



# Diet and habitat of the saiga antelope during the late Quaternary using stable carbon and nitrogen isotope ratios



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## ABSTRACT

Saiga antelope (*Saiga tatarica*) is one of the typical late Pleistocene species of the cold and arid mammoth steppe that covered a large area of northern hemisphere. The species is currently endangered and persists only in small areas of Central Asian steppe and desert ecosystems. The investigation of the ecology of the Pleistocene saiga using stable isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) aimed to decipher how different their diet and habitat were from those observed nowadays in relict populations. Up to 76 samples of bone collagen of ancient saiga from Western Europe, Siberia and Eastern Beringia were analysed and compared with 52 samples of hair and bone collagen of modern specimens from Kazakhstan, Russia and Mongolia. The  $\delta^{13}\text{C}$  values of the ancient saiga do not exhibit a clear trend over time. They cover the same range of values as the modern ones, from a C3-dominated to a C3-C4-dominated mixed diet (including probably Chenopodiaceae). In contrast, the  $\delta^{15}\text{N}$  values of fossil saigas are more variable and lower on average than the extant ones. The lowest  $\delta^{15}\text{N}$  values of ancient saiga are found around the Last Glacial Maximum, reflecting the influence of the cold conditions at that time. On the other hand, fossil saiga occupying the same regions as the historical and modern populations exhibit high  $\delta^{15}\text{N}$  values similar to the modern ones, confirming ecological continuity over time. Modern saiga is thus occupying just one of its potential diverse habitats they used in the past. Therefore, the extant saiga is not a refugee species confined to a suboptimal habitat. During the late Pleistocene, the saiga occupied a separate niche compared with the other ungulates of the mammoth steppe. However, this species could also adapt to a lichen-dominated diet normally seen in reindeer, leading to an isotopic overlap between the two species in south-western France and Alaska around the Last Glacial Maximum. This adaptation allowed a geographical expansion that does not correspond to a habitat-tracking episode. Hence, the realized niche currently observed for the saiga is reduced compared with their potential capacity for adaptation, a crucially important factor for the conservation of this endangered species.

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## 1. Introduction

During the Pleistocene, until around 12,000 years ago, saiga antelope (*Saiga tatarica*) was part of a steppe-tundra ecosystem, the so-called mammoth steppe, which spread from Western Europe north of the Pyrenees and the Alps to north-western North America

(Guthrie, 1990). The climate was dry and cold, but soils were richer in nutrients than present-day Arctic soils, allowing different plants to grow and produce more biomass, allowing them to be grazing tolerant (e.g. Zimov et al., 2012). This productive ecosystem supported a wide range of large mammals. Those common to both regions include: woolly mammoth (*Mammuthus primigenius*), steppe bison (*Bison priscus*), cave lion (*Panthera spelaea*), musk ox (*Ovibos moschatus*), moose or Eurasian elk (*Alces alces*), elk or wapiti (*Cervus canadensis*), caribou or reindeer (*Rangifer tarandus*) and horse (*Equus* spp.). Others such as woolly rhinoceros (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*), cave bear (*Ursus*

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*spelaeus*) and spotted hyena (*Crocuta crocuta*) were confined to northern Eurasia, whereas helmeted musk ox (*Bootherium bombifrons*), short-faced bear (*Arctodus simus*) and sabre-tooth cat, (*Homotherium serum*) occurred only in North America (e.g. Vereshchagin and Baryshnikov, 1982; Guthrie, 1990, 2001; Stuart, 2015).

This ecosystem appears very different from that of modern saiga antelope. Saiga is now found in the open and flat dry steppes, semi-deserts and deserts of Central Asia, where they have avoided human pressure (Lushchekina and Struchkov, 2001; Berger et al., 2008; Buuveibaatar et al., 2009, 2011, 2014). The characteristic large bulbous nose of the saiga seems not only well adapted for breathing and filtering the dusty air, but also helps to warm cold air before it reaches the lungs. In addition to thick winter fur, the abilities to feed through thin snow cover and not requiring much drinking water (Bannikov, 1963; Clifford and Witmer, 2004) may have resulted from adaptations to the cold mammoth steppe environment. Studies of skull morphology (e.g. Baryshnikov & Tikhonov 1994, Ratajczak et al., 2016) and genetics (e.g. Campos et al., 2010) discussed the existence of distinct *Saiga* lineages in the past, such as the possible occurrence of subspecies including *S. t. borealis*. This subspecies is thought to have been bigger and more robust and to have disappeared from most of its former distribution, like most of the large mammals of the mammoth steppe. Although there are arguments for morphological differences, genetic evidence is less clear and no correlation has been evidenced so far between taxonomy and paleoecology of ancient saiga.

