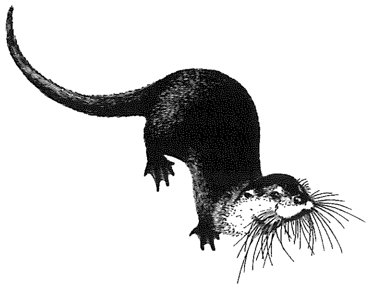

Lutra is back!

Not the journal you are holding, but the mammal that symbolizes our society. And not on its own, but by reintroduction. On July 8, 2002, seven otters from Belarus, Latvia, Czech Republic, and Sweden were released in wetland areas in the north of our country.

When our journal was named Lutra in 1960, the otter was already declining for several decades in most of its range. In 1988, the species was considered extinct in The Netherlands when the last otter was killed by a car.

What caused the extinction of a species that once inhabited waters all over the country? Persecution by man did much of the work, and had been a considerable pressure on the population for centuries. In the 20th century, decreasing habitat quality became a problem, mainly because of water pollution. Another recent threat was mortality from collisions with cars and loss of habitat, and as a result of this, habitat fragmentation. Since hunting has stopped and water quality has improved, most attention was given to the restoration of an area large enough to support a viable population.

Nowadays, reintroductions are not easily done. In general, the actual release of animals is preceded by a long and costly process of establishing the factors causing the species' decline, followed by creating the right conditions for a population that is viable. Monitoring of the released animals is essential to be able to evaluate the reintroduction. Reintroducing a species may very well work, or may not. For the brown bear in the Pyrenees it did not work so far. However, the reintroduction of yet another wetland species, the beaver, has been a great success story. In The Netherlands as well as in other parts of Europe. Let us hope the otter will follow the latter.

The vulnerability of the otter and many other mammals to habitat fragmentation is now widely recognized and receives much attention in recent mammal research. Many studies focus on the restoration of landscape linkages. Two articles in this issue deal with this field of interest. One presents an analysis of the spatial cohesion of habitat for the red deer in The Netherlands and neighbouring parts of Belgium and Germany. The last article deals with possible effects that the Iron Rhine railroad will have on badger population viability in the Meinweg National Park. Several scenarios for reactivating this historic railroad are compared, including bypasses outside the park borders.

This issue starts with a review of current knowledge on the extinct aurochs. Like the otter, these ancestors of the cow were intensely hunted for thousands of years, resulting in their extinction several centuries ago. Furthermore, you will find in this Lutra a short note on a find of partial albinism in a long-eared bat, overviews of recent literature on mammals, and two book reviews. Recently, the editorial board of Lutra has undergone some changes. We regret the resignation of our editor-in-chief Geert Groot Bruinderink. He joined us for a very short period only. However, we expect to introduce a new editor-in-chief soon. Marcel Huijser started a new position at the Western Transportation Institute of Montana State University and decided to resign from our board. We thank Marcel for being an excellent secretary over the past few years and wish him all the best in his new environment. For the time being, Liesbeth Bakker has taken over most of his tasks. Fortunately, we can also introduce a new editor, Jasja Dekker. This makes our editorial board viable again!

History, morphology and ecology of the Aurochs (*Bos taurus primigenius*[1])

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Abstract: In this article, the results of a research into the history, the morphology and the ecology of the extinct aurochs are briefly reviewed. Questions about the appearance of the natural Holocene landscape of Europe and the breeding-back experiments by the Heck brothers are addressed as well. After a millennia-long process of being hunted and ousted by man, the aurochs became extinct in Central Poland in 1627. Based on bone finds, pictures and descriptions it is possible to roughly outline the characteristics of the aurochs. It is evident that there is little morphological resemblance between aurochs and Heck cattle (results of the breeding-back experiments by the Heck brothers in Germany). From palynological and entomological data, descriptions by Roman writers, and from the last European wilderness (the 'Great Wilderness' in former East Prussia) it is likely that the natural landscape that covered most of Europe, consisted of extensive dense forests, intermingled with fens and bogs, lakes and rivers. Probably, the favourite living area of the aurochs in this landscape were sedge marshes along rivers. For aurochs August and September were the mating season and May and June the birthing season. The main predator of the aurochs in Europe was the wolf. Based both on the appearance of the former natural European landscape and recent research into the impact of large herbivores on forest growth, it is concluded that this impact is marginal. Only with the help of man large herbivores are able to create and maintain an open park-like landscape.

Key words: Bos taurus primigenius, history, morphology, ecology, Heck cattle, natural landscape, feeding impact.

Introduction

Since the extinction of the aurochs in the beginning of the 17th century, this animal has almost been mystified during the last century, especially by people who are interested in nature conservation. Notably its size and supposed impact on the forest structure were subject of discussion (Van der Lans & Poortinga 1986, Guintard 1999). In the 20th century, the interest of the general public in the aurochs at first has been evoked by the Heck brothers (Germany), who tried to 're-create' the aurochs in the 1920s and 1930s by crossing certain domestic cattle breeds and selecting in their offspring (Heck 1934a, Heck 1934b). In the 1970s, nature conservation agencies in Europe started to use domestic cattle, horses and sheep to maintain certain types of landscape in a cheap way. Added to this trend was the idea that in former times large indigenous herbivores have been able to create or maintain certain vegetations. Especially interactions with forest vegetations were emphasized (Vera 2000). These ideas, together with the introduction of Heck cattle (being the result of the Heck brothers' experiments), have triggered a lot

[1] According to the Code of the International Commission on Zoological Nomenclature (Wilson & Reeder 1993) here the species name *Bos taurus*, given by Linnaeus in 1758, is used, instead of the formerly usual name *Bos primigenius*, given by Bojanus in 18827; this is because of the rule of priority and the fact the Linnaeus, to all appearance, included the aurochs in his description. Since *Bos taurus* comprises both aurochs and all domestic cattle breeds, which originated from it, I purpose to use the denomination *primigenius* for the wild type in Europe.

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of discussion (e.g. Nederlands Bosbouw Tijdschrift 1998, 70, May/June; Symposium Palynologische Kring, 6-5-1998).

The aurochs was subject of research by both mammalogists and archaeozoologists. In the past 200 years numerous aurochs bones have been found and analysed. Many researchers tried to reconstruct both the aurochs morphology and its way of living (Nehring 1900, Von Leithner 1927, Lehmann 1949). Yet the results of these reconstructions were not always really satisfying. Moreover, data concerning the aurochs remained scattered and hidden in many articles, often in not easily accessible languages.

The policy of creating large-scale nature reserves in The Netherlands, in which undisturbed nature was to be restored, combined with the introduction of Heck cattle in 1983 in one of these areas, caused questions about the suitability of Heck cattle for this purpose. Would Heck cattle be the most suitable bovines to replace the original aurochs, both in its physical and feeding abilities; are we really close to primeval nature in this way? These questions lead to the start of a research into the extinct aurochs. Main goals of this research were to elucidate what the extinct aurochs looked like and how it lived. From these main questions several others originated, e.g. what did the natural European landscape look like, what was the influence of large herbivores (including aurochs) on the (forest) vegetation at the time and how to translate all this to present-day nature conservation? The breeding-back experiments of the Heck brothers were to be analysed and judged as well.

Material and methods

Research into an extinct animal species like the aurochs is not restricted to the bounds of biology, but extends into other fields of science. Within biology important aspects like the ecology of plants and mammals, mammal morphology, entomology and palynology, as well as archaeozoology, palaeontology and historical ecology are very useful for this type of research. In addition to these directly relevant fields of science, also philology is important, especially when studying original texts that describe the former European landscape and the aurochs when it still existed. These sources are written mainly in Latin, but also in mediaeval Germanic and Slav languages.

This study is mainly based on a literature search, both from historical sources and from present-day research. Special effort was put in finding the old original texts concerning physical appearance, ecology and the former management by man (in the Royal forests in Central Poland) of the aurochs and its landscape. The original meaning of old sources is frequently obscured by later incorrect translations (e.g. Gesner 1602, Kędzierska 1959).

Additionally, information was obtained during visits to Heck cattle breeders and herds of Heck cattle in the Netherlands, Belgium, Germany and Austria, and to breeders of Spanish fighting cattle in the Spanish province of Salamanca. Furthermore, data were gathered (such as length and width of long bones and horn cores) during visits to museums (Leiden, Münster, Warsaw) and research institutes in the Netherlands, Belgium, Germany and Poland. Also nature reserves were visited, to observe more or less wild cattle: the Oostvaardersplassen (The Netherlands), the Białowieża Forest (Poland) and the Basque country (in the western Pyrenees of France). In Poland, moreover, the former Forest of Jaktorów was visited: the area where the last aurochs lived.

Results

History

Research into the aurochs in Europe started in the second half of the 18th century. Zoologists were wondering more and more about the former presence of wild bovines here, encouraged by finds of animal bones and complete skeletons and the existence of old faunal descriptions. The memory of the aurochs, of which the last one had died in 1627, had become almost completely blurred by Linnaeus' time. Two schools of thought emerged, which lasted for about a century. One group thought that naturally, there had only been a single wild bovine species in Europe, the European bison (*Bison bonasus*), while the other group argued that there had been more species: the European bison and the aurochs (Wrześniowski 1878, Von Leithner 1927). Even two species of aurochs were thought to have existed: a larger one and a smaller one. Reliable data were scarce at the time and former oral tradition, gratuitous copying, ignorance and poor communication caused a lot of obscurity concerning the aurochs. Eventually, partly by means of the Inspection Reports from the former Forest of Jaktorów (Central Poland) (Kędzierska 1959), the former existence of the aurochs during the Holocene was definitively determined and generally accepted (Wrześniowski 1878). However, even today some people mix up aurochs and European bison because of ignorance of the former (Geerts et al. 1999). The supposed two species of aurochs turned out to be the bull and cow of one species. From that moment on research could be intensified and has yielded since then many data.

The area of origin of the aurochs was probably in India (Thenius 1980). The aurochs is estimated to have evolved there between 1.5 and 2 million years ago. In the course of the Pleistocene it spread to other parts of Asia, to northern Africa and to Europe (Von Koenigswald 1999). The earliest remains of the aurochs in Germany date from about 275,000 years ago (Lehmann 1949). During the Pleistocene cold and warm periods alternated. In Europe, the aurochs withdrew during cold periods to the Mediterranean area and expanded in warmer periods to the north (Von Koenigswald 1999). Obviously they were not as well adapted to cold and dry circumstances as were woolly mammoths (*Mammuthus primigenius*) and woolly rhinos (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*) and horses (*Equus spp.*).

Figure 1 gives the total distribution area of the aurochs for both the Pleistocene and the Holo-

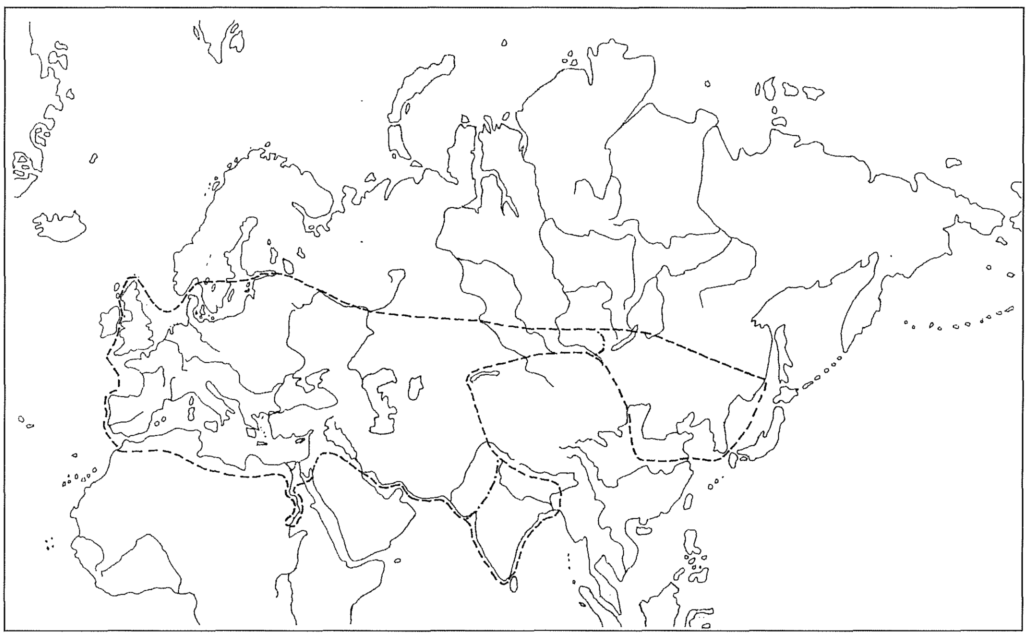

Figure 1. The former distribution area of the aurochs during Pleistocene and Holocene periods (after many authors and own interpretations): - - - - Utmost border during the Pleistocene. For Europe, North Africa and West Asia this border roughly holds for the Holocene too; ·—·—· Probable utmost east- and southeast border during the Holocene.

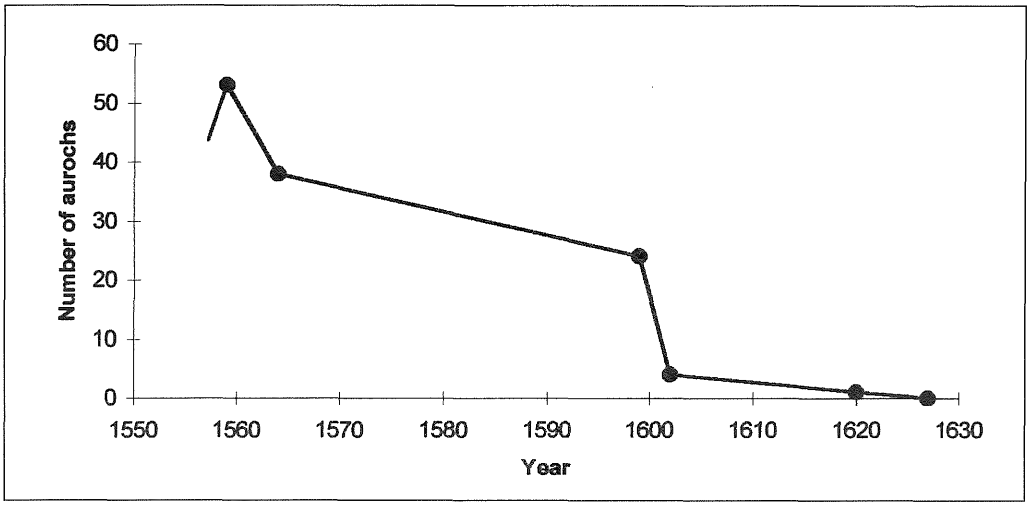

Figure 2. Changes in the number of aurochs in the forests at Jaktorów (Central Poland). After data from Schneeberger (in Gesner 1602) and Łukaszewicz (1952).

cene. In Europe it did not live in Ireland and northern Scandinavia. The most northerly bone remains were discovered at 60° N, at the southern border of Lake Ladoga (near St. Petersburg, Russia). The northern boundary, both in Europe and Asia, roughly coincided with the present boundary between the northern boreal forests and the more southern mixed coniferous/deciduous forests (Gromova 1931).

Extinction of the aurochs in Europe was likely due to both hunting and ousting by man. The more the human population grew, the stronger was the hunting pressure and the more cattle had to be pastured. The latter ousted the aurochs from their favourite feeding grounds (Heymanowski 1972). Extinction started in South- and West-Europe and proceeded to the northeast. The rarer the aurochs was, the more hunting it became the privilege of the nobility. In written records of such privileges the aurochs holds a special place among the various types of game (Wrześniowski 1878).

In the Netherlands aurochs have not later been recorded (by bone finds) than the 4th century A.D. (Lauwerier 1988). Eventually Poland was the last country where the aurochs lived, but its occurrence there was gradually restricted to an area southwest of Warsaw, where there were large forests and where an aurochs population could still survive due to protective measures (Heymanowski 1972). This was a forest area of roughly 25,000 ha, divided into several smaller forests. One of them was the Forest of Jaktorów, where the last aurochs lived. Since aurochs management was reported to the king on a regular basis, the situation at the time is well documented (Kędzierska 1959). Figure 2 offers a graphic representation of the changes in the last population of aurochs, during the last 70 years of their existence.

In spite of an initially well-organized management of guarding and hay-feeding in winter, the aurochs population slowly diminished. Finally the aurochs population perished in this area as well, through a combination of disinterest, corruption, cattle diseases, competition for food (with domestic cattle) and, to a lesser degree, hunting. The last aurochs, a cow, died in 1627 (Heymanowski 1972).

Morphology

From the extinct aurochs a large amount of separate bones, some 15 more or less complete skeletons (photo 1), some keratin horns and some hairs are left at the moment; no soft tissues like meat or skin. Moreover we possess quite a number of pictures and descriptions of it; pictures from the last ice age (e.g. Lascaux and Chauvet caves) and pictures and descriptions from the 16th century (e.g. Schneeberger's description in Gesner 1602, pp. 141-142). However, only a few turned out to be useful enough to approximately visualize the animal (e.g. Smith 1827).

