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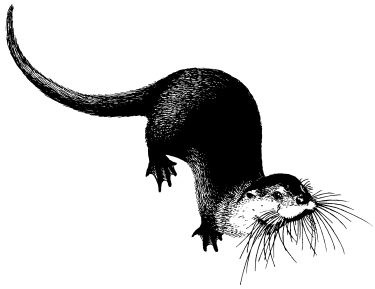

Just normal

Every scientific publication is preceded by observation of a phenomenon. Questions about it have to be properly framed and the results clearly understood before an article can be produced. Very unusual phenomena tend to be noticed earlier, explored earlier, and the results published earlier. Less unusual phenomena that appear to be 'just normal', can often go unnoticed for a long time. This is particularly true of situations where changes of biological phenomena occur very slowly; when the crucial step of posing questions may not be taken and the phenomenon may not be investigated for a long time, if at all.

This issue of Lutra contains examples of both unusual, as well as rather more usual, phenomena. Striking examples of the first are given in *Longevity records in the red fox* by Jaap Mulder, *Partial albinism in the red squirrel (Sciurus vulgaris Linnaeus, 1758)* by Bauke Hoekstra and *Evidence of lesser horseshoe bat (Rhinolophus hipposideros) predation by otter (Lutra lutra) in a Welsh cave system* by Dan Forman et al.; all these are noteworthy observations. Yet there may be many other unpublished observations or studies of the ages of red foxes, of non-albino red squirrels, or otter spraints without traces of lesser horseshoe bats. These phenomena were not published, or maybe not even investigated in depth, because they appeared to be just normal.

Long-term population trends of rabbits (Oryctolagus cuniculus) on Pleistocene sands in the central and northern Netherlands by Rob Bijlsma, is an exceptionally good example of what dedicated, consistent observation can achieve. This author described a phenomenon that is not based on a single observation of a rabbit but on a long and valuable list of observations, gathered over many years. Through these observations the author provides this edition of Lutra with a pearl. When he started his observations in 1974 he could not have foreseen how, 30 years later, disease, severe winters or predators would affect the long-term development trend of several populations of rabbits. Students or scientific employees of research institutes can perhaps spend five to ten years on long trend observations. A period of thirty years is very exceptional. However, observer bias can cause problems in comparing numbers over the years. The oft-cited long-term trend derived from more than 65 years of counting hibernating bats in the marl pits in Zuid-Limburg is impressive. However, improvements in the amount of light emitted by flashlights hinders a precise comparison of numbers of identified bats. Perhaps only the list of stranded cetaceans, carefully started by Van Deinse, shows no bias, at least for the bigger cetaceans.

Generally, there is a need for studies and publications on long-term trends in all sorts of mammal populations. The work of Jeremy Kiszka et al. in their *Distribution and status of small cetaceans along the French Channel coasts: using opportunistic records for a preliminary*

assessment is hopefully the start of a long series of observations that in the future will provide interesting insights into changes in the populations and distribution of small cetaceans.

Three book reviews are presented in this issue of Lutra, two of which focus on herbivores. Maurice Hoffmann reviews the PhD thesis *Herbivores as mediators of their environment. The impact of large and small species on vegetation dynamics* by Liesbeth Bakker. It explores the intricate relation between three herbivorous mammals: cattle, rabbit and common vole. In another book review Bart Nolet reports on Dries Kuijper's PhD thesis *Small herbivores losing control.* It studies the plant-herbivore interactions of cattle, geese and hares along the natural productivity gradient on the small Dutch isle of Schiermonnikoog. For those interested in historical aspects of cetaceans, early marine "biologists", and ichthyology the review by Erwin Kompanje et al. of *Het Walvisboek. Walvissen en andere zeewezens beschreven door Adriaen Coenen in 1585* gives a concise impression of Kees Lankester's findings.

Earlier issues of this journal, especially in the first decades, also presented articles on non-European mammal species. *New records of Latidens salimalii (Chiroptera; Pteropodidae) in the Western Ghats, India* by Juliet Vanitharani et al. resumes this tradition and demonstrates that the editorial board is still interested in manuscripts dealing with mammals outside Europe. This is especially true for genera related to European species or articles with a special interest for members of the *Society for the Study and Conservation of Mammals*.

In the summer of 2004 Steve Geelhoed was appointed as assistant of the editorial board. Steve has much experience in publishing nature journals and will specifically focus on improving the graphic content of the journal. He will also be our key-person linking the board with the office of the *Society for the Study and Conservation of Mammals*.

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.*

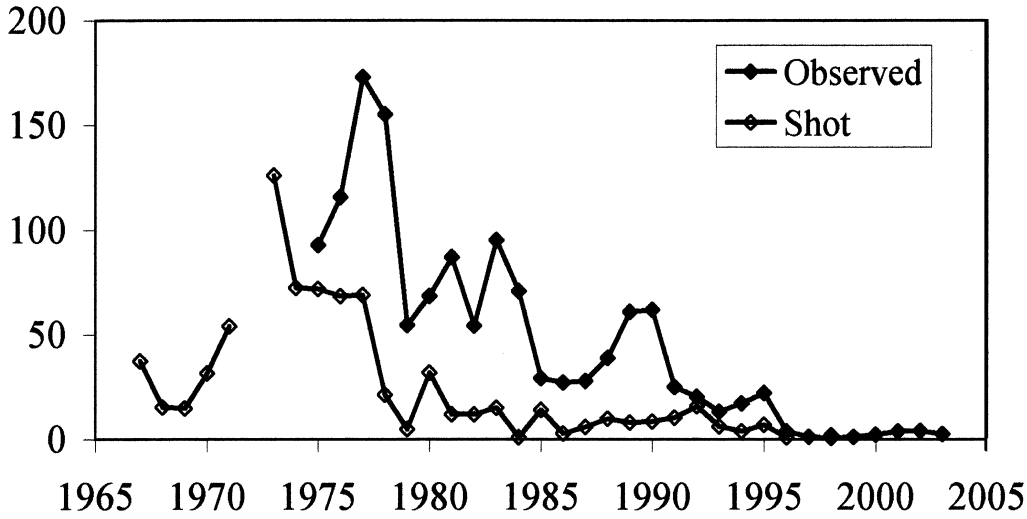

Figure 1. Rabbit counts (mean number observed hour^{-1} in June) and game bags (mean number shot month^{-1}) on Planken Wambuis, southern Veluwe, in 1967-2003.

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

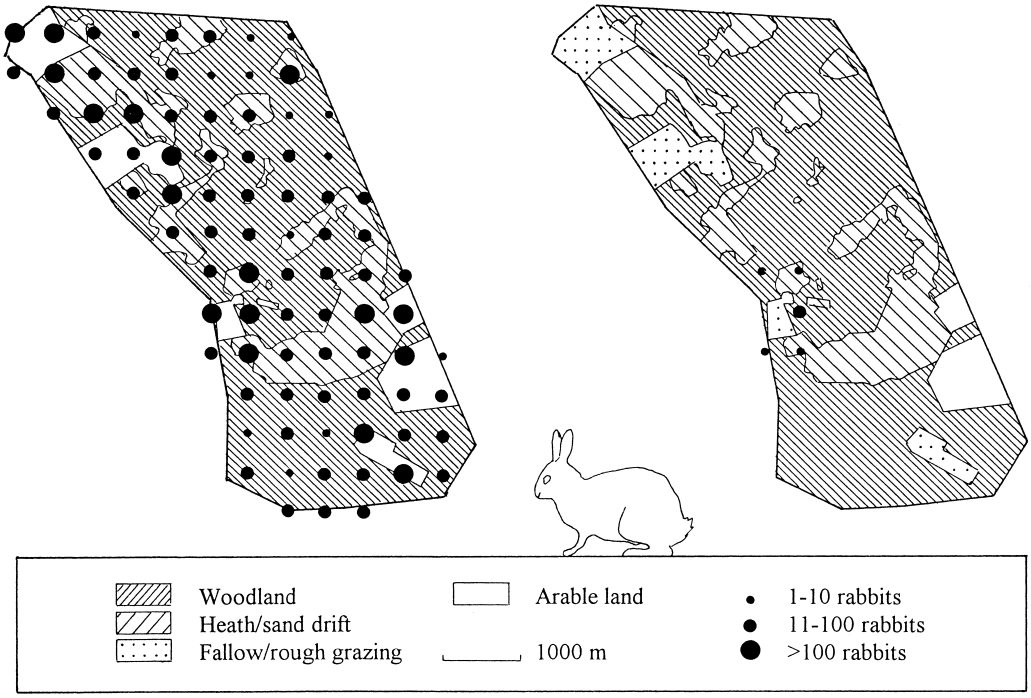

Figure 2. Distribution and abundance of rabbits per 0.25 km^2 on Planken Wambuis in June 1978 (left) and in June 1998. Notice demise of clusters except one (Nieuw-Reemst), and complete loss from forests and heaths.

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).

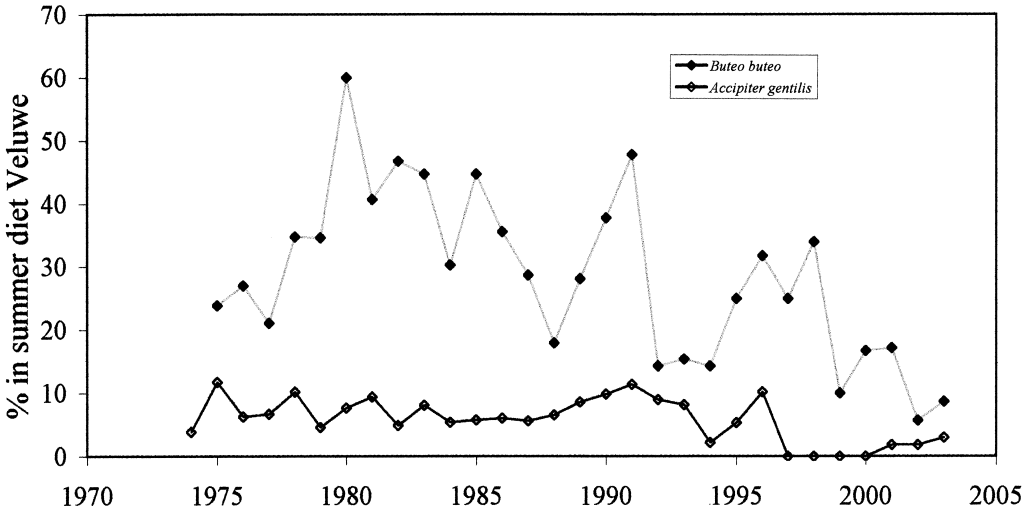

Figure 3. Proportion of rabbits in summer diets of common buzzard (n=10-734 prey remains summer^{-1}) and northern goshawk (n=19-2,486 prey remains summer^{-1}) on the southwestern Veluwe in 1974-2003; prey collections <50 are based on smaller samples of raptor nests from 1991 onwards (Planken Wambuis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

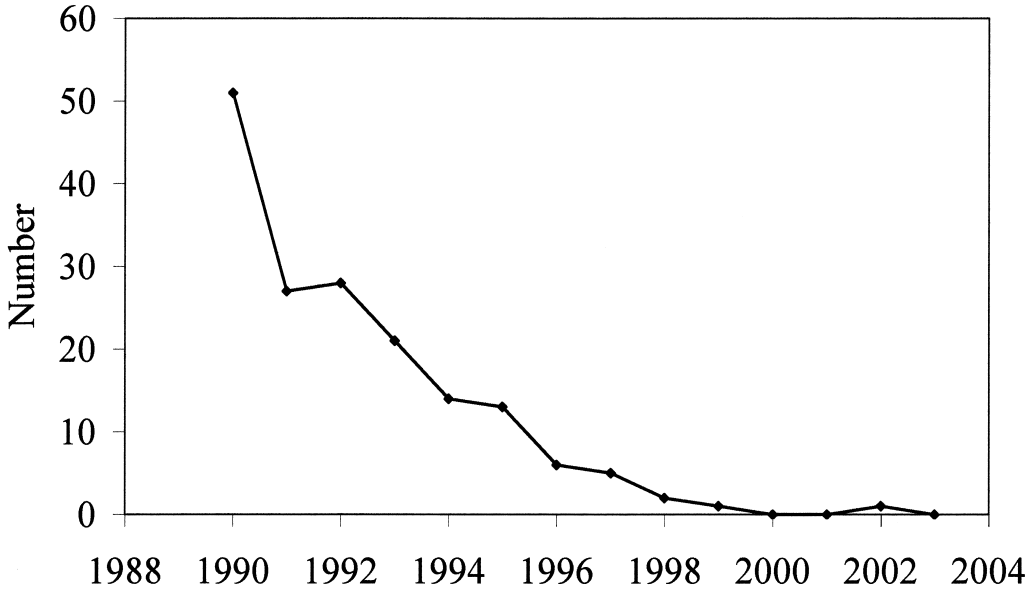

Figure 4. Number of rabbits counted on two transects (combined length 4,350 m) at Berkenheuvel, Drenthe, in June 1990-2003.

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

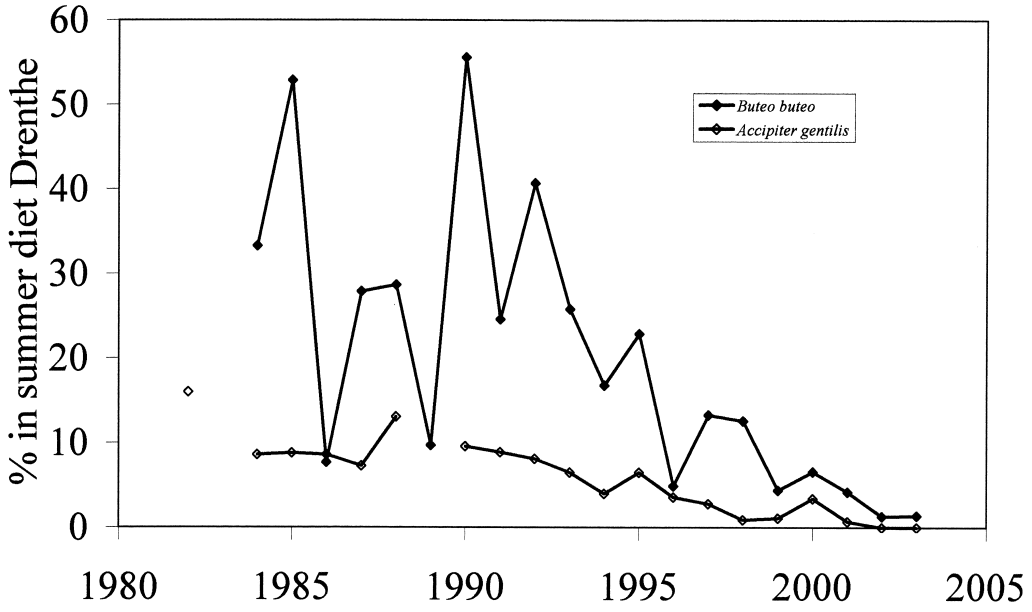

Figure 5. Proportion of rabbits in summer diets of common buzzard (n=24-305 prey remains summer^{-1}) and northern goshawk (n=35-505 prey remains summer^{-1}) in Drenthe in 1982-2003; prey collections in 1982-1989 are based upon raptor nests in northern, eastern and central Drenthe, those from 1990 onwards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

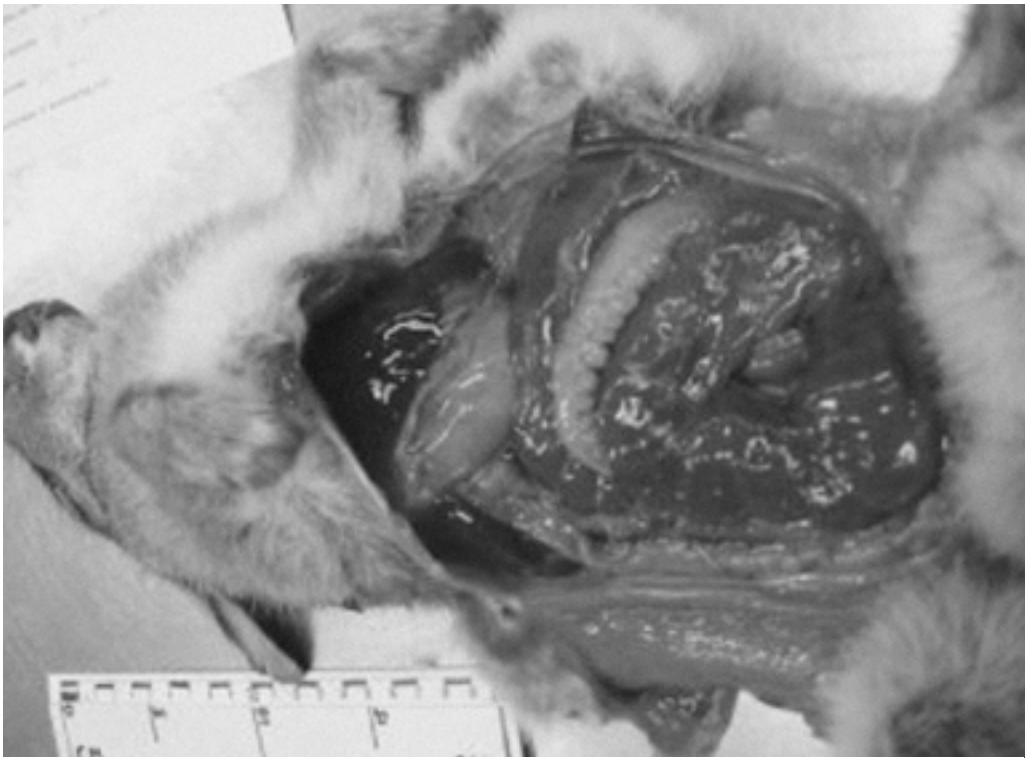

Photo 3. Post-mortem analysis of female rabbit, freshly collected on 10 December 2003 at Planken Wambuis; the liver is normal but the abdominal cavity held bloody fluids. *Photograph: Hugh Jansman, Alterra.*

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

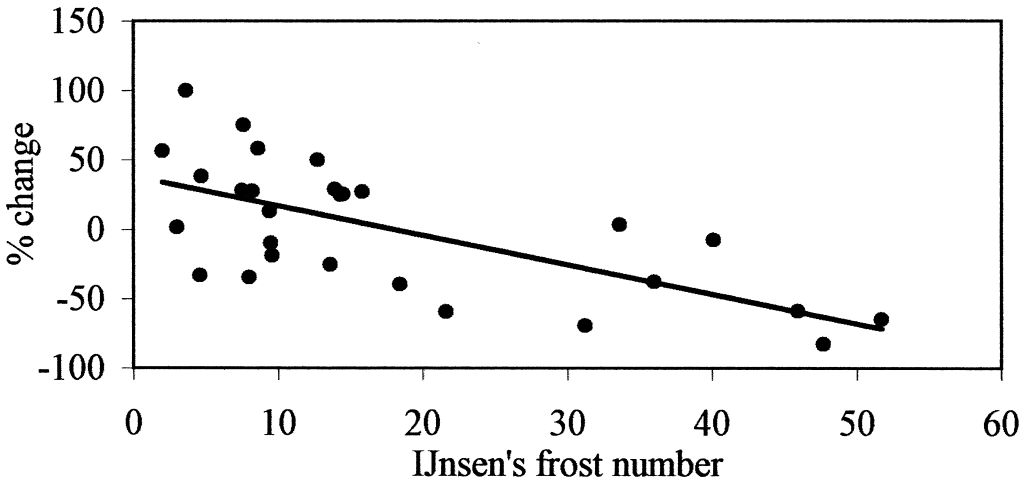

Figure 6. Proportional change in rabbit numbers (June-count) at Planken Wambuis in 1974-2003 in relation to the severity of the preceding winter (expressed as IJnsen's frost number, in which severe winters have a frost number >44.4). The regression is significant (r^2=0.446, P=0.0001).

