Long-term population trends of rabbits (*Oryctolagus cuniculus*) on Pleistocene sands in the central and northern Netherlands

Rob G. Bijlsma

Doldersummerweg 1, 7983 LD Wapse, The Netherlands, e-mail: rob.bijlsma@planet.nl

Abstract: As part of a large-scale study on the population dynamics of avian predators, major prey species, including rabbits (*Oryctolagus cuniculus*), were systematically monitored in two areas in the Netherlands, i.e the Veluwe (mainly Planken Wambuis, central Netherlands, 1974-2003: coniferous forest and heaths on sandy soil interspersed with some arable land) and Drenthe (Berkenheuvel, northern Netherlands, 1990-2003: coniferous forest and heaths on light-loamy sandy soil). Peak numbers were recorded in the late 1970s, probably a recovery from recurrent outbreaks of myxomatosis in the 1950s and 1960s. Severe winters, starting with the one in 1978/79, resulted in steep declines by 59-82%; the recovery afterwards never reached pre-crash levels. Consequently, the overall trend since 1979 was one of steady decline, with numbers in the 1990s being more than decimated compared with the 1970s (decrease of 95-99%). The reliability of this trend was validated by a similar trend in numbers shot at Planken Wambuis, and by the steeply declining proportion of rabbits in summer diets of goshawk (*Accipiter gentilis*) and buzzard (*Buteo buteo*) over the decades. It is suggested that habitat changes triggered the decline, following acidification and eutrophication of food-poor habitats on sandy soils (*Deschampsia flexuosa* became the dominant undergrowth in pine forests and on heaths), conversion of farmland into fallow land and - on the Veluwe only - a negative impact of rooting wild boars (which tripled in numbers between 1987 and 2003) on the remaining feeding grounds of rabbits. This trend was aggravated by a series of severe winters, and reached its nadir following the advent of rabbit viral haemorrhagic disease (RVHD) in the 1990s (although clinical proof is only circumstantial). RVHD probably wiped out already depleted rabbit groups and decimated thriving populations, with a serious impact on vegetation dynamics and the food base of avian predators (mainly buzzard and goshawk).

Keywords: Oryctolagus cuniculus, long-term decline, habitat changes, winter severity, myxomatosis, rabbit viral haemorrhagic disease, raptor predation.

Introduction

In the first half of the 20th century, rabbits (*Oryctolagus cuniculus*) were so abundant on the Pleistocene sands of the eastern Netherlands as to be considered a pest by foresters and farmers (de Rijk 1988). Quantitative information is largely lacking for this period, but qualitative statements are unequivocal, as for example in Wigman (1938): "This species occurs in large numbers on the 'Hoge Veluwe' and in adjoining areas, despite very intensive hunting during autumn and winter".

When I entered the scene myself, in the mid-1960s in the same region on the southern Veluwe where A.B. Wigman was still tramping, rabbits abounded despite recurrent outbreaks of myxomatosis. As part of a large-scale study on raptor dynamics, I started systematic data collection of numbers and reproduction of several important prey species, including rabbits. Initiated in 1974, this study continues to the present day. A similar study was started in western Drenthe in 1990, and is also ongoing.

Long-term rabbit studies in the Netherlands have been largely confined to the coastal dunes (Wallage-Drees 1986, Drees 1998, Olff & Boersma 1998, Drees & Olff 2001). Inland habitats received much less attention (Bakker 2003). For example, transect counts in forestries in

Drenthe in the late 1980s were discontinued shortly afterwards (Bijlsma 1993: 61). In this paper, rabbit fortunes since the late 1960s and early 1990s at two inland sites, Planken Wambuis (Southwest-Veluwe) and Berkenheuvel (West-Drenthe) respectively, will be quantified. Originally started as a monitoring scheme of a major prey base of avian predators, notably goshawk (*Accipiter gentilis*) and buzzard (*Buteo buteo*), the trends provide additional insight in the impact of changing local conditions and other mechanisms affecting rabbit numbers.

Study areas

Planken Wambuis (Southwest-Veluwe)

The Veluwe is the largest forested region in the Netherlands, covering some 1,230 km^2 of continuous woodland on fine and coarse sandy soil between 10 and 100 m above sea level. Planken Wambuis, a nature reserve of 1,965 ha situated between Ede and Arnhem (52°03' N, 5°40' E), constitutes a characteristic cross-section of the Veluwe. It comprises Scots pine (*Pinus sylvestris*) on coarse sandy soil, interspersed with Calluna-heaths and relicts of shifting sand. The few stands with larch (*Larix leptolepis*), Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) used to be managed for timber production, but were mostly clear-felled in the 1990s. In the 1970s, the vegetation was characterised by successional stages from *Spergulo-Corynephoretum* and *Genisto anglicae-Callunetum* into *Leucobryo-Pinetum deschampsietosu* (Vrijlandt & Vrijlandt-Kuiper 1971, Hommel et al. 1999). Since then, eutrophication and acidification have favoured the growth of *Deschampsia flexuosa*, which is now the dominant plant species underneath Scots pine forests (Heij & Schneider 1991), and alternated with dense growth of *Vaccinium myrtillus* where oak (*Quercus robur*) and birch (*Betula* sp.) form an understorey.

From the late 1980s onwards, about 140 ha of arable land was successively converted into fallow land and grazing pastures. These fields used to be cropped with cereals (mainly summer rye) in the 1970s, with a scattering of potatoes and beets. Green maize was the favoured crop type in the 1980s (allowing dumping of manure, imported from the nearby Gelderse Vallei), alternated with potatoes, beets and winter barley. The area is grazed by red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Since the late 1980s, New Forest ponies were introduced in a fenced part of Planken Wambuis which was gradually enlarged to cover the greater part of Planken Wambuis by August 1994. Fourteen Scottish Highlander bulls were introduced in January 2003. Numbers of herbivores have steadily increased over the past decades. Red deer, for example, increased from 116-138 in 1973-1977 to 225-284 in 2000-2003 (summer census, covering the entire Southwest-Veluwe, of which Planken Wambuis accounts for some 50%). The number of New Forest ponies varies between 40 and 65. An important role is played by wild boars (*Sus scrofa*), which tripled in numbers between 1987 and 2003, and numbered 331 on the Southwest-Veluwe in summer 2003 (all data on large mammals: H. ten Seldam [Vereniging Natuurmonumenten], unpublished data). With the present density, wild boar activities have a large impact on vegetation succession and ground-dwelling animals, including rabbits, on former farmland.

Berkenheuvel (West-Drenthe)

The study area of Berkenheuvel and Forestry of Smilde (52°51' N, 6°19' E) lies on fine and loamy fine sand overlying glacial till (6-12 m above sea level) in the northern Netherlands. The landscape is mainly forested (64%), with some heaths, small-scale farmland and a brook valley. It is managed as a nature reserve, with a steeply growing input of recreational activities. Woodland is mostly coniferous with Scots pine, Norway spruce and larch as major tree species, planted from the 1940s onwards. The understorey of oak, birch, rowan (*Sorbus aucuparia*), black cherry (*Prunus serotina*) and European

alder buckthorn (*Rhamnus frangula*) is sparse, or lacking in spruce plantations.

Farming within the study area has become obsolete, resulting from enlargement of the nature reserve at the expense of farmland. Some (partly organic) farming still takes place, with a mixture of spring barley, rye, triticale (cross between wheat and rye), beets, potatoes and peas. Crop husbandry on farmland bordering the study area is mostly restricted to green maize, potatoes, some winter barley and rye, and increasingly cultivation of lilies.