One of the intriguing aspects of the Holocene aurochs is its size. Many authors did their utmost best to describe this size, especially the height at the withers. Based upon several methods of measuring bones, skeleton observation and sometimes a rich imagination, the reported withers height varied between 130-150 cm (the size of present-day cattle) and 200-220 cm (Guintard 1999). Since Matolcsi (1970) proposed to use conversion factors to determine the height at the withers from the length of certain limb bones, most often the metacarpus is being used for this purpose (Bergström & Van Wijngaarden-Bakker 1983), because of all aurochs bones this bone is mostly found. Evaluating the results of the measurements by Matolcsi and comparing them with bone measurements in mounted skeletons by Degerbøl & Fredskild (1970) a plausible shoulder height of 160-180 cm in the aurochs bull and ca. 150 cm in the cow result. For more details of these measurements, see Van Vuure (in press). Both aurochs bull and -cow were relatively long-legged, especially when compared to modern cattle. In the aurochs the height at the withers nearly equalled the length of the trunk (research by Duerst, cited by Matolcsi 1970).

Another conspicuous characteristic of the aurochs were its horn form and –size. We are well-informed about these, because many horn cores (often still attached to the skull) and some dozens of horn sheaths have been found (Nehring 1900, Von Leithner 1927). From these we can conclude that aurochs had a very typical and, within certain borders, stable horn form. By this specific horn form the aurochs can be distinguished well from other bovine species of the

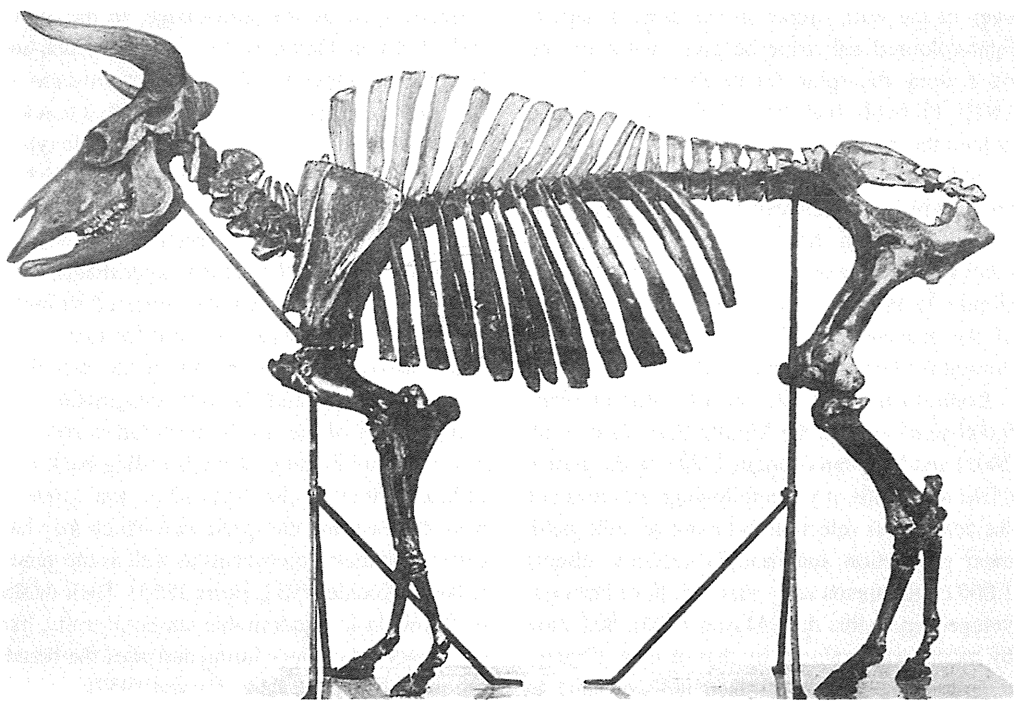

Photo 1. Left skeletons of aurochs are rare. This nearly complete skeleton of a Holocene aurochs bull was found in a peat bog at Hammerslöv (South Sweden) (after Von Leithner 1927).

Bovini tribe. The basic horn form is as follows. From the skull the horns grow outside, then curve forward (in an angle of ca. 60° with the forehead) and inward (toward each other). The tips of the horns sometimes curve upward (Von Leithner 1927). Aurochs horns were light-coloured and had dark-coloured tips.

In the aurochs a striking sexual dimorphism was present, as in many other bovine species (Schneeberger in Gesner 1602, Von Leithner 1927). The bull looked very different from the cow. The male had a larger body size (table 1) and longer and thicker horns (e.g. horn length in the male: up to 107 cm (Stone 1961), in the female: probably up to 70 cm). Also the fur colour in the male was entirely different from that of the female. From ice age cave paintings, 16th century-descriptions and data from modern research in many cattle breeds we can reconstruct this. Both sexes were born with a reddish-brown coat. Within half a year coat colour in the bull calf changed into a deep blackish-brown and that in the cow calf remained nearly unchanged. Moreover in the bull, unlike in the cow, a narrow light-coloured eel stripe became visible on the back along the spine (Schneeberger in Gesner 1602). Probably both had a light-coloured zone around the muzzle.

Udder sizes as we see in dairy cattle nowadays are a typical domestication trait. The aurochs cow had a small, hardly visible udder, like in other wild bovine species (Von Lengerken 1955) (figure 3). In table 1 the separate characteristics of the aurochs (and of Heck cattle, to be reviewed further on) are summarized.

Domestication of the aurochs started some 9,000 years ago, in the Middle East (Troy et al. 2001) and Pakistan (Badam 1984). In the course of the thousands of years following, as a result of the continuous selection in favour of milk yield, meat production and draught capacity, almost 1,000 cattle breeds and –varieties have been developed up to this day (Mason 1996). Selection by nature was replaced by that of man. Characteristics which were till then indispensable to survive in the wild and to live in the social structure of free-roaming bovine groups became useless. No selection for these traits was practised any more, so strongly deviating genetic changes were not removed but remained in existence. This is why modern cattle breeds show a tremendous variety of fur colours, horn sizes, horn shapes, body sizes and udder sizes. A general feature of domestic cattle is that sexual dimorphism has decreased strongly; in many characteristics (e.g. height at the withers, coat colour, horn length) bulls and cows resemble each other more and more (Bohlken 1964, Grigson 1978).

Nevertheless, in several cattle breeds and in some individuals features of the extinct aurochs can still be seen. Not only in old cattle breeds (e.g. Spanish fighting cattle, Steppe cattle), but also in modern thoroughbred breeds. For instance in Holstein-Friesians the original aurochs horn form (not its size) can be seen and in Jersey and Brown Swiss bulls the genes for the aurochs bull coat colour (including eel stripe) are still present (French et al. 1966). The wild curling hairs between the horns of a bull remind of those of the aurochs bull (Schneeberger in Gesner 1602).

Encouraged by this knowledge, in the 1920s and 1930s in Germany the brothers Lutz and Heinz Heck started breeding-back experiments to re-create the aurochs. Each of them tried to reach his goal with his own selected set of cattle types. According to their own statements (Heck 1934a, Heck 1934b) they 'succeeded' within an amazingly short period (12 respectively 11 years). However, when analysing the experiments, their method and results have to be criticized strongly. A lack of basic knowledge about the extinct aurochs, broad selection criteria in the breeding-back experiment and the rich imagination and complacency of the two brothers led to their excessive simplification of the breeding-back procedure. Criticism also focused on the carelessness, the ease and the speed with which they had carried out their experiments as well as the genetic basis (Koehler 1952, Herre 1953). Their denial of throw-backs (undesirable ancestral traits, like e.g. a piebald colour) during and after the breeding turned out to be false (Frevert 1957).

In table 1 the characteristics of the Heck cattle, being the result of the experiments, are shown in

Table 1. Physical characteristics of the aurochs as compared with those of Heck cattle.

Characteristic	Aurochs	Heck cattle
Withers height	♂: 170 cm on average ♀: 150 cm on average	♂: 142 cm on average ♀: 131 cm on average
Fur colour	Clear difference in colour between the sexes. ♂: A deep blackish brown to black. Along the back was a narrow light-coloured eel stripe. Light zone around the snout. ♀: Reddish brown, rarely black. Possibly a light zone around the snout. Calf: Reddish brown, rarely black.	The difference in colour between the sexes is often unclear. Bulls are generally darker than cows. ♂: From black pied via red, brown and grey to black. Colour saddles. Lighter as well as darker eel stripes. Ligth-coloured zone around the snout, sometimes also between the horns. ♀: From light brown via red, brown and grey to black. Light-coloured zone around the snout and sometimes also between the horns. Eel stripes sometimes occur. Calf: Usually reddish brown, otherwise varying from light brown to black.
Horns	Very characteristic and relatively stable as to shape and position. The horns curve forward and inward. Relatively long and thick.	The (slightly) curved horns point upward strongly. Often lyre-shaped. Very rarely as in the aurochs. Relatively short and thin.
Build	Since the shoulder height more or less equals the trunk length, the body is squarely built. Clear difference (relative to volume) between forehand and hindquarters.	Because of the relatively short legs, the body is longish (rectangular) in shape. Little difference (relative to volume) between the forehand and hindquarters.
Head	Relatively long and narrow.	Relatively short and broad.
Udder	Small. Hardly visible.	Very variable in size. Both small ones and large ones occur.

comparison to those of the aurochs. As can be seen, Heck cattle do not really resemble their original ancestor. Only in the fur colour there is some resemblance. Other traits like body size, body proportions and horn form do not match at all.

Way of living

To learn about the aurochs' way of living, we can obtain information from the Inspection Reports (Łukaszewicz 1952), the aurochs description by Schneeberger (in Gesner 1602) and modern research of still existing wild cattle (e.g. Schloeth 1961).

Nearly all data concerning aurochs ecology date from the second half of the 16th century (the last phase of their existence), from the forests at Jaktorów, which were their last living area. Already in the 13th century, the aurochs population in these forests, owned by the Polish kings, was managed by a well-organized game keeping service. Every day the hunters of this service had to look after and guard the aurochs. They protected them from poaching and other threats. The farmers of the village of Jaktorów had to make hay in summer, which was fed to the aurochs by the gamekeepers in winter. Fortunately, several eyewitness accounts of this population have been transmitted to us, so we can form a good notion of the situation in that period (Schneeberger in Gesner 1602, Kędzierska 1959, Heymanowski 1972).

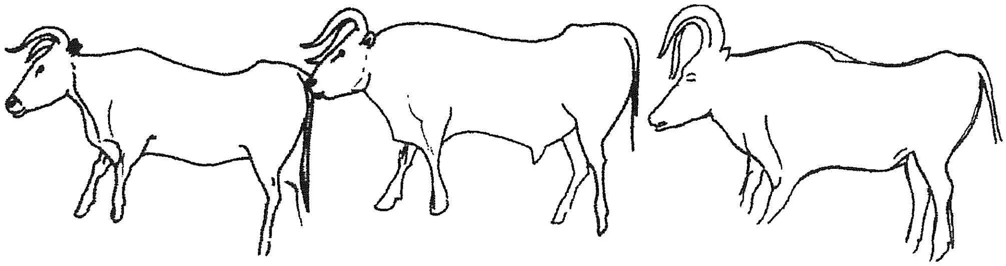

Figure 3. Drawing from the cave of La Mairie (Dordogne, France), ca. 15,000 years old. An aurochs bull with two –cows. In these cows it can be seen that the udders are small and not visible in this way.

When the animals were fed with hay in winter, they gathered in a large group. In summer there were both groups of cows with calves and young bulls and separate groups of older bulls and apart from them solitary bulls. Towards the mating season (August-September) the bulls, which previously lived apart from the cows, moved to the mixed groups to mate with the cows. During this period there was sometimes heavy fighting between bulls. Afterwards, they resumed their previous living. The next year, in May or June, the calves were born. Especially calves and elderly or diseased animals fell prey to predators (i.e. wolves (*Canis lupus*), according to Schneeberger). The healthy age classes in between did not suffer from predation. During the Holocene outside Europe lions (*Panthera leo*), tigers (*Panthera tigris*) and wolves were predators of the aurochs (Von Lengerken 1955); within Europe, where lions only lived in the Balkans, the wolf was the main predator. Without doubt, man was the reason for aurochs extinction, brought about by hunting and ousting. The latter has been shown in the Forest of Jaktorów, where aurochs had to compete for grass with cattle of local farmers (Łukaszewicz 1952).

Aurochs in the above-mentioned area were not afraid of humans and would not flee when people came near. Only when they were teased or hunted they got very hot-tempered and dangerous (Schneeberger in Gesner 1602). This specific behaviour is still lingering on in Polish and Russian phraseology. In Russia, a person who behaves rowdily when drunk was said to be 'behaving like an aurochs' (Pusch 1840). In Poland, there is an expression like 'a bloke like an aurochs' (said of a person who is big and strong; Skorupka 1968).

Habitat

To obtain information on the habitat of the aurochs, it is important to know what the natural landscape of West- and Central Europe looked like during the Holocene and what the diet of the aurochs was. By combining these data we can make an attempt to determine the former habitat of the aurochs.

There are several ways which make it possible to draw a likely picture of the natural landscape that covered Europe thousands of years ago. Since the beginning of the 20th century the most usual method for this has been palynology. In palynological research the most important item, as for the aurochs' habitat, was the partitioning of pollen into arboreal (AP) and non-arboreal pollen (NAP), not the portion of certain tree species in the forest. The partitioning into AP and NAP can elucidate the openness (or afforestation) of a landscape. The more open a forest is/was (that means more grasses), the higher the NAP will be. Research by Aaby (1994), Janssen (1974) and Zoller & Haas (1995) shows that a NAP-percentage of less than 20 indicates a closed forest. Pollen diagrams of early Holocene forests show a NAP percentage of 5-15 (Zoller & Haas 1995). Under natural conditions, grazing herbivores in large-scale grassy vegetations are not able to prevent grass pollen from occurring massively in pollen diagrams of those areas

(Kendall 1969, Hahne & Melles 1995), as put forward by Vera (2000).

Before palynological data became available, texts by Roman writers like Tacitus, Julius Caesar (58-52 B.C.) and Cassius Dio, describing the landscapes of Gaul (France and Belgium) and Germania (The Netherlands and Germany) were already known. Their accounts clearly sketch the difficulties the Romans faced during their warfare in the landscape, especially in Germania. In this region, beside villages and agricultural fields, the landscape must have consisted of extensive woods and marshes ('silvae et paludes', as the Romans regularly titled it; Caesar 58-52 B.C., Mela ca. 49 A.D.). The meaning of the word 'silva', used by the Romans in this context, must be translated as 'forest' in the sense we still use it (Caesar 58-52 B.C., Forcellini 1940). The difficulties for the Roman army to penetrate these forests and to perform military manoeuvres in them are well described by among others Caesar and Cassius Dio (ca. 200 A.D.). Partly due to these problems, eventually the Romans were forced to give up these regions.

To these data results can be added from research (in the last quarter of the previous century) on fossil insects. Since the presence of certain insect species indicates the presence of a certain plant or vegetation, it turned out to be possible to determine the then existing vegetation from fossil insects found in soil layers. This research has especially been practised in England (Dinnin & Sadler 1999) and to a lesser degree in the Netherlands (Brussaard 1985). From these studies it is very likely that before human settlement in the early Neolithic (ca. 3000 B.C.) the landscape of northwest Europe mainly consisted of extensive woods, judging from the insect fauna, which was completely dominated by species specifically tied to trees. Especially the species associated with dead trees, in various phases of decomposition, were prominently present (Dinnin & Sadler 1999). Apparently from ca. 3000 B.C. the landscape began to change, judging from the insect fauna in which dung beetles (associated to large grazing herbivores) appeared. Insect species that live on grass roots and that are typical for high grassy vegetations then appeared as well. Not until the Roman period a composition of insect species did appear, similar to the one we still know nowadays, and which is attached to a mosaic agricultural landscape of meadows, fields, hedges and woodlots (Dinnin & Sadler 1999).

Evidence which has never been used in this discussion before consists of data from the last Central European wilderness, the Great Wilderness in former East Prussia (northeast Poland). During the middle ages, a wilderness situation existed in this area for several centuries, nearly untouched by man (Mortensen & Mortensen 1938, Mager 1960). All original indigenous herbivores (including the aurochs) and predators were present at the time and human settlements and agricultural fields were absent. Descriptions of that area, by eyewitnesses, show the widespread presence of extensive forests and marshes. Just like the Romans in Germania, here army units also had great difficulties to penetrate the wilderness forests. A large number of route descriptions through this area have been handed down (Hirsch 1863); from these we can learn about the density of the forests and the problems people had in cutting and clearing paths through them. Medieval people did not like these wild woods and saw it as their task to order and cultivate this 'highly inhospitable' landscape. It was not before the 18th century that they succeeded in this (Mager 1960).

The quadruple evidence mentioned above strongly points to a landscape which, before man settled down for agriculture, originally was covered by extensive forests, interlarded with fens and bogs.

The kind of food the aurochs ate can be deduced from contemporary descriptions as well as from characteristics of their skull and teeth (Heymanowski 1972, Grigson 1978). From both sources the aurochs emerges as a grazer, feeding mainly on grasses and graminoids. Moreover, according to the description by Schneeberger (in Gesner 1602), in autumn acorns and in winter branches of bushes and trees were added to the menu. Present-day domestic cattle, running wild in nature reserves, greatly resemble their wild ancestor in their choice of food (Groot Bruinderink et al. 1997).