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.

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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.

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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)

A review of the distribution and status of *Latidens salimalii* (Chiroptera: Pteropodidae) with new records from the Western Ghats, India

Juliet Vanitharani[1], Malcolm Pearch[2*], L. Jeya Praba[1] & Ramar Annamalai[3]

[1] Bat Research Laboratory, Department of Zoology, Sarah Tucker College, Tirunelveli – 627 007, Tamil Nadu, India

[2] Harrison Institute, Centre for Systematics and Biodiversity Research, Bowerwood House, St. Botolph's Road, Sevenoaks, Kent TN13 3AQ, UK, e-mail: hzm@btinternet.com

[3] Field Director and Conservator of Forests, Project Tiger, Tamil Nadu Forest Department, Kalakkad-Mundanthurai Tiger Reserve, Tirunelveli – 627 007, Tamil Nadu, India

Abstract: Salim Ali's fruit bat (*Latidens salimalii*) is endemic to southern India and is classified as Critically Endangered by IUCN. This classification is based on an assessment of the species in 1996 when only seven individuals had been recorded, all of which were from the High Wavy Mountains in the state of Tamil Nadu. This paper documents the expansion in the known range of *Latidens* and includes details of four further localities at which the bat has been found together with information on the species' reproductive status and diet. As the increase in recorded numbers and distribution of the taxon calls into question the validity of *Latidens*' current classification, an argument is put forward for a reassessment of the species' status that concludes in a recommendation that *Latidens salimalii* be reclassified as Endangered.

Keywords: *Latidens salimalii*, Western Ghats, distribution, status, Critically Endangered, India.

Introduction

In 1948, a fruit bat, believed at the time to be *Cynopyterus sphinx*, was collected by Angus Hutton from the High Wavy Mountains in the Madurai District of Tamil Nadu, southern India. The specimen was placed in the collection of the Bombay Natural History Society and it was not until its re-examination in 1970 by Kitty Thonglongya that a number of its characteristics were found to be incompatible with those of *Cynopterus sphinx*. As a result, the specimen was assigned to a new genus and species, *Latidens salimalii* Thonglongya, 1972, so named on account of its broad cheekteeth and in honour of the Indian ornithologist Dr. Salim Ali. *Latidens salimalii* was known only by the holotype, skin, and skull until 1993, when six further specimens were collected from Yeni Kodai Cave on the Kardama Coffee Estate (approximately 09° 50' N, 77° 24' E) in the High Wavy Mountains during a survey of the bat fauna of the region by the Harrison Institute (= The Harrison Zoological Museum) and the Bombay Natural History Society (Bates et al. 1994, Muni 1994). The High Wavy Mountains remained the only recorded distributional record of *Latidens* until 1999, when its presence was recorded, but without details, in the Kalakkad-Mundanthurai Tiger Reserve, Tamil Nadu (Ghosh et al. 1999), thereby extending its range between 110 and 160 km southwards. Agoramoorthy (2000) confirmed the species' existence in the vicinity of the Kardama Coffee Estate during an examination of 46 individuals from a colony with an estimated population of 250, while Singaravelan & Marimuthu (2003a) collected 28 individuals from an unidentified cave at the same location during two trap nights and a further ten from a loosely estimated colony of 350 resident in a further cave located

* Corresponding author

nearby (Singaravelan & Marimuthu 2003b). Ten *Latidens salimalii* were reportedly collected from the "Agastiyamalai hill complex" by members of the Zoological Survey of India, presumably prior to January 2002 (Singaravelan & Marimuthu 2003a). During the course of a bat species diversity assessment and conservation management study conducted between February 2002 and May 2003 by the Department of Zoology, Sarah Tucker College, Tirunelveli, 28 specimens of *Latidens*, including five subadults and one juvenile, were collected from four further locations in western Tamil Nadu: (1) Therkumalai Estate in the Courtallum Hills, (2) Nagapodigai Cave and (3) Vudumbukal Cave in the Agasthiyar Hills, and (4) Sengaltheri Cave in the Kalakkad Hills. Locations 2, 3, and 4 lie within the perimeter of the Kalakkad-Mundanthurai Tiger Reserve, whilst location 1 is positioned just outside the Reserve's north-eastern boundary.

Latidens salimalii is endemic to India (Bates & Harrison 1997) and is classified as Critically Endangered in the 2003 IUCN Red List of Threatened Species (IUCN 2003).

Geography

The Agasthiyar Hills, together with the adjoining ranges of Courtallum to the north and Kalakkad to the east (referred to collectively hereafter as "the Agasthiyar Hill Range"), form the southernmost extension of the Western Ghats, a series of hill ranges running parallel to India's western seaboard from approximately 08° 20' N to 21° N (figure 1). The Kalakkad-Mundanthurai Tiger Reserve occupies an area of 895 km^2 and stretches from 08° 23.50' to 08° 53.60' N and 77º 09' to 77° 33.3' E, the western part of its perimeter being delineated by the state border between Tamil Nadu and Kerala. On the western fringes of the Reserve rise the closely connected peaks of Agasthiyar (1847 m), Ainthalaipodigai (1800 m), and Nagapodigai (1745 m). The seasonal drainwaters from these mountains form the headwaters of the perennial Tambraparani River, which flows east to the Gulf of Mannar, some 90 km distant. The waters of the Tambraparani are augmented by a number of tributaries; some of these have been dammed to form reservoirs, which are used for hydroelectric power generation and crop irrigation around Ambasamudram (08° 42' N, 77° 27' E). In addition to numerous peaks, the Agasthiyar Hill Range is characterised by the presence of two plateaux: the Upper Kodayer Plateau (08° 29'N – 08° 34'N), which enjoys an average elevation of 1800 m and supports numerous tea plantations; and, at the lower average elevation of 300 m, the Mundanthurai Plateau (08° 37.50' N – 08° 42' N). Therkumalai Estate is located at an elevation of 900 m in a belt of tropical dry deciduous forest that gives way at about 1000 m to moist deciduous forest. Nagapodigai Cave, Vudumbukal Cave, and Sengaltheri Cave lie between 1300 m and 1600 m amidst tropical wet evergreen rainforest, which occupies elevations in excess of 1200 m.

The south-west monsoon (June to September) and the north-east monsoon (October to January) bring heavy rain and strong winds to the Agasthiyar Hill Range with elevations above 1000 m experiencing frequent mists and cloud cover that may persist for many days. The Hill Range enjoys a warm tropical monsoon climate with an annual rainfall ranging from 2300 mm to 5000 mm. Maximum temperatures range between 23 °C and 34 °C and minimum temperatures between 16 °C and 25 °C (Rajendran 1996).

Land use within the Kalakkad-Mundanthurai Tiger Reserve is strictly controlled by the Tamil Nadu Forest Department. Whilst only a few local tribespeople are known to inhabit areas of the Reserve above 1200 m, the plains to the east are densely populated. Many of the villagers on the plains graze livestock in, or collect wood from, the Reserve. These activities may result in some disturbance of the dry deciduous forest below 1000 m but do not appear to have any adverse affect on land at higher elevations, which remains largely intact.

The Agasthiyar Hill Range is included in two

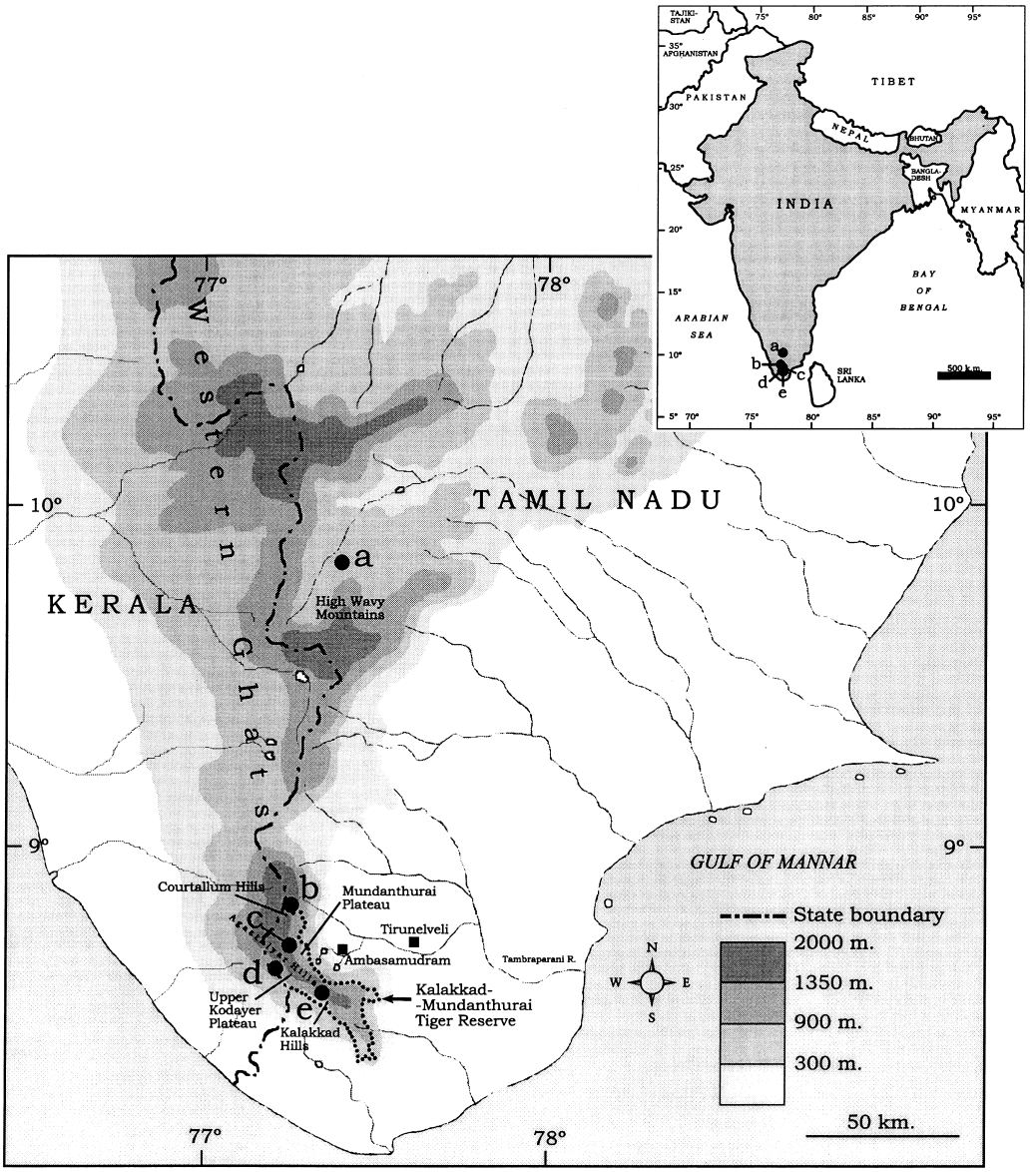


Figure 1. The recorded distribution of *Latidens salimalii*: a. Kardama Coffee Estate, High Wavy Mountains; b. Therkumalai Estate, Courtallum Hills; c. Vudumbukal Cave, Agasthiyar Hills; d. Nagapodigai Cave, Agasthiyar Hills; e. Sengaltheri Cave, Kalakkad Hills.

of the WWF Global 200 Ecoregions, which have been selected for their outstanding biodiversity (no. 20: Southwestern Ghats Moist Forests; and no. 171: Western Ghats Rivers and Streams; see World Wildlife Fund 2004).

Method and materials

Twelve metre two-ply, four shelf, nylon mesh mist nets were used to collect voucher specimens, which were either preserved as wet specimens in 70% ethanol (JVR-1 and JVR-2, see 'Systematic review' section) or tagged and released.

Systematic review

New material

1. Therkumalai Estate, Courtallum Hills, Tirunelveli District, Tamil Nadu
   08° 54' N, 77° 15' E
   900 m a.s.l.
   23 February, 2002
   2 males (1 subadult) (adult male = JVR-1), 1 female (pregnant[1]) (JVR-2)
   1 March, 2003
   1 female (released)

2. Vudumbukal Cave, Agasthiyar Hills, Kalakkad-Mundanthurai Tiger Reserve
   08° 46' N, 77° 15' E
   1400 m a.s.l.
   8 September, 2002
   1 male (released)

3. Nagapodigai Cave, Agasthiyar Hills, Kalakkad-Mundanthurai Tiger Reserve
   08° 35' N, 77° 20' E
   1600 m a.s.l.
   8 April, 2002
   1 male (released), 1 female (with a single juvenile attached) (released)

4. Sengaltheri Cave, Kalakkad Hills, Kalakkad-Mundanthurai Tiger Reserve
   08° 32' N, 77° 28' E
   1300 m a.s.l.
   8 March, 2003
   12 males (4 subadult) (released)
   6 May, 2003
   7 males (released), 1 female (released)

Taxonomic description

Specimens from the Therkumalai Estate in the Courtallum Hills exhibit external characteristics commensurate with recorded data of the genus *Latidens*, notably a short, soft, dark brown to black dorsal pelage with an infusion of chestnut hairs on the posterior back, on the flanks above the wings, and on the elbows and forearms; dark ears with narrowly rounded tips; uniformly black wings; and no external tail (Bates et al. 1994, Bates & Harrison 1997). Forearm measurements of both specimens (72.0 and 72.0 mm) are greater than those of specimens secured in the High Wavy Mountains (66.0 – 69.0 mm) (Bates et al. 1994). Cranial characteristics include a shortened rostrum; short postorbital processes without postorbital foramina; a long, narrow palate with a notable postdental extension; and well-developed basioccipital pits (Bates et al. 1994, Bates & Harrison 1997). The single pair of upper incisors present in both specimens distinguishes *Latidens* from other species of fruit bat known from the Indian Subcontinent (Bates & Harrison 1997).

External, cranial, and dental measurements of JVR-1 and JVR-2 are listed in table 1. Definitions of measurements given follow Bates & Harrison (1997) and are as follows: HB: head and body length; HF: (hind) foot length; FA: forearm length; E: ear length; GTL: greatest length of skull; CBL: condylo-basal length; CCL: condylo-canine length; ZB: zygomatic breadth; BB: breadth of braincase; M: mandible length; C-M^n: maxillary toothrow; C-M_n: mandibular toothrow; M^1-M^1: posterior palatal width; C^1-C^1: anterior palatal width.

Habitat and behaviour

Therkumalai Estate (night roost)
Latidens salimalii was found to roost within a dilapidated, abandoned building known as "Kannadimazhligai" in this former British Raj resort. Bats were observed arriving at the roost with uneaten figs, a fruit of which *Latidens salimalii* is reportedly fond (Ghosh et al. 1999), which they proceeded to consume in areas of the building that moonlight did not penetrate. One adult male, one sub-adult male, and a pregnant female *Latidens salimalii* were collected around 5 am on 23 February, 2002 and a single female on 1 March,

[1] The bat was not evidently gravid at the time of capture and was found to be pregnant only when being prepared as a scientific specimen.

Table 1. External, cranial, and dental measurements (in mm) of two specimens of *Latidens salimalii* from Therkumalai Estate, Courtallum Hills, Tirunelveli District, Tamil Nadu, India. HB: head and body length; HF: (hind) foot length; FA: forearm length; E: ear length; GTL: greatest length of skull; CBL: condylo-basal length; CCL: condylo-canine length; ZB: zygomatic breadth; BB: breadth of braincase; M: mandible length; C-M^n: maxillary toothrow; C-M_n: mandibular toothrow; M^1-M^1: posterior palatal width; C^1-C^1: anterior palatal width.

Feature	JVR-1	JVR-2
HB	123.0	117.0
HF	15.0	14.0
FA	72.0	72.0
E	17.0	19.0
Mass (g)	69.0	77.0
GTL	33.5	33.5
CBL	32.0	32.5
CCL	31.0	32.0
ZB	21.4	21.0
BB	14.2	14.0
M	25.5	25.0
C-M^n	11.5	11.1
C-M_n	13.0	12.6
M^1-M^1	10.6	10.7
C^1-C^1	6.2	6.1
Sex	Male	Female

2003 in a mist net set up within the building.

Threats: Therkumalai is a private estate and is not subject to government control of its land use. Since February 2002, estate workers have removed several corrugated iron roofing panels from "Kannadimazhligai" with the result that the interior of the building is more exposed with many of its formerly dark recesses now penetrated by moonlight.

Vudumbukal Cave (day roost)

Approximately 50 *Latidens salimalii* were observed at 11 am on 8 September, 2002 within Vudumbukal Cave at an elevation of some 1400 m in the Agasthiyar Hill Range. The cave measured approximately 6 m in both height and width with a lower and narrower entrance and was located near a branch of the Servalar River, itself a tributary of the larger Tambraparani River. The depth of the cave could not be determined due to the difficulty of access. A single adult male of the species, which was subsequently tagged and released, was collected in a mist net erected at the cave mouth.

Threats: local people have been known to capture *Latidens* for food while collecting honey in the vicinity of Vudumbukal Cave. A recent government order prohibiting the collection of honey in the area may or may not be beneficial to the security of the roost.

Nagapodigai Cave (day roost)

A colony of 350–400 *Latidens salimalii* was observed at 10 am on 8 April, 2002 in Nagapodigai Cave, which lies near the source of the Tambraparani River at an elevation of approximately 1600 m in the Agasthiyar Hill Range. The cave's principal chamber is approximately 15 m high and 9 m deep before it narrows and disappears within the hill. There are a number of small exits. An adult male *Latidens salimalii* together with a female and a single offspring were collected in a mist net established at the cave's triangular mouth. A number of birds' nests, which were attached to the walls of the cave mouth, were evident.

Threats: human disturbance of the Nagapodigai colony may be occasioned by the known collection of birds' nests by members of the local Kani Tribe, who occupy a small collection of huts at an elevation of 1200 m *en route* to Nagapodigai Cave. Evidence of camp fires has been found in the cave's entrance.

Sengaltheri Cave (day and night roost)

Approximately 25 *Latidens salimalii* were observed flying around the entrance to Sengaltheri Cave on 8 March, 2003. On a subsequent visit to the cave on 6 May, 2003, bats were heard and seen within the cave, where they were noted to roost in narrow chambers. The mouth of the cave is approximately 15 m wide and 10 m in height. The depth of the cave is not known due to the impossibility of human access beyond the first few metres. Large boulders up to 6 m high occupy the area in front of the cave, which is situated at an elevation of 1300 m next to the Pachaiaru

River, a rocky cascade that flows north to join the Tambraparani River east of Ambasamudram. The area around the cave is well forested and is noted to support *Ficus* sp. Twelve male *Latidens salimalii* (four of which were subadult) were collected in a mist net established at the entrance to the cave on 8 March, 2003 whilst 7 males and 1 female of the same species were caught in a mist net set in a similar position on 6 May, 2003.

Threats: none is known. The habitat around Sengaltheri Cave is tightly controlled by the Tamil Nadu Forest Department. The leases of a small number of cardamom plantations in the area expired in the late 1990s, since when the region has been uninhabited.