Methods

Planken Wambuis

The Planken Wambuis area is being visited since 1968, but systematic surveys of birds and mammals started in 1974 (after two pilot years). From 1968-2003, a total of 764 field days covering 3,772 hours, were spent in the field, mostly between one hour before sunrise and two hours after sunset during March-August (69% of all field hours). From mid-March through late July, birds were counted and mapped during five surveys covering the complete study area, using standardised census techniques but not fixed routes. All mammals encountered were also counted and mapped, including dens and rabbit warrens. Rabbits are mostly active during twilight and at night (Wallage-Drees 1986), and therefore difficult to quantify when large census plots (as Planken Wambuis) are also covered during daytime. I allocated the precious twilight hours to areas where rabbits abounded, covering the remaining areas during the rest of the day. Presence of rabbits was also recorded by checking for fresh burrows, fur, scrapes and latrines. This method clearly underestimates total numbers, and implies some imbalance in the comparison of numbers between various parts of the study area. However, it should be stressed that this census is mainly used to depict relative changes in numbers within and between seasons, rather than providing absolute figures. To further standardise census effort, only counts during the June survey are used in this study (young of first litter have emerged from warrens, highest activity of rabbits), expressed as the number of rabbits seen per field hour, to compensate for annual variations in census effort in mid-June (i.e. 750-2,020 minutes/June with a mean of 1,297 ± 329 minutes in 1974-2003). The intensity of the surveys varied within the study area, depending on habitat, specific research interest (bird mapping, nest searching, measuring habitat variables, collecting food data, locating nocturnal species), mode of movement (mostly on foot, bicycle) and weather. In some years, this may have accounted for poor timing relative to the circadian rhythm of rabbits, but overall intensity and standardisation of fieldwork are thought to suffice to reliably detect changes in numbers over time, especially since the entire 30-year census has been carried out by the same person. The field experience of the local warden Han ten Seldam, working in the area since the 1970s and specialised in game species, served as an independent check on the outcome of my rabbit census. His description of rabbit distribution and density corresponded in detail with my quantitative census, and was further supported by information from game bags (see below).

Berkenheuvel

The study area Berkenheuvel is traversed on an almost daily basis since June 1990, mainly while researching birds. From June 1990 through December 2003, I spent a total of 13,537 hours in the field (including the Forestry of Smilde and the adjacent valley of the Vledder Aa, a small brook), of which 77% in March-August.

Rabbits and European hares (*Lepus europaeus*) are censused one hour after sunset along the adjoining line transects of Doldersummerweg (Midzomer-Klaasberg: 3,100 m of dirt road through forest and fields) and Klaasberg (Doldersummerweg-Wapserveld: 1,250 m of dirt track between heath and brook valley). The transects are covered once per two months (starting

in the last week of February, choosing a day with favourable weather conditions, i.e. wind force <3 Beaufort and no rain) by bicycle, with an average speed of 20 km/hour. When the census is frustrated by human activities (frightening rabbits into cover), another effort is made the following day. All rabbits caught in the head light are counted and categorised as small, medium-sized or full-grown. This method has been tested in several mammalian species (Morrison & Kennedy 1989), including rabbits (Wallage-Drees 1986, Kivit 1987, Bankert et al. 2003), and is considered a reliable predictor of relative rabbit numbers (despite some provisos).

Hunting statistics

On Planken Wambuis, rabbits were routinely hunted until 1998, mostly during September through April (of 2,535 rabbits shot in 1967-1998, 98.5% in September-April; incomplete data for 1967-1969, 1972-1973 and 1976-1979). Most rabbits were shot near the farmland enclaves of Dennenkamp (permanently laid fallow in 1984), Mosselse Veld (ditto 1989), Nieuw-Reemst (ditto 1991), Mossel (ditto 1996) and Oud-Reemst (still farmed), where densities were highest and most warrens were situated. Normally, shooting sessions were performed by three persons (driver, marksman, retriever) using a car and a light box (maximum bag: 65 on 6 December 1973). Some ferreting took place by 2-4 persons, but this activity was not quantified (H. ten Seldam [Vereniging Natuurmonumenten], unpublished data). Hunting activities never interfered with my censuses.

Visiting raptor nests: collection of prey remains

Annually, all raptor nests within the boundaries of the study areas are located and climbed 2-6 times (Planken Wambuis) and 2-50 times (Berkenheuvel) per breeding cycle to determine clutch and brood size, take measurements and collect prey remains (Bijlsma 1997). At Planken Wambuis, the number of nesting pairs in 1974-2003 varied between 5 and 12 for buzzards and 3-7 for goshawks (Bijlsma 2003). In Berkenheuvel and Forestry of Smilde in 1990-2003, 10-16 goshawk nests and 28-44 buzzard nests per year were located and checked; this time series is enlarged with data collected elsewhere in northern, eastern and central Drenthe during fieldwork in 1982-1989 (Bijlsma 1993). All prey remains on and near nests were identified, aged, sexed, weighed and measured if possible. In rabbits and hares, the length of the hind foot including the claws was measured to the nearest mm with a stopped ruler. This latter measure correlates closely with body mass, and is a reliable method to approximate age and body mass of captured animals (Bijlsma 1997: 85 and 91).

Prey collection at/near nests is prone to several biases, depending on seasonal and diel timing of nest visits (nutritional needs of nestlings increase with age, hence remains of large prey species tend be over-represented later in the nestling cycle; more hungry in early morning than in late afternoon, hence smaller chance of finding small prey in early morning; more prey remains in years with an abundant food supply), individual variation in nest sanitation (some females systematically remove legs, wings or carcasses) and double counts when prey is not marked during nest visits (Bijlsma 1997: 85-86). In the case of rabbits, raptors start eating at the head; remains therefore often consisted of the hind part of the body including hind legs. Although the relative importance of rabbits as prey of raptors, based on nest visits, tends to be overrated compared to that of voles and mice, the proportion of rabbits in the prey collections allows for between-year comparisons when methods of collecting are the same between years (as in this study; photo 1). It should be noted, however, that buzzards tend to cluster around pockets of rabbits when widespread rabbit declines occur, thus biasing the proportion of rabbits in buzzard diets (but not nearly to the point that rabbit declines are obliterated from prey collections). Furthermore, territorial behaviour prevents that more than a few buzzard pairs profit from isolated rabbit pockets.

Weather

Mean monthly temperatures (in 1961-1990, based on 15 weather stations evenly distributed over the Netherlands) ranged between 2.2°C in January and 16.7°C in August. Annual precipitation averaged 760.4 mm (621.8 hours), varying between 43.4 mm in February and 78.1 mm in November; 65.6% of the annual precipitation (in mm) fell during the breeding season, i.e. March through October. Both study sites are situated in areas with on average >825 mm of precipitation per annum (Heijboer & Nellestijn 2002).

The severity of winters (mild to extremely severe, based on temperature data from November through March) is expressed as IJnsen's frost-number $V = 0.00275\ v^2 + 0.667\ y + 1.111\ z$, where v = number of frost days (daily minimum temperature minus zero), y = number of ice days (daily maximum temperature minus zero), z = number of very cold days (daily maximum temperature minus 10°C) (IJnsen 1991). In the terminology of IJnsen (1991), three winters in the period 1974-2003 qualified as severe (1978/1979, 1984/1985 and 1995/1996) and four as cold (1981/1982, 1985/1986, 1986/1987 and 1996/1997). The winter of 1978/1979 was also accompanied with deep snow and ice sleet, extending well into March.

Results

Planken Wambuis

Rabbit numbers on Planken Wambuis, as re-

Photo 1. Typical buzzard nest, with nestlings 2-6 days old, on Wapserveld, 19 May 1994; the rabbit weighed 150 g (minus head) and had a hind foot length of 56 mm. When plucked on a nest with a deep cup, as this one, rabbit hair often got stuck underneath the eyelids of buzzard chicks, sometimes leading to infection and blindness; this was not recorded anymore after 1996, indicating the loss of rabbits from the diet of buzzards since then. *Photograph: Rob G. Bijlsma.*

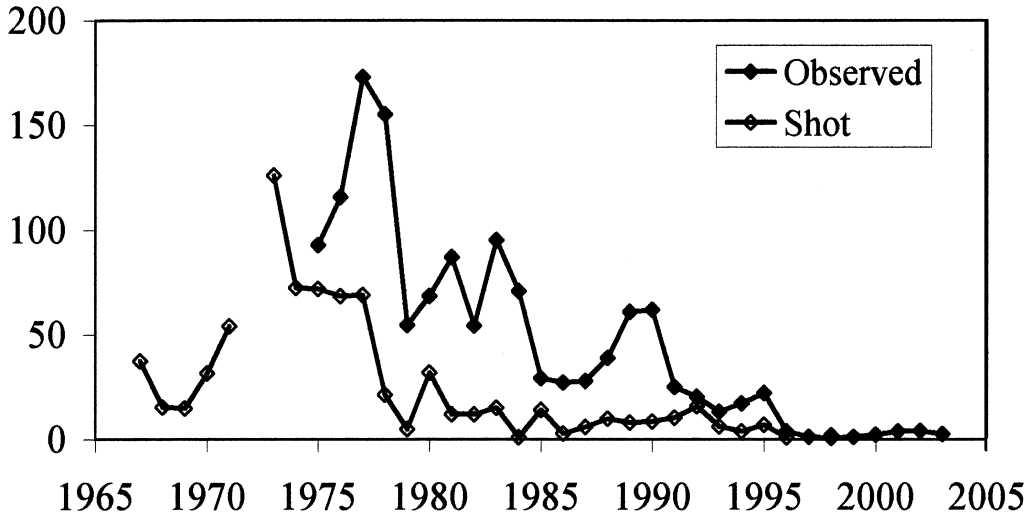

Figure 1. Rabbit counts (mean number observed hour^{-1} in June) and game bags (mean number shot month^{-1}) on Planken Wambuis, southern Veluwe, in 1967-2003.

