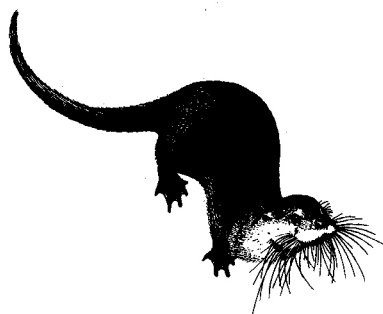


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THE STOAT *MUSTELA ERMINEA* IN THE DUTCH DUNE REGION, ITS LOCAL EXTINCTION, AND A POSSIBLE CAUSE: THE ARRIVAL OF THE FOX *VULPES VULPES*

by

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1. Introduction

The North Sea coast of the Netherlands is lined with a strip of sand dunes, 1-5 km wide, which in many respects forms an elongated ecological island between the sea and the vast area of low-lying (mostly below sea level) wet grasslands of western Holland. As far back as written accounts go, this dune region has always been famous for its rich animal life, the rabbit *Oryctolagus cuniculus* being the predominant mammal. Mammalian predators present were polecat *Mustela putorius*, weasel *M. nivalis* and stoat *M. erminea*. Of these three, the stoat was the main predator of the rabbit, as was already recognized by the unknown author of a manuscript on game practices, dating from about 1635 (Swaen, 1948):

“De Armelijnen oft Harmels zijn cleijnder als een Bonsum [= bunzing] doch is 't schaedelijckste ende 't quaetste ongedierte van alle 't geene wij hier te Lande hebben. Doen meer quaet als den bonsum uijtgenomen als die voedende is, inde lamprey [= jonge konijnen]-tijdt.” [The stoat is smaller than the polecat but it is the most noxious vermin of all we have in the country. They do more harm than the polecats except when the latter are raising young, in the young-rabbit season.]

At the time of the cited manuscript rabbits were an important economic resource. They were kept in warrens, tended by “duijnmeijers” (De Rijk, 1988) who did their utmost to control the predators.

Until about 1980 the stoat has been common in the dunes, but then the number of observations decreased sharply and eventually the species became completely extinct in many parts of the dune region. In this paper I will try to document this extraordinary event as well as to analyse its cause. Since nothing has been written about the life of the stoat in the dunes, I will also seize the opportunity to describe the natural history of the species as far as data are available. Most information refers to the North Holland Dune Reserve (NHD), an area of about 4800 ha north-west of Amsterdam, where Heitkamp & Van der Schoot (1966) conducted some research on the biology of the stoat and where I have observed stoats in the field since 1978. The annual reports of the game wardens of this reserve are a useful source of information as well; I will illustrate my account with anecdotes extracted from these reports, translated into English.

2. The natural history of the stoat in the dune area

2.1. Food

The staple food of the stoat in the dunes undoubtedly was the rabbit. Rabbits are very numerous in the area; roughly 80-200 rabbits per 100 ha are shot each year in the NHD without having a noticeable effect on their numbers. Young rabbits are available from April to July and many were taken by stoats:

“On May 16 I saw a young rabbit (its age was known exactly: 36 days) running as quick as lightning with a stoat on its heels. They disappeared into a rabbit burrow, but a few moments later the stoat reappeared, dragging the rabbit away. A further two young rabbits (19 and 32 days old, resp.) were found freshly killed in front of rabbit burrows some days later. These rabbits showed canine punctures in the neck and in the skull just in front of the ears. In an enclosure six young rabbits were found (about 20 days old), all lined up along the fence, apparently killed by a stoat” (Mulder, 1979).

Stoats usually jump onto the back of a rabbit and bite firmly into the neck. This bite is, at least to adult rabbits, not lethal in itself: the canines are too short to reach vital parts such as the large veins or the vertebral column. Instead, the attack seems to induce a state of shock from which the animal eventually dies (Hewson & Healing, 1971). Usually the rabbit utters a piercing distress cry (in Dutch: “gieren”). The people working in the dunes always welcomed the hearing of this shriek; they waited until they had heard it two or three times and then went to collect an easy meal, forcing the stoat to find another one.

Many people seem to believe that stoats and weasels merely suck blood from their victims. This is probably quite untrue. From inspection of the fresh remains of an adult rabbit it is clear that the stoat eats deep into the neck muscles and may subse-

quently eat its way into the thoracic cavity. Wallage-Drees (1988) estimated that on average about 40 grams of flesh was missing from adult rabbits killed by stoats. This compares well with data in the literature: the daily food requirement of the stoat (in captivity) is about 35 to 60 grams (Day, 1963; Müller, 1970). Higher food demands, of up to 100 grams per day, are mentioned by Delattre (1987). Small rabbits may be eaten (almost) completely and stoats occasionally detect and enter rabbit breeding burrows, as we discovered during two years of research on the reproduction of the rabbit in the NHD. More than 100 rabbit breeding burrows ("stops") were kept under observation. Many rabbit nests were dug out by foxes (Mulder & Wallage-Drees, 1979) and the young in one stop were killed by a stoat. This burrow, the existence of which was known for a week, was inspected at 3 p.m.:

"The stopped entrance showed a small hole, approx. 5 × 3 cm. As soon as we had opened the stop completely, a stoat escaped from it. In the nest we found the remains of three nestling rabbits: a head, a young of which the hind legs had been eaten, and a complete young weighing 126 grams. The estimated weight eaten by the stoat was 105 grams, which indicates that the stoat must have been there for longer than one day. The nestlings were about ten days old and had their stomachs full of milk" (J. L. Mulder, pers. observ. 23/4/1979).

The presence of milk means that the stoat must have killed the young rabbits early in the morning, because they are generally nursed shortly before the first light (Broekhuizen & Mulder, 1983; Broekhuizen et al., 1986).

It is not always easy for a stoat, however, to catch young rabbits. The stoat runs the risk of being attacked by the adult rabbits:

"Twice I observed how a stoat, whilst pursuing a young rabbit, was chased away by one or more adult rabbits. The stoat was completely knocked over by the fast running rabbits, which lowered their heads like a charging bull. At first I was amazed to see adult rabbits above ground in broad daylight, but soon I discovered, by catching and handling young rabbits myself, that the piercing shriek of a young rabbit in distress will lure adults out of their burrows" (Mulder, 1979).

The remains of larger rabbits are usually left on the spot after the stoat has finished its meal; at least, many rabbits killed and partly eaten by stoats can be found in the field. A female stoat with young drags or carries her prey to the nest. Stoats also make caches in which they may store a considerable amount of prey. Stoats will take the opportunity, if offered, to kill more than they need for the day. This has led many people to think that stoats kill just from "bloodthirstiness":

"Once I saw two rabbits playing in the sun, when suddenly a stoat appeared on the spot. It jumped on the back of one of the rabbits and bit it in the neck. The other rabbit froze, as if mesmerized, and within moments the same happened to him. It all took less than half a minute. The rabbits were not dead, but paralysed. The strangest thing, however, was that the stoat went his way as if nothing had happened. From this it is clear that the stoat is a very murderous creature." [It is not clear from the account whether the rabbits recovered or not. They may have been taken by the observer.] (T. Kaij, annual game warden's report, 1953).