In general, colonies of *Latidens* were found to favour the darker recesses of caves, which, at the most, were penetrated only by dappled light coming through cracks or openings in the rock, and typically concentrated their roosts some four to five metres from the cave entrances. If disturbed, the bats would seek refuge further within the caves. Owing to the inaccessibility of the caves, bats were only able to be collected in mist nets established at cave mouths. All caves were located adjacent to or near streams or rivers.

Latidens salimalii was noted to be the host of a species of parasitic mite, believed, from a preliminary identification, to be *Meristaspis lateralis*, Kolenati 1857.

Reproductive status

Examinations of the reproductive status of male and female *Latidens salimalii* collected in mist nets at "Kannadimazhligai" on the Therkumalai Estate and at Nagapodigai, Vudumbukal, and Sengaltheri Caves were undertaken on an irregular basis in the months of February, March, April, May, and September between 23 February, 2002 and 6 May, 2003 (table 2).

Adult male *Latidens salimalii* with descended testes were found on 23 February at "Kannadimazhligai", on 8 March and 6 May at Sengaltheri Cave, on 21 April at Nagapodigai Cave, and on 8 September at Vudumbukal Cave. Subadults were observed on 23 February at

Table 2. Observations taken between February and September of the reproductive status of male and female *Latidens salimalii* from four localities in the Agasthiyar Hill Range.

Date	Locality	Male	Female
23 February 2002	"Kannadimazhligai", Therkumalai Estate (night roost)	1 adult with descended testes 1 subadult	1 pregnant Body mass: 77g
1 March 2003	"Kannadimazhligai", Therkumalai Estate (night roost)		1 lactating adult with prominent teats
8 March 2003	Sengaltheri Cave (day and night roost)	8 adults with descended testes 4 subadults	
21 April 2002	Nagapodigai Cave (day roost)	1 adult with descended testes	1 adult with juvenile attached Body mass adult: 64 g Body mass juvenile: 25 g
6 May 2003	Sengaltheri Cave (day and night roost)	7 adults with descended testes	1 adult with prominent "weaned" teats
8 September 2002	Vudumbukal Cave (day roost)	1 adult with descended testes	

"Kannadimazhligai" and on 8 March at Sengaltheri Cave.

At "Kannadimazhligai", a pregnant *Latidens salimalii* with a body mass of 77 g and a lactating adult with prominent teats were recorded on 23 February and 1 March, respectively. An adult female with a body mass of 64 g with an attached juvenile, whose body mass was 25 g, were found at Nagapodigai Cave on 21 April, whilst an adult female with prominent "weaned" teats was recorded at Sengaltheri Cave on 6 May.

Diet

Within the Therkumalai Estate, *Latidens* was observed to gather fruits from *Ficus* and to transport them to its night roost at "Kannadimazhligai" in order to consume them. Fruits were not seen to be consumed at the point of collection. Seeds and partially eaten fruits gathered from the floor of "Kannadimazhligai" have been identified preliminarily as those from the fruit of *Ficus racemosa* Linnaeus, 1753 (V. Chelladurai, personal communication), a species that is known to bear fruit for much of the year (P. Lakshminarasimhan, personal communication). Seeds from the fruit of the same tree were found on the floor of Sengaltheri Cave. Scientific evaluation both of the bark and of leaf extracts from *Ficus racemosa* has shown the tree to be of medicinal value as an anti-diarrhoeal and an anti-inflammatory agent (Mukherjee et al. 1998, Mandal et al. 2000).

Nuts, which appeared to have been ejected orally, were found in abundance alongside the fruits and seeds of *Ficus racemosa* at "Kannadimazhligai" and initial analysis has shown these to be from the following trees: *Elaeocarpus serratus* Linnaeus, 1753, *Elaeocarpus tuberculatus* Roxburgh, 1832, and *Dichapetalum gelonioides* (Roxburgh, 1896). Orally ejected nuts of *Dichapetalum gelanioides* were also evident n the floor of Sengaltheri Cave while partially eaten fruits of the same species were collected from "Kannadimazhligai". Circumstantial evidence would suggest that fruits from these three tree species may form part of *Latidens*' diet.

No food remnants were visible at Vudumbukal or Nagapodigai Caves.

Current population status, extent of occurrence, and area of occupancy

Calculations of the extent of occurrence and the area of occupancy are based upon an interpretation of IUCN Red List guidelines set out under subsections 9 and 10, section III, Annex 6 of the 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2000).

Population status

Table 3 shows an estimate of the number of individual *Latidens salimalii* recorded in published literature.

Bates et al. (1994) and Muni (1994) record the collection of six bats as they flew into a cave on the Kardama Coffee Estate in the High Wavy Mountains. The collectors were of the opinion that "the large number of bats seen flying near the cave during the evening were also *Latidens*" but were unable to establish the fact. Ghosh et al. (1999) describe the netting of an adult male and a young male "and females of different ages" in the Kalakkad-Mundanthurai Tiger Reserve, where "flocks" of *Latidens* reportedly visited a *Ficus* tree. In a report on a study of the population status of *Latidens* in Tamil Nadu State prepared for Fauna and Flora International by Agoramoorthy (2000), 46 individuals (19 males and 27 females) from a cave near the Megamalai Forest Reserve were captured and released. The author observed "250 individuals of *Latidens salimalii* when they emerged from the cave at dusk". Twenty-eight bats were collected from the Kardama Estate as detailed by Singaravelan and Marimuthu (2003a), the authors referring also to the capture of ten specimens by scientists from the Zoological Survey of India in the Agasthiyar Hill Range. A further 24 bats were collected from a cave on the same estate (Singaravelan & Marimuthu 2003b), although the figures given of the total number of *Latidens salimalii* present are confusing: firstly, the bats are

Table 3. Estimated population of *Latidens salimalii* in May 2003.

Reference	N of bats collected*	N of bats observed	Comments
Bates et al. 1994, Muni 1994	6	6**	A large number of bats seen flying (near the cave) were thought to be *Latidens* but this remains unproven.
Ghosh et al. 1999	3	>3**	Ghosh mentions "flocks" of *Latidens* visiting a *Ficus* tree.
Agoramoorthy 2000	46	250	
Singaravelan & Marimuthu 2003a	38***	38**	
Singaravelan & Marimuthu 2003b	24	>110 - <350	
This paper			
Therkumalai Estate	4	4*	
Vudumbukal Cave	1	50	
Nagapodigai Cave	3	350-400	
Sengaltheri Cave	20	25	
Total	>145	>826 - <1126	

* Assumes all bats collected were released.
** No mention is made of bats being observed other than those that were collected.
*** Includes ten individuals collected by the Zoological Survey of India.

identified as roosting inside the cave in "two clusters, each comprising 50 to 70 individuals" with "several individuals" hanging separately; secondly, "a total of nearly 350 bats" was counted "during their outflights", "24 of which were captured in a mist net". It is stated that "apart from a pair of male *Rhinolophus rouxi*….. no other species of bats were observed inside the cave". An assumption is made, therefore, that the minimum number of *Latidens salimalii* (if the visual identifications are correct) was more than 100 (50 plus 50 plus "several individuals") and that the maximum number was less than 350 ("nearly 350" minus "a pair of male *Rhinolophus rouxi*"). The figures for this paper are given in the sections entitled "New material" and "Habitat and behaviour", *supra*. If the number of bats collected is taken to be included in the number of bats observed, a minimum estimate of the total number of *Latidens salimalii* is (more than) 826 individuals with a maximum estimate of (less than) 1126.

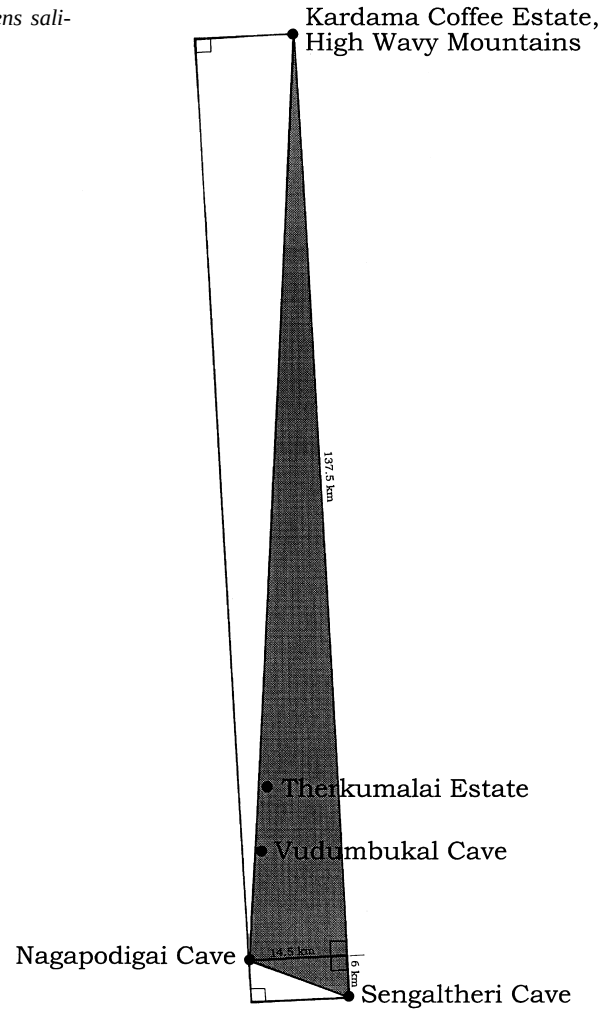
Extent of occurrence

The shaded area delineated by the lines drawn between the Kardama Coffee Estate in the High Wavy Mountains, Sengaltheri Cave, and Nagapodigai Cave in figure 2 represents the known distributional range of *Latidens salimalii*. By dividing the area into simple triangles, the following calculation may be made in order to arrive at a measurement of the extent of the taxon's occurrence:

Extent of occurrence = (137.5 x 14.5 ÷ 2) + (6 x 14.5 ÷ 2) = 1040.38 km^2

As there is more than a reasonable likelihood, on account of a similarity of topography, habitat, and

Figure 2. The extent of occurrence of *Latidens salimalii*.



elevation, that fieldwork carried out between the High Wavy Mountains and the Agasthiyar Hill Range will disclose further populations of *Latidens salimalii*, this area has not been excluded from the extent of occurrence as calculated above (see Annex 6, III: 9 of the 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2000)).

Area of occupancy

Singaralvelan and Marimuthu (2003b) suggest that *Latidens. salimalii* may cover a distance of at least 0.8 km from its diurnal roost to nocturnal feeding grounds, although the morphologically similar species *Cynopterus sphinx* has been observed carrying fruits up to 2 km from feeding grounds to the roost site (Agoramoothy 2000).

If each of the five known roost sites of *Latidens salimalii* is circumscribed by a circle with a radius of 0.8 km., the following formula may be used to calculate the sum of the areas of the circles and, accordingly, the species' total area of occupancy:

$5\pi r^2$, where $\pi = 3.142$ and $r = 0.8$

Total area of occupancy = 5 x 3.142 x 0.8 x 0.8 = 10.05 km^2

Discussion

From studies of *Latidens salimalii* carried out on the Kardama Coffee Estate, Singaravelan and Marimuthu (2003a) suggest that parturition in the species may occur at the end of May or the beginning of June. However, the observations recorded here of a pregnant female *Latidens salimalii* on 23 February, a lactating female on 1 March, a female with young attached on 21 April (the mass of the offspring being 39% of that of the mother at this date), and a female with prominent "weaned" teats on 6 May would indicate, at least in respect of the more southerly colonies of *Latidens salimalii*, that parturition occurs as early as late February. If the production and nurturing of the young of *Latidens* is compared to that of *Cynopterus sphinx* and *Rousettus leschenaulti*, juveniles can be expected to reach 40% of the body mass of adults when 55 to 65 days old and to be fully weaned by 75 days (Singaravelan & Marimuthu 2003a). By applying these periods to the observation of the female with young on 21 April and the female with weaned teats on 6 May, the inference is that these two females gave birth between 14 and 24 February.

The absence of food remnants at Vudumbukal and Nagapodigai Caves would suggest that although these two localities are used as day roosts, seeds gathered by the Vudumbukal and Nagapodigai colonies are consumed elsewhere. In contrast, "Kannadimazhligai" is utilised only as a nocturnal feeding roost, whereas Sengaltheri Cave is employed both as a nocturnal feeding roost and as a day roost. Favoured fruits may be abundant in the vicinity of Sengaltheri Cave but may be too far from Vudumbukal and Nagapodigai Caves to warrant the level of energy expenditure required in returning to these localities for the sole purpose of food consumption. Further studies, perhaps using radio-tracking equipment, may be helpful in determining the positions of day and night roosts relative to the most proximate feeding grounds. It is suggested that further fieldwork around Therkumalai should be undertaken to locate the day roost of the population that utilizes "Kannadimazhligai" as a nocturnal feeding site.

Latidens' preference for establishing roosts in dark recesses in caves raises the question of the navigational methods used by the species in this environment. It may be the case that some form of echolocation is employed similar to that known to be used by the genus *Rousettus* Gray, 1821 (Roberts 1975). A study to determine the use (if any) of echolocation by *Latidens salimalii* was propounded by Singaravelan & Marimuthu (2003b) and that view is reiterated here.

The IUCN Red List of Threatened Species, 2003, classifies *Latidens salimalii* as Critically Endangered with the extent of its occurrence estimated to be less than 100 km^2 or its area of occupancy less than 10 km^2 (IUCN 2003). IUCN suggests that the species is severely fragmented or known to exist at only a single location and that its numbers are expected to decline in respect of the area, extent and/or quality of habitat and that the current population is estimated to number fewer than 50 mature individuals. Whilst the accuracy of these data and projections may have been acceptable at the time of IUCN's assessment of *Latidens salimalii* in 1996 (the date of the assessment on which the 2003 Red List is based), it is now the case that the numbers and distributional range of the species are greater than was known at the time of the assessment, when only seven specimens of the species had been recorded, all of which were from a single location (the High Wavy Mountains). From current and recent field studies of populations of *Latidens*, it would seem reasonable to assume that the species' present extent of occurrence is in the region of 1040 km^2 and that its area of occupancy is at least 10.05 km^2. It may also be estimated that the current number of individuals of the species is not less than 826. If the above data are accepted, the species would no longer meet Criterion B (extent of occurrence estimated to be less than 100 km^2 or area of occupancy estimated to be less than 10 km^2) or Criterion D (population estimated to number less than 50 mature individuals) of the Critically Endangered classification.

On current information, however, the taxon would satisfy the criteria for an Endangered classification under Criterion B (extent of occur-

rence estimated to be less than 5000 km^2 or area of occupancy estimated to be less than 500 km^2 and [sub-criterion 1] the taxon is severely fragmented or known to exist at no more than five locations and [sub-criterion 2c] a continuing decline is estimated in the area, extent, and/or quality of habitat). There are, obviously, extant threats to *Latidens*' habitat. Human activity on the Therkumalai Estate and at Nagapodigai and Vudumbukal Caves poses a threat to the security of the roosts at these locations, particularly the latter two as these are permanent day roosts. The worsening state of disrepair of "Kannadimazhligai" may not be of such concern, as this is a transitory night roost, but any interference with the arboreal ecostructure of the Therkumalai Estate may be detrimental to *Latidens* in terms of the diminution of available feeding grounds. Singaravelan and Marimuthu (2003b) report that tree cutting on the Kardama Coffee Estate in the High Wavy Mountains may pose a threat to the habitat occupied by *Latidens* at that location.

It is likely that further colonies will be discovered during the course of subsequent field studies, especially as the area between the northernmost point of *Latidens*' current known range and the southernmost point offers similar habitat. In this event, the species would be known at more than five locations and would only continue to meet Criterion B1 of the Endangered classification if the taxon is regarded as severely fragmented. It is a moot point whether populations of *Latidens* are "severely fragmented" within the meaning of Annex 6, III: 8 of the Red List (Hilton-Taylor 2000). Whilst it may be said that "most individuals within (the) taxon are found in small and relatively isolated subpopulations", an inference may be drawn from reading Criterion C2a (of the Endangered category) that a subpopulation is not "small" if it exceeds 250 individuals. The same Criterion states that a taxon may not be "severely fragmented" if any subpopulation is estimated to exceed that number (250); the population at Nagapodigai Cave is estimated at no fewer than 350 individuals and a similar number of individuals may exist in another cave roost in the High Wavy Mountains (Singaravelan & Marimuthu 2003b). If further populations are found that bring the total number of known locations to more than five and the taxon is not considered to be severely fragmented at that time, *Latidens* would not meet the criteria for an Endangered classification but would meet the current criteria for a classification of Vulnerable under Criteria B1 and B2c, C2a, and D1 and/or D2 (*q.v.*).

It is suggested here that, at the appropriate time[2], *Latidens salimalii* be reclassified as Endangered on the ground that the taxon no longer meets any of the criteria of the Critically Endangered classification but that it does satisfy Criteria B1 and B2c of the Endangered classification.

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[2] Annex 6, II: 13 of the 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2000) states that: "A taxon may be moved from a category of higher threat to a category of lower threat if none of the criteria of the higher category has been met for five years or more".

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Samenvatting

Een herwaardering van de IUCN-status van *Latidens salimalii* (Chiroptera: Pteropodidae), gebaseerd op nieuwe gegevens uit de Westelijke Ghats, India

India, staat op de Rode Lijst van de IUCN vermeld als 'Critically Endangered'. Deze classificatie is gebaseerd op de vondst van zeven individuen in de High Wavy Mountains (Tamil Nadu, India) in 1996. Recente vondsten van de soort in de westelijke Ghats laten echter zien dat de huidige aantallen en het verspreidingsgebied groter zijn dan voorheen werd aangenomen. De auteurs stellen daarom voor de IUCN-status van *Latidens salimalii* te wijzigen in 'Endangered'. Naast aantals- en verspreidingsgegevens presenteert het artikel gegevens over de voedselkeuze en de reproductieve status van de gevonden dieren.

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Distribution and status of small cetaceans along the French Channel coasts: using opportunistic records for a preliminary assessment

Jeremy Kiszka[1,2], Sami Hassani[3] & Sylvain Pezeril[2,4]

[1] Coordination Mammalogique du Nord de la France, groupe mammifères marins, Maison des associations, Hemmes de Marck, France, e-mail: jeremy.kiszka@wanadoo.fr

[2] Groupe Ornithologique et Naturaliste du Nord-Pas-de-Calais, Maison de l'Environnement, 59 140 Dunkerque, France

[3] Laboratoire d'Etude des Mammifères Marins, Oceanopolis, Port du Moulin Blanc, 29 200 Brest, France

[4] Groupe Mammalogique Normand, Mairie d'Epaignes, Place de l'Eglise, 27 260 Epaignes, France

Abstract: Small cetaceans can use a variety of habitats and are generally wide-ranging. The study of their distribution and abundance is time-consuming and dedicated surveys are very expensive. In order to assess the diversity, distribution, and frequency of small cetaceans off the French Channel coasts, we collated opportunistic sightings collected by French mammalogist organisations, from the French/Belgian border to Pointe du Raz, western Brittany. A total of 1,350 small cetacean sightings are presented in this paper, collected between 1980 and 2000. Bottlenose dolphins (*Tursiops truncatus*) are common off the western French Channel coast. Long-finned pilot whales (*Globicephala melas*), Risso's dolphins (*Grampus griseus*) and common dolphins (*Delphinus delphis*) occurred infrequently in the Channel, mostly on a seasonal basis. The harbour porpoise (*Phocoena phocoena*) occurred regularly off the northern French coast. These results are important for planning systematic assessments of the distribution and abundance of small cetaceans off the French Channel coasts.

