

Review

Mammals of the Mediterranean islands: homogenisation and the loss of biodiversity

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Abstract

There is possibly no other location in the world which has been so intensively influenced by human activity over a prolonged period as the Mediterranean. Virtually no ecosystems have been left untouched. Since prehistory, the human settlers of the Mediterranean islands brought about a radical turnover between ancient and modern mammalian faunas, introducing a variety of allochthonous continental taxa. The data available for the Mediterranean islands point to endemic mammalian extinction being largely the result of human activities of land clearance and the introduction of allochthonous animals. Today, this fauna is no longer characterised by the majority of the endemic mammals previously reported. It displays virtually the same species composition, being almost exclusively characterised by continental mammals whose appearance on the islands has essentially been influenced by man, and dominated by generalist species. The invasion of ecosystems by exotic taxa is currently viewed as one of the most important causes of the loss of biodiversity. Today, in view of the vulnerability of the insular ecosystems it is critically important to prevent further introductions. But this results in the question of how to treat the allochthonous mammalian populations of certified ancient anthropochorous origin, which instead deserve to be protected and considered in terms of a veritable “cultural heritage”. Moreover, their protection and their study can provide an opportunity for testing a range of different evolutionary theories.

Keywords: anthropochorous mammals; endemic faunas; generalist species; Holocene; Mediterranean islands; Upper Pleistocene.

Introduction

The Mediterranean shores have always offered a unique range of peculiar biological elements. Amongst these, it may be interesting to recall the former existence of endemic insular mammals. In fact, the late Quaternary island ecosystems were quite different in some ways from the adjacent continental ecosystems. Palaeontolog-

ical and archaeozoological evidence demonstrates that several of the fossil and subfossil island faunas differed considerably from contemporary continental faunas, and were characterised by a very low taxonomic diversity (Azzaroli 1971, 1977, Sondaar 1971, 1977). The great number of islands in the Mediterranean made this region highly favourable to the evolution of island endemics (Sondaar and Boekschoten 1967, Dermitzakis and Sondaar 1978, Kotsakis et al. 1980, Sondaar et al. 1986, Marra 2005). Examples from the Balearics, Corsica and Sardinia, the Tuscan archipelago, Capri, Sicily, Malta, Crete, many Aegean islands, and Cyprus are significant (Azzaroli 1971, 1977, Sondaar 1971, 1977, Vigne 1992, Masseti and Mazza 1996) (Figure 1). From a biogeographical point of view, all these insular territories have to be regarded as “oceanic islands” (cf. Wallace 1876, Ghigi 1950, Dermitzakis and Theodorou 1994). In effect, within the Mediterranean basin it is almost impossible to ascertain the existence of islands of an authentically “oceanic type”, which is the term generally adopted to indicate volcanic islands formed independently of continental land masses. In conceptual terms, oceanic islands are indeed the opposite of “continental islands”, the latter being territories that are instead close to a continental landmass, and geologically related to it, having been formed by separation from the nearest mainland (cf. Lincoln and Boxshall 1987). Perhaps it would be more precise to refer to them as “oceanic-like islands” (cf. Alcover et al. 1998), or genuinely “true islands”, which is an expression used to designate insular territories that have been separated from the closest mainland for a very long time, since at least the beginning of the Upper Pleistocene (Vigne 1999, cf. Gorman 1979). Addressing the obvious difficulties faced by most organisms in trying to cross salt water, biogeographers used to postulate that most remote islands were once linked to continents by land-bridges now sunk from view (Gorman 1979). It is in fact commonly assumed that, before becoming dwarfed, many of the Mediterranean macromammals reached the islands from the mainland via temporary land-bridges that originated as a result of the lowering of the sea level during glacial episodes. According to Azzaroli (1971, 1977, 1983), this may have happened in Sardinia and Sicily. On the basis of tectonic factors, Malatesta (1980) observes that Crete may also have been joined to continental Greece during the Pleistocene. However, as noted by Davis (1987), it is then difficult to explain why the Pleistocene faunas of the latter islands are relatively rich compared to that of Cyprus. It may be that only a few species migrated to this eastern Mediterranean island, which was somewhat more difficult to reach (cf. Azzaroli 1977).

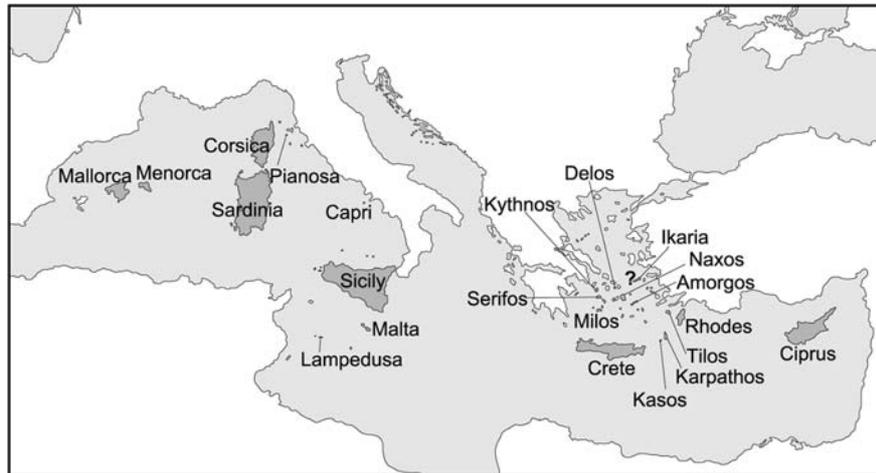


Figure 1 Mediterranean islands yielding remains of Late Pleistocene endemic mammals.

Sweepstake routes and endemic insular mammals

Today, the general opinion is, however, that most of the “true islands” of the Mediterranean could not have been reached over the last 130,000 years by non-Volant vertebrates except by rafting or swimming (Vigne 1999). For instance, Schüle (1993) observed that most suggested Quaternary land-bridges to Mediterranean islands are geologically impossible. Thus, it is assumed that micro-mammals, such as shrews and rodents, may also have reached some islands by jumping onto floating logs and/or rafting. Some larger mammals could be relics of the desiccation of the Mediterranean on the Mio/Pliocene border, whereas others may have reached most of the islands by swimming, being able to cross sea barriers. Sondaar (1977) has noted that endemic island faunas were dominated by good swimmer taxa, such as elephants, hippopotami and deer. Indeed, some authors have suggested that proboscideans may perhaps have swum to some of the islands (Johnson 1980). New evidence today shows unequivocally that elephants are excellent swimmers. Swimming speeds up to 2.70 km/h have been measured, with maximum distances estimated at 48 km. For these reasons, Johnson (1980) suggests reappraising the origin of land vertebrates on all the islands that held elephants, as well as the geological reconstructions that assumed that land-bridges once connected these islands to the mainland. There are also known records of the swimming abilities of hippopotami and deer (Dermitzakis and Sondaar 1978). Although not aquatic animals, cervids have long been known for their migratory water crossing (Held 1989). However, it is possible that the deer are not such good swimmers as elephants and hippopotami. For Davis (1987), this might explain why they never managed to make the crossing to Cyprus while elephants and hippos did, the distance between the island and the closest mainland being too great for the deer (cf. Masseti and Zava 2002a). Animals that can migrate over long distances also include flying taxa, such as birds and bats (Sondaar 1977).

This sporadic and highly selective dispersal from a continent to an island has been referred to as ‘sweepstakes migration’, i.e., possible only via the so-called *sweepstake routes* (Simpson 1940, Sondaar 1971, 1986, Dermitzakis and Sondaar 1978, Theodorou et al. 2007a). As we can imagine, the chances of such a dispersal are extremely low, and largely due to chance combinations of favourable circumstances. The *sweepstake routes* differ from biogeographical filters not merely in degree, but because the organisms that used the former are capable of exploiting them to disperse from island to island (cf. Cox and Moore 1993). During the Pleistocene, the fluctuations of the sea levels caused by climate change favoured *sweepstake* migrations, and the subsequent evolution of endemic faunas, by altering the distances between the mainland and the islands. Low sea levels made the sea barrier easier to cross, but the subsequent high levels then rendered the channel crossing practically impossible, so that the founding population on the island would find itself isolated. Populations reaching the islands by such routes become genetically isolated from the respective continental population. The rapid evolutionary adaptation to the new insular environment usually affects body size and the pattern of locomotion (Sondaar 1977, Lomolino 2005, Theodorou et al. 2007a). Thus, the endemic mammalian assemblages of many of the Upper Pleistocene Mediterranean islands were oligotypic, characterised by a very low taxonomic diversity.