Knowing the appearance of the natural landscape and the aurochs' choice of food and adding some scarce references of the aurochs' way of living, we are now able to outline its habitat. Among others from bone finds and old descriptions, in one of which the aurochs is nicknamed 'morstapa' (i.e. 'moorstalker') (Rodrigues 1992), we may conclude that the aurochs had a special relation with marshes and marshy forests. In a predominantly forested landscape, where it had to compete with two other specialized grazers (European bison and wild horse), it must have been constantly in search of open areas. Such open areas for instance were the sedge marshes of the *Magnocaricion* type along small and large rivers (photo 2). Its choice of habitat probably resembled that of the still existing forest buffalo (*Syncerus caffer nanus*) in African rain forests (Hoppe-Dominik 1988) and the wood buffalo (*Bison bison athabascae*) in Central Canada (Carbyn et al. 1993).

Impact on the forest vegetation

Since the 1970s domestic cattle are used for management purposes in nature reserves in the Netherlands; at first used because of their cheapness, later because of their supposed large impact on the forest vegetation. During the 1980s a discussion started about this impact of large herbivores in Europe (Remmert 1985, Van de Veen 1985). Some have argued that naturally large herbivores (especially European bison) would be able to restrain and regulate forest growth, which would result in a park-like mosaic landscape of grasslands, woodlots, thorny bushes and solitary trees, in which large herds of herbivores roamed (Bunzel-Drüke et al. 1994, Vera 2000).

When we look at the results (Van Vuure, in press) reviewed in this article, it is likely that the natural European landscape has not been such a park-like landscape, but a landscape covered with extensive, dense forests intermingled with fens and bogs, lakes and rivers. This is a first indication that in fact former large herbivores (including aurochs) were apparently not able to oppose or control forest growth. Only beavers (*Castor fiber*), from which there is prehistoric evidence of their clearing and flooding activities (Garrison 1967), locally were and are able to change forest growth along rivers (Johnston & Naiman 1990).

A second indication comes from modern research on effects of large herbivores in nature reserves. In many nature reserves, these animals live or are being kept in divergent manners of management; from situations in which man has complete control of the area to strictly natural ones, in which man does not interfere at all. An example of the former is the New Forest area in South England. Here very high densities of large herbivores are kept (locally up to 3 animals per hectare). At first sight the area seems to remain park-like or treeless by feeding of herbivores. In fact this is being performed by the activities of man (Edlin 1969). Both by artificial maintenance of extremely high animal densities and by regular burning and mowing of vegetation by man the landscape remains open and park-like. Population densities of large herbivores in naturally forested areas (not influenced by man) are relatively low, compared to savanna or steppe regions (Jędrzejewska et al. 1997, Alverson et al. 1988, Sperber 2000). An example where nature can have its way is Wood Buffalo National Park in Central Canada. Here bison and deer species (*Alces alces, Rangifer spp., Odocoileus hemionus*), not influenced by man, are not able to restrain growth of willows (*Salix spp.*) and poplars (*Populus tremuloides*) (e.g. Schwarz & Wein 1997). The extensive sedge marshes (*Carex spp.*) and wet grasslands (mainly *Calamagrostis canadensis*), on which bison depend, are situated along rivers. The existence of these marshes is, like in Europe (Kulczyński 1949), being warranted and entirely governed by the water regime of rivers (Jaques 1990, Carbyn et al. 1993).

In Europe, the European bison is considered by some as a key species concerning control of forest growth and creation of a park-like landscape (Van de Veen 1985, Vera 2000). However,

Photo 2. Sedge marshes along the Narewka River in eastern Poland. In the background the forest of the national park of Białowieża. Such sedge marshes probably played a major role in the life of the aurochs.
Photograph: Cis van Vuure.

several studies in the Forest of Białowieża (East Poland) show that its role there is and was not so prevailing (Fruziński et al. 1975, Jędrzejewska et al. 1997). These bison (actually grazers) feed mainly on grasses and to a lesser degree on branches, tree leaves and -bark. In the present situation they do not really affect forest growth. If this situation would change into a natural one, with no supplementary feeding in winter and no clear cuts, population density of bison would decline as a result and accordingly their presently small impact on the forest.

Discussion

The results concerning the morphology have shown a rough picture of the physical appearance of the former aurochs. Unfortunately not all details could be unveiled; e.g. the exact nuance in coat colour on each part of the body is not yet known and more research is necessary to determine the exact shoulder height. Hopefully in the future still more characteristics will be discovered as a result of more aurochs finds and more advanced technologies (e.g. DNA research). Since we do not know sufficient details of the aurochs at the moment, it is impossible to recreate exactly its original appearance by breeding. However, breeding an aurochs-like bovine, according to the characteristics known by now, and more resembling than Heck cattle do, must certainly be possible; it will only take a long time. Important for this breeding program are the right starting material and suitable techniques. If (Heck) cattle in nature reserves will be left to natural selection, it will take a far longer time before an aurochs-like bovine will emerge. Nevertheless, in complete natural ecosystems this gradual change in physiology and physique will be an inevitable trend, because specific wild-bovine features like body size and -proportions, sexual dimorphism, horn form etc. are indispensable functional properties for survival in the long run, in the presence of predators, a certain microclimate and specific social structure.

The choice for a certain bovine type, for nature conservation, strongly depends on the target one aims at and the kind of nature which has to be maintained or created. As explained before in this article, for a natural ecosystem an aurochs-like bovine, well adapted to a natural situation, is desired; for nature management based on semi-natural landscapes regular cattle types are sufficiently suitable. This choice is also related to the question whether the natural landscape in Europe was an open park-like landscape or a densely forested one. From the results of the study reviewed in this article, it is likely that a policy intending the creation of an open park-like landscape by means of natural grazing and browsing is doomed to fail. However, a lively discussion is going on on the topic of the appearance of the natural European landscape during the Holocene. Some (e.g. Zoller & Haas 1995, Litt 2000, Sperber 2000) argue that large herbivores have only marginal impact on forest vegetations and therefore a landscape with extensive dense forests results. Others (e.g. Beutler 1997, Hofmann & Scheibe 1997, Vera 2000) claim that large herbivores are able to control forest growth and an open park-like landscape emerges. The only way to settle this dispute is to carry out a field experiment, on which both 'parties' should agree. In a large-scale fenced-off nature reserve inhabited by large herbivores (including European bison), without any interference by man, it must be possible to analyse the basic mutual interactions between herbivores and forest growth and draw definitive conclusions from it.

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Samenvatting

Historie, morfologie en ecologie van de oeros (*Bos taurus primigenius*)

In dit artikel worden in het kort de resultaten beschreven van een onderzoek (Van Vuure, in press) naar de historie, de morfologie en de ecologie van de in 1627 in Centraal-Polen uitgestorven oeros (*Bos taurus primigenius*). Er wordt beschreven hoe de oeros eruit zag, hoe hij leefde, hoe het natuurlijke Holocene landschap van Europa eruit zag, wat de invloed is/was van grote planteneters (o.a. de oeros) op de bosgroei en hoe het terugfokexperiment van de gebroeders Heck in zijn werk is gegaan en beoordeeld moet worden.

De uiterlijke kenmerken van de oeros zijn weergegeven in tabel 1; tevens zijn ze daar vergeleken met die van de huidige Heckrunderen, waarmee weinig overeenkomsten blijken te zijn. De oeros leefde in een overwegend bebost landschap, waarin hij waarschijnlijk vooral zeggemoerassen langs rivieren bezocht om te foerageren. Afgezien van de bever, hadden grote planteneters gedurende het Holoceen slechts marginaal invloed op de bosgroei.

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Perspectives for an ecological network for red deer (*Cervus elaphus*) in the Belgian-Dutch-German border area

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Abstract: In the densely populated Belgian-Dutch-German border region, the relicts of natural areas are highly fragmented. The remaining reserves form completely isolated 'islands', i.e. the habitat is surrounded by a 'sea' of intensively cultivated areas. Impoverishment of large ungulate species diversity must be counteracted by restoration of connectivity between these habitat patches and by re-population of its former range. Because of its former widespread distribution and range size, in this study the red deer (*Cervus elaphus*) is chosen as a key species in the design of large-scale ecological networks, which consist of large nature reserves, in this region. An ecological network analysis, assessing habitat connectivity, is carried out for an area covered by The Netherlands, Belgian Flanders and bordering parts of Germany, using the landscape-ecological model LARCH. The results are compared with the habitat suitability analysis of ecological core areas for red deer in the southern parts of The Netherlands. In this way chances for restoring ecological networks and re-establishment of viable populations of large ungulates are visualised. Despite fragmentation, it is shown that some areas have good potentials for the establishment of free roaming large ungulate populations. In particular: the areas of Maasduinen, Kempens Plateau and Vijlener Bos, areas that all extend across the Belgian and German borders. The method used proved to be effective in assessing functional ecological networks and defining measures for improvement of the spatial cohesion of suitable habitat for large ungulates. The results could very well serve EU nature conservation policies.

Key words: red deer, habitat network, habitat connectivity, viable population.

Introduction

Over the past ten years the evidence in support of larger spatial and organisational scales of conservation efforts is accumulating (Wallis De Vries 1995, Soulé & Terborgh 1999a). Large nature reserves have the ability to capture a mosaic landscape of different habitats, protect species with large habitat demands, minimise negative impacts of reserve borders and edge effects, and typically support large populations with lower extinction probabilities (Schwartz 1999). For many species chances of successful dispersal and colonisation decrease as the proportion of a given habitat declines (Andrén 1996, Vos et al. 2001a). In fragmented landscapes, ecological networks are of vital importance for survival of wildlife populations. An ecological network comprises physically separated habitat patches, each supporting a population of a particular species or set of species with similar requirements. Between these habitat patches individuals exchange by dispersal.

Mammals are particularly vulnerable to habitat fragmentation, since small populations in isolated reserves are susceptible to the effects of stochastic demographic, environmental and genetic processes that may result in high extinction rates (Shaffer 1981, Newmark 1987, Roelke et al. 1993, Backbier et al. 1998). To constitute an effective ecological network, robust corridors should connect the large reserves (Soulé & Terborgh 1999a, Broekmeyer & Steingröver 2001). Robust corridors serve to link small natural areas for mobile species, to facilitate colonisation of new habitat, and to allow for wildlife movements in case of unpredictable environmental changes like climate change (Broekmeyer 2002). For nature restoration in the Belgian-Dutch-German border area it is therefore important to create large nature reserves and to improve the spatial cohesion of habitat. The spatial cohesion is a relative measure that can visualise the weakest parts in the ecological network for a certain species or set of species.

Viable populations of large ungulate species like wild boar (*Sus scrofa*) and red deer, demand large, natural areas. This also forms a safer basis for conservation of other species groups, particularly species vulnerable for habitat fragmentation and species requiring mosaic landscapes e.g. birds, insects, amphibian and reptile species (den Boer 1990, Wallis De Vries 1995, Broekmeyer 2002). Therefore, it has been argued to use habitat requirements of ungulates as a key in the architecture of sustainable conservation networks and the design of large-scale nature reserves (Wallis De Vries 1995, Soulé & Terborgh 1999a, van Opstal 2000).

The Belgian-Dutch-German border area is densely populated and characterised by a dense infrastructure network. The remaining fragments of forests and natural lands are small and already more or less isolated. Spontaneous re-colonisation by dispersing red deer or wild boar is actively discouraged by the national governments because of the damage to crops and the risk of collisions with traffic. Except for a population of wild boar in the Dutch-German Maas-Swalm-Nette nature reserve, the roe deer (*Capreolus capreolus*) is the largest mammal in the area.

In this specific region we have reached the point that, without active intervention by conservation management (for example by introducing species after nature restoration), loss of mammalian species diversity will be irreversible. The existing reserves and the land in between these reserves are not large enough to sustain the full range of ecological processes needed for viable populations. Linkage of these areas into an ecological network that enables local populations to form a metapopulation, seems an obvious solution (Wallis De Vries 1995, Soulé & Terborgh 1999a). In this paper we analyse the potential habitat network for red deer in this Belgian-Dutch-German border region, and the spatial cohesion of the network. Furthermore, we assess the potential for re-establishment of populations of red deer.

Methods

The landscape-ecological model LARCH

The landscape-ecological model LARCH (Landscape ecological Analysis and Rules for the Configuration of Habitat), developed at the Alterra Green World Research Institute in The Netherlands, assesses the viability of metapopulations in a fragmented environment. LARCH is based on the assumption that the potential of a landscape for persistence of a metapopulation can be assessed on the basis of ecologically scaled landscape indices (Vos et al. 2001a). Landscape characteristics are ecologically scaled in relation to the spatial requirements of species. LARCH is designed as an expert system, and used for scenario analysis and policy evaluation. The model has been fully described elsewhere (Foppen et al. 1999, van der Sluis & Chardon 2001, Verboom et al. 2001, Groot Bruinderink et al., in press) and only major steps in the method will be dealt with here briefly.

We use following definitions (cf. Verboom et al. 2001): *Habitat network*: a set of habitat patches, positioned close enough to each other to have a reasonable level of inter-patch dispersal; *Key patch (KP)*: a patch with a carrying capacity large enough to sustain a key population; *Key population*: a population in a key patch, viable under the condition of at least one immigrant per generation; *Metapopulation*: a set of populations in a habitat network connected by inter-patch dispersal; *Minimum viable metapopulation (MVMP)*: metapopulation size or network carrying capacity corresponding to a probability of exactly 95% to survive 100 years; *Minimum vi-*

able population (MVP): a population with a probability of exactly 95% to survive 100 years under the assumption of zero immigration; *Patch carrying capacity (PCC)*: patch area x patch quality x average density in the patch type; *Viable population*: a population with a probability of at least 95% to survive 100 years.

Step 1: from a vegetation map to an energy availability map

The main input for LARCH is a vegetation map, in this analysis the CORINE land cover database (European Commission 1994), with a grid of cells of 250x250 m^2. Late winter forms the energetic bottleneck for red deer that lives on natural foods only. Therefore, for each grid cell standing crop (kg dry weight) of the main natural foods for red deer in February was calculated and converted into total available digestible organic matter DOM (kg dry weight). Based on available DOM the carrying capacity can be defined as the population that can be sustained by each habitat patch (Groot Bruinderink et al. 2000).

Step 2: from energy availability map to reproductive units map

One red deer reproductive unit (RU) is defined as three individuals: a reproductive stag and hind and the proportional part of the non-breeding population. Using DOM requirements for one red deer in late winter, each grid cell can be assigned the number of RUs that can be sustained by the available natural food. In this way the 'February-DOM map' is converted into a 'RU map'. For large vertebrates the standard number of RUs for a key patch (KP) is 20 (range 10 – 100) (Verboom et al. 2001).

Step 3: from reproductive units map to habitat network map

To calculate whether adjoining RU cells can be taken together and considered one population, LARCH uses criteria on dispersal capacity and barrier effect of roads based on empirical data, literature and expert judgement. Cells within home-range distance from each other (Carranza et al. 1991) fuse into a local population of a size that equals the sum of the RUs. The highways and primary roads on this chart are considered absolute barriers to day-to-day red deer movements, preventing cells from fusing into one local population. Data on highways and roads are derived from the Digital Chart of the World (ESRI 1993).

Local populations within dispersal distance of each other form together a network population or metapopulation (Schreiber et al. 1994), again of a size that equals the sum of the RUs of the local populations involved. Here, roads are not considered to be absolute barriers, since dispersing red deer might cross even major roads (Groot Bruinderink & Hazebroek 1996). The RU map is thus converted into a habitat network map, showing the spatial configuration of potential red deer habitat in the area. The habitat network map shows the ecological network of potential MVMPs and potential populations outside MVMPs, which are too small to form a viable population. This way also MVPs and key patches will be identified, i.e. important areas which form in potential the core areas for red deer populations.

Step 4: assessment of the spatial cohesion of the habitat

With LARCH the spatial cohesion of habitat was assessed, using habitat features, dispersal characteristics of red deer and data on the presence of barriers to the dispersal of red deer. LARCH uses a grid base, and therefore calculates the connectivity per grid cell. Based on the dominant land use type for each grid cell, a carrying capacity for red deer is calculated, expressed in the number of reproductive units RU_j. So, each grid cell is surrounded by other grid cells, each of which has an RU related to the potential contribution to the stream of immigrants reaching cell i. To determine which cells potentially contribute, it is necessary to know the dispersal range of red deer and the effect of the landscape on the dispersal distance. The number of migrants S_i reaching a patch of habitat at a distance of d_{ij} from other patches is estimated as:

$$S_i = \sum_{j=1}^{n} Y_j A_j^b B_{ij} \cdot e^{-\alpha \cdot d_{ij}} \qquad (j \neq 1) \text{ (Vos et al. 2001b)}$$

where:

Y_j equals 1 for occupied patches and 0 for unoccupied ones, and

A_j is the area of patch j, and

B_{ij} is an indicator of the presence of a barrier between i and j.

In this equation, α is a constant, setting the survival rate of migrants over the distance between the contributing patch j and the receiving patch i. We transformed the product of Y_j and A_j to an ecologically scaled measure, the carrying capacity of a grid cell j. We assumed on the basis of expert knowledge that highways reduced the contribution of a grid cell j to the connectivity of cell i by 10%, but we took no account of the variation in traffic frequency between the regions. Vos et al. (2001b) explained how to transfer empirical data on dispersal distance to an estimate of α. We used the same approach for the red deer. A conservative estimate for dispersal distances for red deer in Northwestern Europe is 50 km (Darling 1937, Carranza et al. 1991), this coincides with α values of 0.05, assuming a landscape with no barriers. As yet, we are unable to validate this assumption.