Keywords: small cetaceans, French Channel coasts, Normandy, Brittany, distribution, status, opportunistic records.

Introduction

Small cetaceans can use a variety of habitats and are generally wide-ranging. For this reason, extensive sighting surveys to assess their distribution, abundance, and habitat preference are needed (see for example: Buckland et al. 1993, Hammond et al. 1995). In some areas, where weather conditions are often difficult, these surveys can be rarely undertaken. However, the most limiting factor for setting-up dedicated cetacean sighting surveys is their prohibitive cost, which is a deterrent for attracting sources of funding. The use of opportunistic sighting records provides an alternative source of information on the distribution and diversity of cetaceans in a given area, and on a long-term basis.

The English Channel is an epicontinental sea. It constitutes a relatively narrow link between the Atlantic Ocean and the North Sea (figure 1) and is influenced by strong tides and freshwater inputs, which create well-mixed waters. This area is also characterised by the presence of hydrological fronts (at various spatial and temporal scales), which induces an important primary and secondary productivity (Brylinski 1997, Southward et al., in press). Large and varied stocks of fishes occur in the English Channel, and are heavily exploited. Only one dedicated cetacean sighting survey has been conducted in recent times, the SCANS programme (Small Cetacean Abundance in the North Sea and adjacent waters, summer 1994). This survey did not observe any cetaceans in "Block B" (the English Channel and southern North Sea), although this may be explained by the limited time spent in this area (Hammond et al. 1995, 2002). Some other surveys have been done in the area using sighting

networks, data collected from onboard platforms of opportunity (especially the ferries between France and England), and dedicated sighting surveys focussing on resident populations of bottlenose dolphins (*Tursiops truncatus*) (see for example: Pourreau & Marin 1989, Tregenza 1992, Guinet et al. 1993, Lahaye & Mauger 2000, Ridoux et al. 2000, Brereton & Williams 2001, Coles et al. 2002, Kiszka et al., in press - a, MacLeod & Walker, in press). Several groups of bottlenose dolphin are known to occur in the English Channel, particularly along the southern coast of England and the coasts of the Brittanian peninsula and Normandy (Tregenza 1992, Williams et al. 1996, Lahaye & Mauger 2000, Ridoux et al. 2000). Data for the other species are relatively scarce. The common dolphin (*Delphinus delphis*) and the harbour porpoise (*Phocoena phocoena*) occur mainly in the western English Channel, and rarely in the central and eastern part (Evans 1980, Northridge et al. 1995, Rosen et al. 2000, Kiszka et al., in press - a). The presence of these species has also been documented through their incidental catches in fishing gear in the western English Channel and Celtic Sea (Tregenza et al. 1997a, Northridge, in press). The harbour porpoise is regularly sighted along the French and Belgian coasts of the southern North Sea, especially during the winter and early spring (Kiszka et al. 2004). Other cetacean species can be found in the English Channel too, such as the long-finned pilot whale (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), killer whale (*Orcinus orca*), striped dolphin (*Stenella coeruleoalba*), white-beaked dolphin (*Lagenorhynchus albirostris)*, and minke whale (*Balaenoptera acutorostrata*) (Evans 1980, Collet et al. 1994, Hammond et al. 1995, Williams & Brereton 2001, Pezeril & Kiszka, in press). However, their status and occurrence remain unclear.

The aim of this study was to investigate the diversity, distribution, and frequency of small cetaceans in the coastal waters of the French side of the English Channel. However, no attempt is made to provide relative abundance estimations due to the lack of data related to observation effort. The harbour porpoise and the bottlenose dolphin are placed under Appendix II of the European Union Habitats Directive, and an assessment of their status and distribution in the English Channel, very exposed to human activities, is much needed to identify conservation and management strategies. This preliminary assessment could help to define areas that are of special interest for some species, and could provide the basis for setting-up dedicated surveys in areas where sightings have been particularly numerous.

Materials and methods

The French Channel coasts (figure 1) are delimited in the north-east by the Belgian border, and in the south-west by the Pointe du Raz, i.e. approximately between 51°00' - 48°00' N of latitude and 06°00' W - 03°00' E of longitude. The topography of the study area is uniform, and maximum depth is approximately 70 metres, north of the Cotentin peninsula. The French Channel coasts are strongly influenced by tide cycles, especially in estuaries and bays, which are numerous throughout the area (from north to south the most important are: the Authie, Somme, Seine and Veys estuaries, and Mont-Saint-Michel Bay). Various biotopes can be found along the French Channel coasts, from mainly rocky (western French Channel coast) to sandy coasts (northern France). Channel waters are well mixed, turbid, and range, on average, from 4 to 20 °C, in winter and summer, respectively (Castel et al. 1997). In the western Channel, during summer, an important hydrological front permits high primary productivity, contributing to a huge amount of biomass in the higher trophic levels, a potential food source for cetaceans (Evans 1987).

Cetacean sightings data were collected from 1980 to 2000, by diverse organisations located along the coast, from the Belgian border to western Brittany. In northern France, records were collected by the Coordination Mammalogique du Nord de la France (CMNF), in Normandy most records were collected by the Groupe Mammalogique Normand (GMN), and finally,

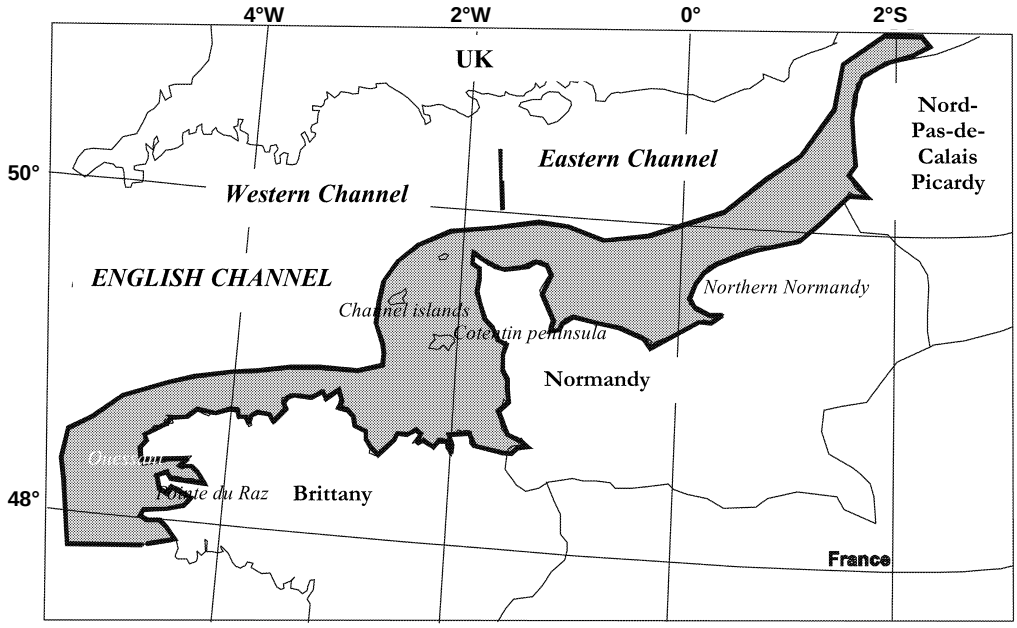

Figure 1. The study area; grey = areas where sighting data were collected.

in Brittany, records were collected by the Laboratoire d'Etude des Mammifères Marins, Océanopolis (LEMM).

The data were recorded by naturalists (particularly ornithologists), and also by recreational and, a few, professional fishermen, yachtsmen, and tourists. However, the bulk of the records we used (78%), were collected by accredited observers, and some marine mammalogists. A sighting was assigned to a species when the description of the animals was judged to be correct on the sighting form (pattern of behaviour, colouration, morphology, and pictures, if available). Consequently, we consider the bulk of the species identifications as valid. Nevertheless, it is still possible that some identifications are mistaken. Collection of the sighting data was undertaken with the collaboration of correspondents involved in the local sighting network. This was implemented in the early 1980s in Brittany and in Normandy, and in the late 1990s in northern France. For this study, we analysed the frequency (based only on the number of sightings for each species, and not calibrated with observation effort), distribution, and diversity of small cetaceans in French coastal waters.

Results

Overview

From 1980 to 2000, 1,350 small cetacean sightings data were collected along the French Channel coast. A total of eight species was recorded. In order of frequency, they are the bottlenose dolphin (*n*=1,031; 76.4% of the records), long-finned pilot whale (*n*=123; 9.1%), common dolphin (*n*=83; 6.1%), harbour porpoise (*n*=47; 3.5%), Risso's dolphin (*n*=44; 3.2%), killer whale (*n*=10; 0.7%), striped dolphin (*n*=7; 0.5%), and white-beaked dolphin (*n*=5; 0.4%).

Temporal and spatial distribution of sightings

The temporal analysis of the records shows a high heterogeneity (figure 2). Many sightings were reported from the mid-1980s to the early

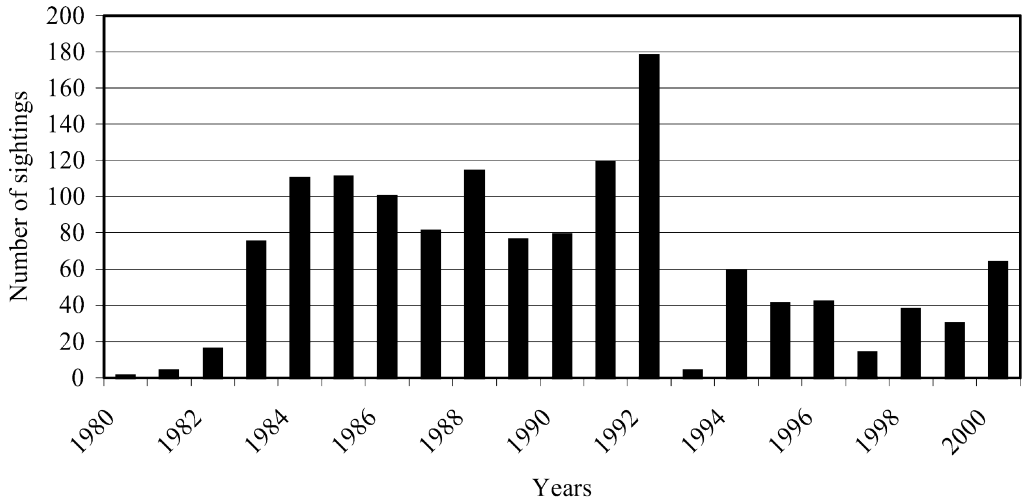

Figure 2. Inter-annual distribution of small cetacean sightings off the French Channel coasts between 1980 and 2000 (*n*=1,350).

1990s. After this period, the records decreased significantly. The average intra-annual distribution of sightings records from 1980 to 2000 shows that sightings are significantly more frequent during the summer months (notably in July and August; figure 3). The spatial distribution of opportunistic small cetacean records off the French Channel coasts indicates a higher number of sightings in the western part of the study area; 181 records (13%) in the eastern part as against 1,169 in the western part (87%) (figure 4). To investigate the spatial distribution of small cetaceans off the French Channel coasts, a specific analysis is needed.

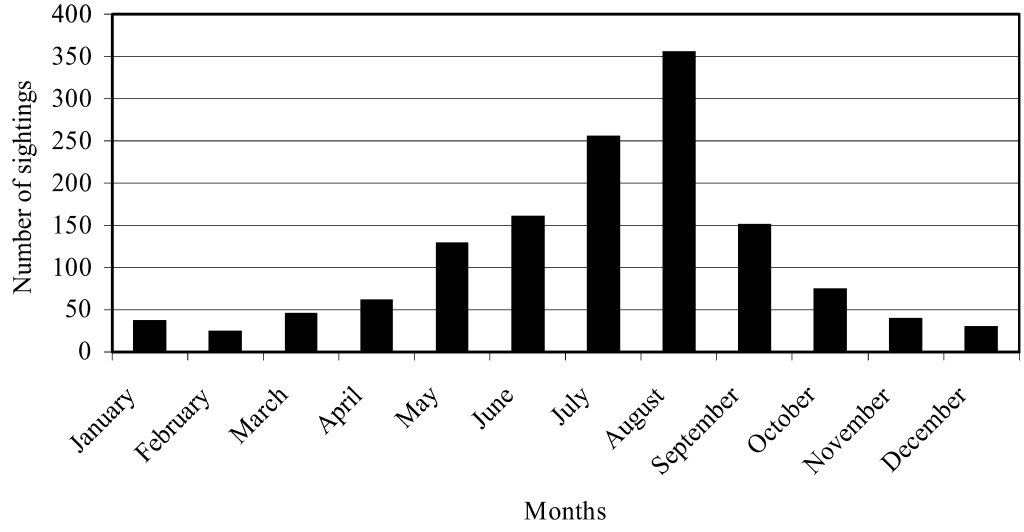

Figure 3. Intra-annual distribution of small cetacean sightings off the French Channel coasts between 1980 and 2000 (*n*=1,350).

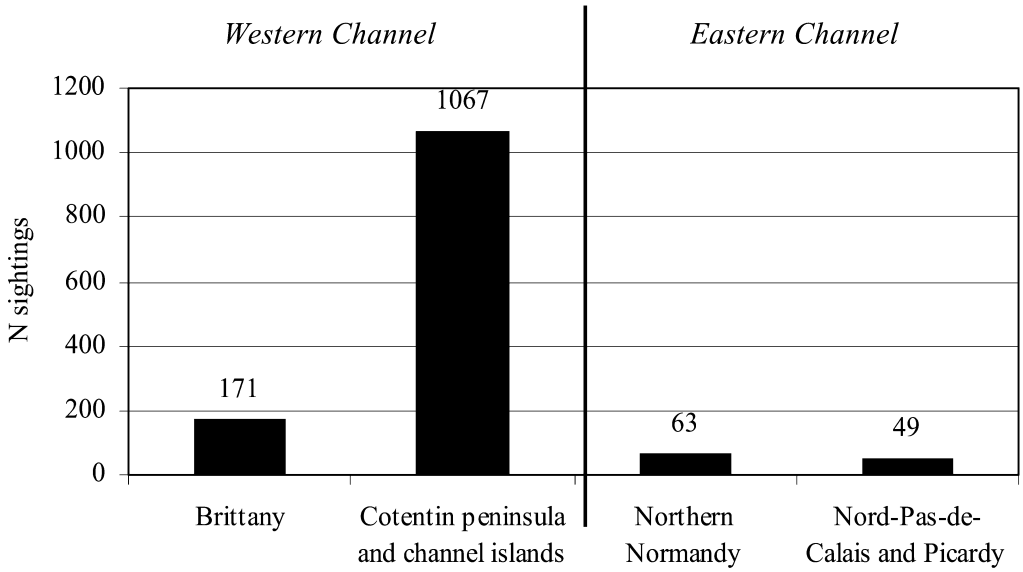

Figure 4. Number of sightings within each region (*n*=1,350).

Distribution and group size of each encountered species

The bottlenose dolphin was by far the most frequently encountered species: 1,031 sightings, i.e. 76% of all records. Sightings were mainly concentrated around the Cotentin peninsula and in the Mont-Saint-Michel Bay, especially during the summer months (figure 5). Few sightings have been reported in northern France and in Brittany. Group size ranged from 1 to 30 individuals, with an average group size of eleven dolphins.

The long-finned pilot whale (*n*=123 sightings; 9.1%) was encountered throughout the study area, but essentially in north-eastern Normandy and around the Channel Islands (figure 6). However, several records have been collected in northern France and northern Brittany. Group size was highly variable, ranging from a single individual to over 150 animals, with an average group size of 17 whales. 33% of the groups were made up of one to four animals.

The common dolphin has been recorded on 83 occasions (6.1% of all records) off the French Channel coasts from 1980 to 2000. The species has been recorded mainly around the island of Ouessant (western Brittany), and north of the Channel Islands (figure 7). Only a few sightings were recorded in the eastern Channel and in the Mont-Saint-Michel Bay. Group size was highly variable, ranging from 2 to 500 individuals, with an average group size of 25 dolphins. The largest aggregations were observed north of Guernsey.

The harbour porpoise has been sighted on 47 occasions (3.5% of all records) during the study period. The bulk of the records have been collected in northern France, and a few in Normandy and Brittany (figure 8). Harbour porpoises were mainly singles (62%), but pairs (18%), groups with more than two individuals (11%) and even more than ten (9%) have been observed. The most important aggregations were found in northern France. The largest group involved more than 40 individuals near the Belgian border, probably foraging.

The Risso's dolphin was recorded on 44 occasions (3.2% of records). None were recorded in the eastern Channel. The bulk of the sightings were concentrated in the Mont-Saint-Michel Bay, with several also off the northern Brittany coast (figure 9). Group size ranged from one to

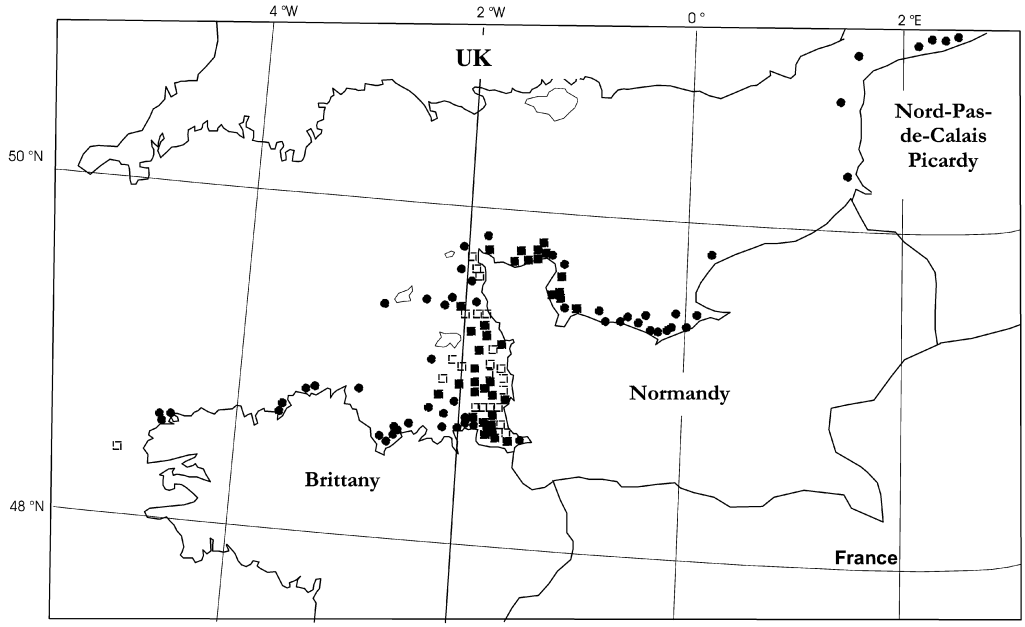

Figure 5. Distribution of bottlenose dolphin by opportunistic sightings off the French Channel coasts between 1980 and 2000 (*n*=1,031); ◆ = 1 sighting; ■ = 2-10 sightings, □ > 10 sightings.