Cyprus, for example, having been separated from the mainland for a very long time (cf. Swiny 1988), has yielded a very peculiar endemic mammalian composition. The main element was a dwarf hippopotamus, *Phanourios minor* Desmarest 1822, known from more than 30 sites on the island (Forsyth Major 1902, Bate 1906, Boekschoten and Sondaar 1972, Reese 1995, Theodorou et al. 2005). Another common endemic species was a dwarf elephant, *Elephas cypriotes* Bate 1903 (Bate 1903a, 1905a). There are also some proboscidean remains of a somewhat larger size than *E. cypriotes*, but as yet the information regarding these and what they might represent is still inadequate (Boekschoten and Sondaar 1972, cf. Theodorou et al. 2007b). Other, generally quite sparse,

findings include a genet *Genetta plesictoides* Bate 1903, as well as some lesser known small mammals: one or two species of rodent (*Mus* sp.) – with the possible inclusion of the recently discovered extant Cypriot mouse, *Mus cypriacus* Cucchi T., Orth A., Auffray J.-C., Renaud S., Fabre L., Catalan J., Hadjisterkotis E., Bonhomme F., and Vigne J.-D. 2006 (Reumer and Oberli 1988, Bonhomme et al. 2004, Cucchi et al. 2006) – one or two species of bat and, perhaps, one shrew (Boekschoten and Sondaar 1972, Reese 1995, Theodorou et al. 2007b). The two largest Balearic islands, Mallorca and Menorca, are the only Mediterranean islands where the dominant mammalian species was a representative of the Caprinae subfamily, possibly of the tribe Rupicaprini, the so-called “cave goat”, *Myotragus balearicus* Bate 1909 (cf. Kurtén 1968, Waldren 1982, Alcover et al. 2000) (Figure 2). From a geological point of view, Mallorca was isolated from the nearest land masses for at least 5.35 million years (Mya). The phyletic lineage of *M. balearicus* evolved starting from this era, as further confirmed by recent studies on the fossil DNA of the species (Lalueza-Fox et al. 2000, 2002, 2005) (Figure 3). The other two mammalian species of the greatly impoverished local fauna were the large-sized shrew *Soriculus hidalgo* Bate 1945, and the giant

dormouse *Eliomys morpheus* Bate 1918. Both of these were also clearly relics from the Tertiary (Alcover 1979, Alcover et al. 1981, 1999).

The composition of the endemic insular mammalian assemblages, despite consisting of only a few taxa, were repeated monotonously on most of the islands. Nevertheless, they displayed peculiar endemic elements which differed greatly from one island to another. The most common trends of endemisation are the decrease in the size of macromammals, such as proboscideans and artiodactyls, and the increase in the size of micromammals, such as shrews and rodents (Azzaroli 1971, 1977, Sondaar 1971, 1977, 1986). Regarding this aspect, it is assumed that the specific genome of these taxa is so plastic as to allow these phenomenic modifications to take place. Effectively, if the characteristics of the genome did not permit such adaptation, the species would logically be destined to extinction. All these modifications are generally assumed to be primarily a consequence of the genetic isolation from continental populations, a quantitative and qualitative reduction in food supply, an alteration of intraspecific competition, the absence of large carnivores and perhaps, where the micromammals are concerned, also of endothermic adaptations (cf. Masseti and Mazza 1996). Islands that provided such faunas can be considered as “natural laboratories” (cf. Davis 1987).



Figure 2 Complete skeleton of the Mallorcan cave goat, *Myotragus balearicus* Bate 1909, on display at the Museo Arqueológico Nacional, Madrid (courtesy of the Museo Arqueológico Nacional de Madrid).



Figure 3 Artist's reconstruction of *Myotragus balearicus* (courtesy of Joan Mayol Serra, Govern de les Illes Balears).

Soricomorpha and Rodentia on islands

As observed above, one of the most common trends of endemisation is the increase in size of both Soricomorpha and Rodentia. The Sicilian giant dormouse, *Leithia melitensis* Adams 1863, was, for example, twice the size of the extant edible dormouse, *Glis glis* (L. 1766) (Petronio 1970). There is also evidence of the occurrence in the Middle/late Pleistocene of the Siculo-Maltese archipelago of at least two other dormice, such as *Leithia carthai* Adams 1863 and *Eliomys wiedincitensis* Zammit Maempel and de Bruijn 1982, from the faunal stages of Spinagallo and Maccagnone (Burgio 1997). The first taxon was described as a form of smaller size, but according to Adams (1870): “...not differing in any other respect” from the Sicilian giant dormouse. And we have already seen that a giant dormouse was also comprised within the endemic fauna of the Balearics. Palaeontological evidence, however, suggests that Late Pleistocene dispersal of the representatives of the Gliridae family occurred only on the islands of the western Mediterranean basin (Figure 4). According to Boekschoten and Sondaar (1972), glirids are in fact absent from the eastern islands where they were more or less replaced by diversified murids. This difference may be caused by faunal differences on the nearest mainland, and would lead us to assume a predominance of glirids in the western Mediterranean coastal areas and of murids in the eastern Mediterranean at the time of immigration.

Rodents and shrews of large dimensions have also been yielded by the archaeological exploration of several other Mediterranean islands. Two large shrews, *Episori-*

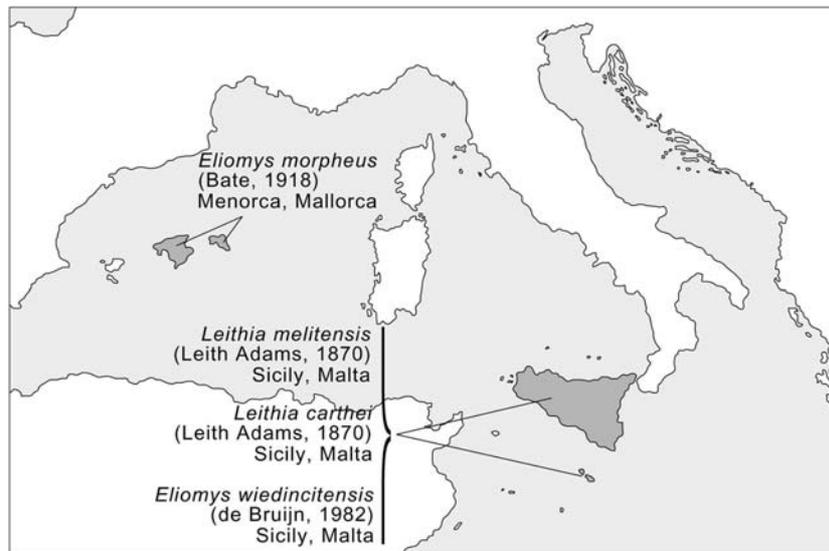


Figure 4 Middle and Upper Pleistocene distribution of endemic glirids on the Mediterranean islands (from Masseti 2005).

culus similis Hensel 1855 and *E. corsicanus* Bate 1944, are known from Late Pleistocene sites in Sardinia and Corsica, respectively, while the late Quaternary faunas of both the latter islands were characterised by the occurrence of the large field vole *Microtus (Tyrrenicola) henseli* Forsyth Major 1881, and the big rat *Rhagamys orthodon* Hensel 1856 (Vigne 1988a, 1992). Morphometrical analyses carried out on remains of *Microtus* recently discovered in a deposit on Monte Tuttavista, in the vicinity of Orosei (western Sardinia), have led to the establishment of a new fossil species *Microtus (Tyrrenicola) sondaari* Marcolini, Caterinella, Arca and Kotsakis 2006 (Marcolini et al. 2005, 2006). A fossil endemic species, *Microtus (Terricola) melitensis* (Bate 1920), has also

been recorded in the Late Pleistocene of Malta (Bate 1920, Burgio and Kotsakis 1986, Brunet-Lecomte and Chaline 1991).

From the post-Tyrrhenian deposits of south-eastern Capri, Cinque et al. (1986) and Gliozzi (1988) reported a giant long-tailed field mouse, *Apodemus sylvaticus tyrrenicus* Gliozzi 1988, also characterised by peculiar dental patterns. The same islands also yielded the remains of the endemic Capri hazel dormouse, *Muscardinus malatestai* Gliozzi 1995 (Gliozzi 1995) (Figure 5), whereas a large *Apodemus* sp. was reported from the Middle or Late Pleistocene assemblages of Naxos, Cyclades (Greece) (Sondaar 1971, Kotsakis 1990). Furthermore, subfossil black rats, *Rattus rattus* (L. 1758), of large

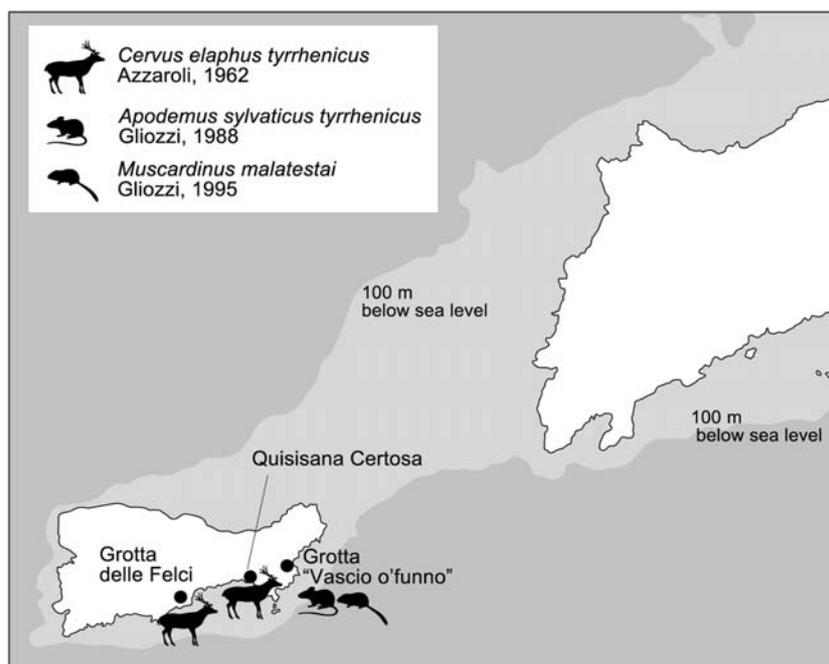


Figure 5 A giant long-tailed field mouse, *Apodemus sylvaticus tyrrenicus*, the Capri hazel dormouse, *Muscardinus malatestai*, and the Capri red deer, *Cervus elaphus tyrrenicus*, are all endemic taxa reported the exploration of the post-Tyrrhenian deposits of the island of Capri, Tyrrhenian Sea (Italy). The pale grey area represents land lost when the sea level rose during the Holocene.

size have been reported from the archipelago of Lavezzi, off the southernmost coast of Corsica (Vigne et al. 1994).