LARCH determines the connectivity SC_i of a habitat grid cell 'i' by weighting the carrying capacity of all grid cells within the potential dispersal distance according to the distance and barrier effect of intervening roads:

$$SC_i = \sum RU_j \cdot e^{-\alpha \cdot d_{ij}} . p_n$$

where:

d_{ij} is the distance between the contributing grid cell j and cell i, measured as the shortest distance between j and i, avoiding built-up areas;

RU_j is the maximum number of reproductive units in cell j (taking account of differences in carrying capacity between habitat types, and the effect of roads);

p_n is the coefficient of the 'permeability' (i.e. ease of crossing) of all roads that are crossed ($p_1 * p_2 * p_3$). If no roads are present, $p_n = 1$.

If no barriers are encountered, the Eucledian distance ('as the crow flies') is calculated. If a barrier is encountered (built-up area, road) the permeability of the barrier is accounted for in the algorithm by the parameter p, *or* the barrier is avoided by a detour. This detour will increase the distance (d_{ij}) in the algorithm. The choice is based on the least costs.

Results

In figure 1 we see the result of the habitat network analysis (step 3). All important habitat is shown. Based on the total area of a patch it was assessed whether the patch is large enough for a small population (red colour), or whether it may form a key population (yellow) or minimum viable population (green).

The results show that a potential minimum viable population can exist in large natural areas in the centre of The Netherlands (Hoge Veluwe (population 1) and Utrechtse Heuvelrug). In Belgium the large forested areas from the Ardennes (population 9) can in potential support a minimum viable population. The Belgian-Dutch-German border area shows a highly fragmented pattern. Many smaller habitat patches could constitute a minimum viable metapopulation, since the (green) habitat patches are all within the homerange of the red deer. However, in reality the presence of urban and sub-urban areas, as well as infrastructure results in a less favourable situation.

The large number of potential local populations illustrates that many of the smaller areas do not function at all as habitat, since they do not form a part of a larger network. They cannot fuse into MVPs, hampered as they are by infrastructure. As a result, the red deer ecological network shows a MVMP structure (Hanski et al. 1996, Hanski & Gilpin 1997, Soulé & Terborg 1999b, Verboom et al. 2001).

The spatial cohesion map (figure 2) shows that

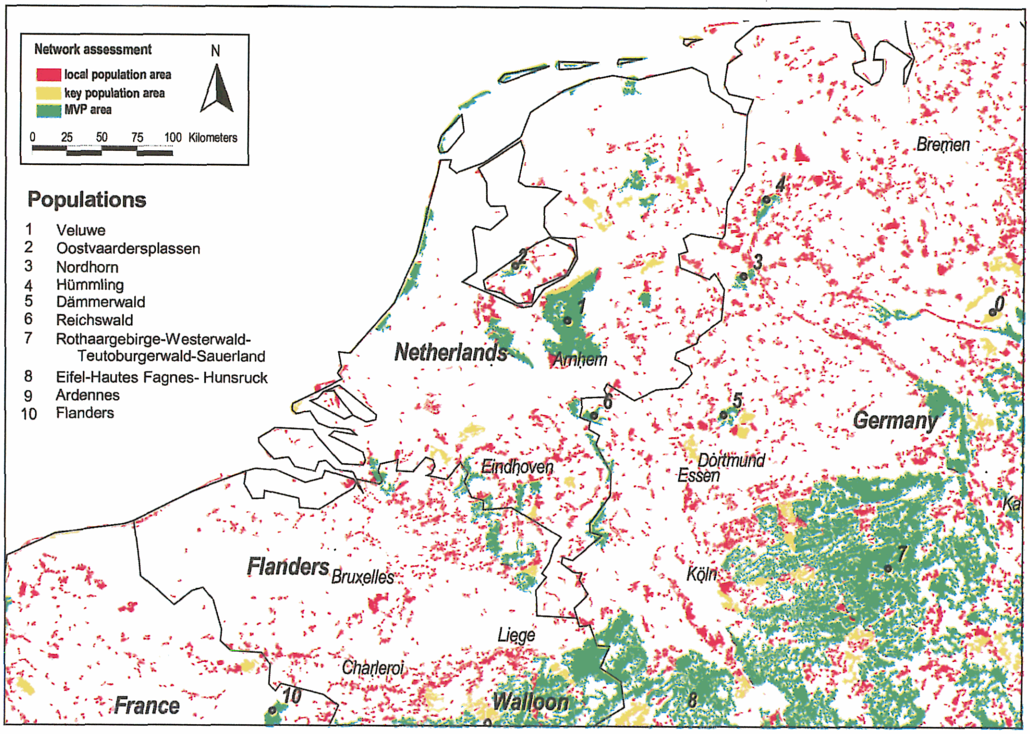

Figure 1. Network analysis for red deer in the Belgian-Dutch-German border area, as calculated by the landscape ecological model LARCH. Numbers refer to existing populations.

the area still harbours large areas of well connected potential red deer habitat. The Eiffel, Hautes Fagnes, and Hunsrück (population 8), the Ardennes (population 9), and Sauerland and Rothaargebirge (population 7) are obviously well connected core areas for red deer, which is illustrated by the intense red colour. They roughly coincide with the potential MVPs from figure 1. These areas are also well connected with large forest areas in central Europe.

Discussion

The analysis results show the potentially important areas for red deer. Areas presently populated with red deer (indicated as populations in the map) confirm the analysis results. The other MVP areas show potential for increase or expansion of red deer populations. This could result in larger, more stable populations where natural population dynamics can occur, which require fewer management interventions. The MVPs should in fact form the backbone for one widespread, cohesive red deer population. However, this is not the case, as some areas with potential to form a MVP do not form a part of this network at present. It will require active management to bring back red deer to the more isolated areas, since spatial cohesion with still inhabited areas, like the Veluwe in the central part of The Netherlands, is too small for natural colonisation by dispersal.

Areas that have potential as red deer habitat are Kempens Plateau and Maasduinen. The area of Kempens plateau is situated south of the city of Eindhoven, but most potential habitat is in fact situated in Belgium. Improving connections between MVP areas and key population areas by development of robust corridors can result here in sufficient habitat for viable red deer populations. Even with the planned robust corridors (LNV 2001), the area will not be connected to

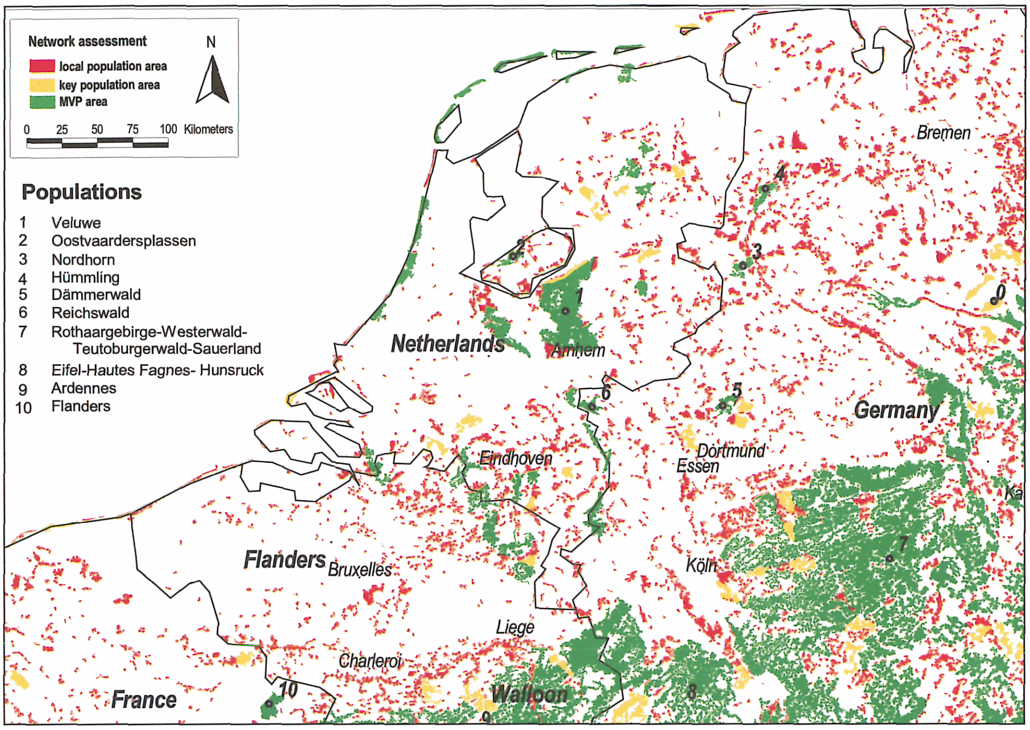

Figure 2. Spatial cohesion of red deer habitat in Northwest Europe, as calculated by the landscape ecological model LARCH. Barriers (roads) and urban areas are taken into account. Numbers refer to existing populations.

existing red deer populations and therefore it should be considered whether re-introduction would be desirable here.

The Maasduinen area is situated along the German-Dutch border south of the Reichswald (population 6). The area is not so well connected with existing core areas, e.g. the Veluwe, Rothaargebirge, and Sauerland (figure 2), but presence of a population will result in colonisation of the other areas if barriers can be overcome. As shown, all areas are trans-national, and realisation would therefore require cooperation of the governments involved.

These potentials for viable red deer populations are based on the network analysis, however, also the ecological qualities and potential risks should be taken into account. For six selected areas in Noord-Brabant and Limburg, Netherlands, the ecological value as well as the potential risks were analysed, e.g. requirements for agriculture (figure 3, Groot Bruinderink et al. 2000). This study confirms that the area Maasduinen and Kempens Plateau have important ecological qualities, based on available food and water, and thus offer chances for establishment of viable populations of large ungulates. Risks involved are smallest in these areas, due to low (human) population density (Groot Bruinderink et al. 2000). Also the potentials for red deer of the Vijlener bos, the border area of Belgium, Germany and The Netherlands, was assessed in this study. This area may have potential since it can be well connected with e.g. the Eifel-Hautes Fagnes area (population 8). For The Netherlands the Vijlener bos area may constitute an important connection with these populations abroad.

Conclusions

The analysis presented in this paper shows how ecological modelling, combined with expert knowledge and an analysis of regional land use, may result in an assessment of areas suitable for nature restoration. There is potential to develop

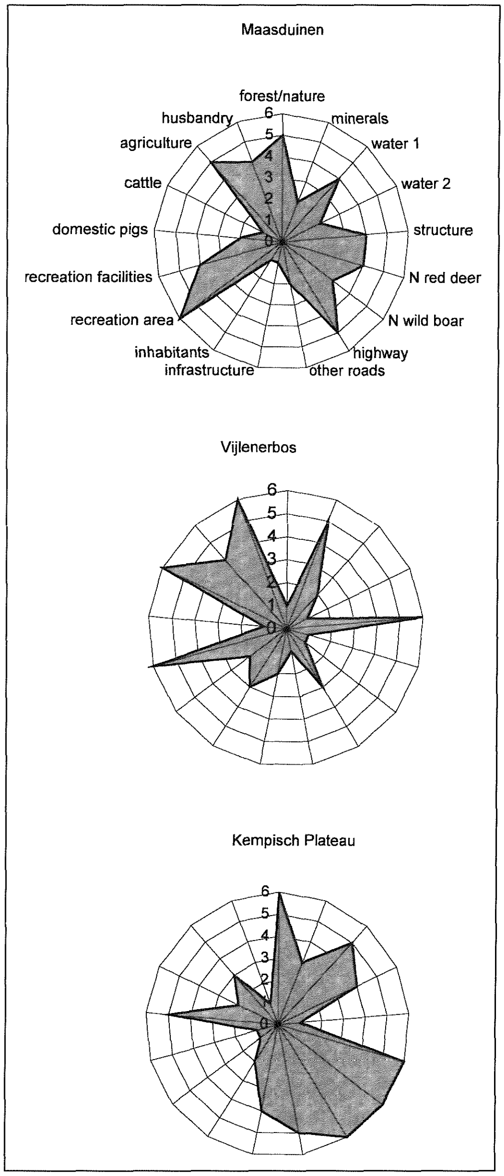

Figure 3. Habitat suitability analysis for red deer and wild boar in the southern provinces of The Netherlands, Noord-Brabant and Limburg (Groot Bruinderink et al. 2000). High ranking in 'ecological' (7) and 'risk' (10) factors means, in order, improving and decreasing quality.

new populations of red deer in the southern part of The Netherlands and bordering areas in Germany and Belgium. Of those areas assessed here, the Kempens Plateau and Maasduinen areas are most suitable to re-establish populations of large ungulates. However, no assessment has been done of the potential risks of establishment for areas in Germany and Belgium. Such an assessment is necessary for the establishment of important robust trans-border corridors.

The large scale assessment of the spatial cohesion shows the importance of a larger ecological network in which populations should be embedded. This can finally result in populations of red deer where more natural population dynamics can take place, with fewer management interventions. The results of this analysis also clearly show the need for international co-operation in creating new large mammal habitat in this region. This would be fully in accordance with the Bonn Convention (1979), which aimed at the conservation of wild animals that migrate beyond national boundaries, and with article 10 of the EU Habitat Directive, dedicated to the issue of connectivity. The results presented in this paper could be helpful in the implementation of EU policies on nature conservation, in particular for the realisation of the Pan-European Ecological Network PEEN (Action Theme 1 of the Pan-European Biological and Landscape Diversity Strategy PEBLDS, Foppen et al. 2000).

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Samenvattting

Mogelijkheden voor een ecologisch netwerk voor edelherten (*Cervus elaphus*) in het grensgebied van België, Nederland en Duitsland

In het dichtbevolkte grensgebied van België, Nedeland en Duitsland, is sprake van een sterke versnippering van de in deze regio nog aanwezige natuurgebieden. Veel van de natuurreservaten kunnen min of meer gezien worden als 'eilanden'; plekken met hoge natuurwaarden die volledig omgeven zijn door intensief gebruikte cultuurgronden met lage natuurwaarden. De afname van het aantal soorten grote hoefdieren in de regio dient te worden tegengegaan door het opnieuw onderling verbinden van de verschillende leefgebieden. In deze studie is het edelhert (*Cervus elaphus*) gekozen als sleutelsoort voor het ontwerp van een grootschalig ecologisch netwerk van natuurgebieden in deze regio. Hiertoe is een ecologische netwerkanalyse uitgevoerd met het landschapsecologisch model LARCH. Met behulp van deze analyse is de mate van connectiviteit tussen de verschillende habitatplekken gekwantificeerd. Deze analyse bestrijkt heel Nederland, Belgisch Vlaanderen en de van onderzoek naar de geschiktheid van ecologische kerngebieden voor edelherten in zuidelijk Nederland. Op deze manier zijn de kansen voor herstel van ecologische netwerken en levensvatbare populaties voor grote hoefdieren gevisualiseerd. Het onderzoek toont aan dat, ondanks habitatfragmentatie, er in sommige gebieden goede kansen zijn voor het herstel van vrijlevende populaties grote hoefdieren. In het bijzonder: het gebied Maasduinen, het Kempens Plateau en het Vijlener Bos. Al

Restoring ecological networks will create new chances for viable red deer populations in north-west Europe. *Photograph: Edgar van der Grift.*

deze gebieden zijn grensoverschrijdend. De gebruikte methodiek is effectief gebleken voor het bepalen van functionele ecologische netwerken en het bepalen van maatregelen voor de verbetering van de ruimtelijke samenhang van geschikte leefgebieden voor grote hoefdieren. De resultaten kunnen een rol spelen bij de ontwikkeling en uitvoering van het natuurbeschermingsbeleid van de EU.

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Will reactivation of the Iron Rhine railroad decrease survival of badgers (*Meles meles*) in Meinweg National Park, The Netherlands?

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Abstract: The impact of reactivating the historic railroad Iron Rhine on badger population viability in Meinweg National Park was investigated. Five scenarios for reactivation were compared: (1) temporarily reactivating the railroad, (2) permanently reactivating the railroad, without sound barriers, (3) permanently reactivating the railroad, with sound barriers, (4) a bypass north of the park, and (5) a bypass south of the park. Based on field data on distribution and occupation of badger setts, configurations of both (potential) badger habitat and badger (meta)populations were analysed. For each scenario the impacts of habitat loss, destruction of setts, mortality caused by train-badger collisions and barrier effect on badger population viability were quantified. Impacts on potential badger habitat were addressed qualitatively. Reactivation of the railroad Iron Rhine will have greatest impact on badgers within the park if the historic railroad is permanently reactivated and sound barriers are constructed. If no mitigation measures to facilitate the exchange of badgers are taken the badger population will be split in two groups, neither of which will be viable. Both a northern and southern bypass will not endanger the existence of badger groups that currently inhabit the park. Further, the decline in carrying capacity of both the key patch and habitat network as a result of either of these new railroad sections is small enough not to impact the viability of the badger population. Temporarily reactivating the Iron Rhine will have no severe impact on badger survival of the current population. The population viability can be increased by enhancing and improving areas which are potentially suitable for badgers within and around the park. However, habitat enhancement and the future badger population will be negatively affected by reactivation of the historic railroad (with or without sound barriers) and the construction of a southern bypass. Nevertheless, mitigation measures may reduce most of the described impacts of railroad reactivation in Meinweg National Park.

Key words: railroad, badger, *Meles meles*, habitat fragmentation, mortality, habitat loss, barrier effects, impact assessment, population viability.

