Rabbits in the coastal sand dunes : weighed and counted = Konijnen in de kustduinen : geteld en gewogen
Drees, J.M.

Author: Drees, Johanna Marijke
Title: Rabbits in the coastal sand dunes : weighed and counted
Issue Date: 1988-06-21

RABBITS IN THE COASTAL SAND DUNES;
WEIGHED AND COUNTED

KONIJNEN IN DE KUSTDUINEN;
GETELD EN GEWOGEN

Proefschrift

ter verkrijging van de graad van doctor aan de Rijksuniversiteit Leiden, op gezag van de Rector Magnificus Dr.J.J.M.Beenakker, hoogleraar in de faculteit der wiskunde en natuurwetenschappen, volgens besluit van het college van dekanen te verdedigen op dinsdag 21 juni 1988, te klokke 15.15 uur

door

Johanna Marijke Drees

geboren te Washington,D.C., U.S.A., in 1950

Drukkerij Mostert, Leiden

Promotiecommissie:

Promotor	:Prof.K.Bakker
Co-promotor	:Dr.E.van der Meijden
Referenten	:Dr.S.Broekhuizen
	Dr.N.Croin Michielsen
Overige leden	:Prof.J.L.Dubbeldam
	Prof.E.Gittenberger
	Prof.P.Sevenster

1988 J.M.Drees, Haarlem
Tekeningen door H.Reiling, Utrecht
Het Provinciaal Waterleidingbedrijf Noord-Holland ondersteunde het onderzoek materieel.

aan mijn grootmoeders,
Catharina Drees-Hent en Johanna Gescher-Kemper

ACKNOWLEDGEMENTS

I am grateful to directors, staff and employees of the PWN for their cooperation and support, especially for maintaining the study area and building rabbit traps. The game wardens helped with collecting much of the data on rabbit body weights. Dr.S.Broekhuizen and F.Maaskamp (Research Institute for Nature Management) showed much interest during the study and provided instruction on some techniques. F.J.S.W.Korner and the men at the workshop of the Zoological Laboratory made the tags and adapted the equipment to field circumstances. Drs.Mimi Roetering helped me in finding the literature. M.L.Brittijn, J.M.J.Herzberg and H.Heijn drew the figures. J.Simons and Fieneke Speksnijder set them up. Rina van der Niet en Ceciel Sassen typed parts of the manuscript. Dr.H.E.van de Veen (Free University,Amsterdam) and prof.dr.R.A.Prins (University of Groningen) inspired the study on the quality of food for wild-living animals. I thank Evelien Zantman for advice on the chemical analysis, which was carried out by Irene Ettinger, H.Halm and the author. Dr.J.F.W.Nuboer (University of Utrecht) stimulated the observations on the activity of wild rabbits. Dr.N.Straw was so kind as to correct the english of the first and last chapter.
Furthermore, the following helped me in gathering the data, in good and bad weather and at the most unsociable times of the day and night: R.Akkermans, R.Bakker, Th.Bakker, J.Damm, W.Denneman, Dory van Dierendonk, G.Dinsbach, F.Distelbrink, Erica Drees, Corrie Elders, Dorien Farjon, Judith van Genderen, Gerda Geut, Heleen Goddijn, A.Guldemond, C.ten Haaf, H.J.Immink, A.James, Els Jans, Elsje Jansen, Marielle Jansen, N.Jonker, Yvonne van Manen, J.van Mourik, J.L.Mulder, M.van Nierop, Sari van Noorden, Els Nijssen, J.Roggeveen, Marjon Rutz, Mies Schollard, Maud Scholten, Margriet Stapel, A.Steeman, D.Tanger, Henny van Veen, Sj.de Waard, W.de Wart, H.van de Water, A.Weeda.

RABBITS IN THE COASTAL SAND DUNES;

WEIGHED AND COUNTED

TABLE OF CONTENTS

KONIJNEN IN DE KUSTDUINEN;

GETELD EN GEWOGEN

SAMENVATTING

Onderwerp van deze studie is de populatiedynamiek van het konijn in de Nederlandse kustduinen, toegespitst op de aantallen in de winter. De vraag is: wordt de populatiedichtheid beperkt door dichtheidsafhankelijk gedrag, door predatie en/of ziekte, of door het beschikbare voedsel.

Het onderzoek werd uitgevoerd in het Noordhollands Duinreservaat (NHD), ter hoogte van Castricum (zie fig.1 en 2 bij hfdst.1).

In hoofdstuk 1 wordt voorts de geschiedenis van het konijn in de duinen gerefereerd, hun invloed op verstuivingen en het optreden van myxomatose bediscussieerd. Er wordt ook nagegaan welke conclusies kunnen worden getrokken uit de omvang van het afschot van konijnen door de jaren heen in een aantal duinreservaten. Veranderingen in beheer en in vangstmethoden maken dat de relatie tussen populatiedichtheid en afschot over de jaren niet gelijk bleef. Uit de afschotgegevens konden geen conclusies worden getrokken over de sleutelfactor die de dichtheid van de populatie bepaalt.

Hoofdstuk 2 behandelt de conditie van konijnen gedurende de herfst en de winter. De lichaamsgewichten en vetgehalten kunnen aangeven of er sprake is van voedseltekort. Van konijnen die in de periode augustus tot april in een deel van het onderzoeksgebied door de jachtopzieners werden geschoten, werden de leeftijd, het lichaamsgewicht en de hoeveelheid vet rond de nieren bepaald. De leeftijd kon worden geschat aan de hand van het gewicht van de ooglens.
Konijnen ouder dan 1 jaar waren zwaarder en hadden een grotere vetreserve dan de eerstejaars konijnen. Het percentage sterfte lag op een lager niveau. Er waren geen verschillen in gewicht en mortaliteit tussen de sexen. Alle konijnen gingen echter in de winter in lichaamsgewicht achteruit, maar alleen in de koude winter van 1978-'79 trad sterfte op door voedselgebrek.

Hoofdstuk 3 en 4 behandelen de kwaliteit van het voedsel gedurende herfst en winter. In hoofdstuk 3 wordt aan de hand van elders verzamelde gegevens de variatie in voedselkeuze binnen een etmaal gedemonstreerd: een maaltijd is niet representatief voor de totale voedselopname per etmaal.

De kwaliteit van het 'diet' (het feitelijk opgenomen voedsel) is bepaald aan de hand van maaginhouden van geschoten konijnen, met eiwitgehalte en verteerbaarheid als parameters. Het eiwitgehalte van de maaginhoud wordt sterk beinvloed door coprophagie, het opnemen van de 'zachte keutels'. De verteerbaarheid wordt daardoor minder beinvloed. De verteerbaarheid van het voedsel was van december tot en met maart onder het niveau zoals dat voor tamme konijnen geldt als het minimale om te overleven.

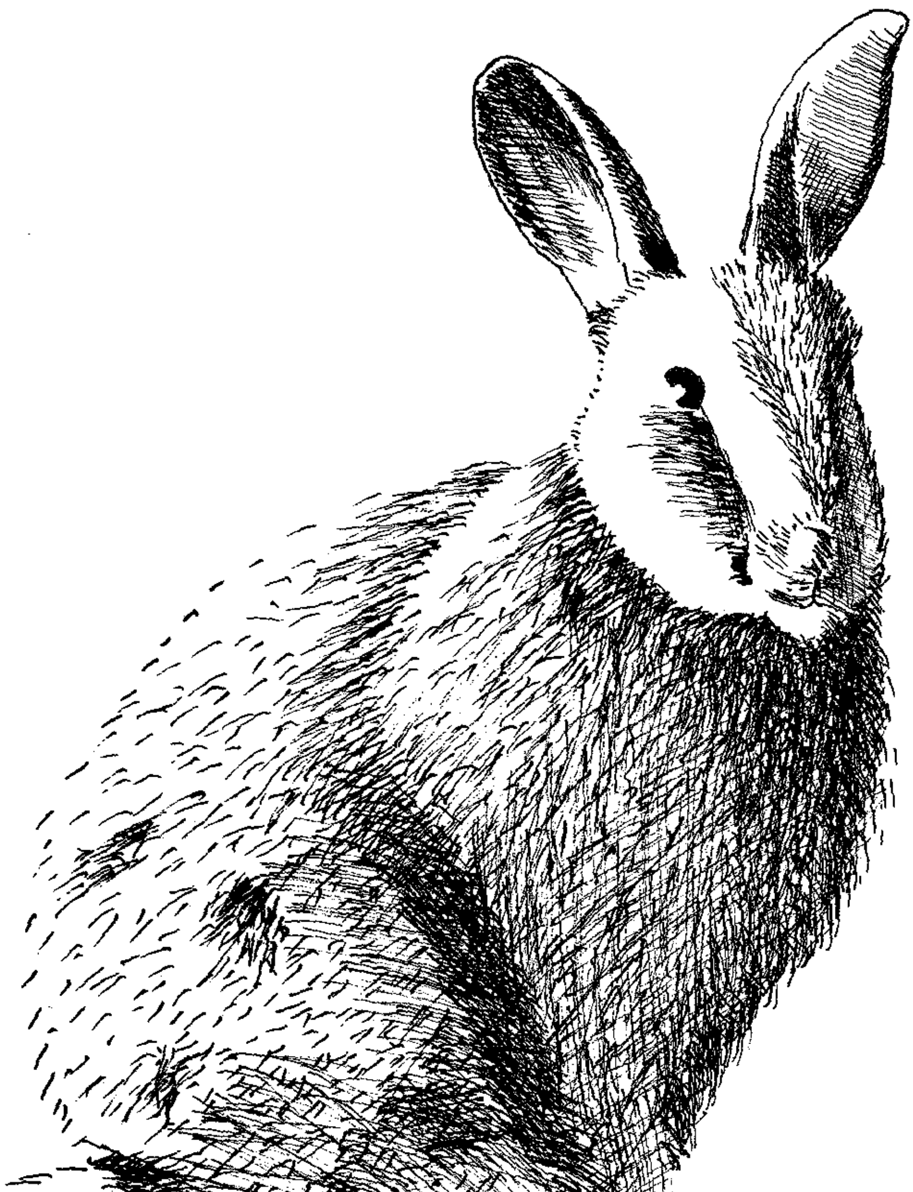
Hoofdstuk 5 behandelt de variatie in de loop van het jaar in de duur van de dagelijkse activiteit van konijnen. De activiteit van konijnen per etmaal varieert gedurende het jaar: van december tot maart zijn konijnen beduidend minder boven de grond. Dat zou kunnen samenhangen met een besparing in engergieverbruik. Deze resultaten zijn van belang bij interpretatie van de veldwaarnemingen voor het bepalen van levenskalenders en aantallen.

De hoofdstukken 6 en 7 behandelen de resultaten van een veldexperiment gedurende de jaren 1978-1981, waarbij de voorplanting en de overleving van een kleine bijgevoerde populatie werd vergeleken met die van andere populaties. De voornaamste methoden waren vangen, merken, terugvangen en observeren.

De lengte van het voortplantingsseizoen bleek afhankelijk van de voedselkwaliteit en de populatiedichtheid. Het moment waarop de meeste vrouwtjes hun eerste worp zogen lijkt samen te vallen met de verbetering in het voedsel aanbod door de toename van kruiden in de vegetatie (hoofdstuk 6). Het aantal worpen per vrouwtje per jaar was relatief laag, wat een reactie zou kunnen zijn op de vrij hoge populatiedichtheid. Bijvoeren leidde tot een vroegere start van het voortplantingsseizoen, maar weinig van de (te) vroeg geboren jongen overleefden. In 1979 (na de voorafgaande strenge winter) werden de eerste jongen later geboren dan in de andere onderzoeksjaren. De voortplanting werd langer voortgezet, maar in september bleek de aanwas toch kleiner dan in andere jaren.

In de koude winter van 1978-'79 trad sterfte tengevolge van voedselgebrek op. In de daarop volgende jaren nam de populatiedichtheid toe en trad er geen sterfte door voedseltekort op, hoewel lichaamsgewicht en gedrag wel duidden op voedselschaarste. Volgroeide konijnen werden gepredeerd door vos, hermelijn en incidenteel door bunzing en kat. Deze predatie bepaalde niet de maximale populatiedichtheid, maar had wel invloed op de snelheid waarmee de populatie naar dat niveau toegroeide.

Op grond van de onderzoeksresultaten wordt geconcludeerd dat de maximale dichtheid van de voortplantingspopulatie uiteindelijk bepaald wordt door kwantiteit en kwaliteit van het voedselaanbod. Dit varieert met het weer. Vooral de duur van de sneeuwbedekking in de winter is van belang.



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.

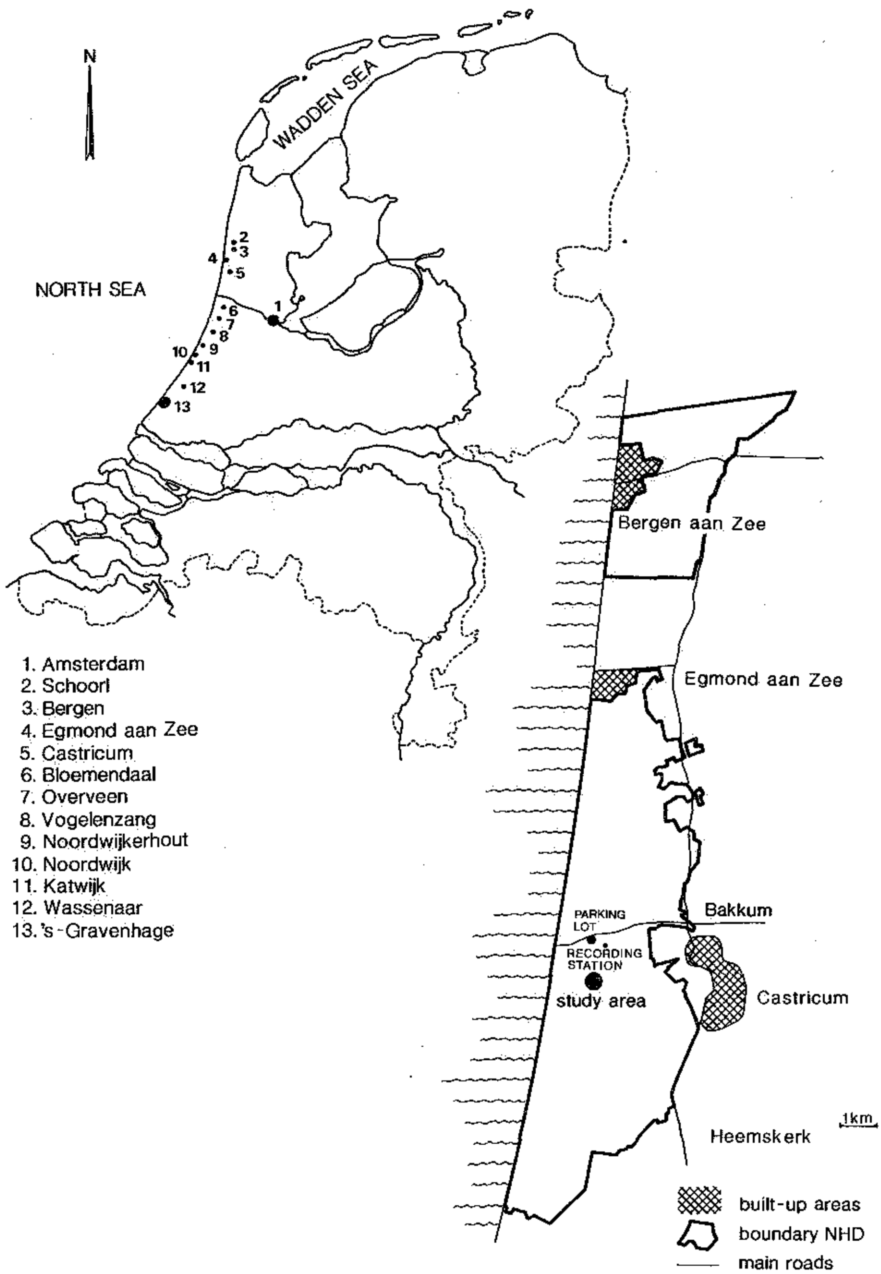


Fig 1 left: Map of The Netherlands with the towns and villages named in ch.1.2.
right: Outline of the Noord-Hollands Duinreservaat with location of the experimental study area, the parking lot where stops were found, and the the weather recording station of the PWN.

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.

Afforestation

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.

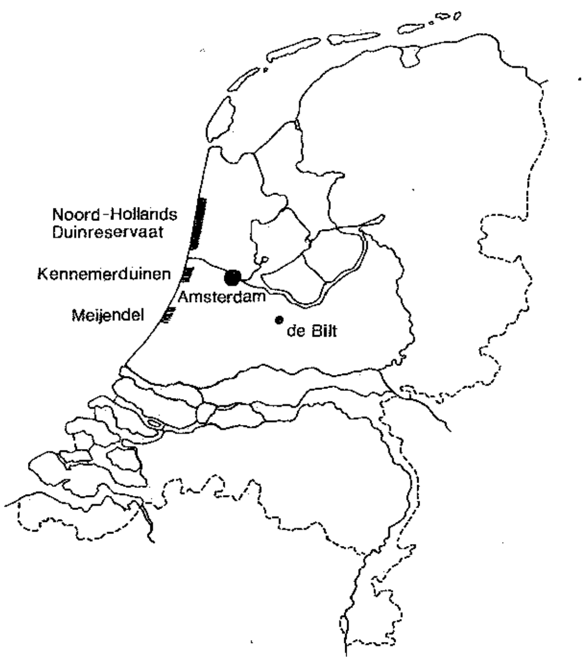


Fig.2 Map of The Netherlands with three dune reserves

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.

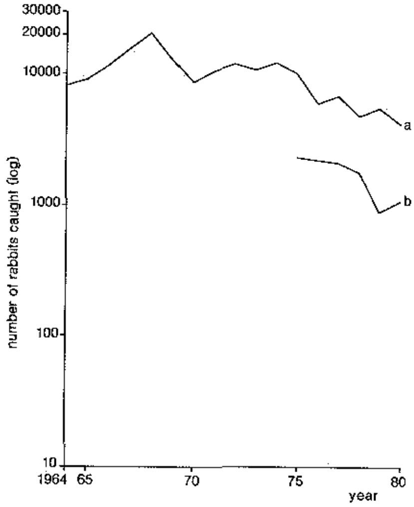

30000
20000
10000
1000
100
10
number of rabbits caught (log)
1964
65
70
75
80
year
a
b

Fig.3

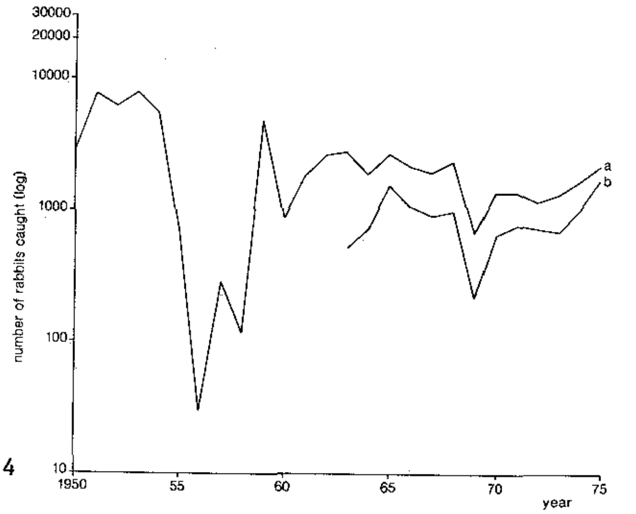

30000
20000
10000
1000
100
10
number of rabbits caught (log)
1950
55
60
65
70
75
year
a
b

Fig.4

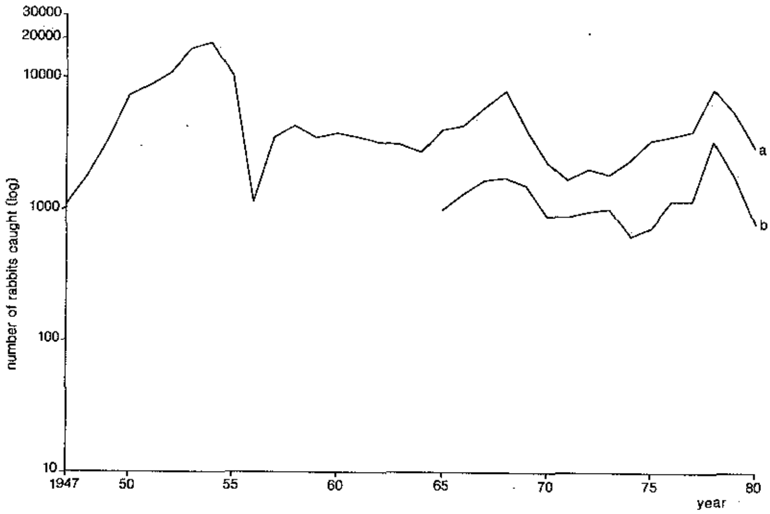


Fig.5

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. $-2.1\ ^0C$), and the next coldest, 1970 (average temperature in Jan. & Feb. $2.3\ ^0C$), 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.

5 REFERENCES

Begon, M., J.L. Harper & C.R. Townsend, 1986. Ecology. Blackwell Sci. Publ., Oxford.

Belonje, J., 1979. Hertenjacht in Noord-Kennemerland. Holland: regionaal-historisch tijdschrift 11: 166-172.

Boerboom, J.H.A., 1958. Begroeiing en landschap van de duinen onder Scheveningen en Wassenaar van omstreeks 1300 tot heden. Bijlage 2 bij: Beplanting en recreatie in de Haagse duinen. ITBON mededeling nr. 39, Arnhem.

Bruyn, G.J. de, in press. Animal communities in Dutch dunes. In: Ecosystems of the world (ed. E.v.d.Maarel)

Bull, P.C., 1956. Some facts and theories on the ecology of the wild rabbit. New Zealand Scientific Review 14: 51-57.

Burggraaf-van Nierop, Y.D., & E. van der Meijden, 1984. The influence of rabbit scrapes on dune vegetation. Biological Conservation 30: 133-146.

Cooke, B.D. & L.P. Hunt, 1987. Practical and economic aspects of rabbit control in hilly semiarid South Australia. Australian Wildlife Research 14: 219-223.

Caughley, C., 1977. Analysis of vertebrate populations. Wiley & sons, Chichester, New York, Brisbane, Toronto.

Dieren, J.W. van, 1932. De ontwikkeling van het duinlandschap van Terschelling. Tijdschrift KNAG 1932: 553-571 en 680-702.

Dieren, J.W, van, 1934. Organogene Dünenbildung. Dissertatie Universiteit van Amsterdam. Uitg. Nijhoff, Den Haag.

Doude van Troostwijk, W.J., 1964. De problematiek van het wildbeheer. In: Recreatie en natuurbescherming in het Noord-Hollands Duinreservaat. ITBON-mededeling nr. 69.

DWL, 1983. Beheersplan Meijendel.

Edmondson, S., 1987. The effect of rabbit grazing in dune slack vegetation at Ainsdale Sand Dunes National Nature Reserve, Merseyside, U.K. Poster paper. Perspectives in coastal dune management; European Workshop and symposium, Stichting Duinbehoud, Leiden.

Feen, P.J. van der, 1963. Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biologisch Jaarboek Dodonea, Gent: pp. 237-243.

Fenner, F. & F.N. Ratcliffe, 1965. Myxomatosis. Cambridge University Press.

Gevers van Endegeest, D.T., 1826. Verhandelingen over het toegangbaar maken van de duinvalleien langs de kust van Holland. Verhandelingen van de Maatschappij ter bevordering van de Landbouw 18.

Gillham, M.E., 1955. Ecology of the Pembrokeshire islands III. The effect of grazing on the vegetation. Journal of Ecology 43: 172-206.

Groenendaal, J. van, R. Boot, D. van Dorp & J. Rijntjes, 1982. Vestiging van meidoornstruwelen in duingrasland. De Levende Natuur 84(1): 11-18.

Hewson, R. & H.H. Kolb, 1973. Changes in the numbers and distribution of foxes (Vulpes Vulpes) killed in Scotland from 1948-1970. Journal of Zoology (London) 171: 285-292.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91: 385-398.

Houlihan, R.B. & W.A. Derrick, 1945. Infectious myxomatosis in malnourished rabbits. Science 101: 364.

Jaksic, F.M. & R.C. Soriguer, 1981. Predation upon the European rabbit (Oryctolagus cuniculus) ,in mediterranean habitats of Chile and Spain: a comparative analysis. Journal of Animal Ecology 50: 269-282.

Jelgersma, S., J. de Jong, W.H. Zagwijn & J.F. van Regteren Altena, 1970. The coastal dunes of the western Netherlands: geology, vegetational history and archeology. Mededeling Rijks geologische Dienst, N.S., nr. 21.

Jelles, J.G.G., 1968. Geschiedenis van beheer en gebruik van het Noordhollands Duinreservaat. Itbon mededeling nr. 87, Arnhem.

Jungerius, P.D., 1986. Erosie door water, wind en konijnen; geomorfologische processen in het Nederlandse duinlandschap. Duin 9: 123-125.

Jungerius, P.D., 1987. Erosiekartering in het Noordhollands Duinreservaat. Duin 10: 75-77.

Jungerius, P.D., A.J.T. Verheggen & A.J. Wiggers, 1981. The developments of blowouts-'De Blink', a coastal dune area near Noordwijkerhout, The Netherlands. Earth surface processes and landforms 6: 375-396.

Klijn, J.A,, 1981. De Nederlandse kustduinen; geomorfologie en bodems. Pudoc, Wageningen.

Kluyver, H.N., 1971. Regulation of numbers in populations of Great Tits (Parus m.major). In: Dynamics of Populations. Eds. P. J. den Boer & G.R. Gradwell: 507-523.

Knorr, F., 1983. Kaninchen Krankheiten. 4e Auflage. VEB, Berlin.

Koersveld, E. van, 1955. De verspreiding van myxomatose. De Ned.Jager 59: 760-764.

Koning, F.J., 1984. Konijnen, muizen en uilen. Duin 7, nr. 3: 29-32.

Kops, J., 1798. Tegenwoordige staat der duinen in het voormalige gewest Holland, zijnde het eerste deel van het algemeen rapport der Commissie van Superintendentie over het onderzoek der duinen.

Kops, J., 1799. Ontwerp tot vruchtbaarmaking der duinen, zijnde het tweede deel van het algemeen rapport der Commissie van Superintendentie over het onderzoek der duinen.

Leeuwen, Chr.G. van & V. Westhoff, 1960. Myxomatose en successie op Schiermonnikoog. RIVON, Bilthoven.

Lloyd, H.G., 1970. Variation and adaptation in reproductive performance. Symp. Zoological Society, London 26: 165-188.

Loo,W.van der, 1986. Geographical immunogenetics of European rabbits. Mammal Review 16:99.

Loo, W. van der, Ch.P. Arthur, B.J. Richardson, M. Wallage-Drees and R. Hamers, 1987. Nonrandom allele associations between unlinked protein loci: Are the polymorphisms of the immunoglobulin constant regions adaptive? Proc.National Academy of Sciences of the USA 84: 3075-3079.

Mabelis, A.A., 1977. Inventarisatie en onderzoek van ongewervelde dieren ten behoeve van het natuurbeheer. De Levende Natuur 80: 204-210.

Marshall, I.D., 1959. The influence of ambient temperature on the course of myxomatosis in rabbits. Journal of Hygiene, Cambridge 57: 484.

Mead-Briggs, A.R. & J.A. Vaughan, 1975. The differential transmissibility of myxoma virus of differing virulence grade by the rabbit flea, Spilopsyllus cuniculi (Dale). Journal of Hygiene, Cambridge 75: 237-247.

Merula, D.G.F.P.N., 1605: Placaten en Ordonnancien op tstuck van de Wildernissen. Delen 1, 2 en 3.

Meulen, F. van der & E.A.J. Wanders, 1984. Stuifduinen: overwegingen betreffende natuur-en duinbeheer in Meyendel. De Levende Natuur 85: 18-23.

Mörzer Bruyns, M.F., 1958. De myxomatose op Vlieland. De Levende Natuur 61: 227-231.

Mulder,J.L., 1982. De vos in de duinen. Duin 5(2):26-30.

Mulder, J.L. & J.M. Wallage-Drees, 1979. Red fox predation on young rabbits in breeding burrows. Netherlands Journal of Zoology 29: 144-149.

Mykytowycz,R., 1956. The effect of season and mode of transmission on the severity of myxomatosis due to an attenuated strain of the virus. Australian Journal of Experimental Biology and Medical Science 34: 121-132.

Mykytowycz,R., 1959. Social behaviour of an experimental colony of wild rabbits, Oryctolagus cuniculus (L.).II First breeding season. CSIRO Wildlife Research 4:1-14.