The above-mentioned observations of dead young rabbits found uneaten also suggest such excess killing. However, stoats often return to collect their prey, abandoned because of disturbance or because there was an opportunity to kill more. This behaviour was sometimes used by the game wardens to capture stoats, in the days that killing "vermin" to protect game was common practice.

	N	S	P	Totals
Rabbit	33	3	30	66
Hare, adult	3			3
Hare, juvenile			1	1
Small mammals	2	2		4
Mole		1		1
Pheasant, adult			3	3
Pheasant, juvenile	5	6		11
Pheasant, egg	4			4
Other birds *)	6			6

*) Four species were identified: willow warbler *Phylloscopus trochilus*, wren *Troglodytes troglodytes* (twice), greenfinch *Chloris chloris* and blackbird *Turdus merula*.

Table 1. Prey remains of the stoat (data from Heitkamp & Van der Schoot, 1966). N = found in nests; S = stoats seen with prey; P = prey recognized from bite wounds.

"I saw two of these bloodthirsty predators chasing a pheasant *Phasianus colchicus* hen with very young chicks, killing these one by one without taking time to consume them. I chased the stoats away, went home to fetch two leghold traps, which I placed with the dead chicks as a lure behind them. Both stoats were caught within two hours" (T. Kaij, annual game warden's report, 1951).

There are no reliable data on the exact composition of the stoat's diet in the dune area. Some prey remains found in the field, especially in and near the nests of a stoat have been listed, but obviously many of the smaller prey items such as small mammals leave no traces. The market gardeners living along the dunes liked stoats because of their alleged destruction of rats (Heitkamp & Van der Schoot, 1966). After rabbits, the most frequent prey are various bird species, ranging in size from wrens *Troglodytes troglodytes* to adult pheasants (Heitkamp & Van der Schoot, 1966); see also section 4. Small mammals probably make up a substantial part of the diet, but will rarely be found as prey remains. Table 1 shows the data on food, gathered by Heitkamp & Van der Schoot (1966) in the years 1965-66. Many of the rabbits they examined appeared to have suffered from myxomatosis. On the other hand, the game wardens always stressed the point that stoats used to take the "best" rabbits (P. Woudsma, pers. comm.).

2.2. Reproduction

The reproduction of the stoat is characterized by the phenomenon of delayed implantation. Copulations take place during spring and summer, but the fertilized eggs develop into blastocysts only, to be stored until implantation in the following spring. Implantation is triggered by a certain critical day length, which at our latitude falls somewhere in early April. The period between implantation and birth is about 28 days, so the young are born early May (King, 1989).

In 1965 and 1966 ten litters were found, caught or observed in the NHD, with 1×2 , 3×4 , 4×5 , 1×6 and 1×9 young. The last litter, with nine young, was considered exceptional by the game wardens (Heitkamp & Van der Schoot, 1966). In

a period during which all observations of mammalian predators in the NHD were recorded, between 1979 and 1983, three stoats were observed accompanied by 3, 5 and 7 young. All three observations were in the last week of June or the first week of July.

The average number of young in these 13 litters was 4.92 (S.D. 1.75). In the literature the number of young born per litter ranges from 1 to 18, with a mean value ranging from 6 to 9 (King, 1989). Compared with these records, the number of young in the dune area seems to be rather low, but we have to take into account that many of the dune litters were already well grown by the time of observation, and some of them may have suffered losses or may have begun to split up already. Lactation ends when the young are 7-12 weeks old. They can kill their first prey at the age of 10-12 weeks (King, 1989); in the dune area the 10th week probably coincides with early July.

Compared with the weasel, the average litter size in the stoat is slightly larger; weasels, however, have no delayed implantation and may produce more than one litter per year. This means they are able to react more quickly to favourable conditions such as an increasing prey population. On the other hand, stoats generally live longer, up to eight years; in New Zealand 25% (sexes combined) and in Sweden 14% (males) and 9% (females) of the stoats live longer than two years (King, 1989; Erlinge, 1983) as compared to 2% (males) and 4% (females) in British weasels (King, 1989). Van Soest & Van Bree (1970) analysed the sex and age composition of the stoat population in the NHD in 1965-67 by examining 150 carcasses collected by wardens. They concluded that among the 87 males, 12.6% were older than two years and only 3.4% were older than four years.

Heitkamp & Van der Schoot (1966) found four stoat nests which were being used or had been used to raise young. All four were shallow scoops in the ground, very well hidden beneath piles of cut trees or other material and lined with fur and feathers from prey animals. Faeces and prey remnants such as the heavier bones of rabbits were scattered around the nests. It is likely, although nothing is known about it apart from a passing reference by Roderkerk (1957), that stoats also made nests in rabbit burrows; the nests of the rabbits themselves seem to offer especially suitable breeding dens. The game wardens, however, have the impression that stoats did not use rabbit warrens for this purpose, but rather made their nest in mole *Talpa europaea* runs, under piles of branches, under man-made structures etc., strongly preferring to have only small entrances to their nests (P. Woudsma, pers. comm.).

3. Population density in the past

The number of stoats (and of all other species) caught annually in the 4800 ha NHD have been recorded since 1952. Before 1970 the majority of the stoats were killed in autumn and winter, by making scent trails and placing leghold traps. In spring and summer some stoats were taken by shooting (P. Woudsma, pers. comm.). In December 1969, however, the use of leghold traps was made illegal in the Netherlands, which resulted in a drastic change in the yearly pattern of the catches, with most animals taken in spring and summer (fig. 1). The total number killed each year dropped to about one sixth of the number before 1970.

Although there are obvious drawbacks in using bag records as a reflection of population density, these are the only data we have; until the drastic change in control tech-

