Title:
Bos primigenius in Ancient Egyptian art – historical evidence for the continuity of occurrence and ecology of an extinct key species

Journal Issue:
Frontiers of Biogeography, 7(3)

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Publication Date:
2015

Permalink:
http://escholarship.org/uc/item/2cc00316

Acknowledgements:
This study was supported by a travel grant related to archaeological studies in Thebes. I would like to thank Rainer Drewello and Michael Hauck for the good time in Thebes, and Christian Laag and Reinhold Stahlmann for support in data management and Richard Field for helpful edits in the manuscript.

Keywords:
archaeozoology, aurochs, hunting, biodiversity loss, biogeography, extinction

Local Identifier:
fb_21527

Abstract:
Knowledge of the habitat requirements and temporal stability of populations of extinct aurochs (*Bos primigenius*) is surprisingly scarce. Reliable reports of this species, which by its domestication remains tremendously important for humans, are rare. As the species became extinct about 400 years ago and regionally disappeared much earlier, its behaviour and morphology are also under debate. Aurochs is also a crucial component of the mega-herbivore theory in nature conservation, but in fact its natural habitat and behaviour are unknown. Here, I report records of aurochs for the time period of Ancient Egypt. They are found in archaeological sites and literature, and in collections. Records of the species continue through all the periods of Ancient Egypt. In particular, hunting scenes illustrating the merits of high-ranking persons, in their graves (mastabas) and temples, provide insights into the behaviour and ecology of the depicted game. Here, special attention is given to one outstanding hunting scene that is documented in a relief at the mortuary temple of Ramesses III (1175 BC, Medinet Habu, Egypt). Assisted by a group of hunters, the pharaoh kills three specimens of aurochs. The whole scene is stunningly realistic. The adult specimen is fleeing towards the reed belt of the River Nile, suggesting that the species' habitat was probably in large valley bottoms, where open grassland is regularly created by flooding.

Endemic species of fish and game confirm that this scene took place in Lower Egypt. The regional populations of the North-African subspecies of aurochs probably went extinct shortly after this piece of art was produced. Records of species in ancient art can be very informative in terms of ecology and behaviour of species, especially when extinct species are addressed. In addition, the dating of old pieces of art containing biological information can be very precise, for instance when these refer to a historic personage.

Supporting material:

Table of occurrences of aurochs in art

opinions, perspectives & reviews

ISSN 1948-6596

opinion

Bos primigenius in Ancient Egyptian art – historical evidence for the continuity of occurrence and ecology of an extinct key species

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Abstract. Knowledge of the habitat requirements and temporal stability of populations of extinct aurochs (*Bos primigenius*) is surprisingly scarce. Reliable reports of this species, which by its domestication remains tremendously important for humans, are rare. As the species became extinct about 400 years ago and regionally disappeared much earlier, its behaviour and morphology are also under debate. Aurochs is a crucial component of the mega-herbivore theory in nature conservation, but in fact its natural habitat and behaviour are unknown. Here, I report records of aurochs for the time period of Ancient Egypt. They are found in archaeological sites and literature, and in collections. Records of the species continue through all the periods of Ancient Egypt. In particular, hunting scenes illustrating the merits of high-ranking persons, in their graves (mastabas) and temples, provide insights into the behaviour and ecology of the depicted game. Here, special attention is given to one outstanding hunting scene that is documented in a relief at the mortuary temple of Ramesses III (1175 BC, Medinet Habu, Egypt). Assisted by a group of hunters, the pharaoh kills three specimens of aurochs. The whole scene is stunningly realistic. The adult specimen is fleeing towards the reed belt of the River Nile, suggesting that the species' habitat was probably in large valley bottoms, where open grassland is regularly created by flooding. Endemic species of fish and game confirm that this scene took place in Lower Egypt. The regional populations of the North-African subspecies of aurochs probably went extinct shortly after this piece of art was produced. Records of species in ancient art can be very informative in terms of ecology and behaviour of species, especially when extinct species are addressed. In addition, the dating of old pieces of art containing biological information can be very precise, for instance when these refer to a historic personage.

Keywords. archaeozoology, aurochs, biodiversity loss, biogeography, extinction, hunting

Introduction: an iconic species

The motivation for this study is to bridge the gap between natural science and humanities in a field that is relevant for both sides. Pictures and artefacts in ancient cultures can be of high biological and ecological precision, they can be exactly dated, and they can be more abundant or frequent than remnants of organisms (e.g. bones). Traditional proxies for past environments and ecosystems such as pollen are preserved only under very specific conditions, refer to only few species, and dating precision can be low. Here, I focus on a key species of former ecosystems across the northern hemisphere, the aurochs, in order to improve the understanding of the ecology and biogeography of this important component of historical ecosystems. Besides woolly mammoth (*Mammuthus primigenius* Blumenbach 1799), aurochs (*Bos primigenius* Bojanus 1827) is perhaps the most prominent extinct large herbivore in Europe, Northern Africa and Asia. Four centuries after its complete disappearance, this species is still vivid in tales and myths. Vernacular names exist in many languages (e.g. auerochs, auroch, ur, urus, bour, tur, tarva, reem) (van Vuure 2005).

