



Extinction of the autochthonous small mammals of Mallorca (Gymnesic Islands, Western Mediterranean) and its ecological consequences

Pere Bover¹ and Josep Antoni Alcover^{1,2*}

¹Department of Mammalogy, American Museum of Natural History, New York, NY, USA, ²Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Palma de Mallorca, Spain

Abstract

Aim To investigate the chronology, causes and consequences of the extinction of the autochthonous Pleistocene small mammals of Mallorca.

Location Mallorca (Gymnesic Islands, Balearics, Western Mediterranean).

Methods We have obtained the first direct ¹⁴C ages from the bone collagen of selected samples of two extinct endemic small mammals from Mallorca: the Balearic dormouse, *Eliomys morpheus* (Rodentia: Myoxidae) and the Balearic shrew, *Asoriculus hidalgoi* (Soricomorpha: Soricidae). We also present evidence for the absence of both endemics from the earliest Mallorcan archaeological sites and for the introduction of the garden dormouse, *Eliomys quercinus*, and the wood mouse, *Apodemus sylvaticus*. Combined information from direct dating of bone collagen of *E. quercinus* and *A. sylvaticus* and from cultural associations provides an adequate framework to establish the chronology of the faunal change and to compare it with the chronological information available on climatic change and the first arrival of humans on the islands.

Results The chronological record includes the latest evidence available for the survival of endemic species and the earliest introduction of small mammals into Mallorca. We present 'uncertainty periods for extinction' (UPEs) of both endemic mammals based on the chronology of their last occurrence and on the inferred timing of their extinction (restricted UPEs).

Main conclusions Possible causes for the extinction of autochthonous small mammals on Mallorca are discussed. Once we have discarded climatic causes, predation by invasive species, competition with newcomers and habitat deterioration, the introduction of diseases emerges as the most reasonable explanation for these extinctions. Based on the identification of changes in keystone species in Mallorcan ecosystems, we propose a tentative schedule of key ecological changes that have taken place over the past 5 millennia.

Keywords

Anthropogenic extinctions, *Asoriculus hidalgoi*, disease, *Eliomys morpheus*, Holocene extinctions, island ecology, last occurrence date, Mallorca, Mediterranean islands.

*Correspondence: Josep Antoni Alcover, Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Ctra. Valldemossa km 7.5, 07122 Palma de Mallorca, Spain.
E-mail: vieapba@uib.es

INTRODUCTION

The Eastern Balearics or Gymnesic Islands (Mallorca, Menorca and surrounding islets) are the most isolated territories in the Western Mediterranean (Fig. 1). Because of this isolation, a highly impoverished, unbalanced mammalian fauna has evolved on these islands. During the upper Pleistocene and

Holocene, only three terrestrial mammals, all endemic, were present: the Balearic cave 'goat', *Myotragus balearicus* (Artiodactyla: Bovidae: Caprinae); the Balearic dormouse, *Eliomys morpheus* (= *Hypnomys morpheus* (Bate, 1919); Rodentia: Myoxidae); and the Balearic shrew, *Asoriculus hidalgoi* (= *Nesiotites hidalgoi* (Bate, 1944); Soricomorpha: Soricidae). Although there is abundant literature on *M. balearicus*,

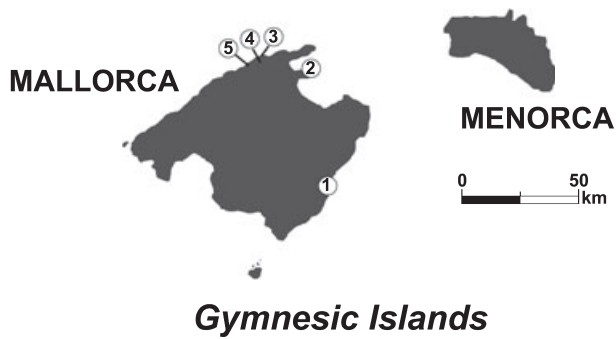


Figure 1 Map of the Gymnesic Islands showing the sampling localities mentioned in the text. 1 Cova des Moro (Manacor), 2 Cova des Garrover (Alcúdia), 3 Cova des Ninot (Pollença), 4 Cova Estreta (Pollença), 5 Cova de sa Tossa Alta (Escorca).

including accurate data on its extinction chronology (Burleigh & Clutton-Brock, 1980; Bover & Alcover, 2003; Quintana *et al.*, 2003), chronological information on the extinction of the other two small mammalian species is scarce and is not based on directly dated bone collagen.

In order to establish the accurate timing and causes of species extinction, it is important to have robust chronological data (MacPhee *et al.*, 1999). Chronological accuracy is particularly required in late Quaternary extinctions, the causes of which have been the subject of much debate (Burney & Flannery, 2005; Koch & Barnosky, 2006; Wroe *et al.*, 2006). Such chronological accuracy was not possible until direct dating of small mammal bones was introduced in the early 1990s (Stafford & Semken, 1990, 1991) with the development of accelerator mass spectrometer (AMS) ^{14}C techniques. Although at first these techniques gave some questionable results, methodologies have gradually improved and radiocarbon dates are currently considered to be reasonably reliable (Anderson, 2000). AMS ^{14}C techniques have occasionally been used to date autochthonous insular small mammals (Michaux *et al.*, 1996; McFarlane *et al.*, 2002; Bocherens *et al.*, 2006), although some of the dates derived cannot be used to resolve extinction chronologies because they clearly do not correspond to the extinction event (Michaux *et al.*, 1996). Nevertheless, the chronological information provided by direct AMS ^{14}C dating has become a powerful tool with which to date the first occurrence of small mammals on islands (Holdaway, 1996, 1999; Anderson, 2000; Burney *et al.*, 2001; Athens *et al.*, 2002; Wilmshurst *et al.*, 2004; Hunt, 2007), and also the best method to date the last occurrence of endemic species (MacPhee *et al.*, 1999). The quality of the chronological information derived from direct dating of small mammal bones is usually considerably higher than that derived from assumed stratigraphic associations, as post-depositional or even depositional anomalies cannot be ruled out from the latter (MacPhee *et al.*, 1999; Bernabeu *et al.*, 2001).

Accurate chronologies are required in the analysis of extinction events and their likely causes, and although multiple age estimates may be available when analysing the chronology of an extinction event, only the last one is significant when

determining the extinction of a species, so even a single radiocarbon age can be highly informative. The last record for an extinct species is important because it provides a *terminus post quem* for the extinction event, which clearly post-dates this age. It is also important to establish the earliest documentation for species absence (an age representing a *terminus ante quem* for the extinction event). Estimates of extinction chronologies pre-dating the Modern Era (before 1500 AD), however, are usually highly imprecise (Diamond, 1984; Bover & Alcover, 2003).

There are a great number of direct datings available on bones from large mammals, including some from isolated or insular regions (MacPhee *et al.*, 2002). In contrast, direct ^{14}C ages on bones from small mammals (weighing < 5 kg) are still scarce, especially in insular regions. In the Mediterranean islands, only the radiocarbon ages of bones of the Sardinian pika, *Prolagus sardus*, have been published to date (Klein Hofmeijer, 1996; Vigne *et al.*, 1998). Radiocarbon chronologies have also been obtained from small mammal bones from the West Indies (MacPhee *et al.*, 1999) and the Canary Islands (Bocherens *et al.*, 2006) in efforts to establish geochronologies for the study of insular extinctions. Similar work is required to understand the chronology of extinctions from Western Mediterranean islands. In this paper, we use radiocarbon dates from bone collagen to investigate the chronology of extinctions of two small mammals of Mallorca: the Balearic dormouse, *E. morpheus*, and the Balearic shrew, *A. hidalgoi*. We then discuss the causes and consequences of these extinctions.