During some intervals of the late Pleistocene, saiga occurred widely across Eurasia and into North America (e.g. Nadachowski et al., 2016). In contrast, current populations have declined dramatically since the end of the last century, and are now critically endangered (Mallon, 2008). Fragile relict populations remain only in parts of south-western Russia, Kazakhstan (sometimes also Uzbekistan and Turkmenistan) and Mongolia (Lushchekina and Struchkov, 2001; Mallon, 2008) (Fig. 1). Four modern populations of the subspecies *Saiga tatarica tatarica* remain in: south-western Russia (Kalmykia) and Kazakhstan (Ural/Volga River, Ustiurt and Betpak-Dala) together with a smaller one of *S. t. mongolica* in western Mongolia, which in turn can be split into 4 sub-populations: Mankhan, Shargiin Gobi, Khuisiin Gobi and Dorgon Plain (Mallon, 2008; Milner-Gulland et al., 2001; Buuveibaatar et al., 2013). In many European areas, saiga antelope was common until the 17th or 18th century, first disappearing from Bulgaria, later from the Moldavian, Romanian and Ukrainian steppes, because of agricultural development and human population growth (Lushchekina and Struchkov, 2001). In China's north-eastern Junggar and Tacheng Basins, they became extinct due to hunting for their high-priced horns used in traditional medicine. The last reports from local herdsmen, who sighted several small groups of 3–4 individuals, are from 1984 (Gao et al., 2011).

A better understanding of past saiga ecology and comparing them with modern populations may help in evaluating the quality of the current habitats. Indeed, areas from which saiga have disappeared, but with vegetation and climatic conditions similar to past habitats, could be considered for future reintroduction in order to sustain genetic variability and limit the risks of mass mortalities, such as was seen in late spring 2015 during which more than 130,000 individuals died, representing more than half of the biggest population in Kazakhstan (e.g. Science, 2015; Saiga Conservation Alliance, 2015).

Comparing past and present saiga ecology, the central questions are: did saiga antelope live in much broader ecological conditions in the past? And if yes, does the much smaller present-day home range reflect the optimal habitat of the saiga antelope whose range has varied over time, or is their current habitat a refugium where

conditions differ from a past optimum? To answer these questions, differences and similarities in the ecology and habitat of past and present saiga antelope need to be studied. For reconstructing the ecology of the late Pleistocene mammals and food webs from the mammoth steppe, stable carbon and nitrogen isotope ratios ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) provide valuable information on the diet of herbivores, reflecting the isotopic compositions of the local vegetation, which is influenced by environmental factors such as aridity, temperature and soil quality. Previous studies of endangered species, e.g. by Crowley et al. (2012) on Madagascan lemurs, by Holdaway et al. (2013) on the brown teal *Anas chlorotis* from New Zealand, and by Bocherens et al. (2015) on European bison *Bison bonasus* used the same approach to discuss whether or not these are refugee species, namely confined in suboptimal habitat.

## 2. Material and methods

### 2.1. Sample overview

We investigated previously unpublished fossil saiga antelope bone samples selected from the Late Quaternary megafaunal extinction project of Tony Stuart and Adrian Lister. Published data of samples from south-western France (Drucker and Henry-Gambier, 2005) and Crimea (Péan et al., 2013) have been included (Table 1). These total 76 samples from Belgium, France, Bulgaria, Ukraine, Russia, Kazakhstan, Turkmenistan and the United States (Alaska). They all have been either directly radiocarbon dated or indirectly dated by stratigraphy, ranging from the 11th to 12th century to older than 47,500 years. Isotopic data from 48 hair and 4 bone samples of modern saiga antelope were used for comparison. These originated from the Kazakh Betpak-Dala (22), Russian Kalmykia (11), Volga River (4), Turkmenistan (2) and Mongolian (13) population; the latter collected by Bayarbaatar Buuveibaatar (Schneider et al., 2015).

Various isotopic data from the coexisting mammoth steppe megaherbivores, namely woolly mammoth, horse, reindeer and *Bos/Bison* from the same time range as the saiga antelope were taken from the literature (Bocherens et al., 1996, 1997, 2011; Drucker et al., 2003, 2011; Fox-Dobbs et al., 2008; Iacumin et al., 2000, 2010; Leonard et al., 2007; Szpak et al., 2010). With the exception of the samples from south-western France, these species have not been found in the same sites as saiga but do occur in the same fossil contexts. Accordingly, the following wider regions were defined: Western Europe, Siberia and Eastern Beringia (Table 1).

### 2.2. Sample preparation and analysis

Saiga antelope bone and hair were sampled for analysis of carbon and nitrogen stable isotope ratios of bone collagen or hair keratin (Table 2). For bones, small samples were sawn from the specimen. These were cleaned with acetone and water in an ultrasound bath and then crushed to powder (0.7 mm grain size) using a mortar, pestle and sieves. Fresh samples of modern saiga antelopes underwent pretreatment to remove the lipid components, using chloroform/methanol 1:2, rinsed twice with millipore water and then left to dry. Collagen extraction was performed following a protocol based on Longin (1971) and modified by Bronk Ramsey et al. (2004) for the samples with the reference OxA-22422 to OxA-25670, and by Bocherens et al. (1997) for the other samples (Table A2 in supplementary material).

The elemental and isotopic measurements were performed at the Department of Geosciences at the University of Tübingen (Germany), using an elemental analyzer NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. The stable isotope ratios are expressed using  $\delta$  values (in ‰), with the international

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