The functional role of this species is currently under debate in European ecology and nature conservation (Birks 2005, Johnson 2009). It is seen as a lost key species. The occurrence of species that are dependent on open habitats, which applies for instance to a large proportion of the Central European flora, can only be understood if open gaps were created in densely wooded landscapes. Here, the impact of large herbivores on vegetation structure is discussed as one possibility (e.g. Vera 2000, Svenning 2002, Birks 2005, John-

son 2009). The mega-herbivore hypothesis in nature conservation is used as an argument to support the back breeding (towards aurochs; see below) of cattle that exhibit primordial traits. These animals are then utilized in the management of nature reserves.

Bos primigenius is the origin for domestic cattle (*Bos primigenius taurus* or *Bos taurus*). European cattle were probably derived from Near-Eastern populations of aurochs (Troy et al. 2001). However, early domestication, which began about 8000 years ago, took place independently in different regions, and also in North Africa (Loftus et al. 1994). Breeding was mainly directed towards transport, meat and milk production. Bone finds and historical sources indicate that remnant wild populations persisted for centuries in landscapes with domestic cattle (e.g. Lasota-Moskalewska and Kobryn 1990).

The body size of aurochs contributed both to its attraction and to its vulnerability. Skeletons indicate that aurochs were significantly larger than modern forms of cattle (Lasota-Moskalewska and Kobryn 1990). Even though less than 20 complete skeletons are known, it is clear that the north-eastern African populations of aurochs varied regionally in size (Linseele 2004).

The animal weighted approximately one tonne. The withers height (i.e. the height of the top of the shoulder blades) was 170 cm on average for males (maximum 200 cm) and 150 cm for female animals (van Vuure 2002). In contrast, domesticated cattle rarely reach 150 cm. Aurochs legs were longer that those of modern cattle, and the shape differed considerably, height of the aurochs' withers almost equalling the length of the whole body (Matolcsi 1970).

Paintings and pictures that show the colour of the fur and the animal's posture are prominent in Stone Age caves, especially in Spain and Southern France (e.g. Feruglio 2006). Then there is a gap in European figurative documents until Renaissance times, though the behaviour of the animal was still reflected in tales and myths. Several pictures, however, tend to reflect or exaggerate a romantic impression of the animal, and realistic scenes in natural settings are missing over millennia.

As was the case in Poland for the last 'wild' population of aurochs, it seems that as the aurochs became increasingly rare it was increasingly managed as game for the hunting privilege of the nobility (Guintard 1997). Possibly, such populations were kept in habitats that did not reflect the species' ecological niche. However, in Egypt this was not necessary because close to the banks of River Nile unmanaged floodplains always existed. There, it seems unlikely that bulls were kept and released to the wild just for hunting (Brewer et al. 1994).

Historical evidence of Aurochs distribution and regional climatic changes within the range of the species

Because of the importance of aurochs (as ancestor of cattle) and its assumed relevance as an ecosystem engineer for nature conservation and forestry, various attempts to back-cross primordial forms of *Bos primigenius* have been and still are undertaken (Heck 1951). Bone finds are the main form of evidence used to compare between the original and the bred forms of cattle with original characteristics. Realistic pictures of the species are rare in mediaeval European art. A famous mediaeval painting from Augsburg (Nehring 1898) that is copied in zoological textbooks is probably lost (van Vuure 2005). Other mediaeval and renaissance depictions are rare and of low precision (see also Pyle 1994).

Stone Age cave paintings of aurochs (and other species) represent the dawn of art and civilisation, with most prominent examples in the SE European caves Chauvet (32,000 years ago), Altamira (18,000 to 13,000 years ago) and Lascaux (17,000 to 10,000 years ago). The abundance of such *Bos primigenius* pictures indicates its outstanding importance both as game and as a threat for the human societies of the time. After the Neolithic period, there appears to be a gap in aurochs artefacts until the 16th century (van Vuure 2002).

Bos primigenius is known to have occurred in North Africa since the early Middle Pleistocene (Martinez-Navarro et al. 2014) and is from then on continuously documented until the late Pleisto-

cene (Churcher 1972, Uerpmann 1987, Gautier 1988, Kowalski and Rzebik-Kowalska 1991) and during the Holocene (Faith 2014). The most southern Pleistocene bone finds range as far south as Kashm el Girba in eastern Sudan, close to Eritrea (14°51' N, 33°25' E), and Erg Tihodaine in the Ahaggar Mountains, which is today in the centre of the Sahara (approx. 25°12' N, 6°30' E; map in Linseele 2004). During the Holocene, bone finds of aurochs range from the Nile delta down to Elephantine, which is 200 km south of Thebes (Linseele 2004). Many of the finds are not precisely dated.