Many of the extant shrews and rodents of the Mediterranean islands are also generally reputed to be distinguished from their mainland relatives by the increase in body size (Felten and Storch 1970, Kahmann and Niethammer 1971, Adler and Levins 1994, Vigne et al. 1994, Fons et al. 1995, Amori and Masseti 1996, and many others). Shrews and rodents regarded as large taxa are, for example, the lesser white-toothed shrew, *Crocidura suaveolens* Pallas 1811, of Corsica (Kahmann and Kahmann 1954, Vlasák and Niethammer 1990); the *Suncus etruscus pachiuus* Küster 1835 from Sardinia (Sans-Coma et al. 1985); the *Eliomys quercinus liparensis* Kahmann 1960, of Lipari (Kahmann 1960); the *Apodemus sylvaticus ilvanus* Kahmann and Niethammer 1971, of Elba (Kahmann and Niethammer 1971, Filippucci 1992); and the long-tailed field mice of Formentera (*A. s. frumentariae* Sans-Coma and Kahmann 1977), Ibiza (*A. s. eivissensis* Alcover and Gosálbez 1988), the archipelago of Hyères (Libois and Fons 1990), and Marettimo (cf. Krapp 1970, Alcover and Gosálbez 1988, Sarà and Casamento 1995). According to some authors, such as Orsini and Cheylan (1988) and Libois et al. (1993), the wood mice of Corsica may also reveal a degree of dimensional increase. The small island of Pantelleria, in the Sicilian channel, is also inhabited by two micromammals of large dimensions: the Pantelleria shrew, *Crocidura pachyura cossyrensis* Contoli 1990 (Contoli and Amori 1986), and the long-tailed field mouse of Pantelleria, *A. sylvaticus hermani* Felten and Storch 1970 (Felten and Storch 1970). Populations of large-sized black rats have been reported from Lipari (Cristaldi et al. 1985), and many other Mediterranean islets, as well as the Atlantic islands of the Açores archipelago (Portugal) (Libois et al. 1996). Medieval populations of large black rats are known from southern Corsica (Bonifacio) and the small islet of Lavezzi (Vigne et al. 1993). Another phenotypic modification is the tendency to produce dark-coloured forms, such as the edible dormouse, *Glis glis melonii* Thomas 1907, and the garden dormouse, *Eliomys quercinus sardus* Barrett-Hamilton 1901, of Corsica and Sardinia, which are, however, smaller than their continental counterparts (cf. Amori and Masseti 1996).

It has been observed that these modifications as a whole are not to be regarded as the effects of the so-called "insular syndrome", a phenomenon that was described several years ago as an essay of the manifestations that most markedly distinguish insular micromammals from their continental counterparts (cf. Libois et al. 1993, Adler and Levins 1994, Fons et al. 1995). Masseti and Mazza (1996) attempted to verify this assumption in the light of palaeontological evidence. In reality, the constancy of patterns shown by the insular mammals of the past attests to the fact that their endemic modifications are the rule rather than the exception. They may be the essential outcome of a tendency towards a redefinition of ecological equilibria under very peculiar environmental conditions (cf. MacArthur and Wilson 1967, Blondel and Vigne 1993). The endemisation of island faunas is in fact the result of a normal and repetitive reorganisation of a few faunal entities distributed in restricted areas with lim-

ited trophic resources and in the absence of large-sized carnivores (Masseti and Mazza 1996). This phenomenon has been better described as the "Island Rule" by Foster (1964), with mammals providing the classic case studies. It can be seen all over the world wherever mammals develop on "oceanic" islands. Moreover, according to several authors, such as Felten and Storch (1970) and Krapp (1984), the insular gigantism would be comprehensible only as a consequence of genetic drifts, in which a role of particular importance could have been played by the so-called "founder effect".

Oak jungles for endemic proboscideans and ungulates

Fossil bones of endemic deer have been reported from a number of Mediterranean islands, including Pianosa, in the Tuscan archipelago, Corsica and Sardinia, Capri, Sicily, Malta, Amorgos, Crete, Kasos, Karpathos, Tilos and Rhodes, whereas dwarf hippopotami are known only from Sicily, Malta, Crete and Cyprus (Sondaar and Boekschoten 1967, Kuss 1973, 1975, Dermitzakis and Sondaar 1978, Ambrosetti et al. 1980, Sondaar et al. 1986, Anastasakis and Dermitzakis 1990, Kotsakis 1990). Remains of elephants have been described from the Middle-Late Pleistocene of the islands of Giglio (Tuscan archipelago, northern Tyrrhenian Sea), Sardinia, Favignana (Egadi islands), Sicily, Malta, Kythera, Euboea, Cyclades (Milos, Kythnos, Seriphos, Delos, and Naxos), Crete, Dodecanese islands (Rhodes, Tilos and Kos), Icaria, Samos, Chios, Gökçeada (Imbros), and Cyprus (Symeonidis and Theodorou 1982, Kotsakis 1990, Masseti 1993a, Caloi et al. 1996). Recently, fossil proboscidean teeth have also been discovered on the islands of Astypalaia and Kalymnos (Dodecanese, Greece) (Masseti 2002a, 2006) (Figure 6). Dwarf endemic elephants are known amongst the Quaternary faunas of Cyprus (Bate 1903a, 1904a,b,c, Vaufrey 1929, Boekschoten and Sondaar 1972), Rhodes and Tilos (Bachmayer et al. 1976, 1984, Symeonidis et al. 1973), Naxos, Delos and Serifos (Johnson 1980, Symeonidis and Theodorou 1982, Davis 1987), Crete (Kuss 1970, Sondaar 1971, Symeonidis and Theodorou 1982, Schlager 1991), Malta (Falconer 1862, Adams 1870, Adams 1875, Vaufrey 1929), and Sicily (Ambrosetti 1968, Ambrosetti et al. 1980, Belluomini and Bada 1985, Bada et al. 1991). Most of these forms appear to derive from the straight-tusked elephant, *Elephas antiquus* Falconer and Cautley 1847, a species dispersed up to the Late Pleistocene in the western Palaearctic (cf. Kurtén 1968, Boekschoten and Sondaar 1972, Symeonidis and Theodorou 1982, Caloi et al. 1996, Herridge and Lister 2007) (Figure 7). The dwarf elephant, recorded from Sardinia, is instead reputed not to belong to the lineage of *E. antiquus* and is described as *Mammuthus lamamorae* Major 1883 (Azzaroli 1983, Caloi et al. 1996).

Several explanations for the dwarfing of island mammals have been suggested (Azzaroli 1971, 1977, 1982, Sondaar 1977, 1986, Heaney 1978, Davis 1984), and departures from the predictions of this rule are common amongst mammals of differing body size, trophic habits



Figure 6 Third inferior molar of straight-tusked elephant, *Elephas (Palaeoloxodon) antiquus* Falconer and Cautley 1847, reported from the island of Kalymnos, Dodecanese (Greece) (courtesy of the 22nd Ephorate of Prehistoric and Classical Antiquities, Rhodes).

and phylogenetic affinities (cf. Raia and Meiri 2006). Dwarfism seems to be the only alternative large-sized animals have to lower selective pressure when they move into insular settings (Mazza 2007). Most of all, the low availability of resources sets insular populations under the strict control of both genetic and ecological constraints. Population densities are therefore confined between a critical minimum number of individuals needed to avoid extinction and a maximum number determined by the carrying capacity of the environment (Mazza 2007). Recently, Raia et al. (2003) and Raia and Meiri (2006) proposed a new explanation for the evolution of body size in large insular mammals – and of elephants in particular – using evidence from both living and fossil island faunal assemblages. They observed that the dimensional evolution of large mammals in different trophic levels has different underlying mechanisms, resulting in different patterns. Absolute body size may be only an indirect predictor of size evolution, with ecological interactions playing a major role. Raia et al. (2003)

focused their speculation on the former existence in Middle-Pleistocene Sicily of a pygmy proboscidean, the elephant of Falconer, *Elephas falconeri* Busk 1867, which was only 0.90 m tall at the withers, with this being, according to Roth (1992) and Lister (1993), the smallest elephant that ever lived (Figure 8). A very abundant fossil population (at least 104 specimens) of this species was recovered at the cave of Spinagallo, in eastern Sicily (Ambrosetti 1968). Raia et al. (2003) computed the survivorship curve for this fossil population in order to investigate both the great juvenile abundance and the high calf mortality revealed. Through the analysis of the survivorship of the elephant of Falconer, certain reconstructed life-history traits, and its supposed ecology – and taking into account the theory of “island rule” – they concluded that *E. falconeri* veered somewhat towards the ‘fast’ extreme of the slow-fast continuum in life-history traits in comparison to its mainland ancestor, the straight-tusked elephant, i.e., it was somehow *r*-selected. Thus, Raia et al. (2003) proposed a new explanation for the common occurrence of dwarfism in large mammals living on islands: the interplay of competition, resource allocation shift and feeding niche width could successfully explain this pattern. Furthermore, Raia and Meiri (2006) suggested that the extent of dwarfism in ungulates depends on the existence of competitors and, only to a lesser extent, on the presence of predators. According to Raia and Meiri (2006), dwarfism in large herbivores is an outcome of the increase in fitness resulting from the acceleration of reproduction in low-mortality environments.