vealed by counts and numbers shot, showed wide fluctuations with an overall decline from the late 1970s onwards (figure 1). To illustrate the extent of the decline, it suffices to note that my June-counts in 1975-1978 revealed between 2,158 and 3,015 rabbits, whereas only 22-39 were counted during the nadir in 1997-1999; the slight increase since then to 116 rabbits in 2003 is marginal compared to the numbers in the late 1970s. Consistent with the decline in numbers, the distribution narrowed down from a widespread occurrence in 1978 (all eighty-four 25 ha-squares occupied, with 17 squares of >100 rabbits each) to a single cluster (five 25 ha-squares occupied in 1998, of which only one had a reproducing territorial group of >10 individuals). At the peak, rabbits even occupied shifting sands, pure pine stands and extensive heaths (figure 2). The surviving rabbit pocket at Nieuw-Reemst occupies a well-grazed and fenced (excluding wild boars but not rabbits) area bordering dense *Sambucus nigra* and *Rhododendron ponticum* scrub near a solitary house. From this site, numbers started to recolonise the vicinity in the early 2000s, radiating in all directions via short-grazed banks of dirt roads and having reached distances of 800-1000 m from Nieuw-Reemst by 2004.

The match between counts and shooting statistics indicates that the latter method of monitoring is probably reliable in this particular case (1975-1996, Spearman test, r_s=0.618, P< 0.01). If so, it may mean that numbers in the late 1960s and early 1970s at Planken Wambuis had been at a lower level than in the second half of the 1970s (by >50%), i.e. that my counts started when numbers were at a peak.

The frequency of rabbits in the summer diets of buzzards and goshawks fluctuated strongly over the years. Up to the early 1990s, rabbits constituted on average 31.4% of the summer diet in buzzards (n=2,606 prey items), which dropped to an average of 20.2% in 1994-2003 (n=228). A stronger decline, reaching its lowest point around 1997, would have been apparent if the surviving rabbit pocket near Nieuw-Reemst had not been the specific target of two buzzard pairs, which nested successfully within 500 m of the warrens and profited from the annual outpour of young rabbits in May and June; the proportion of rabbits in the buzzard diet therefore declined only by 26% in 1994-2003 (compare with goshawks and data from Berkenheuvel, where declines of 64-75% were prevalent). A marked

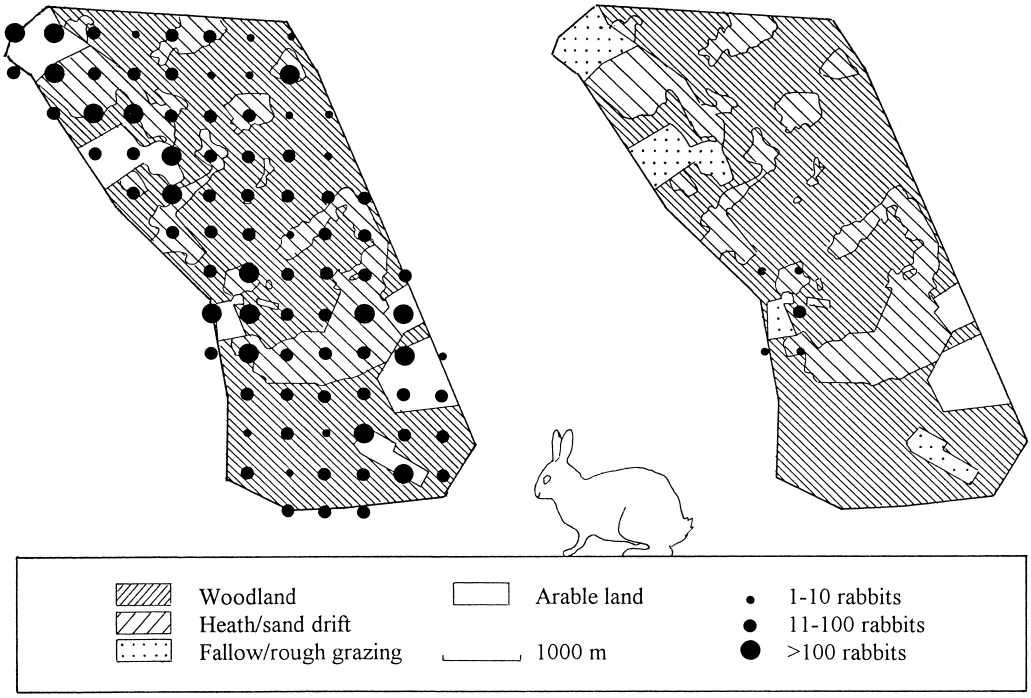

Figure 2. Distribution and abundance of rabbits per 0.25 km^2 on Planken Wambuis in June 1978 (left) and in June 1998. Notice demise of clusters except one (Nieuw-Reemst), and complete loss from forests and heaths.

decline was noticed in the proportion of rabbits in goshawk diets: rabbits formed 7.2% of the summer diet up to and including 1993 (*n*=12,890 pluckings), but only 2.6% in 1994-2003 (*n*= 418), i.e. 64%. The declines became most evident in the latter half of the 1990s and onwards (figure 3).

The three raptor species actively preying upon rabbits, i.e. goshawk, sparrowhawk (*Accipiter nisus*) and buzzard, showed differential predation, with female sparrowhawks only catching nestling rabbits upon first emergence (mean hind foot length ± standard deviation 38.9 ± 2.3 mm, *n*=11), buzzards taking kittens up to 50-60 days old (60.9 ± 8.2 mm, *n*=425;), male goshawks taking small and medium-sized rabbits (77.0 ± 9.6 mm, *n*=62) and female goshawks preying upon medium-sized and (almost) full-grown rabbits (96.8 ± 6.1 mm, *n*=13). This distinct partitioning of rabbit sizes corresponds with body mass and foot span (including claws) of the respective raptors, the latter being on average 79 ± 2.8 mm in female sparrowhawks (*n*=30), 91 ± 4.4 mm in buzzards (*n*=50), 107 ± 3.6 mm in male goshawks (*n*=107) and 124 ± 4.5 mm in female goshawks (*n*=46) (Bijlsma 1993: 261, with additions).

Therefore, as both predators mostly or exclusively preyed on kittens and medium-sized young, this decline could also have been caused by a failure of rabbits to reproduce, rather than a decline in numbers per se. However, even when rabbits were scarce, reproduction was recorded as usual. Moreover, the decline in the proportion of rabbits captured was not caused by a disproportionate increase of other profitable prey species. On the contrary, several main prey species declined as well, resulting in a more diverse prey list for goshawks since the 1980s (Rutz et al., in press).

The proportional change in rabbit abundance from one year to the next showed a significant negative correlation with winter severity (r^2= 0.446, *P*=0.0001; figure 6).