Introduction

Meinweg National Park (MNP) is bisected by a former, one-track railroad, the so called 'Iron Rhine'. Until 1991 cargo was transported by this railroad between Antwerpen (Belgium) and the Ruhr area (Germany). Since then the railroad has been out of use. Recently pro's and con's of reactivating the railroad were investigated, initiated by a Belgian request to reopen the railroad for cargo transport (Ministerie Verkeer en Waterstaat 1999, Wieman et al. 2000, Ministerie Verkeer en Waterstaat 2001). For reactivation different scenarios are being investigated: reopening the historical railroad (temporary or permanently), building a bypass north of the national park, or building a bypass south of the national park.

MNP is part of a proposed European network of protected sites called "Natura 2000" (Osieck 1998a). To establish this network, both the European Bird Directive and the European Habitat Directive is used as an instrument to enforce protection of species and habitats within the countries of the European Union (Osieck 1998b). MNP is a designated Special Protection Area under the Bird Directive, while the status of a Special Area for Conservation under the Habitat Directive is applied for (Osieck 1998a). The two directives require the evaluation of plans that may affect the biological diversity or habitat sustainability of these protected areas. The reactivation of the Iron Rhine railroad in MNP is one such project (Wieman et al. 2000, Etienne et al., in prep.).

Apart from the presence of fourteen endangered plant and animal species, including the mouse-eared bat (*Myotis myotis*), five distinct habitat types motivated the application of MNP under the Habitat Directive. Wieman et al. (2000) selected seven mammal species that are a target or indicator species for one or more of these five habitat types (see table 1). Today only one of these mammals actually inhabits the area: the European badger (*Meles meles*).

Since badgers are sensitive to habitat fragmentation by transportation corridors, it may be expected that the badger population in MNP will be negatively affected by the reactivation of the railroad (van Apeldoorn & Kalkhoven 1991, Lankester et al. 1991, Clarke et al. 1998). Apart from habitat loss from the construction of a railroad, badger populations are expected to be affected by increased mortality caused by collisions with trains and the isolation of (sub)populations or badger groups because of the barrier effect of railroads (Bergers 1997). The aim of this study was to assess the impact of reactivating the Iron Rhine railroad on the badger population within MNP and to predict if this badger population would still be viable thereafter. In addition the impact of the proposed alternatives (northern and southern bypass) are evaluated and the future suitability of MNP for badgers after reactivation of the Iron Rhine railroad are discussed.

Methods

Study area

To study impacts of the railroad on the badger

Photo 1. Forest-heathland ecosystem in Meinweg National Park. *Photograph: Edgar van der Grift.*

population in MNP, it is necessary to analyse changes in spatial configuration of badger habitat and badger populations both within the park and outside this protected area. Therefore, the whole of central Limburg is defined as the study area; between the cities of Venlo in the north (approximately 6° 10' N, 51° 22' E) and Echt in the south (approximately 5° 53' N, 51° 6' E). The river Maas forms the western border of the study area, while the eastern border largely coincides with the Dutch-German border.

MNP (1600 ha) is located along the German border, east of Roermond (figure 1). Two streams that are part of the Roer tributary form the northern (Boschbeek) and southern (Roode Beek) border of the park. The park mainly consists of decidious, evergreen and mixed forests and heathland vegetation (photo 1). Moorland pools and ponds are found throughout the whole area.

The historic one-track Iron Rhine railroad intersects the park from west to east (figure 1; photo 2). Natural changes in elevation cause both height and width of railroad embankments to differ frequently. At some locations the railroad is constructed on a high embankment, while the railroad is constructed beneath the surface of the surrounding landscape at other locations. On average the width of the railroad (tracks, shoulders and verges) is 20-30 m. At locations where the railroad is elevated or is located in a cut the width can be up to about 45 m (van der Grift 1995).

Badgers in Meinweg National Park

MNP is mostly suboptimal habitat for badgers.

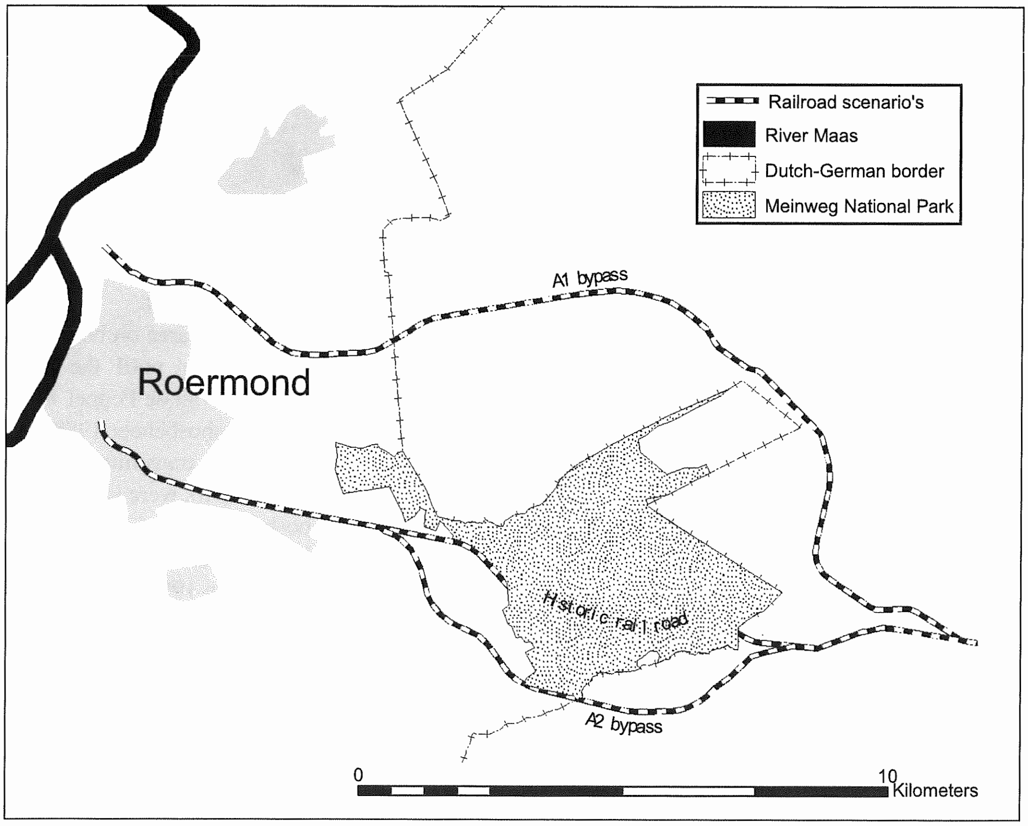


Figure 1. Location of Meinweg National Park, the historic railroad and the proposed northern (A1) and southern (A2) bypass.

Table 1. Mammals that are considered indicator species by Wieman et al. (2000) for the habitat types that motivated the application of Meinweg National Park (MNP) under the Habitat Directive (Annex I). To assess the indicator species the habitat types of the Habitat Directive were first related to the national Target Nature Types, based on Bal et al. 1995.

Protected habitat type in MNP	Dutch Target Nature Type	Indicator species	
		Common name	Scientific name
European dry heaths	dry heathland	badger mouse-eared bat Natterer's bat	*Meles meles* *Myotis myotis* *Myotis nattereri*
dry sand heaths with *Calluna* and *Genista*	open sand	–	–
Northern Atlantic wet heaths with *Erica tetralix*	wet heathland and bogs	otter European water shrew Natterer's bat	*Lutra lutra* *Neomys fodiens* *Myotis nattereri*
alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae)	lowland creeks and forest communities of spring and creeks	badger otter pine marten European water shrew mouse-eared bat Natterer's bat Geoffroy's bat	*Meles meles* *Lutra lutra* *Martes martes* *Neomys fodiens* *Myotis myotis* *Myotis nattereri* *Myotis emarginatus*
natural dystrophic lakes and ponds	heathland ponds	otter European water shrew Natterer's bat	*Lutra lutra* *Neomys fodiens* *Myotis nattereri*

Large areas are characterised by dry and poor sandy soils, covered with evergreen forest and heathland with few suitable food resources for badgers. Thus, badgers are expected to be most abundant along the periphery of the park, where forest-heathland ecosystems border small-scale agricultural areas with more suitable feeding grounds. Apart from providing some badger habitat, MNP is believed to form an important ecological corridor connecting badger populations in the Swalm Valley and Roer Valley, respectively north and south of the park (Wieman et al. 2000). Urban development between the cities of Roermond and Herkenbosch increasingly inhibits the dispersal of badgers between these two areas. Except for a narrow ecological corridor between Melickerheide and Breidberg, planned at the industrial area north of Herkenbosch, no ecological linkages are present west of MNP (Bureau Natuurbalans 2000).

Badgers used to inhabit the area on both sides of the Dutch-German border until the early 1960s (van Wijngaarden & van de Peppel 1964, Wiertz & Vink 1983, Staatsbosbeheer 1988). As part of the fight against fox transmitted rabies, the last badgers within the park were killed in the late 1960s (Staatsbosbeheer, unpublished data). In the 1970s and 1980s badgers were occasionally seen in the area (Lenders 1982, Staatsbosbeheer 1988). However, recolonisation of the area did not take place spontaneously. In 1990 the National Forest Service, owner and manager of the park, decided to reintroduce badgers. In November 1990 three badgers were released in a fenced area, that included a former sett in the north-eastern part of the park (Kombergen). After a period of adaptation the animals were set free (end of February 1991). Additional reintro-

Photo 2. Impression of railroad Iron Rhine in Meinweg National Park. *Photograph: Edgar van der Grift.*

ductions took place in 1991 and 1993: three badgers were set free in the west (Vogelkooi area) and four badgers were released at Steenheuvel (van Moll 1999).

Scenarios

For reactivating the Iron Rhine railroad five scenarios are suggested: (1) temporarily reactivating the historic railroad (5 years maximum; 15 trains per day), (2) permanently reactivating the historic railroad (43 trains per day), without the construction of sound barriers, (3) permanently reactivating the historic railroad, with the construction of sound barriers, (4) construction of a bypass north of the park (A1 bypass; see figure 1), and (5) construction of a bypass south of the park (A2 bypass; see figure 1). Table 2 gives the specifications for each scenario.

Mapping badger habitat

Based on field data of distribution and status of badger setts in both 1993 and 2000 (Ministerie Landbouw, Natuurbeheer en Visserij 1993, Taken Landschapsplanning 2000), actual and potential badger habitat was schematically mapped, both within MNP and outside the national park (see Study area). For this purpose around every used and non-used badger sett, defined as either a main sett, annexe/subsidiary sett or outlier (Neal & Cheeseman 1996), a hypothetical circular territory (800 m radius) of about 200 ha was projected. Although such schematic circular projections of badger territories are a simplification of reality, we believe it corresponds well with empirical knowledge on form and size of badger territories. And this is for three reasons: 1) Badger setts usually are in the centre of the territory of a social group, facilitating efficient use of their foraging areas around the sett (Neal & Cheeseman 1996). 2) Territorial borders between social groups are often located half-way two main setts. Studies in different parts of The Netherlands (i.e. the Veluwe area, Drenthe, the surroundings of Nijmegen and Staphorst) show that the distance between two main setts is about 1600 m in 50% of the cases (van Apeldoorn et al. 1997). 3) The badger habitat in the study area is similar to the badger habitat in the northern parts of the same province (Limburg). In both locations their habitat consists of a mix of arable land, grassland, small forest patches and linear landscape elements, in the transition zone of lowland river banks along the river Maas to elevated dry sandy soils along the German border. In northern Limburg the size of badger territories varies between 130 and 190 ha (Vereniging Das & Boom 1981): an additional argument to use 200 ha as the average size of a badger territory in this study (see also Vink & van Apeldoorn 1995).

Defining the metapopulation configuration

Based on the configuration of badger habitat, the spatial configuration of the badger population in central Limburg was analysed. Badgers are social animals, which live together in groups with well-defined territories. Clusters of neighbouring badger territories form habitat patches. Groups of habitat patches form a habitat network. Habitat patches are inhabited by a certain number of badger groups: the local population. The size of these local populations is related to size and quality of that specific habitat patch. The local populations within a habitat network form a metapopulation (see table 3 and figure 2).

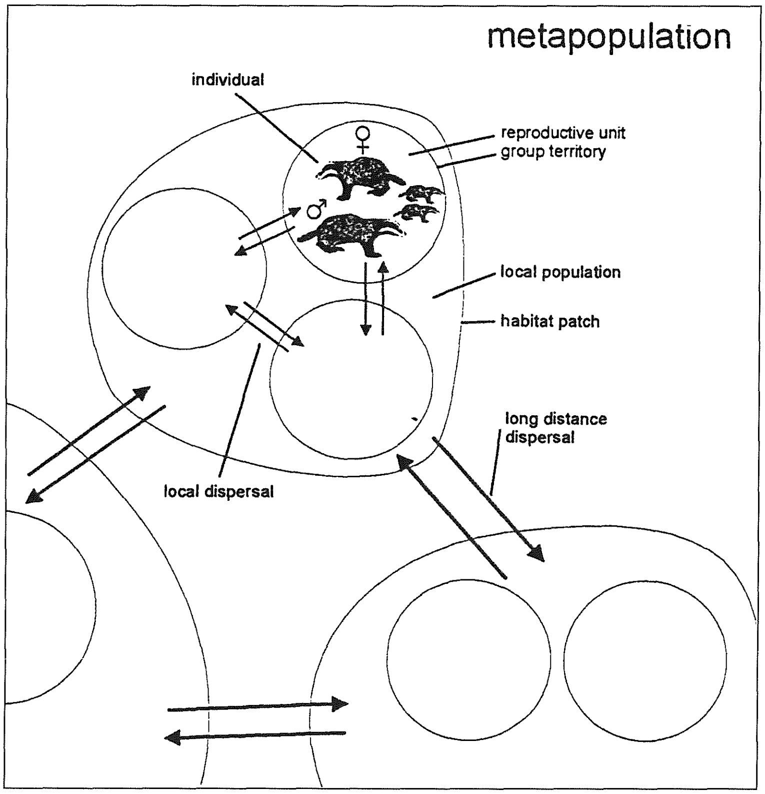
Badgers are mobile animals, able to cover considerable distances. In this study it was assumed that badgers within a local population will encounter each other frequently, e.g. for mating (Evans et al. 1989, Neal & Cheeseman 1996). Badger territories within a local population border each other or are within a distance that can be easily travelled during foraging movements. During a night badgers move on average about 1.5 km (if measured in a straight line) from their main sett searching for food (see review in Müskens & Broekhuizen 1993). In this study two local populations were distinguished when the distance between two (clusters of) badger territories exceeded 1000 m (table 3). This rule of thumb implies that the distance a badger has to cover from its main sett to the border of another local population is at least 1800 m: 800 m from the sett to the border of his territory and 1000 m from this border to the border of a neighbouring local population. This distance can be covered by badgers but on *average* they stay within these limits during feeding movements.

Occasionally, badgers leave their local population without returning. Little is known about the frequency of these dispersals and distances covered. A Dutch study on the movements of displaced badgers showed dispersal distances of 5.1 and 9.1 km as the crow flies (Broekhuizen et al. 1986). A female migrated almost 7 km to an occupied sett after her release at country-seat

Table 2. Characteristics of construction and use of railroad Iron Rhine by scenario; scenario 1: temporarily reactivating the historic railroad; scenario 2: permanently reactivating the historic railroad, without the construction of sound barriers; scenario 3: permanently reactivating the historic railroad, with the construction of sound barriers; scenario 4: construction of a bypass north of the park (A1); scenario 5: construction of a bypass south of the park (A2).

Railroad feature	Scenario				
	1	2	3	4	5
number of trains per day	15	43	43	43	43
train speed (km/hour)	40	80	80	80	80
sound barriers (height: 2 m)	no	no	yes	no	no
construction width (m)	–	–	–	40	40

Figure 2. The spatial structure of the badger metapopulation. Individuals live in social groups, or "reproductive units". Several groups make a local population. Several local populations make a metapopulation. Badger groups inhabit group territories. Several territories make a habitat patch. Several habitat patches make a habitat network (after: Verboom 1996).



Eerde, Friesland (The Netherlands) (Müskens & Broekhuizen 1993). The maximum recorded movement of male and female badgers in Gloucestershire (UK) was 8.3 and 7.8 km respectively (Cheeseman et al. 1988). Dispersals over greater distances do occur (10 to 30 km; Müskens & Broekhuizen 1993), but these are likely to be exceptional in The Netherlands, not least because of the many barriers (built-up areas, infrastructure). Therefore, in this study two habitat networks were distinguished if the distance between two (clusters of) habitat patches exceeded 10 km (table 3).

Assessing carrying capacity

The carrying capacity of a habitat patch is equal to the total number of badger groups that can potentially inhabit that habitat patch. The carrying capacity was expressed as the number of reproductive units (RU) (see figure 2). An RU is defined as a group of usually not more than 5-6 adult badgers and several young, with one dominant and reproductive female and male. The reproductive male of a group may also mate with females from other groups (Evans et al. 1989). To estimate carrying capacity of a habitat patch, each occupied main sett was usually equaled to 1 RU. Only if the distance between two occupied main setts is less than 400 m, i.e. half the distance between sett and hypothetical territory border, these setts would together contribute 1 RU to carrying capacity. Currently non-inhabited main setts and subsidiary setts also counted for 1 RU, if these setts were located outside the hypothetical badger territories around occupied main setts (radius = 800 m). Finally, it was assumed that one sett houses only one badger group (Kruuk 1989). The carrying capacity of connected badger habitat east (Germany) and west (west of river Maas) of the study area was estimated at 15 RU each.