In any case, I personally am of the opinion that we should not undervalue the importance of the selection exerted in relation to such specialisations by the principal characteristics of the physical environment. If we pause to reflect on the general appearance of the Mediterranean islands in the Upper Pleistocene, or even only in the Early Holocene, we realise how incommensurably different it was from that of today. In fact, there is possibly no other place in the world which has been so intensively influenced by human activity over a prolonged period as the Mediterranean. Civilisations have been continuously present for over 10,000–12,000 years, modifying entire landscapes, disrupting or destroying the majority of

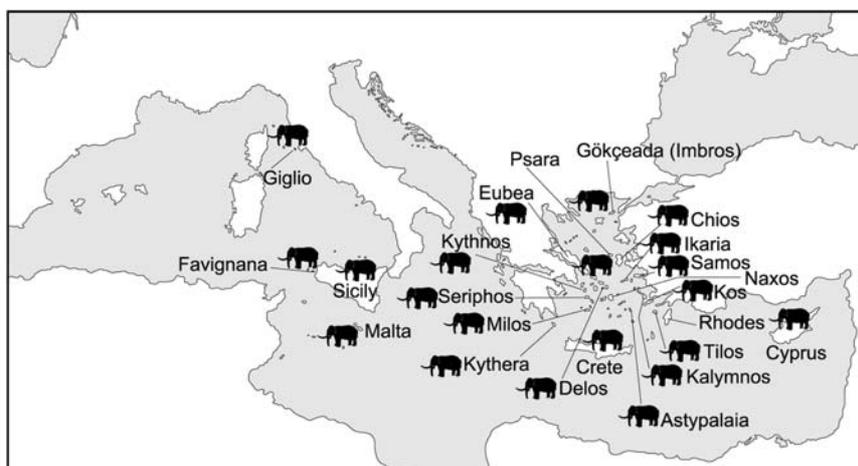


Figure 7 Map of the Mediterranean basin showing the islands where Middle and Upper Pleistocene remains of elephants have been discovered.

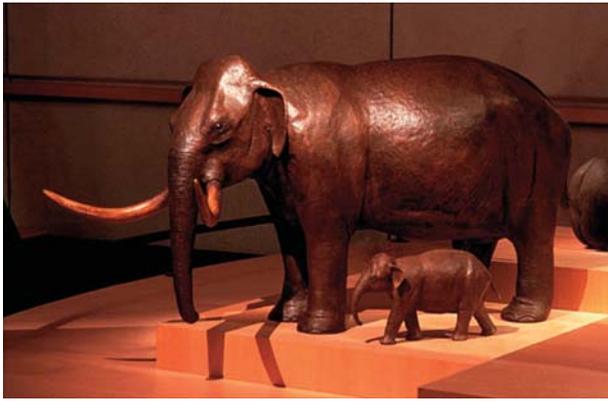


Figure 8 Ideal reconstruction of the elephant of Falconer, *Elephas falconeri* Busk 1867, which was only 0.90 m tall at the withers, thus representing the smallest elephant that ever lived (courtesy of the Muséum National d'Histoire Naturelle, Paris).

native biocenoses, and introducing many new species. Virtually no ecosystems have been left untouched. Few other regions of our planet have been maltreated by man more than the Mediterranean, to the extent that we can now have only the vaguest impression of what the ancient natural riches, vegetable lushness and primaevial faunal luxuriance of the region may have been. Much of the environment of the Mediterranean islands is by now reduced to little more than a mineral skeleton. In the Upper Pleistocene, when the existing botanical and faunal assemblages were already defined, the majority of the Mediterranean islands must still have been cloaked in the densely tangled vegetation that covered most of these environments before any human explorer set foot on them. Oak jungles consisted of downy oaks, *Quercus pubescens* Willd., evergreen oaks, *Q. ilex* L. 1753, Kermes oaks, *Q. coccifera* L. 1753, and of endemic species, such as the golden oak of Cyprus, *Q. alnifolia* Poech 1842, (cf. Haslam et al. 1977, Rackham 1978, 1990, Turner 1978, Meikle 1977, Turland et al. 1993, Rackham and Moody 1996, Ntinou 2002, Masseti 2008). Not to mention the dense undergrowth. The “true” islands of the Mediterranean were inhabited by extraordinary creatures which might have proved to be intriguing aberrations from the most simple rules of evolution. These practically impenetrable vegetable formations must have been home to an entire fauna that was particularly adapted to living, moving, feeding, resting and hunting each other in such an environment. This is still the case, for example, in certain relic fragments of the rain forests of western Africa, where peculiar biological elements, such as the last pygmy hippopotami, *Hexaprotodon liberiensis* Morton 1849, still survive. This is a species dispersed at present only in western Africa from Sierra Leone to the Côte d'Ivoire (cf. Grubb 2005). Its main habitat consists of forested watercourses where it shelters by day in ponds, rivers and swamps. At night, it follows tunnel-like paths through dense riverine vegetation to graze in glades, or along grassy trails (Kingdon 2004). Recently, pygmy hippos have also been “rediscovered” in Liberia, in the Sapo National Park. It cannot be excluded that some of the dwarf hippopotami of Sicily, Malta, Crete and Cyprus might have lived in similar environmental condi-

tions too. The Cypriot dwarf hippo was even smaller and more slender than the extant Liberian hippo (Boeckschoten and Sondaar 1972), being about the size of a pig (Sondaar 1991) (Figure 9). Furthermore, the odontology and morphology of the Cypriot species suggest a mode of living similar to that of leaf-eating pigs and it may have been an animal that was better adapted to walking than to swimming (Boeckschoten and Sondaar 1972). The dwarf endemic elephant which characterised the Late Pleistocene/Holocene faunal horizons of the small island of Tilos, in the Eastern Aegean sea (Greece), has been described as a very agile animal well adapted to the island environment, capable of moving through rough terrain (Theodorou et al. 2007b).

It seems plausible that the reduced body size of the large mammals was one of the best adaptive responses to this type of environment. Analogous examples can be found in the populations of other large herbivores that still populate the primeval forest regions of Africa. Dwarf populations of African buffaloes, for example, taxonomically defined as *Syncerus caffer nanus* Boddaert 1785 (Basilio 1962, Eisentraut 1973, cf. Grubb 2005), and also known as forest, red or dwarf buffaloes, are regarded as still occurring in what remains of the African primeval forests, from Gambia to southern Zaire and northern Angola, and eastwards to lakes Edward and Kivu and south-western Ethiopia (Halthenorth and Diller 1977, Yalden et al. 1984).

Elephants of reduced body dimensions are still reputed to inhabit the rain forests of west-central Africa too (Basilio 1962, Roeder 1970, 1975, Halthenorth and Diller 1977, Kingdon 2004, Shoshani 2005). However, the existence of a species of African pygmy elephant is not generally recognised. In this regard, Halthenorth and Diller (1977) observed that they are often believed to be small exemplars of the African forest elephant, *Loxodonta cyclotis* Matschie 1900. The latter form was until recently considered a subspecies of the African bush elephant, *Loxodonta africana* Blumenbach 1797, but DNA testing has now shown that there may possibly be two extant elephant species in Africa. In fact, the forest elephant has recently been shown to be genetically distinct from the

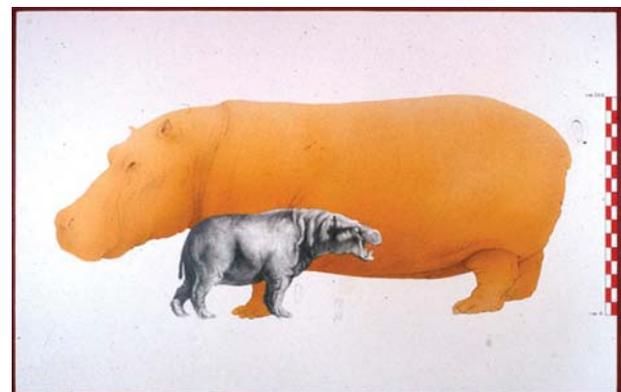


Figure 9 Artist's reconstruction of the extinct pygmy hippopotamus *Phanourios minor* Desmarest 1822, of Late Pleistocene Cyprus, adapted from the specimen in the London Natural History Museum and compared in size with the extant *Hippopotamus amphibius* L. 1758 (Drawing by Alessandro Mangione).

bush elephant, and hence probably a different species (Roca et al. 2001, Debruyne et al. 2003, cf. Kingdon 2004). Not all authorities, however – notably the IUCN African Elephant Specialist Group – consider currently available evidence sufficient for splitting the African elephant into two species. More specifically, the disputed pigmy elephants of the Congo basin, often assumed to be a separate species, *Loxodonta pumilio* Noack 1906, are probably forest elephants whose diminutive size and/or early maturity is due to environmental conditions (Debruyne et al. 2003). Nevertheless, Basilio (1962) gave an accurate description of the latter supposedly existing form, which he considered to be widespread in the pluvial forest of west-central Africa, from the Congo and Gabon to Guinea and southern Cameroon (Figure 10). Not long ago, researchers of the authority of Martin Eisentraut and Wolfgang Böhme (Eisentraut and Böhme 1989, Böhme and Eisentraut 1990) have also come out in favour of the existence of this pygmy form, still diffused in the Congo basin and possibly identifiable as *L. pumilio*. Addressing the principal objections against the specific status of the African pygmy elephants (e.g., ecological “race”, ecotype, juvenile of *L. cyclotis*), they systematically refuted them on the basis of morphological, craniological and biological evidence. As for the size of these pygmy proboscideans, for the first time they offered photographic documentation – obtained in the north of the People’s Republic of Congo – of the objective scale by juxtaposing forest elephants with dwarf buffaloes and above all with a great white egret, *Egretta alba* L. 1758 (Böhme and Eisentraut 1990) (Figure 11).

