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Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus*) and brown bear (*Ursus arctos*) from Austria: Isotopic evidence from fossil bones

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ABSTRACT

In the Austrian caves of Gamssulzen and Ramesch, two genetically distinct cave bears, *Ursus ingressus* and *Ursus spelaeus eremus*, apparently lived side by side for 15,000 years, together with brown bears *Ursus arctos*. The possible ecological partitioning of these three types of bears was investigated using multi-isotopic tracking of organic ($\delta^{13}\text{C}_{\text{coll}}$, $\delta^{15}\text{N}_{\text{coll}}$) and inorganic ($\delta^{13}\text{C}_{\text{carb}}$, $\delta^{18}\text{O}_{\text{carb}}$, $\delta^{18}\text{O}_{\text{PO4}}$) fractions of bone. The cave bears from Ramesch, *Ursus spelaeus eremus*, were ecologically distinct from the cave bears from Gamssulzen, *Ursus ingressus*, both being ecologically distinct from brown bears from Ramesch, *Ursus arctos*. Both cave bear types were purely herbivorous but likely consumed different plant types and/or plants from different habitats, while brown bears included some animal proteins in their diet. Bone apatite $\delta^{18}\text{O}$ values strongly suggest that both types of cave bears used isotopically distinct water sources, indicating that they may not have occupied the same landscape, either separated in space or in time due to climatic shifts. Therefore, the influence of environmental conditions strongly constrained the genetic structure of these bears.

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1. Introduction

The cave bear (*Ursus spelaeus* Rosenmüller 1794) is probably the Upper Pleistocene species that has yielded the highest number of fossil remains in Europe. Since its recognition by the scientific community as an extinct species, this taxon has been extensively studied, especially its palaeoecology. Based on functional anatomy, Kurtén (1958) suggested that this extinct group of bears had

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a herbivorous diet, a hypothesis that was recently confirmed by taphonomical and stable isotopic investigations (e.g., Bocherens et al., 1994, 1997, 2001, 2006; Fernandez-Mosquera, 1998; Stiner, 1999; Bocherens, 2008). Indeed, the high proportion of males in hibernating populations of cave bears point to a depletion of dietary resources available to this species during winter. This is not the case for male carnivorous bears which do not need to hibernate, as opposed to females who give birth during hibernation (Stiner, 1999). The stable nitrogen isotopic ($\delta^{15}\text{N}$) results on cave bear bones from Europe are mostly as low as or even lower than those of herbivorous species, pointing to the near-absence of animal protein in their diet. Isolated reports indicate higher $\delta^{15}\text{N}$ values as indicators of omnivory or carnivory (Hilderbrand et al., 1996; Richards et al., 2008). However, cave bears with high $\delta^{15}\text{N}$ values have unusually low stable carbon isotopic ($\delta^{13}\text{C}$) values that are not