

ORIGINAL PAPER

Why did wisents outlive aurochs?

Maciej Augustyn⁽¹⁾, Kajetan Perzanowski⁽²⁾✉

⁽¹⁾ Museum and Institute of Zoology, Polish Academy of Sciences, Carpathian Wildlife Research Station, Ogródowa, 38-400 Ustrzyki Dolne, Poland

⁽²⁾ Institute of Biological Sciences, Catholic University of Lublin, Konstantynów 1H, 20-708 Lublin, Poland

ABSTRACT

Two native European large herbivores: the aurochs *Bos primigenius* Bojanus, 1827 and the wisent *Bison bonasus* Linnaeus, 1758 lived simultaneously until the end of the Medieval period. Between the 15th and beginning of the 17th century, however, the aurochs population declined rapidly, while wisents continued to live in the wild until the end of World War I. In western Europe, both aurochs and wisents went extinct much earlier than in the east, so by the 16th century the two species were commonly confused, as illustrated by a drawing from 1571, showing the differences in appearance, and providing proper nomenclature for both species. The extinction of aurochs took place despite their strict protection and even supplementary feeding imposed by Polish kings. Since in central and eastern Europe there is a number of traditional geographical names associated with both species, we made an attempt to determine their distribution in four areas of eastern Europe (Poland, Lithuania, Romania + Moldova, and Ukraine), and by comparing historical changes in land cover, identify possible reasons for such a substantial difference in their survival. Numbers of geographical names were much higher for the aurochs than for the wisent: >5-fold in Poland and >4-fold in Ukraine, indicating much greater recognition of the aurochs by the human population. The suggestion is either that aurochs were more abundant, or were more frequently present in open areas. Between 1000 and 1400 (when in Poland and Lithuania hunts for the aurochs by the kings of the Jagiellonian dynasty were organised only occasionally), there was a drastic decline in forest cover, estimated at almost 50% in Poland, nearly 40% in Lithuania, and almost 30% in Ukraine. This deforestation was associated with the development of agriculture and settlements, which resulted in much greater areas of open land with attractive forage for herbivores. Therefore, the most probable factor for differences in the survival of the two species, we suggest, was preference by aurochs for open landscapes, making them more conspicuous, leading to more frequent encounters with people and conflicts with cattle breeders and farmers. This case indicates the critical importance of socio-economic circumstances for the survival of endangered species, despite strict protection.

KEY WORDS

aurochs, European bison, extinction, history, land cover

✉e-mail: kajperz@wp.pl

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Introduction

Aurochs *Bos primigenius* Bojanus, 1827 and wisents (or European bison) *Bison bonasus* Linnaeus, 1758 were fairly common in ancient Europe until the Medieval period. Cave paintings of both species have been dated from more than 10 thousand years ago (Kuemmerle *et al.*, 2011; Wright, 2013).

According to fossil records, wisents occurred in north-western Europe in the Early Holocene, but no such evidence from the Middle and Late Holocene have been found in this part of the continent. The species mainly lived in central and eastern Europe (Kysely, 2005; van Vuure, 2015). Aurochs, as prominent game animals for German tribes, were mentioned even by Julius Caesar under the name 'uri' in his famous work '*De bello Gallico*'. Also, the ancient Roman naturalist Pliny the Elder properly distinguished *E. bison* and aurochs, referring to them as '*iubatos bisontes*' and '*velocitate uros*' in his '*Naturalis Historia*' from the 1st century AD. During the Middle Ages, wisents and aurochs in the west of Europe were given many various names and frequently misidentified (Rokosz 1995; van Vuure 2015). Quite detailed descriptions of these species' appearance were provided only by Conrad Gessner in his '*Historiae Animalium*' (1551-1558). In eastern Europe, both species were commonly known, and as important and respected game, they became symbols on numerous coats of arms, both of nobility and townships, *e.g.*, in Poland, Lithuania, and Moldova (Dzieduszycki *et al.*, 2010; Marszałek and Perzanowski, 2018).