Predators in unbalanced faunas

A peculiar aspect of the endemic insular mammalian fauna is that they were all unbalanced. In fact, entire taxonomic groups, such as perissodactyls and felids, are almost completely absent (Masseti and Mazza 1996). Outside the Mediterranean, islands with unbalanced Pleistocene faunas occur in the Japanese archipelago, Indonesia, the Canary islands, Madagascar and off the coast of California. However, the Mediterranean island faunas have been defined as unbalanced mainly due to the general absence of carnivores of large body size



Figure 10 Adult male pygmy elephant killed in the pluvial forest of Spanish Guinea (extant Equatorial Guinea) in September 1957 (from Basilio 1962).

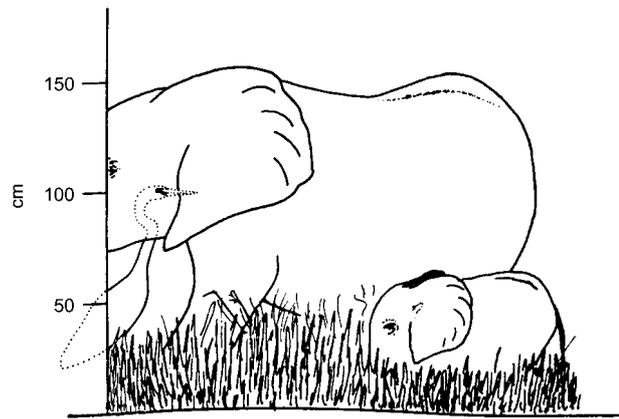


Figure 11 Sketch reconstructing the size of an adult Congo forest pygmy elephant and a calf, compared with the dimensions of an individual of white egret, *Egretta alba* L. 1758 (from Böhme and Eisentraut 1990).

(Sondaar 1977, Dermitzakis and Sondaar 1978). Willemssen (1992), followed by Theodorou et al. (2007a), tries to explain this feature of the faunal composition by observing that carnivores are worse swimmers than the other taxa that dominated the endemic faunas. Schüle (1993) also observed that islands of less than 20,000 km² do not support carnivores larger than an ermine, *Mustela erminea* L. 1758. Furthermore, Raia and Meiri (2006) observed that competition and predation have little or no effect on insular carnivore body size, which is influenced by the nature of the resource base, dependent on the abundance and size of their prey.

However, it can be generally stated that all the carnivores of the unbalanced insular faunas show strong endemic patterns and almost all of them are characteristic of a different insular complex. Indigenous to Sardinia and Corsica (Malatesta 1962, 1970, Bonifay 1976), *Cynoterium sardous* Studiatii 1857, for example, is the only endemic canid of the Late Pleistocene known for the Mediterranean islands. It was approximately the size of a fox, but its origin is still uncertain (cf. van der Geer 1988, Eisemann 1990, Lyras et al. 2006). According to Eisemann and van der Geer (1999), craniological comparisons do not indicate a close relationship with any of the extant canids, supporting a full generic rank for this species. The occurrence of *C. sardous* in the Sardo-Corsican insular complex may have been made possible by the availability of prey of a size and quantity sufficient to offer a permanent food supply. Here, in fact, the presence of the ocothonid rat-like hare, *Prolagus sardus* Wagner 1829 (Figure 12), an endemic sort of pika, fairly large in size, with a high reproduction rate, and not available on any of the other contemporary Mediterranean islands, fulfilled the essential requirement for a medium-sized terrestrial predator (cf. Sondaar et al. 1986).

On the other side of the Mediterranean basin, in Cyprus, Bate (1903b) described a fossil mandibular ramus of a Pleistocene island carnivore as the endemic form *Genetta plesictoides*, intermediate between the extant viverrid *G. genetta* (L. 1758), and a mustelid of the European Oligocene, *Plesictis crozetii* Pomel 1846. Little is known of *G. plesictoides*, with scant material solely from a few Cypriot localities. Recent excavations in the



Figure 12 The ocothonid rat-like hare, *Prolagus sardus* Wagner 1829, was an endemic mammal of Corsica and Sardinia which survived up to historical times (photo: Marco Masseti, courtesy of the Naturhistorisches Museum of Basel).

site of Aghia Napa have, however, provided new remains of skull and skeleton of the species (Theodorou et al. 2007a). Its dental morphology reveals adaptation towards a more carnivorous diet in comparison to the extant *G. genetta*. The co-occurrence of *G. plesictoides* with the Cypriot dwarf hippo in the same archaeological site dates to between 13,500 and 11,000 years BP (G.E. Theodorou 2008, personal communication).

A few other carnivores of possible endemic taxonomic status have been provided by paleontological exploration, such as an undetermined *Mustela* sp. quoted amongst the Pleistocene fauna of Pianosa, in the northern Tyrrhenian sea (Gastaldi 1866, Rutimeyer 1866, Simonelli 1889, Forsyth Major 1882, Stehlin 1928, De Giuli 1970, Azzaroli 1978). Furthermore, *Enhydriactis galictoides* Forsyth Major 1901, was a semi-aquatic or, more probably, a land mustelid, possibly a polecat-like carnivore from the Middle Pleistocene of Sardinia (Ficcarelli and Torre 1967, Kurtén 1968, Azzaroli 1971). However, according to Willemssen (1992), the most common carnivores of the endemic Mediterranean insular faunas are the otters, which are adapted to an aquatic lifestyle and are found in many of the endemic island ecosystems. Being the only carnivores compatible with the unbalanced island faunas, they effectively represent the

exception, since in view of their specialised eating habits they cannot be considered as genuine mammal predators (Burgio and Fiore 1988, Schüle 1993, Masseti 1995). The endemic otters described to date from the Pleistocene of the Mediterranean islands are indicated in Table 1.

While it is true that there were no carnivores of large dimensions on Mediterranean islands of the Late Pleistocene-Holocene, the same cannot be said of the birds of prey. Golden eagles, *Aquila chrysaetos* L. 1758, Bonelli's eagles, *Hieraaëtus fasciatus* Vieillot 1822, and eagle owls, *Bubo bubo* (L. 1758), must have been, then as now, the most widespread raptors of large dimensions. They prey on small and medium-sized mammals, such as rabbits, *Oryctolagus cuniculus* (L. 1758), hares, *Lepus* sp, and even subadult wild goats, *Capra aegagrus* Erxleben 1777, and mouflons, *Ovis orientalis* Gmelin 1774. The island skies were also inhabited by other birds of prey, which have now vanished from most of the Mediterranean area. There was, for example, the white-tailed eagle, also known as sea eagle, *Haliaeetus albicilla* (L. 1758), a massive bird with a very broad wing-span, which feeds mainly on fish but without disdaining the occasional small mammal. This species is in fact regarded as the super-predator of the Late Pleistocene Ibiza ecosystem (Pytiusic islands, western Mediterranean) (Alcover et al. 2000). Several Pleistocene species of birds of prey also displayed a type of gigantism, although the modification was not accompanied by loss of flight (cf. Azzaroli 1982). Raptors of large size have been described from the Balearics, from Malta and from Crete (cf. Mourer-Chauviré et al. 1980). The *Aquila chrysaetos simurgh* Weesie 1988, was, for example, a Cretan subspecies of golden eagle, which on the basis of its known skeletal elements appears to be osteologically closely related to the western Palaearctic subspecies of *A. chrysaetos* (L. 1758), albeit larger. To date, this taxon is known only from Crete (Weesie 1988). The *Tyto balearica* Mourer-Chauviré, Alcover, Moya and Pons 1980, was instead a giant barn owl also dispersed in continental Spain and southern France, which was originally described as endemic to the Balearics (cf. Mourer-Chauviré and Sanchez Marco 1988). The endemic Cretan owl *Athene cretensis* Weesie 1982 (Weesie 1982, 1988) differed from its putative mainland ancestor, the little owl, *A. noctua* Scopoli 1769, in a

Table 1 Endemic otter thus far been described from the Pleistocene of the Mediterranean islands.

Species	Island	Stratigraphic occurrence	References
<i>Algarolutra majori</i> (Malatesta 1978)	Corsica	Late Pleistocene	Malatesta 1978, Helbing 1935, Malatesta 1970, 1978, Willemssen 1992
<i>Sardolutra ichnusae</i> (Malatesta 1977)	Sardinia	Probably Upper Pleistocene or Holocene	Malatesta 1977, Willemssen 1992
<i>Algarolutra majori</i> (Malatesta 1978)	Sardinia	Late Pleistocene	Helbing 1935, Malatesta 1970, 1978, Willemssen 1992
<i>Megalenhydriis barbaricina</i> (Willemssen and Malatesta 1987)	Sardinia	Presumably Late Pleistocene or Holocene	Malatesta 1977, 1978, Sondaar 1978, Willemssen and Malatesta 1987, Willemssen 1992
<i>Lutra trinacriæ</i> (Burgio and Fiore 1988)	Sicily	Middle or Late Pleistocene	Esu et al. 1986, Pennacchioni and Cassola 1986
<i>Lutra euxena</i> (Bate 1935)	Malta	Pleistocene	Burgio and Fiore 1988, Willemssen 1992
<i>Lutrogale cretensis</i> (Symeonidis and Sondaar 1975)	Crete	Late Pleistocene	Bate 1935, Thenius 1951, Thenius 1962, Kurtén 1968, Esu et al. 1986, Willemssen 1992
			Symeonidis and Sondaar 1975, Sondaar 1977, Willemssen 1980, 1992

slightly larger overall body size, longer wings, a morphologically different humerus, and disproportionately longer legs (Weesie 1982, 1988). Furthermore, Lydekker (1890) described the vulture *Gyps melitensis* Lydekker 1890, from the Pleistocene of Malta. This closely resembled the extant griffon vulture, *G. fulvus* Hablizl 1783, but was approximately one-fifth larger. Moreover, the osteological peculiarities of this Maltese vulture clearly correspond to the remains of other fossil vultures described from Crete (Weesie 1988) and from Pleistocene sites of continental Europe (Boule 1910, 1921, Jánossy 1963, 1974, Mourer-Chauviré 1975, 1977). These osteological affinities suggest that the dispersion of *G. melitensis* was not necessarily restricted to island environments, raising doubts about the effective inclusion of the species amongst the endemic taxa of the Mediterranean islands.