With the sudden onset of humid conditions around 8500 BC, which was caused by a specific planetary constellation, currently hyper-arid desert was replaced by savannah vegetation (Ritchie and Haynes 1987). In this period, the Indian Ocean monsoon brought much more precipitation to NE Africa and floods of river Nile were much more intense (Maley 1977, Preusser 2009, Pross et al. 2009). Gradual aridification began 7300 years ago (Jung et al. 2004). Palynological data show the ecosystem transition over a period of about 2000 years (Kröpelin et al. 2008).

The expansion of the desert forced people to leave the degrading savannahs and establish settlements in the moist valleys, which was the start of advanced civilization (Kuper and Kröpelin 2006). The declining water levels of river Nile are well documented from the 1st up to the 5th Dynasty (until 2400 BC) (Pachur and Altmann 2006), which means that climatic changes continued during the early periods of Ancient Egypt.

Dobson (1998) suggests that native populations of aurochs in North Africa might have become extinct after the mid-Holocene. However, the high number of Holocene bone finds, reports, and especially the documented pieces of art in this study confirm the presence of the species until approximately 1000 BC. In agricultural literature, in archaeology, and in art, the appearance of the species in Egypt is cursorily pointed out (Hilzheimer 1917, Wildung, 2011). Aurochs populations must have been relatively large up to the Egyptian New Kingdom (1550–1050 BC), but it is very likely that hunting was reserved for the pharaoh. Hieroglyphs report that Amenhotep III (who reigned 1388–1351 BC) killed 96 animals (Strouhal 1989). It is unclear exactly when the species became locally extinct; van Vuure (2005) doubts whether the reported aurochs hunts of Ramesses II (1197–1165 BC) still took place at the River Nile.

In the Middle East, aurochs is documented in several Mesopotamian sources such as the epic of Gilgamesh (approx. 3000 BC) (van Vuure 2005). The aurochs population in Mesopotamia appears to have been very large, and its hunting is known in the cases of Assurnassirpal II (883–859 BC) and Senacherib (704–681 BC) (van Vuure 2005).

In the Southern Levant, aurochs became probably extinct at the end of the Iron Age (records up to 500 BC) (Tsahar et al. 2009). Human population density increased strongly during this period, concentrated especially in the valleys that provided water for irrigation and substrate for agriculture. If the species was bound to wetlands and valleys, there would have been a conflict with human land use. Even so, it is very likely that hunting of the remnant populations was the final cause of aurochs.

The species was part of the late-glacial overkill, and was definitely erased from large parts of its Pleistocene distribution during the Greek and Roman civilisations. In his book on zoology, Aristotle lists the European bison (*Bison bonasus*) but does not explicitly mention the aurochs (cf. Balme 2002). He would not have ignored such an important species. At his time the species might have been extinct in Greece and Turkey, but the original zoological writings of Aristotle do not exist and what we know comes only from Arabian translations of them.

During Roman times, sporadic notes on aurochs in the Mediterranean exist, for instance by Julius Caesar, Seneca and Pliny the Elder (Pyle 1994). Presumably, some of these may relate to animals that were imported for performances in Roman arenas (Gautier 1988). It is unclear which aurochs populations were used for these shows, but it is unlikely that specimens were caught in remote Eastern European forests. Roman mosaics in Leptis Magna in Libya also show aurochs hunts or fights, but this does not necessarily confirm

remnant local populations. Leptis Magna was an important trading place for exotic wild animals for Roman circus games from the 1st to the 4th century AD (Bianchi Bandinelli et al. 1966). Further, without clear attribution to locations, the species is mentioned in the Bible under the Hebrew word for aurochs, "reem" (e.g. Books of Moses, Job and Isaiah). There, it is clearly stated that these bulls could not be tamed or used in agriculture.

In less developed continental Europe, aurochs populations could persist in the enormous forests. Mediaeval reports say that aurochs fought furiously when being hunted and trapped. The hot-tempered animal was very dangerous, especially when injured (van Vuure 2002). The rarer the species became, the more it was an exclusive privilege of the nobility to hunt this outstanding game. Aurochs had special status in the hunting rights of the European nobility (Wrzesniowski 1878, van Vuure 2002). The last remaining population was recorded in a large royal hunting reserve in Poland (Jaktórow Forest), including estimated numbers of individuals, until the early 17th century (Heymanowski 1972, van Vuure 2002). The last specimen died of natural causes during the chaos of the Thirty Years' War, in 1627 AD. The population had not been protected and managed any more and had presumably declined below its viable population size.