Impact assessment

In order to asses the impact of railroad reactivation on the viability of badgers in MNP, the effects of (1) habitat loss, (2) mortality due to collisions, and (3) loss of connectivity between current and potential population networks were studied. Possible reduction of effects from mitigation or compensation measures was not included in the impact assessment. Neither were impacts of disturbance by passing trains. So far, little is known about how badgers respond to disturbance by trains, but incidental observations suggest low sensitivity of badgers to this kind of disturbance. Badgers seem to become quickly habituated to the noise of traffic (Neal & Cheeseman 1996). Badgers have been known to select railroad embankments for their sett on several occasions (NS Railinfrabeheer 1999). Badgers in a sett in the embankment of a frequently used railroad in England seemed to take no notice of the vibrations and noise whenever a train passed (Neal & Cheeseman 1996). However, sudden or unusual noises may cause a fear reaction or even the abandonment of the sett. This is particularly obvious around the time badgers emerge from their sett (Neal & Cheeseman 1996). Based on these observations, one may expect badgers to be mainly affected by disturbance during the construction of a railroad when unexpected noises will alarm the animals, especially when construction takes place close to badger setts. Once construction activities are completed further disturbance seems unlikely. So the impact of disturbance was not addressed in this study which focussed on the situation in which train traffic has been resumed.

Habitat loss

Habitat loss caused by railroad construction was quantified for both the A1 and A2 bypass. This was done by assessing the area (in ha) necessary for construction, using the length over which badger habitat will be dissected by the railroad and the average construction width (see table 2). In addition the number of occupied and unoccupied main setts was determined within this construction zone and a buffer zone of 50 m at either side of the new railroad. The 50 m-buffer zone was used to take into account the loss of setts due to the construction of roads, construction sites, and material or sand depots. Applying this buffer zone in detecting the loss of setts can be interpreted as a worst-case scenario as all setts within the construction and buffer zones are assumed to be abandoned by badgers. Both the amount of habitat and number of setts that might be lost due to railroad construction were used to determine loss of carrying capacity (in RU) of the dissected local population(s). The following rules were applied: (1) for every (part of) 200 ha (the size of an average badger territory) that is lost to railroad construction, carrying capacity decreases by 1 RU, and (2) for every occupied or unoccupied main sett that is destroyed or abandoned because of railroad construction, carrying capacity decreases by 1 RU.

Train-badger collisions

Badgers are susceptible to collisions with trains. Although no extensive monitoring studies of railroad-kills have been conducted in The Netherlands, incidental observations show that badgers are frequently hit by trains (e.g. van der Grift 1999; Vereniging Das & Boom, unpub-

Table 3. The spatial configuration of badger habitat and standards used in this study to distinguish the different levels.

Habitat	Description	Inhabited by	Standards
territory	home range	badger group	800 m around sett
habitat patch	group of territories	local population	distance between territories within habitat patch ≤ 1000 m
habitat network	group of habitat patches	network population	distance between habitat patches within a habitat network ≤10 km

lished data). This is especially true when the railroad separates different badger setts which are used by one social group, and dissects connecting paths between the setts. In England, badgers were frequently killed at more or less the same spot, which turned out to be a traditional crossing place (Neal & Cheeseman 1996). Except for the bisection of established territories, badgers may also be endangered when lured to the proximity of the railroad by attractants. Carcasses of train-killed animals form attractive food sources for badgers (Neal & Cheeseman 1996). Railroads are sometimes used as corridors to reach different parts of their habitat (Müri & Stammbach 1991). Railroad embankments may be attractive places for digging setts, especially when natural sett sites are lost to anthropogenic activities (Neal & Cheeseman 1996, NS Railinfrabeheer 1999). When, as a result of these attractions, more time is spent in the proximity of the railroad, the chances of being hit by trains will increase.

Compared to the number of badgers killed on roads, annual badger casualties on railroads seem small in number (Rijkswaterstaat 1997). However, much higher road densities within badger habitat obscure any comparison of absolute numbers. Also, badger casualties on railroads may be underestimated because, in contrast to roads, railroads and railroad premises are usually closed to the public. Therefore, badgers killed on railroads often remain undetected.

Badger mortality caused by collisions with trains was estimated for all scenarios. To do so, data of badger casualties in the period 1995-1999 on the railroad between Roermond and Reuver (km 48.0-58.0) were used (Vereniging Das & Boom, unpublished data). This is a one-track, non-electrified railroad that crosses the same network population of badgers in central Limburg and thus is similar to the Iron Rhine. Differences in frequency of railroad use were corrected for, assuming the number of casualties to be proportional to the number of passing trains. Badger densities around both the historic Iron Rhine railroad and proposed bypasses were assumed to be similar to densities of badgers around the railroad Roermond-Reuver. The estimated number of badger-kills within badger habitat per kilometre railroad per year was respectively 0.08 and 0.23 for temporary (15 trains per day) and permanent (43 trains per day) reactivation of the Iron Rhine railroad.

For each scenario the length of railroad sections within badger habitat was determined for each local population. Together with the estimated mortality figures for each kilometre railroad this results in an estimate of the number of badgers that may be killed by trains per local population per year. When sound barriers are constructed (scenario 3), mortality numbers were considered to be zero because in this scenario there is no access to the tracks.

Mortality of badgers from collisions with trains cannot easily be expressed in loss of carrying capacity (RUs). It was assumed that each railroad-kill resulted in the disappearance of one reproductive unit. This can be seen as a worst-case scenario, since not every killed badger will be an animal actively reproducing, and the loss of any reproducing badger will not always result in the loss of a reproductive unit. The loss of a dominant female may be overcome by other females becoming reproductive, while killed adult males may quickly be replaced by migrating males from neighbouring social groups. However, the loss of a reproducing female may cause the loss of her offspring as well, and if the same social group suffers losses in consecutive years, the reproduction potential of the group may be severely endangered for a longer period. Therefore it is considered sufficient justification to equate the loss of one animal to collisions with the loss of one reproductive unit.

Barrier effect

A railroad may inhibit movement of badgers within their territory, migration between social groups or dispersion to new territories or neighbouring population networks. Fences or sound barriers contribute significantly to the barrier effect of railroads. In this study the railroad was assumed to be an absolute barrier for badgers when

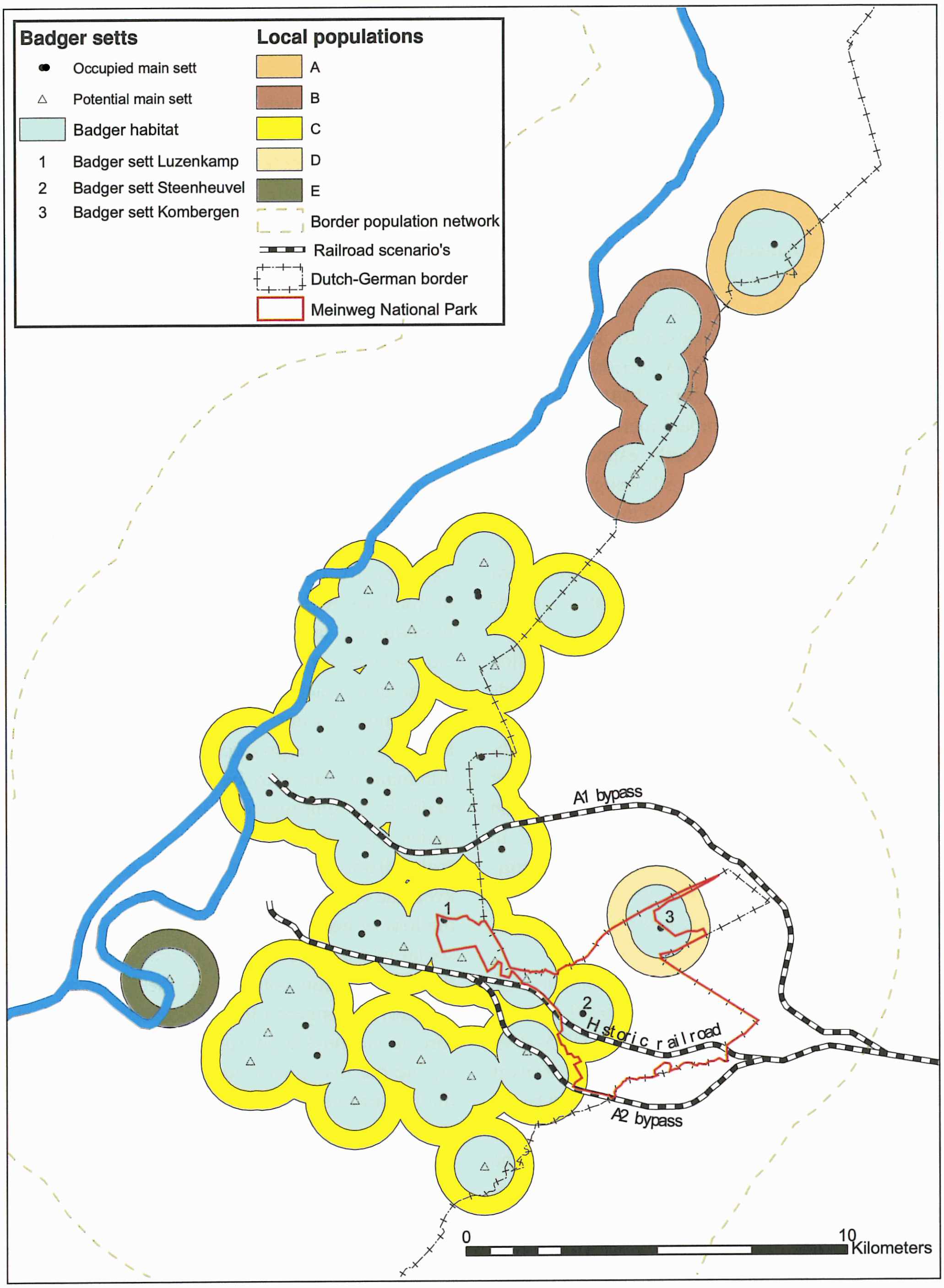


Figure 3. Distribution of occupied and potential main setts, badger habitat, and local populations within the network population of central Limburg.

sound barriers are constructed, hence the exchange of badgers between populations north and south of the railroad was expected to be absent. Also the use by badgers of over- or underpasses intended for human use was assumed to be absent. The presence of such a barrier coincided with the division of (meta)populations in the study area.

Population viability analysis

In this study the metapopulation was considered viable if the survival probability of the metapopulation is ≥ 95% likely to survive 100 years. This probability is highly influenced by the presence of a so called *key patch*: a relatively large habitat patch in a habitat network, inhabited by a local population, which is persistent under the condition of one immigrant per generation (Verboom et al. 2001). For long-lived, large vertebrates the standard for key patch size is considered 20 RU (Verboom et al. 2001). Minimum viable metapopulation (MVMP) size in configurations with and without a key patch was estimated at 80 and 120 RU respectively (Verboom et al. 2001). These standards were used to assess viability of badger (meta)populations in the study area for the present situation and the different scenarios for railroad reactivation. Note that in a metapopulation a large proportion of the habitat may be uninhabited; a carrying capacity of 80 or 120 RU corresponds to a much lower number of badger groups that actually inhabit the area.

Future habitat suitability

In addition to the analysis of the impact of railroad reactivation on survival probability of badgers in the present situation, the impact of reactivation on future potential of the area for badgers was determined. To do so management- and nature development plans (Staatsbosbeheer 1988, Staatsbosbeheer, in prep.) for MNP and surrounding areas were analysed, and all proposed measures that may influence future suitability of the area (carrying capacity) for badgers listed. In other words: where will suitable badger habitat disappear and where will such habitat be developed? Based on the above described population viability analysis (for both the present situation and the scenarios), the impact of reactivating the railroad on future habitat potentials were qualitatively evaluated for each scenario.

Results

Present situation

In MNP eight badger setts are present, of which three are presently occupied as main setts (T. Lenders, personal communication). Two of these occupied setts are located near the boundary of the national park, far in the northwest (Luzenkamp) and close to the former Beatrix State mine in the northeast (Kombergen) (see figure 3). Both setts are located on the edge of forest and adjacent agricultural areas. The third occupied

Table 4. Carrying capacity of the badger metapopulation in central Limburg. Estimates between brackets.

Local population	Number of present main setts	Number of potential main setts	Carrying capacity (RU)
A	1	0	1
B	3	2	5
C	29	21	50
D	1	0	1
E	0	1	1
Germany	–	(15)	15
West of river Maas	–	(15)	15
Total	34	54	88

Photo 3. Badger tunnels may be effective measures to restore habitat connectivity.
Photograph: Edgar van der Grift.

main sett is located in a more forested part of the park (Steenheuvel), but close to the central heathlands and a number of small meadows. These three occupied main setts had a distance to the historic railroad of respectively 1.2, 3.0 and 0.5 kilometre.

Badgers in Luzenkamp and Steenheuvel belong to the same local population that extends from the Roer valley below Herkenbosch in the south to the outskirts of Reuver in the north (local population C; figure 3). This local population is the largest in central Limburg, and expected to function as a key population within the network population. Carrying capacity of the key patch is estimated at 50 RU. About 40% of this carrying capacity is formed by badger territories which are (temporarily) unoccupied, indicating that badger densities can increase in the area. The badgers at Kombergen form a more or less isolated group and this group is not expected to be part of the key population to the west. It is more likely that the Kombergen group is connected with badger clans in Germany, but no data is available. The size of this local population (at carrying capacity) is estimated at 1 RU (local population D; figure 3).

The two local populations mentioned are part of the same network population, that extends from the Roer valley in the south to the town of Venlo in the north (figure 3). The city of Venlo and the road network that surrounds it form serious barriers to the exchange of badgers between populations north and south of this built-up area (Hoogeveen 1989). That is why, despite the relatively small distance between badger populations north and south of Venlo, these populations are assumed to be part of different population networks.

Carrying capacity of the central Limburg network is about 88 RU, including carrying capacity estimates for connected habitat patches east and west of the study area (table 4). The population is assumed to be viable, because its size matches the standards for a minimum viable metapopulation in configurations with a key population.

Future habitat suitability

In the near future several management and nature development initiatives in and around MNP will affect suitability of the area for badgers. Positive impacts are expected of: (1) the transformation of forest into heathland with a year-round grazing regime, increasing the diversity in vegetation composition and structure in the central areas of the national park; (2) restoration of wet heathland, wet grasslands and fens, both in the central and western parts of the park; (3) development of more natural woodlands with an increased percentage of deciduous forest; (4) development of heathland and grassland vegetation around the historic railroad; (5) restoration of species-rich grasslands, meandering streams and linear landscape elements within the small-scale agricultural area around the Venbeek, immediately south of the historic railroad. Nature development plans for the Wolfsplateau in the northeastern parts of the park that include the transformation of grasslands and arable lands into forest and heathland, a shift to less intensive use of the small meadows in the central parts of the park, and a possible increase in recreational use of the area, may result in a decline in both quality and quantity of badger habitat.

These developments are likely to result to some extent in additional badger habitat in the central and western parts of MNP, while the northeastern areas will probably become less attractive for badgers. This may lead to the disappearance of the Kombergen badger group (local population D; figure 3), while the number of badger groups in the key population (local population C; figure 3) may slightly increase. Changes in the small-scale agricultural area around Venbeek are of importance for better connectivity between badger habitat north and south of the built-up area Roermond-Herkenbosch. Increased connectivity will facilitate movements of individual badgers between clans, which will likely strengthen the internal structure of the key population within the central Limburg badger population, and consequently increase network population viability.

Reactivating Iron Rhine

Historic railroad

When the historic railroad is temporarily reactivated (scenario 1) no habitat loss will occur (table 5) nor loss of connectivity between badger habitat north and south of the railroad. In this scenario approximately 0.7 badgers will be killed by trains per year on the tracks between Roermond and the German border (total length railroad 9.1 km; table 6). The risks of getting killed is especially high for badgers with territories bisected by the railroad. Within MNP this is the case for the Steenheuvel badger group. The relatively small distance between main sett and railroad results in the bisection of the territory over a length of about 1.5 km. This implies that on average every eight years one badger of the Steenheuvel badger group will be killed by a train (since annual mortality is 1.5 * 0.08 = 0.12; see table 6). The decline of carrying capacity (<1 RU) affects only one local population: the key population. Both the key population and the network population are still considered viable.

Habitat loss and reduced connectivity of habitat north and south of the railroad due to physical barriers will not occur if the railroad is permanently reactivated *without* the construction of sound barriers (scenario 2; table 5). However, like the scenario with temporary reactivation of the railroad, this scenario will result in increased mortality of badgers from collisions. On average about 2 badgers within the key population will be killed on the tracks between Roermond and the German border each year (table 6). Thus the carrying capacity of the key population will decrease by about 2 RU. This decline is too small to affect sustainability of both the key population and network population significantly. Again, within MNP the badger group at Steenheuvel will suffer most from increased mortality. On average every three years one badger of the Steenheuvel badger group will die on the tracks

Table 5. Loss of habitat and badger setts due to the construction of new tracks per scenario.