In the light of all this, the threat to the endemic mammals of the Mediterranean islands may have come from the sky (Figure 13). It has even been suggested that the tendency often displayed by endemic insular shrews and rodents to become larger than their mainland counterparts may have been the result of adaptation engendered as a defence against the attacks of birds of prey.

The disappearance of the endemics

The circumstances of the insular endemics changed drastically around the end of the Pleistocene/Holocene, the most significant cases of extinction over the past few thousand years having been those of the insular species (Howald et al. 2007). The most significant reason for this appears to be linked to human action. As far as is known today, the data available for the Mediterranean islands point to endemic faunal extinction being largely the result of human activities.

Human exploration of the shores and coastlines of the Mediterranean region began in ancient times, as man sought to exploit new natural resources and/or discover new geographical areas suitable for settlement. This was

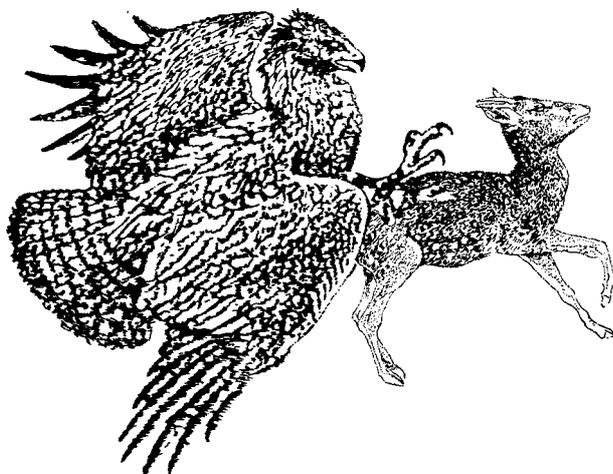


Figure 13 The threat to the endemic mammals of the Mediterranean islands may have come from the sky. In the picture, an artist's reconstruction of a golden eagle, *Aquila chrysaetos* L. 1758, attacking an individual of the endemic cave goat of Mallorca is shown (drawing by Silvia Cantagalli Masseti).

a lengthy process that began in pre-Neolithic periods and continued up to historical times. It now appears sufficiently plausible that, up to the Late Pleistocene/Early Holocene, this basin increasingly represented less a barrier than a bridge (Uerpman 1979, Lewthwaite 1987, Binder 1989, Guilaine 1994, Orliac 1997), in a relatively short time promoting and multiplying the circulation of ideas, merchandise, faunal and botanical elements and human groups, which spread into new and different environments and, over time and in different ways, became grafted onto the autochthonous substratum (Masseti and Vianello 1991, Masseti 1998). The available archaeological documentation, based on still quite fragmentary evidence, tends to indicate that the first relocations by sea in the Mediterranean basin were already carried out by hunter-gatherers in expression contexts of a Mesolithic type (Jacobsen 1976, Perlès 1979, Cherry 1981, 1990, 1992, Simmons 1991, Masseti and Darlas 1999). Evidence from the islands of Corsica (Camps 1988, Vigne and Desse-Berset 1995), Milos in the Western Cycladic archipelago (Perlès 1979, Renfrew and Aspinall 1990), possibly Kythnos (Cherry 1979) and Cyprus (Simmons 1988, 1991, 1999) indicate improved seafaring capacities. In fact, from the late Mesolithic onwards the Mediterranean sea can be considered as a preferential route for the exploration and subsequent colonisation of its coastlines and islands (cf. Payne 1975, Perlès 1979, Shackleton et al. 1984, Fedele 1988, Pennacchioni 1996).

For some islands it would appear that the endemic oligotypic associations and/or single species vanished prior to periods for which there is evidence of permanent human occupation (cf. Masseti and Darlas 1999). According to the 'theory of island biogeography', outlined by MacArthur and Wilson (1967), island environments tend to be characterised by a reduced biodiversity, to which animal populations, similar to human communities, have to adapt. Thus, it has been suggested that the extinction of the insular endemics may have been related more to their inability to adapt further in the face of a basically unfavourable environment than to the hunting prowess of pre-Neolithic man. In any case, this theory could prove more cogent for small and remote islets than for islands, such as Sardinia, Corsica, Sicily, Crete or Cyprus, still characterised by a great variety of natural resources. In the light of the archaeological evidence, one might even conclude that the impact of hunter-gatherer communities on the ecology of Mediterranean islands was relatively limited. Nevertheless, as argued by Rackham and Moody (1996), if in the Early Mesolithic trips to find obsidian, to Milos, for example, were combined with hunting trips to other islands, many of the endemic mammals may have disappeared before there was any settlement, such as to leave an archaeological record. In reality, in the case of Crete, for example, any overlap between the endemic Pleistocene fauna and the human occupation of the island has scant support from archaeological data, despite considerable efforts to uncover evidence of pre-Neolithic occupation (cf. Cherry 1992, Patton 1996). This is not to say, however, that the Corsico-Sardinian ochotonid lagomorph *Prolagos sardous* has not been hunted and eaten by people since pre-Neolithic times, as far back as the 9th millennium as

evidenced by the radiocarbon dating of its bone remains from the site of Monte Leone, Corsica, which indicated 8225 ± 80 BP (Vigne and Desse-Berset 1995, Vigne et al. 1998). On Cyprus, excavations of the site of Akrotiri-*Aetokremnos* have brought to light the possible conjunction of cultural material and great quantities of bone from the extinct endemic fauna (Simmons 1988, 1989, 1991, 1999). Associated with this site is a huge faunal assemblage that consists of endemic mammalian species previously thought to have become extinct during the Pleistocene, prior to the arrival of humans on the island. Most of the osteological material is referable to the endemic hippopotamus, while pygmy elephants are also represented by several subadult individuals. Simmons (1991) estimates that a minimum of 200 specimens of *Phanouris minor* were represented amongst the fossil remains of *Aetokremnos*. Approximately 20% of the bone was burned and almost none was articulated, but no clearly butchered bone was identified (Simmons 1991, 1999). A consistent group of a dozen ^{14}C dates (shell, bone, charcoal) arguing in favour of an 11th millennium BP occupation, with a weighted average of $10,030 \pm 35$ BP, sets the findings of Akrotiri-*Aetokremnos* only a few centuries before the earliest record now available for the pre-pottery Neolithic period, recently discovered at Shilloukambos and dated to the first half of the end of the 9th/8th millennium (see Guilaine et al. 1996, 2000, Briois et al. 1997). Thus, Akrotiri-*Aetokremnos* has implications for early seafaring technology and, more importantly, for the adaptive strategies adopted by these early Mediterranean human colonists (Hadjisterkotis and Masala 1995). Equally interesting is the association of cultural materials with extinct late Pleistocene vertebrates. *Aetokremnos* appears, in fact, to represent one of the few good examples of a late Pleistocene/early Holocene cultural adaptation directly associated with the extinction of an endemic vertebrate fauna. In the light of all this, Cyprus is the first Mediterranean island where some of the endemic vertebrates effectively appear to have been wiped out by the hunting of human prehistoric groups.

However, not all the endemites became extinct in ancient times. Several indigenous mammals survived up

to late Holocene chronologies (Figure 14). For instance, the extinction of *Myotragus balearicus* is well documented on the Balearics, where it persisted up to the 3rd millennium BC (Burleigh and Clutton-Brock 1980, Lax and Strasser 1992, Alcover et al. 1999, Ramis and Bover 2001), or perhaps even later (cf. Guerrero Ayuso 1997). The subfossil evidence that we have for Corsica and Sardinia indicates the survival of the rat-hare *Prolagus sardous* up to very recent epochs, datable between the Bronze and the Iron Age (Fonzo 1986, Gallin and Fonzo 1992, Delussu 1997, 2000, Manconi 2000, Wilkens 2005). Moreover, the persistence of this animal up to even more recent times, such as the period of classical antiquity, cannot be ruled out (cf. Vigne 1997, Wilkens and Delussu 2003, Masseti 2009a). In Sardinia, the presence of the vole *Microtus henseli* has also been documented up to archaeological contexts of the Iron Age (Delussu 2000, Wilkens 2005). In the eastern Aegean sea, a population of dwarf elephants seems to have survived on the island of Tilos, perhaps at least up to the Bronze Age (Symeonidis et al. 1973, Masseti 2001, 2003a), much longer than the last endemic Cypriot proboscideans and hippos, hunted to extinction several millennia earlier (cf. Simmons 1999).

Nothing beside remains...