MATERIALS AND METHODS

In order to obtain relevant radiocarbon ages, we first selected potentially useful datable material. Bones of small mammals were selected from the uppermost stratigraphic layers from localities in Mallorca that had been sampled using sufficient stratigraphic controls (Cova Estreta, Cova des Moro; Fig. 1). In other cases, datable bones were selected on the basis of the quality of preservation and the absence of mineralization (Cova des Garrover, Cova de sa Tossa Alta; Fig. 1). All the materials studied were curated at the Vertebrate Collection 'Museu de la Naturalesa de les Illes Balears' (MNIB, Palma de Mallorca).

The following material was dated by AMS radiocarbon analysis: Cova Estreta: *E. morpheus* femur (MNIB unaccessioned); Cova des Moro: *E. morpheus* tibia (MNIB unaccessioned); Cova de sa Tossa Alta: *E. morpheus* femur (MNIB 68320) and a pelvis (MNIB unaccessioned); Cova des Garrover: 6.5 g of *A. hidalgoi* bones (MNIB unaccessioned).

Our purpose was to establish two dates for each species, delimiting the temporal range in which extinction occurred: a *terminus post quem* (a date that pre-dates the time at which extinction occurred) and a *terminus ante quem* (a date that post-dates the extinction). In establishing both *termini*, we used established criteria for ^{14}C ages (Spriggs, 1989; Anderson, 1991; Spriggs & Anderson, 1993; Housley *et al.*, 1997; Tuggle &

Spriggs, 2000; Alcover *et al.*, 2001; Zilhão, 2001; Ramis *et al.*, 2002; Bover & Alcover, 2003). Thus ^{14}C ages are expressed as 2σ intervals ($P = 95.45\%$), and their interpretation is based exclusively on the extreme values of these intervals (the approach assumes that the true age of the dated material is more recent than the lower extreme of the 2σ interval and it is, independently, older than the upper extreme of the 2σ interval; Alcover *et al.*, 2001). The lower extreme of the 2σ interval of the last documented occurrence date represents the *terminus post quem* for the extinction event, while the upper extreme for the earliest evidence of absence represents the *terminus ante quem*. The temporal range in which the extinction occurred, placed somewhere between both *termini*, will be called the 'uncertainty period for extinction' (UPE) of *E. morpheus* and *A. hidalgoi*.

Dates derived from the calibration of radiometric results (using the program OxCAL ver. 3.5; Bronk Ramsey, 1995) are written as 'cal. BC'. Uncalibrated radiocarbon ages and Th/U ages are presented as 'BP'. Calendar dates not derived from radiocarbon analyses are expressed as 'BC'.

RESULTS

Terminus post quem

The new radiocarbon ages are presented in Table 1. All samples of *E. morpheus* provided sufficient quantities of collagen for accurate AMS analysis. All analytical steps proceeded normally for the beta-analytic samples, according to the laboratory reports. Pre-treatment of beta-analytic samples involved collagen extraction with alkali; the Brussels Laboratory reported no problems during the process. The sample of *A. hidalgoi* initially submitted to the laboratory proved to have too little collagen to be analysed accurately, so it was replaced by a new sample that yielded the required quantity of collagen.

Eliomys morpheus

Radiocarbon ages were obtained from four samples of *E. morpheus* (Table 1). The most recent ^{14}C age obtained from a sample of *E. morpheus* is 5890 ± 35 BP (KIA 30353,

4840–4690 cal. BC). This suggests that, with $P > 95.45\%$, *E. morpheus* disappeared from Mallorca later than 4840 cal. BC.

Asoriculus hidalgoi

The only available ^{14}C age for *A. hidalgoi* is 4280 ± 50 BP (beta-163133; range 3030–2690 cal. BC), suggesting, with $P > 95.45\%$, that *A. hidalgoi* disappeared from Mallorca later than 3030 cal. BC.

Terminus ante quem

The earliest archaeological sites on the island of Mallorca date back to the end of the 3rd millennium cal. BC and are related to the Bell Beaker cultural tradition (Coll, 2001). The earliest available evidence for human occurrence in Mallorca has recently been placed within the last third of the 3rd millennium cal. BC, pre-dating 2030 cal. BC (Alcover *et al.*, 2001; Ramis *et al.*, 2002). Calvo & Guerrero (2002) updated the last limit to before 2040 cal. BC.

Microfaunal analyses of the most ancient archaeological contexts, e.g. Coval Simó (Coll, 2001), Cova des Ninot and Ca na Cotxera, all show the absence of endemic mammals, but the introduced *Eliomys quercinus* and *Apodemus sylvaticus* are present in some of these deposits (Coval Simó and Cova des Ninot). Whereas systematic sieving was applied in the case of the first two sites (excavations of 1998–2001 and 2006, respectively), it is unclear whether this method was used in the open-air site of Ca na Cotxera (excavated in 1968). Also, there is no documentation of the presence of autochthonous small mammals in more recent archaeological deposits in Mallorca.

In Cova des Moro (Manacor, stratigraphic unit 406), the remains of 13 indigenous examples of *E. morpheus* and six of *A. hidalgoi* were recovered through systematic sieving (2001–02 fieldwork results), while remains of the immigrant *E. quercinus* and *A. sylvaticus* have also been identified in this faunal assemblage. Pottery types belonging to two different prehistoric phases were recorded in this archaeological level. Remains belonging to the earliest phase are characteristically undecorated, and appear to be related to the incised Bell Beaker pottery found in several other archaeological sites on

Site	Laboratory number	Conventional date (BP)	Calibrated 2σ range (cal. BC)	$\delta^{13}\text{C}/^{12}\text{C}$ (‰)
<i>E. morpheus</i>				
Cova Estreta	UtC 5175	6357 ± 44	5480–5250	–22.2
Cova de sa Tossa Alta	Beta 143116	8200 ± 50	7450–7070	–15.7
Cova de sa Tossa Alta	KIA 30353	5890 ± 35	4840–4690	–15.74
Cova des Moro	Beta 162613	$12,250 \pm 80$	13,500–11,800	–17.1
<i>A. hidalgoi</i>				
Cova des Garrover	Beta 163133	4280 ± 50	3030–2690	–18.1

Table 1 Direct ^{14}C ages of the bone collagen of the extinct Balearic dormouse *Eliomys morpheus* and the extinct Balearic shrew *Asoriculus hidalgoi* from Mallorca.

The range of isotopic values of $\delta^{13}\text{C}$ for *E. morpheus* is very large and probably related to an omnivorous diet. All the extractions were performed with alkali.

the island. The latter was present in Mallorca during the uppermost part of the 3rd millennium and possibly the beginning of the 2nd millennium cal. BC (Coll, 2001). Nevertheless, the main bulk of the material is chronologically attributed to the end of the 2nd millennium cal. BC or the beginning of the 1st millennium, on the basis of the presence of the same pottery types in habitation structures of this period (Pons, 1999; Salvà, 2001). Two different AMS ^{14}C ages were obtained for this stratigraphic unit, both based on collagen from two introduced bovid bone samples: 3750 ± 40 BP (beta-155645, range 2290–2030 cal. BC) and 2860 ± 50 BP (beta-162619, range 1190–900 cal. BC). These radioisotope results are consistent with those obtained through analysis of the archaeological materials. An AMS ^{14}C age was obtained from a sample of *E. morpheus* bone in order to determine if it was contemporaneous with the introduced taxa. The result obtained was beta-162613 ($12,250 \pm 80$ BP; 13,500–11,800 cal. BC). This date indicates that the remains of *E. morpheus* from stratigraphic unit 406 of Cova des Moro were deposited before the archaeological context from which they were recovered. We consider that the same holds for the *A. hidalgoi* bones from the same level; however, the sample is too small to be dated properly.