Scenario	Length of new tracks within badger habitat (km)[#]	Habitat loss (ha)*	Number of lost actual/potential setts[$]	Loss in carrying capacity (RU)
1	0	0	0	–
2	0	0	0	–
3	0	0	0	–
4	8.2	33	2/0	ca. 2-3
5	4.5	18	0/1	ca. 1-2

[#] including the areas outside badger territories but within the borders of local populations
* within the 40 m railroad construction zone
[$] within the 40 m railroad construction zone and a buffer zone of 50 m on either side of this construction zone

(annual mortality is 1.5 * 0.23 = 0.35; see table 6).

Neither habitat loss or mortality from collisions occur if the historic railroad is permanently reactivated and sound barriers are constructed on both sides of the tracks (scenario 3). The sound barriers keep badgers from getting on the tracks. However, the screens form absolute barriers prohibiting badgers from crossing the railroad. As a result badger groups south of the railroad will be isolated. Consequently, local population E and the southern part of local population C, the key population, would form a second network population (see figure 3). Carrying capacity of this second habitat network will be 14 RU, not including (potential) badger groups in Germany or west of river Maas. The number of RU within this habitat network is much less than the minimum requirement for a viable metapopulation size and consequently the population will be threatened with complete extinction.

In scenario 3, the habitat network north of the railroad (local population A, B, C (northern part) and D) will have a carrying capacity of 74 RU, including the estimations for badger groups in both Germany and west of the river Maas. Carrying capacity of the remaining parts of the key patch north of the railroad decreases from 50 to 37 RU, and thus is still large enough to house a key population. However, the standard for minimum viable metapopulation size in configurations with a key population is not met. Consequently, sustainability of the habitat network changes from sustainable to non-sustainable.

On a local scale, within MNP the existence of the Steenheuvel badger group is threatened by railroad reactivation in scenario 3. The railroad intersects the territory of this group, which makes about one-fifth of their territory inaccessible.

Reactivating the historic railroad will impact future habitat potential for badgers in and around MNP. In case of temporary reactivation of the historic railroad (scenario 1) or permanent reactivation of the historic railroad without the construction of sound barriers (scenario 2), colonisation of newly developed and restored badger habitat at a short distance of the historic railroad may be frustrated by increased risks of being killed on the tracks. Construction of permanent sound barriers (scenario 3) that prevent badger migration across the rail track will completely negate any positive impact on the local badger population that improvements to the Venbeek area habitat may have.

Northern bypass

The construction of a bypass north of MNP (A1 bypass) results in the loss of about 33 ha of badger habitat (table 5). Also two presently occupied badger setts will be lost because they are located within the construction site or buffer zones. Loss of both habitat and setts all occur outside MNP but within the key patch of the central Limburg habitat network. Approximately 1.9 badgers will be killed by trains per year in this scenario (table 6). All expected mortality attributed to collisions takes place within the key population. No sound barriers are projected in this scenario, so no loss of connectivety is expected.

Table 6. Badger mortality and loss of carrying capacity from train-badger collisions per scenario.

Scenario	Length of railroad within badger habitat (km)#	Mean mortality on tracks within badger habitat per km per year	Badger mortality per year	Loss in carrying capacity (RU)
1	9.1	0.08	0.7	<1
2	9.1	0.23	2.1	ca. 2
3	9.1	0	0	–
4	8.2	0.23	1.9	ca. 2
5	8.9	0.23	2.0	ca. 2

including the areas outside badger territories but within the borders of local populations.

Loss of habitat, setts, and increased mortality will reduce the carrying capacity of the key patch by 4-5 RU. However, because standards for minimum viable metapopulations will still be met, both the key population and the network population will remain sustainable. Badger groups within the national park are not threatened.

As the northern bypass is planned at a considerable distance to the park, no loss of future habitat or future badger setts within the park will occur. Consequently no possible future badger territories within the park will be intersected by the new railroad, thus avoiding increased mortality from collisions.

Southern bypass
The construction of a bypass south of MNP (A2 bypass) results in the loss of about 18 ha of badger habitat (table 5). One potential badger sett will be lost because it is located within the construction site. Again, loss of both habitat and sett all occur outside MNP but within the key patch of the central Limburg habitat network. In this scenario approximately 2.0 badgers will be killed by trains per year (table 6). All expected collision mortality takes place within the key population. As no sound barriers are projected in this scenario no loss of connectivety is expected.

Loss of habitat, setts, and increased mortality will reduce the carrying capacity of the key patch by 3-4 RU. As standards for minimum viable metapopulations will still be met, both the key population and the network population will remain sustainable. Badger groups within the national park are not threatened.

In contrast with the northern bypass, the bypass south of MNP is situated close to the park border. It intersects the Venbeek area and consequently will impact future potential habitat and the possible establishment of new badger groups in this small-scale agricultural landscape.

Discussion

Methodology

The method used to assess whether reactivation of the Iron Rhine railroad will reduce population viability of badgers or not, can best be characterised as a 'quick scan'. In this approach, impacts on badger survival are based on static analyses of habitat configuration and population size, using thresholds to determine whether populations are viable or not. It is recommended however, if time and budgets allow, that dynamic (meta)population models are used, which result in more precise predictions of the consequences of an increased mortality, habitat loss, or barrier effect on badger populations (e.g. van der Grift & Verboom 2001).

The use of thresholds for population viability allows for a quick exploration of possible impacts, but has considerable downsides too. Our method implies that a situation is described as 'viable' or 'non-viable', even if the difference in carrying capacity is only one RU. In case of this study a habitat network with a carrying capacity of 80 RU is indicated persistent, while a habitat network with a carrying capacity of 79 RU is judged as non-persistent. If a population is highly viable (i.e. carrying capacity is significantly higher than the threshold), even a considerable decline in carrying capacity will not result in a shift in population viability. Results should not be interpreted as exact predictions of future population developments, but as rough indications or trends of what will happen after railroad reactivation. In this regard, the method is especially useful if different scenarios have to be compared for the selection of the scenario with the least impact.

Badger survival

Temporarily or permanently reactivating the historic railroad without sound barriers (scenario 1 and 2) would result in a small decline of carrying capacity in the key patch. This decline is solely caused by increased mortality of badgers from train-badger collisions. Both the key population and the network population remain viable in these scenarios. Within MNP the badger group at Steenheuvel will suffer most. If the railroad is temporarily reactivated, this group may not disappear because of reproduction and immigration. In scenario 2, it is expected that losses will be too high to be compensated for. In this scenario chances are considerable that the Steenheuvel group will disappear.

The greatest impact is expected when sound barriers are constructed, without additional mitigation measures (scenario 3). The present network population will be split into two separate populations; both too small to be characterised as a MVMP. For simplicity it was assumed that in the new situation only the population north of the railroad, which is the largest and most accessible, will be connected with (potential) badger groups east and west of the study area. This implies that 30 RU (see also table 4) is added to the carrying capacity of badger habitat north of the historic railroad. However, some of these badger groups may be part of the network population south of the railroad. If this is the case, carrying capacity of the northern habitat network will be even less than 74 RU, reinforcing the conclusion that the barrier effect of the railroad with sound barriers will result in two non-sustainable populations. Within MNP, the Steenheuvel badger group seems most threatened by railroad reactivation because a considerable part of this group's territory is cut off, increasing chances that this badger group becomes extinct.

With the construction of either a northern or southern bypass (scenarios 4 and 5) the key population size would decrease. However, the decline would be too small to endanger the sustainability of the key population and the network population. All losses are expected in badger groups outside MNP. Badger groups within the national park are all likely to survive.

Mitigation measures

Mortality from train-badger collisions in scenario 1, 2, 4 and 5 can be prevented by the construction of fences on both sides of the tracks (e.g. van der Grift & Kuijsters 1998, van der Grift 1999). The barrier effect of such fences, as well as the barrier effect of sound barriers (scenario 3), can be reduced by the construction of wildlife over- and underpasses. Research has shown that badgers are able to use different types of wildlife passages, varying from small badger pipes to large wildlife underpasses and ecoducts (Derckx 1986, Bekker & Canters 1997, Berris 1997, Georgii 1997, Hermann et al. 1997) (photo 3). The effectiveness of such measures depends on the location, the presence of linear landscape elements, like hedgerows that guide the badgers towards the passages, length, height and quality of fences, as well as frequent and proper management of passages (Derckx 1986, Broekhuizen & Derckx 1996, Vereniging Das & Boom 2002). The construction of these mitigation measures at either the historic railroad or one of the bypasses is believed to reduce most described impacts of railroad reactivation, most benefit being seen in scenario 3. If connectivity between badger populations north and south of the railroad is restored, and effective wildlife passages are built, both the key population and the network population will remain viable. However, mitigation measures offer no solution for loss of habitat and badger setts (scenario 4 and 5). Expected reductions in carrying capacity as a result of these losses should be compensated for by developing suitable habitat and sett sites on surrounding agricultural lands.

Conclusion

Reactivation of the Iron Rhine railroad through MNP will have most impact on badgers within the park if use of the historic railroad is permanently resumed. If no sound barriers are constructed, habitat suitability decreases because of an expected increase in mortality from train-badger collisions. In this scenario there is a likelihood that one of the badger groups in the park will become extinct. If sound barriers are constructed, the barrier effect of the railroad will cause the greatest impact on badger movements. If no mitigation measures are taken, the network population will be split in two. These separated network populations north and south of the railroad may not be viable.

The loss of RU is higher with the construction of either a northern or southern bypass, because of a combination of habitat loss, destruction of setts and increased mortality. However, the distance of these new railroad sections to badger groups in the park is too large to endanger their existence. Also, the decline in carrying capacity of both the key population and network population is too small to impact population viability.

Temporarily reactivating the Iron Rhine railroad will have no severe impact on badger survivability within the park. This will result in a moderately increased chance of badgers being killed on the tracks but it is believed that this will not cause the disappearance of badger groups within MNP.

If habitat potential within and around MNP are fully developed, population viability will be positively affected by both the colonisation of new habitat and higher badger densities in extended and qualitatively improved habitat. These positive developments will be frustrated most by reactivation of the historic railroad (with or without sound barriers) and the construction of a southern bypass. Mitigation measures such as underpasses are believed to reduce most described impacts of railroad reactivation in MNP.

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Samenvatting

Zal reactivering van de spoorlijn IJzeren Rijn de overlevingskansen van dassen (*Meles meles*) aantasten in nationaal park De Meinweg?

We onderzochten het effect van reactivering van de goederenspoorlijn 'IJzeren Rijn' op de levensvatbaarheid van dassenpopulaties in nationaal park De Meinweg. Hierbij werden vijf scenario's voor reactivering met elkaar vergeleken: (1) tijdelijke reactivering van het historisch tracé, (2) permanente reactivering van het historisch tracé, zonder geluidschermen, (3) permanente reactivering van het historisch tracé, met geluidschermen, (4) een omleiding ten noorden van het park, en (5) een omleiding ten zuiden van het park. Op basis van gegevens over de ligging en bezetting van dassenburchten in Midden-Limburg is een analyse gemaakt van de ruimtelijke structuur van (potentieel) dassenleefgebied in en rondom het nationaal park. Tevens is de configuratie van de Midden-Limburgse dassenpopulatie onderzocht, waarbij lokale populaties en netwerkpopulaties zijn onderscheiden. Per scenario zijn de effecten van habitatverlies, verlies van burchten, sterfte als gevolg van aanrijdingen en de barrièrewerking van de spoorlijn op de levensvatbaarheid van de dassenpopulatie gekwantificeerd. De effecten van reactivering van de spoorlijn op voor dassen gunstige autonome ontwikkelingen in het gebied zijn kwalitatief beoordeeld. Het permanent in gebruik nemen van

het historisch tracé heeft de grootste gevolgen voor de dassen in nationaal park De Meinweg. Vooral wanneer aan weerszijden van de spoorlijn geluidschermen worden aangebracht. Als geen mitigerende maatregelen worden getroffen, zoals de aanleg van faunatunnels of ecoducten, betekent dit dat de netwerkpopulatie in twee delen wordt gesplitst. Zowel de dassenpopulatie ten noorden als die ten zuiden van de spoorlijn zijn in deze situatie niet levensvatbaar. De omleidingen noord en zuid van het park vormen geen bedreiging voor het voortbestaan van dassen in De Meinweg. Wèl neemt de draagkracht van zowel het sleutelgebied als het habitatnetwerk af, maar deze afname is naar verwachting te gering om de levensvatbaarheid van de dassenpopulatie in gevaar te brengen. Tijdelijke reactivering van het historisch tracé heeft geen ernstige gevolgen voor de overlevingskansen van dassen binnen De Meinweg. Als voorgenomen plannen voor natuurontwikkeling en habitatverbetering binnen en nabij De Meinweg plaatsvindt, zal dit op de meeste lokaties positief uitwerken voor de dassenpopulatie in het gebied. De aanleg van nieuw habitat en de verbetering van de kwaliteit van bestaand habitat zal leiden tot een verhoging van de draagkracht van het gebied voor de das. Deze positieve ontwikkelingen voor de das worden vooral doorkruist wanneer het historisch tracé opnieuw in gebruik wordt genomen (zonder of met geluidschermen) of men overgaat tot de aanleg van een zuidelijke omleiding. Mitigerende maatregelen kunnen naar verwachting de meeste negatieve gevolgen van reactivering van de IJzeren Rijn op de dassenpopulatie in De Meinweg wegnemen.

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Short Note

First record of an albino long-eared bat *Plecotus auritus* in The Netherlands

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Every summer, we carry out a survey of church loft dwelling bats in the northern half of the Dutch province of Limburg (figure 1). This survey is part of a nation-wide monitoring program (de Wijs 1995, Buys et al. 1999), and focuses on both indigenous *Plecotus* species, *P. auritus* and *P. austriacus*.

On September 18th 1999, we observed an albino specimen of *P. auritus* in the loft of the (partially medieval) church in the village of Nunhem (figure 2, 51°14' N – 05°57' E). The animal was one of a group of 21 individuals of the same species (figure 3). The bat was brightly white, except for the eyes, which showed black. This indicates that the retina had the usual pigment. As far as visible, other parts of the body lacked any pigment. Therefore, we conclude this was a case of partial albinism. To use the alternative qualification, leucism, the fur should have had pigmentation to some extent.

Whereas both *Plecotus* species occur in this area (Buys & Vergoossen 1997), we paid particular attention to the identification of this albino specimen. In this survey we never handle the animals, in order to minimise disturbance of the bats. Moreover, there is a practical reason as most animals hang out of reach in the top of the loft. Hence, we based the identification of the group on the shape of the head, the colour of the skin and tragus, and the colour of the fur (Buys 1996). All animals had the *P. auritus* characteristics. Although the characteristic 'colour of the fur' and 'colour of skin and tragus' were not applicable to the albino bat, the shape of the head was typical for *P. auritus*. The albino bat had the typical blunt nose and swollen glands between the nostrils and eyes. The shape of the head is the most distinctive criterion, for it is related to the measurable differences in skull characteristics between both *Plecotus* species.

We revisited the Nunhem church twice after-

Figure 1. The survey area.

wards in 2000 and 2001. In both visits a group of *P. auritus* was present. However, the albino bat was not found, suggesting that the animal either had not survived or used another, unknown, roost at the time.

This is the first record of an albino *P. auritus* in The Netherlands. Bekker (1989) and Van Laar (1994) describe partial albinism in *Myotis daubentonii* and *M. mystacinus* respectively. An albino *Myotis dasycneme* was reported from the village of Kollum (province of Friesland) around 1955 (W. Bongers, personal communication).

Albinism is known to exist in both European *Plecotus* species. Lehnert (1991) and Weidner (1994) report a completely and a partially albino specimen of *P. auritus* respectively. Haensel et al. (1993) describe a whitish specimen of *P. austriacus*. It is unlikely that the specimen of Lehn-

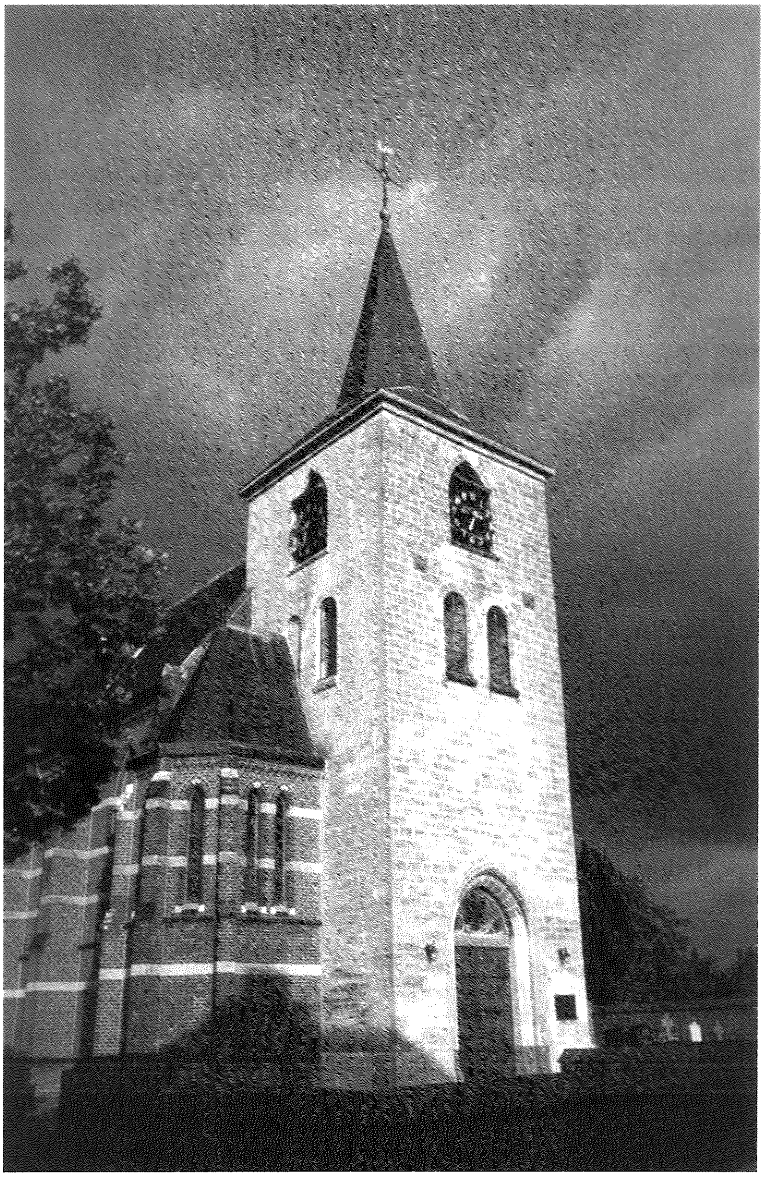

Figure 2. The Nunhem church.
Photograph: Jan Buys.