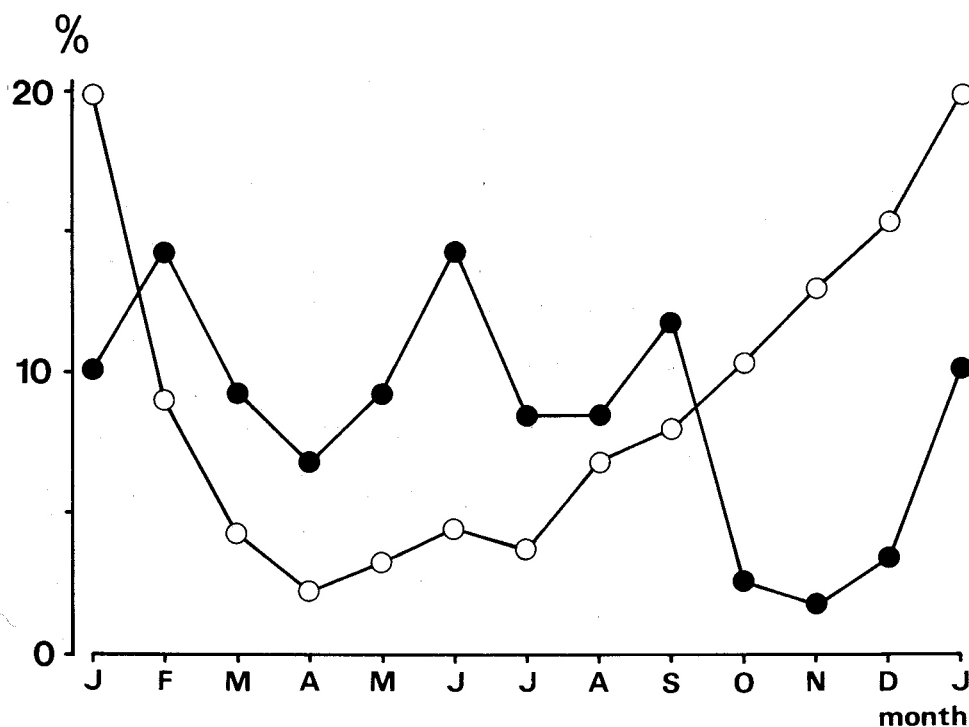


Fig. 1. The effect of the use of leghold traps on the relative numbers of stoats taken each month in the NHD. Percentage of stoats caught per month during the years 1966-69, $n = 679$ (○) and 1971-74, $n = 119$ (●), before and after the ban on leghold traps, resp. (P. Woudsma, pers. comm.)

nique in 1970 they may at least give a picture of the relative changes in numbers from year to year, since the circumstances (e.g. number of game wardens and their catching methods) were more or less the same throughout the period 1952-69. Fig. 2 shows the bag records between 1952 and 1969 of all three mustelid species in the NHD. The average number of individuals taken each year was: stoat 193.2 (S.D. 46.5), weasel 52.6 (S.D. 26.5) and polecat 26.1 (S.D. 20.0). There is clearly a large fluctuation between years in the bag records of all three species, sometimes with parallel tendencies, e.g. in 1955-60 and 1963-69. This may indicate either parallel fluctuations in real population densities, or fluctuations in catching effort having a similar effect on all three species.

On average about four stoats per 100 ha were killed each year during this period. The lack of stoat control during the Second World War did not lead to an increase in the number of observations of stoats in the area, nor did local and temporary (Heitkamp & Van der Schoot, 1966) and eventual complete abandonment of control in 1976 (P. Woudsma, pers. comm.). It is therefore likely that the toll taken from the stoat population must in general have been less than the annual production of young. Assuming an average productivity of five young per female, the average density of

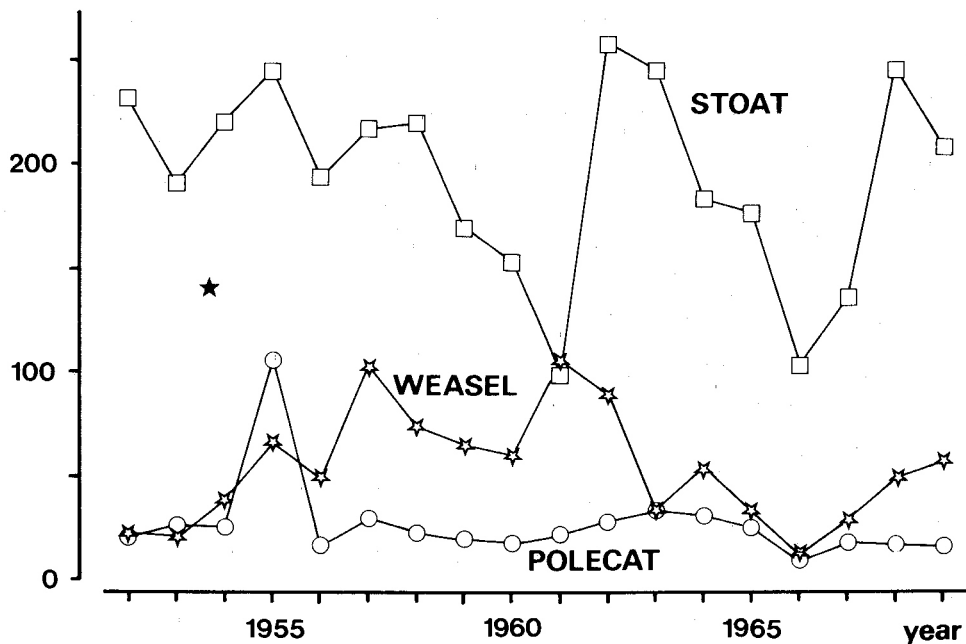


Fig. 2. Numbers of stoats, polecats and weasels caught in the NHD between 1952 and 1969. * indicates the arrival of myxomatosis.

females must have been at least 0.8 females per 100 ha. The sex ratio in the sample examined by Van Soest & Van Bree (1970) was 63 females and 87 males, or about 2:3. Assuming, however, for this purpose that the real sex ratio in the field is 1:1, the total population density of the stoat must have been at least 1.6 animals per 100 ha in the period just before the birth of the young. Assuming that the subsequent addition to the population of four young per 100 ha decreases linearly to zero throughout the year (which it probably does not, since there is a large fluctuation in the number of stoats caught throughout the year: fig. 1), the average number of stoats per 100 ha throughout the year must have been at least 3.6 animals (1.6 adults plus 4/2 young). Heitkamp & Van der Schoot (1966), merely from their field observations, estimated that the density of stoats in 1966 was about three animals per 100 ha. They mention that the game wardens thought that there was one stoat per 15 ha, i.e. 6.7 per 100 ha, just before the reproductive season.

Erlinge (1983) gives the density of stoats in southern Sweden as 3-10 per 100 ha in autumn in rough pasture areas where rabbits and voles *Microtus* sp. are the staple food, and up to 22 per 100 ha in marshy areas with the abundant water voles *Arvicola terrestris* as the staple food. Home ranges are generally smaller in females than in males, ranging from 2-17 and 8-40 ha, respectively, in a variety of habitats in western Europe (King, 1989). In spring and summer some males may range over much more extensive areas (Erlinge & Sandell, 1986).

It is impossible to estimate the impact of the stoat on the rabbit population, but the following tentative suggestion may be made. Assume that stoats ate rabbits on eight out of ten days and that each stoat killed one adult or young rabbit per day, the adults being eaten only partly and the smaller young completely. This results in a total of at least $0.8 \times 3.6 \times 365 = 1051$ rabbits killed per 100 ha per year. The annual bag of rabbits in the same years averaged 5970 rabbits in the NHD, i.e. 124.4 rabbits per 100 ha. These figures suggest that the stoat probably had a larger impact on the rabbit population than the game wardens.