Niethammer, H., 1938. Ergebnisse von Markierungsversuche an Widkaninchen. Zeitschrift für Morphologie und ökologie der Tiere 33: 297-312.

Noest, V., 1987. Stabilisatie van stuifkuilen. Zuidhollands Landschap 16: 12-13.

Oosterveld, P., 1983. Eight years of monitoring of rabbits and vegetation on abandoned arable fields grazed by ponies. Acta Zoologica Fennica 174: 71-75.

Phillips, P. 1936. The distribution of rodents in overgrazed and normal grasslands in Central Oklahoma. Ecology 17: 673-679.

Pluis, J.L.A., 1986. Landschapsecologisch onderzoek van het wilde konijn, Oryctolagus cuniculus (L.), in Meijendel. Rapport, Universiteit Amsterdam, Fysisch Geografisch en Bodemkundig Lab.

Pluis, J.L.A., 1987. Duinvergraving in het klein. Graverij van holen en graafjes door konijnen in Meyendel. Duin 10: 52-54.

PWN 1985a. Jaarverslag over 1984.

PWN 1985b. Beheersnota Noordhollands Duinreservaat en Provinciale Landgoederen in Zuid-Kennemerland 1985/1990.

Ranwell, D.S., 1960. Newborough Warren, Anglesey III. Changes in the vegetation on parts of the dune system after the loss of rabbits by myxomatosis. Journal of Ecology 48: 385-395.

Ranwell, D.S., 1972. Ecology of salt marshes and sand dunes. Publ. Chapman and Hall, London.

Rentenaar, R., 1978. De vroegste geschiedenis van het konijn in Holland en Zeeland. Holland: regionaal-historisch tijdschrift 10: 2-16.

Ricker, W.E., 1940. Relation of 'catch per unit effort' to abundance and rate of exploitation. Journal of the Fisheries Research Board of Canada 5: 43-70.

Ross, J. & M.F. Sanders, 1984. The development of genetic resistance to myxomatosis in wild rabbits in Britain. Journal of Hygiene 92: 255-261.

Ross, J. & A.M. Tittensor, 1981. Myxomatosis in selected rabbit populations in southern England en Wales 1971-1977. In: Proc. 1st World Lagomorph Conference, Guelph, 1979. Eds. K. Myers & C.D. McInnes: 830-833.

Rijk, J.H. de, 1988. Geschiedenis van het konijn Oryctolagus cuniculus (L., 1758) in Nederland. Lutra 31: in press.

Salman, A. & E. van der Meijden, 1985. De opmars van de meidoorn in de Wassenaarse Duinen. Duin 8: 6-10.

Sheail, J., 1971. Rabbits and their history. David & Charles, Newton Abbot.

Sloet van Oldruitenborgh, C.J.M., 1982. Waarheen met het beheer van natuurreservaten? De Levende Natuur 84: 133-143.

Soriguer, R.C. & P.M. Rogers, 1981. The European rabbit in mediterranean Spain. In: Proc. 1st World Lagomorph Conf., Guelph, Ontario. Eds. K. Myers & C.D. McInnes. Pp. 600-613..

Spittler, H., 1976. Witterungsfaktoren als Grundlage für Vorhersagen über die Entwicklung des Hasenbesatzes. In: Ecology and Management of European hare populations. Eds. Z. Pielowski & Z.Pucek: 115-118.

Swaen, A.E.H., 1948. Jacht-Bedrijff. Naar het oudst bekende document in de Nederlandse taal, een handschrift uit ±1635. Publ.Brill, Leiden.

Tinbergen, N., 1970. Konijnenwentels. De Levende Natuur 73: 193-199.

Tittensor, A.H., 1981. Rabbit population trends in southern England. In: Proc. 1st World Lagomorph Conf., Guelph, Ontario. Eds. K. Myers & C.D. McInnes. Pp. 629-632.

Vegte, F.W. van der, J. Faber & L. Kuiters, 1985. Vegetation, land use and management of the inner-dune zone in the North-Holland Dune Reserve, The Netherlands. Vegetatio 62: 449-457.

Verster van Wulverhorst, A.H., 1840. Geschiedkundige aantekeningen over het Jagtwezen sedert de vroegste tijden. Publ. L. van der Vinne, Amsterdam.

Visser, G., 1979. Honderd jaar Terschellinger flora. Eigen uitgave, Terschelling.

Wallage-Drees, M., 1982. Konijnen als duinbeheerders. Duin 5, nr. 2: 7-12.

Wallage, M., 1982. Duinkonijnen. Waddenbulletin 17: 123-125.

Watkinson, A.R., A.H.L. Huiskes & J.C. Noble, 1979. The demography of sand dune species with contrasting life cycles. In: Ecological processes in coastal environments. Eds. R.L. Jefferies & A.J. Davy. Pp. 95-112. Publ. Blackwell Scientific Publ., Oxford.

Watt, A.S., 1937. Studies in the ecology of Breckland. II. On the origin and development of blow-outs. Journal of Ecology 25: 91-112.

Watt, A.S., 1981. Further observations on effects of excluding rabbits from grassland A in East Anglian Breckland: the pattern of change and factors affecting it (1936-73). Journal of Ecology 69: 509-536.

Westhoff, V., 1967. De invloed van het wild op de vegetatie. Ned. Bosbouw Tijdschrift 39: 218-232.

White, D.J.B., 1961. Some observations on the vegetation of Blakeny Point, Norfolk, following the disappearance of the rabbits in 1954. Journal of Ecology 49: 113-118.

Williams, R.T. & I. Parer, 1971. Observations on the dispersal of the European rabbit flea, Spilopsyllus cuniculi (Dale), through a natural population of wild rabbits, Oryctolagus cuniculus (L.). Australian Journal of Zoology 19: 129-140.

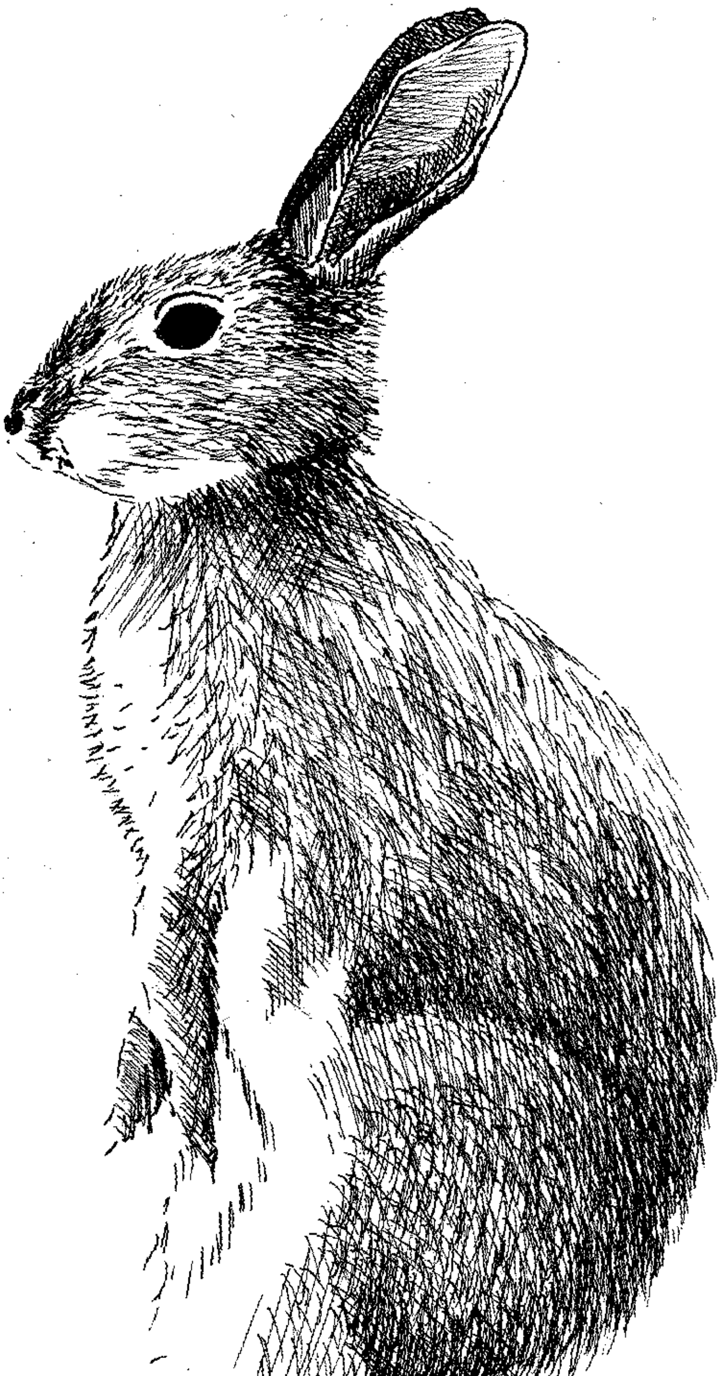
Williams, O.B., T.C.E. Wells & D.A. Wells, 1974. Grazing management of Woodwalton Fen: seasonal changes in the diet of cattle and rabbits. Journal of Applied Ecology 11: 499-516.

Wood, D.H. 1980. The demography of a rabbit population in an arid region of New South Wales, Australia. Journal of Animal Ecology 49: 55-80.

Zagwijn, W.H., 1984. The formation of the Younger dunes on the west coast of The Netherlands (AD 1000-1600). Geologie en Mijnbouw 63:259-263.

Zeevalking, H.J. & L.F.M. Fresco, 1977. Rabbit grazing and species diversity in a dune area. Vegetatio 35: 193-196.

Zeuner, F.E., 1963. A history of domesticated animals. Publ. Hutchinson, London.



Chapter 2

SEASONAL CHANGES IN THE CONDITION OF RABBITS, *ORYCTOLAGUS CUNICULUS*(L.), IN A COASTAL SAND DUNES HABITAT

ABSTRACT

Studied the condition of a wild rabbit population to assess whether it has reached the carrying capacity of its area. Therefore age and condition of rabbits shot from September to March, in 1977 through 1981, were determined from eye-lens weight, body weight and kidney fat. Rabbits older than one year (adults) could be separated from rabbits aged less than one year (juveniles) by eye-lens weight. Both kidney-fat weight and body weight were highly correlated with total fat content and with each other. There were no significant differences in body weight nor detectable differences in autumn or winter mortality between sexes. The overall sex ratio (males:females) was 1.14.

Adults were heavier and had larger fat reserves than juveniles. In every winter they suffered less mortality. Only in a very severe winter did weight loss together with starvation occur. Juveniles suffered more from starvation than adults. After a winter like that the population did not reach the limit set by the food resources of the area.

INTRODUCTION

Rabbits (*Oryctolagus cuniculus* (L.)) have been living in the Dutch coastal dunes since the 13th century (Rentenaar 1978). Their numbers were diminished by myxomatosis during 1955-58, but now the population has recovered and they are abundant in a large part of the area. The sand dunes protect the low-lying country behind them from the sea. For this reason there is popular concern about the possibility that rabbits may cause erosion by burrowing or overgrazing. In this context,it is important to determine whether the rabbit population has reached the carrying capacity of the vegetation.

Wintertime seems to be the most difficult period for rabbits to get an adequate amount of good quality food. The 'duinmeiers', who used to make their living by catching and selling wild rabbits (like the British 'warreners'), supplemented the rabbits' diet with hay in winters with much snow (Rentenaar 1978). Since the winter season seems crucial for the rabbits' survival, I studied the condition of rabbits in this season.

Whether the population has reached the limit of available food, where the survival of individuals and the growth of the population become impaired by food shortage, would be indicated by the animals' condition at this time.

It has been established that the condition of individuals is related to population dynamics. Myers and Poole (1963) as well as Gibb et al.(1978) found a positive correlation between body weight and the probability of survival in wild rabbits. Vaughan and Keith (1978) found the same correlation in another Lagomorph, the Snowshoe hare (*Lepus americanus*).

Caughley (1970) and Martin (1977) considered the level of fat reserves as an indicator of an animal's well-being, its general state of nutrition and the favourability of its environment. They demonstrated a positive correlation between the level of fat reserves and the rate of increase of a population, while Batzli and Pitelka(1971)found a positive relation between low fat reserves and population decline.

These relations are useful in comparing animals in a single environment, although Malpas (1981) and Millar (1981), who studied African elephants (*Loxodonta africana*) and white-footed mice (*Peromyscus leucopus*) respectively, warned that the relation between fat reserves and the well-being of an animal should be used with care when comparing individuals of populations living in different environments. The deposition of fat is an adaptation of the animal to the variability of the environment: in an environment with little variation only small reserves are formed, while large fat reserves are advantageous when foraging conditions are uncertain.

As fat deposition and body weight are influenced by age and sex (Martin 1977) body weight, fat reserves, age, and sex all had to be considered in this study.

MATERIAL AND METHODS

This study was done in 'het Noord-Hollands Duinreservaat', (NHD), a 4765 ha coastal dune area northwest of Amsterdam, which is used as a catchment area and managed by the provincial water company 'het Provinciaal Waterleidingbedrijf Noord-Holland' (PWN). In order to control the rabbit population, the PWN has appointed game wardens to shoot rabbits from August till December, and sometimes until March. The average hunting pressure is 1.1 rabbit per hectare per year.

Changes in body weight were studied from rabbits bagged in this way. It seems probable that there is some bias in the material,but since no data could be collected in another way, it is impossible to characterize or correct for this bias. It is assumed, however, that the direction and extent of the bias is constant throughout the season and in different years

Altogether 2024 rabbits, shot in a selected area of ca. 1000 ha over four years, were studied. The length of the sampling period depended on the management policy of the PWN.

In the season 1980-81, 191 rabbits were collected more systematically by shooting every two weeks from August to December and every three weeks from January till March in a smaller part of the study area ('Vogelduin').

The game wardens use two methods of hunting. From August until the middle of November they customarily hunt at night, and from then until the end of the season they hunt in the daytime. When hunting at night, they use lights mounted on their guns to spot the rabbits. In the daytime, they or their dogs flush the rabbits from above-ground hiding places.

Possible differences in the data collected through these two methods were checked by comparing the results of hunts that were near to each other in time.

Sex, age and body weight were assessed. Age was determined from eye-lens weight, which has been shown to be a reliable measure of age till the age of 24 months (Myers and Gilbert 1968). The fresh lens was kept in 10% formol for three weeks, dried at 80 °C for a week and weighed on a Mettler electronic balance to 10 mg.

Body weight was measured to 10 g. Because the variation in body size was small, a correction for body size was not considered necessary.

From the 'Vogelduin' samples kidney fat (=abdominal fat deposit) and stage of moulting were also determined. These measures depend on Martin's (1977) observation that 'the abdominal fat index appears to be a consistent measure of relative changes in fat reserves in rabbits'. Kidney fat was taken as the total fat deposit which lies in the abdominal cavity, after removing mesenteric fat and fat adhering to testes.

Since moulting could influence body weight, the time of moulting was assessed by noting how many rabbits in a sample had broad black patches or stripes on the inner side of the fur.

From a sample of 12 rabbits the relation between body weight, kidney fat, and total body fat was examined. Total body fat was determined by extraction of all fat from the dried carcass with petroleum ether in a Soxhlet apparatus.

RESULTS

SEX RATIO

The effects of daytime and nighttime hunting on the sample were evaluated by comparing the results of the two kinds of hunt that took place close together in time.

With regard to sex ratio, age class distribution and mean body weight, no consistent difference was found between samples from the same period taken with different methods.Consequently the data from both hunting methods are pooled.

The overall sex ratio (males:females) was 1.14. Comparing Aug. + Sept. + Oct. to Jan. + Feb. + March of all years together there is no change in the ratio.

AGE CLASSES

Fig.1 gives the frequency distribution of eye-lens weights for a few dates in 1978-79. There are two distinct age groups recognizable: juveniles, less than one year old, and adults, more than one year old, separated by a gap caused by the pause in reproduction from August to February. From this graph the discriminating lens weight for the different months is derived.

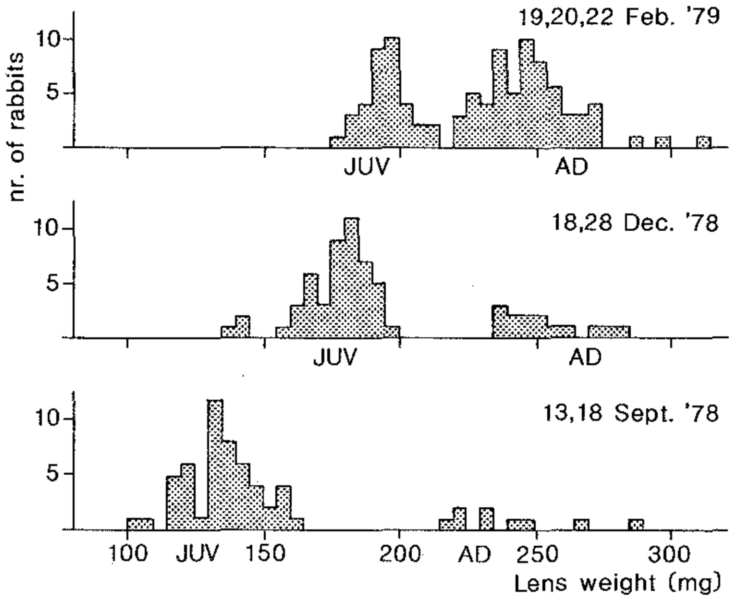


Fig.1 Frequency distributions of eye-lens weight in a few samples from 1978-79.

Table 1 shows how the percentage of adults in the game bagged increases during the course of the season. This indicates a higher mortality among juveniles than in adults. The highest percentage of adults is found in winter 1979.

Table 1

PERCENTAGE ADULTS IN SAMPLE

Month	1978-1979		1980-1981	
	n	% ad	n	% ad
Augustus	-		153	14
September	93	12	103	13
October	45	18	48	21
November	72	35	102	27
December	95	24	84	31
January	16	64	19	47
February	170	60	11	27
March	-		8	63

Aug.+Sept.+Oct. vs. Jan.+Feb.+March 1978-79: $X^2 = 81$ $p<0.001$
1980-81: $X^2 = 23$ $p<0.001$

FAT RESERVES

Table 2 gives the total fat content of the carcass and two other parameters frequently used to determine fat reserves : kidney fat (KF) and body weight (BW). Both these parameters have a high positive correlation with total body fat (TBF).

Table 2

THE RELATION BETWEEN TOTAL BODY FAT (g), KIDNEY FAT (g) AND BODY WEIGHT (g)
n=12

Sex	Age	Month	Total body fat	Kidney fat	Body weight
	juv	Oct.	2	0	1320
	juv	Oct.	7	0	1240
	juv	Jan.	6	0	1250
	juv	Jan.	41	2	1400
	juv	Jan.	95	17	1500
	juv	Jan.	61	11	1450
	ad	Jan.	87	8	1630
	ad	Jan.	141	46	1760
	ad	Jan.	88	11	1600
	ad	March	90	18	1550
	ad	March	80	19	1600
	ad	March	91	14	1610

Body weight and total body fat are linearly related as follows: BW = 1270 + 3.4 TBF, n=12, r=0.90. This means that after reaching a body weight of 1270 g, 1.0/3.4, i.e. about 1/3 of the additional weight increase is laid down as fat.

The relation between TBF and KF is best expressed as a logaritmic function: TBF = 7 + 31 ln(KF), n=12, r=0.96. As overall body weight increases, the kidney fat deposit becomes an ever greater part of the fat reserves.

In Fig.2 the relation is shown between the total body weight and the amount of kidney fat for the rabbits from the 'Vogelduin' sample.

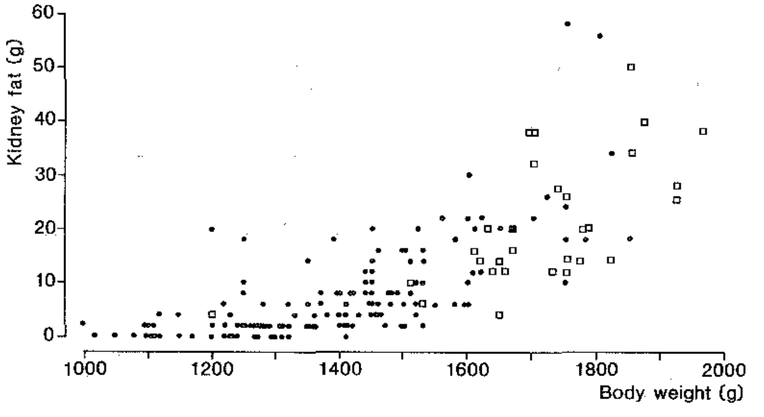


Fig.2 Kidney fat weight in relation to body weight. 'Vogelduin' sample, 1980-1981. Legend: □=adults; •=juveniles.

The mean weight of the kidney fat in adults was 21 ± 2 g (n=33), in juveniles 7 ± 1 g (n=147).

In Jan-March females deposit slightly more fat than males. Mean body weight of females in Jan.-March is 1500 ± 50g, of males :1530 ± 40g, while mean weight of the kidney fat was for females:20 ± 3g and for males: 11 ± 2g.

BODY WEIGHT

Males and females

To analyze whether males and females differ in the relation of body weight to age the regression of body weight on lens weight is calculated. The regression of body weight (g) on lens weight (mg) is (with 90% confidence limits):

BW = 802 + 3.5 lens   n = 153   r = 0.97

For males only:

BW = 802 + 3.6 lens   n = 79   r = 0.98

This indicates that the group of males can be considered a sample from a statistically identical population. In the following calculations the data from the two sexes are pooled.

Fig.3 gives the relation between body weight and lens weight for the juveniles bagged in 1980-'81. The amount of scattering increases with lens weight. If one calculates a linear regression, the standard error of estimate (145 g) is about the same size as the SD of 11% given by Myers and Gilbert (1968) for the estimation of age from eye-lens weight. Nonetheless the concentration of values on the top-left side in the scattergram suggests maximal growth, while the zone on the lower right suggests impaired survival.

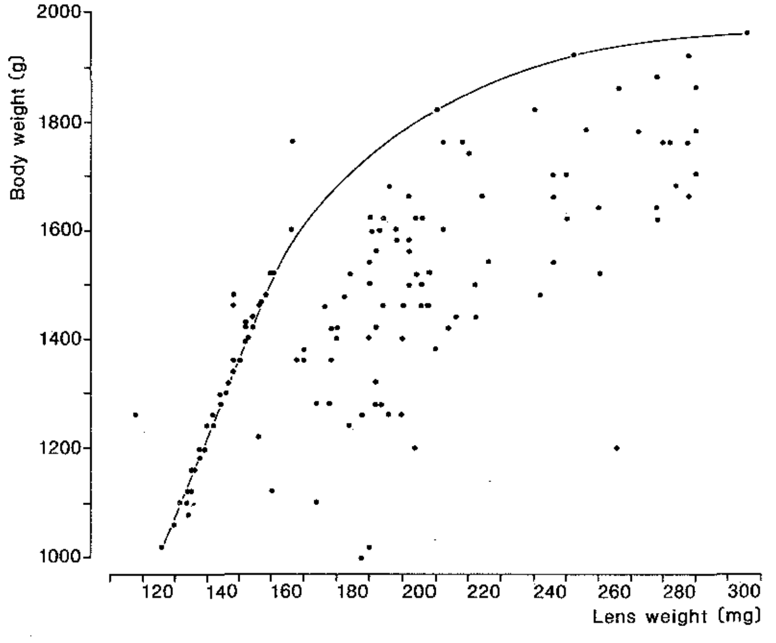


Fig.3 Body weight in relation to eye-lens weight. 'Vogelduin' sample, 1980-81. Juveniles only.

I hypothesize that the curve represents the optimal growth. This curve seems to be logistic in shape. The formula is:

BW= 1900 / 1+e (0.28-0.0068*Lens), n=82, r=0.81.

Rabbits below this weight are in suboptimal condition. Individuals from both autumn and winter are found below the curve.

TREND DURING THE SEASON

Fig.4 shows the mean body weight of adult and juvenile rabbits in the game bagged during the hunting season of 1977-81. To reach sample sizes of at least 5, sometimes results from hunts are combined and represented by a weighted mean.

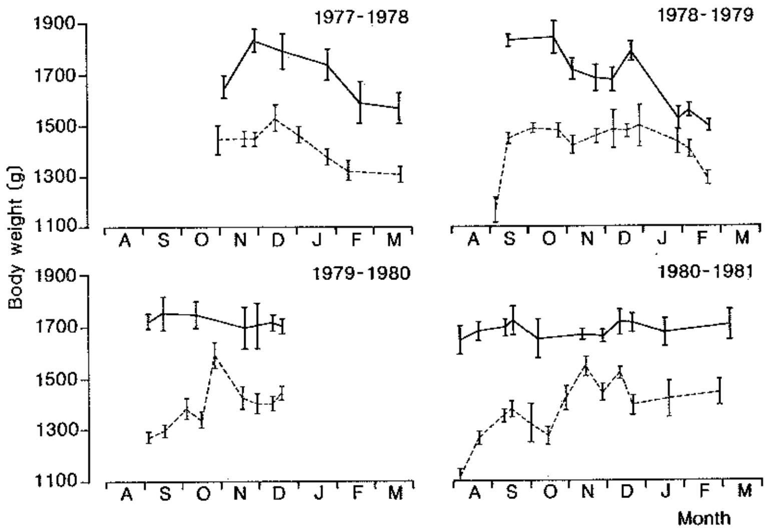


Fig.4 Mean body weight of rabbits per hunt. Vertical bars indicate standard error. Legend: —— =adults; --- =juveniles.

The average weight of the adults is consistently higher than that of the juveniles. Between the mean weight of the juveniles in February and that of the adults in September there is a difference of ca.300 g, which indicates a weight increase in spring and summer.

It is impossible to calculate this more precisely, as the composition of the adult age class is not known and may vary from year to year.

Fig.5 gives an example of the distribution of the weights on a few hunts. It is clear that there is a considerable overlap in weights of adults and juveniles as determined by lens weight, and that weight can not be used as a reliable indicator of age. The overlap becomes larger during the season.

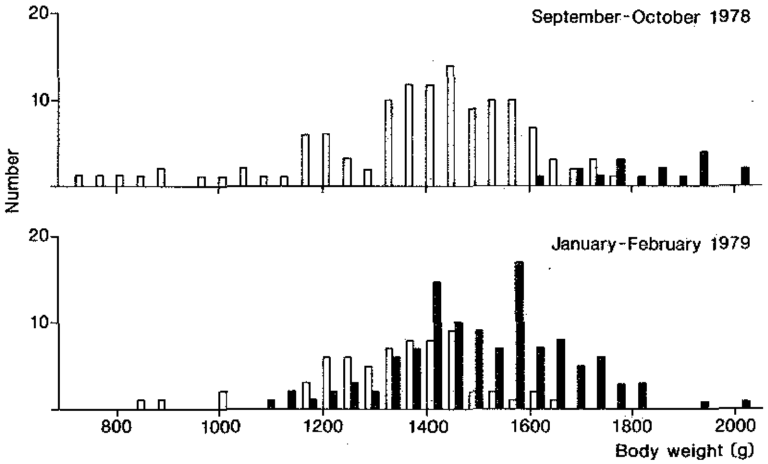


Fig.5 Distribution of specimens by body weight.
Legend: ■ =adults; □ =juveniles.

Table 3

INFLUENCE OF TIME OF THE YEAR ON BODY WEIGHT OF JUVENILES
Data 'Vogelduin', Aug.1980-March 1981

	Constant	Partial r	n
Body weight-Age	(Time)	0.77	124
Body weight-Time	(Age)	-0.66	124

Time-Day of the year, continually increasing from August to March
Age-Calculated from eye-lens weight according to Myers and Gilbert (1968).

The adults show a weight decrease during the season in two out of four years (fig.4).

For the juvenile age class there is a general increase in body weight until December, but growth is interfered with by the winter. To separate the simultaneous effects of aging and time, the partial correlations of these two factors with body weight are calculated (see table 3). The results show that in juveniles growth is adversely affected by the progress of time, i.e. by the winter season, even in the favourable circumstances of 1981.

Moulting takes place mainly in September and October. In November only 2 out of 24 rabbits showed signs of moulting. So decrease in growth is not caused by moulting.

COMPARISON BETWEEN YEARS

In 1978-'79 there were a relatively great number of snowy days in January and February (36 days on which the soil was snow-covered), and mean monthly maximum temperatures were below 0 °C, while the other years were normal compared with the previous 30 years, with just a few days of snowfall and mean monthly temperatures a few degrees above 0 °C(data from the Royal Netherlands Meteorological Institute KNMI).

Fig.4 shows that the body weights of the adult rabbits were lower in January and February 1979 (mean: 1510 g) than in 1978 (mean: 1660 g) or 1981 (mean: 1700 g).