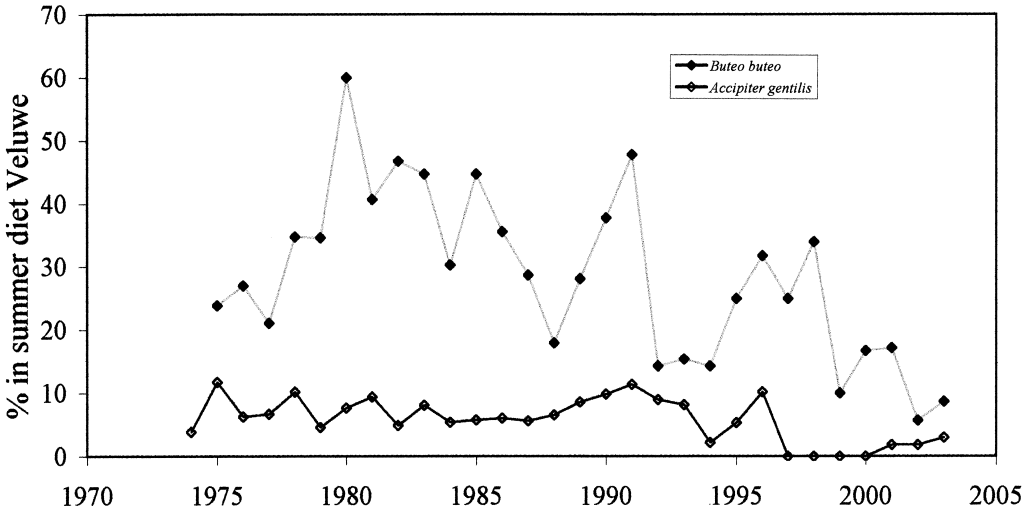

Figure 3. Proportion of rabbits in summer diets of common buzzard (n=10-734 prey remains summer^{-1}) and northern goshawk (n=19-2,486 prey remains summer^{-1}) on the southwestern Veluwe in 1974-2003; prey collections <50 are based on smaller samples of raptor nests from 1991 onwards (Planken Wambuis only).

Berkenheuvel

The overall trend on Berkenheuvel showed a steep decline (figure 4). Numbers almost halved from 1990 to 1991, then remained more or less stable for a few years, to decline again after 1994 and 1996. By 2000, this census population had disappeared completely, despite the existence of a nearby group territory on the heath of Wapserveld (distance from transect <200 m, in 2000-2001 <15 rabbits left of a population exceeding 200 in 1990; Bijlsma 2001) and the camping site/residential area of Midzomer (<150 m from transect, circa 15 rabbits left by 2003). Both extant pockets were in a poor state by 2003. The only site within 5 km of the study area in western Drenthe with some numbers left in the early 2000s is Leggelderveld. This isolated pocket still held about 20 rabbits in late 2003 and early 2004 (a decline by >90% as compared to the early 1990s; R. Vierhoven and R.G. Bijlsma, unpublished data). Exchange with nearby woodland and heaths is unlikely, as Leggelderveld is surrounded by inhospitable farmland on all sides, and effectively isolated from Berkenheuvel and Forestry of Smilde by a canal (Drentsche Hoofdvaart) and from the Forestry of Dwingeloo by a stream (Dwingelerstroom-Beilerstroom).

Rabbits as part of the summer diets of buzzard and goshawks showed declines similar to or steeper than those found on the Veluwe (figure 5), i.e. from a diet proportion in April-June of 34.3% (n=750) to 8.6% (n=1,922) for buzzards in 1984-1993 respectively 1994-2003, and from 9.3% (n=2,119) to 2.5% (n=1,363) in the same periods for goshawk. This signifies a marked reduction of rabbits in diets of avian predators, i.e. by 75% in buzzards (indicating that – unlike Planken Wambuis – rabbit clusters had been wiped out or could not be profitably exploited anymore; see above) and by 73% in goshawks (photo 2).

Discussion

The inland rabbit populations in this study showed a decline similar or stronger to the ones recorded in the Dutch dunes north of the North Sea Canal (Olff & Boersma 1998), Schleswig-Holstein, northern Germany (since 1978/1979 and especially since the mid-1990s; Anonymous

Photo 2. Some buzzards, here on the heath of Wapserveld, nested close to rabbit warrens, and preyed intensively on kittens. The chicks of 14-16 days old are surrounded by remains of three rabbit kittens, with hind feet lengths of 70, 73 and 76 mm. After 1996, such scenes have become rare in the Netherlands north of the river Rhine. *Photograph: Rob G. Bijlsma*.

2002), France (from 1989 onwards, reaching Paris in 1995; Marchandeau & Boucraut-Baralon 1999) and in Spain (since 1988, following the outbreak of rabbit viral haemorrhagic disease (RVHD); Tella & Mañosa 1993, Martínez & Zuberogoitia 2001). However, the trend recorded at Planken Wambuis indicates that long before RVHD entered the Netherlands (about 1990; Marsman & Siebenga 2002) inland rabbits were already in serious decline.

The game bag series and early counts from Planken Wambuis suggest that rabbit numbers were lower in the late 1960s and early 1970s than in the late 1970s (figure 2). Whether or not the population was then still recovering from the ravages of myxomatosis, which reached the Netherlands in 1953 (Drees 1992) and the Veluwe between 1953 and March 1955 (van Koersveld 1955), is uncertain. However, studies of goshawk diets in the first half of the 20th century show that rabbits must have been abundant in those days. Systematic collection of goshawk pluckings on the southern Veluwe (in exactly the same area where I am still collecting data) in 1928-1935 revealed 69 rabbits on 415 prey remains (16.6%); another sample, in Montferland (eastern Netherlands), showed 21 rabbits on 161 prey remains (13.0%; Tinbergen 1936). A smaller sample from the Southwest-Veluwe, based on 105 pluckings collected near goshawks nests between 1939 and 1946, held 23 rabbits, i.e. 21.9% (Versteeg s.a.). Given the excellent observation skills and field experience of this generation of ornithologists (see for example Tinbergen & Tinbergen 1931), it is likely that their data are representative of goshawk diet in these areas before myxomatosis took its toll. This can be interpreted as much higher rabbit densities in those days (my highest proportion of rabbits in goshawk diets on the Veluwe in any one year

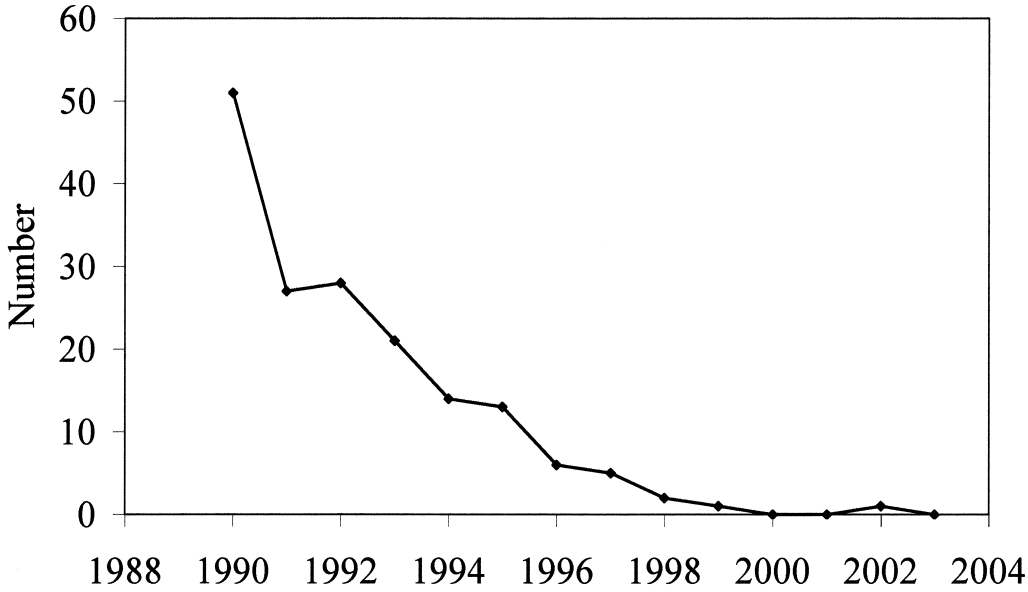

Figure 4. Number of rabbits counted on two transects (combined length 4,350 m) at Berkenheuvel, Drenthe, in June 1990-2003.

hardly ever exceeded 10%), a poorer prey base with fewer dominant prey species in general (as inferred from the predominance of shifting sands, sandy heaths and young pine plantations on poor sandy soil; Bijlsma et al. 2001), or a combination of both.