4. Effects of the arrival of myxomatosis

King (1989) describes how the sudden decline of rabbits, as a result of the arrival of myxomatosis, affected the number of stoats and weasels caught in England. The number of stoats decreased sharply whereas many more weasels were caught than before. One possible explanation is that the stoat experienced much fiercer competition with the larger predators (fox, feral cat, birds of prey) for the remaining rabbits whereas the weasel profited from the increased number of voles. The vole populations flourished as a result of the more abundant vegetation, which was no longer grazed short by the rabbits.

The effects of the arrival of myxomatosis in the Dutch dune area do not seem to have been as drastic as in England. In the NHD myxomatosis was first noticed in October 1954; within a year the disease had reached every corner of the reserve, and dead and dying rabbits were found everywhere. There was, however, no effect on the number of stoats killed for at least the first five years after the arrival of myxomatosis (fig. 2).¹ The number of polecats killed rose sharply in 1955, returning to a more normal level the next year. The diseased rabbits were an easy source of food, which probably enhanced either the reproduction rate or the survival of young polecats, or both, but for one year only. Interestingly, Weber (1989) predicts, on the basis of a study of the polecat's population biology in Switzerland, that polecat populations will react positively to favourable summer and autumn conditions (more so than to favourable winter conditions), as a result of a better survival of young.

Between 1955 and 1962 the bag record of weasels was on average 122% higher than before or after this period, which, as in England, may also have been an indirect effect of myxomatosis. The lack of an effect on the numbers of stoats may have been due to an increased reproduction rate of the remaining rabbits, as a result of which many young rabbits were available in the years directly after the arrival of myxomatosis (Heitkamp & Van der Schoot, 1966). In contrast to the English situation, there were no larger predators in the Dutch dunes except feral cats *Felis catus*, to compete with stoats for rabbits: foxes *Vulpes vulpes* and the larger birds of prey, e.g. buzzard *Buteo buteo* and goshawk *Accipiter gentilis* had not yet arrived in the area though buzzards were regular winter visitors.

¹) The same data, at least for the years 1953-61, were previously published by Doude van Troostwijk (1964); he corrected the figures for the number of people officially employed as game wardens each year. However, the actual number of people actively involved in control operations in the field was more or less the same from year to year (Heitkamp & Van der Schoot, 1966; P. Woudsma, pers. comm.).

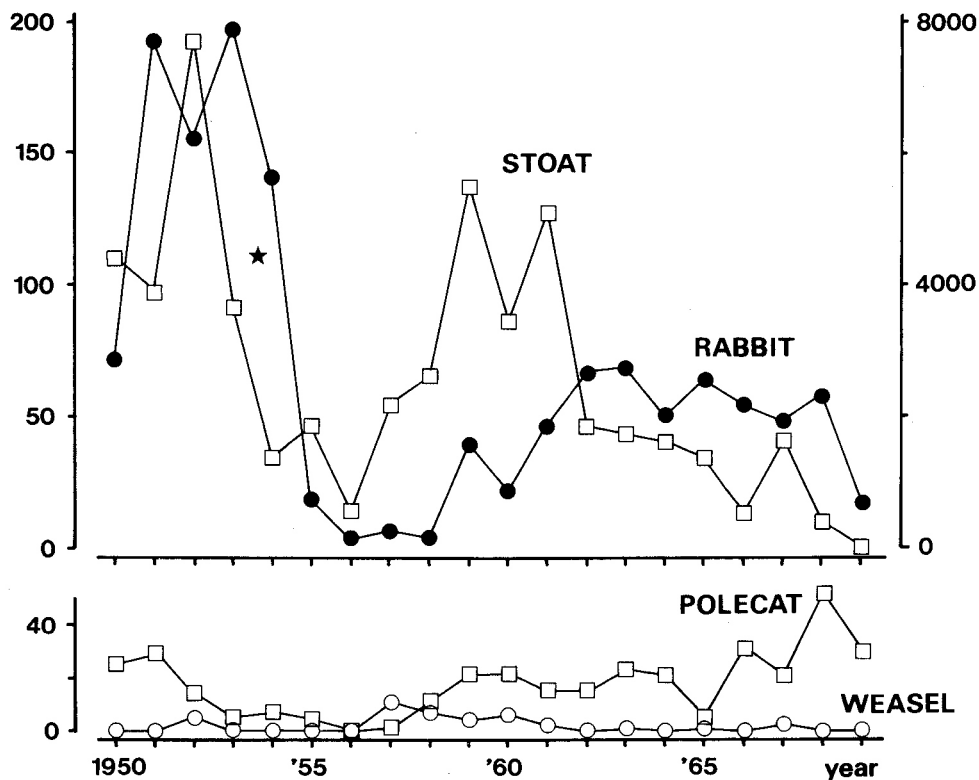


Fig. 3. Number of stoats, polecats, weasels (left y-axis) and rabbits (right y-axis) caught in the Kennemerduinen between 1950 and 1969. * indicates the arrival of myxomatosis (after Heitkamp & Van der Schoot, 1966; archives Nationaal Park Kennemerduinen).

However, in another part of the dunes, the Kennemerduinen (1240 ha), the bag records give a completely different picture (fig. 3): the number of stoats killed shows a high peak two years *before* the arrival of myxomatosis and was already declining, perhaps in reaction to this peak. Myxomatosis may have kept the stoat population at a lower level for the next few years than was to be expected under unchanged conditions. The population of polecats in this area too, seems to have been negatively affected for a few years. We know too little of the circumstances in this area at the time to offer an explanation for the differences between the two areas.

The wardens expected that the disappearance of the rabbits would lead to a decrease in the number of other game such as pheasants, due to an increased predation by stoats, but this did not happen. Pheasants were positively affected by the increased cover for nests and broods as well as by the increased supply of insects for their chicks (Roderkerk, 1975). A change by the stoat to other prey species (birds) was, however, noted by the wardens of the NHD:

"It has struck me that, as a result of the strong decline in rabbit numbers, the stoats are taking to climbing trees. I found two nestling wood pigeons *Columba palumbus*, with bite wounds in the neck, next to a pile of branches; further inspection revealed a nest with young stoats underneath the pile, together with the following prey remains: 4 young pheasants, 2 blackbirds *Turdus merula*, 1 grey partridge *Perdix perdix*, some juvenile redstarts *Phoenicurus phoenicurus* and 1 nightingale *Luscinia megarhynchos*" (A. van Amersfoort, annual warden's report, 1955).

5. The local extinction of the stoat and its possible cause

5.1. The decline

In the early seventies a decrease in the number of stoat observations in the Kennemerduinen was noted by Roderkerk (1975):

"As to the stoats, since a few years something mysterious is going on. They have suddenly become very rare. This cannot be the result of too strong control measures, because we only regulated this species. Lack of food cannot be the case either; in short, it is an unsolved mystery."

In the NHD the same drop in numbers was observed by the game wardens, but they suggested a cause as well:

"According to the game wardens the foxes have destroyed virtually all the stoats and weasels, and possibly the polecats and young feral cats too" (annual report of the Provinciaal Waterleidingbedrijf van Noord-Holland, 1975).