Nevertheless, together with the growing density of human population, and drastic changes in land cover resulting from the development of agriculture and settlements, both species gradually became rare, beginning in western Europe. In England, no aurochs bones dated after 1300 BCE have yet been found. In Scandinavia, aurochs survived until the 11th century. In Germany, the latest findings of aurochs remains have been dated the 9-13th centuries, but in Poland, aurochs and wisents lived contemporaneously until the 16th century (Miechowita, 1521; Degerbøl and Fredskild, 1970; Vörös, 1985; Clutton-Brock, 1986).

Together with a sharp decline in population numbers in western Europe by the 16th century, the two species notoriously became confused (van Vuure, 2015). Heberstein (1571), in his work published at Basel, included drawings of both animals with the following descriptions: for the wisent – *Bisons sum, polonis suber, germanis avrox. Ignari uri nomen dederant* (I am the bison, in Polish zubr, in German bisont. Ignorants call me the aurochs) and for the aurochs – *Urus sum, Polonis tur, Germanis aurox. Ignari bisontis nomen dederant* (I am the aurochs, in Polish tur, in German aurox. Ignorants call me the bison) – clearly indicating mutual differences and confirming the common confusion about the two species (Fig. 1).

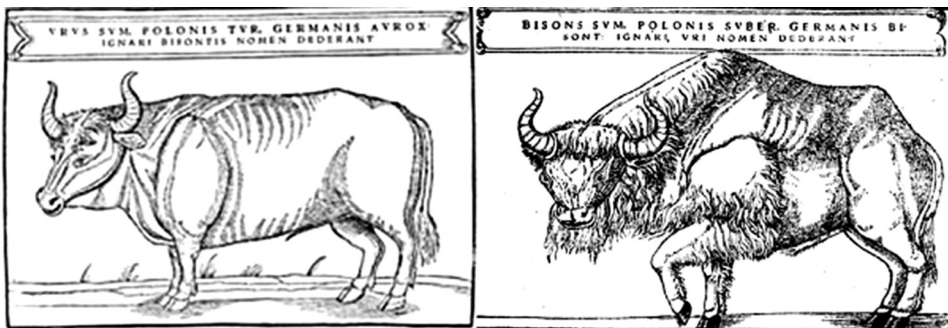


Fig. 1.

Drawings of an aurochs and a wisent from 16th century (after Heberstein, 1571)

In Poland, the aurochs survived until 1627, when the last remaining cow died in the royal menagerie. Wisents lived in the wild until 1919, when the last individuals were killed at Białowieska Primeval Forest, presumably by marauders from the fighting armies of World War I or by local poachers (Rokosz, 1995; Dzieduszycki *et al.*, 2010; Krasieńska and Krasieński, 2017).

The intriguing question is why the survival in the wild differed by about 300 years for those two large herbivores of comparable size and similar gregarious behaviour, originally occupying the same ranges within Europe, and apparently having very similar foraging niches. In this paper we try to analyse some factors that could be crucial for the different fates of the two species.

Materials and methods

Registers of geographical names (toponyms), related to aurochs and wisents, listed in indexes of contemporary atlases of Poland, Lithuania, Romania + Moldova (historically forming one country), and Ukraine were compared. The most important source, however, was the Geographical Dictionary of Polish Kingdom and other Slavic countries (Sulimierski *et al.*, 1880-1902) (Table 1).

Also, we analysed available historical documents referring to the occurrence of aurochs and wisents, distinguishing whether present geographical names (townships, villages, small settlements, watercourses, hills, etc.) derive from the name of an animal or are of anthropogenic origin (*e.g.*, settlements named after the first owner). Therefore we did not consider contemporary names of streets or squares, which (*e.g.*, in Lithuania) are quite popular (Miechowita, 1521; Karcov, 1903; Krasieńska and Krasieński, 2017; <https://maps.lt/map/>).

To assess the influence of land cover upon the range of occurrence of aurochs and wisents, the extent of the historical toponyms reflecting the presence of both species was compared with the estimated area dominated by forests in our selected European countries in medieval times (Kaplan *et al.*, 2009).

Results

An inventory of geographical names derived from wisents and aurochs shows that in all four countries considered, toponyms connected with aurochs are much more numerous. In Poland this proportion is ~5:1, similarly in Ukraine and Romania + Moldova ~ 4:1, in Lithuania this ratio is much lower (Table 2).

