NHD. Together with the bag from the game wardens, this means that in recent times about 5 rabbits/ha have been killed there each year. The influence of these actions on rabbit density will be discussed in ch.7.

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