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Analysis of coprolites from the extinct mountain goat *Myotragus balearicus*

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A B S T R A C T

Humans colonized the Balearic Islands 5–4 ka ago. They arrived in a uniquely adapted ecosystem with the Balearic mountain goat *Myotragus balearicus* (Bovidae, Antilopinae, Caprini) as the only large mammal. This mammal went extinct rapidly after human arrival. Several hypotheses have been proposed to explain the extinction of *M. balearicus*. For the present study ancient DNA analysis (Sanger sequencing, Roche-454, Ion Torrent), and pollen and macrofossil analyses were performed on preserved coprolites from *M. balearicus*, providing information on its diet and paleo-environment. The information retrieved shows that *M. balearicus* was heavily dependent on the Balearic box species *Buxus balearica* during at least part of the year, and that it was most probably a browser. Hindcast ecological niche modelling of *B. balearica* shows that local distribution of this plant species was affected by climate changes. This suggests that the extinction of *M. balearicus* can be related to the decline and regional extinction of a plant species that formed a major component of its diet. The vegetation change is thought to be caused by increased aridity occurring throughout the Mediterranean. Previous hypotheses relating the extinction of *M. balearicus* directly to the arrival of humans on the islands must therefore be adjusted.

Introduction

The Balearic Islands are an archipelago in the Western Mediterranean Sea (Fig. 1). Their isolated position may have probably played an important role in the late arrival of humans when compared to other Mediterranean islands (Bover et al., 2008). Both the time of arrival and the archaeological culture associated with the first human inhabitants have been debated since the start of archaeological studies on the Balearics (Waldren, 1982; Guerrero, 2001; Calvo and Guerrero, 2002; Ramis et al., 2002; Alcover, 2008). In the present study we follow a conservative view of the available radiocarbon dates, and argue that human settlement on the island must have occurred between 5000 and 4050 ^{14}C yr BP (Fig. 2; Ramis et al., 2002; Alcover, 2008). This time span is based upon radiocarbon dates taken from charcoal samples, and has been established after reviewing the reliability of the available radiocarbon dates (Ramis et al., 2002). The established time span can be reduced to 4350–4150 ^{14}C yr BP (Alcover, 2008) when cultural indicators, or their absence, and comparison to the cultural chronologies of nearby mainland Spain and France are taken into consideration. This approach is not followed here, as this shorter time span, 4350–4150 ^{14}C yr BP, is based on relative dating, and therefore not supported by a confidence of $p > 95.4\%$ (as is the case with the 5000–4050 ^{14}C yr BP interval). Also, the shorter time span is dependent on chronologies established in other regions, each with their own chronological problems (Alcover, 2008). This adds further uncertainties to the use of these shorter chronologies.

Some ecological information is available for the period when humans arrived on Mallorca. After the separation of the Balearics from

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Figure 1. Location of the Balearic Islands in the Mediterranean Sea. Numbers refer to location of samples studied (1 = Balma de Son Matge; 2 = Cova de Muleta).

the mainland, about 5.3 Ma (Krijgsman et al., 1999), a unique combination of flora and fauna developed on the different islands (Bover et al., 2008, 2010; Quintana et al., 2011) for an overview of the faunal developments). Differences between the islands were present during parts of the last 5.3 Ma, although Mallorca and Minorca have shared the same biogeographic history since the beginning of the Holocene. Vertebrates present on Mallorca included mammals (*Myotragus balearicus*, *Hypnomys morpheus* and *Nesiotites hidalgo* and some bats), two amphibian species, a lizard and some birds (Bover et al., 2008). *Myotragus balearicus* is considered to be the key species in understanding Balearic paleoecology, mainly because of its size when compared to the other vertebrates present on the islands. Environmental conditions changed dramatically during the period of human colonization of the islands, leading to the extinction of endemic mammals (Bover and Alcover, 2003, 2008), the disappearance of existing vegetation composition (Yll et al., 1997), and the introduction of new mammals and plants by humans (Alcover, 2008) (Fig. 2).