Between 1000 and 1400, *i.e.*, before the period of rapid development of agriculture and built-up areas, the proportion of forested land decreased dramatically (almost by twofold) in Poland, but considerably less in the remaining three countries, where forest dominated-landscapes still prevailed (Table 3).

Therefore until the 15th century, the highest proportion of open areas, providing the best grazing conditions, appeared in Poland, where geographical names connected with aurochs are still the most numerous.

Table 1.

Names of wisents and aurochs in native languages of four considered countries of central and eastern Europe

Species \ Country	Poland	Romania and Moldova	Lithuania	Ukraine
Wisent	żubr	zimbru	stumbr	zubr
Aurochs	tur	bour	taur	tur

Table 2.

Numbers of geographical names derived from wisents and aurochs in four considered countries of central and eastern Europe

Species \ Country	Poland	Romania and Moldova	Lithuania	Ukraine
Wisent	22	4	10	16
Aurochs	114	16	14	65

Table 3.

Estimated percentage of forests within usable land (*i.e.*, potentially suitable for agriculture and settlements) in four countries of central and eastern Europe in 1000 and 1400 (according to Kaplan *et al.*, 2009)

Year \ Country	Poland	Romania and Moldova	Lithuania	Ukraine
1000	46.1	89.1	71.7	90.9
1400	24.8	78.3	43.9	65.4

Discussion

We selected for our analysis four countries of Central and Eastern Europe, because in the western part of the continent, aurochs and wisents were commonly mistaken, and geographical names there may not correctly reflect the association of a site with an occurrence of a particular species. Moreover, proper identification of bone remains of both species is difficult and without DNA analysis often impossible, so fossil findings cannot be always a reliable proof of the former occurrence of a given species (van Vuure, 2015).

Although historical records for both species are rather scarce, there is evidence that even when the density of human population was much lower than now, in some areas the presence of considerable numbers of such large mammals could pose a serious economic problem (Karcov, 1903; Gloger, 1907).

Nevertheless, it is well documented that quite early, hunting for both species became strictly regulated and regarded as a royal privilege (Rokosz, 1995). Since we do not have any estimates on population numbers from that time, it is difficult to say whether such a rule was imposed just because of high attractiveness of those animals as game, or it was stimulated by a considerable decrease of their populations.

In Poland already in 1288, Bolesław the Prince of Masovia allowed his serfs to hunt various animals, except aurochs. During the reign of King Władysław Jagiełło (1386-1434), hunts for aurochs were organized only occasionally (*e.g.*, in 1422). From 1520 on, aurochs remaining at Jaktorowska Forest (southwest of Warsaw) were strictly guarded by royal rangers and provided with hay in winter. King Zygmunt II August in 1523 took aurochs under official protection, but by 1564 only 38 animals survived. By 1599 just 24 individuals were recorded in Poland, and finally King Zygmunt III Waza ordered creation of a special reserve at Jaktorowska Forest, where the last representative of this species died in 1627. Surprisingly, no historical records on aurochs exist from Białowieża Primeval Forest, so must have disappeared from there before the 15th century (Rokosz, 1995; Dzieduszycki *et al.*, 2010; Krasieńska and Krasieński, 2017).

Wisents, however, appeared to maintain their numbers much longer. Until the 12th century they occurred in all sizeable forests of Poland. A description of a hunt for wisents by Prince Bolesław Krzywousty dates from 1107. After the 15th century, their area of occurrence shrank to several large forest complexes, *e.g.*, between the Vistula and San Rivers, the Białowieża, Kozi-

nickie, Jedlińskie, Kurpiowska and Niepołomska Forests, and east of present Polish borders in Volyn Province and along the Prypiat River. Nevertheless, before the battle of Grunwald (1410), the Polish king Władysław Jagiełło ordered a big hunt for wisents and other game to supply the army. At Białowieża Forest, wisents were hunted by the Polish king Aleksander Jagiellończyk in 1504, and in 1774 by King August III Mocny. In the Carpathians, the last wild wisent found in Transylvania was captured in 1810, and transferred to the imperial menagerie at Schönbrunn. Until the end of the 17th century, lowland wisents were recorded in Lithuania and East Prussia, but by the 19th century they occurred only in Białowieża Forest, which after the partition of Poland belonged to the Russian Empire until the end of the World War I. Wisents there were hunted by Russian tsars, *e.g.*, Aleksander II in 1860, who killed as many as 28 animals. The last wisent observed there in the wild was killed by poachers in 1919 (Hussoviani, 1523; Gloger, 1907; Perzanowski and Marszałek, 2012; Krasieńska and Krasieński, 2017).