The adult cohort lost, on average, 225 g between December 1978 and February 1979, which is far more than their fat reserve (ca. 90 g, see table 2).

The juvenile class had a light average weight in September 1979. This last fact can be explained by a mean younger age, caused by a later start of the breeding season in '79 than in other years (table 4 and Wallage-Drees 1983).

Table 4

MEAN AGE OF JUVENILES IN GAME BAG IN SEPTEMBER

	n	Lens weight±s.e.	Age
Sept. 78	82	135±2	158
Sept. 79	146	127±1	143
Sept. 80	91	132±1	152

Age(days) estimated according to Myers and Gilbert (1968).

The body weight of the juveniles in January and February 1978 and 1979 is plotted against lens weight and the regression line drawn (fig.6). The line of 1979 is siginificantly below the one in 1978 (more than 1.96 * s.e.,p < 0.05).

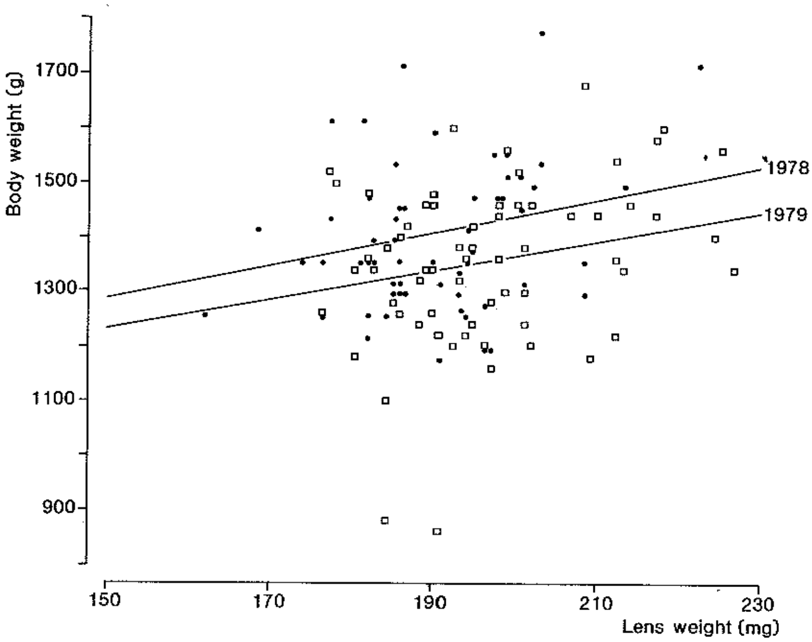


Fig.6 Body weight in relation to eye-lens weight of juveniles in January and February. Legend: • =1978; □ =1979.
Regression formulae:
1978 BW(g)=829+3.02 Lens(mg). S.e.b=0.09, n=57, r=0.30.
1979 BW(g)=829+2.66 Lens(mg). S.e.b=0.09, n=64, r=0.30.

DISCUSSION

In this study no difference was found between males and females in body weight (fig.3) and mortality rate. There is a difference between the sexes in the seasonal pattern of fat deposition. Females store slightly more fat in January and February than males. This may be a preparation for the breeding season, which starts in this area in March(Wallage-Drees 1983). The same was shown by Gibb et al.(1978), Myers & Poole (1963), Parer (1977) and Skira (1980), where different fat deposition was accompanied by distinctly different trends in body weight.

This study shows that rabbits in a temperate zone increase in weight even after reaching maturity. Weight increase stops or is reversed during wintertime, but continues in spring and summer. Consequently the weight of individual rabbits studied here shows an upward oscillating trend much like that described for hares in Poland (Pielowski 1971), and different from the more asymptotic weight curve of rabbits living in less variable circumstances in Spain (Soriguer 1980) and New Zealand (Watson 1957, Wodzicki & Roberts 1960).

In all years of the study period, the mean body weight of the juveniles stayed below that of the adults (fig.4). The proportion of the adults in the game bag increased during the winter season (table 1), indicating a higher mortality rate in juveniles compared to adults. This is probably the result of a higher vulnerability to predation and hunting due to less experience and to myxomatosis (Wallage-Drees in prep.).

In the winter 1978-79, with many days of snow, juveniles suffered a higher mortality than in other years (table 1). These findings parallel the data of other studies on Lagomorphs (Gibb et al.1978, Myers and Poole 1963, Mykytowycz 1961, Vaughan and Keith 1981) which show that adults have a higher rate of survival than juveniles when starvation occurs. It is an advantage to have had time to grow and lay down reserves. Kleiber (1975) formulated the general rule that the basal metabolic rate of mammals is 293xBW Joule/day(BW in kg). Accordingly, when a rabbit increases its weight by 1 g, its basal metabolic rate increases by 2 J and its fat reserves by 1.0/3.4 g = 11 J (this study, table 2).

In times of severe food shortage, body weight decreases by more than the weight of the fat reserves. Obviously other body tissue is degraded as well.

Body weights of individuals in a population can indicate whether the population suffers from food shortage. In the sand dune area where this study was done, a general decrease in body weight with accompanying mortality occurred only in a year with severe weather conditions, in 1978-79. The limit set by the food resources was exceeded not because of fluctuations in population density, but because of fluctuations in this limit.

In the 'normal' winter 1977-'78 there was a weight decrease, but not in 1980-'81. This suggests that in 1978 the population had reached the limit of the carrying capacity of the area, while in 1980-'81 it had not yet recovered from the reduction in numbers caused by the severe winter of 1978-'79. This confirms observations from people working in the area and the results of seasonal hunting (PWN, 1984),both of which indicate an increase in population density from 1980 onward. Hunting could have promoted this situation. I do,however,consider the hunting pressure to be small and did observe the same population fluctuations in an experimental area where no hunting was done (Wallage-Drees unpublished).

In conclusion: data on the condition of wild rabbits in the study area indicate that the population density was limited by the available food in a year with a severe winter.

LITERATURE

Provinciaal Waterleidingbedrijf Noord-Holland (1984): Beheersnota '85-'90 Noord-Hollands Duinreservaat, Provinciale landgoederen en overige Provinciale natuurgebieden. PWN, Bloemendaal.

Batzli,G.O.; Pitelka,F.A. (1971): Condition and diet of cycling populations of the California Vole, Microtus californicus. J.Mammal. 52,141-163.

Caughley,G. (1970): Fat reserves of the Hinalayan Thar in New Zealand by season, sex, area and age. N.Z.Jl.Sci. 13,233-248.

Gibb,J.A.;Ward,C.P.;Ward,G.D. (1978): Natural control of a population of rabbits, Oryctolagus cuniculus (L.), for ten years in the Kourarau enclosure. N.Z.Dep.Sci.Ind.Res.,DSIR Bulletin 223.

Kleiber,M. (1975): The fire of life. An introduction to animal energetics. Robert E.Krieger Publishing co.,Huntington.

KNMI (1978-81): Dagelijks weerbericht. Daily publication of the Royal Netherlands Meteorological Institute, De Bilt.

Malpas,R.C. (1977): Diet and the condition and growth of elephants in Uganda. J.appl.Ecol. 14,489-504.

Martin,J.T. (1977): Fat reserves of the wild rabbit, Oryctolagus cuniculus (L.). Aust.J.Zool. 25, 631-639.

Millar,J.S. (1981): Body composition and energy reserves of the northern Peromyscus leucopus. J.Mammal. 62,786-794.

Myers,K.;Gilbert,N. (1968): Determination of the age of wild rabbits in Australia. J.Wildl.Manage.32,841-849.

Myers,K.;Poole,W.E. (1963): A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations.V.Population dynamics. CSIRO Wildl.Res.8,166-203.

Mykytowycz,R. (1961): Social behaviour of an experimental colony of wild rabbits, Oryctolagus cuniculus (L.).IV. Conclusion:outbreak of Myxomatosis, third breeding season, and starvation. CSIRO Wildl.Res. 6,142-156.

Parer,I. (1977): The population ecology of the wild rabbit, Oryctolagus cuniculus (L.), in a Mediterranean-type climate in New South Wales. Aust.Wildl.Res.4,171-205.

Pielowski,Z. (1971): The individual growth curve of the Hare. Acta theriol. 16,79-88.

Rentenaar,R. (1978): De vroegste geschiedenis van het konijn in Holland en Zeeland. Holland:reg.-hist.tijdschr.10,2-16.

Skira,I.J. (1980): Some population parameters and seasonal changes in weights of internal organs of rabbits Oryctolagus cuniculus (L.) at Macquarie Island. Aust.Wildl.Res. 7,235-245.

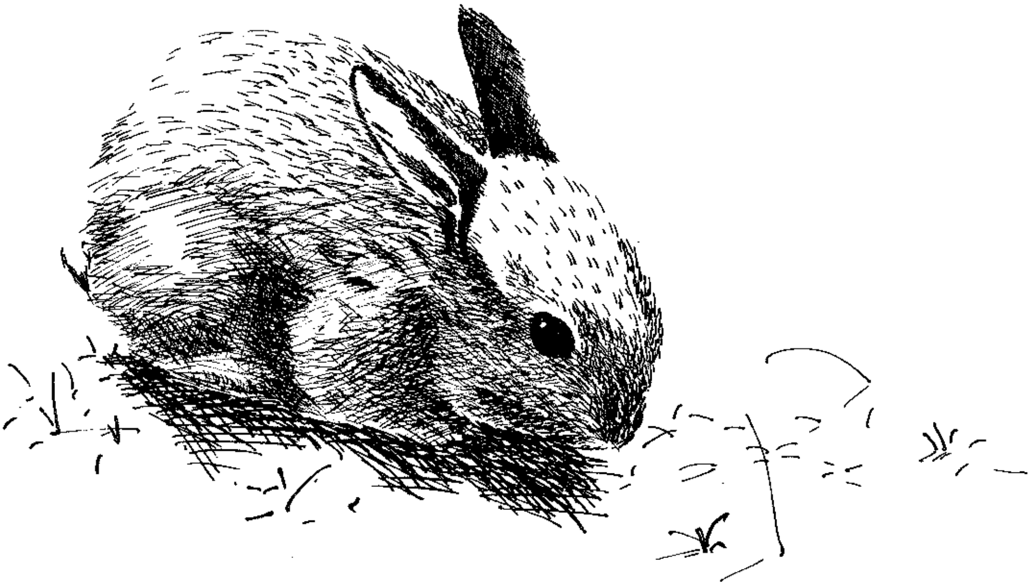
Soriguer, R.C. (1980): El conejo, Oryctolagus cuniculus (L.) en Andalucia Occidental: Parametros corporales y curva de creciemento, Doñana Acta Vert. 7,83-90.

Vaughan,M.R.;Keith,L.B. (1981): Demographic response of experimental Snowshoe Hare populations to overwinter food shortage. J.Wildl.Manage.45, 354-381.

Wallage-Drees,J.M. (1983): Effects of food on onset of breeding in rabbits, Oryctolagus cuniculus (L.), in a sand dune habitat. Acta zool.fenn. 174,57-59.

Watson,J.S. (1957): Reproduction of the Wild Rabbit in Hawke's Bay, New Zealand. N.Z.Jl.Sci.Techn.B. 38,451-482.

Wodzicki,K.;Roberts,H.S. (1960): Influence of population density on the adrenal and body weights of the wild rabbit Oryctolagus cuniculus (L.) in New Zealand. N.Z.Jl.Sci.3,103-120.



Chapter 3

THE USE OF FRAGMENT-IDENTIFICATION TO DEMONSTRATE SHORT-TERM CHANGES IN THE DIET OF RABBITS

ABSTRACT

Microscopical analysis of epidermal fragments in stomach contents or faeces is a helpful tool in assessing the diet of herbivores. Two aspects can cause differences between stomach and faecal samples and should be taken into account in establishing correction factors for diet composition:

1)differential digestion or retention of different plant species or plant parts and

2)differences between meals (short-term changes in diet).

In the present study faeces mean/stomach mean presence of a plant species is interpreted as a measure of digestibility and used as conversion factor for differential digestion of that species. By application of cluster analysis to the modified stomach and faecal contents it is revealed that some rabbits,<u>Oryctolagus cuniculus</u>(Linnaeus,1758), have shifted their foraging areas during the night.

Observations on short-term changes in the diet give information on foraging behaviour in a heterogeneous environment.

INTRODUCTION

Histological identification of plant fragments in stomach contents or faeces is commonly used for analysing the diet of wild herbivores (Bhadresa, 1982; Chapuis & Lefeuvre, 1980). To recognize plant species the prints of the epidermal structure on the cuticula constitute a helpful tool.

Differences between stomach and faecal contents are usually ascribed to differential digestion or retention of foodplants (Batzli & Pitelka, 1971; Neal et al., 1973; Owaga, 1977). Differential digestion means that some food particles are digested more fully on their way through the gastro-intestinal tract than others. Actually the waxen cuticula is never digested, but can become unidentifiable (Neal et al.,1973).

It has been realized that differential digestion or retention complicates the quantitative analysis of the diet from faeces composition. To calculate conversion factors for the main foodplants Bhadresa (1982) did experiments with captive rabbits, relating the proportions in the faeces to the proportions consumed.

Analyzing stomach and faeces contents of the same animals seems a time saving method to determine the degree of differential digestion for all foodplants. Wydeven & Dahlgren 1982), however, mentioned short-term changes in the diet as the major cause of dissimilarities between stomach and faeces samples. In the present contribution we will explore the field of differences between stomach and faeces more systematically.

This study forms part of an extensive research program by the Research Institute for Nature Management on the influence of grazing by ponies and rabbits on the succession of the vegetation in the nature reserve Baronie Cranendonck in The Netherlands (Van de Laar & Slim, 1979; Oosterveld, 1983). In this study it was necessary to know the habitat use of the rabbits. We studied to what extent one can get information on habitat use by the technique of fragment-identification.

STUDY AREA

The study area (51.18'N.; 5 33'E.) is situated south of Eindhoven, near the Belgian border. The site within the reserve where this study was conducted covers ca. 100 ha of woodland, heathland with drift sands, and abandoned arable fields (Fig.1).

The woodlands consist of 50 year old plantations of Pinus sylvestris* with only Deschampsia flexuosa or without any undergrowth. The heathland is characterized by species-poor remnants of a dry heathland community, Genisto pilosae-Callunetum * and of stabilized sand, Spergulo-Corynephoretum.
Locally patches of Molinia caerulea and spontaneous growth of Pinus sylvestris, Quercus robur, Juniperus communis and Frangula alnus occur.

The former arable fields are plots of between 0.5-5.5 ha. They were abandoned in 1972 and originated from heathlands reclaimed for cultivation around 1900. The vegetation succession on these plots is from Chenopodietea and Aperetalia associations to vegetation with species from Artemisietea vulgaris and Plantaginetalia majoris associations and finally to Koelerio-Corynephoretea and Nardo-Callunetea associations. The last two syntaxa were almost absent in 1975, when the rabbits were sampled (Van de Laar & Slim, 1979). In 1975 the burrows were still mostly situated in the heathland.

Outside the study area there are meadows, Poo-Lolietum, heavily fertilized with manure.

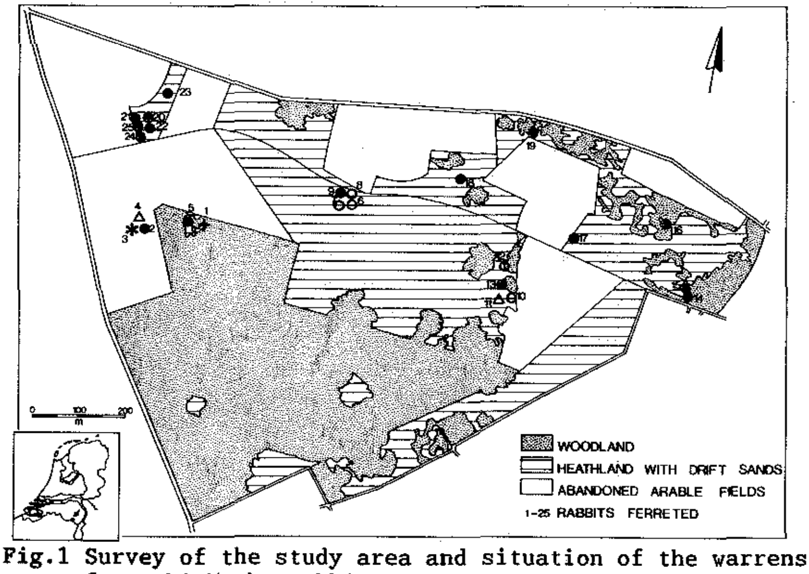


Fig.1 Survey of the study area and situation of the warrens from which the rabbits were ferreted (○=cluster I, (△=cluster II, ✱=cluster III, ●=cluster IV and ✚=cluster V).

*Nomenclature of taxa and syntaxa according to Heukels & Van Ooststroom(1977) and Westhoff & Den Held(1975) respectively.

METHODS

Stomach contents and last faecal (hard) pellets in the colon minus('rectum')of 25 rabbits ferreted and shot in Cranendonck between 10.00 and 14.30 h on 14 January 1975 were collected for analysis (Fig.1).
The analysis was conducted as described in Brüll (1973) with modifications by Immink (1977). Stomach and faeces contents were homogenized and from every sample (n=50) 200 particles were determined to species. Particles <1mm were discarded. The presence of a plant species in the sample is expressed as the percentage of the particles that belonge to that species.

Rabbits eat about 300 g roughage in 24 hours (Aitken & Wilson, 1962) and the mean stomach fill of a wild rabbit is 45 g (Wallage, unpubl.) This means that the stomach contents collected represent one out of several meals of the previous night.

With faeces the case is less simple, as mixing of the contents of several meals happens in the digestive tract, especially in the caecum (Björnhag, 1972).

With the use of stained straw particles Björnhag (1972) showed that the first particles reach the distal part of the colon minus in 4 hours after the meal.The mean retention time in the rabbit for Phleum pratense was 5.3 hours (Uden et al., 1982).

Rabbits do practise coprophagy. Smaller particles (<100) are collected in the colon, packed into caecotrophes (soft pellets) and after defecation taken from the anus and consumed. Coprophagy need not concern us here as these very small particles are probably unidentifiable and lost in the analysis procedure as applied in the present study.

The set of 50 stomach and faecal contents is subdivided into groups by a cluster analysis based on group averaging. The program used is a part of BIOPAT, a program system for bioinformatic pattern analysis, developed by P.Hogeweg and B.Hesper, Department of Bioinformatics, University of Utrecht, The Netherlands. The stomach and faecal contents are considered as points in a multi-dimensial space, spanned by the composing plant species. Discontinuities in this cloud of points are depicted in dendrograms in which the vertical axis is a measure of mean square distance between subgroups. A set is split up at a high level when the distance between the subsets is large.

RESULTS

Table 1 gives the means and standard deviations of percentages of plant fragments per species in 25 stomach and 25 faecal samples. The last column shows the quotient: faeces mean / stomach mean, interpreted as a measure of digestibility.
The diet of the groups of 25 rabbits contained 24 foodplants identifiable in at least 6 of the samples. Poa trivialis and 5 species of dicotyledons found in the stomaches were not found in the faeces at all. Plantago and Taraxacum were in the faeces only found once. Generally, dicots have a higher digestibility than monocots. Exceptions here are Poa with a relatively high and Calluna and Ranunculus with a low digestibility.

Table 1

PRESENCE OF PLANT SPECIES (%) IN STOMACH AND FAECES
25 shot rabbits

Plant species	Stomach		Faeces		Quotient
monocotyledons	mean	s	mean	s	
Agrostis spec.	1.3	1.8	0.3	0.8	0.23
Apera spica-venti	4.1	11.6	1.7	6.1	0.41
Corynephorus canescens	0.8	1.3	2.9	4.1	3.63
Deschampsia flexuosa	1.4	1.6	1.6	2.8	1.14
Elytrigia repens	3.6	4.5	1.7	2.5	0.47
Festuca ovina	2.3	4.8	10.1	12.2	4.39
Holcus lanatus	2.8	5.4	2.5	7.0	0.89
Lolium perenne	20.1	15.7	16.7	16.0	0.83
Nardus stricta	3.8	7.3	2.2	3.2	0.58
Phleum pratense	12.6	8.9	18.1	11.8	1.44
Poa pratensis	2.8	3.7	0.2	0.8	0.07
Poa trivialis	1.7	2.0	0.0		0.0
	57.3 %				
dicotyledons					
Achillea millefolium	0.8	1.5	0.0		0.0
Calluna vulgaris	7.2	8.8	18.6	7.4	2.58
Cerastium spec.	2.8	3.2	0.6	1.0	0.21
Erodium cicutarium	0.4	0.9	0.0		0.0
Plantago major	0.6	1.1	0.1	0.6	0.17
Ranunculus repens	0.4	0.7	0.6	1.8	1.50
Rumex acetosella	1.6	2.3	0.0		0.0
Rumex obtusifolius	1.6	1.7	0.0		0.0
Stellaria media	3.2	4.4	0.3	0.7	0.09
Taraxacum spec.	15.0	7.5	0.1	0.4	0.01
Trifolium repens	0.9	1.8	0.0		0.0
Urtica dioica	4.5	3.4	3.2	3.3	0.71

Figure 2 is a dendrogram of the stomach contents. Only the 16 plant species found more than once in the faeces were used. The 25 stomach contents can be subdivided into 5 clusters.

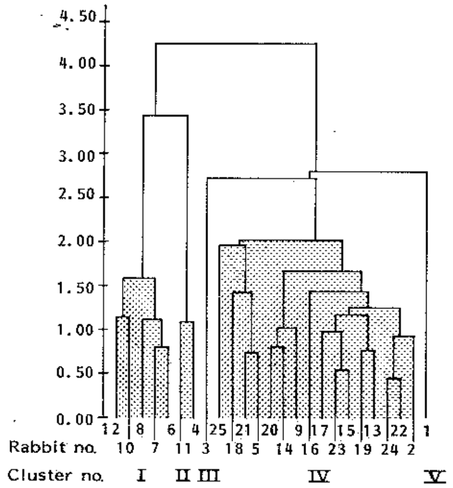


Fig.2 Dendrogram of stomach contents. Horizontal axis: rabbit number (1-25); vertical axis:mean square distance between subgroups

Table 2 gives per cluster the means of percentages of plant fragments per species. These clusters represent different vegetation types in which the rabbits recently took their meals. So rabbits of cluster I recently foraged in heathland with Calluna and Nardus, whereas rabbits of cluster IV recently took their meals in a vegetation with Lolium and Phleum.

Table 2

MEANS OF PERCENTAGES OF PLANT FRAGMENTS IN STOMACH CONTENTS IN 5 CLUSTERS

Cluster number	I	II	III	V	IV
Rabbit number	6-8,10,12	4,11	3	1	2,5,9,13-25
Agrostis spec.	3	1	2	0	1
Apera spica-venti	1	42	3	0	1
Calluna vulgaris	20	3	0	0	5
Cerastium spec.	3	4	4	12	2
Corynephorus canescens	3	2	0	0	0
Deschampsia flexuosa	2	3	2	2	1
Elytrigia repens	0	0	10	0	5
Festuca ovina	1	3	2	24	1
Holcus lanatus	3	2	1	0	3
Lolium perenne	2	0	0	23	30
Nardus stricta	18	0	0	0	1
Phleum pratense	2	2	14	5	18
Poa pratensis	1	0	3	0	4
Ranunculus repens	1	0	2	0	0
Stellaria media	8	13	0	0	1
Urtica dioica	5	4	1	9	4
Vegetation type	Heathland	Abandoned arable field	Abandoned arable field, meadow outside reserve & heathland		Meadow outside reserve

We can assume to eliminate differences between stomach and faeces contents due to differential digestion by dividing the percentages of plant fragments per species in the faeces by the digestibility quotient. Cluster analysis of the 25 stomach contents and the 25 modified faeces contents together results in the dendrogram shown in Figure 3.

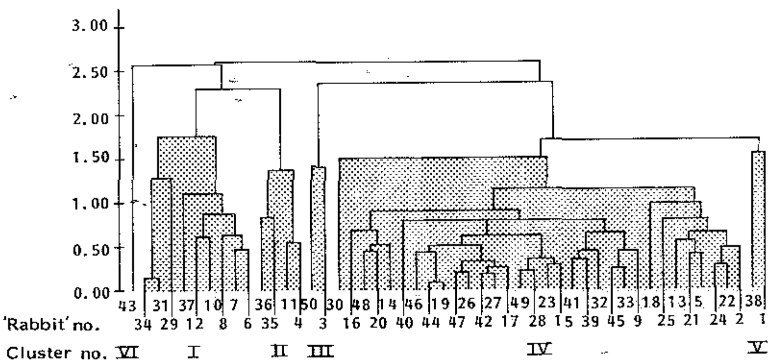


Fig.3 Dendrogram of stomach contents and faeces contents together. Horizontal axis: rabbit number (faeces of rabbit i = i+25); vertical axis: mean square distance between subgroups.

The 5 clusters of Figure 2 can be recognized in Figure 3 and all the faeces contents, except no.43 (rabbit no.18) can be classified in those clusters. In 15 cases the faeces content of a certain rabbit can be found in the same cluster as the stomach content of that rabbit. However, 10 rabbits have their faeces content in another cluster than their stomach content. Evidently they did forage successively in different vegetation types. Table 3 gives an enumeration of these changes.

Table 3

RABBITS WHICH TOOK MEALS OF DIFFERENT COMPOSITION; NUMBER OF CLUSTER[1] INTO WHICH THE CONTENTS OF STOMACH AND FAECES ARE CLASSIFIED RESPECTIVELY

Rabbit	Stomach	Faeces
1	V	IV
3	III	IV
4	II	I
7	I	IV
8	I	IV
9	IV	I
10	I	II
13	IV	V
18	IV	VI
25	IV	III

[1] See table 2 for the composition of the clusters

DISCUSSION

Several authors have paid attention to the differential digestibility of plant species as complicating the assessment of the diet of a herbivore from the composition of its faeces, even in nonruminants. Batzli & Pitelka (1971) and Neal et al. (1973),working respectively with Microtus californicus and M.Pennsylvanicus, and Owaga (1977) working with Equus burchellii found a higher correlation between stomach and faecal contents and used discrepancies between stomach contents and faeces to establish correction factors for different plant species. They all noted that dicotyledons more than monocotyledons became unidentifiable or were digested. Wydeven & Dahlgren (1982) pointed to the importance of 'short-term changes in the diet' in causing these differences, but failed to separate the effects from those of differential digestion.

In a patchy environment with different vegetation types, the information regarding the habitats in which the animal has been foraging can be used to assess habitat use and daily dispersion.

In this study it could be shown that the rabbits foraged either on abandoned arable land (cluster II), heathland (cluster I) or on fertilized meadow outside the reserve (the largest cluster: IV). Some rabbits must have travelled more than 200 m to reach the foraging places (see Fig.1). No evidence for foraging in the woodlands was found, even for the rabbits living in it.

The present study reveals clearly the change of foraging areas by studying individual rabbits. Rabbits 7 and 8 for example, have probably taken their last meal, early in the morning, in the heathland around their burrows, while they foraged earlier on the fertilized meadow outside the study area. Observations like the ones presented in this study can therefore contribute to the understanding of habitat use (especially foraging) by rabbits in a diverse, patchy, environment.

REFERENCES

1. Aitken, F.C.& Wilson, W.K., 1962. Rabbit feeding for meat and fur. Rowett Institute,Aberdeen.Techn.Comm.no.12: 1-63
2. Batzli, G.O. & Pitelka, F.A.,1971:Condition and diet of cycling populations of the Californian vole. J.Mamm.,52: 141-163.
3. Bhadresa, R., 1982: Plant-rabbit interactions on a lowland heath.Thesis, King's College, University of London:1-263. versity of London: 1-263.
4. Björnhag,G., 1972: Separation and delay of contents in the rabbit colon. Swedish J.Agr.Res.,2:125-136.
5. Brüll,U.,1973:Wildfutterpflanzengesellschaften und Futterwerk der von Feldhasen (Lepus europaeus Pallas) genutzten Pflanzen. Dissertation,Universitat Hamburg:1-162.
6. Chapuis,J.L. & Lefeuvre, J.C., 1980: Evolution saisonniere du regime alimentaire du lapin de garenne , Oryctolagus cuniculus (L.),en Lande: Resultat de deux ans d'analyses. Bull.Ecol.,3: 587-597.
7. Heukels,H.& Ooststroom,S.J.van, 1977: Flora van Nederland. 19th ed. Wolters-Noordhoff:1-925.Groningen.
8. Immink,H.J.,1977:Voedselkeuze en graasdrukbepaling van het wilde konijn Oryctolagus cuniculus L. (1758) in het CRM-reservaat 'Baronie Cranendonck'. Internal report, Rijksinstituut voor Natuurbeheer, Leersum.
9. Laar,J.A.J.van de & Slim,P.A.,1979:Veranderingen in flora en vegetatie van de verlaten landbouwgronden in het CRM-reservaat Baronie Cranendonck na vijf jaar begrazing door IJslandse pony's (1972-1977). Internal report,Rijksinstituut voor Natuurbeheer, Leersum.
10. Neal,B.R., Pulkinen,D.A. & Owen,B.D., 1973: A comparison of faecal and stomach contents analysis in the meadow vole (Microtus pennsylvanicus). Can.J.Zool.,51: 715-721.
11. Oosterveld,P., 1983: Eight years of monitoring of rabbits and vegetation development on abandoned arable fields grazed by ponies. Acta Zool.Fenn., 174:71-74.
12. Owaga,M.L.A.,1977: Comparison of analysis of stomach contents and faecal samples from zebra. E.Afr.Wildl.J., 15: 217-222.
13. Uden,P., Rounsaville,T.R., Wiggans,G.R. & Van Soest,P.J., 1982: The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (Phleum pratense) hay. Br.J.Nutr.,48: 329-339.
14. Westhoff,V. & Held,A.J.den, 1975: Plantengemeenschappen in Nederland. Thieme:1-324.Zutphen.
15. Wydeven,P.R.& Dahlgren,R.B., 1982: A comparison of prairie dog stomach contents and faeces using a microhistological technique. J.Wildl.Manage., 46: 1104-1108.