Continuity of Bos primigenius in Ancient Egypt

During the early Holocene, aurochs was abundant across the Holarctic realm in Europe, Northern Africa and Asia ranging from the coast of the Atlantic Ocean to Korea (van Vuure 2002, Pushkina 2007). Subarctic regions and high mountains were not part of the species' habitat.

Three subspecies of aurochs are differentiated in the literature: *Bos primigenius* ssp. *primigenius* (Bojanus 1827), *Bos primigenius* ssp. *namadicus* (Falconer 1859) and *Bos primigenius* ssp. *mauretanicus* (Thomas 1881, syn.: *B. primigenius africanus*, *B. primigenius ophistonomous*).

England was reached because large parts of the North Sea were terrestrial surface during the last glaciation period, with sea level about 120 m below current. Hall (2008) supports the hypothesis, for the geographical distribution of post-glacial finds of aurochs in England, that the species was bound to low-lying flat sites such as broad valleys, which are exposed to floods and were unattractive for human settlements. Nevertheless, these sites are fertile and produce large amounts of biomass.

Knowledge of the occurrence of aurochs along the River Nile is based on bone finds (see also Gautier 1988, Linseele 2004) as well as historic references (Boessneck 1988, Yeakel et al. 2014). Archaeological records exist from the Pleistocene through Stone Age periods up to the rise of advanced cultures in Ancient Egypt.

In this study, additional aurochs records are documented (Table 1, Appendix). We can distinguish between hunting scenes in the wild, single depictions of the species in artefacts and scenes in captivity. Pictures of aurochs can be clearly distinguished from scenes with domesticated cattle. Cattle differ from aurochs in shape (and colour), but importantly cattle are mainly shown in an agricultural context, for instance pulling ploughs.

The documented pictures and artefacts show that aurochs was continuously present along river Nile over millennia. Wild aurochs existed during all flourishing periods of Ancient Egypt (Fig. 1). The phases of low numbers of records are the intermediate periods between the Old, Middle and New Kingdoms, where historical evidence is generally low.

The ecological content of the hunting scene in Medinet Habu

Hunting was an important activity of the upper class in Ancient Egypt. In order to continue hunting in the afterlife, realistic hunting scene paintings and reliefs were put for example in tombs and mortuary temples. Hunting of bovines was common (Manlius 2000) and aurochs was the only bovine game. Neither European bison (*Bison bonasus*) nor water buffalo (*Bubalus arnee*) occurred in Egypt and African buffalo (*Syncerus caffer*) was recorded only during the Pleistocene and moist periods of the mid Holocene (Yeakel et al 2014).

