

HISTORY, MORPHOLOGY AND ECOLOGY OF THE AUROCHS (*BOS PRIMIGENIUS*).

by

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Abstract

In this article, the results of a research (Van Vuure, in press) 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 resemblance as to morphology 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 primigenius*, history, morphology, ecology, Heck cattle, natural landscape, feeding impact.

1. 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 (Guintard 1999, Van der Lans & Poortinga 1986). In the 20th century, the interest of the general public in the aurochs at first has been evoked by the Heck brothers (Germany), who in the 1920s and 1930s tried to 're-create' the aurochs by crossing certain domestic cattle breeds and selecting in their offspring (Heck, H. & L. 1934). 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 of discussion (Nederlands Bosbouw Tijdschrift 1998, 70, May/June; Symposium Palynologische Kring, 6-5-1998).

The aurochs was object 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 (Von Leithner 1927, Lehmann 1949, Nehring 1900). 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.

2. 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 Bia³owieża 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.

3. Results

3.1. 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 ever been a single wild bovine in Europe, the European bison (*Bison bonasus*), while the other argued that there had been more: the European bison and the aurochs (Von Leithner 1927; Wrzeñniowski 1878). 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 (Wrzeñniowski 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.*).

Fig. 1 gives the total distribution area of the aurochs for both the Pleistocene and the Holocene. In Europe it did not live in Ireland and northern Scandinavia. The most northerly bone remains were discovered at 60° NL, 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 increasingly became the privilege of the nobility. In written records of such privileges the aurochs holds a special place among the various types of game (Wrzeñniowski 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). Fig. 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 disinterestedness, 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).

3.2. 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 (Von Leithner 1927, Nehring 1900). 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 *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 (Von Leithner 1927, Schneeberger in Gesner 1602). 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)(Fig. 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 (Grigson 1978, Bohlken 1964).

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, H. 1934; Heck, L. 1934) 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 (Herre 1953, Koehler 1952). 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 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.

3.3. 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 gamekeeping 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 eye-witness accounts of this population have been transmitted to us, so we can form a good notion of the then situation (Schneeberger in Gesner 1602, Heymanowski 1972, Kêdzierska 1959).

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); inside 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).

3.4. 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 BC, Mela ca. 49). 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 BC, 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). 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 BC) the landscape of NW-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 BC 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 (NE Poland). During the middle ages, a wilderness situation existed in this area for several centuries, nearly untouched by man (Mager 1960, Mortensen & Mortensen 1938). 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 (viz. 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).

3.4. 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 (*Bison bonasus*)) 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 (Vera 2000, Bunzel-Drücke et al. 1994).

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 (Jêdrzejewska 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 (*Bison bison athabascae*) 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 (Carbyn et al. 1993, Jaques 1990).

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, several studies in the Forest of Bia³owie¿a (East Poland) show that its role there is and was not so prevailing (Fruziñski et al. 1975, Jêdrzejewska 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.

4. 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 re-create 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 be certainly 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. Sperber 2000, Zoller & Haas 1995, Litt 2000) argue that large herbivores have only marginal impact on forest vegetations and therefore a landscape with extensive dense forests results. Others (e.g. Vera 2000, Hofmann & Scheibe 1997, Beutler 1997) 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.

Samenvatting

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

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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. Light-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.



Fig. 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.

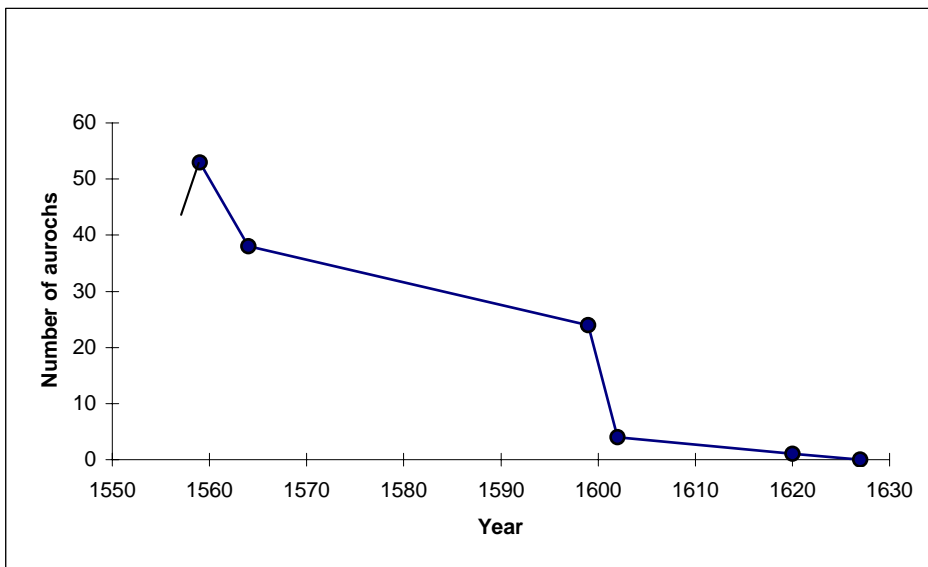


Fig. 2. Changes in the number of aurochs in the forests at Jaktorów (Central Poland). After data from Schneeberger (in Gesner 1602) and Łukaszewicz (1952).