The annual report of the subsequent year, 1976, again mentions the decline of stoat and weasel. Unfortunately we have no quantitative data for this period, and very few thereafter, because the wardens were no longer using leghold traps. Shooting was the only control measure allowed since 1970, and very few mustelids were taken that way. Control of predators in the NHD was abandoned completely in 1976. No systematic records were kept of predator observations until the start of a fox study in the area in 1979. Then the people working in the field were asked to enter their observations of foxes, stoats, weasels and polecats on maps attached to the walls of the canteens. The number of observations can only be regarded as a rough relative estimate of the predator density, because the workers' readiness to enter observations probably varied considerably with time and between different workers and areas of the reserve.

The available data are presented in fig. 4. Whereas the number of polecat observations remained rather stable between 1979 and 1983 and weasel observations fluctuated considerably, the number of stoat observations dropped suddenly from 1981 to 1982. In fact, according to the game wardens, the stoat population had been declining since 1975, well before these records started. In 1984 stoats were seen only occasionally in the NHD (P. Woudsma, annual game warden's report, 1984). My own last observations of stoats in the NHD were made in 1981 (fig. 5, 6).

The difference in stoat density between the years 1965-66 and 1978-81 may be illustrated by the number of animals seen per 100 hours of field observations. The carefully kept field notes of H. Schekkerman, a frequent visitor to the NHD, reveal an observation rate of 0.5 to 2.1 stoats per 100 hours in 1978-81 (fig. 4). By contrast, Heitkamp & Van der Schoot (1966) mention having observed about four stoats per 100 hours of field work in 1965-66. These data are, however, not directly comparable, because Heitkamp & Van der Schoot visited the reserve in spring and summer only,

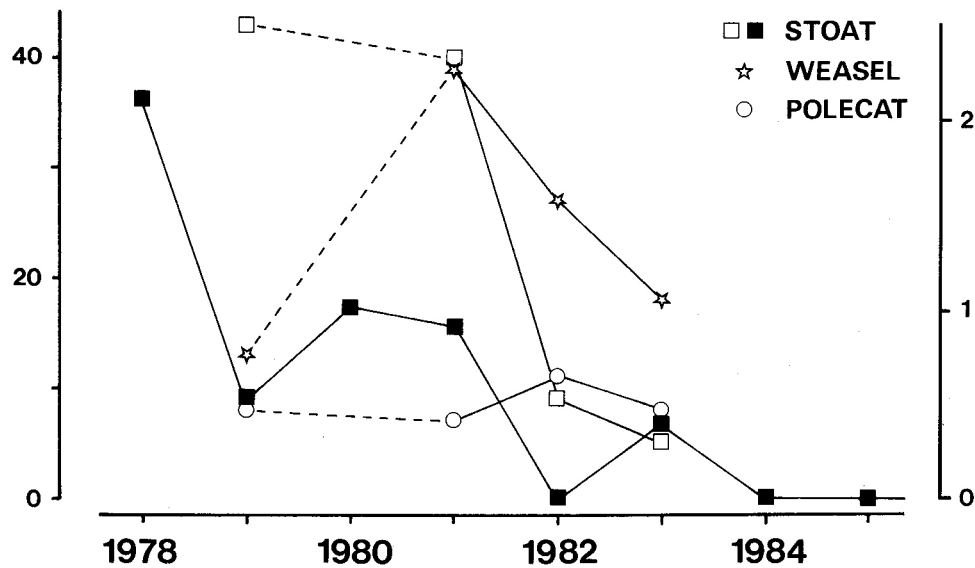


Fig. 4. Number of times mustelids were observed by staff members of the NHD in 1979 and 1981-83 (left y-axis, open symbols), and number of stoat observations per 100 hours of bird watching by H. Schekkerman in 1978-85 (right y-axis, solid symbols). The NHD data for 1980 were lost.

and were specifically looking for stoats, whereas Schekkerman visited the reserve the whole year round, mainly for bird watching.

Data on the decline of stoat populations in other parts of the dune region were gathered by interviewing the managers and game wardens of seven dune reserves, mapped on fig. 7. The results are shown in table 2. It seems safe to conclude that the stoat has become extinct in the whole of the dune region except perhaps in the northernmost part, the Zwanenwater. This area is different from the others in three respects: the stoat has always been rare here, the fox arrived rather late (1977), and foxes are shot on sight to protect a spoonbill *Platalea leucorodia* breeding colony.

5.2. Possible causes of the extinction

There are many accounts of the disappearance of predators from larger areas, most of them clearly caused by human interference. The classic examples are, of course, the extinction of wolf *Canis lupus* and bear *Ursus arctos* in most of Europe, but smaller predators have been exterminated from some places as well. In Great Britain, for instance, the polecat and the pine marten *Martes martes* were wiped out except in parts of Wales and Scotland, respectively, by human persecution in the 19th century. Stoat and weasel were killed in even greater numbers but did not become extinct, because their opportunistic life history makes them much less vulnerable to man-induced mortality (King & Moors, 1979).



Fig. 5. Stoat with dying subadult rabbit. De Kruisberg, summer 1981 (from colour slide).



Fig. 6. Stoat on the look-out. De Kruisberg, summer 1981 (from colour slide).

The arrival of a new predator can displace another resident species. In parts of North America where wolves have disappeared as a result of human persecution, coyotes *Canis latrans* have extended their range, and consequently red foxes have vanished from these areas (Voigt & Earle, 1983). Next to human persecution and interspecific competition, the most likely causes of local extinction are a major change in food supply, a sudden infectious disease (like rabies or mange), and predation. To determine which of these could have destroyed the established population of the stoat