In the light of current knowledge, less than approximately one-fourth of the mammalian species found in the continental Mediterranean region have been described as endemic to the area. The number of endemites decreases drastically, however, if we consider the composition of the extant fauna on the islands. In fact, in comparison to the Pleistocene, it can be observed that the extant insular mammalian fauna is richer in species but with a greatly reduced level of endemics (cf. Vigne 1997, Masseti 1998). Today, the almost complete absence of endemic species is quite surprising. The insular endemics are restricted to just four taxa, possibly comprising two species of shrew, the Sicilian shrew, *Crociodura sicula* Miller 1900, and the Cretan white-toothed shrew, *C. zimmer-*

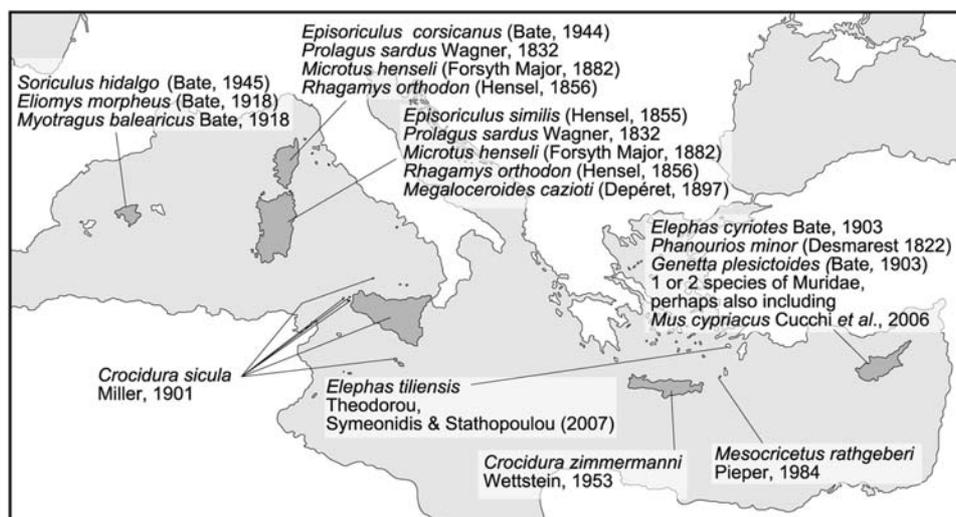


Figure 14 Endemic non-volant mammalian species that survived in the Holocene of the Mediterranean islands.

manni von Wettstein 1953, and two rodents, the recently discovered, and already mentioned, Cypriot mouse, *Mus cypriacus*, and perhaps also the Kerkennah islands dipodil, *Dipodillus zakariai* Cockrum, Vaughan and Vaughan 1976, from the namesake Tunisian archipelago (Figure 15).

From a cytogenetic analysis of shrews found on Sicily and the island of Gozo (Maltese archipelago), it became evident that all the members of the *Crocidura* genus from the Siculo-Maltese archipelago actually belong to the same species *C. sicula* (Vogel et al. 1989). This taxon is endemic to Sicily, the archipelago of Egades (Levanzo, Favignana and Marettimo), Ustica and Gozo, and is considered as being extinct on Malta (Vogel et al. 1990, Sarà 1995, 1996). It is a probable survivor from the Pleistocene, but not related to the endemite *C. esuae* Kotsakis 1986, living in the Middle Pleistocene of Sicily (Kotsakis 1986, Hutterer 1990, Sarà, 1995), and apparently replaced by *C. sicula* since the terminal Pleistocene (Bonfiglio et al. 1997). The Sicilian shrew has also been identified as a conspecific form of *C. canariensis* (Hutterer et al. 1987), endemic to the Canary islands (Sarà 1995). According to certain authors (Vogel et al. 1990, Sarà 1995, 1996, 1998), that of *C. sicula* is to be comprised amongst the extinctions that took place also on the small island of Lampedusa in the Sicilian channel in the course of the Holocene. Nevertheless, considering the markedly African character of the terrestrial mammal fauna yielded by the fossil horizons of Lampedusa (cf. Burgio et al. 1997), the presence of a Sicilian-Maltese endemite within this would raise a number of questions and should in any case be considered with caution (Masetti and Zava 2002b).

The Cretan white-toothed shrew has instead been recognised by Reumer (1986) as a relic of the Early and Middle Pleistocene group of European *Crocidura* species, and of the Pleistocene Mediterranean fauna. Effectively, fossils of this species have probably been present since the Early Pleistocene, being found in association

with the endemic mammals that lived on Crete. It regressed after the man-made introduction of the species that characterise the current fauna (Reumer and Payne 1986). Today, this shrew is not known anywhere outside Crete (Reumer 1996) and is therefore considered endemic to this island (Vogel et al. 1990, Reumer 1996, Hutterer 2005).

Recently, a phylogenetic survey has confirmed that the non-commensal mouse of Cyprus, *Mus cypriacus*, was an unknown sister species of the European wild mice (Bonhomme et al. 2004, Cucchi et al. 2006). Genetic and morphometric analyses provide satisfying criteria for the diagnosis of this new species in relation to other Mediterranean taxa. The most obvious phenotypic characteristics are its long tail and the allometric gigantism and robustness of its cranial and dental characters. According to Cucchi et al. (2006), the molecular clock and the history of the murine settlement on Cyprus are congruent and suggest that the common ancestor of *M. cypriacus* and the Balkan short-tailed mouse, *M. macedonicus* Petrov and Ružić 1983, arrived on Cyprus during the Middle Pleistocene through a founder event on natural raft. The remoteness of Cyprus through time has prevented introgression from the mainland gene pool and favoured phenotypic adaptation to competition release, leading to the allopatric speciation of *M. cypriacus*.

The Kerkennah islands dipodil is regarded as endemic to the homonymous archipelago (Cockum et al. 1976, Lamine Cheniti 1988, Cheylan 1988, 1990, Pavlinov et al. 1990), and it is no longer synonymised with the North African mainland Simon's dipodil, *Dipodillus simoni* Lataste 1881 (cf. Musser and Carleton 2005), as instead reported by Gippoliti and Amori (2006) apparently following Musser and Carleton (1993). It could be interesting to note that, apart from the latter species, rodents on Kerkennah are today represented only by non-endemic species, such as the greater jerboa, *Jaculus orientalis* Erxleben 1777, the house mouse, *Mus musculus* L. 1758, and the black rat (Cockum et al. 1976, Cheylan 1988,

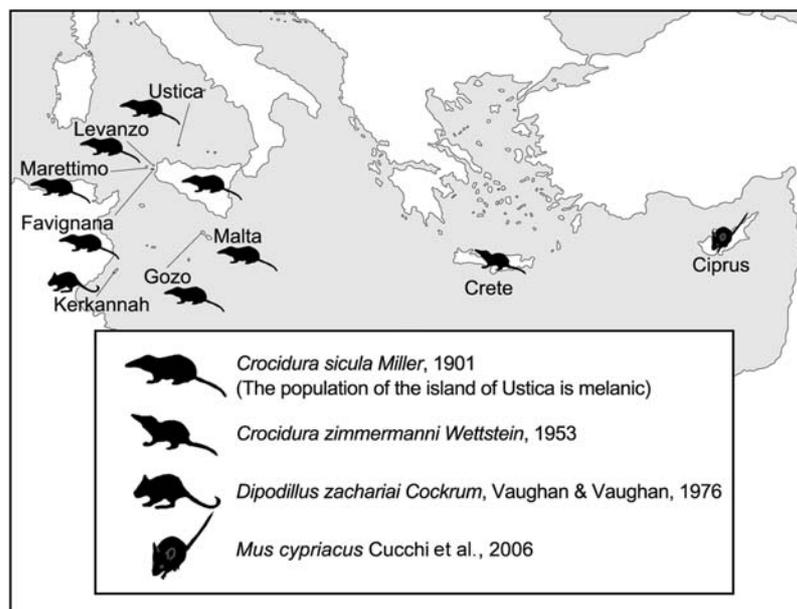


Figure 15 Present distribution of the mammalian species currently regarded as endemic to the Mediterranean islands.

Lamine Cheniti 1988, Vigne and Callou 1996). Moreover, arguing against the formerly supposed endemism of the Cretan and the Cypriot spiny mice is the absence of any Pleistocene fossil of the genus recorded so far from either of these islands, whereas genetic researches demonstrate the vicinity of the spiny mice to the populations of the *Acomys cahirinus-dimidiadus* group, distributed in south-western Asia (Macholán et al. 1995, Barôme et al. 1998, 2001, Masseti 1998, 2003a).

Modern research emphasises the susceptibility of bats to geographical barriers, even a narrow tract of sea (Azzaroli Puccetti and Zava 1988, de Naurois 1994, Castella et al. 2000). Thus, only a few species of the order Chiroptera are today recognised as endemic to the insular complexes between the Mediterranean Sea and the Atlantic Ocean. As far as is presently known, the Sardinian long-eared bat, *Plecotus sardus* Mucedda, Kiefer, Pidinchedda and Veith 2002 (Kiefer and Veith 2001, Kiefer et al. 2002, Mucedda et al. 2002), is the only endemic bat recognised for the Mediterranean islands. It is also the only extant mammalian species endemic to Sardinia and the sole endemic bat of Italy.