Consequently, there is currently no strong evidence for the presence of both species of endemic small mammals in archaeological deposits in Mallorca. Waldren's (1982) claims for the presence of endemic small mammals in archaeological levels of Cova de Moleta have recently been questioned (Alcover *et al.*, 2001; Ramis & Alcover, 2001; Ramis *et al.*, 2002; Alcover, 2004, 2005) on the basis of the scarce reliability of the stratigraphic record. The chronological information currently available for the first arrival of humans and associated fauna indicates that *E. morpheus* and *A. hidalgoi* were absent in Mallorca by 2040 cal. BC.

Establishment of UPEs on the basis of available radiocarbon ages

Based on the available data, a UPE can be established for each species studied. The uncertainty period for the extinction of *E. morpheus* in Mallorca corresponds to an interval of 2800 years (4840–2040 cal. BC). For *A. hidalgoi*, the UPE spans from 3030 to 2040 cal. BC, representing an uncertainty period of 990 years. Within these UPEs, there are currently no direct radiocarbon ages that enable a more constrained chronology for the extinction of both species to be established, although restricted UPEs can be derived from the archaeological framework (see below). The overlap between the two UPEs as currently established impedes determining the order in which the two species became extinct.

DISCUSSION

Although the chronological framework for the extinction of *M. balearicus* has recently been resolved (Bover & Alcover, 2003; Quintana *et al.*, 2003), the chronology of the extinction of

Mallorcan small mammals remains unknown. Adrover (1966) was the first to document the Holocene occurrence of the two species in the fossil record of Cova de Moleta, whereas Reumer (1980) and Alcover *et al.* (1981) presented divergent views on the chronological order of the extinction of these species. According to Reumer (1980), *E. morpheus* disappeared before *A. hidalgoi* in Mallorca, while Alcover *et al.* (1981) and Waldren (1982) consider that *A. hidalgoi* could have been the first species to vanish. All these investigators assume that the extinction of the endemic small mammals in Mallorca is related to human settlement.

These views are based on (1) data available at the start of the 1980s, and (2) the assumption of stratigraphic accuracy in the absence of direct chronological data for the fossil record of the different deposits. During the 1970s, some deposits were reported to contain only one of the two autochthonous small mammals. While Alcover *et al.* (1981) based their view on the deposits containing only *E. morpheus*, Reumer (1980) emphasized the absence of this species in some deposits containing only *A. hidalgoi*. Nevertheless, no taphonomic biases that may have originated from selective predation or even by specific behaviour and ecology were adequately considered by these authors. On the other hand, the accuracy of the reported stratigraphy of some deposits from Mallorca, usually considered as key sites, has recently been questioned (Ramis *et al.*, 2002; Alcover, 2004, 2005). Consequently, there is no basis to support any of these views, and the order of the extinction events remains unresolved.

Likely causes of extinction

Two hypotheses are considered to explain the extinction of the autochthonous small mammals in Mallorca: (1) climatic change, and (2) human settlement on the islands. The following discussion attempts to correlate possible causes of extinction with UPE chronologies.

Extinction caused by climatic change

Climatic change as the cause of extinction of the Mallorcan autochthonous small mammals seems inconsistent with the palaeoclimatic and palaeontological data currently available. Assuming that the maximum sea-level stand of the Holocene had a palaeothermal significance, the maximum temperature at this period apparently occurred slightly before 6600 ± 300 BP ($^{230}\text{Th}/^{234}\text{U}$ age; Versilian, OIS 1). Between 4900 and 5800 BP ($^{230}\text{Th}/^{234}\text{U}$ age) the sea reached a roughly similar level to its current level. Since that time, no noticeable sea level changes have been recorded (Tuccimei *et al.*, 2000). The occurrence of a climatic change event post-dating 3030 cal. BC (the *terminus post quem* for the *A. hidalgoi* extinction) is not documented by the palaeosea-level oscillation record preserved in Mallorca (Ginés & Ginés, 1993; Tuccimei *et al.*, 2000). Consequently, the documented date for the last occurrence of *A. hidalgoi* does not correlate with a known change in climate.

In contrast, the available *terminus post quem* for the extinction of *E. morpheus* lacks sufficient resolute power by itself to discriminate directly between the likely causes of the species' extinction. The *E. morpheus* UPE embraces both a climatic change that occurred in the Versilian, and the first arrival of humans in Mallorca. Thus, on the basis of the direct chronometric data available, although a climatic cause for the extinction of *A. hidalgoi* can be discarded, whether it could explain the extinction of *E. morpheus* remains unresolved.

Two other approaches offer supplementary clues to distinguish between possible causes of the extinction of *E. morpheus*: (1) an analysis of the climatic events affecting the two small mammal lineages during their evolution in Mallorca, and (2) the application of a parsimony criterion. The ancestors of *E. morpheus* and *A. hidalgoi* appear to have colonized Mallorca during the Messinian (Alcover *et al.*, 1981), between 5.7 and 5.35 Ma (Gautier *et al.*, 1994), and both lineages evolved in Mallorca for at least 5.35 Myr. Major climatic changes took place during this time, including one from a subtropical to a Mediterranean climate (Late Pliocene), and there was also a succession of glaciations and interglacial periods during the Late Pliocene and Pleistocene (Shackleton & Opdyke, 1973, 1977; Emiliani, 1992), all of which clearly pre-date the small mammal extinction in Mallorca. During the last interglacial (OIS 5), the climate of the Balearic Islands showed a wide seasonal range of temperature, moisture and precipitation, including recorded periods with a mean annual temperature about 2°C higher than today, with very dry moisture regimes, limited plant biomass (Rose & Meng, 1999; Rose *et al.*, 1999), and a sea-level rise of 2–2.5 m (Tuccimei *et al.*, 2000; Vesica *et al.*, 2000). The absence of extinction records of vertebrates in the Gymnesics during the most arid and unproductive phases of the Pleistocene suggests that climatic deterioration is unlikely to have been involved in the extinction of both species during the Holocene.

The parsimony criterion favours one single cause to explain both small mammal extinctions, rather than different causes. Although not impossible, the extinction of *E. morpheus* from a climatic cause seems to be highly unlikely, while it definitely does not account for the extinction of *A. hidalgoi* and *Myotragus balearicus* (Burleigh & Clutton-Brock, 1980; Bover & Alcover, 2003; Quintana *et al.*, 2003). It clearly seems to be more parsimonious to assert that only one key factor could have affected the whole terrestrial mammal fauna of the Gymnesic Islands, and climate cannot be identified as such a factor. The exclusion of a climatic change as the cause for this global insular mammalian extinction event points to human-related causes.