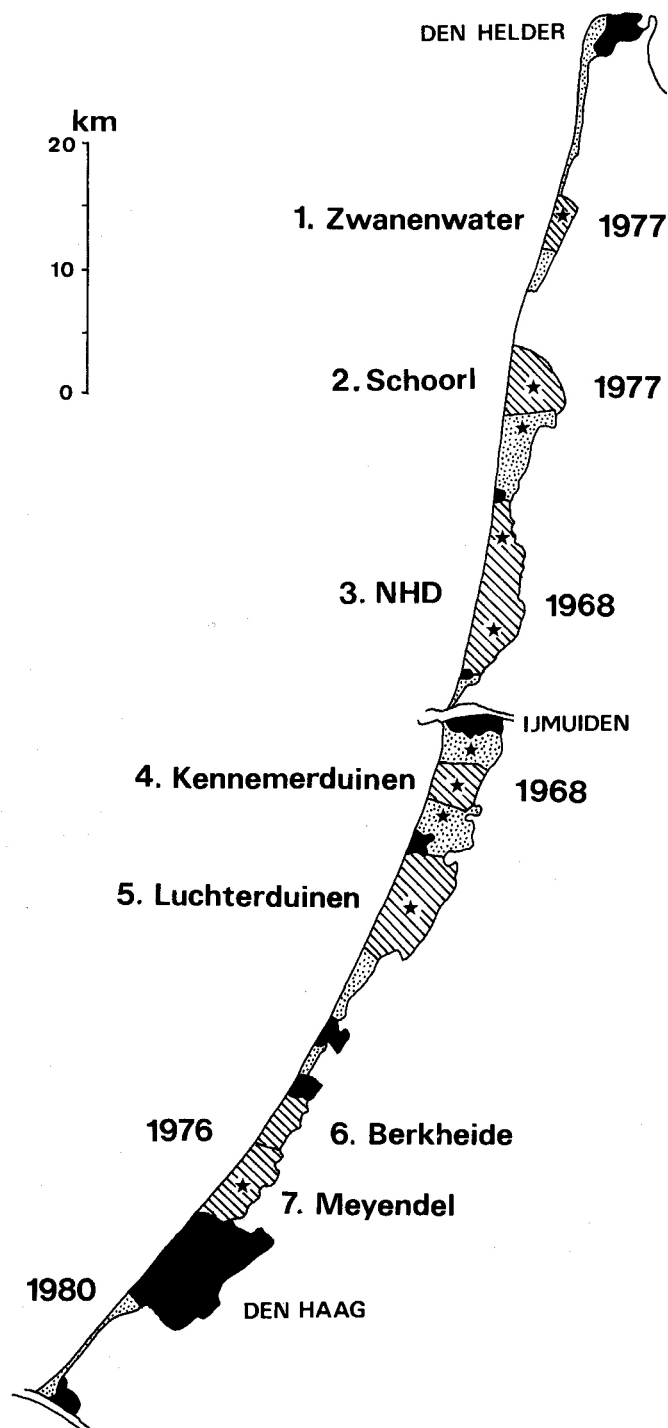


Fig. 7. The dune region along the mainland coast of Holland, with the numbered dune areas listed in table 2 (hatched) and the other dune areas (dotted). The years of first recorded fox sightings, if known, are mentioned as well. Built-up areas in black. * Area where rabbits are being censused.

No. (see fig. 7)	Area and source of information	Species	Former occurrence (-1970)	Present occurrence (1985-)	Year of last stoat observation
1	<i>Zwanenwater</i> W.H. Klomp	Stoat	—	—	1988
		Weasel	+	+	
		Polecat	+	+	
2	<i>Schoorl</i> F.H. Nieuwenhuizen	Stoat	+	—	1980
		Weasel	—	—	
		Polecat	+	+	
3	<i>NHD</i> this paper	Stoat	++	—	1984
		Weasel	+	+	
		Polecat	+	+	
4	<i>Kennemerduinen</i> J. Verdel	Stoat	++	—	1983
		Weasel	+	+	
		Polecat	—	—	
5	<i>Luchterduinen</i> H.J. Verdonk	Stoat	++	—	1978
		Weasel	+	+	
		Polecat	+	—	
6	<i>Berkheide</i> J. Hoogenkamp, J. Dros, N. Aarts	Stoat	+	—	> 1972 (1987) (1988)
		Weasel	+	+	
		Polecat	+	+	
7	<i>Meijndel</i> Th. J. van Leeuwen, G. van Ommerring	Stoat	++	—	1982 (1985) (1986)
		Weasel	+	+	
		Polecat	+	+	

Table 2. Observations of mustelids in various parts of the dune region. ++ very common; + common; — rare; — absent. Years of incidental last observations of stoats in brackets.

in the Dutch dune region, it would help to compare the field conditions before, during and after the decline.

Human interference cannot have been a significant factor unless the intensive control measures before 1970 had been actually maintaining the population, which is inconceivable. The control measures were relaxed in 1970 as a result of the ban on leghold traps, and (at least in the NHD) abandoned entirely in 1976. In some places in the dune region there has been some illegal poisoning of foxes between 1979 and 1984 (Mulder, 1988b). This may have affected polecats as well, but it seems unlikely that stoats would have taken the poisoned baits to any great extent, because small mustelids (at least the longtailed weasel *Mustela frenata*; Devan, 1982) strongly prefer live or at most freshly dead prey.

Small mustelids have no diseases capable of drastically reducing the population density. Their best-known disease is skrjabinoglyosis, caused by an infection of the nasal sinuses by the nematode *Skrjabinoglyus nasicola*. This disease is, however, not lethal except perhaps in older animals, beyond their first year of reproduction, and therefore cannot have any appreciable effect on the population level (King, 1989). The incidence of this disease in the dune region before 1972, as judged from the signs of distortion of and damage to the skulls, was 21% in young stoats (less than one year old, n = 141) and 28% in older animals (n = 53) (Van Soest et al., 1972).

Variations in the main food supply do not seem to have played a role either. The rabbit populations gradually recovered from the first outbreak of myxomatosis, and

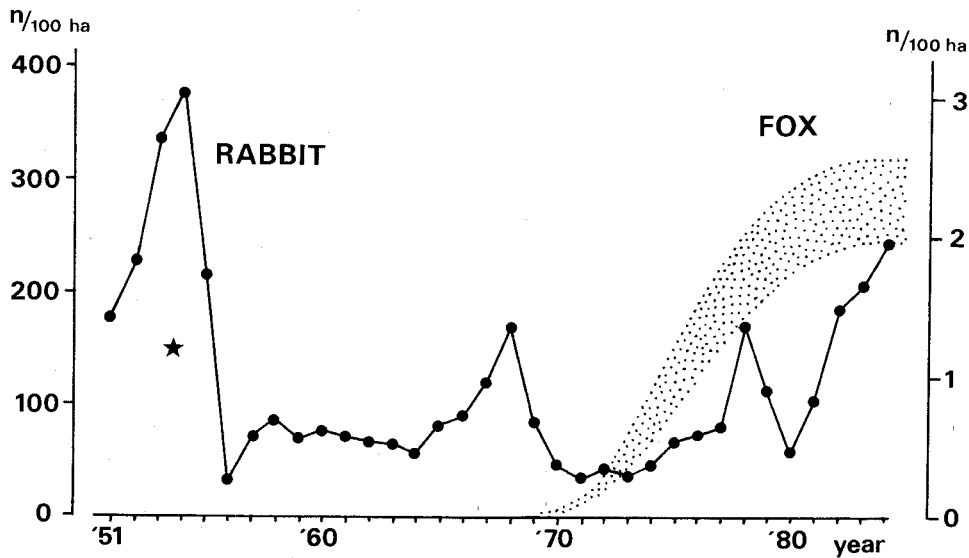


Fig. 8. Number of rabbits shot per 100 ha in the NHD between 1951 and 1984 (left y-axis) and estimated number of foxes per 100 ha in early spring (right y-axis) (from Mulder, 1988a). * indicates the arrival of myxomatosis.

this recovery has not been inhibited or reversed by the arrival of the fox (fig. 8). The number of rabbits shot in the NHD has even increased recently, although small changes in shooting practice render the figures for these last years not entirely comparable with those for previous years. Between 1982 and 1987 systematic transect counts of rabbits were made in ten areas of the dune region (fig. 7) and the results show a stable pattern over the years in four, a decrease in three, and an increase in the remaining three areas (Kivitt & Snater, 1988). So the arrival of the fox and its subsequent rapid increase have had no obvious effect on the rabbit populations in the dunes, and there are no reasons to assume a substantial reduction in the main food of the stoat. Alternatively, perhaps stoats were prevented from hunting by foxes, by continuous harassment for instance. If this were so, we should have expected the stoats to hunt more frequently by day, to avoid confrontations with foxes: at least in the northern half of the dune region the foxes are almost exclusively nocturnal (Mulder, 1988b). This suggestion is, however, not supported by field observations.