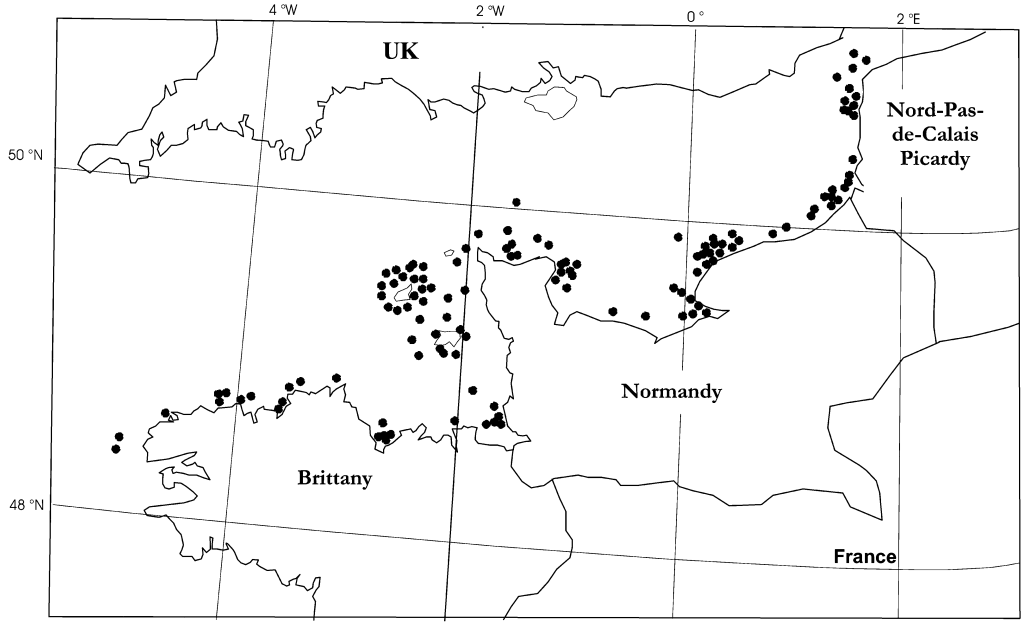

Figure 6. Distribution of long-finned pilot whale by opportunistic sightings off the French Channel coasts between 1980 and 2000 (*n*=123).

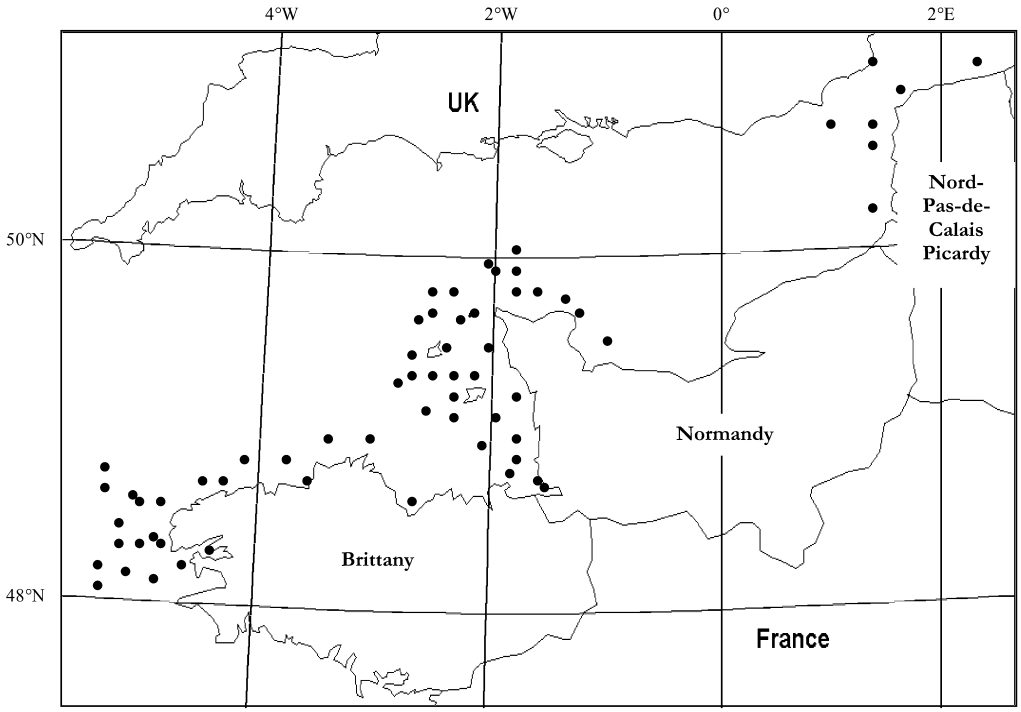

Figure 7. Distribution of common dolphin by opportunistic sightings off the French Channel coasts between 1980 and 2000 (*n*=83).

eight individuals, with an average group size of five dolphins.

Some other rare small cetacean species have been recorded off the French Channel coasts, including the killer whale (*Orcinus orca*), the striped dolphin (*Stenella coeruleoalba*), and the white-beaked dolphin (*Lagenorhynchus albirostris*). Killer whales have been recorded on three occasions in the Dover Strait (between November to March, in 1994, 1996 and 1997), on three occasions off eastern Normandy (between June to September in 1981, 1983 and 1989), and on four occasions off western Brittany, i.e. near Pointe du Raz off Ouessant and a long the northern coast (from April to October in 1996, 1997, 1998 and 1999). Striped dolphins, regularly stranding along the French Channel coast (Van Canneyt 2001, Van Canneyt 2002), were observed once in the Dover Strait in April (2000), once in northern Brittany (in November 1993), and off the western coast of Normandy, essentially in winter. White-beaked dolphins were sighted once in Normandy (near the Channel Islands, during winter 1989) and in northern France (November, January and March 1998).

Discussion

Overview

This study reveals the limits of the use of occasional observations. Although there appears to be a decrease in the number of sightings after 1992 and this decrease is most probably due to a lower number of cetaceans, although it may also be due to a decrease in observational effort (not quantified), as the observers were not regularly approached during the latter period. Indeed, we suspect a lower motivation of the observers after the 1990s, probably due to less funds and active leaders in the organisations dedicated to marine

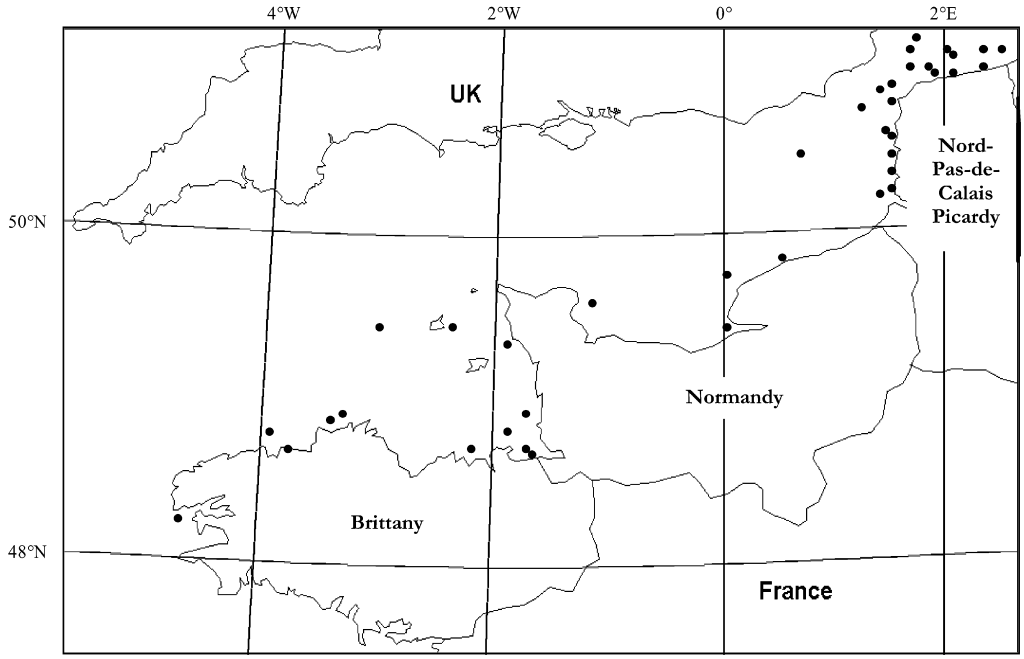

Figure 8. Distribution of harbour porpoise by opportunistic sightings off the French Channel coasts between 1980 and 2000 (*n*=47).

mammals. The summer records (from May to September) represent, by far, the bulk of the information presented in this study. The winter data may also be an underestimation, as observations are easier to undertake in the summer (due to better weather conditions) and recreational sailing activities increase during this period. However, the investigation of spatio-temporal trends of stranding records along the French Channel coasts, from 1972 to 2001, indicates a higher occurrence of cetaceans during winter in the area, especially involving the common dolphin (Van Canneyt 2001). Finally, there is a significant difference in the number of cetacean sightings between the eastern and western French Channel coasts. Our records indicate far more sightings off the western coasts (figure 4 to 9), except for the harbour porpoise and the long-finned pilot whale. This may be due be a higher presence of cetaceans in the western English Channel, better reporting and/or higher observation effort in this area (especially west of the Cotentin peninsula), or a combination of these factors. Opportunistic data collection started much later in northern France (in 1996) than in the other two regions, where it started in the early 1980s.

Although we do not have the answers to the questions relating to distribution patterns (for the seasonal distribution of bottlenose dolphin, see the results; however, the global trend follow the same pattern than the one in figure 3, as for the other species such as pilot whales and Risso's dolphin), the English Channel, especially the French Channel coastal waters, seems to constitute an important area for several cetacean species. There are resident groups of bottlenose dolphins (Lahaye & Mauger 2000, Ridoux et al. 2000) and other species appear to use this region, at least seasonally. As the western part of the Channel is open to the Atlantic Ocean, oceanic species such as common dolphins, long-finned pilot whales and Risso's dolphins can easily make incursions in their hunt for prey. Even

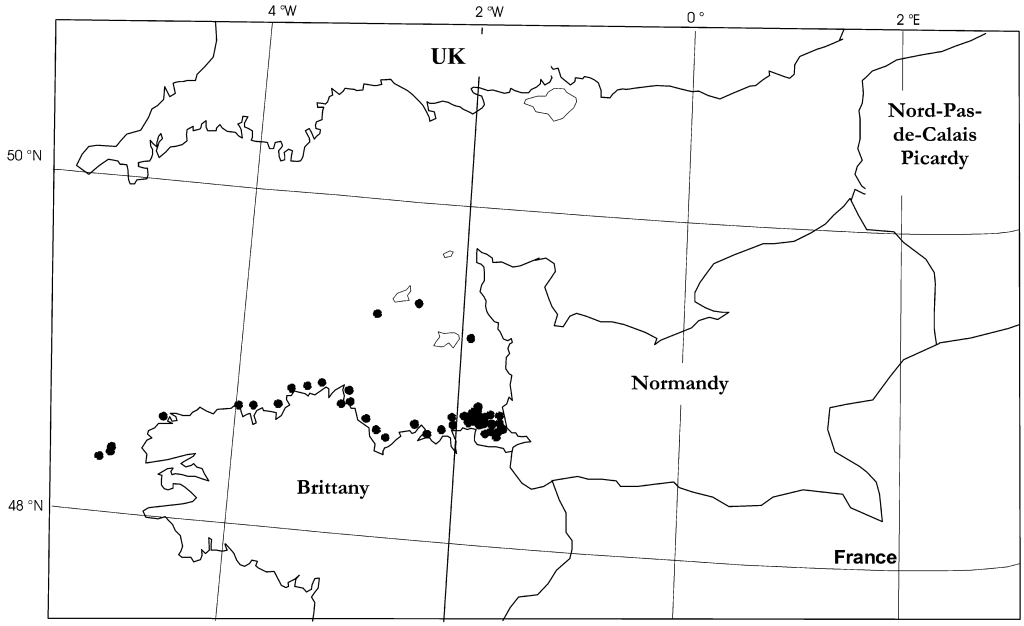

Figure 9. Distribution of Risso's dolphin by opportunistic sightings off the French Channel coasts between 1980 and 2000 (*n*=44).

though it is difficult to interpret these occasional observations in order to assess the abundance (or relative abundance), occurrence and distribution of cetaceans off the French coast in the English Channel (for reasons discussed earlier) these data can help to define particular locations for cetaceans and encourage more accurate studies following scientific protocol (for example, line transect surveys for abundance estimates and/or photo-identification surveys for site fidelity assessment).

Comparisons with previous knowledge of the status of small cetaceans in the English Channel

The bottlenose dolphin is the most commonly encountered species along the French Channel coasts. The high number of sightings is due to the presence of several resident populations in the French Channel coastal waters, especially around the Cotentin peninsula. Few data have been recorded in Brittany. This may be because local observers consider the species as resident, so less interesting to record and report than, for example, pilot whales. There are two important groups of resident bottlenose dolphins in western Brittany: one around Île de Sein, and the other one in the Molène archipelago. The first one consisted in 2001 of 17 individuals, and the second of 35-50 individuals (Guinet et al. 1993, Ridoux et al. 2000, Liret 2001). In Normandy, the bulk of observations of bottlenose dolphins are located off the west coast of the Cotentin peninsula (in accordance with the observations by Pourreau & Marin 1989), yet many sightings were also made off the east coast, and in the Seine Bay – a phenomenon that has hardly been commented on before. Off the western and northern coast of the Cotentin peninsula, this species occurs on a year-round basis, with a substantial increase of records during summer, i.e. the same seasonal distribution pattern as in other species, such as pilot whales, Risso's dolphins and common dolphins. In Normandy, the resident bottlenose dolphin population probably involves more than 80 individuals, and individuals/groups seem to exploit all the coastal waters

of the Cotentin peninsula during summer (Lahaye & Mauger 2000, Pineau et al. 2000). In northern France, there have been only a few sightings of bottlenose dolphins.

Little is known about the status of the long-finned pilot whale in the English Channel. It has been recorded regularly off the south-west coast of England, notably during autumn and early winter (Evans 1980). This species, considered as oceanic (Bernard & Reilly 1999), regularly enters into shallow coastal waters, including those off the French Atlantic and Channel coast (Desportes 1983, Van Canneyt et al. 1999). Our data suggest a regular presence of pilot whales, especially around the Channel Islands, in north-eastern Normandy as well as in northern Brittany. In Normandy, pilot whales are considered as regular during the summer months. Movements of groups of pilot whales have been documented (Pezeril & Kiszka, in press), mainly between July and September, but also during winter. The main areas where the whales have been seen are the Channel Islands and the north-eastern coast of Normandy. Their presence in coastal waters could be linked to feeding behaviour, but more investigations are needed in order to prove this (Pezeril & Kiszka, in press).

Our results suggest that the common dolphin is a regularly occurring species in the western Channel, particularly around the Channel Islands and the island of Ouessant (western Brittany). Some sightings were made in the eastern Channel. The common dolphin is abundant in the western English Channel, especially during the winter months, but is rare in the eastern English Channel (Tregenza et al. 1997a, Rosen et al. 2000, Brereton & Williams 2001, MacLeod & Walker, in press). The presence of the common dolphin has been frequently associated with incidental catches in fishing gear in the western English Channel (Collet et al. 1994, Tregenza et al. 1997b, Northridge, in press).

It is generally considered that the harbour porpoise is rare in the English Channel, and in the southern North Sea (Hammond et al. 1995). In northern France, recent sighting and stranding records have indicated a probable recovery of the harbour porpoise, which is borne out by similar results from the Belgian and the Dutch coasts (Camphuysen 1994, Kiszka et al. 2004). In the western English Channel, the harbour porpoise is relatively common, with a higher presence during summer (Brereton & Williams 2001, Rosen et al. 2000, Kiszka et al., in press - a). The presence of the species is, like the common dolphin, mentioned due to recurrent incidental catches in fishing nets in the western English Channel, Celtic Sea, and along the French Channel coasts (Collet et al. 1994; Tregenza et al. 1997a).

Our data suggest that the Risso's dolphin is absent in the eastern part of the study area, as suggested by Collet et al. (1994). However, in the western English Channel, Risso's dolphins were sighted on a regular basis in the Mont-Saint-Michel Bay, which seems to be a summer feeding ground for a small group of individuals, and along the northern Brittany coast. Beaulieu (1996) suggested that the species would occur in Brittany, and in the Mont-Saint-Michel Bay in summer, when cuttlefish (*Sepia officinalis*) come to reproduce in the shallow waters of the bay. A relatively stable group of eight to ten individuals was studied in the 1980s, notably using photo-identification (Hussenot 1985, Beaulieu 1996). This group was re-identified over several years, although no long-term follow-up studies have been undertaken in recent years. Risso's dolphins are still regularly seen, but more research would allow us to confirm the status of the group and provide new information about this little known species.

Certain other cetacean species, including the killer whale, striped dolphin and white-beaked dolphin have also been observed. These three species are generally considered as very rare off the French Channel coasts (Duguy 1983, Collet et al. 1994, Kiszka et al., in press - b). Striped dolphin sightings were mostly made in winter. Two unusual stranding records were made along the northern French Channel coasts, in the winter of 2001, but the bulk of stranding data were collected along the western French Channel coast (Van Canneyt 2002, Kiszka & Labrune 2003). Since the late 1990s, there has been a substantial

increase of striped dolphin observations around the North Sea and the Baltic (Isaksen & Syvertsen 2002). Environmental changes, linked to an increase of the sea surface temperature in the North Sea and adjacent waters could explain this phenomenon, as striped dolphins mostly occur in oceanic tropical, subtropical and warm temperate waters of both hemispheres (Evans 1987). However, no in-depth investigations have been undertaken to confirm this hypothesis. White-beaked dolphins were sighted in Normandy and in northern France. The species is rare, except in the southern North Sea French coast where some groups are regularly observed during the winter months (Kiszka & Labrune 2003, Kiszka et al., in press - b, J. Haelters, personal communication).

Conclusions

Some short-term quantitative studies have suggested that the English Channel is not an important area for cetaceans (Hammond et al. 1995). However, at least for the western French coastal waters, this long-term qualitative study underlines that several species do occur on a regular basis. The data we present here might be helpful in identifying areas where it might be justified to protect cetaceans. Before this more accurate studies would need to be carried out within a scientific protocol. Consequently, more research is needed in Normandy, especially on bottlenose dolphin distribution, movement patterns, and abundance. In the Mont-Saint-Michel Bay, a study focusing on the status of Risso's dolphins would also be interesting. This species, considered as mainly oceanic, has been regularly observed feeding in very shallow waters in this area during summer. The same phenomenon was observed with pilot whales, but at a larger spatial scale**,** i.e. along the French Channel coast and not in a localised site. Such behaviour seems to be relatively rare elsewhere. More knowledge about the ecology of both species could be obtained by implementing new long-term follow-up research along the French Channel coasts. At the local scale, dedicated surveys on species making regular coastal incursions, such as pilot whales and Risso's dolphins, would confirm their abundance (using photo-identification, for example), site fidelity and behaviour (habitat use, movement patterns). At a broader scale, the use of platforms of opportunity (especially the ferries between France and England) on a regular basis could provide, at a low cost, more quantified data (with observation effort) on the distribution and seasonal occurrence of cetaceans in the English Channel. This research, both regional (French) and international (in cooperation with England for the broader studies) could also contribute to the conservation of small cetaceans in the highly disturbed habitat of the English Channel.