It would be reasonable to assume that Mallorca, like the rest of the world, was affected by climatic changes at several levels. Nevertheless, the long stability of the Mallorcan biota suggests that these changes did not influence the composition of the fauna. A major climatic change recorded during the evolution of the lineages of small mammals in Mallorca occurred in the Late Pliocene, with the beginning of the succession of glacial and interglacial periods, yet no small mammal extinctions were

reported to have occurred during this dramatic episode of climatic change. On the contrary, they became extinct during times that appeared to have been climatically stable.

Anthropogenic causes

Once a climatic cause for their extinction is ruled out, and as no other natural causes can be advocated for them in the Balearic Islands, *E. morpheus* and *A. hidalgoi* may reasonably be assumed to have been present in Mallorca at the time of the first arrival of humans.

A quantitative approach to the knowledge of the causes and chronology of the extinction of *E. morpheus* and *A. hidalgoi* derives from the comparison of the respective UPEs and the uncertainty period for human arrival (UPHA; Fig. 2). The UPHA has been defined – following the criteria of Alcover *et al.* (2001) – as the temporal range during which the arrival of humans occurred, embracing the period from *c.* 3000 to 2040 cal. bc.

A comparison between UPEs and UPHA in Mallorca (Fig. 2) shows that the UPE of *E. morpheus* spans 2800 years (from 4840 to 2040 cal. bc), the UPHA comprises *c.* 960 years (Alcover *et al.*, 2001; Ramis *et al.*, 2002), and the UPE of *A. hidalgoi* spans 990 years (from 3030 to 2040 cal. bc). Thus the overlap of both UPEs and the UPHA is *c.* 960 years. This

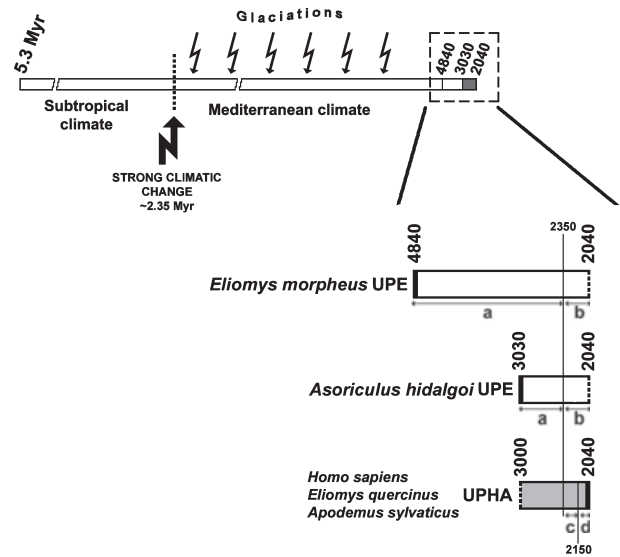


Figure 2 Chronology of the small mammal extinctions recorded on Mallorca. Upper left: complete temporal range of the lineages, starting in the Messinian and ending before 2040 cal. bc. Arrows indicate glaciations. In detail: uncertainty periods for extinction (UPEs) for the last species of each lineage and the uncertainty period for human arrival (UPHA). Thick vertical line extremes are used to express a great degree of robustness for the considered event ($P > 95\%$). The spotted vertical line extremes are used for good indicators of the considered event. (a) Minimal unrecorded last occurrence of endemic small mammals; (b) restricted UPE; (c) restricted UPHA (J.A.A., unpublished data); (d) minimal unrecorded first presence of humans.

figure indicates that, with the current knowledge available, the maximum possible period of contact between humans and *A. hidalgoi* (and *E. morpheus*) in Mallorca is less than *c.* 960 years, although the actual overlap could have been shorter, maybe even considerably so – which is an important point. Recent work (J.A.A., unpublished data) suggests a UPHA of only 200 years based on archaeological correlates on the mainland, and that the first arrival of humans on Mallorca (and, consequently, the extinction of the endemic fauna) would have occurred after 2350 cal. BC.

The existence of an overlap between UPHAs and UPEs is informative, as the long period of the evolution of both small mammal lineages in Mallorca (> 5.35 Myr) demonstrates beyond doubt that the island supported viable, stable populations of both species. Under such circumstances, the overlap between UPEs and UPHAs suggests that the first arrival of humans and the extinction of the autochthonous small mammals were closely related events, just as they were in the case of the extinction of *M. balearicus* (Quintana *et al.*, 2003). If such a relationship is accepted, the disappearance of *E. morpheus* and *A. hidalgoi* from Mallorca would have actually occurred at an undetermined time between 2350 and 2040 cal. BC, this range representing the restricted UPE for both species. The time lapse running between 3030 cal. BC (the available chronological evidence for the last occurrence of *A. hidalgoi* in Mallorca) and post-2350 cal. BC (the assumed chronology of its extinction) suggests that the unrecorded part of the presence of this species is > 680 years, while the unrecorded part of the presence of *E. morpheus* is > 2490 years.

Once humans have been implicated as the key factor explaining the Holocene mammalian extinctions in Mallorca, the precise cause should be identified. Four possible human-related causes, acting independently or in combination, can be put forward (MacPhee & Marx, 1997; MacPhee & Flemming, 1999; Worthy & Holdaway, 2002; Steadman, 2006): (1) the introduction of predators (including humans), (2) the introduction of competitors, (3) habitat transformation and cascade extinctions, and (4) the introduction of diseases.

Predation

The introduction of alien predators on islands has frequently been considered the most important factor leading to the extinction of autochthonous species (Worthy & Holdaway, 2002). Nevertheless, the introduction of alien predators may not have been relevant in the extinction of the autochthonous small mammals of Mallorca.

In Mallorca, humans can be excluded as efficient direct predators of the autochthonous small mammals, as humans hunting the shrew, even occasionally, is highly improbable, and human predation on dormice, although possible, has never been documented. Moreover, it is unlikely that predation by humans could have been so widespread as to produce a demographic decline in the Mallorcan population of *E. morpheus*.

The first human settlers documented on Mallorca introduced some domestic and wild species, but only herbivorous species have been adequately documented: the domesticated artiodactyls, sheep (*Ovis aries*), goats (*Capra hircus*), cows (*Bos taurus*) and pigs (*Sus scrofa*); and the wild rodents, the wood mouse (*A. sylvaticus*) and the garden dormouse (*E. quercinus*). No unquestionable documentation regarding the early presence of dogs on the island currently exists, although canid gnawing is inferred from taphonomic analyses of remains of domestic species from cultural levels (D. Ramis, unpublished data).

The current mammalian fauna in Mallorca includes two domestic carnivores (the dog and the cat) and three wild carnivores (the weasel *Mustela nivalis*, the genet *Genetta genetta* and the marten *Martes martes*). The expansion of cats is related to the Romans (Clutton-Brock, 1999) and, consequently, this species could have colonized Mallorca during Roman times (later than 123 BC) or slightly earlier (see Sanders & Reumer, 1984, for the first documented occurrence of cats in Menorca). The weasel was also introduced by the Romans, according to classical literature sources. The zooarchaeological record from Menorca suggests that the weasel was present in the island by the 1st century BC (Sanders & Reumer, 1984). The genet is believed to have been introduced into the Iberian Peninsula by Muslims (Morales, 1994), and probably also to the Balearic Islands. Although predation by genets has been claimed as the cause for the extinction of *E. morpheus* (Waldren, 1982: 100), there is no proof of the coexistence of both species. Finally, there is no information on the chronology of introduction of the marten, a species that is much less carnivorous than the rest of the introduced species of Carnivora (Moreno *et al.*, 1988; Ruiz-Olmo & Nadal, 1991).

