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Review

Holocene distribution and extinction of the moose (*Alces alces*, Cervidae) in Central Europe

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Abstract

Moose (*Alces alces* L.) were among the first large mammals to recolonize Central Europe after the last glaciation. Already during the Allerød they established themselves in most parts of the area. In the early Holocene their distribution range extended from the Pyrenees to Denmark and from Austria to Great Britain and also covered eastern Central Europe where they still occur today. In the Preboreal, the moose slowly vanished from the southwestern parts of its distribution range, leading to its extinction in France and, later, in England. During the Atlantic period, the moose died out in large parts of Denmark and population densities apparently decreased in the rest of Central Europe as well. Around the birth of Christ only relict populations were left in western Central Europe, which finally became extinct in early medieval times. In Thuringia and in the region northeast of the river Elbe as well as in central Poland, some stocks persisted until the high and late Middle Ages. The causes of the gradual extinction in Central Europe during the Holocene are complex. Changes in vegetation, climate and sea-level, the increasing fragmentation of habitat through human activities and hunting were, at different times, important factors. In the recent past, however, moose have repeatedly migrated from the east towards the west. The development of its distribution range since the end of the Second World War as well as experiences with Scandinavian populations show that moose are able to thrive in close proximity to humans and that a future expansion of its distribution range towards the west seems possible.

Key words: Alces alces, Holocene, Europe, archaeozoology, palaeoecology

Introduction

The moose (*Alces alces*) is the largest living cervid and one of the biggest terrestrial mammals in Europe, second only to the European bison. Its present distribution range extends from northern, central and eastern Europe across northern Asia to North America. Moose occur almost continuously between 50 and 70°N latitude and south to about 40° (Nygrén 1986; Geist 1998).

Systematically, moose (Alcinae) are related to the New World deer and branched off in the late Tertiary, being present in the Palaearctic mainly as *A.* (*Libralces*) *gallicus* and *A.* (*Libralces*) *latifrons* (Nygrén 1986; Geist 1998). According to the orthodox view of Alcine phylogeny, *A. latifrons* gave rise to the modern moose *A. alces* (cf. Kurtén 1968; Heintz and Poplin 1981; Lister 1987, 1993;

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Kahlke 1990, 1994; but see von Koenigswald 2002 and Sher 1987 for criticism). The origin of the Alcine lineage is Central Asia (Kahlke 1990) or Europe (Heintz and Poplin 1981), while modern moose originated in Asia and then subsequently colonized Europe and America (Hundertmark et al. 2002).

Alces alces, as compared to the fossil forms, is characterized by shorter antler beams and the loss of any contact between the premaxillary and nasal bones. It first occurred in the Riss/Saale glacial. Modern moose were absent from North America until after the last glacial maximum when they moved in from eastern Siberia via Beringia, being part of the Siberian fauna that filled the vacuum left by the late Pleistocene "megafaunal" extinctions some 10,000 years ago (Geist 1987; Guthrie 1990). Moose have traditionally been divided into two types: European-West Siberian (up to the Yenisei River) and East Siberian-American (Flerov 1952). These two groups differ in antler plan (three-pronged in European-type, four-pronged in American-type moose, Geist 1987, 1998) and also in karyotype ($2n = 68$ for European, $2n = 70$ for eastern Asian and American moose, Gustavsson and Sundt 1968; Hsu and Benirschke 1973; Boeskorov 1996, 1997). The European moose, which this review is dealing with, is referred to as *Alces alces alces*.

Based on genetic data, Hundertmark et al. (2002, following Avise 2000) suggested a recent bottleneck in European moose although the sample size for Europe in their study is too small to draw definitive conclusions. Nevertheless, this scenario is in line with the history of moose in the European part of the former Soviet Union, an area covered by Hundertmark et al. (2002), as described detailedly by Heptner et al. (1966) and Heptner and Nasimowitsch (1967). According to these authors, moose populations drastically declined in the first half of the 19th century following the rapidly increasing demand of moose leather since Peter the Great, some 100 years earlier, had decided to clothe the army almost exclusively with this material. When the use of moose leather was stopped, populations slowly recovered from this bottleneck, but after the Revolution poaching exploded and moose stocks again declined catastrophically. After that, due to strict protection measurements, moose numbers increased again. Similar bottlenecks have been reported from Scandinavia, where the species was nearly extinct at the beginning of the 19th century (Rülcker and Stålfelt 1986), and Poland (see below).

Table 1. Subdivision and timescale (BP=years before present) of the Late Pleistocene and the Holocene (after von Koenigswald 2002).

Holocene	Subatlantic	3000 BP–present
	Subboreal	5600–3000 BP
	Atlantic	9100–5600 BP
	Boreal	10,000–9100 BP
	Preboreal	11,500–10,000 BP
Late Pleistocene	Younger Dryas	12,700–11,500 BP
	Allerød	13,500–12,700 BP

Being present since the Allerød period (Table 1), the moose was one of the first large mammals to immigrate into Central Europe at the end of the Pleistocene (Willms 1987; von Koenigswald 2002). Studies from Denmark show that *A. alces* survived in a woodland or open park tundra 350 km south of the ice front (Aaris-Sørensen 1992). According to Willms (1987; see also Andersen et al. 1990; Döhle 1996; Szymczyk 1973), the Holocene history of the moose was as follows. During the late Pleistocene, moose were very rare north of the Alps but became more abundant (and in the Baltic countries even the most frequent ungulate species) in the Preboreal. In the Boreal, the English moose population, now separated from the mainland, declined, and Scandinavia, with the ice sheets retreating, was colonized, on the one hand, via Denmark and Scania (Sweden), and, on the other hand, from Russia via Karelia to Finland and north Sweden. At the same time, the southern edge of the species' distribution shifted northwards with the moose-dominated zone (i.e. the area in which moose were the most abundant ungulates) already being north of Scania. From the following Atlantic period on, northern Europe was free from glaciers. At most Central European excavation sites from this period, the moose was rare while in