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Samenvatting

Verspreiding en status van kleine walvisachtigen langs de Franse Kanaalkust: het gebruik van incidentele waarnemingen voor een voorlopig overzicht

Kleine walvisachtigen kunnen een grote verscheidenheid aan habitats bewonen en komen over het algemeen op veel plaatsen voor. Onderzoek naar hun verspreiding en aantallen is tijdrovend en het maken van verantwoorde overzichten is buitengewoon kostbaar. Om de diversiteit, verspreiding en frequentie van voorkomen van kleine walvisachtigen langs de Franse kust van het Engelse Kanaal te achterhalen, vergeleken wij willekeurige waarnemingen verzameld door Franse zoogdierkundige organisaties, dat wil zeggen, vanaf de Frans-Belgische grens tot en met Pointe du Raz, in het westen van Bretagne. In dit artikel worden in totaal 1.350 waarnemingen van kleine walvisachtigen gepresenteerd, verzameld tussen 1980 en 2000. Tuimelaars (*Tursiops truncatus*) kwamen algemeen voor in het westelijk deel van het onderzoeksgebied; er konden drie afzonderlijke populaties worden on-

derscheiden. De griend (*Globicephala melas*), de gramper (*Grampus grisues*) en de gewone dolfijn (*Delphinus delphis*) kwamen onregelmatig voor in het Kanaal, meestal in een bepaald seizoen. De bruinvis (*Phocoena phocoena*) kwam regelmatig voor langs het noordelijk deel van de Franse kust. Deze resultaten zijn van belang voor het opzetten van systematische schattingen van het voorkomen en de aantallen van kleine walvisachtigen langs de Franse Kanaalkust.

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Kort bericht

Een geval van partieel-albinisme bij de eekhoorn (*Sciurus vulgaris* Linnaeus, 1758)

Bauke Hoekstra

Bornsestraat 118, NL-7601 GK Almelo, The Netherlands, e-mail: b.hoekstra@home.nl

Inleiding

Het is algemeen bekend dat de kleur van de pels bij de eekhoorn (*Sciurus vulgaris* Linnaeus, 1758) sterk kan variëren. In een populatie kunnen naast elkaar diverse kleurslagen voorkomen, variërend van helder roodbruin tot bruinzwart. Over de geografische verspreiding van de diverse kleurfasen bestaat een uitgebreide literatuur (Wiltafsky 1973). Naast de vermelding van diverse geografische variëteiten wordt van tijd tot tijd gewag gemaakt van het voorkomen van albinisme. Albinisme, het ontbreken van pigment met als uiterlijke kenmerken kleurloosheid (witte huid en vacht) en rode ogen, kan in beginsel bij alle diersoorten optreden.

Het optreden van albinisme berust op een genetisch bepaalde aanmaakstoornis van melanine. Partieel-albinisme kan ook het gevolg zijn van ziekte, operaties, bevriezing en parasieten. In die gevallen wordt doorgaans gesproken van verworven albinisme of vitiligo.

Albinisme is vooral bekend bij huisdieren, konijnen, katten, cavia's, laboratorium-ratten en -muizen, en ook bij de mens. Bij in het wild levende zoogdieren is het fenomeen veel zeldzamer. Dit is waarschijnlijk het gevolg van het feit dat albinistische dieren door hun opvallende uiterlijk veel sneller het slachtoffer worden van predatoren.

Het voorkomen van witte staarten bij het in Groot-Brittanië voorkomende endemische eekhoorn-ras *leucourus* Kerr, 1792 valt niet in de categorie albinisme. Bij dit ras verandert in het voorjaar de staart van kleur en wordt geleidelijk aan geheel wit. Dit is een genetisch bepaald kenmerk van deze vorm.

Verspreiding van albinisme bij eekhoorns

Bij de eekhoorn komt albinisme zelden voor. Barrett-Hamilton & Hinton (1910-1921) sommen voor Groot-Brittannië een tiental gevallen op over een periode van 25 jaar, van 1885 tot 1910. Onder deze gevallen was één partieel-albinistisch dier. Vrijwel alle meldingen waren ontleend aan korte berichtjes in de tijdschriften Field en Zoologist. Shorten (1954) voegt aan deze lijst nog vier gevallen toe.

Veel min of meer populaire werken (IJsseling & Scheygrond 1950, Gurnell 1987, Corbet & Harris 1990) volstaan met het signaleren van het verschijnsel zonder exacte gegevens te vermelden. Andere handboeken gaan zelfs geheel aan het verschijnsel voorbij (Niethammer & Krapp 1978).

Op het vasteland van Europa lijkt albinisme nog zeldzamer te zijn dan in Groot-Brittanië. Een uitgebreide speurtocht in de literatuur leverde slechts enkele concrete gegevens van totaal-albinisme bij de eekhoorn op. In december 1954 werd in de provincie Lerida in het noordoosten van Spanje, een albino-eekhoorn (♂) geschoten. In de omgeving van Barcelona zou 25 jaar daarvoor ook eens een albino zijn gesignaleerd (Balcelles & Palaus 1955).

Voorkomen van albinisme in Nederland

Op 27 oktober 1935 werd in het Heerenbosch te Velzen een geheel witte eekhoorn waargenomen (Van den Voet 1935). In de winter van 1950-1951 werd een totaal witte eekhoorn gesignaleerd in de omgeving van Lochem (Pettinga 1951). In maart 1998 ontfermde de Stichting Eekhoornopvang te Meern zich over een jonge albino-eekhoorn (♂) die kort daarvoor was gevonden op Oostvoorne (Anonymus 1998). Het sterk verzwakte dier moest wegens de slechte conditie na enkele dagen worden geëuthanaseerd. Huid en schedel van dit exemplaar zijn opgenomen in de collectie van het Nationaal Natuurhistorisch Museum te Leiden (registratienummer RMNH 38678). De collectie in Leiden telt nog een tweetal albino-eekhoorns. Het ene exemplaar werd op 24 februari 1865 verzameld op het landgoed Den Wildenborch bij Vorden. Van het tweede exemplaar, gedateerd 1866 is geen nadere vindplaats bekend dan "Europa".

Een recente waarneming van partieel-albinisme

Partieel-albinisme, dat bij diverse diergroepen, waaronder vleermuizen en woelmuizen, vrij regelmatig voorkomt, is bij de eekhoorn nauwelijks bekend. Uitgebreid literatuuronderzoek leverde, behalve het bovengenoemde exemplaar van Barret-Hamilton & Hinton, geen enkel geval op.

Het hieronder beschreven exemplaar werd op 7 maart 2003 door een hond gegrepen en gedood toen het de oprit van een boerderij overstak, enkele kilometers buiten de bebouwde kom van het dorp Weerselo, Overijssel (atlasblok 28-38-21, Amersfoort-coördinaten: 255.8 - 485.9). Het dier was door omwonenden al geruime tijd gesignaleerd.

De vachtkleur van deze eekhoorn is zeer merkwaardig. De buikzijde, inclusief de voor- en achterpoten, is zuiver wit. Van de linker achterpoot loopt het wit geheel door tot en met de voetzool. Het wit van de rechter achterpoot begint ongeveer ter hoogte van het hielgewricht. Ook de beharing van de voetzolen is geheel wit. Het haar aan de basis van de staart is zeer donkergrijs. Schijnbaar loopt dit grijze haar aan de bovenzijde van de staart enkele centimeters verder door, doch dat is vooral het gevolg van de grotere lengte van de staartharen. Het wit van de buikzijde verloopt volkomen asymmetrisch via de rechter zijde, naar het midden van de rug. Vandaar wordt het via een smalle witte band verbonden met de linker buikzijde (foto 1). Van de gebruikelijke roodkleuring in de donkere delen van de pels is vrijwel niets terug te vinden. Slechts bij de extremiteiten en de basis van de oren valt een zweem van roodkleuring te bespeuren. Een klein deel van de witte rugharen vertoont aan de basis, diep in de pels verscholen, ook een geringe roodkleuring. De overige, niet witte delen van de pels zijn blauwachtig grijs, een kleurvariant die normaliter bij eekhoorns niet voorkomt. De karakteristieke agoeti-kleuring zoals we die bij elke eekhoorn kunnen vaststellen, is wel aanwezig. Deze kleuring wordt veroorzaakt door een afwisseling van lichte en donkere banden in de dekharen. In de beharing van de oorpluimen en de staartwortel ontbreken deze lichte banden. Hierdoor lijken deze delen veel donkerder dan de overige delen. In de beharing ontbreken blijkbaar de rode pigmentkorrels waardoor de pels haar blauwgrijze uiterlijk verkrijgt**.** Het is moeilijk na te gaan waarvan het ontbreken van gebruikelijke pigmenten het gevolg is. Het kan genetisch bepaald zijn, doch het kan ook fysiologische oorzaken hebben. De binnenzijde van de huid vertoonde geen ruivlekken.

Sectie wees uit dat het hier om een volwassen, seksueel actief mannetje gaat. De afmetingen van de testes bedroegen 18,3 x 9,5 mm. De kop-romplengte mat 247 mm, de staart vanaf anus tot laatste wervelpunt 173 mm, het rechteroor 32,4 mm (het linkeroor was beschadigd door de hond) en de voet inclusief nagel 69,3 mm, zonder nagel 63,0 mm. Het bruto gewicht bedroeg 380 g. Alle maten werden genomen aan het vers dode dier. Door de beet van de hond was de schedel ernstig beschadigd en konden slechts enkele maten wor-

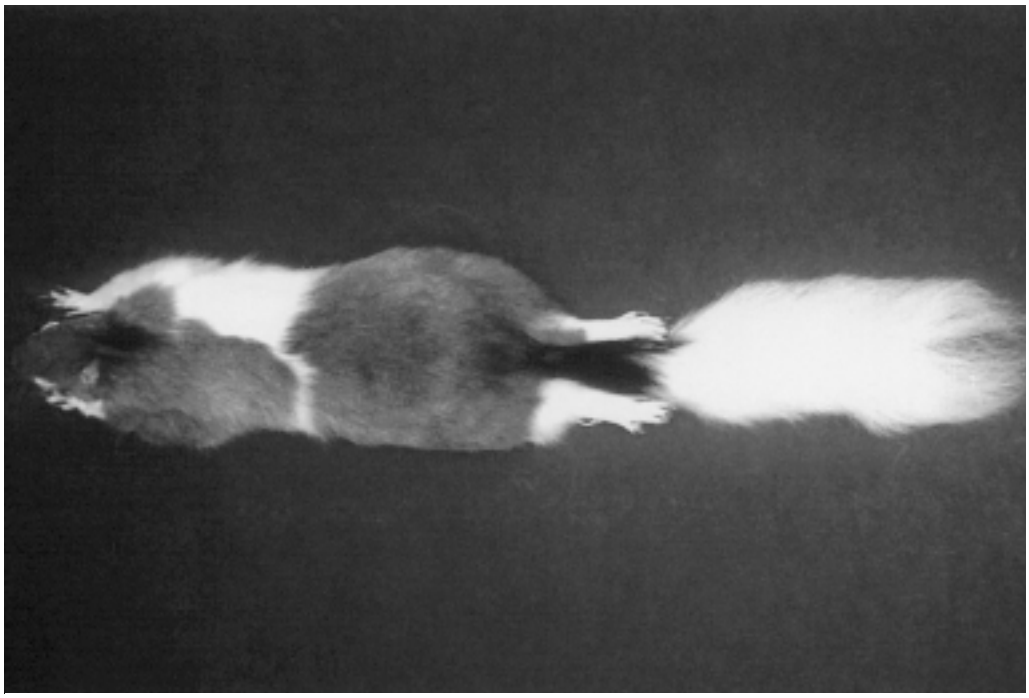

Foto 1. Rugzijde van de eekhoorn. *Foto: Bauke Hoekstra*.

den genomen. De jukbeenbreedte bedroeg 31,6 mm, de kiezenrij van de linker bovenkaak mat 13 mm. De ogen van het dier waren niet rood. Op basis van de slijtage van de kiezen wordt de leeftijd op minstens 2 jaar geschat. Lengte van de onderkaak mat 31,6 mm. De verbening van de schedelnaden is optimaal en duidt ook op een volgroeid dier. De eekhoorn (huid en schedel) is onder nummer 2192 opgenomen in de collectie van de auteur.

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Summary

Partial albinism in the red squirrel (*Sciurus vulgaris* Linnaeus, 1758)

A partially albinistic specimen (♂) of the red squirrel (*Sciurus vulgaris* Linnaeus, 1758) was

killed by a dog near Weerselo, a small village in the province of Overijssel, in the eastern part of the Netherlands. The belly, tail and feet are pure white, as well as the foot soles and hands. The base of the tail is very dark grey. In addition, a large part of the right side of the back is covered with white fur, and the left side of the pelage is divided into two parts by a small white band. The principal colour of the unaffected, normally coloured parts is blue-grey. This is the first documented observation on partial albinism in the red squirrel.

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Short note

Longevity records in the red fox

Jaap L. Mulder

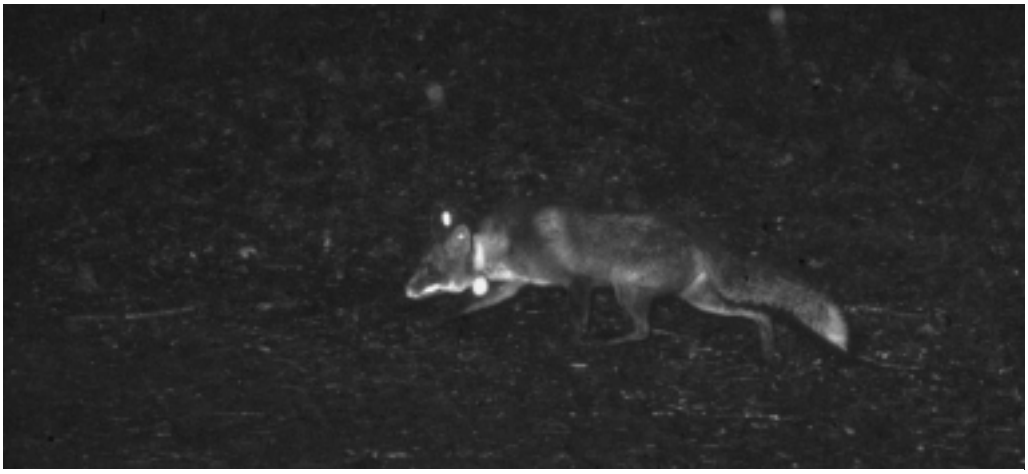
De Holle Bilt 17, NL-3732 HM De Bilt, The Netherlands, e-mail: jaapmulder@freeler.nl

In the course of a research project on the red fox (*Vulpes vulpes*) in the coastal dunes of Holland (North-Holland Dune Reserve), red foxes were tagged with earmarks and equipped with radio-collars between 1979 and 1984. On the 12th of April 1993, long after the end of the project, a radio-collared fox was observed in a neighbouring village, Castricum. It was cornered and captured, and subsequently clubbed to death by a police officer, out of fear for rabies, although the last and nearest case of rabies had been five years ago and about 200 km away (Anonymous 1989). The fox appeared to be a female, ear tagged as the smallest cub in a litter of six in April 1981. From the end of June 1981 she was equipped with a radio-collar, and her whereabouts were followed till the end of the project, three and a half years later.

At the time of her unfortunate death, this female thus was 12 years and about 1 month old, a longevity record for an ear tagged wild red fox, as far as reported in the literature. In the same research project a tagged male reached the age of almost ten years: 9 years and 11 months. There is no fox control in this area, which may have helped these foxes to become so old.

Most longevity records mentioned in the literature are based on examination of tooth sections. Counting the number of the yearly formed cementum layers around the root of teeth, however, is not always straightforward, hence there always remains some doubt about the real age of the animal, unless the animal was tagged as a juvenile. This uncertainty increases with growing age, as can be concluded by the following. We sectioned canine teeth of 331 foxes of unknown age. In age-classes 0-3 years the age of 9 out of 281 individuals was estimated with an uncertainty of 1 year (3.2%) and of 2 with an uncertainty of 2 years (0.7%), because of unclear lines. In age-classes 4-6 years (41 individuals) these numbers were 9 (22.0%) and 1 (2.4%) respectively, and in age-classes 7-9 years (9 individuals) 5 (55.6%) and 2 (22.4%) respectively (J.L. Mulder, unpublished data). Conversely, checking the number of cementum lines in known age individuals never yields a 100% fit either, in larger samples; Grue & Jensen (1973) for instance determined the age of only 93% of 135 known age foxes (age 0.5 - 4.5 years) accurately from cementum lines.

The highest age of a red fox has been reported from Hokkaido, Japan. This animal was a female with 14 dark lines in the cementum (Maekawa et al. 1980). Since this fox was captured in winter and the dark lines are formed during spring and summer (Grue & Jensen 1979), this number of lines probably corresponds with an age of almost 15 years. Kappeler (1985) found, among nearly thousand foxes examined from Switzerland, a single fox (sex unknown) of almost 13 years old (shot in late winter), and as the next oldest fox a female of almost 11 years old. Chubbs & Phillips (1996) reported upon two foxes from Labrador, which were determined to be 8 years and 7 months (female) and 10 years and 8 months (male) old, respectively. The oldest fox Baker & Harris (2001) found in a sample of 1,628 dead foxes from Bristol was two weeks short of 10 years old. In a recent fox research project in another part of the Dutch coastal dunes (Meyen-



The female red fox, which would live to be 12 years old, with radio-collar and ear tags, just after the release following a recapture on 31 January 1983. *Photograph: Jaap Mulder*.

del), the oldest fox, a female, reached the age of exactly 9 years, according to her tooth sections (Mulder 2000).

In captivity foxes may reach higher ages than in the wild. Harris & Lloyd (1991) mention ages of 14 years or even more for captive red foxes.

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Samenvatting

Leeftijdsrecords van de vos

Een vos, die in 1981 als juveniel vrouwtje gemerkt en gezenderd werd in het Noord-Hollands Duinreservaat, werd in april 1993 doodgeslagen in het dorp Castricum. Zij bereikte dus met zekerheid een leeftijd van twaalf jaar, een record voor een gemerkte, in het wild levende vos. Bij leeftijdsonderzoek aan dode, ongemerkte vossen zijn weliswaar af en toe nog oudere dieren gevonden (tot bijna 15 jaar), maar aan de leeftijdsbepaling door middel van groeilaagjes in het tandcement kleeft altijd enige onzekerheid, die nog toeneemt met opklimmende leeftijd.

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Short note

Evidence of lesser horseshoe bat (*Rhinolophus hipposideros*) predation by otter (*Lutra lutra*) in a Welsh cave system

Dan W. Forman[1], Geoff Liles[2] & Pauline Barber[3]

[1] School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea, SA2 8PP, UK, e-mail: d.w.forman@swansea.ac.uk
[2] Otter Consultancy, Llwyneinon Isaf, Capel Iwan, Newcastle Emlyn, Carmarthenshire, SA38 9LY, UK
[3] Countryside Council for Wales, North Region, Victoria Buildings, Stryd Meurig, Dolgellau, Gwynedd. LL40 1LN, UK

Introduction

A significant number of studies have demonstrated unequivocally that the diet of otters (*Lutra lutra*) is strongly biased towards fish species (Jenkins et al. 1979, Kruuk 2001). A variable and occasionally significant proportion of this species' diet can, however, be derived from non-fish prey types. The relative importance of these non-fish inputs to the overall dietary intake of otters can vary considerably, seasonally and between locations (Beja 1991, Beja 1997).

It is well documented that otters regularly predate amphibians at specific times of the year (e.g. Sidorovich et al. 1998). It is also noted that otters are not averse to opportunistically and selectively pursuing mammalian prey on occasions. For example, in a two-year study on the seasonal diet of otters in north-east Scotland, Jenkins et al. (1979) found that otters actively preyed upon a wide range of mammals including lagomorphs and rodents.

The following short paper reports the first known occurrence of otter predation of a bat species.