Consequently, the only likely carnivores that could be responsible for the extinction of the autochthonous Mallorcan small mammals are dogs and martens. Nevertheless, the presence of these carnivores is not adequately documented at the time of the first arrival of humans or even throughout Mallorcan prehistory, and there is no evidence for the coexistence of these carnivores with the small autochthonous mammals of Mallorca.

To attribute the extinction of both endemic species to dogs, two additional assumptions should be met: (1) that dogs – if present – were living outside the human settlements, and (2) that dogs achieved a density high enough to produce a demographic decline in the small mammal populations (high densities are usually reflected in the zooarchaeological record, e.g. the presence of the weasel in Menorca). Neither of these assumptions appears to have been met in Mallorca or even elsewhere (Worthy & Holdaway, 2002). Consequently, dogs can reasonably be ruled out as a possible cause of the extinction of the small endemic mammals of Mallorca.

The attribution of these extinctions to the marten also remains undemonstrated, and seems unlikely given the absence of this species from the archaeological record and its feeding behaviour. Consequently, predation by carnivores apparently did not play an important role in the extinction of the

Mallorcan autochthonous small mammals. In addition, there is no evidence that the introduction by humans of alien predatory birds took place. Predatory birds were present in Mallorca throughout the Pleistocene without having had a devastating influence on the populations of autochthonous small mammals. Hence the only other introduced mammalian species that could have played some sort of predatory role on the autochthonous small mammals of Mallorca is the garden dormouse *E. quercinus*. Currently there is no compelling evidence for their coexistence, suggesting that their contact was short. Even though this species seems to incorporate some animal items in its diet (Kahmann & Lau, 1972), it is unlikely to have contributed significantly to the disappearance of the autochthonous species.

Competition

The introduction by humans of alien species that are potential competitors of insular autochthonous small mammals is frequently proposed as an explanation of extinction episodes. Nevertheless, this seems irrelevant as a cause for the extinction of the autochthonous small mammalian fauna of Mallorca.

Whereas the introduction of alien shrews in Mallorca remains to be documented, the closest introduced relative to *A. hidalgoi* is the hedgehog, *Atelerix algirus* (Erinaceomorpha), which also shares its insectivorous habits, but there is no evidence of their coexistence in Mallorca; the hedgehog has never been found in the rich Mallorcan prehistoric zooarchaeological record. It appears that it was introduced into the islands during the Middle Ages by Muslims from Northern Africa (J. Rofes and A. Morales, unpublished data).

There is evidence for the presence of two introduced rodents in the earliest human occupation levels of Mallorca: bones of the garden dormouse (*E. quercinus*) and wood mouse (*A. sylvaticus*) have been documented in stratigraphic unit 67 of Cova Simó, dated as 3650 ± 40 BP (beta-161787, range 2140–1890 cal. BC) through a direct radiocarbon age on a caprine bone. Both species are also present in stratigraphic unit 9 of Cova des Ninot, below fragments of incised Bell Beaker-like pottery. However, there is no compelling evidence for the coexistence of these aliens and the autochthonous species. The currently available direct datings on collagen of small mammals introduced on Mallorca are presented in Table 2.

The current Mallorcan mammalian assemblage includes six introduced rodents living in 'natural' habitats, suggesting that in the past the addition of two rodent species to the

autochthonous fauna could not have produced the collapse of the sole autochthonous rodent population. If six rodent species coexist nowadays in Mallorca, it seems reasonable to assume that the introduction of two rodent species would easily be supported by the Mallorcan ecosystems. Mallorca is a relatively large island (> 3600 km²), and several rodent species are known to coexist currently on smaller Mediterranean islands. The same rodent species living currently in Mallorca also coexist in Menorca (600 km²), whereas five of them coexist in Eivissa (540 km²) and four on the small island of Formentera (80 km²).

Habitat modifications

Habitat transformation is one of the first consequences of human arrival on islands (Burney *et al.*, 2001). A late Holocene vegetation change has been recorded in Mallorca and Menorca (Pérez-Obiol *et al.*, 2002), although its chronology and causes remain insufficiently documented. Even if a sudden vegetation change occurred at the beginning of the human colonization of the Gymnesic Islands, its consequences for the fauna remain unclear. Moreover, the proportions of the vegetation change remain unknown. The current presence of relict woodland on the Mallorcan mountains suggests that although the change could have been very important, it was not complete. Some autochthonous vegetation patches are very likely to have survived the first impact of humans on the island. Furthermore, it seems reasonable that, in the absence of other factors, the autochthonous small mammals would have been able to consume the resource supplied by the human-modified ecosystems. Consequently, some influence on the demography of the autochthonous small mammals derived from habitat modifications should be expected, but not the complete disappearance of these species, as insects remained available for *A. hidalgoi* in the modified habitats, as well as edible plants for *E. morpheus*.

Introduced diseases

The introduction of alien diseases is sometimes argued as a cause of insular extinctions (Diamond, 1984) and, with the exclusion of other possible human-related causes, emerges as the best explanation for the extinction of Mallorcan small mammals.

The effect of introduced pathogens may be a relevant factor to explain insular extinction events, as has been proposed in

Site	Laboratory number	Conventional date (BP)	Calibrated 2σ range (cal. BC)	δ ¹³ C/12C (‰)
<i>E. quercinus</i>				
Cova Estreta	Beta 143114	2440 ± 40	770–400	–19.0
<i>A. sylvaticus</i>				
Cova Estreta	Beta 143115	3180 ± 40	1530–1320	–20.2

The two extractions were performed with alkali.

Table 2 Direct ¹⁴C ages of the bone collagen of two small mammals introduced to Mallorca: the garden dormouse *Eliomys quercinus* and the wood mouse *Apodemus sylvaticus*.

the Caribbean (MacPhee & Marx, 1997). In fact, MacPhee & Iturralde-Vinent (2000) suggest a close relationship between the extinction of most small mammals in the Antilles and the arrival of rats (*Rattus rattus*) from the Old World, which were likely to have carried diseases to which the natives had no immunity. Devastating consequences could be expected from the introduction of new viruses, bacteria or parasites (such as protozoa, helminths and arthropods) transported by humans, their domesticated animals and wild species transported to Mallorca. Some viruses, including rodent-borne viruses, display a trend to be shared by multiple species (Van Blerkom, 2003) and, although the potential to share viruses and bacteria is more pronounced in closely related species (as could have been the case for the congeneric *E. morpheus* and *E. quercinus*), there are multiple cases of pathogens shared by species belonging to different mammalian orders. This is a necessary condition for an assumption of the infection of *A. hidalgoi*. The shift of a host can be associated with high levels of pathogenesis. Additionally, shared parasites are suspected to be an important force in structuring communities, and even in explaining extinction (Logiudice, 2003).

In summary, the archaeological and palaeontological record from Mallorca is not conclusive with regard to the ultimate causes of the extinction of autochthonous small mammals, although there is no doubt that it is correlated with the first arrival of humans. Some likely factors may be reasonably excluded, and the introduction of alien diseases by humans emerges as a preferred explanation for these extinctions. Nevertheless, empirical evidence for this potential cause remains to be found.

An improvement in knowledge of the palaeontological and archaeological record of the 3rd millennium cal. BC of Mallorca will be pivotal in improving our understanding of the causes and mechanisms of the extinction of the endemic fauna, and in testing the conclusions of the present paper.