Chapter 4

QUALITY OF THE DIET SELECTED BY WILD RABBITS (ORYCTOLAGUS CUNICULUS(L.)) IN AUTUMN AND WINTER

ABSTRACT

Diet quality for a population of wild rabbits was determined by assessing the quality of the stomach contents. Two parameters were measured: digestibility(energy content) and crude protein. Digestibility of the food was analysed by comparing the contents of stomach and faeces with an internal tracer. Rabbits digest only one-third of the cell wall constituents(CWC). The total digestibility of the food was below the standard of maintenance from December till March. So winter diet may influence the survival of the rabbits. Crude protein(CP) was determined by the Kjeldahl procedure. The CP value of the stomach content remained high in all seasons. It is discussed to what extent CP in the stomach equates CP in the diet.

INTRODUCTION

The coastal sand dunes of The Netherlands provide an opportunity to study factors that influence rabbit population dynamics in a natural situation. One of these factors is the influence of diet quality on body weight and consequently on survival (Hoover and Heitmann 1972, Vaughan and Keith 1981, Wallage-Drees 1986). In the sand dunes their diet consists of grasses (mainly Festuca ovina and Deschampsia caespitosa) and dicotyledons, grazed in a short turf, supplemented with roots and bark.

Suitable food can be in short supply even if standing vegetation is abundant (Sinclair 1974) for plant cell walls can only be partly digested by monogastric mammals. They consist largely of structural carbohydrates (cellulose and hemicellulose) and of lignin and the enzymes of these mammals can only break down part of the hemicellulose. The cell contents,however,contain e.g. proteins, organic acids, lipids and non-structural carbohydrates and are considered very digestible in monogastrics (Deinum 1973). The digestibility determines the energy content of the food (Kleiber 1975).

Most herbivores have microflora in a part of the digestive tract as an aid in fermenting the plant cell walls. In rabbits, microbes are mainly found in the caecum. The volatile fatty acids into which they transform the substrate are absorbed in the caecum and colon (Björnhag 1972, Henning and Hird 1972, McBee 1970). Rabbits are therefore classified as 'hindgut-fermentators' (Hintz 1969). Hindgut fermentation extracts less energy out of plant cell walls than does rumen fermentation in ruminants. Feeding trials have shown that rabbits cannot survive on a diet of grass alone (Voris et al.1940).

All herbivores make a specific food selection from the available vegetation. So one should measure the diet quality actually eaten and not the available food (Sinclair et al.1982). Selection by larger herbivores can be studied in the field and may be followed by digestibility trials on animals in captivity with hand-picked forages (for example van de Veen 1979). Reports on small herbivores (snowshoe hare, mice), however, reveal that such animals could not be kept in captivity on natural food, probably because the researchers were not able to select as well as the animal (Golley 1960, Pease et al. 1979, Servello et al. 1983).

We therefore decided to use an indirect method for measuring the quality of food taken by free-living rabbits and its changes. Stomach contents were collected as representing the food eaten and analyzed for protein content and digestibility as estimates of the nutritive value.

The diet quality thus found is compared to the requirements for maintenance in rabbits as stated by the NRC (1977) : 55% for digestibility of organic matter and 12% for crude protein content.

MATERIAL AND METHODS

The study was conducted in the nature reserve "Noord-Hollands Duinreservaat", a coastal dune area northwest of Amsterdam.

For the assessment of diet quality in autumn and winter, rabbits were sampled by shooting at night from August 1980 till March 1981 (Wallage-Drees 1986). Whole stomachs and faeces from the 'rectum' (better called the colon minus, Björnhag 1972) were collected and frozen.

The weight of the total stomach contents was taken, because this is a measure of intake rate (Collins and Smith 1976, Golley 1960).

ANALYSES

The digestible-organic matter content of herbivore diets can be estimated as the sum of the digestible amounts of the cell contents and of the cell walls.

Before analysis the contents of the fundus of the stomach were discarded as these may contain the caecotrophes or 'soft pellets' (Björnhag 1972, Hörnicke 1972, Hörnicke and Björnhag 1979). The remaining stomach contents and faeces from the constituents of organic matter (CWC_{om}), indigestible residue (used as tracer) and ash by the method of Goering and Van Soest(1970). For production of the indigestible residue the inoculum of a hay-fed steer was used.

For calculation of the digestibility of organic matter (D_{om}) the cell contents(CC) were assumed to be 90% truly digestible (Deinum 1973, Short and Reagor 1970, Parra 1978).

THE CHOICE OF TRACER

The digestibility of a forage depends on
-the percentage of CWC
and
-the digestibility of the CWC (Goering and Van Soest 1970).

In conventional in vivo trials on digestibility the animals are given a known amount of feed for a certain period of time and the faeces are collected quantitatively for analysis. In this study we used stomach contents and faeces collected from the colon minus of the same individuals. We assumed that the contents of the stomach were not yet subject to digestion and so identical to the feed as consumed.

To measure the fraction of CWC in the stomach that is digested a naturally occurring indigestible substance which can be found unchanged in the faeces is needed. There is a wide choice of internal tracers. None was found to be reliable (Streeter 1969). Even lignin has been found to be partly digested or absorbed (Servello et al. 1983, Van de Veen 1979). There is absorption of ash in the digestive tract (Johnson and Groepper 1970, Kaufman et al. 1976).

Prins et al.(1981) tested the potentially indigestible plant cell wall components, after incubation of feedstuffs with mixed rumen microorganisms for a long time. They found it a reliable tracer for different species of herbivores. We have followed their method but used stomach contents instead of the actual food.

PROTEIN

To calculate apparent digestibility of protein(ADP) for each individual animal a faeces weight unit is converted to the original stomach unit by multiplying the CP in faeces with the conversion value: (1-D_{om}). Next the percentage CP from the stomach that was digested before reaching the faeces can be calculated(=ADP).

RESULTS

CELL-WALL CONSTITUENTS AND DIGESTIBILITY

Table 1 gives the digestibility of CWC from wild rabbits, analyzed from 57 shot animals, taken at all times of the year. The digestive capacity was low (D_{cwc} =0.29), half of that of the ruminant inoculum on the same material (0.57). The correlation between the D_{cwc} of the rabbit and the D_{cwc} of the steer was: $r=0.63$, $n=57$, $p<0.005$. This shows that the digestive capacity of both depends on the composition of the cell-wall fraction. The standard deviation of D_{cwc} was high (0.26) and D_{cwc} even reached negative values when the cell wall of the faeces were more digestible than those from the food in the stomach. Very high values were also measured. Evidently stomach and faeces did not always contain the same food in different stages of digestion, but consecutive meals could have a different composition.

As a result of the high variation in D_{cwc} there is a high variation in D_{om}.

Table 1

THE DIGESTIBILITY OF STOMACH SAMPLES (n=116)

	mean	sd	range
CWC	57	9	35 - 71
D_{cwc}	0.29	0.26	-0.71 - 0.68
D_{om}	0.54	0.18	-0.12 - 0.77

Legend:
CWC =cell-wall constituents of organic matter(%)
D_{cwc} =digestibility of the organic cell-wall constituents
D_{om} =digestibility of the organic matter

PROTEIN

Table 2 gives the values for crude protein content (CP) and its digestibility. The apparent digestibility of protein(ADP) has a curvilinear relation to CP, because the metabolic faecal protein is constant (Holter and Reid 1959).

Table 2

CONTENT AND DIGESTIBILITY OF PROTEIN

	n	mean	sd	range
%Crude protein(stomach)	155	19.8	3.6	13-32
%Crude protein(faeces)	109	16.1	4.8	11-27
Apparent digestibility (ADP)	27	0.58	0.15	
True digestibility (TDP)	27	0.93		
Metabolic Faecal Protein (MFP)	27	-6.5%		

True digestibility of protein(TDP) and metabolic faecal protein(MFP) are calculated from the linear regression of ADP*CP on CP as described by Holter and Reid (1959), Slade and Robinson (1971):

ADP*CP=0.93 * CP − 6.5 ($r=0.8$, $n=27$, $p<0.005$).
So TDP=0.93 and MFP=6.5%

RELATION BETWEEN CWC AND CP

In plants CWC and CP generally show a negative correlation. The CWC and CP in the stomach contents of the rabbits were also correlated in this population, but less strongly.

For rabbits and plants collected in the same area the linear regressions for January till March are calculated:

plant species %CWC =81-2.2%CP ($r=-0.91$, $n=33$, $p<0.005$, s.e.=0.09)

stomach contents %CWC =81-1.0%CP ($r=-0.33$, $n=40$, $p<0.05$, s.e.=0.07)

These regressions are significantly different. (They have the same intercept and the regression coefficients differ with more than twice their s.e.).

SEASONAL TRENDS IN FOOD QUALITY

Table 3 gives the parameters for food quality during autumn and winter. By grouping samples according to the period of sampling seasonal differences in food quality become evident.

Table 3

ANALYSES OF STOMACH CONTENTS OF SHOT RABBITS.1980-81. means±s.e.

Month	n	Stomach contents (g)/Body weight(kg)	cwc (%)$_{om}$	D_{cwc}	D_{om}	CP (%)
August	15	37±2	51±1	0.40±0.03	0.63±0.02	24±1
Sept.	11	35±2	55±2	0.37±0.07	0.61±0.04	20±1
Oct.	31	34±3	54±1	0.29±0.04	0.57±0.05	21±1
Nov.	35	27±2	61±2	0.26±0.05	0.51±0.04	21±1
Dec.	5	34±2	61±2	0.11±0.03	0.36±0.04	17±1
Jan.	3	31±2	65±1	0.07±0.06	0.34±0.05	18±1
Feb.	11	31±3	62±3	0.22±0.07	0.44±0.05	18±1
March	5	37±5	61±1	0.25±0.24	0.50±0.16	22±1

While the proportion of CWC increases, D_{cwc} decreases ($r=-0.31$, $n=57$, p 0.01).There is a deterioration of quality in wintertime.

DISCUSSION

The method of Prins et al.(1981), to use the potentially indigestible CWC as a tracer for in vitro studies, has been found useful for determining diet digestibility of free-living rabbits. A deviation from the method was the use of stomach contents instead of the actual food. It is the only way to know the actual quality of the diet in the field whilst avoiding the bias of hand-picked forage samples.

From the weights of the stomach contents (Table 3) it appears that, like its relative the Snowshoe hare (Sinclair et al.1982), the rabbit maintains a relatively constant intake rate as quality decreases in autumn.They do not in that season increase their foraging time (Wallage-Drees 1987). So mean diet quality can be considered an indicator of the food situation.

This poses the question whether the stomach contents are representative of the diet. There are three complications:

- short-term changes in the diet
- the possibility of differential retention of parts of the food
- the addition of saliva, gastric juice, enzymes and caecotrophes to the food.

Short-term changes in the composition of the diet result in stomach and faeces representing different meals (Wallage-Drees et al. 1986). This results in much variation in D_{om} among individual rabbits. In some cases, where the faeces originated from well digestible food, even negative values for D_{om} appeared. By grouping samples according to date, however, an average picture of the changes during the year can be made.

Differential retention of food particles is well-known in ruminants. Smaller particles have a shorter retention time than larger ones (Gaare et al. 1977). This is not the case in rabbits. Uden et al.(1982) have shown that in rabbits liquid and solid markers and food particles of different sizes all have the same turnover time in the gastro-intestinal tract. Grützner (1905) describes the movements of food in the stomach: food leaves the stomach in about the same order as it is eaten. So we can assume stomach contents to be representative of the food taken with regard to particle size and proportion of CWC. There are,however, some problems with regard to CP.

PROTEIN

Crude protein content of the feed in the stomachs is relatively high. CWC and CP in the plants are highly negatively correlated because both are influenced antagonistically by plant species ,growing conditions and age (Deinum 1981). We found a correlation in the stomach contents also, but with a different proportion of CP to CWC.

The stomach contains ingested food and the caecotrophes, N-rich products of the caecum (Björnhag 1972). They are concentrated in the fundus. In this study the fundus was discarded before analysis. There is, however, a mixing of the fresh food from the cardiac part of the stomach with the contents of the caecotrophes as the food moves from the cardiac part first outward and then to the pylorus (Grützner 1905). This mixing is shown in domestic rabbits by the production of lactic acid in the stomach by bacteria from the caecotrophes (Griffiths and Davies 1963, Hörnicke 1972), but Henning and Hird(1972) did not find any lactate in the wild rabbit stomach. This mixing will result in a higher CP in the stomach than in the food really taken. The addition of saliva,mucous and pepsin enhances this effect.

Comparing CP in food with that in stomach contents has not often been done. Researchers on domestic rabbits were more interested in the processes within the intestinal tract. Catala(1976) gives figures that show a much higher N in stomachs than in the food. She, however, used the whole stomach contents, including the fundus. The possible size of the effect of complete mixing on the CP content of stomach contents will be demonstrated with an example. Jilge(1974) found a mean caecotrophe production of 64 g/day at a mean food intake of 125 g/day. We found that the caecotrophes had a mean CP of 33%.If a rabbit takes food of 17% CP complete mixing of food and caecotrophes would lead to 21% CP in the stomach, a rise of 4%!

Our rabbits were shot at night, when they were foraging. Caecotrophe production and consumption takes place in the morning for about 7 hours from the beginning of the light phase (Hörnicke 1978, Jilge 1974). In this study the amount of caecotrophe relative to the amount of food in the stomach was far less than in the example given above.

To know more about the influence of mixing on CP in the stomach we analyzed eight stomach contents in four separate parts, following the food on its way through the stomach (Grützner 1905). The results are given in table 4. They show a large standard deviation, probably caused by short-term changes in the diet. There is some differential retention at the (small) pyloric part. The fundus not only contains caecotrophes, but also food, which results in a relatively lower CP than in pure caecotrophes.

We may conclude that in wild rabbits, shot at night, the food in the stomach is not much mixed with caecotrophes.

Table 4

FOOD QUALITY IN DIFFERENT PARTS OF THE STOMACH
means ± s.e.

	CWC	CP (%)
fundic	0.34±0.04	28±3
cardiac	0.48±0.04	21±2
peripheral	0.42±0.03	23±2
pyloric	0.55±0.02	18±1

Myers and Bults(1977) report results quite contrary to ours. They found that food contained 1.4 times as much N as stomachs. They explained this by a fast passage of cell contents through the stomachs. The differential retention in the pyloric part of the stomach (Table 4) supports this assumption, but it would cause a much smaller effect.

We found a true protein digestibility of 93% and a metabolic fecal protein of 6.5%, not very different to the 92% and 5.0% from in vivo trials on domestic rabbits (Slade and Robinson) 1971). True digestibility could be assessed too high when the presence of caecotrophes leads to an overestimation of CP in the diet.

ASESSING PROTTEIN OR ENERGY

Sinclair and Smith(1984) defend the assessment of protein only instead of both protein and energy with the argument that in wild animals protein content of the food is easier to monitor than energy. In the case of a non-ruminant, however, it suffices to analyze the percentage of CWC in the food to monitor energy content.

Pehrson(1984) suggests that energy rather than protein is the limiting resource. Our results suggest that net energy, not protein is in short supply in winter. This is in agreement with the results of Cooke(1981) in arid inland Australia: fiber sometimes reached maximum tolerable limits while CP remained above the minimum tolerable level in all seasons.

ENERGY

The level of D_{cwc} found in this study (29%) is within the range for domestic rabbits fed on roughage (value for grassmeal: 11-17%, Partridge (1980); for whole cornplant pellets: A1%, Schurg et al. (1977)). Most studies measure the digestibility of Acid Detergent Fiber (ADF), which is cellulose +lignin. CWC also contains the hemicellulose. ADF is the least digestible part of the cell-wall. Rabbits, however, digest such a small part of the cell-wall in the food that to know the digestibility of the food one should first and foremost measure D_{cwc} rather than D_{adf}.

The digestibility of the rabbit's diet in the rumen inoculum was low (0.57) compared to the digestibility of forage of the usual agricultural quality by ruminants.This shows the low quality of cell walls in the natural dune vegetation.

QUALITY OF THE DIET IN WINTER

From December till March D_{om} was below the NRC(1977) standard of 55% for maintenance, so there was a shortage of energy content of the food in these months. Quality was sufficient in the other parts of the season. Content of crude protein was never a limiting factor.

The winter of 1980-'81 was mild with hardly any snow. The rabbit population had not yet recovered from the reduction in numbers in the severe winter of 1979. So one would expect that the population was below the carrying capacity of the available food. In this winter juvenile rabbits did not grow, but I did not find indications of starvation (Wallage-Drees 1986). Even in these mild conditions the quality of the food in the winter was inadequate. This points to food quality limiting the population density of rabbits in the coastal dunes.

REFERENCES

Björnhag,G.,1972.Separation and delay of contents in the rabbit colon. Swedish J.Agric.Res. 2:125-136.

Catala,J.,1976. Etude sur les repartitions hydrique, ponderale et azotee dans le materiel digestif chez le lapin. 1er Congres Int.Cunicol,Dijon. Comm.no.58.

Collins,V.R. & M.H.Smith, 1976.Field determination of energy flow in a small nocturnal mammal. J. Mammal.57:149-158.

Cooke,B.D.,1981. Food and dynamics of rabbit populations in inland Australia. Proc.World Lagomorph Conf., Guelph. Ed.K.Myers and C.D.MacInnes pp.633-648.

Deinum,B.,1973. Structural inhibitors of quality in forage. Växtodling 28:42-51.

Deinum,B. 1981. The influence of physical factors on the nutrient content of forages. Meded.LH Wageningen 81-5

Gaare,E.,A.Sorensen,&R.G.White,1977. Are rumen samples representative of the diet? Oikos 29:390-395.

Goering,H.K. &P.J.Van Soest,1970.Forage fiber analyses (Apparatus,Reagens,Procedures and some Applications). Agriculture Handbook no.379. U.S.A.Dept. of Agric.

Golley,F.B.,1960. Energy dynamics of a food chain of an old-field community. Ecol.Monogr. 30:187-206.

Griffiths,M. & D.Davies,1963. The role of the soft pellets in the production of lactic acid in the rabbit stomach. J.Nutrition 80:171-180.

Grützner,P., 1905. Ein Beitrag zur Mechanismus der Magenverdauung. Pflugers Archiv 106:463-522.

Henning,S.J. & F.J.R.Hird ,1972. Transport of acetate and butyrate in the hind-gut of rabbits. Biochem.J. 130: 791-796.

Hintz,H.F.,1969.Effect of coprophagy on digestion and mineral requirements in the Guinea pig. J.Nutr. 99: 375-378.

Holter,J.A. & J.T.Reid,1959. Relationship between the concentrations of crude protein and apparently digestible protein in forages. J.An.Sci.18:1339-1349.

Hoover,W.H. & R.N.Heitmann,1972. Effects of dietary fiber levels on weight gain, cecal volume and volatile fatty acid production in rabbits. J.Nutrition 102:375-380.

Hörnicke,H.,1972. Neuere Befunde über Blinddarmfunktionen und Coecotrophie bei Kaninchen. Z.Tierphys.Tierenahrg.u.Futtermittelkde 30:121

Hörnicke,H.,1978. Futteraufnahme beim Kaninchen. Ablauf und Regulation. Ubers.Tierernahrg.6:91-148

Hörnicke,H. & G. Björnhag,1979. Coprophagy and related strategies for digesta utilization. In: Proc. of the 5th Int.Symp. on Rum.Phys. pp:707-730.

Jilge,B. ,1974. Soft faeces excretion and passage time in the laboratory rabbit. Lab.An.8:337-346.

Johnson,D.R. & K.L.Groepper,(1970).Bioenergetics of North Plain rodents. Am.Midl.Nat. 84:537-548.

Kaufman,D.W., M.J.O'Farrel & G.A.Kaufman,1976. Digestibility and elemental assimilation in cotton rats. Acta theriol. 21:147-156.

Kleiber,M.,1975.The fire of life.Publ.R.E.Krieger, Huntington, New York.

McBee,R.H.,1970. Metabolic contributions of the cecal flora. Am.J.of Clin.Nutr. 23:1514-1518.

Myers,K. & H.G.Bults 1977. Observations on changes in the quality of food eaten by the wild rabbit. Austr.J.Ecol. 2:215-230.

NRC ,1977. Nutrient requirements of farm animals no.9. Nutrient requirements of rabbits. National Research Council.

Parra,R.,1978.Comparison of foregut and hindgut fermentation in herbivores.In: The ecology of arboreal folivores. Ed.G.C.Montgomery.pp.205-229. Publ.Smithsonian Inst.Press, Washington D.C.

Partridge,G.C.,1980. The effect of age on fibre digestion in the rabbit. Proc. 2 World Rabbit Congress.pp.29-36.

Pease,J.L.,R.H.Vowles & L.B.Keith,1979. Interaction of snowshoe hares and woody vegetation. J.Wildl.Mgmt. 43:43-60.

Pehrson,Å. ,1984. Faecal nitrogen as an index of hare browse quality. Can.J.Zool.62:510-514.

Prins,R.A.,W.C.Cline-Theil & A.Th.Van't Klooster, 1981. An in vitro procedure for estimation of in vivo digestibility of roughage plant cell wall components in herbivores using mixed rumen micro-organisms. Agric. and Env. 6:183-194.

Schurg,W.A.,D.L.Frei,P.R.Cheeke & D.W.Holtan, 1977. Utilization of whole corn plant pellets by horses and rabbits. J.An.Sci.45:1317-1321.

Servello,F.A.,K.E.Webb jr. & R.L.Kirkpatrick,1983. Estimation of the digestibility of diets of small mammals in natural habitats. J.Mamm. 64:603-609.

Short,H.L. & J.C.Reagor,1970. Cell wall digestibility affects forage value of woody twigs. J.Wildl.Manage.34:964-967.

Sinclair,A.R.E.,1974. The natural regulation of buffalo populations in East Africa IV. The food supply as a regulating factor, and competition. E.Afr.Wildl.J.12:291-311.

Sinclair,A.R.E., C.J.Krebs & J.N.M.Smith,1982. Diet quality and food limitation in herbivores: the case of the Snowshoe Hare. Can.J.Zool. 60:889-897.

Sinclair,A.R.E. & J.N.M.Smith,1984. Protein digestion in snowshoe hares. Can.J.Zool.62:520-521.

Slade,L.M. & D.W.Robinson,1971. Nitrogen metabolism in nonruminant herbivores 2. Comparative aspects of protein digestion. J.An.Sci. 31:761-763.

Streeter,C.L.,1969.A review of techniques used to estimate the in vivo digestibility of grazed forage. J.An.Sci. 29:757-768.

Uden,P., T.R.Rounsaville, G.R.Wiggans & P.J.Van Soest, 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given Timothy (Phleum pratense) hay. Br.J.Nutr. 48:329-339.

Van de Veen,H.E.,1979. Food selection and habitat use in the Red Deer (Cervus elaphus L.). Dissertation, Un. Groningen.

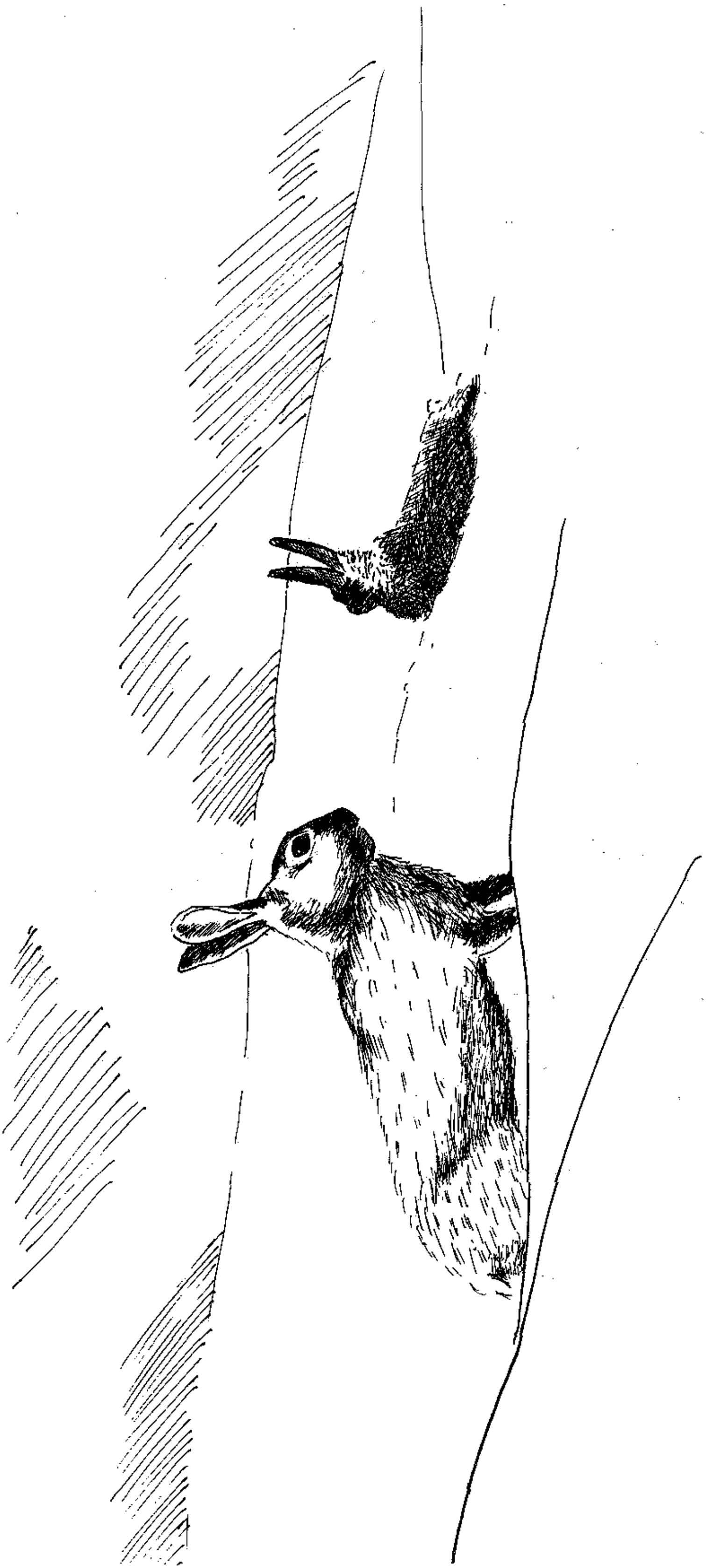
Vaughan,M.R. & L.B.Keith,1981. Demographic response of experimental snowshoe hare populations to overwinter food shortage. J.Wildl.Mgmt.45:354-381.

Voris,L., L.F.Marcy, E.J.Thacker & W.W.Waino 1940. Digestible nutrients in feeding stuffs for domestic rabbits. J.Agric.Res. 61:673-683.

Wallage-Drees,J.M. ,1986. Seasonal changes in the condition of rabbits, Oryctolagus cuniculus (L.), in a coastal sand dune area. Z.für Säugetierk. 51:26-36.

Wallage-Drees,J.M.,1987. Circadian activity in rabbits in a coastal sand dune habitat. Submitted.

Wallage-Drees,J.M.,H.J.Immink,G.J.de Bruyn & P.A.Slim 1986. The use of fragment-identification to demonstrate short-term changes in the diet of rabbits. Acta theriol., in press.