Methodology

Between October 2003 and March 2004, a total of five spraints were recovered from a mine adit (horizontal mining tunnel) in northern Wales at an undisclosed location. In addition to these spraints, a significant (>1 kg in mass) amalgamated pile of spraints was located some 100 m within the adit adjacent to an established and recently used couch. The spraints and couch prey remains were collected (under licence from the Countryside Council for Wales), placed into labelled plastic bags and stored at -17 °C at the University of Wales Swansea until analysis could be conducted. Spraints were subsequently prepared using a standard protocol (see Conroy et al. 1993) and prey species identified using keys produced by Corbet (1964), Conroy et al. (1993), Yalden (1993) and by the use of a previously amassed reference collection of fish and mammalian remains.

Results

Prey within the five spraint samples was identified to species level for fish, and family for other groups (table 1). Due to the low sample size (n=5 + 1), and the specific aim of this paper, i.e. to report on the presence of a new dietary species, it was deemed inappropriate to present the data gathered as frequency of occurrence (%).

Table 1. The presence of different categories of prey in the mine adit spraints. X = prey remain present in spraint.

Prey category	Spraint				
	1	2	3	4	5
Anguilla anguilla	X	X	X	X	
Salmo spp.	X	X	X	X	X
Cyprinidae	X			X	
Percidae		X	X	X	
Gasterosteidae	X				
Pleuronectidae	X			X	X
Amphibia	X	X	X	X	X
Chriroptera					X

A total of three chiroptera scapulae were recovered from one of the spraints. These scapulae were subsequently identified as those of the lesser horseshoe bat (*Rhinolophus hipposideros*). Vertebrae were used to identify fish remains from the spraint mass found near the couch. All remains were identified to species level where possible (table 2). Whilst the number of vertebrae is given in the table to give an indication of relative importance of each fish species, the varying number of vertebrae in different species makes this a very general indication at best. Two incomplete lesser horseshoe skulls (but with upper jaws), a number of vertebrae and several broken humerus (with styloid processes intact) were recovered from this large deposit of spraints.

Discussion

To our knowledge, this is the first documented case of bat predation by otters in the United Kingdom or, indeed, anywhere else. Previous studies elsewhere have noted that generalist carnivores such as raccoons (*Procyon lotor*) and beech martens (*Martes foina*) will opportunistically exploit accessible and localised congregations of bats (Roer & Gudendorf 1994, Sparks et al. 2003). The cave adit at the focus of this baseline study supports a variable number of lesser horseshoe bats over the winter months (D.W. Forman, unpublished data). As the height of the roof within the adit is highly variable, it is not unfeasible that otters passing through these caves might opportunistically predate any bat within easy reach. We acknowledge that there is the possibility that otters were consuming bat carcasses located on the adit floors. Given that the energetic benefit of consuming dead bats is presumably relatively low, the likelihood of this occurring is, on balance, slight. The data presented here reveal that the presumed single otter using the site had consumed at least four lesser horseshoe bats. Individual reinforcement of this predatory behaviour could feasibly occur over time, potentially leading to selection of individual prey preferences within the otter meta-population of northern Wales. Furthermore, there is the potential opportunity for this foraging behaviour to be learnt by offspring observing their mothers feeding in this particular manner (Kitchener 1999). Such suggestions clearly need further, more detailed investigation. The results of such studies would begin to fill the considerable gap in our knowledge of prey selection, foraging strategies and social learning in carnivores.

Whilst the finding of this study is potentially problematic with respect to horseshoe bat conservation efforts, it is hard to imagine that otter predation could be a serious threat to the persistence of specific bat colonies due to the large number of available roost sites in the area. Indeed, it is more probable that human intrusion into such sites during certain times of the year is more of a threat to bats than the natural predatory behaviour of otters. Unpublished data collected over the last six months strongly suggests that otters regularly frequent mine adits in northern Wales. A study is currently underway, therefore, to determine the potential impacts and frequency

Table 2. Prey categories and number of vertebrae recorded from the adit couch prey mass.

Prey category	Number of vertebrae recorded	Notes
Anguilla anguilla (eel)	6071	
Salmo spp.	912	Both trout (*Salmo trutta*) and salmon (*Salmo salar*)
Rockling (Gadidae) spp.	539	Three-, four-, and five-bearded rockling (*Gaidropsarus vulgaris, Rhinonemus cimbruis, Ciliata mustela*)
Hetersomata (flatfish)	335	Flounder (*Platichthys flesus*), plaice (*Pleurinectes platessa*), dab (*Limanda limanda*) and sole (*Micostomus kitt*)
Percidae (perch)	318	Perch (*Percha fluviatilis*) and ruff (*Gymnocephalus cernua*)
Gasterosteus aculeatus	194	Three-spine stickleback (*Gasterosteus aculeatus*)
Non-rockling Gadidae spp.	165	Saithe (*Pollachius virens*) and cod (*Gadus morhua*)
Esox lucius (pike)	160	
Cyprinidae (cyprids)	156	Minnow (*Phoxinus phoxinus*), roach (*Rutilus rutilus*) and gudgeon (*Gobio gobio*)
Mugilidae (mullets)	47	Thick (*Crenimugil labrosus*) and thin-lipped (*Liza ramada*) mullet
Cottidae (bullheads)	35	Miller's thumb (*Cottus gobio*)
Gobiidae (gobies)	24	
Sparidae (sea breams)	19	
Labridae (wrasses)	15	
Callionymidae (dragonets)	9	
Serranidae (bass)	2	
Unidentified fish vertebrae	121	
Amphibia (anura)		67 *Rana temporaria* skulls or partial skulls recovered
Aves (birds)		Rail (Rallidae) remains
Rodentia		Field-vole (*Microtus agrestis*)
Chiroptera		two lesser horseshoe bats (*Rhinolophus hipposideros*)

of bat predation by otters in a larger number of mine adits. Moreover, this study should also highlight the conservation significance of maintaining adit access suitable for otters (as well as bats) within Britain.

The results of this study also provide an interesting 'snap-shot' of the diet of otters in this area of northern Wales. It is apparent that a significant proportion of the diet of otters in this area could be derived from estuarine or marine species, as well as from freshwater. Since the occurrence of some marine/estuarine prey groups is relatively high (although we note the low sample size), it is clear that the coastal zone is an important foraging habitat for otters in northern Wales. Previous anecdotal observations made in mine adits suggest that significant numbers of amphibians inhabit these sites. It is perhaps unsurprising, therefore, to find such a large number of frog skulls within the couch faecal mass. The presence of such prey (as well as the secluded nature of many of these sites) might also explain the willingness of otters to regularly enter adits, although this has yet to be formerly studied.

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Samenvatting

Aanwijzingen voor predatie van kleine hoefijzerneus (*Rhinolophus hipposideros*) door otter (*Lutra lutra*) in een mijn in Wales (Groot-Brittannië)

Uit een analyse van vijf spraints (uitwerpselen) van de otter (*Lutra lutra*) bleek dat deze vooral resten bevatten van verschillende soorten vis en amfibieën. In één van de spraints werden daarnaast drie schouderbladen van de kleine hoefijzerneus (*Rhinolophus hipposideros*) aangetroffen. Dit zijn, voor zover bekend, de eerste aanwijzingen voor predatie van vleermuizen door de otter. Op ongeveer 100 m van de vindplaats werd, dichtbij de ingang van een leger, een grote hoeveelheid samengeklonterde spraints gevonden. Na analyse bleken deze uitwerpselen, naast resten van vissen, amfibieën, vogels en veldmuizen, twee schedels van de kleine hoefijzerneus te bevatten. Vermoedelijk gaat het hier om één otter die tenminste vier individuen van de kleine hoefijzerneus heeft gepredeerd.

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Bauke Hoekstra

Bornsestraat 118, 7601 GK Almelo, The Netherlands, e-mail: b.hoekstra@home.nl

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Book Reviews

Herbivores as mediators

Herbivores as mediators of their environment. The impact of large and small species on vegetation dynamics. E.S. Bakker 2003. PhD thesis. Wageningen University, Wageningen, The Netherlands. 184 pp. ISBN 90-5808-878-2.

This PhD thesis deals with three herbivorous mammals (cattle, rabbit (*Oryctolagus cuniculus*) and common vole (*Microtus arvalis*)) and their impact on vegetation and vegetation constituents of a cool temperate alluvial grassland system (Junner Koeland). Quite some impact determinants are treated, such as plant consumption, treading, burying activity (gap creation), defecation, nutrient redistribution, endozoochory, (perceived) predation and herbivore interactions. Those who expected a book on mammals will be disappointed, only one of the chapters departs from the animal as response variable, all the others actually have vegetation and its constituents as responding subject. But as such many aspects are covered, none of them exhaustively though.

One result of this PhD thesis will be remembered in particular: the present-day underestimation of the possible impact of common voles on a grassland system. Not many biologists will ever have estimated the daily energy expenditure (DEE) of a vole population at any time period during the year to be equal to the DEE of cattle (with a density of 0.4 individuals per ha) in the same environment. Nonetheless, both appear to have an entirely different impact on the grassland environment: the effect of cattle grazing excludes common voles entirely from the grassland system and leads to a compositional and structural constancy of the vegetation, which is never reached with common vole grazing without cattle and rabbits.

What further remains as a general feeling after reading this PhD thesis, is the difficulty to deal with the complexity of field conditions. The field experiments are difficult to replicate and hardly ever lead to clear-cut conclusions. The author often needs to leave questions unanswered, because of the variability in weather and habitat conditions and population dynamics of both wild herbivores. On the other hand, she proofs the absolute necessity of field experiments: ecological questions can hardly be simplified to univariate experiments, ignoring the multivariate interactions. These are well documented in this PhD thesis. The apparent leitmotiv here is the importance of herbivore size.

The impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands

From a field experiment it is concluded that gap creation (colonization opportunity) plays a crucial role for the non-dominant (subordinate) plant species in a grassland system. It was found that cattle disperse much larger amounts of germinable seeds via their dung than rabbits do. Through their burying activities, rabbits on the other hand create bare soil and might be far more important for gap creation than cattle, and, hence, for colonization opportunities for plants. Artificial disturbance improved germination success for the four model plant species (*Prunella vulgaris, Ranunculus acris, Trifolium pratense, Plantago lanceolata*, perhaps not exactly the most critical plant species in nature conservation; selection criteria are not given) that were tested. Cattle are recognized as better seed dispersers, while rabbits are more important as creators of disturbance, necessary for germination and mainte-

nance of plant species-richness in a grassland ecosystem. Hence, different herbivores have different impact on colonization/extinction ratios of plants.

The interactive effects of grazing and litter on grassland plant diversity

In a second contribution to the estimation of herbivore impact on colonization and extinction rates of plants, emphasis is given on the importance of the litter decomposition cycle under grazing. In a nicely designed three-year long exclosure experiment it is proven that large herbivore grazing diminishes (not surprisingly) bio- and necromass accumulation significantly, creating favourable light conditions for plant colonization. Litter removal alone did not effect species richness significantly. Much emphasis is given on the favourable light conditions at soil level, but regrettably other determinants, such as available space and possible soil development are not taken into consideration. It remains unsolved why voles do not have the same impact on bio- and necromass removal and thus on favouring light conditions for colonization, given the general conclusion that the vole population has a daily energy expenditure close to that of the cattle grazing the area.

Compositional constancy in grazed plant communities increases with herbivore size

Again within the framework of the alluvial grassland system of Junner Koeland, and with a herbivore-differentiated exclosure experiment, the impact of the three differently sized herbivores on vegetation compositional stability and the impact of nutrient addition was tested. When grazed by large herbivores (cattle + rabbit), plant species composition of the grassland was very stable during consecutive years, while it fluctuated strongly when exclusively grazed by both smaller herbivores (fluctuations were strongest with exclusive vole grazing). Very interesting for nature managers was the observation that local nutrient addition did not effect plant species composition significantly when vegetation was grazed by large herbivores, since those nutrient-enriched spots were highly preferred by the herbivores. Apparently, seasonal cattle grazing at a density of 0.4 heifer per ha, suppresses species composition fluctuations and promotes structural homogeneity, while exclusive small herbivore grazing enhances structural variation (expressing soil differentiation), while plant species richness increases less. However, one remains with the evident question, which of both is preferable from a nature manager's point of view, taking into consideration that structural diversity in space (perhaps less so in time) is assumed to be favourable for invertebrate diversity. In this respect, the author makes an important note on the fact that the conclusion that large and small herbivores control the vegetation differently depends on the scale of observation: "If the scale of observation was adjusted to herbivore size and for example the vegetation structure of several hectares was compressed to a few square meters, the grazing patterns created by cattle and voles may be very similar. At the landscape scale cattle may even create a structurally more diverse landscape because they prefer certain vegetation types and patches [while others are avoided]. This results in vegetation with a mosaic of high and low patches. Vole grazing on a landscape scale may result in structurally rather homogeneous vegetation, because vole grazing lawns are so small that they are hard to detect at a landscape scale".

Impact of herbivores on nitrogen cycling: contrasting effects of small and large species

Again within an exclosure experiment, in which consecutively cattle and cattle + rabbit were excluded from grazing, the effect of different herbivore combinations on nitrogen cycling was tested. First important conclusion is that cattle grazing (at a heifer density of 0.4 animals per ha) excludes voles almost entirely. Despite comparable daily energy expenditure of all three herbi-

vores given the respective animal densities in the system (peak densities of common vole are extremely high), the impact of the different herbivore combinations was quite different. Net annual in situ N-mineralization was higher in the small herbivore treatments (voles and voles + rabbits, respectively), while turnover of nitrogen was significantly lower under cattle grazing treatment.

Experimental manipulation of food quality and apparent predation risk in the European rabbit: bottom-up versus top-down control in a central-place foraging herbivore

After four chapters on response variables of herbivore grazing, we finally arrive at the herbivores themselves. In her field experiment, the author tries to differentiate between the impact of food quality and predation risk on the foraging behaviour of the European rabbit (*Oryctolagus cuniculus*). A very original and highly appreciated field experimental design, unfortunately with a low replication level, revealed that grazing intensity, not surprisingly, declined with increasing distance from the burrows, situated beneath thorny scrub of blackthorn (*Prunus spinosa*). Fertilizing vegetation increased rabbit foraging four times, and decreased the above-mentioned distance-to-burrow effect. Through more intense grazing close to the burrows, the rabbits increase food quality and facilitate themselves. More surprising was the effect of addition of predator scent (realised through addition of mink pellets as a substitute of potential polecat predation). Although it did not result in different *total* visitation rates by the rabbits, it did cause a significant change in diurnal feeding pattern. Without pellets the rabbit foraged predominantly during the night, while addition of mink pellets made them forage during daylight as well. In fact, no nocturnal foraging preference could be noticed anymore when pellets were added. This shift in activity pattern clearly points at an adaptation to increased perceived predation risk by mustelid predators, which are mainly nocturnal. The results further suggest that the improvement of food quality through frequent grazing and, hence, promotion of new shoot development, is a more important trigger than the accompanying improvement of visibility of the surroundings.

Ecological anachronisms in the recruitment of light-demanding tree species?

After exactly one chapter on one of the herbivores themselves, we return to their environment again. This last contribution deals with vegetation development on the longer time scale. We partly leave Junner Koeland to have a broader view on plant defences that evolved under predation pressure (e.g. thorns of blackthorn). Predation pressure has vanished partly (not forgetting present-day wild herbivores like roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*)) because of extinction of plant predators (aurochs (*Bos primigenius*), tarpan (*Equus caballus gmelini*)). In this context the hypothesis is tested whether grazing by their descendants (cattle, horse) could give evidence to the succession mechanism of shifting mosaics hypothesized by Olff et al. in 1999 and more or less introduced by Vera (1997, 2000). The question is reduced to the impact of both large grazers and the lagomorphic European rabbit on palatable pedunculate oak (*Quercus robur*) and seven thorny (i.e. “defensive”) shrub species. It is shown that oak can regenerate in the presence of large herbivores through spatial association with blackthorn. The palatable species can resist herbivores through association with the defended thorny shrub (so-called associative resistance). However, rabbit presence suppresses this facilitation process, since rabbits do eat oak seedlings and juveniles, whether growing underneath blackthorn scrub or not. Also blackthorn ramets are consumed by rabbit. Through study of consecutive aerial photographs one was able to associate blackthorn encroachment with temporal low rabbit density. Although the author states that the results give some evidence for the shifting mosaic theory, one might equally conclude that the presence of other herbivores than aurochs (cattle) and tarpan (horse), not improba-

ble in historical and pre-historical time (although European rabbit was introduced in the Middle Ages only) is not favouring the same succession theory.

Maurice Hoffmann

Ghent University, Department Biology
Terrestrial Ecology Unit
Krijgslaan 281, S8
B-9000 Ghent, Belgium
e-mail: maurice.hoffmann@UGent.be

Het Walvisboek

Het Walvisboek. Walvissen en andere zeewezens beschreven door Adriaen Coenen in 1585. Redactie en inleiding Florike Egmond en Peter Mason, met commentaar door Kees Lankester 2003. Walburg Pers, Zutphen. viii-xvi, 208 pp. ISBN 90.5730.282.9.

Vier boeken heeft Adriaen Coenen(szoon) van Schilperoort gemaakt: het *'Grote Vis Boeck'* (in 1574 aan Willem van Oranje ten geschenke gegeven, en sindsdien spoorloos), het *'Visboeck'* (1577-1579; bevindt zich in de Koninklijke Bibliotheek te 's-Gravenhage), het *'Walvisboeck'* (1584-1585; in de bibliotheek van de Koninklijke Maatschappij voor Dierkunde in Antwerpen) en het *'Haringkoningboeck'* (in het Gemeentearchief van Keulen). Het betreft in alle gevallen manuscripten die tot nu toe nog nooit in druk zijn verschenen.

Adriaen Coenen werd in 1514 te Scheveningen geboren in een familie van vissers en is in zijn werkzame leven veilingmeester van de vismijn en groothandelaar in vis geweest. Vanuit zijn opvoeding en werk heeft hij een grote interesse gekregen in de mariene fauna en daar voor zichzelf veel aantekeningen en tekeningen van gemaakt. Dit materiaal vormde de basis van de genoemde manuscripten. Coenen stierf in 1587.

Bij Walburg Pers in Zutphen zijn nu de van tekst voorziene platen van het Walvisboeck gereproduceerd en van biologisch commentaar voorzien door de marien bioloog Kees Lankester. Het manuscript is van uitzonderlijk natuurhistorisch belang omdat er strandvondsten van marien gedierte en visvangsten met plaats en datum in worden beschreven. Coenen beschrijft gedetailleerd de allereerste marien-biologische waarnemingen van de Nederlandse kust. De originele tekeningen zijn een genoegen om te bekijken, de reproducties echter zijn van een fletse, nauwelijks acceptabele kwaliteit. Het boek bestaat uit twee delen. Het eerste deel omvat 58 bladen en het tweede 66 bladen. "Dat eerste boock" (1584) heeft als ondertitel: "*Van menich derleij walvisschen ende ander selseme groote wonderlijke visschen*". "Dat tweede boock" (1585) heeft als ondertitel "*Van veel vreemde zeemonsteren, veelderleij meereminnen, zeemans, zeebisschoppen, zeedraken, zeepaarden, zeeleeuwen, zeevossen, zeehasen, zeevarkens, zeeduvels, zeespinnen, zeenetelen, zeekarstangens, zeeridders, zeemonniken, zeekoijen, zeewolven, zeeapen, zeehonden, zeekaluen, zeekatten, zeemuijsen, zeeluijsen, zeekokommers ende noch meer andere vreemde onsiene en oneetbare vischen, cocodrillen, groote vremde schilpaddens"*.