The last occurrence date of *A. hidalgoi* is of additional interest, as it represents the latest evidence for the presence of an endemic mammal in Mallorca. This record reinforces the claim that the Balearic Islands – the most isolated islands in the Mediterranean – were still pristine when the first pyramids were erected in Egypt (Alcover *et al.*, 2001).

Palaeoecological consequences

The extinction of the autochthonous mammalian fauna from Mallorca started after 2350 cal. BC, probably soon after, and was definitely completed by 2040 cal. BC. *Myotragus balearicus* is considered to be the keystone species in Mallorcan ecosystems during the Pliocene and Pleistocene (Palmer *et al.*, 1999). The disappearance of the autochthonous fauna, keystone species included, must have produced huge ecological consequences, one of which was the replacement of *M. balearicus* as a keystone species.

Just after human arrival, the wild mammalian fauna shifted from three species (*M. balearicus*, *E. morpheus* and *A. hidalgoi*) to only two (*E. quercinus* and *A. sylvaticus*). Together with

these wild species, humans introduced four or five domesticated mammals (sheep, goat, cow and pig, and probably also the dog). It is within this pool of species (wild mammals, domesticated animals and humans) from which the key species for the transformed ecosystems were recruited. Although the transformation of insular ecosystems is frequently attributed directly to human activities (such as slash-and-burn), recent research suggests that the transformation of the landscape pre-dates human settlement in some places. The best documented case comes from Hawaii (Athens *et al.*, 2002), where the 'Ewa Plain in O'ahu was deforested before human arrival: the Polynesian rat *Rattus exulans* emerges as the crucial species for the transformation of the 'Ewa Plain. The same pattern occurred in the Taranaki area in New Zealand (Wilmschurst *et al.*, 2004). Another case is found in Rapa Nui, where landscape transformation was initially attributed to direct deforestation by humans, but new research strongly suggests that the devastating effects of the introduced Polynesian rat played a major role (Hunt, 2007).

Although the archaeological record of the Balearics is not definitive, evidence suggests that introduced rodents could have had an important role in the vegetation transformation following human arrival. A rough analysis of the archaeological record of the small mammals introduced into Mallorca and Menorca shows that it comprises remains from prehistoric to Roman Age deposits – some of them very rich ones – while there is a complete absence of post-Roman (historic) deposits until the second half of the last century. The existence of these prehistoric deposits, together with the absence of post-Roman deposits, is informative, suggesting an extraordinary abundance of small mammals during prehistory, with a related high abundance of barn owls at that time, thus multiplying the chance for fossil deposits to be produced. A second indicator of the high densities of small mammals attained during Mallorcan prehistory relies on the presence of owl pellet deposits in places where there is no historic or current evidence for the presence of owls.

Cova des Ninot (Pollença, Mallorca) is a recently excavated site (September 2006) located in the Mallorcan mountains. *Eliomys quercinus* and *A. sylvaticus* are present through the entire stratigraphic column, from before the deposition of the early incised Bell Beaker-like pottery until the Late Talaiotic period (Iron Age). From this period onwards, owl pellet deposition stops completely, suggesting a change in the ecology of the surrounding land, implying a decrease in the former *E. quercinus* and *A. sylvaticus* populations, which could not have supported the presence of a bird of prey in the cave any longer. Finally, the body sizes of prehistoric *E. quercinus* and *A. sylvaticus* in Mallorca were larger than those of the most recent specimens of both species. On the whole, this evidence suggests that both species may well have had a great demographic importance and played a role in the transformation of the island ecosystems. We consider that both were keystone species in Mallorcan prehistory, although we cannot discard landscape transformation as a synergic consequence of the effects of several key species. The direct effects of humans

and feral goats might also have played an important role in the transformation of the landscape.

Following the arrival of *E. quercinus* and *A. sylvaticus* and the quick extinction of the endemic species, the mammalian fauna of Mallorca remained basically unaltered for c. 2000 years. Indirect chronological data obtained in Menorca indicate that a new wave of biological invaders arrived some time within the second half of the 1st millennium cal. BC, probably associated with the Roman expansion (Reumer & Sanders, 1984). As Mallorca and Menorca were settled by Romans at the same time (in 123 BC), the chronology of the species introductions can be reasonably assumed to have been roughly coeval in both islands. The introduction of black rats, domestic mice, rabbits, garden shrews (only in Menorca), red deer (Mallorca), fallow deer (Mallorca), geckos, snakes, cats, horses and weasels appears to date from that time (Uerpmann, 1971; Reumer & Sanders, 1984; Sanders & Reumer, 1984). This new wave of immigrants probably changed the Mallorcan ecosystems once again. The introduction of weasels appeared to have been devastating for the previous fauna; autochthonous lizards and the Balearic midwife toad disappeared after their arrival, and a significant reduction in body size was recorded for both *A. sylvaticus* and *E. quercinus*. From this point onwards, the former role of these small mammals as keystone species was eclipsed, while the weasel simultaneously emerged as a new keystone species in Mallorcan ecosystems. Further research is required to elucidate the consequences of this new change.

ACKNOWLEDGEMENTS

This paper is a product of Research Project BTE2001-0589 of the Dirección General de Investigación, Ministerio de Ciencia y Tecnología (Madrid). We thank Dr Ross MacPhee (New York) and Dr Adrián Tejedor (New York) for helpful comments on our first manuscript, and Dr Bruce J. Shockey (New York) for reviewing the English in this paper and making some interesting suggestions. Mr Darden Hood (Miami) and Mr Mathieu Boudin (Brussels) provided valuable supplementary information on different radiocarbon ages. Mr Juan Rofes and Dr Arturo Morales (Madrid) kindly allowed us to cite unpublished information. One of the authors (P.B.) has an MEC-Fulbright postdoctoral fellowship from the Secretaría de Estado de Universidades de Investigación of the Ministerio de Educación y Ciencia of Spain.

REFERENCES

Adrover, R. (1966) Pequeño intento de lavado de las tierras de la cueva de son Muleta y los resultados obtenidos. *Boletín de la Sociedad de Historia Natural de Baleares*, 99–116.

Alcover, J.A. (2004) Disentangling the Balearic first settlement issues. *Endins*, 1–14.

Alcover, J.A. (2005) Agulles d'ós, domesticació de *Myotragus balearicus*, la cova de Moleta Petita, datacions neolítiques i calcolítiques, productes d'ivori d'elefant i estratigrafia de la

balma de Son Matge: problemes d'higiene documental i cronològica als dipòsits càrstics de Mallorca. *Endins*, 211–224.

Alcover, J.A., Moyà-Solà, S. & Pons-Moyà, J. (1981) *Les Quimeres del Passat. Els vertebrats fòssils del Plio-Quaternari de les Balears i Pitiüses*. Editorial Moll. *Monografies Científiques*, 1–260 (Palma de Mallorca).

Alcover, J.A., Ramis, D., Coll, J. & Trias, M. (2001) Bases per al coneixement del contacte entre els primers colonitzadors humans i la naturalesa de les Balears. *Endins*, 5–57.

Anderson, A. (1991) The chronology of colonization in New Zealand. *Antiquity*, 767–795.

Anderson, A. (2000) Differential reliability of ¹⁴C AMS ages of *Rattus exulans* bone gelatin in South Pacific prehistory. *Journal of the Royal Society of New Zealand*, 243–261.

Athens, J.S., Tuggle, H.D., Ward, J.V. & Welch, D.J. (2002) Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. *Archaeology in Oceania*, 57–78.