Remains of *M. balearicus* were first discovered in 1909 (Bate, 1909). This extinct mountain goat developed special adaptations, probably both as an evolutionary reaction to a resource limited environment as well as to within-species competition (Winkler, 2010; Jordana and Köhler, 2011). The adaptations found in *M. balearicus* evolved during a

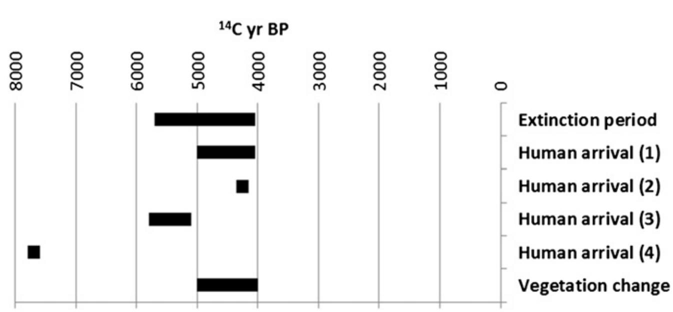

Figure 2. Overview of the most important periods in early Mallorcan prehistory. Extinction period of *Myotragus balearicus*, 5700–4050 ^{14}C cal yr BC, as established by Bover and Alcover (2003). Human arrival periods are shown according to different models: (1) 5000–4050 ^{14}C yr BP, the longer timespan as followed here, after Ramis et al. (2002) and Alcover (2008), (2) 4350–4150 ^{14}C yr BP, the shorter time span, after Alcover (2008), (3) 5800–5100 ^{14}C yr BP, after Calvo and Guerrero (2002), and (4) 7800–7600 ^{14}C yr BP, after Waldren et al. (2002). Vegetation change, 5000–4000 ^{14}C yr BP, after Yll et al. (1997). (See referenced articles for specific radiocarbon details.).

successive series of six chronospecies (Moyà-Solà et al., 2007; Bover et al., 2008, 2010), starting after the separation of the Balearic Islands from the mainland of Spain (Krijgsman et al., 1999).

Three different sets of adaptations can be discerned. These adaptations initially included morphological changes. The first of these was a diminishing in size. Size estimates differ, but the largest individuals were not taller than 50 cm (Ramis and Bover, 2001). Body mass estimates range between an average of 30 kg to a maximum of 70 kg (Bover and Alcover, 1999a; Palombo et al., 2008). Second, a further series of morphological changes observed in the limbs suggests the animal "*reduced the energy costs of locomotion by adopting a slow and powerful walking gait with reduced step length*" (Palombo et al., 2008, 162). Third, additional information obtained from long bones showed that *M. balearicus* had a delayed maturity, with reproduction beginning late in the animal's lifetime (Köhler and Moyà-Solà, 2009).

A relatively strong reduction of brain size when compared with the body size reduction has been observed in *M. balearicus* as well; especially a reduction of the cerebellum, including the vision, auditory and locomotory senses (Palombo et al., 2008, 2013). These relative reductions may be related to the predator-free environment, in which energy otherwise needed for predator avoidance can, by reducing the costs of locomotor abilities and vision, be used for other energy costs (Palombo et al., 2008). Adding to this, there was a more frontal positioning of the eye orbits compared with modern bovids. This reduced the width of the visual field (needed for predator avoidance), but may have given *M. balearicus* a greater form of visual depth (Bover, 2004).

A third adaptation observed in *M. balearicus*, but also evident in the earlier species of the lineage, is the evolution of its dentition. Dental evolution in *Myotragus* probably started with a dentition similar to that of extant continental bovids (the dental formula for *M. antiquus,* the first species for which a dental formula could be established) and resulted in a dental formula for *M. balearicus* unique for bovidae. The only present incisor in adult specimens of *M. balearicus* is the dI_2 that replaces the dI_1 by a horizontal process (Bover and Alcover, 1999b). Both teeth are present in juvenile specimens but located in different alveoli, separated by a bony septum (Bover and Alcover, 1999b). In juveniles, the dI_2 is not yet erupted (Bover and Alcover, 1999b). Furthermore, the dI_2 is ever-growing and, together with an overall increase in the degree of hypsodonty of the teeth in general, this has been related to an increased abrasiveness of the diet consumed (Bover and Alcover, 1999b; Winkler, 2010; Winkler et al., 2013). Crown formation times of molars indicate a slow rate of crown formation,