Of the many factors impacting rabbit populations, long-term habitat changes (cover and food supply), weather (severe winters, high water table) and diseases have been indicated as particularly important (Thompson & King 1994). The data collected for the present study suggest that at one time or another all these factors played a significant role, either as isolated events or in concert. The long-term decline in my study areas, as visible from 1978/1979 onward, was probably triggered by profound habitat changes, and further aggravated and persisting through stochastic events like severe winters (especially 1978/1979, 1984/1985 and 1995/1996) and the advent of RVHD (particularly since 1996). The impact of predation was probably negligible, as avian predators almost exclusively prey on the younger age classes of rabbits, and densities of red fox (*Vulpes vulpes*), badger (*Meles meles*), stoat (*Mustela erminea*) and weasel (*Mustela nivalis*) are low. Furthermore, the latter two species crashed in numbers over the past decades; numbers seen per 100 hours of field work in 1974-1979, 1980-1989, 1990-1999 and 2000-2003 were respectively 3.2, 2.8, 1.5 and 0.2 for weasel, and respectively 0.5, 0.3, 0.2 and 0.0 for stoat. Also, despite some buzzards nesting near surviving rabbit pockets, few (Veluwe) if any (Drenthe) rabbits are presently caught.

Habitat and management changes

During the past three decades, several changes took place at Planken Wambuis, viz. (1) an increasing dominance of *Deschampsia flexuosa* as undergrowth in coniferous forests, and on heaths and clear-fellings (about 50 ha in 1971, >800 ha in 2000; Vrijlandt & Vrijlandt-Kuiper 1971; R.G. Bijlsma, unpublished data), (2) the successive conversion of 140 ha of farmland into fallow land between 1984 and 1996, changing favoured foraging habitat into rough herbaceous growth, (3) changes in hunting regime (advancement of annual closing date for shooting red deer

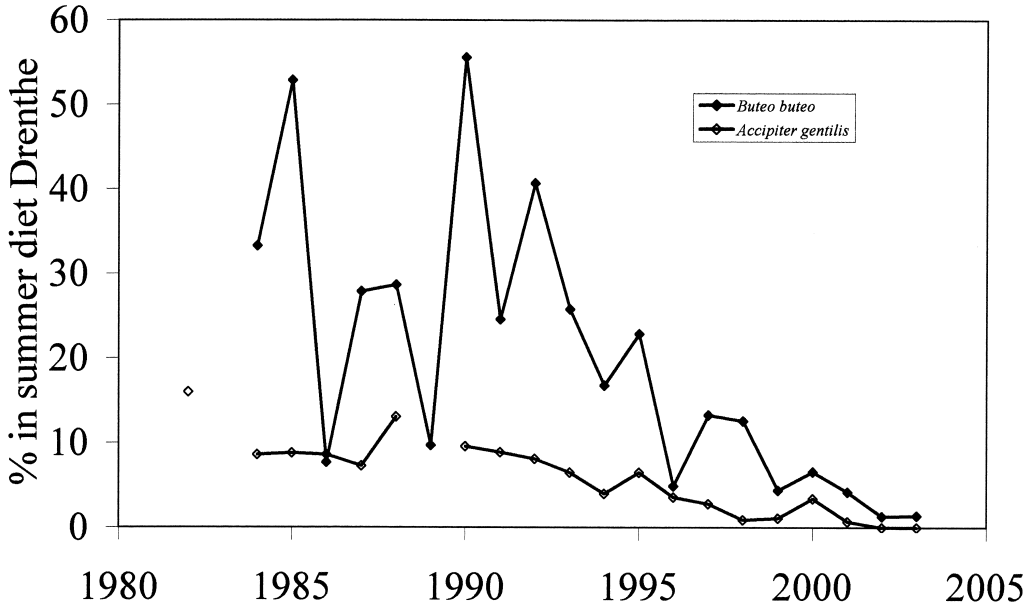

Figure 5. Proportion of rabbits in summer diets of common buzzard (n=24-305 prey remains summer^{-1}) and northern goshawk (n=35-505 prey remains summer^{-1}) in Drenthe in 1982-2003; prey collections in 1982-1989 are based upon raptor nests in northern, eastern and central Drenthe, those from 1990 onwards upon nests in western Drenthe.

and ban on food-supplementing wild boar, leading to intensification of browsing and rooting), and (4) a three-fold increase in the wild boar population between 1987 and 2003 (intensive rooting, feeding grounds of rabbits negatively affected).

The combined effect of these changes has been a reduction in the availability of feeding grounds, especially of short-grazed diverse grasslands, by an estimated 80%. In the past, when herbivores were restricted to forests and heaths, grazing of red deer (later also New Forest ponies) may have locally facilitated rabbits, as it still seems to be doing in an enclosure with ponies near Nieuw-Reemst. When the farmland was converted into fallow land between 1984 and 1996, and the fencing between Planken Wambuis and neighbouring areas was partly removed, much grazing shifted towards the newly available feeding grounds (H. ten Seldam, personal communication). Moreover, wild boars were then still being food-supplemented, and intensively hunted during autumn and winter. Surplus-feeding of wild boars was abandoned in 1999, and hunting has been less effective in reducing boar numbers in the late 1990s due to mast years of *Fagus sylvatica* and/or *Quercus robur*. In years with little or no mast, and no surplus feeding, wild boars face serious food shortage and start rooting wherever grassy habitats occur.

Severe winters

The proportional change in rabbit abundance from one year to the next showed a significant negative correlation with winter severity (r^2= 0.446, P=0.0001; figure 6): sudden, steep declines in the long-term trend of Planken Wambuis coincided with severe winters (in the terminology of IJnsen (1991)), i.e. 1978/1979 (-65%), 1984/1985 (-59%) and 1995/1996 (-82%). Although steep declines were followed by some recovery (early 1980s, late 1980s, early 1990s), rabbit numbers never again reached pre-crash levels, suggesting that the decline was long-term

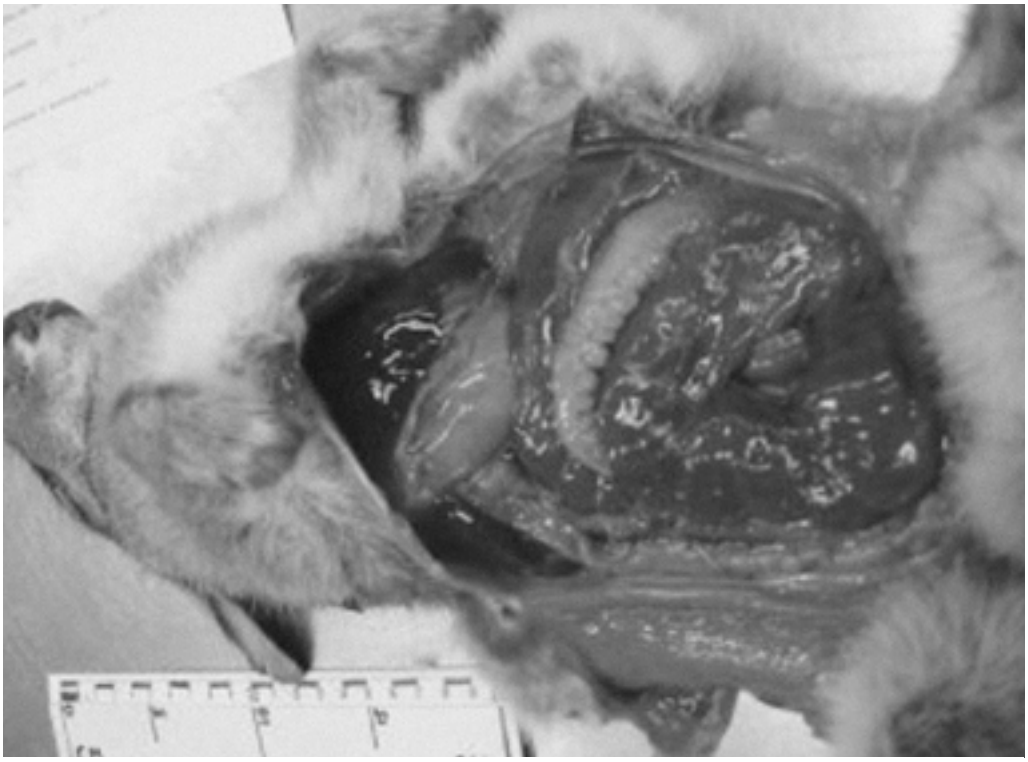

Photo 3. Post-mortem analysis of female rabbit, freshly collected on 10 December 2003 at Planken Wambuis; the liver is normal but the abdominal cavity held bloody fluids. *Photograph: Hugh Jansman, Alterra.*

and, at least partly, independent of severe winter weather. This is also born out by the trend at Berkenheuvel (figure 4), where a decline was already apparent before the severe winter of 1995/1996 took its toll, and where the severe winter of 1996 was not followed by recovery.