Bernabeu, J., Barton, C.M. & Pérez-Ripoll, M. (2001) A taphonomic perspective on Neolithic beginnings: theory, interpretation, and empirical data in the Western Mediterranean. *Journal of Archaeological Science*, 597–612.

Bocherens, H., Michaux, J., Garcia Talavera, F. & Van der Plicht, J. (2006) Extinction of endemic vertebrates on islands: the case of the giant rat *Canariomys bravoii* (Mammalia, Rodentia) on Tenerife (Canary Islands, Spain). *Comptes Rendus Palevol*, 885–891.

Bover, P. & Alcover, J.A. (2003) Understanding Late Quaternary extinctions: the case of *Myotragus balearicus* (Bate, 1909). *Journal of Biogeography*, 771–781.

Bronk Ramsey, C. (1995) Radiocarbon calibration and analysis of stratigraphy: the OxCal program. *Radiocarbon*, 425–430.

Burleigh, R. & Clutton-Brock, J. (1980) The survival of *Myotragus balearicus* Bate, 1909 into the Neolithic on Mallorca. *Journal of Archaeological Science*, 385–388.

Burney, D.A. & Flannery, T.F. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution*, 395–401.

Burney, D.A., James, H.F., Burney, L.P., Olson, S.L., Kikuchi, W., Wagner, W.L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F.V., Gage, R., II & Nishek, R. (2001) Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs*, 615–641.

Calvo, M. & Guerrero, V.M. (2002) *Los inicios de la metalurgia en Baleares. El Calcolítico (c. 2500–1700 cal. BC)*. Editorial El Tall, Palma.

Clutton-Brock, J. (1999) *The natural history of domesticated animals*. Cambridge University Press, Cambridge.

Coll, J. (2001) Primeres datacions absolutes del jaciment de coval Simó. *Endins*, 161–168.

Diamond, J.M. (1984) Historic extinction: a Rosetta stone for understanding prehistoric extinctions. *Quaternary extinctions: a Quaternary revolution* (ed. by P. S. Martin and R. G. Klein), pp. 574–593. University of Arizona Press, Tucson, AZ.

- Emiliani, C. (1992) *Planet Earth: cosmology, geology and the evolution of life and environment*. Cambridge University Press, Cambridge.
- Gautier, F., Clauzon, G., Suc, J.P., Cravatte, J. & Violanti, D. (1994) Age et durée de la crise de salinité Méssinienne. *Comptes Rendues de l'Académie des Sciences Paris, Série II*, 1103–1109.
- Ginés, J. & Ginés, A. (1993) Dataciones isotópicas de espeleotemas freáticos recolectados en cuevas costeras de Mallorca (España). *Endins*, 9–16.
- Holdaway, R.N. (1996) Arrival of rats in New Zealand. *Nature*, 225–226.
- Holdaway, R.N. (1999) A spatio-temporal model for the invasion of the New Zealand archipelago by the Pacific rat *Rattus exulans*. *Journal of the Royal Society of New Zealand*, 91–105.
- Housley, R.A., Gamble, C.S., Street, M. & Pettitt, P. (1997) Radiocarbon evidence for the Late Glacial human recolonisation of Northern Europe. *Proceedings of the Prehistoric Society*, 25–54.
- Hunt, T.L. (2007) Rethinking Easter Island's ecological catastrophe. *Journal of Archaeological Science*, 485–502.
- Kahmann, H. & Lau, G. (1972) Der Gartenschäfer *Eliomys quercinus ophiusae* Thomas 1925 von der Pityuseninsel Formentera (Lebensführung). *Verofften Zoologisches Staatsammlungen*, 29–49.
- Klein Hofmeijer, G. (1996) *Late Pleistocene deer fossils from Corbeddu cave*. PhD Thesis. Utrecht University, Utrecht.
- Koch, P.L. & Barnosky, A.D. (2006) Late Quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution and Systematics*, 215–250.
- Logiudice, K. (2003) Trophically transmitted parasites and the conservation of small populations: raccoon roundworm and the imperiled Allegheny woodrat. *Conservation Biology*, 258–266.
- MacPhee, R.D.E. & Flemming, C. (1999) *Requiem Aeternam. The last five hundred years of mammalian species extinctions. Extinctions in near time: causes, contexts, and consequences* (ed. by R. D. E. MacPhee), pp. 333–371. *Advances in Vertebrate Palaeobiology*. Kluwer Academic/Plenum Press, New York.
- MacPhee, R.D.E. & Iturralde-Vinent, M.A. (2000) A short history of Greater Antillean land mammals: biogeography, paleogeography, radiations and extinctions. *International Symposium. The Ryukyu Islands – the arena of adaptive radiation and extinction of island fauna* (ed. by H. Otsuka, H. Ota and M. Hotta), pp. 145–154. *Tropics*, . The Japan Society of Tropical Ecology Kagoshima.
- MacPhee, R.D.E. & Marx, P.A. (1997) The 40,000-year plague. *Humans, hyperdisease, and first-contact extinctions. Natural change and human impact in Madagascar* (ed. by S. M. Goodman and B. D. Patterson), pp. 169–217. Smithsonian Institution Press, Washington, DC.
- MacPhee, R.D.M., Flemming, C. & Lunde, D.P. (1999) 'Last occurrence' of the Antillean Insectivore *Nesophontes*: new radiometric dates and their reinterpretation. *American Museum Novitates*, 1–20.
- MacPhee, R.D.M., Tikhonov, A., Mol, D., de Marliave, C., van der Plicht, H., Greenwood, A., Flemming, C. & Agenbroad, L. (2002) Radiocarbon chronologies and extinction dynamics of the late Quaternary mammalian megafauna of the Taimyr Peninsula, Russian Federation. *Journal of Archaeological Science*, 1017–1042.
- McFarlane, D.A., Lundberg, J. & Fincham, A.G. (2002) A late Quaternary paleoecological record from caves of southern Jamaica, West Indies. *Journal of Cave and Karst Studies*, 117–125.
- Michaux, J., López-Martínez, N. & Hernández-Pacheco, J.J. (1996) A ¹⁴C dating of *Canariomys bravoii* (Mammalia, Rodentia), the extinct giant rat from Tenerife (Canary Islands, Spain), and the recent history of the endemic mammals in the Archipelago. *Vie et Milieu*, 261–266.
- Morales, A. (1994) Earliest genets in Europe. *Nature*, 512–513.
- Moreno, S., Rodríguez, A. & Delibes, M. (1988) Summer foods the pine marten (*Martes martes*), in Majorca and Minorca, Balearic Islands. *Mammalia*, 289–291.
- Palmer, M., Pons, G.X., Cambefort, Y. & Alcover, J.A. (1999) Historical processes and environmental factors as determinants of inter-island differences in endemic faunas: the case of the Balearic Islands. *Journal of Biogeography*, 813–824.
- Pérez-Obiol, R., Yll, E.I., Pantaleón-Cano, J. & Roure, J.M. (2002) Canvis en el paisatge vegetal de les Illes Balears durant el final del Quaternari. *El canvi climàtic: passat, present i futur* (ed. by G. X. Pons and J. A. Guijarro), pp. 69–89. *Monografies de la Societat d'Història Natural de les Balears*, 9, Palma.
- Pons, G. (1999) *Anàlisi espacial del poblament al pretalaiòtic final i al talaiòtic I de Mallorca*. Consell de Mallorca, Cultura i Patrimoni, Monografies de Patrimoni Històric, Col. lecció La Deixa, 2, Palma.
- Quintana, J., Bover, P., Ramis, D. & Alcover, J.A. (2003) Cronologia de la desaparició de *Myotragus balearicus* Bate 1909 a Menorca. *Endins*, 155–158.
- Ramis, D. & Alcover, J.A. (2001) Revisiting the earliest human presence in Mallorca, Western Mediterranean. *Proceedings of the Prehistory Society*, 261–269.
- Ramis, D., Alcover, J.A., Coll, J. & Trias, M. (2002) The chronology of the first settlement of the Balearic Islands. *Journal of Mediterranean Archeology*, 3–24.
- Reumer, J.W.F. (1980) Evolutie en biogeografie van de kleine zoogdieren van Mallorca (Spanje). *Lutra*, 13–32.
- Reumer, J.W.F. & Sanders, E.A.C. (1984) Changes in the vertebrate fauna of Menorca in prehistoric and classical times. *Zeitschrift für Säugetierkunde*, 321–325.
- Rose, J. & Meng, X. (1999) River activity in small catchments over the last 140 ka, north-east Mallorca, Spain. *Fluvial processes and environmental change* (ed. by A. G. Brown and T. Quine), pp. 91–102. Wiley, Chichester.
- Rose, J., Meng, X. & Watson, C. (1999) Paleoclimate and paleoenvironmental responses in the western Mediterranean