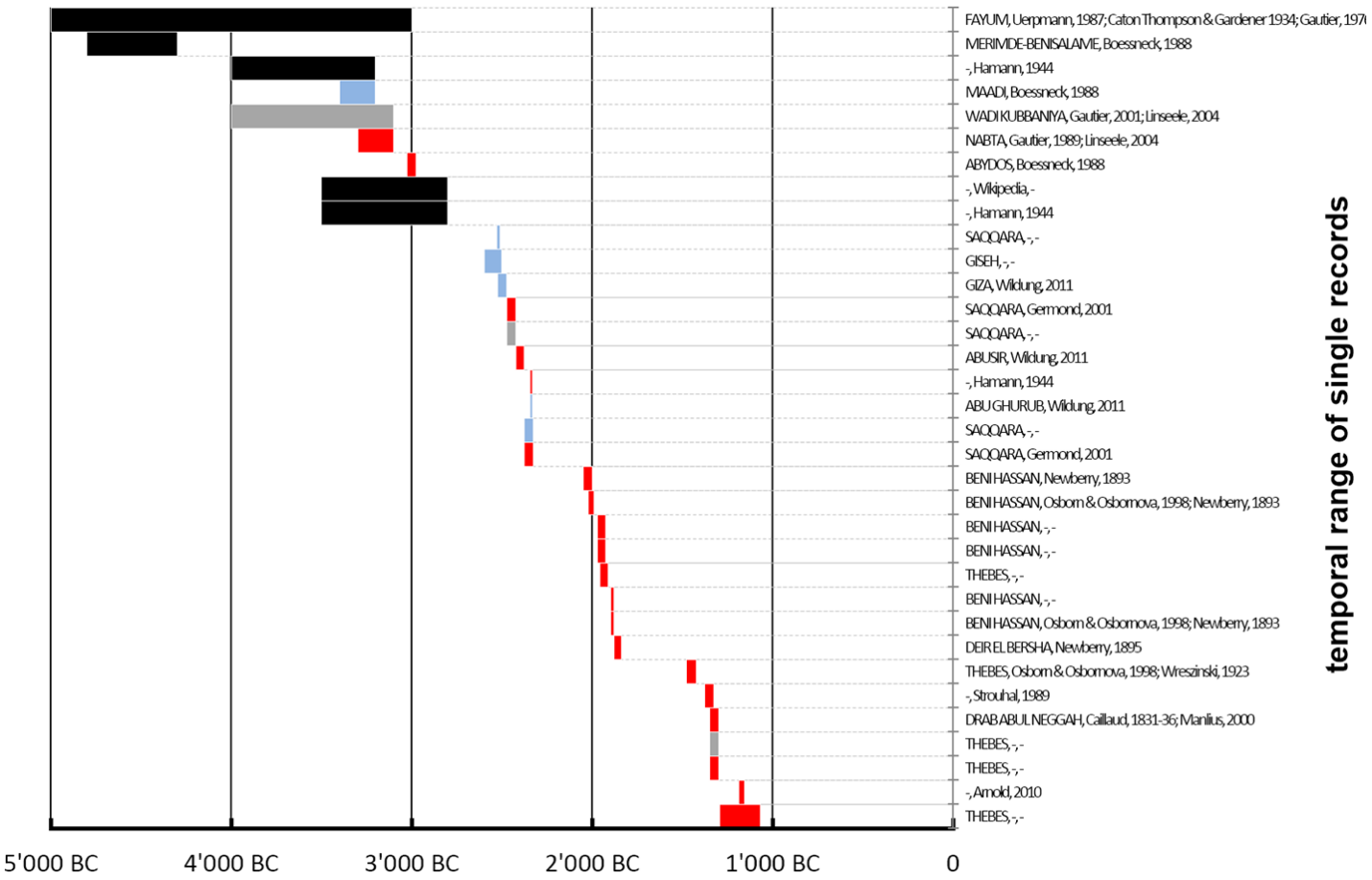

Figure 1. Records of *Bos primigenius* in Ancient Egyptian Art (n=34). Black – bone finds; red – hunting scenes in the wild; blue – animals held in captivity; grey – other artefacts (e.g. sculptures) and pictures. Records continue through all periods but are clumped in the Old, Middle and New Kingdom. Politically chaotic transition phases in between are poor in artefacts. All single records are documented in the electronic appendix (Table 1). Dating uncertainty is shown by the lengths of bars.

Several hunting scenes exist, where aurochs is shown together with ibex (*Capra nubiana*), antelopes (e.g. *Oryx dammah*, *Oryx leucoryx*, *Alcelaphus buselaphus buselaphus*, *Addax nasomaculatus*) and gazelles (*Gazella dorcas dorcas*, *Nanger soemmerringii*). Some of these species or subspecies are also regionally extinct. However, many scenes represent sequential arrangements of hunted species and not realistic impressions of animal communities in natural ecosystems. The scene in Medinet Habu is thus extraordinary (see next paragraph), and reflects the development of ecological knowledge (and art) in Ancient Egypt.

The mortuary temple of Ramesses III (Medinet Habu, Luxor) was completed in 1175 BC, during the life time of the pharaoh (who reigned 1186– 1155 BC) (Murnane 1980). On the southwestern outer wall of this temple there is a stunning example of Ancient Egyptian art, which was made to highlight the successes and achievements of the pharaoh. The hunting scene at the mortuary temple of Ramesses III demonstrates that aurochs lived at his time on the banks of river Nile (Fig. 2). In this period, aurochs hunting may have been reserved for the pharaoh and perhaps this scene shows one of the last hunts of all. In the scene, the large male aurochs is trying to escape towards the river. It has reached the dense reedbed but there is no chance of escape. The injured bull is cornered by the hunters and its legs are collapsing in its struggle to reach the water.

The hunted animals are depicted with high morphological precision. These bovines clearly differ from domestic cattle. It is not only the shape of the horn, which cannot be taken as proof of wild aurochs because among the breeds of cattle in Ancient Egypt a huge variety of horn-shapes existed. As explained above, compared to domes-