To what extent the supply of other prey than rabbits may have changed since 1970 is largely unknown. The number and species of breeding birds have not changed much over the years, according to the unpublished reports of the census work by local bird watching clubs. Only the pheasant population has declined rather strongly between 1970 and 1980, from about 140 to about 40 birds per 100 ha, as a result of a drastic change in pheasant management in 1970 and probably also partly as a result of predation by foxes (Mulder, 1988c). There are no data on small mammals, but it seems that no obvious changes have occurred since the years when stoats were still common. The

wood mouse *Apodemus sylvaticus* is the most widespread rodent species in the dune region, living in both wooded and open areas. The bank vole *Clethrionomys glareolus* lives in the wooded areas of the dunes; the common vole *Microtus arvalis* is more patchily distributed, living mainly in the larger, grassy valleys. Of the insectivores only the mole, common shrew *Sorex araneus* and pygmy shrew *S. minutus* are found in the dune area (data from the Provinciaal Waterleidingbedrijf van Noord-Holland and own observations); the latter three species are, however, avoided by stoats and weasels (King, 1989).

Apart from the fox, two other predators have reached the dune region recently: a few pairs of buzzard now breed in the area and the goshawk is trying to establish itself as a breeding bird. Their numbers are still very low and their presence is unlikely to have influenced the stoat.

5.3. The fox's role

Undoubtedly the most striking change in ecological conditions in the dune region has been the arrival of the fox. According to archaeological data and the manuscript from 1635 referred to in the introduction, foxes probably lived in the coastal regions of Holland until the Middle Ages, when they were exterminated as a result of large-scale deforestation and human persecution. Occasionally dispersing foxes from the east reached the area, but these were quickly caught by the "duijnmeijers" (the warreners) and their dogs, because the drift sand of the dunes offered prime tracking conditions (Swaen, 1948). In later centuries, and especially towards the end of the 19th century, the dunes were more and more planted with marram grass and trees, which gradually restored suitable living conditions for foxes. However, the vast area of low-lying meadows to the east of the dunes prevented the immigration of foxes from the nearest populations, at least 60 km away. Between 1936 and 1968 at least five foxes are known (from press reports) to have been shot or observed in or near the dunes.

From 1968 onwards, increasing numbers of fox sightings have been reported from the dune area. Foxes seem to have been introduced deliberately, more or less at the same time in two areas, the NHD and the Kennemerduinen. An anonymous person told me that in 1968 four young foxes, presumably cubs from the same litter, were released in the NHD. The inbred character of the present fox population in the NHD is apparent from the high incidence of an aberration characterized by strongly shortened mandibles (Bouwmeester et al., 1989). The subsequent spread of foxes through the dune region is indicated in fig. 7. Fig. 8 gives an estimate of the population density of foxes in the NHD; from zero in 1967, the population reached its highest density in 1982, stabilizing or slightly decreasing since (Mulder, 1988b). Although about 90% of the fox's diet (by weight) in the dune region consists of rabbits (Mulder, 1988a), the rabbit population has shown no signs of a decrease since the arrival of the fox (fig. 8). Foxes exploit the rabbits they catch much more efficiently than stoats do, because they eat the rabbits almost completely, temporarily storing what exceeds their daily requirements (about 500 grams). In contrast, stoats generally leave their kill (at least the adult rabbits) on the spot after having eaten only a small part of it (see section 2.1), where they are further consumed by scavengers such as magpies *Pica pica* and carrion crows *Corvus corone*. The respective densities of foxes and stoats are, or rather

were, similar: 2 to 2.5 foxes per 100 ha in early spring and about 6 per 100 ha in summer (Mulder, 1988b), compared with (a minimum of) about 2-3 stoats per 100 ha in early spring and about 6-7 in summer (see section 3).

The decline of the stoat coincides (at least in the NHD) with the increase in foxes, but no correlation is proof of causation. In principle there are two ways in which the fox may have influenced the number of stoats: by competition for food and by direct interference. Although changes in the food situation with the arrival of the fox may not have been obvious (see above), they still may have been important enough to affect the stoat population. The stoats studied by Erlinge (1983) in southern Sweden were limited by food shortage, due to competition for their main prey, water voles, by other, more generalist predators. Stoats are much smaller in Sweden than in England and the Netherlands (Erlinge, 1983; Van Soest & Van Bree, 1970), and in Sweden the rabbit is not an important prey species. When rabbit numbers decreased in Erlinge's study area, the generalist predators (fox, buzzard, domestic cat) turned to other prey and increased their intake of voles and water voles. The total availability of voles and water voles to predators, however, did not change, which implied that the stoats consumed less of these prey species than before. As a result, reproduction of the stoat was markedly reduced and the population declined, although their main prey had not decreased in numbers. Something similar might, in principle, have been the case in the Dutch dune region; besides the rabbit as staple food, there may have been other important prey species during the reproductive period for which the stoat suddenly had to compete with the newly arrived fox, for instance young pheasants or small mammals. However, it is rather difficult to assume such a mechanism in the dune region, in view of the abundant supply of young rabbits during the stoat's reproductive period.

The opinion of the NHD game wardens that foxes interfered with stoats by actually killing them, seems the most likely explanation for the extinction of the stoat. Two stoats and about ten polecats, found dead in the NHD between 1978 and 1985, on examination showed punctures in the chest region or the skull, made by canines 20 to 25 mm apart, the distance characteristic for the fox. Apparently these mustelids are vulnerable to predation by the fox; perhaps foxes take them when hunting by ear, only realizing what they have caught when they have already made the kill. However, P. Woudsma twice observed a fox chasing a stoat in broad daylight in the NHD, in one case for at least a hundred meters (pers. comm.). Foxes do not generally eat mustelids as they apparently find them unpalatable (Macdonald, 1977). Dead polecats were also found in another dune area, Berkheide, during the early eighties (J. Dros, pers. comm.). In yet another dune area, the Luchterduinen, a total of eight polecats were found uneaten among the prey remains at three fox dens in 1980-82 (H. J. Verdonk, pers. comm.). This is the only dune area where the polecat population has strongly decreased since 1970 (table 2).