Chapter 5

A FIELD STUDY ON SEASONAL CHANGES IN CIRCADIAN ACTIVITY OF RABBITS

ABSTRACT

Investigated the circadian activity of wild rabbits during the year. Wild rabbits are more nocturnal than their domestic relatives. Their emergence and disappearance times do not vary with the time of sunset and sunrise, but stay about the same during the whole year. When activity is defined as the presence above ground , then wild rabbits show one activity period with irregular fluctuations during the night. When comparing the average periods spent above ground by individuals there appear large differences between the activity during November to February and the rest of the year. Reasons for this are discussed. The highest percentage of the population above ground at one time during these winter months is lower than in the rest of the year. One should take this into account when trying to assess population size by sight counts.

INTRODUCTION

The rabbit is a prominent inhabitant of the coastal sand dunes of The Netherlands. Despite being of Mediterranean origin (Feen 1963,Zeuner 1963) it thrives at this latitude. There are no published data on the circadian activity rhythm in wild rabbits under natural conditions at our latitude as there are from New Zealand (Gibb,Ward and Ward 1978) and Australia (Mykytowycz and Rowley 1958; Myers and Poole 1961). First impressions (Southern 1940) indicate a much lower level of activity in western Europe.

Sight counts are generally used to assess the trend and size of the fluctuations in rabbit populations. Knowledge on the activity rhythm of rabbits is necessary when trying to assess population fluctuations from sight counts. Crucial aspects are:at what time of the day can one expect the highest and/or least variable proportion above ground.

So this paper has two objectives: to describe the circadian rhythm and its seasonal change in a temperate climate and to give information that is useful in the interpretation of sight counts.

METHODS

The study site covered a 1.4 ha area within the reserve 'Het Noord-Hollands Duinreservaat', about 15 km northwest of Amsterdam (52.35 'N; 4.37 'E). Rabbits were caught in baited live-traps and earmarked. From September 1979 , when a large part of the population (36 out of 41) was earmarked, monthly population size was assessed by constructing live-calendars from sightings and recaptures. Because it took some time to capture and tag the young, population size could not be calculated in all months. This accounts for the absence of data for May,June,July and August in table 1 and 2 and in figure 4. The population was contained on two sides by canals and on the third by a field of high grass not used by the rabbits.
Observations were recorded over 24 hours, once a month from August 1979 till April 1982. They were made from a pit with a shelter behind and above. From there about 70% of the (hilly) area could be covered. The unseen part had the same type of vegetation. Therefore, to relate counts to total population size above ground, counts are multiplied by 100/70. There were always 2 observers, who were changed every three hours. Every 15 minutes it was noted which rabbits were visible. In all calculations the first observation after changing the observers was substituted by the average of the immediately previous and subsequent observation. At dark a red spotlight was used. The rabbits' eyes, and earmarks, lighted up in the beam. As a result of the insensitivity of their retina for this long wave stimulation (Nuboer 1971) the rabbits were not disturbed by this red illumination.

One use of activity rhythm data is to aid interpretation of sight counts. The Ministry of Agriculture, Fisheries and Food (England and Wales) has long experience in conducting rabbit counts. Counts are taken during several consecutive days at dawn and dusk along transects (Tittensor,Wood and Fox 1978). As an index of population size the maximum count is taken. The average is a less reliable measure as it is influenced strongly by incidental low values caused by disturbances (pers.comm. A.M.Tittensor). The index is adopted in this study.

In this article the word 'activity' means any presence above ground.

RESULTS

TIMING OF START AND END OF ACTIVITY

Figure 1 shows the times of the start and end of activity within the population. Activity is arbitrarily said to begin at the start of the first half hour in which at least 2 percent of the total activity of that day occurred and to cease at the end of the last half hour in which at least two percent of the total activity of that day occurred. For an example see Fig.2.

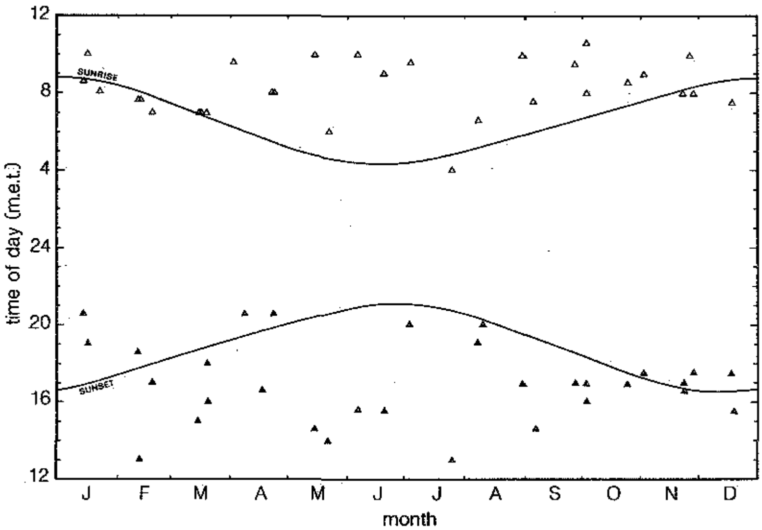


Fig.1 Times of emergence (▲) and disappearance (△). Times of sunset and sunrise are indicated.

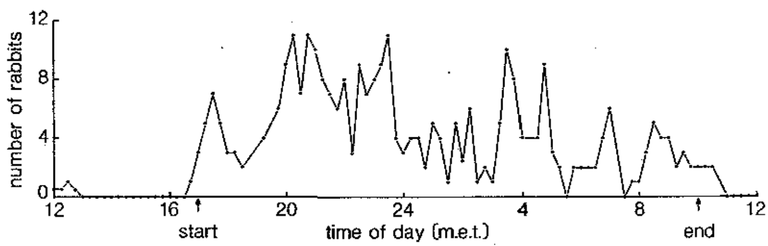


Fig.2 Activity pattern (Number of rabbits/30 min.) on 2 October 1979. Arrows indicate times of emergence and disappearance as they are calculated in this paper.

Sometimes, in the winter, there were periods during the night with no rabbit above ground. These periods could not be taken into account in Fig. 1, but are included in calculations in the tables and Figs. 2 and 3.

In the same way, incidental activity during the daytime separated by at least an hour from the main activity period, is not taken into account in Fig. 1.

A close relation between activity period and times of sunset or sunrise may have been expected. Van Hof, Rietveld and Tordoir (1963) showed that in domestic rabbits the time of light-on (sunrise) is the trigger that determines emergence time. So one would expect a correlation between time of sunrise and start of activity. In this study, however, correlation coefficients are not significant (sunrise-start of activity, r=0.08, n=32, p=0.3;and sunrise-end of activity, r=-0.06, n=31,p=0.4).
Holley and Greenwood (1984),studying the brown hare found the absence of this relationship to be characteristic of the summer. So I calculated sunrise-start of activity for autumn, winter and spring together, but did not find a significant correlation (Sept.-April, r=-0.07, n=23, p=0.4). There are large, apparently irregular fluctuations. The mean times of emergence and disappearance are 16.50±2.10 and 8.20±1.30 hours, respectively.

THE CIRCADIAN ACTIVITY PATTERN

Figure 2 shows an example of the activity pattern during one observation period of 24 hours. The numbers sighted were registered every 15 min. The evident irregularities are quite typical of rabbit emergence in this site and consistent with our observations of individual rabbits re-entering and re-emerging from burrows during the night.

To determine the existence of short-term periodicities, sample autocorrelations (Chatfield 1975) were calculated for 3 series of observations over 24 hours . Fig.3 shows that the only significant correlations are between one observation and the subsequent one to five observations.

Fig.3 Autocorrelation function for activity per 15 minutes on 3 dates (Oct.1979, Oct.1980, Dec.1980). Only the period that the rabbits are active is used. n=74. 90% confidence limits=±0.23

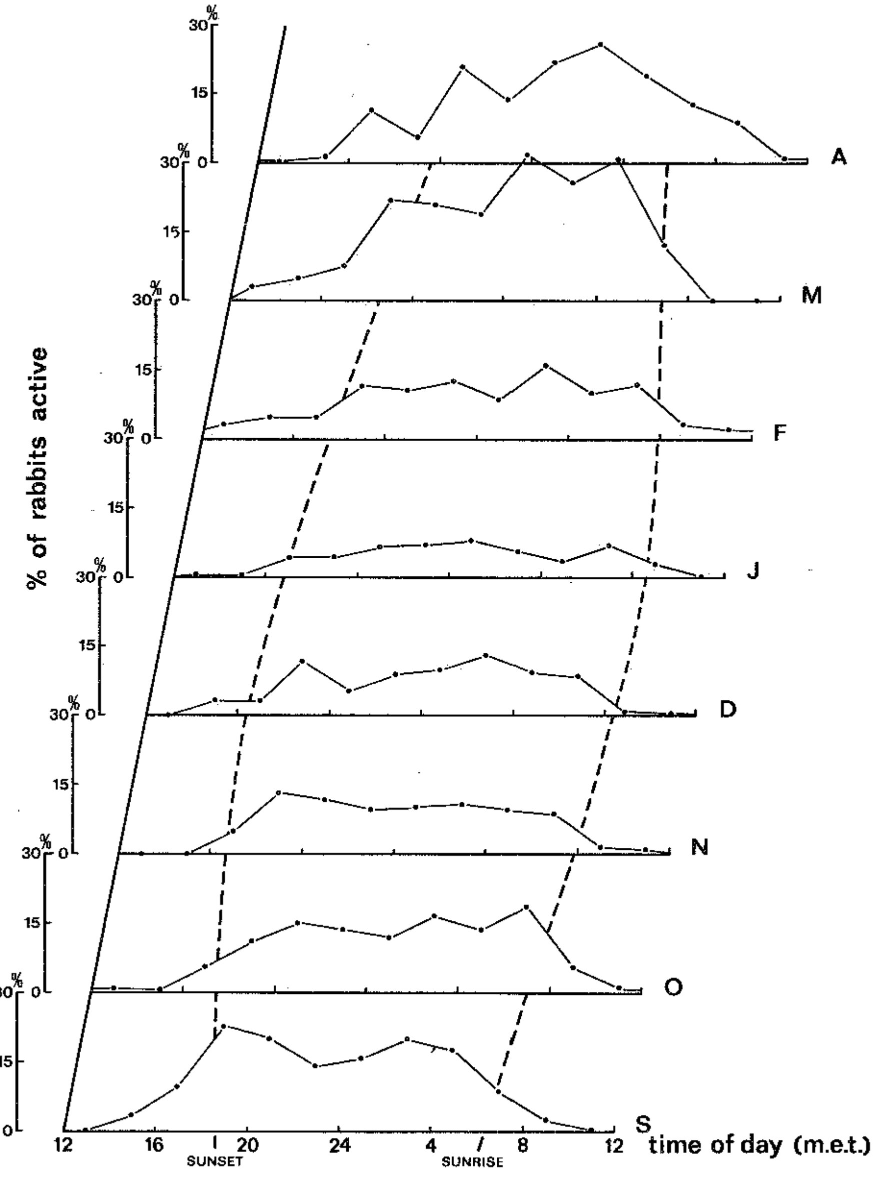


Fig.4 Average activity patterns for each month between September and April. Each point is the mean of 3 observations made in different years.

SEASONAL CHANGES IN THE PERCENTAGE OF RABBITS ACTIVE

Figure 4 is constructed by averaging the monthly observations from the three years (only for those months for which assessments of population size were available). For each year the mean number of rabbits for the observation sessions (in each 2 hour period) is converted to a percentage of the population by dividing by the population size for that particular month. The percentages of rabbits active in corresponding time periods are then averaged for the three years. The figure illustrates the trend in activity over the year. Activity is low in wintertime and increases at the beginning of March.

A homogeneous distribution of activity between 18.00-6.00h can be confirmed or refuted by dividing this period into three equal parts(per day) and comparing the first and second part with Wilcoxon matched-pairs signed-ranks (Siegel 1956). This statistic does not require that the rabbits behave independently of each other. It is computed both for the whole series and for the separate seasons. In all cases $p > 0.05$, so there is no significant tendency to bimodality.
The average period spent above ground per individual is calculated for each month by summing the mean number of active rabbits per hour and dividing this total by the known population size for that month (Tab.1). From November to February it is only 1.5 hours, in March and April 3.1 hours. It may be even higher during the summer months.

Table 1

AVERAGE ACTIVITY (hours above ground) PER RABBIT IN 24 HOURS
Full-grown rabbits only.

year	1979	1980	1981	1982	average
January		-	0,9	1,4	1,2
February		3,1	1,3	1,2	1,9
March		2,9	4,5	2,6	3,3
April		3,3	2,9	2,4	2,9
May		4,8	-		4,8
June		5,0	-		5,0
July		-	-		
August	-	-	-		
September	-	3,2	2,3		2,8
October	2,9	1,9	1,9		2,2
November	1,6	1,5	2,1		1,7
December	-	1,8	0,5		1,2

Sept.+ Oct. versus Nov.to Febr.:p=0.02
Mrch.+ Apr. versus Nov.to Febr.:p=0.02
(Mann-Whitney U-test)

MAXIMUM NUMBER OF ACTIVE RABBITS

To calculate the theoretical results of the sight count method, I have taken the maximum value of 5 consecutive 15 min. sightings starting or ending with at 1 hour after sunset or 1 hour before sunrise, respectively, and divided it by the population size and multiplied it by 100/70 to get the percentage of the population above ground (Table 2).
The data in Table 2 show that the rabbits were never all above ground at the same time. Generally, the percentages in January are lower than in either September or March. Fluctuations are smaller just after sunset (from 5–57%) than just before sunrise (from 0–77%).

Table 2

THE PERCENTAGE OF THE TOTAL POPULATION WHICH IS ACTIVE, ONE HOUR AFTER SUNSET AND ONE HOUR BEFORE SUNRISE.
The highest value of five consecutive observations is given. Full-grown rabbits only.

	Highest percentage of the population observed							
	at 1 hour after sunset				at 1 hour before sunrise			
year	1979	1980	1981	1982	1979	1980	1981	1982
January		5	8	24		5	8	24
February		20	27	34		31	45	34
March		48	48	24		34	76	–
April		48	55	27		16	77	27
May		57	–	–		48	–	–
June		44	–	–		–	–	
July		–	–			–	–	
August		–	–			–	–	
September	35	38	22		–	24	29	
October	40	35	16		33	22	29	
November	30	28	28		8	28	9	
December	–	34	11		–	27	0	

DISCUSSION

START OF ACTIVITY

Our results show that emergence time varies, but does not correlate with the time of sunset as would be expected from experiments and observations on synchronization of activity periods of wild rabbits with daily variations in colour and light intensity of the sky (Nuboer, Nuys and Steenbergen 1983). This 'non-synchrony' was also found in summertime in the hare (Holley & Greenwood 1984).
This is partly due to the fact that in my study area foraging areas were adjacent to the burrows. Nuboer, Nuys & Steenbergen (1983) recorded the movement from hutch to food supply (indoors) or between the warren in the dune and feeding site on the floodplain. I took emergence out of the burrow to be 'start of activity'. In my study site we saw rabbits re-enter or re-emerge from their burrows during the night.This has also been noted by Mykytowycz and Rowley (1958) and Kraft (1978).
Another reason for the lack of synchrony may be the influence of weather. Rowley (1957) found a late emergence during strong winds and/or rain. Kolb(1986) mentions an extremely variable onset of activity for rabbits in a small enclosure. He found a negative correlation with the maximum temperature during the previous day.

In particular a change in the type of weather is expected to influence emergence time. An example is the influence of changes in cloud cover on suckling behaviour of hares (*Lepus europaeus*, Pallas)(Broekhuizen and Maaskamp 1980).
The influence of the period of the moon has been analyzed only by Lord (1964) on *Sylvilagus*.He did not find any effect on activity pattern.
I did not find a significant correlation between either emergence time or maximum percentage active with temperature, wind speed or length of showers. However, the data collected were not sufficient for a detailed analysis of the influence of weather conditions. During the fieldwork I did notice that directly after snowfall rabbits stayed underground at night and that during prolonged snow periods the entire population may be above ground in the afternoon.

THE CIRCADIAN ACTIVITY PATTERN

The rabbits' eyesight is good at low light intensity. Their sensitivity to the "blue" and "green" parts of the spectrum and their "blue-green" dichromacy seems an adaptation to the light environment during twilight (Nuboer ,Nuys and Steenbergen, 1983). One would expect the highest activity in twilight, and therefore a bimodal activity pattern.
Hof, Rietveld and Tordoir (1963) did indeed find this pattern for locomotor activity in domestic rabbits. Rietveld, Tordoir and Hof (1964) showed that changing the irradiance abruptly gave more pronounced activity peaks.

Prud'hon and Goussopoulos (1976) measured locomotor and foraging activity in indoor cages and Kraft(1978) 'total activity' and foraging activity in small outdoor enclosures. Both compared wild to domestic rabbits in this respect. Wild rabbits showed one phase of nearly uninterrupted activity, with more (Kraft) or less (Prud'hon and Goussopoulos) pronounced bimodal foraging peaks. Domes- tic rabbits changed phases of rest and activity a few times during 24 hours. Broekmeyer and Lunen (1986) saw that they kept this pattern after release in the wild. It is thus not advisable to study the behaviour of domestic rabbits to get more insight into that of their wild relatives.
When, in experiments under controlled light conditions, a bimodal pattern for either locomotor or foraging activity is not obvious , it does not surprise us that workers studying overall activity of (more or less) free-living rabbits report no peaks. Generally they find rabbits to be equally active the whole night (Stodart and Myers 1964, Myers and Poole 1961, this study). A similar unimodal acti- vity period is also found in the related Sylvilagus (Lord 1964) and Lepus timidus (Lemnell & Lindlof 1981).

INTERPRETATION OF SIGHT COUNTS

Data on activity levels can be useful to people monitoring rabbit populations by sight counts. Fig.4 can be used to choose the best time for counting.
People wishing to count rabbits on their land often start at either one hour after sunset or one hour before sunrise. Table 2 gives the proportion of rabbits active at these times.
One will have to correct for the proportion of the terrain that is visible , especially when comparing counts done in different areas. Here I will only consider the influence of the circadian and yearly activity patterns on the chance that a rabbit is above ground.
Different figures have been given for the maximum proportion above ground at any one time : Dunnet(1957) 55-60%, Lésel(1968) 50%, Myers(1957)90%, Mykytowycz and Rowley(1958) 66%, von Schantz & Liberg(1982) 57%, Southern(1940) 'usually' 30% and in this study 5-57%.
Gibb, Ward and Ward (1978) found a large effect due to population density: at a high density with food shortage 90-95% were above ground, at a low density only 45%. This is, however, different from the situation in our dunes, where a possible food shortage coincides with the coldest time of the year and being above ground costs energy.
The influence of the weather on short-term fluctuations in the maximum percentage active is probably not as strong as its influence on time of emergence. Gibb, Ward and Ward (1978) found that only wind speeds higher than 6 Bf had an influence on numbers above ground.
For the same population as described here, Geut and Jansen(1980) made 4 series of at least 9 consecutive morning and evening observations. They found that highest daily maxima occurred where there was no or very little rain and low wind speed, and lowest maxima occurred after rainfall. Temperature and wind direction seemed to have no effect.

SEASONAL CHANGES IN ACTIVITY

The level of activity varies strongly with the seasons. Activity reaches a nadir in wintertime, followed by a strong increase in March. The increase corresponds with the onset of reproduction in the study area (Wallage-Drees 1983: 50% of does pregnant in the first week of March, so 50% lactating in the first week of April) . Lactating requires a lot of energy (2 to 3 times the demands for maintenance, Reyne et al. 1977)). Thus does need more food at that time and , consequently, will forage longer. Lloyd(1964) mentions a longer feeding period in pregnant does compared to other rabbits active at the same time.

The short activity period in winter is a surprise, the more so since domestic rabbits (3kg) who had access to food for only 4 hours a day, lost weight. The coldest night during this study was in December 1981. The temperature dropped from 0 to -8 °C. The associated activity pattern, with hardly a rabbit above ground after 23.00 h,was the most extreme. This means that foraging time was short where one would have expected rabbits to need more time to gather a sufficient quantity of good quality food (Wallage-Drees and Deinum 1986).

The demand for food in winter is determined by diametrically opposed factors. Rabbits do not have a large fat reserve (mean:7-21 g, Wallage-Drees 1986). The energy requirement in winter is less than in other seasons because there is hardly any sexual, agressive or burrowing behaviour. On the other hand energy is needed to keep the body temperature stable. In domestic rabbits basal metabolism increases 1,5 times when outdoor temperature drops from 14°C to 4°C (Kleiber 1975). Wild animals that have had time to adapt compensate partly by enhancing their fur thickness (insulation, Hart et al. 1965). Also keeping the fur dry, avoiding strong winds and staying in their burrows will help to reduce heat losses. The burrow presents an environment of moderate, stable temperatures (Hayward 1961). In this dilemma the Dutch rabbits choose to stay underground for many hours a day.
The rabbit originates from the Mediterranean. They have been extensively studied in Australia, where they are very successful in areas with climates resembling that Of the Mediterranean (Myers 1971). Rabbits are also successful in coastal dunes. It looks as if they have adapted to our climate by showing low activity in winter and becoming diurnal on the coldest days.

REFERENCES

BROEKHUIZEN,S. and MAASKAMP,F.(1980).Behaviour of does and leverets of the European hare(Lepus europaeus) whilst nursing. J.Zool.(Lond.), 191,487-501.

BROEKMEYER,M. and LUNEN,K.van (1986). Een onderzoek naar het effect van konijnen op de vegetatie van de Derde Duintjes, Boschplaat, Terschelling. Hugo de Vries-lab., Univ. Amst., intern.rep. 206.

CHATFIELD,C. (1975). The analysis of time series: theory and practice. London:Chapman and Hall.

DUNNET,G.M.,(1957). Notes on emergence behaviour of the rabbit Oryctolagus cuniculus(L.) and its bearing on the validity of sight counts for population estimates. CSIRO Wildl. Res.,2,85-89.

FEEN,P.J.van der (1963). Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biologisch Jaarboek 31, 237-243.

GEUT,G. and JANSEN,M.(1980). Enkele aspecten van de oecologie van het wilde konijn (Oryctolagus cuniculus(L.)). Intern. rep., Univ. Groningen.

GIBB,J.A., WARD,G.D.and WARD,C.P.,(1978).Natural control of a population of rabbits, Oryctolagus cuniculus (L.), for ten years in the Kourarau enclosure. Dept.Sci.Ind.Res.,Bull.223.

HART,J.S., POHL,H. and TENER,J.S.(1965). Seasonal acclimatization in Varying Hare (Lepus americanus). Can. J. Zool.,43,731-744.

HAYWARD,J.S.(1961). The ability of the wild rabbit to survive conditions of water restriction. CSIRO Wild.Res.,6, 160-175.

HOF,M.W.van, RIETVELD,W.J. and TORDOIR,W.E.M.(1963). Influence of illumination on locomotor activity of rabbits. Acta Physiol. Pharmacol. Neerl.,12,266-274.

HOLLEY,A.J.F. and GREENWOOD,P.J.(1984).The myth of the mad March hare. Nature,(Lond.),309,549-550.

HÖRNICKE ,H., DIETZEL,F., AIGNER,E., and SCHULTE,R. (1976).Alimentary behaviour in rabbits under different influences. 1er Congr. Int.cunicole,Dyon, commun. 13.

KLEIBER,M.(1975). The fire of life. R.E.Krieger, Huntington, New York.

KLINE,P.D.,(1965). Factors influencing roadside counts of cottontails. J. Wildl. Manage., 29,65-671.

KOLB,H.H.,(1986). Circadian activity in the wild Rabbit (Oryctolagus cunciculus). Mammal Rev.,16,145-151.

KRAFT,R.,(1978). Beobachtungen zur Tagesperiodiek von Wild und Hauskaninchen. Z.Säugetierkd.43,155-166.

LEMNELL,P.A. and LINDLOF,B.(1981). Diurnal and seasonal activity pattern in the mountain hare.Proc.first World Lagomorph Conf., Guelph,Ontario. (Ed.by K.Myers & C.D.MacInnes),pp.349-356.

LÉSEL,R.(1968). Essai d'estimation de la population d'Oryctolagus cuniculus L. sur la Peninsule Courbet (Iles Kerguelen). Mammalia,32,612-620.

LLOYD,H.G.(1964). Influences of environmental factors on some aspects of breeding in the wild rabbit, Oryctolagus cuniculus (L.). MSc thesis, University of Wales.

LOCKLEY,R.M.(1964). The private life of the rabbit. Worcester and London: Ebenezer Baylis and Son LZD.

LORD,R.D.(1964). Seasonal changes in the activity of penned cottontail rabbits. Anim. Behav.,12,38-41.

MYERS,K.(1957). Some observations on the use of sight counts in estimating populations of the rabbits, Oryctolagus cuniculus (L.). CSIRO Wildl. Res.,2,170-171.

MYERS,K.(1971). The rabbit in Australia. Proc.adv.study inst. 'Dynamics of Numbers in Populations', Oosterbeek, The Netherlands. (Ed.byP.J.den Boer and G.R.Gradwell),pp.478-507.

MYERS,K. and POOLE,W.E. (1961). The effects of season and population increase on behaviour. CSIRO Wildl.Res.,4,14-26

MYKYTOWYCZ,R. and ROWLEY,I.(1958). Continuous observations of the activity of the wild rabbit, Oryctolagus cuniculus (L.), during 24-hour periods. CSIRO Wildl.Res.,3,26-31.

NIETHAMMER,H.(1938). Ergebnisse von Markierungsversuche an Wildkaninchen. Z. Morphol. Okol.Tiere,33,297-312.

NUBOER,J.F.W.,(1971). Visual acuity measurements in a rabbit. PhD thesis, Univ. Utrecht.

NUBOER,J.F.W., NUYS,W.M.van and STEENBERGEN,J.C.van (1983) Colour changes in a light regimen as synchronizers of circadian activity. J. comp. physiol.151,359-366.

PRUD'HON,M and GOUSSOPOULOS,J.(1976). Comportement alimentaire du lapin de garenne en captivite. Ann.Zootech., 25,407-410.

REYNE,Y.,PRUD'HON,M.,DEBICKI,A.M. and GOUSSOPOULOS,J. (1977). Caracteristiques des consommations d'aliments solide et liquide chez la Lapine gestante puis allaitante nourrie ad libitum. Ann. Zootech., 27,211-223.

RIETVELD,W.J., TORDOIR,W.E.M. and HOF,M.W.van (1964). Influence of light to dark ratio, for a 24-hour cycle, on locomotor activity of rabbits. Acta Physiol.Pharmac. Neerl., 13,87-95.

ROWLEY,I.(1957). Observations on evening rabbit activity in relation to weather and sunset. CSIRO Wildl.Res.,2,168-169

SANDERSON,J. and VANDERWEELE,D.(1975). Analysis of feeding patterns in normal and vagotomized rabbits. Physiol.Behav. 15,357-364.

SCHANTZ,T. von and LIBERG,O. (1982). Censusing numbers of medium-sized nocturnal mammals in open landscapes. Proc. XIV Int.Wildl.Congr.,Dublin, 1979. Pp.409-417.

SIEGEL,S. (1956). Nonparametric statistics for the behavioral sciences. Kogakusha: McGraw-Hill,Ltd.

SNYDER,W.I.(1978). Feed constituent digestibility by adult and juvenile cottontail rabbits. PhD thesis, Department of Natural Resources, University of Cornell, Cornell.

SOUTHERN,H.N.(1940). The ecology and population dynamics of the wild rabbit (Oryctolagus cuniculus). Ann.appl.biol., 27,509-526.

STODART,E. and MYERS,K.(1964). A comparison of behavior, reproduction and mortality of wild and domestic rabbits in confined populations. CSIRO Wildl. Res.,9,144-159.

TITTENSOR,A.M.,WOODS,J.A. and FOX,A.P. (1978). Ecology of farmland rabbit populations. Pest Infestation Control Laboratory Report 1974-76,pp.155-157. HMSO,London.

WALLAGE-DREES,J.M. (1983). Effects of food on onset of breeding in rabbits, Oryctolagus cuniculus (L.), in a sand dune habitat. Acta zool. Fenn., 174,57-59.

WALLAGE-DREES,J.M.(1986). Seasonal changes in the condition of rabbits, Oryctolagus cuniculus (L.), in a coastal sand dune habitat. Z. Säugetierkd, 51,26-36.

WALLAGE-DREES,J.M. and DEINUM,B. (1986). Quality of the diet selected by wild rabbits (Oryctolagus cuniculus(L.)) in autumn and winter. Neth. J. Zool.,36:438-448.

ZEUNER,F.E.(1963). A history of domesticated animals,pp.409-415. London:Hutchinson.

RABBIT WITH GRASS FOR NEST

Chapter 6

EFFECTS OF FOOD ON ONSET OF BREEDING IN RABBITS, *ORYCTOLAGUS CUNICULUS* (L.), IN A SAND DUNE HABITAT

ABSTRACT

The influence of body weight of does and quantity and quality of the vegetation on start of breeding is described. An experiment with supplemental feeding in winter is done.
Breeding starts in the first week of March. Between February and March there is no improvement of the quality, there is, however, an increase in quantity of the vegetation. The availability of food in winter modifies the start of the breeding season.