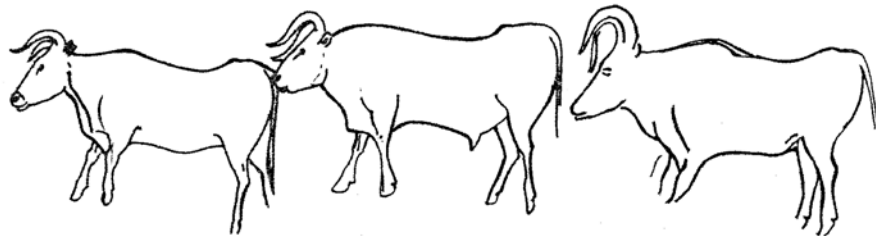


Fig. 3. Drawing from the cave of La Mairie (Dordogne, France), ca. 15,000 years old. An aurochs bull with two cows. In these cows it can be seen that the udders are small and not visible in this way.

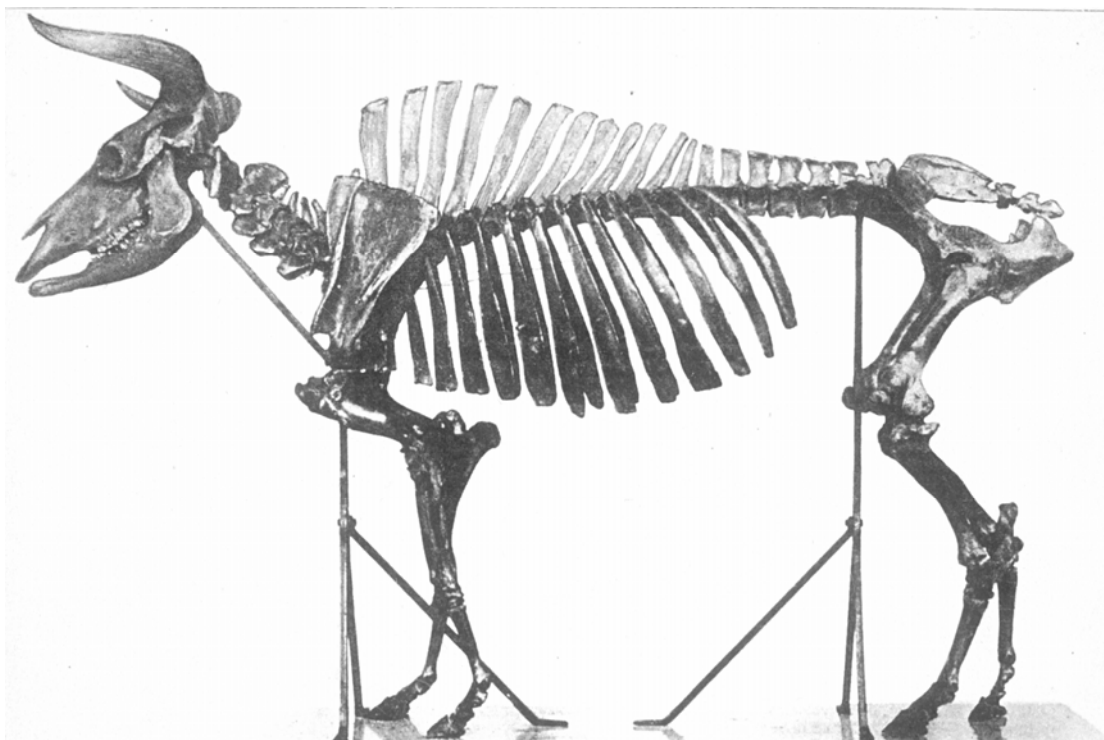


Photo 1. Left skeletons of aurochs are rare. This nearly complete skeleton of a Holocene aurochs bull was found in a peat bog at Hammerslöv (South Sweden) (after Von Leithner 1927).



Photo 2. Sedge marshes along the Narewka River in eastern Poland. In the background the forest of the national park of Bia³owieża. Such sedge marshes probably played a major role in the life of the aurochs (Photograph: T. van Vuure).