In both regions, (partial) recoveries after severe winters were fully natural, i.e. not enhanced through introductions of rabbits by the hunting fraternity.

Diseases

On Planken Wambuis, annually myxomatosis killed large numbers of rabbits in the 1960s, but a decimation of numbers, as recorded in the 1950s (Drees 1992), did not occur. Throughout the next decades, myxomatosis was noticed in most years, however with varying intensity. In the 1990s, when numbers and distribution at Planken Wambuis had already been reduced substantially, myxomatosis was still recorded in 1991, 1992, 1994, 1995 and 1996 (several tens found dead near Nieuw-Reemst; H. ten Seldam, personal communication). At Berkenheuvel in Drenthe, myxomatosis was almost absent in the 1990s; the only, minor, outbreak was recorded in May 1994 (two infected rabbits recorded near Wapserveld).

The advent of RVHD in the Netherlands is shrouded in mystery. Various sources indicate an arrival date in 1988 (Siebenga in Drees 1992), 1990 (Drees & Olff 2001) or 1991 (Marsman & Siebenga 2002), but very little is known about the actual occurrence, spread or impact. In a review of the literature relating to RVHD, for example, not a single Dutch source is mentioned (Westbury et al. 1994). Information from Spain, where the disease spread at a rate of approximately 15 km per month, indicates that RVHD outbreaks are not necessarily synchronised nor

do they affect rabbit populations equally (Cooke 2002). Although local mortality was reported as high as 90%, the genetic diversity in a study population in France stayed as high as at the pre-crash level, suggesting little effect of epizootics on the genetic diversity of wild rabbit populations if remnant populations with sufficient individuals survive (Queney et al. 2000).

The (near-)demise of my study populations in the 1990s, and especially after 1996, is probably caused by the arrival of RVHD. Unfortunately, clinical evidence is lacking; even records of dead rabbits, other than road casualties or from myxomatosis, were non-existent in my study areas until 10 December 2003 when Han ten Seldam (personal communication) found two freshly dead rabbits at Planken Wambuis. A post-mortem of one of these rabbits, a young female of 1,300 g, by Hugh Jansman (personal communication) showed clear signs of RVHD: this animal was in good condition but showed bloodied lungs, bloody fluids in the stomach and >5 ml of blood in the breast cavity (photo 3). The crash to extinction level was too sudden to have been caused by the severe winter of 1995/1996 alone. Still more telling, numbers did not bounce back after the winter of 1995/1996, as they always, albeit partly, did after previous severe winters (figure 1 and 4), again indicating that some other factor was involved in the consistent decline in the 1990s. The virulence of epizootics like RVHD is well-known (Cooke 2002), and may have been the ultimate cause of (near-)extinction in my study areas.

Rabbit trends elsewhere in the Netherlands

In the dunes of the western Netherlands, transect counts of rabbits since the early 1980s revealed a plethora of trends. North of the North Sea Canal, rabbits in two areas fluctuated or increased in synchrony up to 1990; this synchronicity disappeared afterwards, when a marked decline was recorded through the late 1990s. Two populations south of the North Sea Canal either fluctu-

Table 1. Proportion of rabbits in summer diets of northern goshawks and common buzzards in various parts of the Netherlands (March-August 1997-2003: data Dutch Raptor Group, published in series in De Takkeling 6-12, 1998-2004: respectively pages 50-53, 48-51, 48-51, 49-52, 45-48, 52-54, 52-55).

Region	Goshawk		Buzzard	
	No. prey	% rabbit	No. prey	% rabbit
Northern Netherlands				
Groningen (peat, clay)	107	12.1	291	1.0
Friesland (sand, peat)	1,324	1.6	2,670	5.9
Drenthe (sand)	1,235	0.5	2,531	5.9
Eastern Netherlands				
Overijssel (sand)	201	1.5	825	6.3
Central Netherlands				
Flevoland (clay)	296	1.4	779	7.3
Utrecht (sand)	85	2.4	90	22.2
Het Gooi (sand)	497	3.2	475	10.7
Veluwe (sand)	470	3.2	395	13.9
Western Netherlands				
Zuid-Holland (peat, clay)	24	0.0	124	2.4
Southern Netherlands				
Zeeland (clay, sand)	12	0.0	270	19.3
Noord-Brabant (sand)	2,432	3.1	888	15.1
Limburg (sand)	1,666	2.5	1,622	22.9

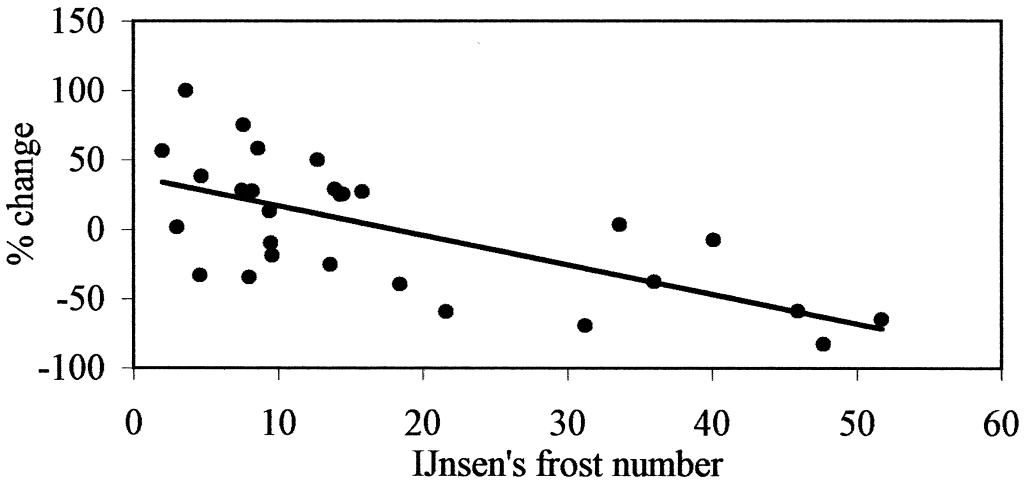

Figure 6. Proportional change in rabbit numbers (June-count) at Planken Wambuis in 1974-2003 in relation to the severity of the preceding winter (expressed as IJnsen's frost number, in which severe winters have a frost number >44.4). The regression is significant (r^2=0.446, P=0.0001).

ated or showed a decline from the beginning (Olff & Boersma 1998). In Junner Koeland, a riverine dune complex near Ommen in the eastern Netherlands, rabbits were facilitated by cattle grazing but numbers steeply declined after 1996, presumably caused by the outbreak of RVHD (Bakker 2003).

The frequency with which rabbits are recorded by raptorphiles as prey of goshawks and buzzards in the breeding season in various parts of the Netherlands can be used as a relative measure of spatial abundance. Compared to mice and voles, rabbits are more likely to be recorded as prey because of their larger size (increased likelihood of indigestible parts being discarded and consequently recorded). Although buzzards always prey more intensively on rabbits than goshawks, the importance of rabbits as a food source varied between regions for both avian predators (table 1). Notwithstanding biases related to frequency and timing of nest controls (cf. Bijlsma 1997), and confounding effects of raptors homing in on remaining pockets of rabbits in depleted populations, regional differences in the proportion of rabbits in raptor diets are probably accurate given the standardisation of raptor field work since the early 1990s (following recommendations of the Dutch Raptor Group; Bijlsma 1993, Bijlsma 1997). Assuming equal hunting opportunities for avian predators, it suggests that in the period 1997-2002, rabbits were least common in the northern Netherlands and more abundant in the southern Netherlands (south of the river Waal); the central and eastern Netherlands are positioned in between. At present, it is not clear what this means: a less drastic impact of RVHD in the southern Netherlands, higher densities in the southern Netherlands to start with (increasing the viability of surviving pockets), differential resilience to infection, earlier accumulation of antibodies in the south (where RVHD probably arrived earlier than in the north, given its south-to-north dispersal through Europe and the timing of the final, possibly RVHD-related, crash in the northern Netherlands, i.e. in 1996), differential stress in rabbit populations, or any combination. It is clear, however, that various rabbit populations are affected differently, as previously recorded for populations in the dunes of the western Netherlands (Drees & Olff 2001).