INTRODUCTION

Rabbits are abundant in the coastal sanddunes of the Netherlands. The dunes provide a good habitat for the rabbits since suitable dry sandy soil for warrens is adjacent to feeding grounds (Rogers 1981).
The coastal dunes form an important protection of the lowlying country behind against the sea. Much care has been given to stabilize the outer range of dunes. To keep this intact and also to protect agriculture, rabbits are traditionally controlled by man. In the 'Noord-Hollands Duinreservaat', the nature reserve where my study is done, the management aims at a natural state, i.e. a minimal influence of man on the fauna. In this context it is important to know which factor(s) determine(s) the population density of rabbits. During this study it became evident that the timing of the start of the breeding season is flexible and in some way connected with the situation in the previous winter. After a cold winter with much snow (1979) breeding started later than average.
Rabbits are known to be opportunist breeders (Flux 1965, Hughes & Rowley 1966). Is has been found that breeding in the rabbit may commence during any season of the year. Recent research by Davies (unpubl.) shows that does possess mature follicles all year round. In Mediterranean-type climate breeding starts rather abrupt when succulent plant species begin to grow (Poole 1960. Myers & Poole 1962, Stodart & Myers 1966). In our climate rabbits have one breeding season in spring. The timing of the start of the breeding season could have an influence on total production per year and hence on the population level.

METHODS

The actual start of breeding is determined by the physiological state of the does. Bucks are often fertile weeks before the first successful conceptions occur (Skira 1978, own observation). Possible factors influencing the start of breeding are: improvement in quantity and/or quality of the food; condition of the does, dependent on food the previous winter; direct influence of the weather; or a combination of these.

With shot animals it was possible to check whether there is a difference between the pre-breeding and the breeding samples in body weight of does and/or quality of the diet. Body weight was used as an indicator of condition. It has been assumed that there is a direct relationship between the stomach content (minus the fundus which contains the soft pellets) and the food actually taken. As measures of quality crude protein percentage and cell-wall contents were analysed. Cell-wall contents can be used to obtain an index of the digestibility of plants.

The reproduction in the rabbit population was monitored at the same time, in winter and spring 1980, as the vegetation growth was measured and its quality as rabbit food analysed. The area was a blown out valley in the outer dunes, 400 m. from the sea. The vegetation consisted of a short grazed cover of grasses, forbs and mosses with some low bushes of Salix repens, Hippophaë rhamnoides and Ligustrum vulgare.

Rabbit populations were monitored by capture, marking and intensive observation. Quantity of food was estimated by measuring height and cover of all grasses and forbs by the point quadrat method (Goodall 1952). The quality was measured by analysing crude protein and cell-wall contents of random samples of the green vegetation, grasses and forbs kept separate. Generally dicotyledons are richer in protein and contain less cell-wall than monocotyledons, so they constitute food of higher quality. The increase in (soil) temperature and the growth of the vegetation could not be separated in this situation.

The influence of the availability of food in winter was studied with an experiment in 1980-1981. One enclosed population (enclosure 1.4 ha) was fed on oat rich mixture as a supplement to the dune vegetation present. There were a fenced and a free-living control population. The enclosures were much larger than the average home-range of rabbits in the dunes. The populations were monitored as above. From captured does the reproductive condition was assessed by feeling for uterine swellings, possible from 10 days onward, and determining whether the belly has been plucked.

RESULTS

ONSET OF THE BREEDING SEASON AND BODY WEIGHT OF DOES

Both 1980 and 1981 were rather mild winters. In March most of the does were pregnant or parous (Fig. 1). No resorption was observed, but the number of embryos around 12 days old was small. The embryos were of different ages. After calculating the age (Minot & Taylor 1905, Brambell 1942) it was estimated that 50% of the does were pregnant in the first week of March. There is an indication that heavy does may become pregnant earlier than the others, but onset of reproduction in individuals shot in March is not significantly correlated with body weight.

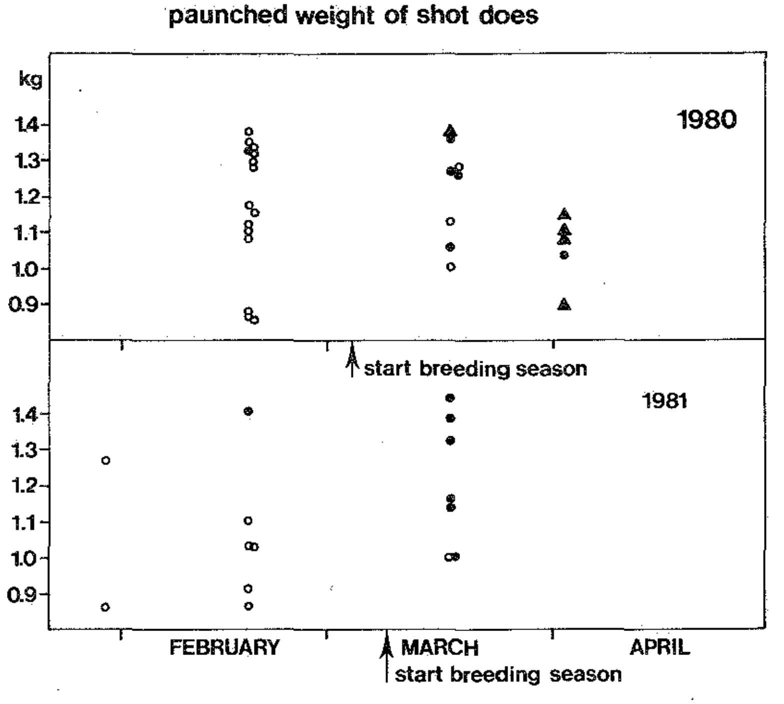


Fig.1 Paunched weight of shot pregnant and non-pregnant does.
●=pregnant ▲=parous O=non-pregnant,non-parous

Breeding in February is possible, as these incidental pregnances show. It is also proven by the supplemental feeding experiment (see below) and is mentioned in research on the British Isles (Lloyd 1970, Brambell 1944). Although there is an increase in the mean weight (Fig. 1) many does are in a good condition in February. Consequently condition cannot be the trigger for the start of breeding in March.

CHANGE IN VEGETATION

There must be some change in the environment between February and March that stimulated the does to start breeding. Quality and/or quantity of food, already indicated by research elsewhere, were considered likely factors. The growth (increase in biomass) of mono- and dicotyledons is compared with the birth dates of young (Fig. 2). To compare dates of birth, given in Fig. 2, with dates of conception, one has to take into account a pregnancy of 30 days.

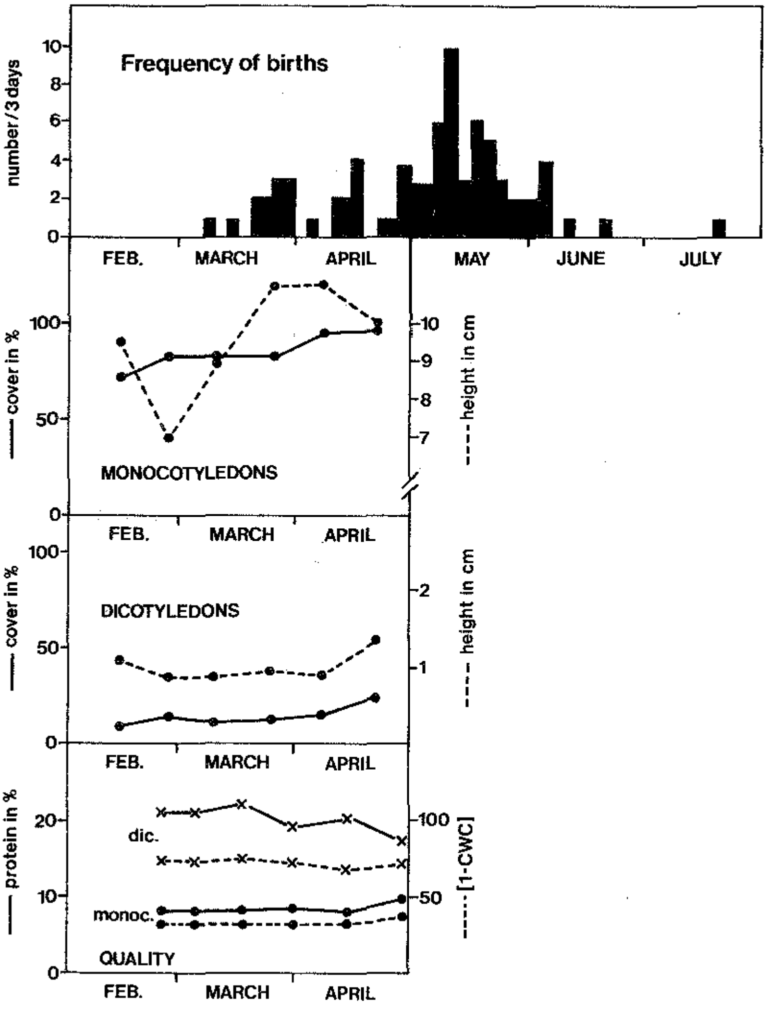


Fig.2 Frequency of births, increase in biomass and quality of the vegetation

We caught only young from 21 days onward. Compared to the data from shot animals (Fig. 1) there seems to be a bias towards catching the very first young rabbits in March. Breeding starts gradually.

Table 1

CELL-WALL CONTENTS AND CRUDE PROTEIN (%,means ± s.e) of stomachs of shot rabbits (males and females)

		n	CWC	n	CP
February	1980	17	53 ± 2	18	20 ± 1
	1981	12	55 ± 2	15	18 ± 1
March	1980	14	55 ± 3	10	20 ± 1
	1981	12	54 ± 2	9	22 ± 1

The growth of the perennial monocotyledons coincides with the start of the breeding season and the increase in biomass of the, mostly annual, dicotyledons coincides with the peak of the first litters, when many does are suckling and the first young take solid food. Suckling and growing both require a lot of energy and a high percentage of protein in the food (Davidson & Spreadbury 1975, Maynard et al. 1979).

Table 2

NUMBER OF PREGNANT OR PAROUS FEMALES IN THE POPULATIONS ON MARCH 5, 1981.
reconstruction from capture around that date. n=number of females caught.

	n	parous & pregnant	not parous or pregnant
control populations	9	3	6
fed population	5	5	0

Difference significant, p=0.028, with Fisher exact probability test.

QUALITY OF THE FOOD

The quality of the food plants does not change between February and March (Fig. 2). Another way to assess a change in quality of the food is to analyse stomach contents, assuming they are representative of the food actually eaten. Table 1 gives the data for the shot rabbits. Data from males and females are pooled, since there was no significant difference between them. The data indicate only an increase in crude protein in the diet in 1981.

INFLUENCE OF WINTER FOOD

Supplementary food was provided in 1980-81. Compared to the control populations the first young rabbits in the fed population were observed and caught exceptionally early. A litter must have been born around January 15; the conception must be dated in December. As this could be an incidental case I also assessed the reproductive condition of does caught in a trap. From these captures I reconstructed the reproductive situation on March 5, 1981 (Table 2). There were significantly more does reproducing in the fed population. Table 3 shows the mean live weight of these does. They were much heavier than the others, even after a correction for the weight of uterus and mammary glands. Their heavy weight by itself is enough explanation for the earlier onset of the breeding.

Table 3

MEAN LIVE WEIGHT (minus estimated weight of uterus and mammary glands) OF FEMALES IN FED AND CONTROL POPULATIONS (kg, mean ± s.e.)

	n	weight
control populations	8	1.41 ± 0.07
fed population	4	1.68 ± 0.05

CONCLUSIONS

In the coastal sanddunes in a temperate climate breeding starts gradually. Fifty percent of the does were pregnant in the first week of March in 1980 and 1981. Between February and March there is no improvement of the quality, there is, however, an increase in quantity of the vegetation on offer, especially of the monocotyledons. The growth of the dicotyledons starts later and coincides with the first peak of suckling does.

These data could indicate that the growth of the grasses, which is phenologically related with the growth of the forbs, is a trigger for the first succesful conceptions. The availability of food in winter modifies the start of the breeding season through the enhanced condition of the does. Some very heavy does in the natural situation also do not wait for the food situation to improve before they start breeding.

REFERENCES

Brambell, F.W. 1942: Intra-uterine mortality of the wild rabbit. Proc.Royal Soc.Lond. (B) 130:462-479.

Brambell, F.W. 1944: The reproduction of the Wild Rabbit, Oryctolagus cuniculus (L.) Proc.Zool.Soc.London 114: 1-45.

Davidson, J. and D.Spreadbury 1975: Nutrition of the New Zealand White rabbit. Proc.Nutr.Soc. 34:75-83.

Flux, J. 1965: Timing of the breeding season in the hare, Lepus europaeus Pallas, and rabbit, Oryctolagus cuniculus (L.) Mammalia 29: 557-562.

Goodall, D.W. 1952: Point quadrat methods for the analysis of vegetation. Austr.J.Botany 1: 457-461.

Hughes, R.L. and I.Rowley 1966: Breeding season of female wild rabbits in natural populations in the Riverina and Southern Tablelands districts of New South Wales. CSIRO Wildl. Res. 11: 1-10.

Lloyd, H.G. 1970: Variation and adaptation in reproductive performance. Symp.Zool.Soc.London 26: 165-188.

Maynard, L.A., J.K. Loosli, H.F. Hintz and R.G. Wagner 1979: Animal nutrition. McGraw-Hill, 601 pp.

Minot, C.S. und E.Taylor 1905: Normentafeln V.Ed.Keibel, Jena.

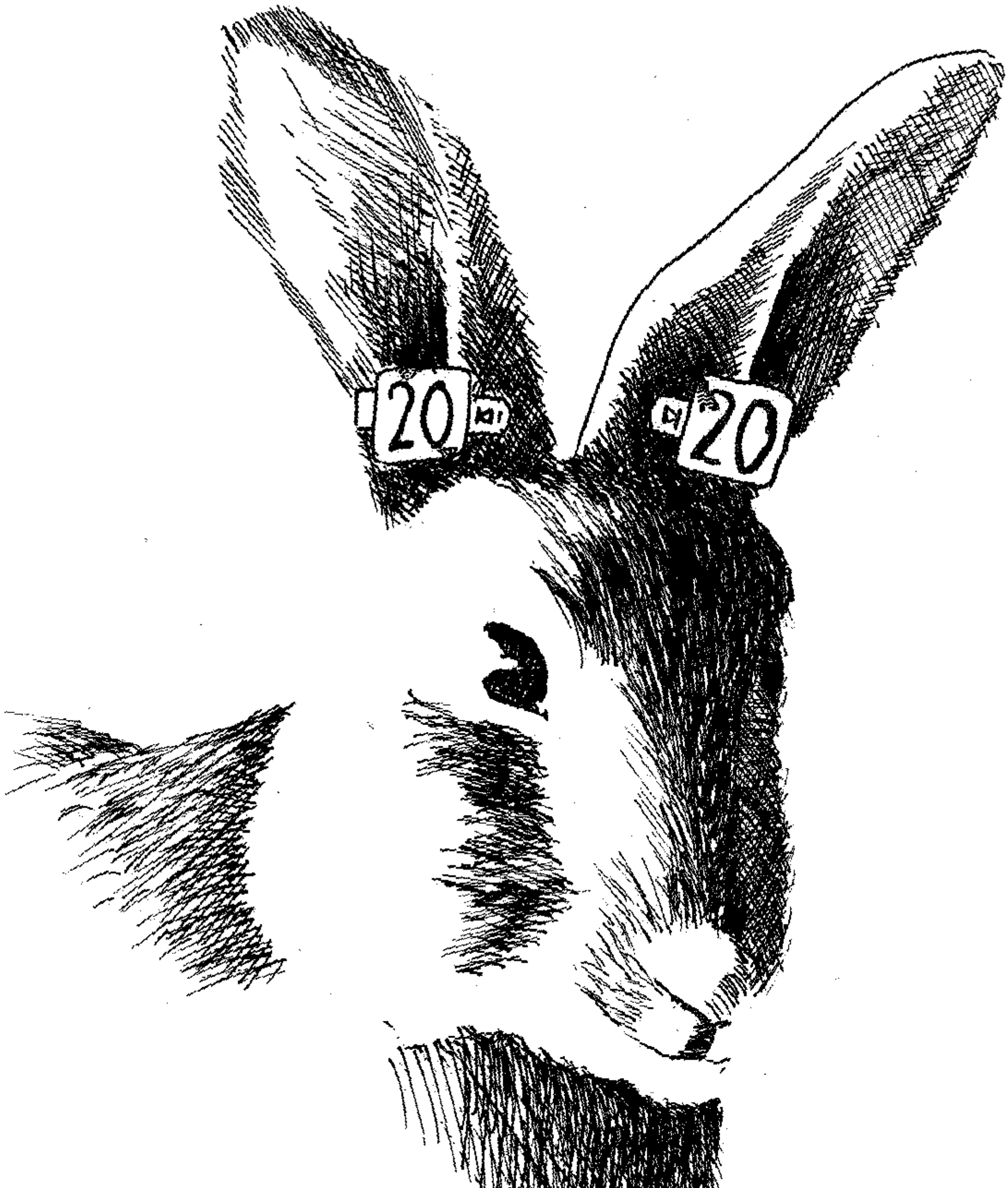
Myers, K. and W.E. Poole 1962: A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations III. Reproduction. Austr.J.Zool. 10: 225-267.

Poole, W.E. 1960: Breeding of the wild rabbit in relation to the environment. CSIRO Wildl.Res. 5: 21-43.

Rogers, P.M. 1981: Ecology of the European wild rabbit Oryctolagus cuniculus (L.) in mediterranean habitats II. J. Appl. Ecol. 18: 355-371.

Skira, I.J. 1978: Reproduction of the rabbit, Oryctolagus cuniculus (L.), on Macquarie Island, Subantarctic. Austr.J.-Wildl.Res. 5: 317-326.

Stodart, E. and K.Myers 1966: The effects of different foods on confined populations of wild rabbits, Oryctolagus cuniculus (L.). CSIRO Wild. Res. 11: 111-124


20
20

Chapter 7

THE INFLUENCE OF THE FOOD SUPPLY ON THE POPULATION DYNAMICS OF RABBITS (ORYCTOLAGUS CUNICULUS(L.)) IN A DUTCH DUNE AREA

ABSTRACT

The population dynamics of rabbits in a temperate, maritime climate were studied in response to the question: are rabbit numbers kept in check by intrinsic responses to density, or by predation and disease,or do they rise to the level permitted by the food supply? The study was carried out in a few small observation plots within a coastal dune nature reserve. An experiment employing supplemental feeding was conducted during autumn and winter. In the severe winter of 1978-79 rabbits died from starvation. In the following years population density increased, but did not reach the upper limit set by food availability. Fullgrown rabbits were eaten by fox, stoat and occasionally cat and polecat. Littering frequency was low and may have been depressed by high rabbit density. The length of the breeding season was determined by an interaction between population density and food quality. Predation and other mechanisms potentially capable of regulating population size were not strong enough to keep rabbit density below the level permitted by the food supply. Reasons for this are discussed.

INTRODUCTION

In the coastal sand dunes of The Netherlands many nature reserves are established. The vegetation is vulnerable to overgrazing, which can lead to rain and wind erosion. Rabbits can cause damage to the dune vegetation, and in many places managers try to control rabbit populations by hunting them during autumn and winter. The question remains, however, whether availability of food during the winter already limits rabbit population densities. This question has become more of present interest since the impact of myxomatosis is lessening.

It has been discussed widely as to whether herbivore numbers are limited by food supply, or whether intrinsic behavioural responses to high density, or predation or disease, prevent populations from reaching the limit set by food availability. Watson & Moss (1970) argued that since changes in behaviour (dominance, spacing behaviour and aggression) invariably attend population limitation, these factors must be all-important in setting population size. However, it is more likely that changes in behaviour arise as inevitable symptoms of over-crowding displayed as the carrying capacity of the habitat is reached (e.g. Lack,1954).
Cowan & Garson (1985) describe how rabbit numbers are limited by the number of burrows on the chalk, but not on the dunes. On the chalk, much more aggression and burrow defense occurred.
Gibb et al.(1978) considered that density-dependent behavioural or physiological mechanisms were too weak to regulate populations of rabbits. They stated that "the population of rabbits appeared to be limited by extrinsic factors alone" and concluded that rabbit populations in New Zealand were kept in check by predators, mainly feral cats and ferrets.

Rabbits have been particularly well studied in Australia. Myers & Poole (1963) concluded that starvation was the only mortality factor of consequence in determining density. Myers (1971) forwards the hypothesis that the characteristics of rabbit population dynamics in Australia reflect the conditions under which the rabbit originally evolved: "The rabbit in Australia possesses no inbuilt physiological or behavioural mechanism to control its numbers. The rabbit evolved in a system where extrinsic mortality factors (mainly predation) are necessary to maintain population stability." The rabbit evolved in the Mediterranean region (Flux & Fullagar,1983) and so, according to Myers, rabbit numbers there should be kept in check by predation.

Compared with the relatively recent introductions of rabbits in Australia and New Zealand, rabbits have been established in north-western Europe since 1250 (Rentenaar,1978;van der Feen,1963). Predation might be expected to have a greater impact on rabbit numbers in these older habitats. However, with regard to predation, the situation in north-west Europe is quite different from that in the Mediterranean. Delibes & Hiraldo (1981) describe that in Spain many more birds of prey

and mammalian predators prey on rabbits than in other parts of Europe.
Historically, foxes, cats, mustelids and birds of prey have been much hunted in the dutch coastal dunes, to protect hunting and commercial interests in rabbits. Predators are protected now, and the fox has re-established itself since 1968. This fact has led to this study on the population dynamics of rabbits.

The study was set up to determine whether rabbit numbers rise to the level permitted by their food supply. It is impossible to quantify food supply correctly. Standing vegetation is not the same as available food. Only part of the vegetation is usable, so suitable food can be in short supply even where vegetation is abundant (Sinclair,1975). In addition, rabbit grazing can effect the composition of vegetation and hence the suitablility of the habitat, and plants may show compensatory growth in response to grazing (McNaughton,1983).
Therefore, to determine whether rabbit numbers have reached the level set by the food supply, we studied whether reproduction and survival are food-dependent.

A few small populations were monitored by catching, marking and observing over several years. By providing supplementary food to one population it could be determined whether relieving food scarcity in wintertime led to reduced mortality and increase in reproduction.
This experimental approach was supplemented by a study on condition and disease of rabbits shot in other parts of that same dune reserve (Wallage-Drees,1986).
Observations on rabbit breeding in stops was done on a former arable field used as parking lot in the same dune reserve.

METHODS

THE STUDY AREA

The study was carried out between January 1978 and June 1981 in the 'Noord-Hollands Duinreservaat' (NHD), an area covering 4765 ha of coastal dunes northwest of Amsterdam . The reserve is managed by the Provincial Waterworks of North-Holland (PWN) and rabbits are hunted by game wardens in order to reduce damage. With their help many data on condition and food of rabbits were collected (Wallage-Drees,1986; Wallage-Drees & Deinum,1986).

The actual study area was situated about 800 m from the sea in a vegetation mosaic of Hippophaë rhamnoides, Rubus caesius, Salix repens ,mosses, forbs,grasses and sedges (mainly Festuca ovina, Carex repens) classified as 'Rubus caesius landscape' (Doing,1964).
This coastal area has a mild, maritime climate(fig.1) with little seasonal fluctuation in rainfall. There is usually some snow in January and February. The first study winter in 1979 was much colder than average; snow covered the ground completely for 23 days in January and February and there were at least 5 days with glazed frost.

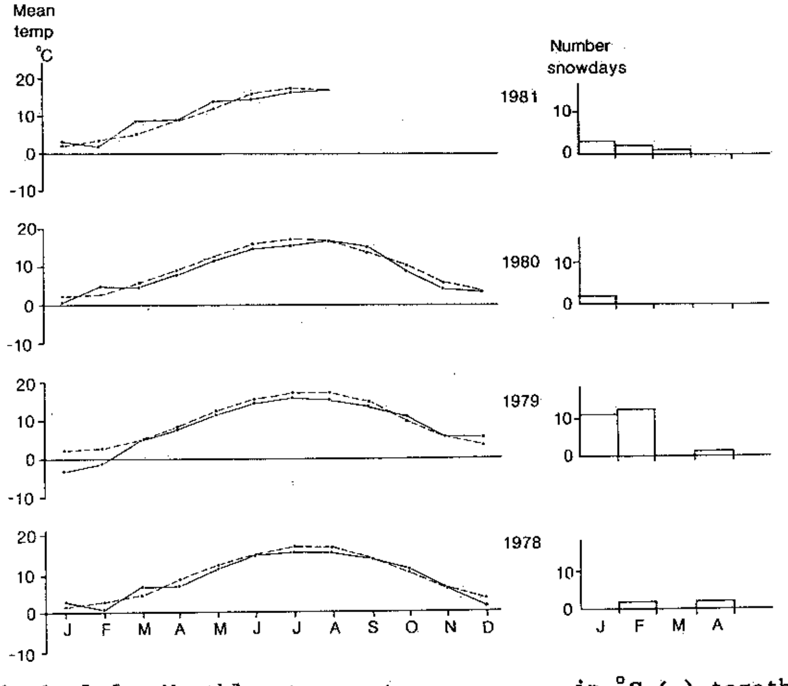


Fig.1 left: Monthly temperatures means in °C (—) together with the means over 1950-'80 (- - -). Data from KNMI, De Bilt.
right: Number of days with complete snow cover. Data from the recording station of PWN (see fig.1 in ch.1).

THE OBSERVED POPULATIONS

Rabbits were observed in seven plots (table 1). Five plots were made by fencing in a few inhabited burrow systems, including foraging areas, while the sixth and seventh populations were left as unfenced controls. Plot 7 was added in 1980 and was bounded on two sides by a canal, on a third side by high grass not used by the rabbits and was open on the fourth side.
The boundaries of plots 6 and 7 were determined from observations on the movements of the rabbits that lived inside the plots.
The size of our plots varied from 0.7 to 1.4 ha (table 1). Myers (1964) did not notice any detrimental effect on behaviour or physiology when keeping rabbits in enclosures of 0.3 and 0.7 ha.
Fences were 1 m high with a mesh width of 3 cm. They were designed to ensure which rabbits got the supplemental food, while (as far as possible) allowing free access to predators.

Table 1

SIZE OF THE PLOTS IN THE STUDY AREA

fenced			unfenced		
nr	size	in use	nr	size	in use
1	1.3 ha	1978-79	6	1.3 ha	1978-79
2	0.7 ha	1978-79, 1980-81	7	1.4 ha	1979-81
3	0.7 ha	1978-79			
4	1.3 ha	1978-79			
5+	1.4 ha	1978-79, 1980-81			

+Plot with supplementary feeding

The drawback of fencing was that it prevented dispersal. However, dispersal in rabbits is generally found to be small and not responsible for regulating population density (Gibb,1977; Myers & Poole,1961; Myers & Schneider,1964; Mykytowycz & Gambale,1965; Southern,1940; Tyndale-Biscoe & Williams,1955). We never noticed immigration of untagged rabbits into our unfenced populations and consequently, also considered that there was no emigration. This was corroborated by the fact that no tagged rabbits from the observed populations were seen or shot outside the study area. Also, from rabbits tagged as nest young on the parking lot, 5 out of 45 were shot in their first year, all not farther than the border of the parking lot.
We believe that fences did not significantly influence predator activity. The main predators in the coastal dunes were stoat, polecat, fox and feral cat. Both stoat and polecat could creep through the fence and cats and foxes could climb over it. From tracks and sightings we know that stoats, polecats and foxes got inside the fences.

The fences possibly increased the chance of predation by making escape more difficult. This could only be checked for predation by stoats. Predation by a stoat can be recognized from bite-wounds on the rear of the animal (only visible by removing the fur), a gaping wound in the neck, and extensive subcutaneous haemorrhage (Hewson & Healing, 1971). The fenced plots and another similar area of the same size (5.4 ha) were searched for rabbit carcasses. Between 1 November 1978 and 1 March '79, 14 carcasses/ha were found in the fenced areas and the same number in the searched area. Therefore, assuming the same population density on both sites, fences do not seem to have influenced the level of mortality caused by stoats.

PARAMETERS OF SURVIVAL AND REPRODUCTION

Two sets of parameters were measured. Population size in autumn and winter, impact of predation, body weight in wintertime were assessed with regard to rabbit survival and litter size, timing of the breeding season, littering rate, growth and survival of the young, the relative participation of adult and juvenile females in breeding were assessed with regard to reproduction.