In the absence of historical data on population size, judging from a much greater number of toponyms for aurochs originating in the Middle Ages, it can be assumed that this species was then more common or better known by people than the wisent (Wright, 2013). Because overwhelmingly the most such geographical names come from Poland, probably aurochs were more common there than in the other countries of Central Europe (Sulimierski *et al.*, 1880-1902, Rokosz, 1995). At the same time, the proportion of open landscapes was also the highest there. This allows us to guess that this species preferred open land, which provided good grazing conditions, compared to closed-canopy forests (Degerbøl and Fredskild, 1970). Therefore, aurochs could on one hand be more conspicuous to people, but also could have higher potential for conflicts either due to a competition for pastures with domestic cattle or due to the damages to crops. Being easy to notice in an open landscape, they were also an obvious target for hunters, but also by sharing the same pastures with cattle, they could be threatened by transmission of infectious diseases.

On the contrary, much lower numbers of historical geographical names associated with wisents may indicate fewer contacts with people and/or that they inhabited areas less important for economy of that period. Since this part of Europe remained mostly forested until the 15th century, it is reasonable to assume that wisents frequented open landscapes to a lesser degree than aurochs.

According to Hofmann (1989), aurochs, being true grazers (roughage eaters), were more dependent on access to open pastures than wisents, which were classified between grazers and intermediate feeders, *i.e.*, being better adapted to a mixed diet of monocotyledons and browse. As an example of the habitat effect, the disappearance of aurochs from Jutland by the beginning of the Boreal Period was attributed to the appearance of dense forests there (Degerbøl and Fredskild, 1970).

The question of whether wisents were true forest dwellers or were just pushed from open lands by the development of agriculture and settlements is still open, but the latest literature tends to support the hypothesis that the species developed from an early, post-glacial steppe form into somewhat of an opportunist preferring mosaic habitats with refuges and access to browse in the forest, but with good grazing conditions within forest meadows and openings (Kerley *et al.*, 2012, 2020; Kueemmerle *et al.*, 2012, 2018, 2020; Perzanowski *et al.*, 2019). On the contrary, limited access to open habitats and strong dependence upon a grassy diet could contribute considerably to the extinction of aurochs, which according to historical sources were initially more widespread and abundant than wisents, although the ranges of both species mostly overlapped during the Holocene (Wright, 2013; Hofman-Kamińska *et al.*, 2019).

An early disappearance of aurochs from central and eastern Europe, and even much earlier from the western part of the continent, which was more economically developed at that time, can be then attributed mostly to their frequent contacts and conflicts with people. Due to their strong affinity for open habitats they were more likely to be a nuisance in cultivated fields. Wisents, though, being not so easy to spot in the forest and rarely present in the open, were less exposed to direct encounters with peasants or hunters. Consequently, despite efforts of rulers of Poland to protect such attractive game, aurochs perished some 300 years before the extinction of the last wisents from the wild at Białowieża (Rokosz, 1995; Krasieńska and Krasieński, 2017).

Conclusions

Two main factors contributing to early and definite extinction of the aurochs were (1) the loss, by conversion to agriculture, of natural open habitats that provided favourable grazing conditions; and (2) human pressure resulting from presumably low social acceptance of the species. Wisents, however, managed to survive in the wild until the first half of the 20th century, because of their ability to adapt to a refuge from human persecution within a mosaic of mixed and deciduous forests, with less accessible glades and forest meadows along watercourses. This example shows how important for the survival of wildlife is the preservation of adequate land cover, representing habitats critical for those species. Our results suggest a selection of the most promising habitats for further reintroductions of wisents in contemporary Europe. Major attention should be paid to land cover and socio-economic conditions within reintroduction sites.