What if rabbits don't bounce back?

The present low numbers of rabbits, as compared with its abundance only a decade ago, has major

consequences on various scales. In poor habitats, as studied by me, the impact is probably even more succinct, as rabbits constituted a specific component within the grazing community, which is otherwise made up by herbivores as red deer, roe deer, New Forest ponies, Scottish highlander cows and wild boars. It should be specially noted that common voles (*Microtus arvalis*), normally having a large impact on vegetation development (Bakker 2003), are scarce or absent in woodland and heaths on poor sandy soil (replaced by the seed-eating bank vole (*Clethrionomys glareolus*), omnivorous wood mouse (*Apodemus sylvaticus*) and insect- and seed-eating harvest mouse (*Micromys minutus*)). The near-disappearance of rabbits is therefore likely to have far-reaching consequences for the development of herbaceous growth, survival of seedlings and regeneration of woodland. The activities of the expanding populations of wild boars and large herbivores, on the Veluwe, are unlikely to counteract the loss of rabbits except in enclosures with a high grazing pressure of herbivores.

Whether or not the present nadir in rabbit numbers is part of a long-term numerical fluctuation, as surmised by Bakker (2003) for Junner Koeland (riverine grassland, grazed with cattle), is difficult to say. The circumstances on the Veluwe and in Drenthe are very different from those in floodplains, not least because of the larger impact of acidification on vegetation succession. The specific quality of a grazer like the rabbit is therefore unlikely to be replaced by browsers like deer and bulk grazers like cows and ponies, nor is a come-back of rabbits likely to be facilitated by the latter's activities (which forage mainly on fallow land). On the contrary, the dominance of *Deschampsia flexuosa* has become a characteristic feature of the vegetation on sandy soils, and may permanently exclude rabbits from forested habitats that were formerly occupied in large numbers. Furthermore, prime foraging habitats on the Veluwe are nowadays partly unsuitable for grazing by rabbits following the rooting activities of wild boars. Therefore, a bounce-back in numbers, as witnessed after the myxomatosis event in the mid-1950s, is unlikely to occur this time in eutrophied habitats, even when rabbits have achieved some protective immunisation against RVHD.

This situation is further complicated by the fragmentation of rabbit populations. The chances of reuniting rabbit pockets, or recolonising isolated patches where rabbits have gone extinct, are probably smaller in the 2000s than during the crash caused by myxomatosis in the 1950s. Road density and traffic intensity have exploded since the 1950s, the latter showing at least a tenfold increase between 1955 and the late 1990s, with a disproportionate steep growth of traffic at night (Huijser 1999). In combination with the industrialisation and upscaling of farming practices (Bijlsma et al. 2001), this will likely hamper dispersion of rabbits from surviving pockets into nearby extinct or depleted populations.

Though outside the scope of this paper, it should be noted that rabbits used to be an indispensable part of the food base of several avian predators, notably buzzard and goshawk. The latter species is particularly affected, as the avian biomass on the Veluwe has also declined by almost 80% over the last few decades (Bijlsma et al. 2001, Bijlsma 2003, Rutz et al., in prep.), especially impacting bird species weighing 75-500 grams, i.e. the prey group selected by goshawks. This has led to a decline in number of territorial goshawks, a decline in the proportion of goshawk pairs laying eggs, a decline in reproductive output per territorial pair, the near-disappearance of floaters (non-breeding surplus birds, only occasionally recorded after the early 1990s as based on findings of individually recognisable moulted feathers), a poor condition of nestlings (probably affecting survival) and an increasing predation pressure of goshawks on middle-sized and large bird species (in its turn resulting in more species at risk, reduced densities in some species and local extinction of others; Bijlsma 2004). The buzzard, although being a generalist predator, was also negatively affected by the precipitous decline in rabbit numbers, as noted in the increasing incidence of non-breeding, de-

cline in reproductive output and decline in nestling condition (R.G. Bijlsma, unpublished Veluwe-data). The substantial decrease of rabbits in summer diets of buzzards, especially after 1996 (in agreement with findings of Willem van Manen in central Drenthe), coincided with an increase of birds' nestlings and fledglings in buzzard diets. This is a poor substitute, as birds are more widely spaced in the breeding season (territorial), many bird species have low densities and their availability (as nestling and naive fledgling) is more peaked than in rabbits (hence harvestable for a shorter period only).

Acknowledgements: After years of illegal trespassing, my presence at Planken Wambuis was eventually considered inevitable, and permission by Vereniging Natuurmonumenten was granted to continue the studies. Han ten Seldam (Stichting Wildbeheer Planken Wambuis, later Vereniging Natuurmonumenten) did a great job in saving and extracting detailed data on game bags at Planken Wambuis since the late 1960s. Additional information was provided by Marijke Drees, Hugh Jansman, Dirk Lieftink, Han Olff and Roelof Vierhoven. The studies in Drenthe took place in nature reserves managed by Vereniging Natuurmonumenten, Staatsbosbeheer and Het Drentse Landschap. Drafts of this paper were improved by comments from Marijke Drees, Koos Dijksterhuis, Willem van Manen, Han ten Seldam and three anonymous referees.

References

Anonymous 2002. Jagd und Artenschutz: Jahresbericht 2002. Ministerium für Umwelt, Natur und Forsten des Landes Schleswig-Holstein, Kiel, Germany.

Bakker, E.S. 2003. Herbivores as mediators of their environment: the impact of large and small species on vegetation dynamics. PhD thesis. Wageningen University, Wageningen, The Netherlands.

Bankert, D., K.C.G. in 't Groen & S.E. van Wieren 2003. A review of the transect method by comparing it with three other counting methods to estimate rabbit (*Oryctolagus cuniculus*) density. Lutra 46: 27-34.

Bijlsma, R.G. 1993. Ecologische atlas van de Nederlandse roofvogels. Schuyt & Co., Haarlem, The Netherlands.

Bijlsma, R.G. 1997. Handleiding veldonderzoek Roofvogels. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, The Netherlands.

Bijlsma, R.G. 2001. Dynamiek van overwinterende Klapeksters *Lanius excubitor*. Drentse Vogels 14: 65-72.

Bijlsma, R.G. 2003. Havik *Accipiter gentilis* legt superdwergei, of: leven en dood in een 30-jarig territorium op het voedselarme Planken Wambuis (Veluwe). De Takkeling 11: 133-142.

Bijlsma, R.G. 2004. Wat is het predatierisico voor Wespendieven *Pernis apivorus* in de Nederlandse bossen bij een afnemend voedselaanbod voor Haviken *Accipiter gentilis*. De Takkeling 12: 185-197.

Bijlsma, R.G., F. Hustings & C.J. Camphuysen 2001. Algemene en schaarse vogels van Nederland (Avifauna van Nederland 2). GMB Uitgeverij, Haarlem / Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, The Netherlands.

Cooke, B.D. 2002. Rabbit haemorrhagic disease: field epidemiology and the management of wild rabbit populations. Revue scientifique et technique/Office International des Epizooties 21: 347-358.

Drees, J.M. 1992. Konijn *Oryctolagus cuniculus* (L., 1758). In: S. Broekhuizen, B. Hoekstra, V. van Laar, C. Smeenk & J.B.M. Thissen (eds.). Atlas van de Nederlandse zoogdieren: 328-333. 3e herziene druk. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, The Netherlands.

Drees, M. 1998. Langoor: over konijnen en vegetatie in de duinen. Duin 21 (4): 4-6.

Drees, M. & H. Olff 2001. Rabbit grazing and rabbit counting. In: J.A. Houston, S.E. Edmonson & P.J. Rooney (eds.). Coastal dune management: 86-95. Liverpool University Press, Liverpool, UK.

Heij, G.J. & T.T. Schneider (eds.) 1991. Acidification research in The Netherlands. Elsevier, Amsterdam, The Netherlands.

Heijboer, D. & J. Nellestijn 2002. Klimaatatlas van Nederland. De normaalperiode 1971-2000. Uitgeverij Elmar, Rijswijk, The Netherlands.

Hommel, P.W.F.M., J.H.J. Schaminée & A.H.F. Stortelder 1999. Vaccinio-Piceeta. In: A.F.H. Stortelder, J.H.J. Schaminée & P.W.F.M. Hommel (eds.). De vegetatie van Nederland, Deel 5: 229-254. Opulus Press, Uppsala, Sweden.