Figure 3. Albino long-eared bat (*Plecotus auritus*). *Photograph: Jan Buys.*

ert migrated to Nunhem because the animal Lehnert describes had reddish / pink eyes. Moreover, the distance between Berlin and Nunhem and the reputation of *P. auritus* as a rather sedentary species exclude migration.

Uieda (2000) gives an overview of complete albinism in bats. Altogether he mentions 64 cases, which underlines the rarity of the phenomenon. Uieda also comments on the occurrence and survival rate of albino bats. First of all, he notes that albinism is seldom found in bats roosting in unsheltered places. This might imply that the survival rate of albino bats in sheltered roosts (e.g. buildings, tree hollows, nesting-boxes) is higher. Nevertheless, Uieda (2000) is not clear whether or not this can be attributed to a relatively higher inspection frequency of these types of roosts. He even argues that in the case of bats roosting in foliage a light (or white) fur is an advantage, as it reflects the (green) colour of the foliage, thus making the bats less visible. Uieda mentions several cases in which albino bats have been observed for several years, which shows that albinism does not necessarily imply a short life for a bat. This is not very surprising, considering the nocturnal habits of bats and the dark roosts they generally select.

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Samenvatting

Eerste waarneming van een albino gewone grootoorvleermuis *Plecotus auritus* in Nederland

In 1999 troffen we tijdens de jaarlijkse kerkzolderinventarisatie een albino gewone grootoorvleermuis (*Plecotus auritus*) aan op de zolder van de kerk in Nunhem (provincie Limburg). Een tamelijk unieke waarneming, getuige het kleine aantal meldingen van albino vleermuizen in de literatuur. Gezien de zwart gepigmenteerde ogen, kunnen we hier niet spreken van volledig albinisme. Tijdens bezoeken in 2000 en 2001 werd geen albino grootoorvleermuis meer aangetroffen; steeds waren er wel gewone grootoorvleermuizen op de zolder aanwezig.

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Publicaties over recente zoogdieren van Nederland, verschenen in de jaren 1985-1999 (aanvulling)

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Introductie: Bij het samenstellen van literatuuroverzichten werd en wordt gestreefd naar volledigheid. Het is echter bijna onvermijdelijk dat er desondanks toch nog publicaties over het hoofd worden gezien. Dit overzicht geeft aanvullingen op de eerdere publicatielijsten over Nederlandse zoogdieren, verschenen in de periode 1985-1999.

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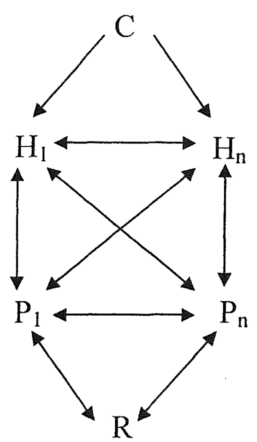
Book Reviews

Can woody species cope with vertebrate herbivory in the extremely nutrient poor conditions of De Hoge Veluwe?

The secret life of woody species. A study on woody species establishment, interactions with herbivores and vegetation succession. R. Smit 2002. PhD thesis. Wageningen University, Wageningen, The Netherlands. 139 pp. ISBN 90-5808-615-1.

Despite the very botanical title of this PhD, it is really very much dealing with vertebrates and their impact on woody species, especially with their first life phases, the seed and the seedling and sapling phase. It tries to contribute to the solution of the basic question how on earth it is possible that woody species dominate most formations on this globe, while they are severely predated by all kinds of herbivores. It brings us back to the very fundamental hypotheses on who is limiting who. Should we follow the 'food limitation hypothesis', stating that herbivores regulate the abundance of plant populations, or is the opposite true, i.e. that herbivorous animals have little impact on plants because their numbers are controlled by the depredations of natural enemies (as Crawley (1983) states in his introduction to "Herbivory")? Or to put it in Ruben Smits' words: which biotic and abiotic factors limit woody species establishment? That's his general focus.



C: carnivory; H_{1-n}: herbivores (h: rodents); P_{1-n}: woody plant species; R: resources (light, water, nutrients)
Conceptual model of species interactions on different trophic levels (Smit 2002)

Smits' model area for our globe is the National Park De Hoge Veluwe, where several field experiments were done between 1994 and 2001. Most important ungulates in the area are red deer, roe deer, mouflon and wild boar. All field experiments are framed into a simple conceptual model on interactions between different trophic levels (see figure).

R → P ↔ P: Woody species in relation to habitat productivity

Through the analysis of vegetation relevés of former agricultural fields that were not cultivated anymore during a period of 1 up to 54 years and that are differentiated according to soil fertility, the establishment success of early- and late-successive woody species is compared. It is concluded that on relatively fertile soil, woody species establishment in general is delayed in comparison with poor soils (woody species dominance after 45 in stead of 30 years), because of earlier canopy dominance by perennial herbs on fertile soil (up to 100% cover); abundance of perennials remains lower (40-60%) on poorer soil. Wind-dispersed, early-successive species (e.g. birch) appear to be less hampered in their establishment than barochoric or zoochoric late-successive species (e.g. common oak), since many individuals arrive and develop before perennials have formed a closed canopy. Arrival of the last mentioned species is expected to depend strongly on the distance to seed sources.

Not denying the interesting results of this study, one should be aware though that relatively little data are available and they are very unequally divided among age classes. With less than five relevés on old fields that were abandoned more than 30 years ago and a strong dominance of relevés on relatively young abandoned fields, one should be very careful in its interpretation towards succession speed.

R → P ↔ H+h: Effects of herbivore guilds on woody species establishment across a succession gradient

Far better founded are the results of the study of the effects of different herbivore guilds. They are obtained from a standardised and controllable field experimental design. In four vegetation types, arranged according to an assumed succession gradient (heathland → pine woodland → pine forest → oak-beech forest) a field experiment was set up, in which seeds of four tree species were introduced (birch, Scots pine, common oak, beech) with three herbivore conditions: (1) large vertebrates (H: ungulate species) + rodents (h) + insects, (2) rodents + insects, and (3) insects.

The results clearly expose the drastic impact of rodents. Almost all sown seeds of oak and beech in the three forested areas have disappeared (81-99%) from both types of rodent-influenced plots. Only in heathland a significant number of seeds remained (26-36%). Whether these seeds were all predated or partly just moved outside the plots can not be revealed from the data though. Since oak and beech are known for their zoochoric dispersal, this is an important issue that remains to be investigated. It nonetheless becomes evident that common oak and beech have a hard time during their establishment phase. If not predated they still have to overcome fungal destruction, desiccation and defoliation by insects. In heathland–insect plots only 14% of the sown seeds of common oak and a mere 2% of beech survived after two years.

A unique chance to study the differential effect of large ungulate herbivores on vegetation, on each other and on other herbivore guilds was the fact that part of De Hoge Veluwe (Hoenderloo (Hoe) and Kemperberg (Kem)) was newly exposed to red deer, wild boar and mouflon herbivory in November 1994, while these areas were formerly only grazed by roe deer. This situation was the basis for the last three chapters of the PhD.

P ↔ H: Botanical changes during 7 years after large herbivore introduction and exclusion across a woodland-forest gradient

This primarily botanical study included three forest types arranged along an assumed succession gradient: first generation Scots pine woodland → second generation Scots pine forest → oak-beech forest. In all three forest types 15x25m large vertebrate herbivore exclosures were raised to be able to compare grazed and ungrazed situations. A detailed botanical survey was performed in 1994 (prior to introduction of red deer, wild boar and mouflon in Hoe and Kem), 1995, 1996, 1997 and 2001.

Surprisingly enough, in neither of the forest types the herb layer composition nor the vascular plant species richness in general significantly altered due to changes in herbivore species composition and density. Grazing introduction did not alter the shrub layer, but grazing exclusion in formerly heavily grazed forest types induced a fast increase in graze-tolerant shrub species. Shrub development influenced perennial grass cover negatively. Important conclusion is that exclusion of a herbivore species has not necessarily the exact reverse effect of its introduction. It is concluded that deer introduction in forests [i.e. of the particular kind studied here] is no successful tool to maintain or create a higher species or community diversity. Whether this statement holds for other forest habitats of richer and more humid soil remains to be investigated.

H (→ P) → h: Effects of introduction and exclusion of large herbivores on small rodent communities

To detect the impact of large herbivores on rodent presence and their seed predation impact,

The introduction of red deer in forests is not always a succesful tool to maintain high species diversity. *Photograph: Edgar van der Grift.*

again an exclosure technique was used in previously ungrazed pine and oak-beech forest, where red deer were introduced three years earlier, and pine woodland and heathland that were previously heavily grazed by red deer, roe deer and mouflon.

The results show that in formerly heavily grazed habitats significantly higher densities of wood mice and field voles appeared in grazer exclosures. On the other hand the introduction of red deer in the other habitats did not influence rodent presence significantly [yet]. Parallel with an increased rodent density (wood mice), predation on [or at least removal of] sown beechnuts and acorns increased as well. It is hypothesized that rodent density increase in absence of large grazers is due to the increase in understory cover after grazer exclusion. Introduction of grazers did not change understory vegetation [yet] in a way to limit rodent density [already]. It is concluded that woody species establishment can be influenced indirectly by the large herbivore species composition through its influence on vegetation structure, of which the rodent density depends heavily, which in itself has a large impact on seed fate.

H ↔ H: Shifts in resource partitioning between large herbivore species in response to interspecific competition

Using again the unique situation of having available two large areas, where formerly only roe deer grazed and where red deer, mouflon and wild boar could invade from one particular moment onwards, and using general ungulate monitoring data (five permanent road transects investigated on a weekly basis and additional ungulate spatial distribution data), it was investigated whether roe and red deer appear to have a competitive relationship or that resource partitioning might prevent severe competition. Since only red deer colonised the new areas on a relatively large scale, interactions between roe deer and both other ungulates were low. Habitat use was reconstructed through recurrent faecal pellet counting.

Not surprisingly the results reveal that roe deer population performance decreased when red deer population performance increased; roe deer habitat use shifted from dominantly deciduous forest and pine forest towards pine woodland and heathland. Both facts point at a direct competitive relationship. It is hypothesized that competition might be due to specific red deer browsing on woody forage, which probably is a preferred component of the roe deer diet and which composes much of the understory structure of which roe deer is dependent for shelter. Much of the data point at competitive exclusion of roe deer by red deer, being the superior competitor. Many of these conclusions should be further underpinned with further research though. Nonetheless it is rightly concluded that resource competition might lead to shifts in resource partitioning in food-limited environments.

What remains in one's mind after reading this interesting plant and animal ecology integrating PhD is ... "rodents". It is clearly proven that the impact of rodents is (extremely) large on the establishment phase of the woody tree species with large heavy seeds (common oak, beech). This impact might well be underestimated until now. It is a pity though that nothing can be said yet about the other side of the coin, i.e. seed dispersal: does common oak or beech in the end benefit from rodent activities through its dispersal potentials or is it harmed by its predatory activities? This remains to be disclosed.

Whether conclusions hold for other habitats on richer or more humid soil types also remains to be discovered. Most of comparable research in Western Europe on herbivory in woody habitats is restricted to equally nutrient poor systems as De Hoge Veluwe. A lot remains to be done in other, less nutrient-limited and water-limited circumstances.

This PhD clearly points out that several trophic levels are involved in the potential success of woody plant establishment. Nature once again presents itself as a complicated network of interactions that all depend on each other. It becomes clear that the question on 'who is limiting who', will never be answered straightforwardly; nonetheless this PhD proves that even to become just a sapling is a hard thing to do. Only when time is introduced as an ecological factor, one starts to understand that woody species with their competitive ability in later life stages in the end are still able to dominate most of the world's terrestrial vegetation.

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Mustelids in a modern world

Mustelids in a modern world. Management and conservation aspects of small carnivore - human interactions. H.I. Griffiths (ed.) 2000. Backhuys Publishers, Leiden, The Netherlands. 342 pp. ISBN 90-5782-066-8.

This book collects 21 invited essays and research papers by 48 authors, and results from the mustelid session of the Euro-American Mammal Congress, held in Santiago de Compostela (Spain) in July 1998. It is remarkable that there are no contributions from continental western Europe. This may be related to the fact that researchers from this region have their own yearly 'Mustelid Colloquium' and, as a consequence, were poorly represented at the Santiago congress.

Besides papers concerning the occurrence and conservation status of mustelids in several parts of the world, e.g. USA, Ontario, the Balkans and Taiwan, the book offers a kaleidoscope of various aspects of mustelid management and interactions with humans. Although the book partly deals with species that do not occur in western Europe, most of the aspects also apply to western

Europe. Some papers deal with the outcome of governmental policy and the lack of proper evaluation. In Norway, for instance, over a century of state-subsidised control has resulted in the practical extinction of wolverines throughout most of the country. After the wolverine became protected in all of Norway, culminating in a government policy paper in 1992, the various counties were still allowed to issue permits and quotas for hunting wolverines to reduce their predation on sheep and semi-domestic reindeer. In Troms County in 1996-1997 this resulted in the removal of more than 25% of the wolverine population due to overestimation of the population size. No data were collected on the possible effect of the control measures on the population's social structure and reproduction, nor on the long term effect on sheep predation. This Norwegian example is a warning to other countries such as The Netherlands that have delegated the issuing of permits for the control of protected species to provinces.

In England, over 20 years of government-organized badger culling to reduce bovine tuberculosis in cattle did not result in a clear insight in the effectiveness of different types of badger removal operations. This is mostly related to the lack of a scientific control experiment. A detailed field study described in this book shows the practical difficulties of the application of removal strategies in the field, but unfortunately some of the legends do not match the illustrating figures.

Several papers deal with a major problem in mustelid studies: the difficulty to determine the animals' numbers, densities and distribution, and, consequently, the result and effectiveness of management measures. The survey methods discussed in different chapters are tracking tunnels, track plates, photographs at bait stations and trails, the collection of fur at bait stations, snow tracking, scat transects and the collection and screening of sightings by the public. The latter, carried out in Britain for the pine marten, shows the strong dispersal capacity of this species, but it could also reflect the possible inaccuracy of the method.

The relationship between habitat and landscape parameters and mustelids' habitat use is the topic of other chapters, e.g. for otters in Ireland and British Columbia, polecats in Britain and mustelids in northern Italy. Other papers discuss the negative effect of human presence and activity (e.g. fur industry, forestry, agriculture, recreation and traffic) on the occurrence of mustelids. On the other hand the book illustrates the recovery of otters in man-made habitats in central Europe.

The application of GIS and computer modelling is discussed and promoted as complimentary tools to the more traditional ecological techniques. These techniques can increase our understanding of the factors that influence mustelid populations at a landscape scale. It is stressed that the high-tech methods do not form the panacea that offers the solution to every problem. They can also not substitute good natural history skills and field research.

A special aspect of population management are reintroduction programs in former occupied areas. An example is the reintroduction of the black-footed ferret in the Great Plains of North America. A review is given of all the research carried out during this project. Among the experience gathered is the realisation that the environment in which the young grow up has a significant effect on the development of their behaviourial patterns and that these influence their survival in the wild. The results indicate that a natural environment increases breeding success and stimulates breeding in on-site pens.

Intra- and interspecific relationships are also important for the management of mustelid populations. A study of the response of badgers' social organisation to increasing population density forms an example of an intraspecific relationship. As the population density approached the carrying capacity of the habitat, the social groups decreased the overlap between their territories and the percentage of badgers with bite wounds also decreased. This indicates a higher stability in social organisation. This also implies that when the population density remains below the carrying capacity, for instance as a result of the culling of badgers or traffic mortality, the social organisation is less distinct and agressive intraspecific contacts are relatively common. This makes it difficult to interpret the effect of population control. This book also deals with interspecific relations in mustelids such as the hybridisation between the polecat and the feral American mink in Britain and between the polecat and the European mink in eastern Europe.

Although this review did not discuss all papers and aspects presented in the book, I think that this collection of mustelid studies is important to everyone who is interested in nature management in general and mustelids in particular. The extensive reference lists have additional value.

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