Authors' contributions

Both authors contributed equally to the manuscript.

Conflicts of interest

Both authors do not declare any conflict of interest.

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STRESZCZENIE

Dlaczego żubry zdołały przetrwać dłużej niż tury?

Dwa rodzime dla Europy gatunki dużych roślinożerców – tury *Bos primigenius* Bojanus, 1827 i żubry *Bison bonasus* Linnaeus, 1758 – występowały równocześnie do końca średniowiecza. Pomiędzy wiekiem XV a początkiem wieku XVII nastąpił szybki spadek liczebności populacji tura, podczas gdy żubry aż do końca I wojny światowej żyły nadal w stanie wolnym. Wyginięcie turów nastąpiło

pomimo ich ścisłej ochrony, a nawet dokarmiania zimowego nakazanego przez polskich królów. W Europie Zachodniej zarówno tur, jak i żubr wyginęły znacznie wcześniej i już w XVI wieku były powszechnie ze sobą mylone, o czym świadczy rycina z 1571 roku ukazująca różnice w ich wyglądzie i podająca właściwe nazewnictwo (ryc. 1).

Ponieważ w środkowej i wschodniej Europie występuje znaczna liczba tradycyjnych nazw geograficznych powiązanych z oboma tymi gatunkami, podjęto próbę oszacowania rozmieszczenia przestrzennego ich zasięgu występowania w czterech krajach (Polska, Litwa, Rumunia z Mołdową oraz Ukraina), a także porównania historycznych zmian w pokryciu terenu, aby zidentyfikować możliwe przyczyny tak znacznych różnic w ich przetrwaniu w stanie dzikim.

Nazwy obu gatunków w czterech wziętych pod uwagę obszarach językowych różnią się wyraźnie, co świadczy o dobrej ich rozpoznawalności w czasach historycznych (tab. 1). We wszystkich uwzględnionych w tym opracowaniu krajach liczba nazw geograficznych związanych z turami jest wyraźnie wyższa: nawet ponad 5-krotnie w Polsce i ponad 4-krotnie w Ukrainie (tab. 2). Pozwala to przypuszczać, że tury we wczesnym średniowieczu były znacznie bardziej liczne lub że gatunek ten był lepiej ludziom znany czy też miał dla nich większe znaczenie.

Według oceny powierzchni leśnej w obrębie terenów użytkowanych rolniczo, a więc niebiożącej pod uwagę obszarów niedostępnych (np. górskich czy bagiennych), zmniejszyła się ona radykalnie pomiędzy rokiem 1000 a 1400, a więc przed okresem panowania Jagiellonów, którzy na tury polowali już jedynie okazjonalnie. W przypadku Polski był to spadek o niemal połowę, na Litwie o niemal 40%, a na Ukrainie o prawie 30% (tab. 3). Proces ten związany był z powszechnym wylesianiem na potrzeby rolnictwa i osadnictwa, a skutkowało powstaniem wielkich otwartych obszarów oferujących atrakcyjną bazę pokarmową dla dużych roślinożerców.

Tak istotne różnice w częstotliwości występowania nazw geograficznych związanych z turami wskazują na ich częstsze niż w przypadku żubrów kontakty z człowiekiem. Można więc przypuszczać, że czynnikiem mającym największe znaczenie dla różnicy w czasie przetrwania obu gatunków była wyższa preferencja turów w odniesieniu do otwartych terenów, co czyniło je łatwiej zauważalnymi przez człowieka, a także sprzyjało powstawaniu konfliktów z rolnikami i hodowcami bydła. Na tę tendencję w odniesieniu do wykorzystywania terenów otwartych wskazuje także zaklasyfikowanie turów do typowych gatunków spասających, podczas gdy żubry uważane są za gatunek o diecie mieszanej, zawierającej też żer pędowy. Redukcja powierzchni leśnej oraz intensywny rozwój terenów zasiedlonych przez ludzi nastąpiły na obszarze Europy Środkowej i Wschodniej właśnie od końca średniowiecza, od kiedy zaznaczył się też drastyczny spadek liczebności tura na tych terenach. Wskazuje to, jak ważne dla przetrwania zagrożonych gatunków są okoliczności socjoekonomiczne.