Huijser, M.P. 1999. Human impact on populations of hedgehogs *Erinaceus europaeus* through traffic and changes in the landscape: a review. Lutra 42: 39-56.

IJnsen, F. 1991. Karaktergetallen van de winters vanaf 1707. Zenit 18: 69-73.
Kivit, H. 1987. Over de methodiek van konijnentellingen in de vastelandsduinen: een evaluatie van de toegepaste telmethode. Vakgroep Natuurbeheer, Landbouwhogeschool Wageningen, The Netherlands.
Koersveld, E. van 1955. De verspreiding van myxomatose. De Nederlandse Jager 59: 760-764.
Marchandeau, S. & C. Boucraut-Baralon 1999. Épidémiologie de la myxomatose et des caliciviroses apparentées à la VHD dans une population sauvage de lapins de garenne (*Oryctolagus cuniculus*). Gibier Faune Sauvage 16: 65-80.
Marsman, G.J.P. & S. Siebenga 2002. Mysterieuze konijnenziekte VHS snel en dodelijk. De Nederlandse Jager 107 (17): 8-10.
Martínez, J.A. & I. Zuberogoitia 2001. The response of the Eagle Owl (*Bubo bubo*) to an outbreak of the rabbit haemorrhagic disease. Journal of Ornithology 142: 204-211.
Morrison, J.L. & P.L. Kennedy 1989. The use of line transects to evaluate the abundance of diurnal mammalian prey. Journal of Raptor Research 23: 172-175.
Olff, H. & S.F. Boersma 1998. Lange-termijn veranderingen in de konijnenstand van Nederlandse duingebieden. Oorzaken en gevolgen voor de vegetatie. Wageningen University, Wageningen, The Netherlands.
Queney, G., N. Ferrand, S. Marchandeau, M. Azevedo, F. Mougel, M. Branco & M. Monnerot 2000. Absence of a genetic bottleneck in a wild rabbit (*Oryctolagus cuniculus*) population exposed to a severe viral epizootic. Molecular Ecology 9: 1253-1264.
Rijk, J.H. de 1988. De geschiedenis van het konijn *Oryctolagus cuniculus* in Nederland. Lutra 31: 101-131.
Rutz, C., R.G. Bijlsma, M. Marquiss & R.E. Kenward, in press. Population limitation in the Northern Goshawk *Accipiter gentilis* in Europe: a review and some case studies. Studies in Avian Biology.
Tella, J.L. & S. Mañosa 1993. Eagle Owl predation on Egyptian Vulture and Northern Goshawk: possible effect of a decrease in European Rabbit availability. Journal of Raptor Research 27: 111-112.
Thompson, H.V. & C.M. King 1994. The European Rabbit: the history and biology of a successful colonizer. Oxford University Press, Oxford, UK.
Tinbergen, L. 1936. Gegevens over het voedsel van Nederlandse Haviken (*Accipiter gentilis gallinarus* (Brehm)). Ardea 25: 195-200.
Tinbergen, L. & N. Tinbergen 1931. Waarnemingen aan roofvogels en uilen. I-III. De Levende Natuur 36: 69-80, 98-104, 131-137.
Versteeg, J. *s.a*. Griepgrauw, de vrijbuiter van het Veluweland. Voorhoeve, Den Haag, The Netherlands.
Vrijlandt, P. & J. Vrijlandt-Kuiper 1971. Het Planken Wambuis: Natuurwetenschappelijke inventarisatie. Vakgroep Natuurbeheer, Landbouwhogeschool Wageningen, The Netherlands.
Wallage-Drees, J.M. 1986. Dag- en nachtaktiviteit bij konijnen en de relevantie voor de telmethode. De Levende Natuur 87: 40-45.
Wallage-Drees, J.M. 1988. Rabbits in the coastal sand dunes; weighed and counted. PhD thesis. Leiden University, Leiden, The Netherlands.
Westbury, H., C. Lenghaus & R.K. Munro 1994. A review of the scientific literature relating to RHD. In: R.K. Munro & R.T. Williams (eds.). Rabbit Haemorrhagic Disease: issues in assessment for biological control: 91-103. Bureau of Resource Science, Australian Government Publishing Service, Canberra, Australia.
Wigman, A.B. 1938. Het voedsel van den zeearend, *Haliaeetus a. albicilla* (L.), in het winterkwartier. Limosa 11: 140-141.

Samenvatting

Lange-termijn trends in populaties van konijnen (*Oryctolagus cuniculus*) op de Pleistocene zandgronden van centraal- en noord-Nederland

Als onderdeel van een lange-termijnstudie naar de populatiedynamiek van roofvogels werd tegelijkertijd de aantalsontwikkeling van belangrijke prooigroepen bijgehouden, waaronder die van konijnen (*Oryctolagus cuniculus*). Dit onderzoek vond plaats in twee voedselarme gebieden, namelijk op de Zuidwest-Veluwe (met name Planken Wambuis, vanaf 1974, naaldbos, heide en cultuurland) en in West-Drenthe (Berkenheuvel, vanaf 1990, naaldbos en heide). Op Planken Wambuis piekte het konijn in de late jaren zeventig. Gezien de tellingen en afschotcijfers daaraan voorafgaande zou dat een herstel kunnen zijn geweest van geregelde uitbraken van myxomatose in de jaren vijftig en zestig. Strenge winters (in termen van IJnsen, met een vorstgetal

van >44,4) bewerkstelligden acute dalingen van 59-82% in de konijnenstand. De eerste klap werd in de winter van 1978/1979 uitgedeeld, en hoewel de stand nadien aantrok, werd nimmer het niveau van vóór de crash bereikt; ook bij daaropvolgende strenge winters trad enig herstel op zonder op het oude niveau terug te keren. Het uitblijven van herstel na de strenge winter van 1995/1996 is mogelijk het gevolg van de komst van het viraal hemorrhagisch syndroom (VHS), al ontbreken daarvoor klinische bewijzen. De stand van het konijn in de late jaren negentig was nog slechts een schim van wat in de jaren zeventig werd vastgesteld; dat geldt voor aantallen (>99% afname) en verspreiding (>90% dito). Gezien het aantalsverloop in beide gebieden is het aannemelijk dat habitatveranderingen de sturende factor zijn geweest in deze ontwikkeling, nog versterkt door strenge winters en, in de jaren negentig, ziektes (VHS). In de jaren zeventig en tachtig veranderde de vegetatie in naaldbossen op arme zandgronden drastisch onder invloed van zure neerslag; zo veranderde de ondergroei in naaldbossen geleidelijk in een dichte mat van bochtige smele. Tegelijkertijd werden landbouwgronden uit productie gehaald en omgezet in ruigtes. Op de Veluwe ging dit gepaard met een toename/introductie van grote grazers (edelhert, ree, ponies, Schotse hooglanders), terwijl het wilde zwijn vanaf 1987 verdrievoudigde in aantal. Tezamen met een vermindering van bijvoedering betekende dit een zware aanslag op resterende graslandjes en jonge opslag; bijna elk foerageergebied van konijnen is tegenwoordig grondig door zwijnen op de kop gezet. Zelfs al zouden konijnen herstellen van de uitbraak van VHS, dan nog is hun leefgebied in de door mij onderzochte gebieden zodanig ten nadele veranderd dat verspreiding en dichtheid vermoedelijk achter zullen blijven bij wat ik in de jaren zeventig heb meegemaakt. De consequenties voor de vegetatieontwikkeling, en voor het prooiaanbod van roofvogels, zijn verregaand. Haviken en buizerds kampen sinds de bijna-verdwijning van het konijn met serieuze voedseltekorten (mede door een afname van de biomassa aan gevleugeld voedsel), wat zich uit in een dalende stand (alleen bij havik), groter aandeel niet-broedende paren, dalende reproductiecijfers, verslechterende conditie van nestjongen (en dus afnemende overlevingskansen?), bijna-verdwijning van floaters uit de havikenpopulatie, en een sterk veranderde predatiedruk op de resterende prooidieren.

Received: 6 January 2004
Accepted: 29 October 2004

When logic and proportion
Have fallen sloppy dead,
And the White Knight is talking backwards
And the Red Queen's "off with her head!"
Remember what the dormouse said:
"Feed your head. Feed your head."

White Rabbit, written by Grace Slick
(Surrealistic Pillow by Jefferson Airplane 1967)