- over the last 140 ka: evidence from Mallorca, Spain. *Journal of the Geological Society*, 435–448.
- Ruiz-Olmo, J. & Nadal, J. (1991) Regime alimentaire de la Marte (*Martes martes* L., 1758) et taille des portées à Menorca, Iles Baléares. *Mammalia*, 639–642.
- Salvà, B. (2001) *El pretalaiòtic al llevant mallorquí (1700–1100 AC)*. Anàlisi territorial. Edicions Documenta Balear, Arbre de Mar, 4, Palma.
- Sanders, E.A.C. & Reumer, J.W.F. (1984) The influence of prehistoric and Roman migrations on the vertebrate fauna of Menorca (Spain). *The Deya Conference of Prehistory: Early Settlement in the Western Mediterranean Islands and their Peripheral Areas* (ed. by W. H. Waldren, R. Chapman, J. Lewthwaite and R. Kennard), pp. 119–144. British Archaeological Reports, International Series, 229. Archaeopress, Oxford, UK.
- Shackleton, N.J. & Opdyke, N.D. (1973) Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V28–238: oxygen isotope temperatures and ice volumes on a 10⁵-year time scale. *Quaternary Research*, 39–55.
- Shackleton, N.J. & Opdyke, N.D. (1977) Oxygen isotope and paleomagnetic evidence of early Northern Hemisphere glaciation. *Nature*, 216–219.
- Spriggs, M. (1989) The dating of the island Southeast Asian Neolithic: an attempt at chronometric hygiene and linguistic correlation. *Antiquity*, 587–613.
- Spriggs, M. & Anderson, A. (1993) Late colonization of East Polynesia. *Antiquity*, 200–217.
- Stafford, T.W. & Semken, H.A. (1990) Accelerator ¹⁴C dating of two micromammal species representative of the Late Pleistocene disharmonious fauna from Peccary cave, North County, Arkansas. *Current Research in the Pleistocene*, 129–132.
- Stafford, T.W. & Semken, H.A. (1991) AMS ¹⁴C dating of individual species of small mammals: paleoenvironmental reconstruction for 20 KA to 8 KA BP. *Rocky Mountains Section, Geological Society of America*, 92.
- Steadman, D. (2006) *Extinction and biogeography of tropical Pacific birds*. University of Chicago Press, Chicago, IL, USA.
- Tuccimei, P., Ginés, J., Delitala, C., Pazzelli, L., Tadeucci, A., Clamor, B., Fornós, J.J., Ginés, A. & Gràcia, F. (2000) Dataciones Th/U de espeleotemas freáticos recolectados a cotas inferiores al actual nivel marino en cuevas costeras de Mallorca (España): aportaciones a la construcción de una curva eustática detallada de los últimos 300 ka para el Mediterráneo occidental. *Endins*, 59–71.
- Tuggle, H.D. & Spriggs, M. (2000) The age of the Bellows Dune site O18, O'ahu, Hawai'i, and the antiquity of Hawaiian colonization. *Asian Perspectives*, 165–188.
- Uerpmann, H.P. (1971) Die Tierknochenfunde aus der Talaiot-Siedlung von s'Illot (Sant Llorenç, Mallorca). *Studien über frühe Tierknochenfunde aus der Iberischen Halbinsel*, 1–111.
- Van Blerkom, L.M. (2003) Role of viruses in human evolution. *Yearbook of Physical Anthropology*, 14–46.
- Vesica, P.L., Tuccimei, P., Turi, B., Fornós, J.J., Ginés, A. & Ginés, J. (2000) Late Pleistocene paleoclimates and sea-level change as inferred from stable isotopes and U-series of overgrowths on speleothems, Mallorca, Spain. *Quaternary Science Reviews*, 865–879.
- Vigne, J.D., Bourdillat, V., André, J., Brochier, J.E., Bui Thi Mai Cuisin, J., David, H., Desse-Berset, N., Heinz, C., Lanfranchi, F., Ruas, M.-P., Thiébault, S. & Tozzi, C. (1998) Nouvelles données sur le Préneolithique corse: premiers résultats de la fouille de l'abri du Monte Leone (Bonifacio, Corse-du-Sud). *Rencontres de Préhistoire récente. Deuxième session. Arles, 1996*, p. 251. APDCA, Antibes.
- Waldren, W.H. (1982) *Balearic prehistoric ecology and culture. The excavation and study of certain caves, rock shelters and settlements. British Archaeological Reports, International Series, 149*. Archaeopress, Oxford, UK.
- Wilmshurst, J.M., Higham, T.F.G., Allen, H., Johns, D. & Phillips, C. (2004) Early Maori settlement impacts in northern coastal Taranaki, New Zealand. *New Zealand Journal of Ecology*, 167–179.
- Worthy, T.H. & Holdaway, R.N. (2002) *The lost world of the moa. Prehistoric life of New Zealand*. Indiana University Press, Bloomington, IN.
- Wroe, S., Field, J. & Grayson, D. K. (2006) Megafaunal extinctions: humans, climate and assumptions. *Trends in Ecology & Evolution*, 61–62.
- Zilhão, J. (2001) Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west Mediterranean Europe. *Proceedings of the National Academy of Sciences USA*, 14,180–14,185.

BIOSKETCHES

Pere Bover has a Fulbright Post-Doc Fellowship of the Spanish Ministerio de Educación y Ciencia and is working at the Department of Mammalogy of the American Museum of Natural History. He works mainly on vertebrate palaeontology in the Balearic Islands. His PhD dissertation was on the evolution of *Myotragus balearicus*, the extinct endemic goat of the Gymnesic Islands. He co-edited the Proceedings of the International Symposium 'Insular Vertebrate Evolution: The Palaeontological Approach, September 16–19 2003, Mallorca' (2005).

Josep Antoni Alcover is on the scientific staff of the CSIC, Spain. His contributions usually focus on insular vertebrate evolution. Recent research concerns the chronology and causes of extinction of endemic vertebrates in the Balearic and Canary Islands, as well as on the establishment of the first human settlement in the Balearics.

Editor: José María Fernández-Palacios