SUPPLEMENTAL FEEDING EXPERIMENT

To determine the influence of food availability on winter mortality an experiment was conducted in which the rabbits in plot no.5 were supplied with additional food. This consisted of oats, wheat and the peel of *Ceratonia siliqua*, producing a mixture of high energy and low protein . Food was scattered ad libitum every two days at three foraging spots from 21 October 1980 until 20 March 1981. The food remained in good condition for at least two days. If little food was left over, the amount supplied was increased. Initially, 2.25 kg was given at each feed, which was increased to 4.5 kg from December onwards.

CONDITION OF RABBITS AND POPULATION SIZE

Rabbits were caught in live traps baited with oats and set at foraging spots. A few were caught by ferreting. After capture weight,sex and length of the hindfoot were recorded. Because rabbits were released we used body weight to distinguish juvenile(first-year) and adult rabbits. In shot rabbits from the same reserve body weight correlated well with eyelens weight,which is regarded as a reliable parameter of age (Wallage-Drees ,1986). To determine whether females were pregnant and/or suckling, the condition of the nipples and the fur on the belly were checked (females line the nest with fur shortly before parturition) and the belly palpated. At first capture, rabbits were marked on both ears with a label that could be recognized at day or night when observing with a telescope: a monel wing band size 4 with an enlarged surface covered with reflecting yellow tape and with an individual code in black letters and numbers.

Two methods were used for estimating population size.
a)Field counts were made just after sunset. The highest value of four counts on consecutive days was divided by the maximum proportion that was above ground in the same area during that month (see Wallage-Drees, in press).
b) From September 1979 onwards ,when the major part of the population had been marked, live-calendars were constructed from recaptures and sightings. The number of unmarked individuals was assessed from sightings.
Population size was not calculated using a capture-recapture method, however, because the chances of being caught were not randomly distributed (Daly,1981;this paper table 2).

The whole observation area was searched intensively during the study and the chances of having missed emergent litters or fullgrown rabbits with severe myxomatosis were low . Also, the game wardens were aware of our study and brought us tags or tagged rabbits whenever they found them.

RECRUITMENT AND JUVENILE SURVIVAL

Young rabbits are born in a nest-chamber,either in a blind diverticulum of a warren system or at the end of a separate blind tunnel called a 'stop' (Lloyd & McCowan, 1968). The doe visits the young only once or twice in 24 hours and leaves the nesting burrow blocked up while she is absent. Young rabbits emerge and make small excursions outside the burrow from about their 22nd day (Broekhuizen et al., 1986). From that age onward they could be caught in traps set in the burrow entrance. The probability of capturing them was increased by finding the places where young emerged. Older young were also caught in traps set at foraging spots. Young were marked with the same tags as the adults.
The populations under observation littered in existing burrows. Many nests appeared to be located in empty burrows of which there were large numbers.
Stops were found on former arable fields in the reserve, which are now used as parking lots or as playgrounds. Nests in stops provided data on litter size and growth of kittens that could not be obtained from the actual study area.

Litter size is affected by the partial loss of embryos during gestation (Brambell, 1943) and by the death of part of the litter in the nest. One has to be careful in opening a stop lest the doe deserts the young. We found that stops with young under 10 days, even when opened carefully and blocked again after inspection , were deserted by the mother. The birth date was estimated from the timing of visits by the doe: once the young are born she opens the stop every night (Myers, 1958). Litter size was defined as the size at the first count 10 days after the birth of the litter.
In 1980 and '81 not enough stops were found to determine litter size from nests in stops. However, in 1981,the litter size in utero from rabbits shot in February and March could be recorded when uterine swellings were visible at dissection. The embryos were aged according to the drawings of Minot & Taylor(1905).

LITTERING RATE

The littering rate is the number of litters born each month divided by the number of adult females present at the beginning of the next month (Parer, 1977). In this study the number of litters per year per doe was assessed by observation and capture of emergent young.
Rabbits have a post-partum oestrus. In this study littering rate was never 100%. No distinction could be made between does that did not conceive post-partum, lost embryos before full-term, or whose young did not survive till emergence.

PATTERN OF THE BREEDING SEASON

The pattern of the breeding season was deduced from the appearance of litters in the study area and the distribution of age cohorts in the autumn bag of the wardens.

THE AGE OF DEAD RABBITS

The age of dead rabbits was determined using their eyelens weight according to the formula given by Myers & Gilbert (1968), i.e. age(days)=-57+181.4/ln(314/lens weight(mg)). A similar formula was found in this study, based on data from 15 rabbits with known birth date who were either shot at the parking lot or found dead in the study area. This sample gave: age(days)=-64+228.8/ln(314/lens weight(mg)) which lies within the 11% standard deviation given by Myers & Gilbert (1968). As their formula was based on a much larger sample, it was used.

AVAILABLE FOOD IN THE BREEDING SEASON

To assess the quantity and quality of food available during the breeding season, the relative biomass of the vegetation was measured from mid-February to mid-June. The relative biomass of a 'species' was defined as the product of cover and average height. Cover was measured by the point-quadrat method (Mueller-Dombois & Ellenberg, 1974) and average height by measuring all plants touching the point quadrat within a distance of 0.5 cm. This was done on a grid of 392 points. Cover was summed and height averaged for monocotyledons and dicotyledons separately, as these show a difference in quality as rabbit food (Wallage-Drees, 1983).

RESULTS

WINTER MORTALITY

CAPTURE RATE

Captures in the baited live-traps were not distributed at random with regard to age and sex . For example, table 2 gives figures for a few months in which the composition of the population was well-known. In autumn juveniles were caught more often than adults(2A), pregnant does were caught more often than bucks (2B) and supplementary feeding reduced the chance of capture(2C).In September, juveniles increased in weight more than adults (table 7), and does need extra food when pregnant or lactating. Generally, one might conclude that rabbits which need more food enter the traps more readily.

Table 2

CAPTURE RATES
n=population size

2A **Frequency of captures of adults and juveniles.**
Plot 2 & 7.

	September 1980			January 1981		
	n	no.of captures	X^2	n	no.of captures	X^2
adults	36	3	85.3($p<0.001$)	8	6	0.76 n.s.
juveniles	12	33		17	8	

2B **Frequency of captures of males and females in the reproductive season (1 March-3 June).**
1981, plots 2,5&7.

	n	no.of captures	X^2
♂♂	14	17	11.9 $p<0.001$
♀♀	18	55	

2C **Frequency of captures in plot 5 with supplementary feeding, compared with the untreated plots 2&7.**
January 1981. (tested: observed vs. expected values).

	n	no.of captures	X^2
plot 5	16	3	3.3 n.s.
plots 2 & 7	25	14	

POPULATION REDUCTION

Table 3 gives the number of rabbits in the plots and the mortality rate during autumn and winter. A variable number of plots were used, because, following heavy mortality in the winter of 1978-79, not enough rabbits survived in the original study area to continue the work there. Consequently, we moved to another area nearby called plot 7. Meanwhile, plots 2 and 5 were restocked with rabbits caught in other parts of the reserve, and so plots 2,5 and 7 could be monitored in 1980-'81. The mortality rate varied between months and years. It was highest from December 1978 to March 1979. In 1980-81 no differences in mortality rate were found between plot 5, with supplemental feeding, and the controls.

For 1979-80 and 1980-81 the mortality of juveniles and adults and of the two sexes were calculated separately. No significant differences were found, either between age-groups or sexes, and therefore, these classes are not treated separately in table 3.

Table 3

POPULATION SIZE AND MORTALITY IN THE STUDY AREAS

	population size			mortality(%)	
	Sept.	Dec.	March	Sept.-Dec.	Dec.-March
1978-'79 plots 1-6 6.7 ha	244	89	25	64	72
1979-'80 plot 7 1.4 ha	41	32	21	22	34
1980-'81 plots 2&7 2.1 ha	48	29	19	40	34
plot 5+ 1.4 ha	29	21	12	28	43

pop. decrease 1978-'79 vs. 1979-'80: X^2=40.6 p<0.001

1980-'81: X^2=24.7 p<0.001

pop. decrease 1979-'80 vs. 1980-'81: X^2=0.79 n.s.

1980-'81, in autumn, plot 5 vs. plot 2&7: X^2=0.68 n.s.

1980-'81, in winter, plot 5 vs. plot 2&7: X^2=0.09 n.s.

+ experimental plot:supplemental feeding during Oct.-March

CAUSES OF DEATH

In table 4 data about the causes of death are summarized and compared to the decrease in total population numbers. The decrease in population numbers shows that the number of rabbits that disappeared without their carcasses being found was higher in autumn 1978 than in winter 1978-79. This was due on the one hand to the lower rate of decay in winter and on the other hand to our attention being drawn to the carcasses by the behaviour of magpies, who were more attracted to carcasses in winter than in autumn.

Table 4

NUMBER OF RABBITS THAT DIED AND CAUSES OF DEATH

	a estimated total number of deaths at the study site	b trap or ferret	c myx	d stoat	e fox	f carcass found, cause unidentified	a-(b to f) missing
1978-79 6.7 ha							
Sept-Oct	44	0	0	3	1	9	31
Oct-Nov	93	0	1	17	0	2	73
Nov-Dec		1	1	20	0	1	
Dec-Jan	46	0	1	5	0	2	15
Jan-Feb	24	1	0	19	0	2	2
Feb-Mrch	22	2	0	8	1	11	0
1979-80 no carcasses or remains found							
1980-81 3.5 ha							
Sept-Oct	3	1	1	0	0	0	1
Oct-Nov	12	1	0	0	0	0	11
Nov-Dec	12	1	0	0	0	0	11
Dec-Jan	9	0	0	0	0	2	7
Jan-Feb	6	0	0	0	0	0	6
Feb-Mrch	4	1	0	0	0	0	3

First, we examine whether the catching procedure caused additional mortality. During the three years of the study 9 rabbits were found dead in traps (table 5). From the study of the warden's game bag we know that the lethal minimum body weight of adults is around 1100 g (Wallage-Drees,1986: fig.5). Therefore, we expect that rabbits of about this weight or less, if they had not been caught in a trap , would have died from starvation. In two cases, two rabbits were found together in the same trap. This could have been responsible for the death of one of them, but because of the small number involved, this was only a minor addition to deaths from natural causes.

Table 5

RABBITS FOUND DEAD IN LIVE-TRAPS 1978-'81

Date	Body weight(g)	Comments
2-03-'78	860	
9-02-'79	1225	myxomatosis
23-02-'79	1150	
23-02-'79	1100	
21-03-'79	890	
16-09-'80	930	2 rabbits in one trap, one dead
13-11-'80	950	
3-03-'81	1280	2 rabbits in one trap, one dead
03-04-'81	1380	weight loss 240g since 15-03

DISEASES AND PARASITES

Rabbits caught in live-traps did not manifest any symptoms of disease, except for myxomatosis. Rabbits shot in another part of the reserve and dissected had intestinal parasites, especially Graphidium strigosum and Taenia sp. These rabbits did, however, seem to be in good condition. Only one out of 175 rabbits showed symptoms of liver coccidiosis.

myxomatosis

Few rabbits with symptoms of myxomatosis were found(table 4). Other evidence also indicated a low rate of mortality from myxomatosis. Over the three years of the study, 29 animals on the study site were seen to have myxomatosis: 23 of these were juveniles and 6 were adults. At least 10 of the rabbits are known to have recovered. Myxomatosis occurred mainly at the end of summer (table 6). Nestlings may die from myxomatosis in spring without showing symptoms (Fenner & Ratcliffe, 1965). In this study causes of death of nestlings were not assessed.

Table 6

NUMBER OF RABBITS ON THE STUDY SITE SEEN WITH MYXOMATOSIS

	1978-79	1979-80	1980-81
Sept	7	0	1
Oct	2	0	0
Nov	2	0	0
Dec	1	0	0
Jan	0	0	1
Feb	0	0	0
March	0	0	0
April	0	1	1
May	0	1	1
June	0	1	-
July	1	3	-
Aug	0	6	-

STARVATION

The chance of capture was higher in rabbits that required more food (table 2). Therefore, if there had been starving rabbits in the study area, they should have been caught. In the winter of 1978-79 three of the 'trap deaths' could be attributed to starvation. In this year I observed that rabbits were less alert: another sign of starvation.

In 1980-81 I did not see any evidence of starvation. The weight changes of ten rabbits that disappeared during December - February, and were assumed to have died, were known up to the time of disappearance. These had all been positive (+0.66 to +5.66 g/day). The comparable figure for rabbits who were observed to be alive in March was -1.10 to +5.40 g/day, (n=13). This does not suggest that starvation was a cause of mortality in this year.

PREDATION

Predation is almost always elusive and hard to measure.
The number of rabbits caught by predators can only partly be deduced from table 4.

Full-grown rabbits in the coastal dunes were eaten by fox,polecat, stoat and feral cat, and the first three species were seen in the study area.

Large numbers of rabbits killed by stoats were found in 1978-79 (table 4,column d) . In addition, many of the carcasses of which the condition did not allow determination of the cause of death (table IV,column f) may also have been killed by stoat. Magpies often found the carcass and ate what was left.
In November and December 1978 we found 15 juvenile rabbits killed by stoats that had not yet been damaged by magpies.

Their mean weight($\pm$s.e.) was 1380$\pm$45 g. When I simulated the wounds to rabbits caused by stoats I concluded that an average of 40 g of flesh were eaten. Adding this eaten part gives a converted mean weight of the juvenile rabbits of 1420 g. The mean weight of juveniles in the warden's game bag for the same months was 1450 g $\pm$ 25 (n=64). During this period only one adult rabbit was found killed by a stoat. This suggests that stoats take healthy, but inexperienced rabbits. Stoats may have had no other choice, however, because there were no weakened rabbits present at this time of year. By taking healthy prey the stoat could be a factor influencing rabbit population density.

Polecat kills were not found, but may have been included in the figures for the stoat. A polecat might drag a full-grown rabbit away from the spot where it was caught, but only in the unfenced plots. The same applies to the cats and foxes. Feral cats were scarce in the Dune Reserve. Foxes are known to carry away their prey and bury it, so reducing the chance of finding the remains of fox kills. Carcasses with the head severed or buried were attributed to foxes. Such prey remains were found only twice during the study (table 4, column e).

The number of rabbits caught by foxes were assessed in the following way. Mulder (1985b), who studied the fox in the same dune reserve, estimated that rabbits constitute 90% of the weight of the diet of foxes. A fox needs 350-550 g (Lloyd,1980) to 480-700 g (Niewold, 1976) of food per day. An average (juvenile) rabbit weighed around 1500 g (Wallage-Drees,1986). Therefore, one rabbit and some other prey may provide a fox with food for two days. Fox territories in the NHD, on average, covered 165 ha and contained three adult foxes and their young at years of high fox population density. In 1980 they ususally contained two adults. Here we calculate the situation at maximum fox density. Assuming that from September until December three adult and three full-sized young inhabit a territory, and that from 1 December the young start to disperse, we might expect 6 foxes/165 ha from September through November and 4 foxes/165 ha from December through April (Mulder, 1985a). Their minimum food requirement would then be:
90 rabbits/165 ha per month during Sept.-Nov., and
60 rabbits/165 ha per month during Dec.-April.
They might waste food in autumn, but it was assumed not in winter.
Foxes were expected, therefore, to remove one or two rabbits per month over the whole of the three plots of the study site in 1980-81; a small loss compared to total rabbit numbers at that time (table 3).

During the study period there was a change in the populations of predators. From spring 1979 onwards, stoats became rare in the whole dune reserve. Foxes have lived in the Reserve since 1968. Their numbers increased up to 1981, after which they remained constant (J.L.Mulder pers.comm.). The increase of the fox population may explain why so few rabbit carcasses were found after spring 1979 (table 4): foxes eat carcasses

as well as live prey and both types of food are carried away and hidden.
The impact of the stoat was quite high during the winter of 1978-79. Rabbits weakened by food shortage might have been more susceptible to predation , but the apparently greater effect could have been due partly to the fact that I noticed the carcasses sooner in winter than in the autumn.
With the fall in stoat numbers in spring 1979, predation pressure on rabbits decreased.

THE EXPERIMENT WITH SUPPLEMENTAL FEEDING

In 1980-81, rabbits in plot 5 were given additional food, but this did not reduce winter mortality (table 3).

Table 7 gives the change in body weight of rabbits that were caught at least twice. In plot no.5 both adults and juveniles showed a weight gain during autumn and winter, but in the untreated plots, adults lost weight over both periods, and juveniles only gained weight during autumn. All differences between treated and untreated plots were significant, even for the juveniles in autumn. Juveniles supplied with extra food gained more weight than did juveniles in the untreated plots.

One effect of supplemental feeding was that young were born in this population weeks ahead of the usual start of the reproductive season (Wallage-Drees,1983). Only three of them emerged, apparently because the conditions in February and March are too harsh for nestlings or suckling does. The ones that emerged had a low growth rate (table 10).

TABLE 7

CHANGE IN BODY WEIGHT IN CONTROL PLOTS AND IN POPULATIONS SUPPLEMENTED WITH FOOD
g/day ± s.e..1980-81. n=number of rabbits that were caught twice or more during the period

		n	1 Sept.-30 Dec.	n	15 Dec.-6 Mrch
adults	plot 2,6&7	5	-1.3 ± 1.6	4	-1.7 ± 0.8
"	plot 5+	5	+3.5 ± 0.9	0	
			t=3.78, p<0.05		
juv.	plot 2,6&7	12	+2.8 ± 0.1	6	-0.9 ± 1.2
"	plot 5+	8	+3.6 ± 0.4	4	+4.9 ± 2.3
			t=4.42, p<0.05		t=6.18,p<0.05

+ Experimental plot:supplementary feeding during Oct.-March

PRODUCTIVITY

LITTER SIZE

The factors which contribute most to a high rate of population increase are early maturation, large litter size, high littering rate and high survival rate of the young.

In 1978 the mean litter size of 34 litters in stops was 5.0 ± 0.2 . Litter size increased from spring to summer (fig.2) as described by the regression equation for March 21 to May 17:
$Y = -0.4 + 0.05X$, $r = 0.478$, $p < 0.005$,
where Y is the litter size and X is the birth date as day of the year.

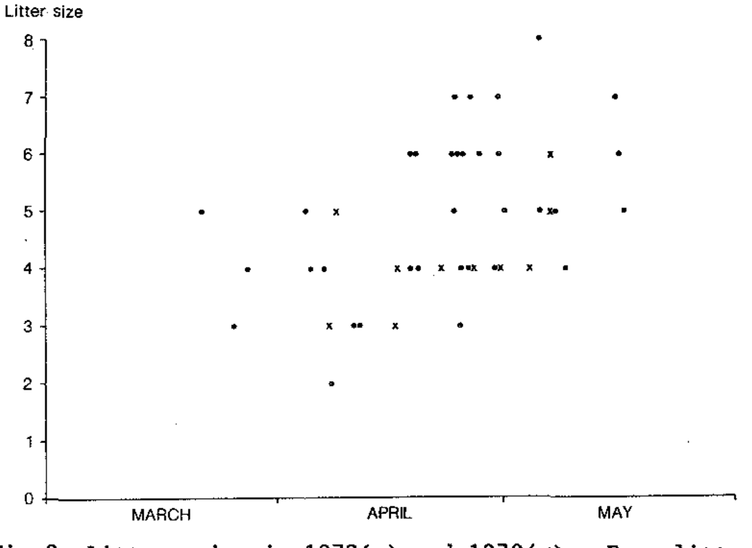


Fig.2 Litter size in 1978(•) and 1979(x). From litters in stops on a parking lot in the dune reserve.

In 1979,10 stops were found before June. The correlation of litter size with time was not significant. Litter sizes were smaller in 1979: mean litter size was 4.1 with a mean birth date of April 24. On that date the expected litter size for 1978 would have been 5.3.

In 1980 and 1981 three and zero stops were found, respectively, thus mean litter size could not be determined. The mean litter size *in utero* from 10 rabbits shot in February and March 1981, with an expected mean birth date of about April 1, was 4.4. This was in the range expected from the regression formula for 1978.

LITTERING RATE AND LENGTH OF BREEDING SEASON

Fig.3 shows the birth dates of litters during the study. Data from plot 5 with supplemental feeding are excluded from this figure. In 1978, young from 27 litters were seen in the study plots, compared to an estimated number of 25 adult does, giving littering rates of 36% in April, 44% in May and 20% in June.
It was not possible to gather similar data in 1979, due to the scarcity of rabbits. In 1980 the birth dates of individual young caught in traps was determined.
In 1981, observations ended in June, so only the first part of the breeding season was recorded. Eight adult does were estimated to be present in the study site in this year, giving littering rates for March of 50% and April of 88%.

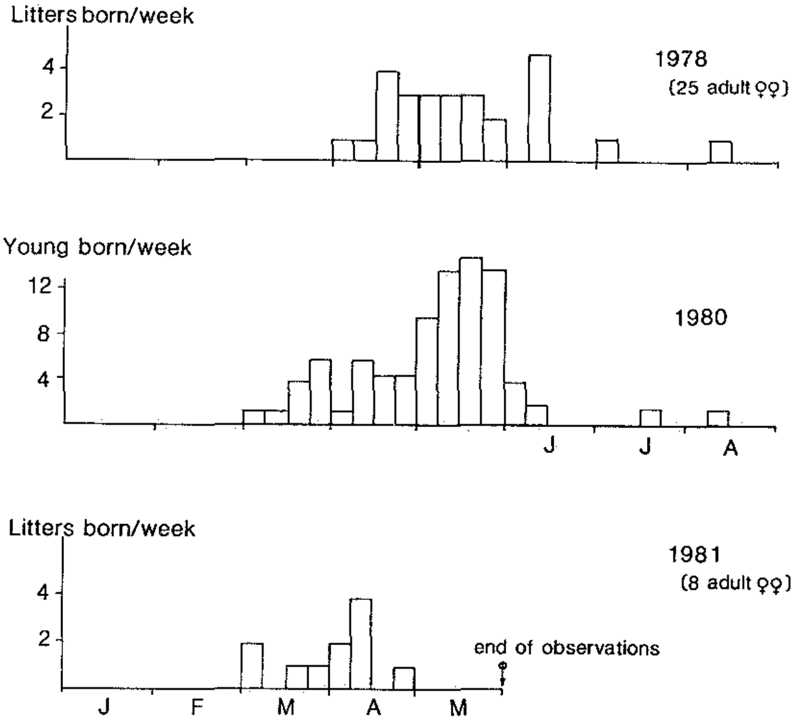


Fig.3 Number of litters or young born per week in the study area

Generally the main breeding season was confined to March, April and May, with a small number of litters produced into August.

In 1979, due to the high mortality in the preceding winter, there were not enough rabbits in the study area to assess the pattern of breeding from observation and capture of young. To compare the length and pattern of the breeding season between years, the frequency of occurrence of young of different age cohorts (born in different months of the year) in the game bag were determined (table 8). This showed that the peak of the frequency distribution of births was later in 1979 than in 1978 or 1980.

Table 8

FREQUENCY OF AGE COHORTS OF JUVENILES
IN THE GAME BAG IN 1978,1979 AND 1980
Totals of September plus October

Month of birth	1978	1979	1980
June	7	45	13
May	27	69	41
April	53	70	36
March	28	16	25
February	8	4	10

Two-sample test Kolmogorov-Smirnov
1978 vs. '79 D=0.283 $p_2 < 0.001$
1979 vs. '80 D=0.182 $0.001 < p_2 < 0.01$
1978 vs. '80 D=0.156 $p_2 = 0.05$

Another indication that the breeding season lasted longer in 1979 was that only in this year lactating does were among the rabbits shot in September (14 out of 20 adult females , and 2 out of 85 juvenile females , Fisher exact probability test for 1979 vs. 1978+1980: p=0.0003).

The extended breeding season in 1979 did not compensate fully for the late start and smaller litter size. Overall, fewer young were born per doe in 1979 compared to the other years. In September 1979 the proportion of juveniles in the study area was 39% (total n=41) , in September 1980 it was 69% (total n=71).

DEVELOPMENT OF THE VEGETATION

The availability of food in the breeding season is shown by the height and cover of the two main plant groups(table 9). The quantity of plant material increased from 1 March, and then decreased before mid-June, particularly in the quantity of dicotyledons which offer the best quality food. As the average height of the plants continued to increase over this period, this decrease seems not to have been caused by rabbit grazing.

Table 9

RELATIVE BIOMASS OF THE VEGETATION DURING THE BREEDING SEASON, 1980
Cover, average height and relative biomass (c x h)

Date	Dicotyledons Cover	Height(mm)	c x h	Monocotyledons Cover	Height(mm)	c x h
13 Feb.	0.10	12	1.20	0.71	19	13.49
27 Feb.	0.14	8	1.12	0.83	17	14.11
10 Mrch	0.11	8	0.88	0.83	22	18.26
24 Mrch	0.13	9	1.17	0.84	22	18.48
7 April	0.15	8	1.20	0.95	22	20.90
21 April	0.24	17	4.08	0.96	18	17.28
11 June	0.02	22	0.44	0.63	19	11.97

GROWTH RATE

The weight of young rabbits caught more than once were plotted against time. For nestlings and young from 200 to 1000 g the increase in weight was arithmetic (table 10). A relationship using the logistic form of the equation failed to improve the correlation. The growth rates found in this study are within the range of growth rates reported in other studies (table 11). Those from the young in the population receiving supplemental food that were born in January, much earlier than usual, were comparatively low.

Table 10

GROWTH CURVES OF YOUNG RABBITS

n= number of individuals that were caught repeatedly and weighed
BW= bodyweight in gramms
GR= 95% confidence interval of the linear growth rate in g/day
t= age in days
r= correlation coefficient

A. Growth curve of nestlings between day 10 and 21
1978 only

BW = 22.3 + 8.9t, n=15, r=0.94

B. Growth curve of young between day 21 and 93

BW = 42.5 + GRt

year	n	GR	r
1978	18	10.0-11.2	0.98
1979	-		
1980	26	9.4- 9.8	0.99
1981	47	8.6- 9.0	0.98
born in the usual season			
1981	3	7.6- 8.4	0.80
born in Jan.in plot 5			

Table 11

GROWTH RATES IN DIFFERENT COUNTRIES

country	author	growth rate(g/day)
England	Southern (1940)	9.6
New Zealand	Tyndale-Biscoe & Williams(1955)	10
Australia	Dudszinski & Mykytowycz(1960)	6-11
	Dunnet (1956)	9.8
	Dunsmore (1971)	8-10
	Myers (1964)	10-11
	Myers & Poole (1963)	10-12
	Parer (1977)	10
	Parer & Fullagar (1986)	9.1
	Wheeler & King(1985)	10.5
	Wood(1980)	9.6-10.5

SURVIVAL

The survival of young in different cohorts (born in different months of the year) was assessed from the composition of the game bag. Table 12 gives the frequencies of occurrence of age cohorts in the game bag and in the study site as a whole. In 1980-81 there was no significant difference in survival rate between young born in June and those born early in the season (i.e. March-May). Young born in March have better chances of survival than the others (April-June).

Table 12

SURVIVAL RATE OF YOUNG BORN IN DIFFERENT MONTHS

12A. Frequency of age cohorts (young with different months of birth) in the monthly game bag of 1979.

	Sept.		Oct.		Nov.		Dec.	
Lens weight (mg)	Cohort	n	Cohort	n	Cohort	n	Cohort	n
92-114	June	33						
115-132	May	54	June	12				
133-147	April	47	May	15	June	3		
148-160	March	9	April	23	May	5	June	4
161-172			March	7	April	7	May	17
173-182			Feb.	4	March	9	April	11
183-190							March	7
total n		143		61		24		39

June cohort shot in September vs. June cohort in December: $X^2_2=2.37$ n.s.
March cohort shot in September vs. March cohort in December: $X^2_2=3.84$ p=0.05

Young up to 3 months seldom appear in the game bag (Myers 1971). The July and August cohorts that appeared in October, November and December are neglected.

12B. Survival of age cohorts in the study area
1980-'81, plots 2,6 & 7

Month of birth	n in Sept.'80	survival(%) till March '81
Mrch.	5	20
April	14	36
May	7	29
June	0	
July	5	20
August	0	

Fisher exact probability test for March + April + May vs. June + July + August:p=0.54, n.s.

DISCUSSION

POPULATION DENSITY

OCCURRENCE OF FOOD SHORTAGE IN AUTUMN AND WINTER

In the field it was impossible to assess the cause of death for every individual.It is assumed here that rabbits that were not seen again or recaught at the site any more had either died from disease or starvation inside the burrow , or had been carried away after predation.
There were no indications of diseases impairing survival, except for some myxomatosis in August and September in each year. Myxomatosis manifests itself only in spring and autumn and is no longer a major factor in determining the number of rabbits.