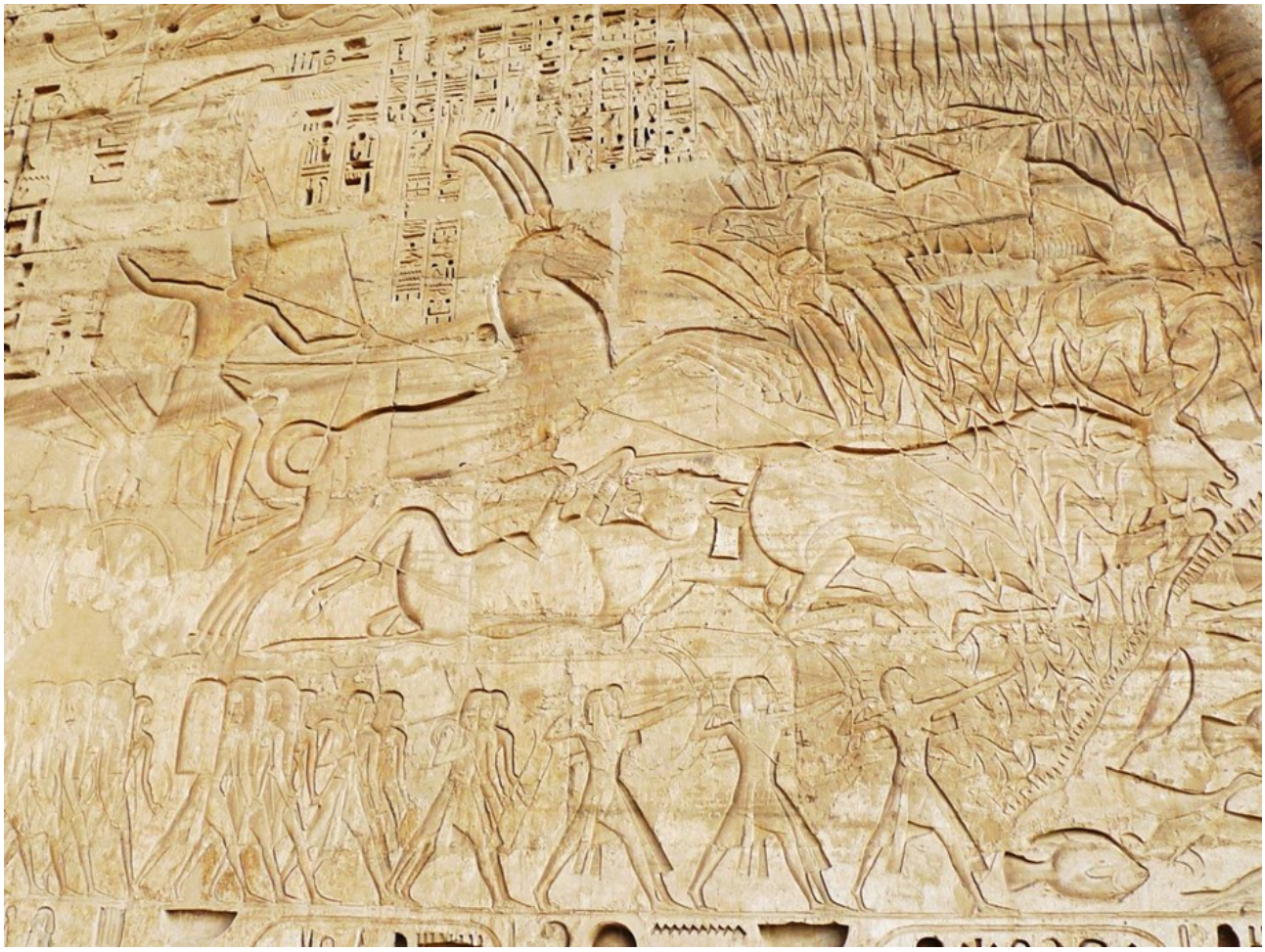

Figure 2. The pharaoh Ramesses III is hunting aurochs on a chariot at the bank of the Nile. He is accompanied by bowmen and armed hunters. A large aurochs is hit by a spear and collapses in the dense reeds at the river margin with its tongue hanging out. Additionally, two juveniles are lying on the ground, one apparently dead with eyes closed and the other one bending its neck up. This relief is located on the back side of the large pylon in the temple of Medinet Habu (Thebes). The whole size of the scene (including Fig. 3 and 4) is approx. 9 x 9 m. The scene was not visible to the public but directed towards the private ritual palace of Ramesses III within the temple area. Photo C. Beierkuhnlein.

tic cattle, the legs of aurochs were long. The whole animal was very tall but Egyptian reliefs do not follow a standard scale. More importantly, it is discernible in the shape of the animal in this relief that the height of the withers almost equals the length of the body – again characteristic of aurochs (Matolcsi 1970; see above).

In pieces of Ancient Egyptian art, domestic cattle are always shown in a schematic way: as a donation to act as food supply for a dead person, in slaughtering scenes or being held on ropes. Hunting scenes, in contrast, are frequent in tombs (mastabas) and mortuary temples, and they always show animals in the wild.

Certainly, hunting domesticated cattle would not be of great honour for a pharaoh. After the regional extinction of elephants in North Africa, aurochs was the most dangerous game. No artist would have been assigned to illustrate a "cow hunt" in such an elaborate way, at such a special and prominent place as on the walls of the mortuary temple of Ramesses III. The location of the relief (which is several meters in breadth) at the back side of the large pylon, is of importance. On the other side of the pylon, facing to the visitors of the temple, the greatest military successes of the pharaoh are documented in scenes where he kills men from other countries. The hunting scene is equally large, but it was to be seen only from the private ritual palace of the pharaoh, and from his temple. Between the chariot and the hunted bull, a calf has fallen down and is lying on its back, with its neck upright. In the upper part of this scene another specimen has already been

Figure 3. Animals of the Nile River shown on the relief can be attributed to certain species of fish (centre on top: *Marcusenius cyprinoides*; upper right side: *Eutropicus niloticus*; bottom centre: *Alestes baremose*; centre and left lower margin: *Oreochromis niloticus*) and geese (cf. *Anser anser*). Photo C. Beierkuhnlein.

killed. The pharaoh himself is the one who kills the animals, though he is supported by a large group of hunters, lined up below the scene.