Zoals uit deze titels blijkt, beschrijft Coenen fantasieschepsels, veelal overgenomen uit vertellingen en de toenmalige schaarse literatuur, maar daarnaast uit eigen waarneming ook gemakkelijk te herkennen bestaande soorten. Met name in het laatste ligt de grote kracht van het werk. De lezer kan zich in gedachten naar het 16de-eeuwse Nederlandse strand verplaatsen en zich een voorstelling van Coenen maken die aangespoelde walvisachtigen bekijkt, met zeepokken begroeide voorwerpen opraapt en bijzondere vissen in de manden van de Scheveningse vissers vindt. Hij beschreef en tekende zijn waarnemingen zeer nauwkeurig. Het manuscript zoals dat in Antwerpen aanwezig is telt 125 bladen, inclusief een uitvouwblad tussen de beide delen. In de nu verschenen uitgave zijn 23 bladen niet opgenomen, zonder dat de redacteuren in de tekst aangeven waarom dat zo is. In ieder geval zijn alle bladen uit het eerste deel gereproduceerd, en de 23 niet gereproduceerde bladen moeten dus in het tweede deel zitten. Een ander hinderlijk man-

co is dat niet de letterlijke tekst van Coenen is weergegeven, maar een selectieve vertaling.

Doordat de platen te weinig contrastrijk zijn afgedrukt is de oorspronkelijke handgeschreven tekst slecht te lezen. Dit had naar onze mening met de huidige druktechniek beter kunnen worden uitgevoerd. Zoogdierkundigen komen bij Coenen aan hun trekken door de weergave van enige goed gedocumenteerde strandingen en vangsten van walvisachtigen. De eerste plaat geeft de stranding van een butskop (*Hyperoodon ampullatus*) weer, die op 18 augustus 1584 was aangespoeld op het eiland Schouwen. Coenen kreeg een schets en beschrijving opgestuurd van Rembert Dodoens (1517-1585), lijfarts van de Habsburgse keizers Maximiliaan II en Rudolf II en hoogleraar botanie aan de Universiteit van Leiden. Vervolgens heeft Coenen een tuimelaar (*Tursiops truncatus*) afgebeeld, die hij 'Hil' noemt. Hij had rond 1534 een jong exemplaar gezien bij Berckheij, hetgeen door vissers was aangevoerd. Zonder enige twijfel is dit de oudst bekende melding van deze, nu in de Nederlandse zeewateren niet meer resident voorkomende dolfijnensoort. Dit soort meldingen maken het manuscript van Coenen tot een waardevol document voor hen die in de geschiedenis van voorkomen van walvisachtigen is geïnteresseerd. Lankester concludeert in zijn commentaar dat de tweede walvis die Coenen bij deze afbeelding beschrijft ook een tuimelaar moet zijn geweest, maar deze mening kunnen wij niet delen. Want Coenen beschrijft hoe hij, vijf of zes jaar na de stranding van dit dier, nog steeds op het strand van Rockanje een groot stuk van een grote vis zag liggen, zo groot dat hij erop kon staan, als op de zijde van een buisschip. Gezien deze grootte kan dit nooit een tuimelaar zijn geweest. Wat het dan wel geweest is zal waarschijnlijk nooit meer opgehelderd worden.

De afbeelding van de bruinvis (*Phocoena phocoena*; p. 7) is zeer herkenbaar. Coenen omschrijft hoe hij een zwanger vrouwtje opensneed en een voldragen jong aantrof. Een tekening van moeder en jong illustreert het voorval. Dat bruinvissen al in de 16de eeuw werden 'bijgevangen' door de visserij en algemeen voorkwamen wordt duidelijk uit Coenen's tekst. Belangrijk is de mededeling van Coenen bij zijn tekening van de gewone dolfijn (*Delphinus delphis*; p. 92). Hij schrijft daar dat de gewone dolfijn niet bekend was bij de Scheveninger vissers, in tegenstelling tot de bruinvis en de tuimelaar. Dit zou kunnen betekenen dat het voorkomen van de gewone dolfijn in onze contreien pas van meer recente datum is.

Coenen beschrijft vier potvisstrandingen: het exemplaar van 11 maart 1566, bij Zandvoort (p. 19), het exemplaar van 2 juli 1577, tussen Haaften en Saaftinge (p. 11), de drie exemplaren van 23 november 1577, bij het dorp Westerheij (Ter Heijde) (p. 9), en de drie exemplaren van juli 1577, in de Schelde (p. 43, 49). Daarnaast nog een stranding in Engeland in de oogstmaand van 1532 bij Tynemouth (p. 49). Coenen was goed op de hoogte van enige historische potvis-strandingen; hij noemt immers alle in de 16de eeuw bekende strandingen van deze indrukwekkende walvissen. Onder de naam 'Balena' beschrijft Coenen een grote walvissoort, waarvan niet geheel duidelijk is om welke soort het gaat. Het dier is met tanden in de bek getekend en heeft twee spuitgaten en buikgroeven (p. 13). Lankester determineert de walvis als Groenlandse walvis (*Balaena mysticetus*), maar het kan net zo goed een Noordkaper (*Eubalaena glacialis*) zijn geweest. Indien het een walvis betreft die in de Noordzee is gevangen of waargenomen, is het laatste zelfs veel aannemelijker. Als het inderdaad een Noordkaper betreft is ook dit een belangrijke historische waarneming.

De grote plaat op pagina 112-113 laat de gewone vinvis (*Balaenoptera physalus*) zien die op 8 mei 1547 bij Egmond op het strand kwam, compleet afgebeeld met een groep monniken. De stranding van een jonge griend (*Globicephala melaena*) op 28 juli 1581 bij Scheveningen heeft volgens de beschrijving van Coenen (p. 47) zelfs de prins van Oranje naar het strand gelokt. Coenen heeft de prins op het strand zijn *'Visboeck'* getoond en het zoontje van Coenen kreeg van de prins een goudstuk. Het *'Visboeck'* dat Coenen op het strand van Scheveningen aan de prins toonde is het exemplaar dat nu in de Koninklijke

Bibliotheek te 's-Gravenhage wordt bewaard. Op pagina 44 vertaalt Lankester *Macrocephalus* als 'langhoofdig', 'groothoofdig' lijkt ons een betere vertaling.

Daar Coenen zich, in tegenstelling tot wat de titel doet vermoeden, niet heeft beperkt tot het beschrijven van de zeezoogdieren, hebben wij gemeend ook wat nauwkeuriger naar de teksten en commentaren van Lankester met betrekking tot de overige diergroepen te moeten kijken. De waarde van het oorspronkelijke manuscript ligt ook in het feit dat het een Nederlands kustbiotoop uit de 16de eeuw beschrijft. In de redactionele commentaren bij de vissen en andere lagere zeedieren worden hinderlijk veel fouten gemaakt en bij een aantal platen ontbreekt het commentaar volledig. Wij geven een aantal van de meest opvallende weer. Op pagina 37 worden de door Coenen getekende haaien afgebeeld. Lankester determineert de grootste haai als doornhaai (*Squalus acanthias*). Wij twijfelen aan deze determinatie, het is volgens ons een zee-engel (*Squatina squatina).* Coenen schrijft dat het dier te Venetië nauwkeurig is afgebeeld. Op pagina 67 wordt de zee-engel opnieuw afgebeeld. Ook hier schrijft Coenen: "*Deze zee-engel heeft mij vanuit Venetië bereikt. Hij was door iemand daar geportretteerd*". Hoogstwaarschijnlijk betreft het hier dus één en dezelfde vis. Aan de andere kant lijkt het kleine exemplaar linksonder op pagina 37 daarentegen wel onmiskenbaar op een doornhaai, waarbij Coenen zeer gedetailleerd de dorsale stekel (doorn) in zijn schets opneemt.

Op pagina 63 wordt de gemarmerde sidderrog (*Torpedo marmorata*) fraai afgebeeld en op pagina 62 beschreven. Slordig is het dat Lankester hier het genus *Torpedo* verwart met de wetenschappelijke familienaam *Torpedinidae*. Ook de soortnaam *Torpedo marmora* is onjuist, dit dient *Torpedo marmorata* te zijn. Op pagina 102 determineert Lankester de op pagina 103 afgebeelde vis als snotolf (*Cyclopterus lumpus*). Dit is onjuist, het is een kogelvis (waarschijnlijk *Lagocephalus lagocephalus*); Coenen noemt hem immers ook *Orbis* (sic, want letterlijk: kogelvis), en omschrijft dat de vis vier tanden heeft en dikwijls opgezet in apotheken etc. wordt opgehangen.

Op pagina 106/107: het verhaal over de "haringkoning", tegenwoordig de riemvis (*Regalecus glesne*) genoemd, een diepzeevis van een meter of zeven, past volgens ons niet bij de vis die Coenen hier beschrijft. Gezien de nauwkeurigheid die Coenen toch wel aan de dag legde (zie op dezelfde pagina ook de afbeelding van de makreel (*Scomber scombrus*), met de duidelijke gezaagde staartvin en laterale streeptekening, kunnen we in zijn omschrijving (*"hij is heel rood als een zeehaan* (rode poon) *en heeft schubben"*) geen riemvis herkennen. De riemvis is zilverkleurig en heeft géén (zichtbare) schubben. De "Coninck van den harinck" die wordt afgebeeld lijkt verdacht veel op de mul (*Mullus surmuletus*). Op zo'n moment lijkt de cirkel weer (bijna) rond: de mul wordt ook heden ten dage nog wel "koning van de poon" genoemd.

Op pagina 137 wordt naast de mossel (*Mytilis edulis)* ook een andere tweekleppige afgebeeld, waar in de beschrijving aan wordt voorbijgegaan. Coenen noemt hem *Chama glycymeris*. Het grappige is dat het genus *Chama* alleen in warmere wateren voorkomt, maar dat de soortnaam verwijst naar een weekdier dat in onze streken leeft: *Glycymeris glycymeris*. De gedetailleerde tekening van Coenen leert ons dat we inderdaad te maken hebben met een schelp uit de orde der Taxodonta, schelpdieren met een fijn gegroefd slot. Deze soort heeft voor zover wij weten geen Nederlandse naam, maar wordt in Frankrijk in grote aantallen voor de consumptie gevist. Wellicht werden er ook in die tijd handelsbetrekkingen tussen Scheveningen en de Noord-Franse vissersplaatsen onderhouden en is Coenen op die wijze met de soort in aanraking gekomen.

Op pagina 166: een afbeelding van de poelomp. Lankester geeft hier informatie over *Architeutis dux*, een 18 meter lange pijlinktvis die zo nu en dan dood op het strand of in een net wordt aangetroffen. Er is echter nog nooit een *Architeutis dux* op de Nederlandse kust aangespoeld of in een net terecht gekomen. Wij denken dat de pijlinktvis die Coenen hier beschrijft eerder een *Ommastrepsus saggitatus* is geweest. Coenen

heeft het over drie voet lang, maar inclusief de uitsteeksels zeven voet. *Ommastrepsus saggitatus* kan een lengte bereiken van circa 1,5 m (vijf voet) en kwam en komt voor op onze kust.

Op pagina 170 vermeldt Lankester dat de afbeeldingen op de naastgelegen pagina betrekking hebben op de adelaarsrog (*Myliobatis aquila*). Het was zinvoller geweest als hij erbij had verteld dat de duizenden rogjes die Coenen in zijn jeugd had gedroogd betrekking hadden op de pijlstaartrog (*Dasyatis pastinaca*) die wél voor onze kust voorkomt. Zonder enige aarzeling stelt Lankester (p. 176) dat de 'kwal' rechts de rode haarkwal is. Coenen heeft het hier echter over zeeanemonen en niet over kwallen: *"...hij kleeft vast aan de rotsen in de zee en zit zo vast dat hij er alleen maar in stukken af te trekken valt", "sommige rood, andere groenachtig of blauwachtig"*. Het gaat hier dus hoogstwaarschijnlijk om de paardenanemoon (*Actinia equina*). De anemoon links van de afgebeelde paardenanemoon zou heel goed het wat fragielere slibanemoontje *Sagartia elegans* kunnen zijn. Op pagina 174 heeft Coenen het wél over kwallen (zee-netelen), maar hier blijft de verklarende omschrijving echter volledig achterwege. Het linker exemplaar op pagina 175 kan met zekerheid worden gedetermineerd als de oorkwal (*Aurelia aurita*).

En zo zijn er nog veel meer voorbeelden van fouten te geven, die met iets meer aandacht voor de tekst en tekeningen van Coenen gemakkelijk voorkomen hadden kunnen worden.

Sommige platen van vissen en ander marien gedierte zijn, zeker voor Coenen's tijd, prachtig gedetailleerd weergegeven. Neem bijvoorbeeld de mola, de zonnevis, de snot(d)olf, de sidderroggen of de koningsvis. Ook had Coenen al feilloos in de gaten hoe de eieren van de zeekat (*Sepia* spec.) er uit zagen (pp. 158/159).

Het originele manuscript van het Walvisboek is een waardevol 16de-eeuws document over de mariene fauna aan de Nederlandse kust en kan zich meten met de werken van Martinus Slabber (*Natuurkundige vertellingen*, 1778) en Job Baster (*Natuurkundige uitspanningen, behelzende eenige waarneemingen over sommige zee-planten en zee-insecten, benevens derzelver zaadhuisjes en eijernesten*, 1759-1765), die de Nederlandse invertebrate kustfauna in de 18de eeuw beschreven.

Concluderend is het 'Walvisboeck' van Coenen zowel voor geïnteresseerden in de Nederlandse cetacea, maar ook voor mariene veldwerkers en ichtyologen een waardevol boek. Het is jammer dat de platen in deze eerste gedrukte uitgave zwak zijn gereproduceerd en de letterlijke oud-Nederlandse tekst niet naast de platen is weergegeven. Ronduit storend en slordig ervaren wij de vele fouten en omissies in de determinaties. Jammer dat een uniek 16de-eeuws, klassiek wetenschappelijk manuscript op deze wijze wordt gedegradeerd tot een populair-wetenschappelijke facsimile. Misschien kunnen biologen en veldwerkers uit de 21ste eeuw toch nog iets leren van de nauwkeurigheid waarmee hun vakgenoten meer dan 400 jaar geleden te werk gingen.

Erwin J.O. Kompanje (conservator zoogdieren)
Frans J.A. Slieker (conservator Crustacea)
A. Frans de Jong (conservator vissen)

Natuurmuseum Rotterdam
Postbus 23452
3001 KL Rotterdam
e-mail: ejokompanje@ilse.nl

Kleine herbivoren verliezen de controle

Small herbivores losing control. Plant-herbivore interactions along a natural productivity gradient. D.P.J. Kuijper 2004. Proefschrift. Rijksuniversiteit Groningen, Groningen, Nederland. 143 pp.

De kwelder van Schiermonnikoog breidt zich geleidelijk naar het oosten uit en vertoont daardoor in die richting een fraaie gradiënt van oud naar jong. Met de ouderdom van de kwelder neemt ook de kleilaag toe en aangezien de klei

veel stikstof bevat is dit tevens een gradiënt van rijke naar arme grond. Een klassieke theorie in de ecologie voorspelt dat de invloed van herbivoren langs zo'n productiegradiënt het hoogst is in het overgangsdeel van rijk naar arm: op het rijke gedeelte zouden roofdieren de aantallen herbivoren reguleren en het arme gedeelte zou wegens een gebrek aan voedselplanten door herbivoren worden gemeden. Alleen in het overgangsdeel zouden herbivoren de planten in toom houden.

Eerder onderzoek aan het kweldersysteem heeft al duidelijk gemaakt dat deze theorie op Schiermonnikoog niet opgaat. De herbivoren mijden de rijke, oude kwelder niet omdat daar roofdieren voorkomen, maar omdat de planten daar minder eetbaar zijn. Op de rijke grond concurreren planten om licht en winnen hoge, slecht verteerbare planten de competitie. Alleen op de armere gronden komen goed verteerbare planten voor. Net als de klassieke theorie voorspelt deze nieuwe theorie de hoogste aantallen herbivoren in het overgangsgedeelte, maar nu door een effect van de bodemrijkdom op de plantenkwaliteit.

Het door NWO gefinancierde promotieonderzoek van Dries Kuijper richtte zich op de vraag hoe de wisselwerking tussen planten en herbivoren veranderde langs deze productiegradiënt en hoe die de vegetatie van de kwelder beïnvloedde. De herbivoren in kwestie zijn ganzen (grote aantallen brand- en rotganzen op hun trek naar de toendra), hazen (ruim 100 jaar geleden op Schiermonnikoog uitgezet) en koeien. De belangrijkste planten zijn rood zwenkgras als vertegenwoordiger van de arme kwelder en strandkweek als vertegenwoordigers van de rijke kwelder.

Vooraf was de verwachting dat strandkweek was aangepast aan groeien op rijke plekken en rood zwenkgras aan groeien op plekken met veel begrazing. Een kasproef leverde echter het onverwachte resultaat dat strandkweek doorgaans de concurrentie van rood zwenkgras won, ook als er begrazing werd gesimuleerd. Strandkweek kan zich dus prima invechten op arme gronden met begrazing. Dat de soort toch ontbreekt op dergelijke plekken komt wellicht doordat kiemplantjes er niet overleven. Deze vervolghypothese werd getoetst met een veldproef waarbij kiemplantjes werden geplant onder verschillende omstandigheden. In overeenstemming met de hypothese bleek herbivorie door ganzen en vooral hazen de overlevingskansen van deze kiemplantjes op de jonge kwelder sterk te reduceren.

Door herbivorie voor kortere of langere tijd middels kooien uit te sluiten kon worden aangetoond dat de grootste effecten optraden in de jonge, arme kwelder, waarbij het vooral hazen waren die de invasie van hoge planten in dit vroege stadium van kweldervorming voorkwamen. Hierdoor vertraagden de hazen de successie met zo'n 20 jaar. In overeenstemming hiermee worden de kwelders op de eilanden Rottumerplaat en Mellum, waar geen hazen voorkomen, in een veel jonger stadium al overheersd door hoge plantensoorten als strandkweek en zoutmelde. Door de geleidelijke toename van de bodemrijkdom kunnen hazen uiteindelijk niet voorkomen dat soorten als strandkweek de vegetatie op Schiermonnikoog gaan domineren. Grotere herbivoren kunnen met een lagere kwaliteit voedsel toe en zouden dit wellicht wel kunnen. Door gebieden mèt en zonder begrazing door koeien te vergelijken kon worden aangetoond dat koeien de begrazing door hazen faciliteren. De koeien reduceren de bedekking van hoge planten en bevorderen daarmee de begrazing door hazen (die de hoge planten mijden).

Deze studie toont derhalve duidelijk aan dat herbivoren een sleutelrol vervullen in dit kweldersysteem met een groot effect op de biodiversiteit. Een onverwacht resultaat is dat de grootste invloed van de herbivoren plaatsvindt op het jonge, arme gedeelte van de kwelder, ondanks het feit dat de hoogste aantallen herbivoren op het overgangsdeel van de kwelder voorkomen. Daarnaast faciliteren grotere herbivoren kleinere, waarbij ganzen profiteren van hazen en hazen profiteren van koeien.

Bart A. Nolet

Nederlands Instituut voor Ecologie (NIOO-KNAW)
Postbus 1299 - 3600 BG Maarssen
Nederland
b.nolet@nioo.knaw.nl