Evidence of the influence of food shortage on mortality was gathered in several ways: by assessing the condition of rabbits in wintertime (described in Wallage-Drees,1986), by assessing the quality of the available food in winter (Wallage-Drees & Deinum,1987) and by providing supplemental food (this paper).
The condition of the rabbits in the study area was assessed by examining live rabbits caught in traps (table 7) and rabbits shot in the dune reserve outside the study area (Wallage-Drees,1986). Both data sets showed the same pattern: in all winters there was a decrease in weight, especially among juveniles. Only in the cold winter of 1978-79, however, did starvation occur. In the other winters very few individuals showed signs of starvation.
Wallage-Drees & Deinum(1987) showed that from December 1980 till March 1981 digestibility of the food was below the maintenance level.
Supplemental food given to one fenced-in population in 1980-81 did not change the mortality rate. This indicates that mortality rate in years with 'normal' weather was determined by causes other than food shortage.

It should be realized that the level of the food supply itself is not constant. It changes stochastically with the weather and is influenced by the actions of rabbits, who deplete it at high density, but on the other hand increase its quality by promoting dicotyledons through their grazing (Gillham,1955).

During the study widely different weather conditions occurred. High mortality in the long winter of 1978-79 reduced numbers to a low level. In the following years, population density increased, but did not return to the pre-1979 level (table 3) . Nevertheless, in 1980-81 a decrease in mean weight occurred in winter and the quality of the food was low.

PREDATION IN AUTUMN AND WINTER

Gibb et al. (1978) found that rabbits in New Zealand hardly ever experienced food shortage because predators kept their numbers below the food limit. We will discuss under what circumstances predators have this impact on rabbits, and whether these are present here.

For vertebrate predators the following characteristics of the ecosystem are mentioned (Erlinge et al.,1983).
a) a rich supply of alternative prey sustaining a high and constant predator density. For example for foxes in Sweden, Erlinge et al.(1983) say that "their diet contained a high proportion of voles in autumn-winter and a low proportion in summer."
b) availability of prey for most of the year. Gibb et al. (1969) mention a year-round breeding and hence year-round availability of young rabbits.
c) a heterogeneous environment where the prey moves through habitats less suitable for them where they are vulnerable to predators (Wolff, 1980).

Gibb et al. (1969) consider characteristic (b) combined with an effective predator like the cat to be sufficient explanation for regulation of rabbit numbers below the food limit.

The main predators in the coastal dunes were the stoat and the fox. Feral cats were rare. The change in the predator population, from stoat plus fox to fox only, occurred at about spring/summer 1979. The decrease of the stoat population could be due to food competition with the fox, especially in the early spring of 1979, when the number of rabbits was low. Also, predation by fox on stoat may be involved (cf.Erlinge, 1983).
The decrease in stoat numbers led to lower predation pressure on rabbits. The number of rabbits/ha estimated to be taken by foxes was lower than the number taken by stoats (table 4). Stoats take only healthy animals, foxes both healthy and diseased ones (J.L.Mulder pers.comm.).
Foxes behave as generalists, even though in the dunes rabbits were their main food. Their numbers are regulated by territorial behaviour and the density of breeding vixens is similar from year to year (Erlinge et al. 1983; von Schantz,1984;J.L.Mulder pers.comm.).

It is not the absolute number killed but the mortality rate inflicted when the prey population cannot compensate by lowering mortality rate from other causes, in this case the food supply, that is important for the impact of a predator on the dynamics of its prey. So, mortality in late winter has the largest impact (Errington,1946; Nicholson, 1954; Solomon; 1969). The 1 rabbit/ha per month taken by foxes in February could have some influence on a population density of about 7 rabbits/ha (table 3).

Looking again at the characteristics mentioned before
ad a): foxes apparently hardly take any alternative prey in the coastal dunes.
ad b): there is a short breeding season of the rabbit, young rabbits are only available from mid April-September.
ad c): it seems that the whole dune system can be considered a refuge or optimal habitat for rabbits in the sense meant by Wolff (1980). There is no suboptimal habitat whereto rabbits disperse at high densities.

In conclusion, in this study rabbit numbers grew to the point where they were limited by food and predation did not regulate rabbit numbers.

THE EFFECT OF RABBIT CONTROL AND POACHING

In the Noord-Hollands Duinreservaat game wardens and poachers together killed about 5 rabbits per hectare each year, mainly between September and December(Bakker & Wallage-Drees, in prep.). This would have decreased rabbit numbers in autumn and have been important to a manager who considered that the main damage is done at that time. However, the effect on the breeding population would be small, especially after severe winters when the kill in autumn would be compensated by lower mortality from food competition in winter. Tittensor (1981) found that only rabbit control just prior to breeding could be effective. Even so, the kills in autumn by man, and during the whole year by predators would depress the recovery rate of the population after a severe winter by acting as a density-independent mortality factor on the new cohort of young.

RECRUITMENT

INTRINSIC FACTORS:INFLUENCE OF DENSITY ON RECRUITMENT

Average litter size was 5, which was within the range expected in high-density populations (Lloyd, 1970). Litter size is strongly related to body weight of the does (Brambell,1943; Poole, 1960). The lower body weight of the does in this study in 1979 explains the smaller litter size in this year.
The low littering rate found in this study seems to be related to population density: it was higher in 1980 than in 1978.

The short breeding season in the study populations can be interpreted as an intrinsic response to high population density or as a response to low food quality in summer.
The beginning of the breeding season (presence of pregnant females) in February or March is timed by the availability of good quality food (Wallage-Drees,1983).

What determines the end of the breeding season? Usually the end is near 1 May. After that date few females become pregnant any more. For an explanation for the timing of the end of the breeding season we may consider the fact that there was a difference in the ending of reproduction between 1979, when reproduction continued or was resumed in summer, and 1978 and '80 when reproduction finished earlier.

Many authors from different countries in the northern and southern hemispheres mention that rabbits show a depression in fertility before or at summer solstice, with sometimes resumed breeding in autumn. They consider this an adaptation to arid conditions in the ancestral mediterranean homelands of the rabbit (Brambell, 1943; Hughes & Rowley,1966; Lloyd, 1970; McIlvaine,1962; Parer 1977; Poole, 1960; Rogers,1981; Soriguer & Rogers, 1981; Wood,1980). Hammond (1965) found that even in domestic rabbits (when they are on a low plane of nutrition) summer anoestrus occurs.
However, Andersson et al. (1979) in South-Sweden, Bell (1977) and Gibb et al. (1978) in New Zealand and Skira (1978) on Macquarie Island report breeding patterns without summer anoestrus.

It is hard to believe that this ancestral pattern would still exist in an animal that has been in our temperate coastal climate at least since 1250 A.D. (Rentenaar 1978). Individuals are supposedly selected for maximum reproductive value. There is individual variation in littering frequency, that, if genetically determined , should enable natural selection to act.
There is evidence for the influence of density, and also for that of food quality on the breeding pattern. In this study summer anoestrus occurred only in 1978 and 1980, years with a high population density, but not in 1979 when population density was low (fig.3 and tab.7).A similar influence of population density was also found by Lloyd (1970). The growth rates of the young found in this study were within the usual range. So, in spring and summer there seems to have been sufficient food of high quality. Young born at summertime had the same chances of survival as the others (table 12) hence the number of offspring from an individual would increase if that individual continued breeding as long as possible. However, the high survival rate of late-born young in 1979 might have been caused by the fact that they experienced less than usual food competition from the early-born young (Garson, 1986).

It is possible that longer breeding would lower the survival chance of the doe and hence her chance to reproduce in the following spring. This has not been measured in our study. However, rabbits are known to be able to breed much longer than three months, even in our temperate climate (Brambell, 1943).
Population density affects food quality. At a low population density (e.g. in 1979) rabbits have more choice of food plant and can enhance the quality of their diet.

Generally, the concentration of protein in grasses is lowest in June/July and increases again in August/September (McNeill & Southwood,1978). Also the species composition of the vegetation changes unfavourably after the end of April (table 9).

Recently Boyd(1986) described that the administration of 6-methoxybenzoxalinone (6-MBOA) to rabbits can prevent reproductive regression when the breeding season would normally end. A precursor of 6-MBOA is especially prevalent in the growing shoots of grasses. A regrowth of the vegetation often occurs in August/September.

So intrinsic responses of production size to population density do occur, but they might to a large extent be the results of the interaction between rabbit and vegetation.

RECRUITMENT INTO THE AUTUMN POPULATION

After the decrease in population numbers in winter 1978-79, the longer breeding season could not compensate for the later start of breeding and smaller litter size that also resulted from the harsh weather conditions. Recruitment was not sufficient to allow recovery of the population from the extra mortality in that winter.

Interestingly, Cooke(1981) found in S.W.Australia that rabbit populations needed two years to recover from a drastic change in density and the same is mentioned by Sheail (1971).

The rate of increase of the population might have been slowed down by predation of foxes on nestlings and young (Tittensor, 1981).

CONCLUSION

Although predation is important and may slow down the rate of increase in rabbit population numbers, the potential maximum density reached by the population was set by the quantity and quality of food. The availability of food varied stochastically with the weather. In some years,e.g.1978-79, severe food shortage caused a major reduction in population numbers. In other years, e.g. 1979-80 & 1980-81, rabbit densities were not curtailed by food shortage. In this latter case, low rabbit numbers and abundant food may give the impression that rabbit numbers are kept below the limit set by the food supply by other factors. However no mechanisms would prevent the population from rising to its food limit again.

REFERENCES

Andersson,M.,M.Dahlback & P.Meurling (1979): Biology of the wild rabbit, Oryctolagus cuniculus , in southern Sweden.1.Breeding season.Viltrevy **11**,103-127.

Bell,J.(1977): Breeding season and fertility of the wild rabbit, Oryctolagus cuniculus (L.) in North Canterbury, New Zealand.Proc.N.Zl.Ecol.Soc.**24**,79-83.

Boyd,I.L.(1986): Effect of daylength on the breeding season in male rabbits.Mammal Rev.**16**,125-130.

Brambell,F.W.(1943): The reproduction of the Wild Rabbit Oryctolagus cuniculus(L.).Proc.Zool.Soc.London **114**,1-45.

Broekhuizen,S.,E.Bouman & W.Went (1986): Variation in the timing of nursing in the Brown Hare (Lepus europaeus) and the European Rabbit (Oryctolagus cuniculus).Mammal Rev.**16**,139-144.

Cooke,B.D.(1981). Food and dynamics of rabbit populations in inland Australia.In:K.Myers & C.D.MacInnes (Eds.):Proc.First World Lagomorph Conf.,Guelph,Ontario:633-648.

Cowan,D.P. & P.J.Garson(1985). Variations in the social structure of rabbit populations:causes and demographic consequences.In:R.M.Sibley & R.H.Smith(Eds.):Behavioural Ecology:537-555. Blackwell Scientific Publ.,Oxford.

Daly,J.C.(1981). Effects of social organization and environmental diversity on determining the genetic structure of a population of the wild rabbit, Oryctolagus cuniculus.Evolution **35**,689-706.

Delibes,M. & F.Hiraldo(1981): The rabbit as prey in the Iberian mediterranean ecosystem. In:K.Myers & C.D.MacInnes(Eds.): Proc.First World Lagomorph Conf.,Guelph,Ontario:614-622.

Doing,H. (1964): Vegetatie. In: Recreatie en Natuurbescherming in het Noordhollands Duinreservaat. Suppl.2. Meded.ITBON nr.**69c**. Belmontia II. Ecology fasc.11.

Dudszinski,M.L. & R.Mykytowycz (1960): Analysis of weights and growth rates of an experimental colony of wild rabbits. CSIRO Wildl.Res.**5**,102-115.

Dunnet,G.M.(1956): Growth rate of young rabbits, Oryctolagus cuniculus (L.).CSIRO Wildl.Res.**1**,66-67.

Dunsmore,J.D.(1971): Biology of the wild rabbit. IV. Austr.J.Zool.**19**,355-370.

Erlinge,S.(1983): Demography and dynamics of a stoat Mustela erminea population in a diverse community of vertebrates.J.An.Ecol.**52**,705-727.

I.N.Nilsson,T.Nilsson,T.von Schantz & M.Sylven(1983):
Erlinge,S.,G.Goransson,L.Hansson,G.Hogstedt,O.Liberg,
Predation as a regulating factor on small rodent populations in southern Sweden.Oikos **40**,36-52.

Errington,P.L.(1946): Predation and vertebrate populations.Quart.Rev.Biol.**21**,144-177,221-246.

Feen,P.J.van der, 1963. Hoe en wanneer zijn wilde konijnen in Europa verspreid geraakt? Biol.Jaarb.Dodonea 31:237-243.

Fenner,F. & F.N.Ratcliffe(1965): Myxomatosis. Cambridge University Press.

Flux,J.E.C. & Fullagar,P.J.(1983):World distribution of the rabbit (Oryctolagus cuniculus).Acta Zool.Fenn.**174**,75-79.

Garson,P.J.(1986): Intraspecific influences on juvenile recruitment rate in Rabbits.Mammal Rev.**16**,195-196.

Gibb,J.A.(1977):Factors affecting population density in the wild rabbit Oryctolagus cuniculus (L.) and their relevance to small mammals. In:B.Stonehouse & Chr.Perrins(Eds.): Evolutionary Ecology:33-46. Macmillan Press Ltd, London & Basingstoke.

Gibb,J.A.,G.D.Ward & C.P.Ward(1969): An experiment in the control of a sparse population of wild rabbits (Oryctolagus cuniculus) in New Zealand.N.Zl.J.Sci.**12**,509-534.

Gibb,J.A.,C.P.Ward & G.D.Ward (1978): Natural control of a population of rabbits ,Oryctolagus cuniculus (L), for ten years in the Kourarau enclosure. N.Zl.Dept.of Sci. and Ind.Res.,Wellington, Bulletin **223**.

Gillham,M.E. (1955): Ecology of the Pembrokeshire islands III. The effect of grazing on the vegetation. J.Ecol.**43**,172-206.

Hammond,J.(1965): The effects of high and low planes of nutrition on the reproduction in rabbits. N.Zl.J.Agr.Res.**8**,708-717.

Hewson,R. & T.D.Healing(1971): The stoat, Mustela erminea, and its prey.J.Zool.**164**,239-244.

Hughes,R.L. & I.Rowley (1966): Breeding season of female wild rabbits in natural poulations in the Riverina and Southern Tablelands districts of New South Wales. CSIRO Wildl.Res.**11**,1-10.

King,C.M.(1977): Stoat Mustela erminea. In: G.B.Corbet & H.N.Southern (eds.). Handbook of British Mammals:331-338. Blackwell Sci.Publ.,Oxford, London, Edinburgh & Melbourne.

Lack,D.(1954): The natural regulation of animal numbers. Clarendon Press,Oxford.

Lloyd,H.G.(1970): Variation and adaptation in reproductive performance. Symp.Zool.Soc.Lond.**26**,165-188.

Lloyd,H.G.(1980): The red fox. Batsford Ltd.,London.

Lloyd,H.G.(1981): Biological observations on post-myxomatosis wild rabbit populations in Britain 1955-1979. In:K.Myers & C.D.MacInnes(Eds.):Proc.First World Lagomorph Conf., Guelph, Ontario:623-628.

Lloyd,H.G. & D.McCowan(1968): Some observations on the breeding burrows of the wild rabbit, Oryctolagus cuniculus, on the island of Skokholm. J.Zool.,Lond. **156**,540-549.

McIlwaine,C.P.(1962): Reproduction and body weights of the wild rabbit Oryctolagus cuniculus (L.) in Hawke's Bay, New Zealand.N.Zl.J.Sci.5,325-341.

McNaughton,S.J.(1983): Compensatory growth as a response to herbivory.Oikos **40**,329-336.

McNeill,S. & T.R.E.Southwood(1978):The role of nitrogen in the development of insect/plant relationships. In:J.B.Harborne(Ed.). Biochemical aspects of plant and animal coevolution. Phytochem.Soc.Europ.Symp.Ser. no **15**, 77-98. Academic Press, London.

Minot,C.S. & E.Taylor (1905): Normentafeln zur Entwicklungsgeschichte der Wirbeltiere. Herausgegeben von F.Keibel.Verlag Gustav Fischer,Jena.

Mueller-Dombois,D. & H.Ellenberg (1974):Aims and methods of vegetation ecology. John Wiley and sons, New York.

Mulder,J.L.(1985a): Spatial organization, movements and dispersal in a dutch red fox (Vulpes vulpes) population: some preliminary results.Rev.Ecol(Terre & Vie) **40**,133-138.

Mulder,J.L.(1985b):Invloed van de vos op wulpen en fazanten in het Noordhollands Duinreservaat. De Ned. Jager **90**,564-566.

Myers,K.(1958): Further observations on the use of field enclosures for the study of the wild rabbit.CSIRO Wildl.Res.**3**,40-49.

Myers,K.(1964): Influence of density on fecundity, growth rates, and mortality in the wild rabbit.CSIRO Wildl.Res.**9**,134-137.

Myers,K. (1971): The rabbit in Australia. In:P.J.den Boer & G.R.Gradwell(Eds.): Dynamics of Populations:478-506. Pudoc,Wageningen.

Myers,K. & N.Gilbert (1968): Determination of age of wild rabbits in Australia.J.Wildl.Manage.**32**,841-849.

Myers,K. & W.E.Poole (1961): A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations.II. The effect of season and population increase on behaviour. CSIRO Wildl.Res. 6,1-41.

Myers,K. & W.E.Poole (1963): A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations.V.Population dynamics. CSIRO Wildl.Res. 8,16-203.

Myers,K. & E.C.Schneider (1964): Observations on reproduction, mortality and behaviour in a small, free-living population of wild rabbits.CSIRO Wildl.Res.9,138-143.

Mykytowycz,R. & S.Gambale (1965): A study of the inter-warren activities and dispersal of wild rabbits, Oryctolagus cuniculus, living in a 45-ac.paddock.CSIRO Wildl.Res.10,111-123.

Nicholson,A.J.(1954): An outline of the dynamics of animal populations. Austr.J.Zool.2,9-65.

Niewold,F.J.J.(1976):De bestudering van de oecologie van de vos (Vulpes vulpes) in verband met zijn rol bij de verspreiding van rabies. 1-119,I-XXXV, Rijksinstituut voor Natuurbeheer, Arnhem.

Parer,I.(1977): The population ecology of the wild rabbit, Oryctolagus cuniculus (L.), in a Mediterranean-type climate in New South Wales. Austr.Wildl.Res.4,171-205.

Parer,I. & P.J.Fullagar(1986): Biology of rabbits, Oryctolagus cuniculus, in subtropical Queensland.Austr.Wildl.Res.13,545-559.

Poole,W.E.(1960): Breeding of the wild rabbit, Oryctolagus cuniculus (L.), in relation to the environment.CSIRO Wildl.Res.5,21-43.

Rentenaar,R. (1978): De vroegste geschiedenis van het konijn in Holland en Zeeland. Holland:reg.hist.tschr.10,2-16.

Rogers,P.M. (1981). The wild rabbit in the Camargue, Southern France. In:K.Myers & C.D.MacInnes(Eds.):Proc.First World Lagomorph Conf.,Guelph, Ontario : 587-599.

Schantz,T.von (1984):'Non-breeders' in the red fox Vulpes vulpes:a case of resource surplus. Oikos 42,59-65.

Sheail,J.(1971): Rabbits and their history. David & Charles,Newton Abbot.

Sinclair,A.R.E.(1975): The resource limitation of trophic levels in tropical grassland ecosystems. J.An.Ecol.44,497-520.

Skira,I.J. (1978): Reproduction of the Rabbit, Oryctolagus cuniculus (L.), on Macquarie Island, Subantarctic. Aust.Wildl.Res.5,317-326.

Solomon,M.E.(1969): Population dynamics. Edward Arnold,London.

Soriguer,R.C. & P.M.Rogers(1981): The European wild rabbit, Oryctolagus cuniculus (L.) in Mediterranean Spain.In:K.Myers & C.D.MacInnes (Eds.):Proc.First World Lagomorph Conf.,Guelph, Ontario:600-613.

Southern,H.N.(1940): The ecology and population dynamics of the wild rabbit (Oryctolagus cuniculus). Ann.appl.biol.27,509-526.

Tittensor,A.H.(1981): Rabbit population trends in southern England. In:K.Myers & C.D.MacInnes (Eds.):Proc.First World Lagomorph Conf.,Guelph,Ontario:629-632.

Tyndale-Biscoe,C.H. & R.M.Williams(1955):A study of natural mortality in a wild population of the rabbit. N.Zl.J.Sci.Techn.36(B),561-580.

Wallage-Drees,J.M.(1983): Effects of food on onset of breeding in rabbit, Oryctolagus cuniculus (L.), in a sand dune habitat. Acta Zool.Fenn.174,57-59.

Wallage-Drees,J.M.(1986): Seasonal changes in the condition of Rabbits, Oryctolagus cuniculus (L.), in a coastal sand dune habitat. Z. Saugetierk.51,26-36.

Wallage-Drees,J.M.(1988): A field study on seasonal changes in the circadian activity of rabbits. Z. für Säugetierk.,in press.

Wallage-Drees,J.M. & B.Deinum(1986): Quality of the diet selected by wild rabbits (Oryctolagus cuniculus (L.))in autumn and winter. Neth.J.Zool. 36,438-448.

Watson,A. & R.Moss(1970):Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: A.Watson(Ed.): Animal populations in relation to their food resources:167-220. Blackwell Sci. Publ.,Oxford and Edinburgh.

Wheeler,S.H. & D.R.King(1985): The European rabbit in south-western Australia.II. Reproduction. Austr.Wildl.Res.12,197-212.

Wolff,J.O.(1980): The role of habitat patchiness in population dynamics of snowshoe hares. Ecol.Monogr.50,111-130.

Wood,D.H.(1980): The demography of a rabbit population in an arid region of New South Wales,Australia.J.An.Ecol.49,55-79.

CONCLUSIONS

HABITAT

The close proximity of dry burrowing areas and feeding grounds make stabilized dunes a good rabbit habitat. At high population density rabbits keep their habitat suitable by grazing and digging. At (temporary) low population densities vegetation succession takes place which reduces the area of suitable feeding ground.
Although rabbit activity can trigger erosion, the cause of the large scale erosions in the coastal dunes from the Middle exploitation of the dunes and not with rabbit activity (Ch.1).

ACTIVITY

Wild rabbits are mainly nocturnal. Their emergence and disappearance times did not vary over the year. However, the highest percentage of the population above ground at one time was lower during the winter months than in the rest of the year. This may be due to the need to conserve energy otherwise lost in maintaining body temperature (Ch.5).
The variation in the level of above ground activity needs to be taken into account when assessing population size by sight counts, and when evaluating the effect of rabbit control measures (Ch.5).

PREDATION AND DISEASE

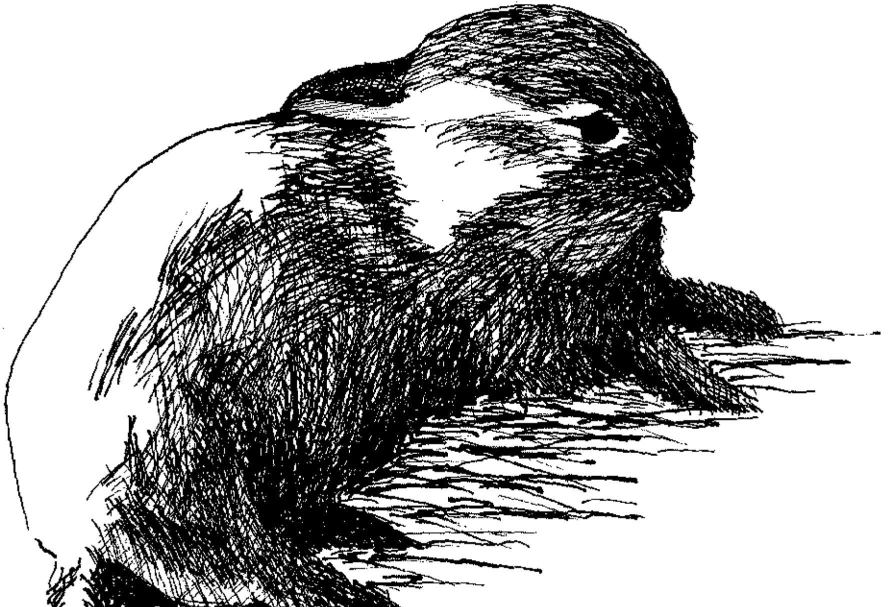
The co-evolution of the virulence of the Myxoma virus and of resistance in the rabbit should result in outbreaks of myxomatosis continuing to occur at irregular intervals in west-european rabbit populations. In the coastal dunes myxomatosis had its main impact in spring an autumn, mostly on the new generation of young (juveniles) (Ch.1.3 & 7).
In addition, juveniles were killed disproportionally more than adults by stoats and hunters (Ch.2 & 7).
Data from the game bag and the field study show that the increase in fox numbers in the Noord-Hollandse Duinreservaat since 1970 has not led to a decrease in rabbit numbers in autumn and winter. The impact of total predation might even be less than before, because of the (unexplained) decrease in stoat numbers (Ch.1.4 & Ch.7).

FOOD IN WINTER

The diet, the food actually taken by rabbits, varied in composition over the course of the day. In a patchy environment with different vegetation types, information about the composition of meals can be used to assess habitat use and daily dispersion (Ch.3).
The winter diet in the coastal dunes, assessed from quality of stomach contents, had a sufficient percentage crude protein but a level of digestibility below that required for body maintenance (Ch.4).
There were no significant differences in body weight or detectable differences in mortality between sexes. In autumn and winter adults were heavier and had larger fat reserves than juveniles. Juveniles were more vulnerable than adults to starvation in severe winters (Ch.2).
The length of the breeding season was modified by an interaction between population density and food supply. The timing of the breeding season seemed to be adapted to the changes in quality of the vegetation. The first young were born when the proportion of dicotyledons in the vegetation increased and in the study area this occurred about the first week of March. Breeding started earlier with supplementary feeding, but few of the young born early survived (Ch.6). High population density kept the breeding season short and litter frequency low (Ch.7).
Almost all does litter in existing burrows. Stops are made only when rabbits are colonizing new habitats or in situations where burrows are systematically destroyed (Ch.1.1).

The main conclusion of the study can be summarized as:

Weight loss in winter, low quality of winter food and the absence of sufficient regulating factors indicate that food supply is the factor which limits the density of the breeding population of rabbits in the coastal dunes.



CURRICULUM VITAE

Johanna Marijke Drees werd geboren op 11 juni 1950 in Washington,D.C.,U.S.A. Na een Gymnasium-b opleiding aan het Gymnasium Haganum in 's-Gravenhage en een jaar met de American Field Service in de U.S.A. (Escondido High School), ging ze in 1969 biologie studeren aan de Rijksuniversiteit Groningen. In maart 1976 werd de studie afgesloten met een doctoraal examen, hoofdrichting plantenoecologie met bijvakken milieurecht en didactiek en een stage bij de landschapsconsulent van het Staatsbosbeheer in Assen.

In 1976 werkte ze tijdelijk bij de Provinciaal Planologische Dienst in Groningen aan de interpretatie van biologische inventarisaties ten behoeve van het streekplan. Vanaf 1977 werd op onbezoldigde basis het onderzoek verricht waarop dit proefschrift is gebaseerd. In 1986 werkte ze tijdelijk bij het Ministerie van VROM als technisch wetenschappelijk medewerkster bodembescherming.

Zij was lid van het dagelijks bestuur van de Stichting Het Groninger Landschap, van de Vereniging voor Zoogdierkunde en Zoogdierbescherming(VZZ) en van de Stichting Duinbehoud. Voor de VZZ was ze lid van de Jachtraad. Ze is sinds 1987 lid van de Provinciale Staten van Noord-Holland voor de PvdA.

Gepubliceerde artikelen, die niet in dit proefschrift zijn opgenomen:

1980. Het wilde konijn. PWN-Wereld 32(9):18-19.

1982. Duinkonijnen. Waddenbulletin 17:123-126.

1982. Konijnen als duinbeheerders. Duin 5(2):7-12.

1982. De Bunzing. Huid en Haar 1:153-156.

1984. Duinen aan de Engelse oostkust. Duin 7(1):6-7.

1985. Het konijn in de duinen. Publ. IVN, Leiden.

1985. Het konijn is weer terug. Spiegel der Natuur 16(4):132-136.

1985. Konijn, <u>Oryctolagus cuniculus</u>. Argus 10(4):18.

1986. Dag- en nachtaktiviteit bij konijnen en de relevantie voor de telmethode. De Levende Natuur 87:40-45.

1986. Konijnen in Groningen. Noorderbreedte 10(4):151-152.

& R.Stevers, 1986. Kustgenese: wat gebeurt er voor onze kust? Duin 9(4): 120-122.

geaccepteerd: Het konijn, <u>Oryctolagus cuniculus</u> (L.). In: Atlas van de Nederlandse Zoogdieren.