Various other species can be identified in this fascinating relief. Most notable is the thicket of reed (*Phragmites australis*) into which the aurochs is trying to flee. This vegetation is still characteristic of the margins of the Nile, today. It indicates the ambition of the artists to show the real habitat of the animal. In the water on the right-hand side, several species of fish can be identified, such as Nile Tilapia (*Oreochromis niloticus syn. Tilapia nilotica*) and others (cf. *Marcusenius cyprinoides, Eutropicus niloticus*, *Alestes baremose*) (Fig. 3). Geese (probably *Anser anser*) feed close to the water or fly away, upset by the hunt. At the top of the relief, more groups of game species can be seen (Fig. 4). *Equus* and *Oryx* are not proof of a location in Northeast Africa, but *Alcelaphus buselaphus buselaphus* was native to North Africa (Holloway 1976) and did not occur in Mesopotamia or Asia. Locating the other mammal herds above the aurochs hunt may indicate a higher location, at the margin of the valley. In the narrow valley of the Nile, wetlands and mountainous habitats are found in close proximity, unlike in Mesopotamia.

This scene is a reflection of a local ecosystem. Together, the endemic fish and mammal species confirm that the depicted scene took place in Egypt. In the biological literature on aurochs, this relief (which is difficult to find, at the rear of the pylon) has hitherto been unknown (van Vuure 2005) or misinterpreted. Osborn and Osbornova (1998) reproduced a copy of an old photo (source Louis Grivetti) of this scene but erroneously assumed that the hunt took place in Mesopotamia. Indeed, following the construction of the Temple in Medinet Habu (1175 BC) there is no further evidence for the existence of aurochs in Egypt.

Figure 4. In the same relief at Medinet Habu, several herds of other herbivores are shown (*Oryx dammah* or *leucoryx, Equus africanus, Alcelaphus buselaphus buselaphus*). The lioness, which is attacking a wild donkey, indicates that this scene did not take place in captivity. Photo C. Beierkuhnlein.

There appears to have been a change in hunting practice over time. In the scene at Medinet Habu, two juvenile animals are killed. Older scenes of 'hunting in the desert' only show the killing of adult bulls, whereas cows and juvenile animals were allowed to escape (Manlius 2000) (Fig. 5). In the Egyptological context, 'desert' refers to natural ecosystems outside the agricultural landscape and settlements. Like in Mesopotamia, the hunting of aurochs was carried out with horse-drawn chariots, arrows and spears, sometimes supported by dogs. Hunting with horses is impressively portrayed on Tutankhamun's hunting chest lid (Sandison 1997).

Van Vuure (2002) argues that sedge marshes may have been the major habitat of *Bos primigenius*. As a large mammal that depended on local resources and did not migrate within its individual life cycle over large distances following seasonal availability of biomass, aurochs is not likely to have built up very large populations. Based on its tooth structures, and on rare verbal descriptions, aurochs probably fed mainly on grasses and herbs (van Vuure 2002). This indicates that the species could hardly exist in closed-canopy forest with low biomass in the herb layer; it was more related to open gaps, grasslands, marshes and reeds. In forested landscapes with dense forests and closed canopies, such habitats depend largely on disturbances such as fire, wind throw or flooding.

Discussion

Regarding the scarcity of records, it comes as no surprise that knowledge of population trends, distribution, morphology and behaviour of aurochs is scarce. Even though pictures of aurochs are prominent in Stone Age caves, especially in Spain and France, there is an almost complete gap in figurative documents until Renaissance times, when only few low quality pictures were produced when the species was on the brink of extinction. Realistic scenes in nature are missing. Memory of the

Figure 5. Hunting scene in the tomb of Antefoquer (1958–1913 BC) in Thebes (tomb number TT60) from the beginning of the 12th dynasty. In the second row, a male aurochs is hit by a spear and attacked by a hunting dog. The female animal (turning her head back) and the calf are allowed to escape. Species in this scene include: *Alcelaphus buselaphus buselaphus, Dama dama mesopotamica, Bos primigenius, Oryx leucoryx, Gazella dorcas dorcas, Vulpes vulpes, Lepus capensis,* and *Ammotragus lervia.* Photo Osiris Net.

species has mainly been passed on in tales and myths (van Vuure 2002).