During nightly observations in the course of the fox study in the NHD, only once was a confrontation seen between a fox and a mustelid, in this case a polecat:

"10.50 p.m. Suddenly I hear the 'geckering' sound of a polecat, and with my infrared binoculars I see a radio-collared female fox about fifty meters away from me; she is standing in front of the noisy polecat, in an inquisitive posture. The polecat retires, walking slowly and very attentively backwards into a rabbit burrow a few meters away; the vixen follows her at a distance of about one meter or less.

As soon as the polecat has disappeared in the burrow, the vixen inserts her head half into the burrow and subsequently token marks the entrance with urine as well as one or two of the other entrances to the warren, after which she walks away'' (J. L. Mulder, pers. observ. 29/7/1981).

From this observation one gets the impression that a fox can kill a polecat only if it catches it by surprise. Weber (1988) has experimentally demonstrated that polecats strongly prefer to stay under cover of dense vegetation, and argues that this behaviour is an adaptation to avoid predation. He also mentions that in his radio-tracking study a polecat kit was killed by a cat, a polecat male was killed by a dog, and another one was eaten and possibly also killed by a fox. So the risk of predation is very real to mustelids, even to the rather large-sized polecat. Powell (1982) has elegantly demonstrated that predation pressure, in this case predation by birds of prey, is apparently so important that it has led to the evolution of the black tail tip in stoats and longtailed weasels *Mustela frenata*. It serves to deflect striking birds of prey from the body, especially in the white winter fur; the weasel does not have a black tail tip, because its tail is too short to hold a black tip far enough from the body to be effective.

The question arises why many more polecats than stoats were found killed by foxes in the NHD, although stoats were wiped out and polecats still live there. Firstly, stoats are much smaller than polecats, hence their carcasses will not be found as easily as those of polecats and their remains will disappear sooner. Secondly, the disappearance of the stoat was a relatively rapid process, and dead stoats probably were to be found during a few years only. Apparently, enough polecats can escape predation by foxes to allow the survival of the population.

Latham (1952) has demonstrated a negative correlation between the number of small mustelids (three species) and foxes (two species) turned in by hunters in Pennsylvania. In years with a relatively high number of foxes relatively few mustelids were presented for bounty payments, and vice versa. This negative correlation was not only temporally, but also spatially demonstrable: counties with low numbers of foxes had high numbers of mustelids and vice versa. He further remarked that dead weasels were often found, uneaten, at fox dens. However, his data, like those from the Dutch dune region, are wholly circumstantial, as is the observation by Delattre (1987) that the number of stoats in the French Jura increased when a wave of rabies passed through the area, decimating the fox population.

I doubt whether the stoat will ever return in appreciable numbers to the dunes. A new population of stoats can establish itself only by an immigration of stoats from outside the area. Stoats are still present in marshy areas not far from the dunes; one was recently observed in a polder about 6 km east of the NHD (H. Kivit, pers. observ. 7/5/1989) and one was found run over on a road about 9 km east of the NHD (J. L. Mulder, pers. observ. 29/4/1989). In the marshes, the main food of the stoat probably is the water vole, as it is in the study area of Erlinge and his coworkers in southern Sweden (Erlinge & Sandell, 1986). If the stoat would be similar in behavioural development to the ferret *Mustela putorius furo*, stoats dispersing from the marshes to the dunes may not readily change to rabbits as food: Apfelbach (1986) has experimentally demonstrated that young ferrets were strongly imprinted with the food they received from the mother when they were between two and three months old. However, in other species of mustelids, i.e. martens *Martes* sp., such imprinting does not occur (Apfelbach, pers. comm.).

King (1989) considers that no conclusive evidence has yet been presented to show that weasel populations are controlled by larger predators. In general mustelid populations will be limited by food, and it is virtually impossible to produce proof of a case in which predators actually control the number of stoats. Only large-scale experiments are likely to produce results which may come near to proof (C. M. King, pers. comm.). To test the hypothesis that foxes and stoats cannot co-exist in the Dutch dune ecosystem, controlled introductions (of sterilized animals?) should be made in separate areas, and experimental and control areas should be interchanged after some years. The only areas suitable for this kind of experiments are the islands in the Wadden Sea, on two of which stoats occur, although recent information indicates that the stoat has become extinct on the island of Terschelling, where they were introduced in 1931 and subsequently established a thriving population (Van Wijngaarden & Mörzer Bruijns, 1961). In view of the great importance of these islands for bird life, it is very unlikely that the authorities would welcome the idea of releasing predators there. So, as long as experimental proof is not available, it remains a matter of opinion whether (and how) the fox has wiped out the stoat in the dune region or not.

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SUMMARY

Until about 1975 the Dutch coastal dune region harboured a thriving population of stoats *Mustela erminea*, which mainly lived on rabbits. Food habits, reproduction and population density, as far as known, are described here. From about 1975 a decline in stoat numbers was noticed, and around 1985 the species had become extinct in virtually the whole dune area. This decline is documented and possible causes are discussed. Human interference, disease and major changes in food supply are all dismissed as possible causes. Only the arrival of the fox *Vulpes vulpes* in the area offers a likely explanation for the extinction of the stoat, either through competition for food, or through direct interference. It is believed that the main cause of the extinction has been predation on stoats by foxes.

SAMENVATTING

De hermelijnen *Mustela erminea* in de Hollandse duinen en hun uitsterven, mogelijk als gevolg van de komst van de vos *Vulpes vulpes*

Tot het midden van de jaren zeventig herbergden de duinen van het Hollandse vasteland een bloeiende populatie van hermelijnen *Mustela erminea*, die voornamelijk van konijnen leefden. Voedsel, voortplanting en populatiedichtheid van deze soort worden hier beschreven voor zover de schaarse gegevens dat toelaten. Vanaf ongeveer 1975 werd een achteruitgang van het aantal hermelijnen opgemerkt; rond 1985 was de hermelijn vrijwel overal in de duinen uitgestorven. De achteruitgang wordt beschreven en mogelijke oorzaken van het uitsterven worden besproken. Menselijk handelen, ziekten en veranderingen in de voedselsituatie worden als mogelijke oorzaken van de hand gewezen. Alleen de komst van de vos *Vulpes vulpes* naar de

duinstreek wordt gezien als een waarschijnlijke verklaring; de hermelijn zou zijn verdwenen, ofwel door een vooralsnog onbegrepen vorm van voedselconcurrentie, ofwel als gevolg van directe confrontatie met vossen. Dit laatste lijkt de meest geloofwaardige oorzaak van het verdwijnen van de hermelijn: de vossen zouden de hermelijnen op grote schaal gedood hebben. Er is echter geen sluitend bewijs voor deze veronderstelling, zolang geen experimenten met het uitzetten van hermelijnen en het verwijderen van vossen zijn gedaan; het uitvoeren van dergelijke experimenten stuit echter op onoverkomelijke praktische bezwaren.

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