The Egyptian culture did not produce natural science literature like the Greek culture did some centuries later. However, artists that decorated buildings such as the tombs and mortuary temples of important personalities had precise perceptions of nature. Until recently, this important source of biogeographical information has been ignored (Yeakel et al. 2014), though pitfalls must be considered (Evans 2015). In this paper I have started to plug this gap, documenting what seems to be a continuous aurochs population alongside the Nile during the Holocene until approximately 1000 BC. These historical archives, most importantly the hunting scenes, have specific advantages and problems. Precision in the dating of these artefacts and pictures is extremely high. In addition, such scenes can include ecological information on the species' habitat. This makes

them superior to most other historical records.

Dating is best when the pieces of art are closely associated with the life of an individual person. Tombs were constructed during the lifetimes of pharaohs or high-ranking civil servants and not typically in the year of death. Nevertheless, this still gives a dating precision that is much higher than for radiocarbon dating. However, not all finds are clearly attributed to a person with a well-known lifespan. Additionally, the production of art is subject to political stability and economic prosperity. In times of chaos, as in the intermediate periods between the Old, Middle and New Kingdoms, evidence is lacking. As a result, the abundance of records is temporally patchy (see also Evans 2015).

Some pieces of Egyptian art are of astounding precision regarding animal morphology. In the Neferhotep tomb hunting scene, aurochs shows the characteristic whitish eel stripe on its back (Manlius 2000). Here, bull and cow are considerably different in size, which confirms the sexual dimorphism of the few complete skeletons. In the scene at Medinet Habu, we can see the reed belt of the River Nile. Such places close to the river were highly dynamic and fluctuating in extent because of seasonal flooding, erosion and sedimentation. The image at Medinet Habu is very likely to depict the characteristic natural habitat of the species. If so, aurochs may not have created open forest gaps for herbs and grasses as the megaherbivore theory assumes (Birks 2005). It is known from other regions that the preferred habitats of aurochs were dense forests on valley bottoms, wetlands and river banks (Hall 2008, Tsahar et al. 2009). Aurochs may still have acted as an ecological engineer and key species in Ancient Egypt. However, open space with grassy vegetation was probably created not by the animal itself but rather by the flooding regime of a braided river.

It is generally assumed that southern habitats served as refugia during the LGM for species such as aurochs (Sommer and Nadachowski 2006). Nevertheless, there is evidence that the Holocene warming did not lead to substantial population growth in aurochs (Mona et al. 2010), which could be a result of human hunting pressure. In northern Africa, during the Pleistocene, arid conditions and sand dune formation coincided with intense Arctic glaciation and low sea levels, resulting in a high degree of connectivity between Africa and Asia because neither the Persian Gulf nor the Red Sea functioned as marine barriers (Williams 2009). The Holocene then brought drastic changes in precipitation regimes. Desert climate was replaced by humid conditions between 8500 BC and 3500 BC (Preusser 2009). The maximum monsoon rainfall occurred around 6500 BC, when lakes and wetlands were common in the present-day Sahara (Pachur and Altmann 2006). The zonal vegetation was characterized by savanna ecosystems. Tropical species occurred up to 500 km north of their present-day distribution, especially in humid depressions (Watrin et al. 2009). No analogue of this historic setting exists today. Large herbivores must have found excellent conditions in the early-Holocene landscapes of northern Africa and could expand their populations.

The period of Ancient Egypt, and the development of its high culture, is linked to remarkable climatic changes. The re-formation of the desert correlates with the establishment of settlements in valleys and the development of high civilization. With increasing aridification around 4000 BC, species that require large amounts of biomass necessarily had to move to the valleys. Since 2300 BC, arid conditions have prevailed and the availability of water was more and more restricted to the valleys. This must have caused increased encounters and conflicts between humans and large herbivore species.

Conclusion

Documents from archaeology and art can be valuable sources of ecological and biogeographical information. In particular, hunting scenes in Ancient Egyptian art represent a surprisingly precise reflection of the historic mammal fauna in northwestern Africa. These pieces of art also demonstrate the regional (and part of the global) loss of vertebrate biodiversity. The scene in Medinet Habu (Thebes) even reflects the ecology and behaviour of extinct aurochs (*Bos primigenius*). Further hunting scenes include more species that are now

extinct in the wild (e.g. *Oryx leucoryx* and *Oryx dammah*) or subspecies that are globally extinct (e.g. *Alcelaphus buselaphus buselaphus*). These examples should encourage biogeographers towards more extensive use of historical sources of information.

Acknowledgements

This study was supported by a travel grant related to archaeological studies in Thebes. I would like to thank Rainer Drewello and Michael Hauck for the good time in Thebes, and Christian Laag and Reinhold Stahlmann for support in data management and Richard Field for helpful edits in the manuscript.

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Submitted: 13 February 2014
First decision: 12 April 2014
Accepted: 04 August 2015
Edited by Jessica Blois