The island of Tilos, in the Eastern Aegean Sea: a case study

Further studies are required for a better understanding of the taxonomic status of the lesser white-toothed shrew, *Crocidura suaveolens* Pallas 1811, from the small island of Tilos in the Dodecanese (Eastern Aegean Sea, Greece). Although this island lies only a few marine miles off the western Anatolian coast, in the late Quaternary its native mammalian fauna was not characterised by continental taxa, but differed considerably from contemporary mainland wildlife. It was dominated by endemic dwarf elephants, only recently specifically described as *Elephas tiliensis* by Theodorou et al. (2007b) (Figure 16). According to detailed comparisons by Theodorou (1983, 1986), this elephant also never arrived at the larger dimensions of some of its bigger endemic relatives of

Sicily and Crete. The morphology of the new species points to a population with numerous changes concerning the postcranial material. It could be interesting to note that the height at the withers of the adult pygmy African elephants photographed by Böhme and Eisentraut (1990) in the north of the People's Republic of Congo is almost the same as that which it has been possible to reconstruct for the Tilos exemplar, it also being adult, symbolically illustrated in Figure 17 (cf. Masseti 2003a, Masseti and Sarà 2003). As we have already seen, however, the supposed ancestor of the dwarf proboscidean of Tilos was not *Loxodonta africana* or a taxonomically related form, but the straight-tusked elephant.

The age of the deposits of the cave of Charkadio, on Tilos, where the elephants were discovered ranges from the very late Pleistocene to the Holocene, some of their osteological remains being attributed to very recent times, between 7.090 ± 680 and 4.390 ± 600 BP (Bachmayer and Symeonidis 1975, Bachmayer et al. 1976). These dates originate from a different place in the cave of Charkadio, in inland Tilos, and are supposed to prove the simultaneous existence of the elephants and post-Palaeolithic man (Bachmayer et al. 1984). Furthermore, if such dating is reliable, we can assume that this taxon survived at least up to the beginning of the Aegean Bronze Age (Masseti 2001). According to Theodorou et al. (2007b), *Elephas tiliensis* is the last Mediterranean and European endemic elephant.

Except for one bat, the lesser mouse-eared bat, *Myotis blythii* Tomes 1857, so far no other micromammal remains have been found associated with the Tilos elephants, the stratigraphy of which also yielded *Testudo marginata* Schoeppf 1795, and *Ursus arctos* L. 1758, the latter presumed to be a hunter trophy (Bachmayer et al. 1976, Caloi et al. 1986, Kotsakis 1990). Nonetheless, other as yet unknown representatives of the limited endemic mammalian fauna of Tilos may have survived much longer than on other Mediterranean islands, possibly thanks to the shelter afforded by the natural morphology of the island, particularly inhospitable and unsuitable for human settlement. On the basis of such a

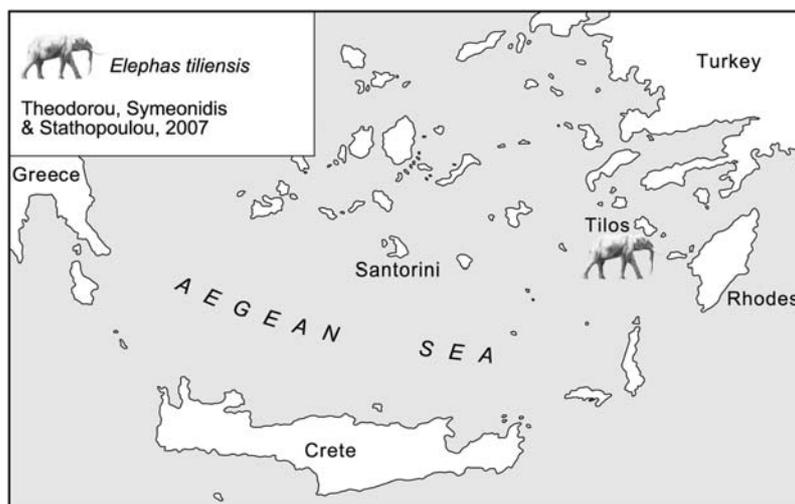


Figure 16 The geographical location of the island of Tilos, only a few marine miles off the western coast of Turkey, in the Eastern Aegean Sea (Greece).

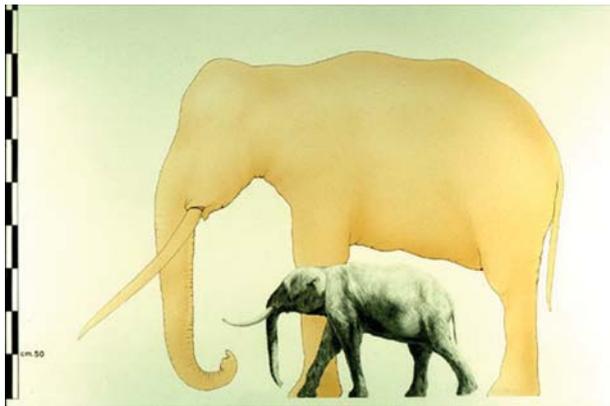


Figure 17 Artist's reconstruction of the extinct dwarf elephant, *Elephas tiliensis* (Theodorou et al. 2007b), of Late Pleistocene-Holocene Tilos, adapted from the osteological material in the Museum of Megalochorio (Tilos, Greece), and compared with the size of its alleged ancestor *E. antiquus* Falconer and Cautley 1847 (drawing by Alessandro Mangione).

supposition, research was carried out several years ago by Masseti and Sarà (2003) to investigate – for the first time – the current composition of the non-flying mammals of Tilos, also with a view to exploring the eventual relationship with species reported for the island for the previous Late Pleistocene-Holocene chronology. The outcome revealed that the extant insular non-volant mammals did not differ fundamentally from those of the great majority of the other Eastern Aegean islands, being almost exclusively characterised by continental taxa whose appearance on Tilos appears to be directly and essentially related to human activity (Table 2). Only the local lesser white-toothed shrew revealed peculiar phenotypic patterns: while the external size and the colour of its coat fall within the variability range for the species, this shrew reveals an unexpected white tail tip (Masseti and Sarà 2003). Colour anomalies have been reported for several species of Soricomorpha (Pearce 1934, Balli

1940, von Lehmann 1961, Fons et al. 1983, Michalak 1983, Chêtnicki et al. 2007). Albinism and white spotting in shrews include *Crocidura suaveolens*, *Crocidura russula* and *Crocidura leucodon* (Pucek 1964). The light colouration of the coat has been recognised as a result of lack of pigment in the entire hair or hair fragments, and it appears that atypically coloured shrews occur more often in isolated populations whose gene transfer with neighbouring populations is limited (Chêtnicki et al. 2007) (Figure 18). Moreover, white tail tips do not appear to be uncommon in shrews of the genus *Sorex* (Pearce 1934, Crowcroft 1957, Corbet 1963, Corbet and Harris 1991, Gelling 2003), but specifically as regards the representatives of the genus *Crocidura*, apart from the Tilos shrew, it is a characteristic reported to date only for the circum-Sicilian endemite *Crocidura sicula* (Vogel et al. 1989, Masseti and Sarà 2003, Masseti 2006, 2007a).

In any case, as we have already observed, the Sicilian and Cretan shrews, together with the Cypriot mouse and perhaps the Kerkennah dipodil, are presumably the relics, the last remnants of the late Pleistocene endemic mammals that characterised the Mediterranean islands. More specifically, Reumer (1986, 1996) observes that the Cretan shrew is a relic in two senses: firstly, it is the direct descendant of the Pleistocene group of *Crocidura* species that have disappeared from Europe and have been replaced by the present living species; secondly, it is the only known representative of the array of endemic shrews that were found in most of the Mediterranean islands during the Pleistocene. In any case, and apart perhaps from the allometric gigantism of certain phenotypic characters of *Mus cypriacus*, it is interesting to note that none of the aforementioned species displays the most common trends of endemisation reputed to affect micromammals on islands: the well known increase in size characteristic of fossil and/or subfossil shrews and rodents, but also documented in many of the extant populations (Masseti 2007a). This fact, together with their almost total absence from the Quaternary fossil horizon

Table 2 Holocene non-flying terrestrial mammals of the island of Tilos (Dodecanese, Greece) in time (from *Masseti and Sarà 2003).

Taxon	Charkadiocave (Late Pleistocene-Holocene fauna)	Charkadio cave, sub-recent fauna	Present fauna
<i>Elephas tiliensis</i>	Bachmayer et al. 1976, Caloi et al. 1986, Kotsakis 1990, Theodorou et al. 2007b		
<i>Erinaceus roumanicus</i>			Masseti and Sarà 2003
<i>Crocidura russula/suaveolens</i>		Symeonidis et al. 1973	
<i>Crocidura suaveolens</i>			Masseti and Sarà 2003
<i>Oryctolagus cuniculus</i> ^a			Masseti and Sarà 2003
<i>Apodemus flavicollis/sylvaticus</i>		Symeonidis et al. 1973	
<i>Apodemus mystacinus</i>		Symeonidis et al. 1973	
<i>Rattus rattus</i>			Masseti and Sarà 2003
<i>Mus domesticus</i>			Masseti and Sarà 2003
<i>Vulpes vulpes</i>		Symeonidis et al. 1973	
<i>Ursus cf. arctos</i> ^b	Bachmayer et al. 1976, Caloi et al. 1986, Kotsakis 1990		
<i>Martes foina</i>		Symeonidis et al. 1973	
Total (n=12)	Total (=2)	Total (=5)	Total (=6)

^aImported in very recent times (around 1997–1998) by hunters.

^bVery probably hunter trophy.



Figure 18 A partial depigmentation of the coat colour is not so unusual in the representatives of the Crocidurinae subfamily, such as the bi-coloured white-toothed shrew, *Crocidura leucodon* Hermann 1780 (photo: Massimo Del Guasta).

of the islands from which they are now reported, raises a series of intriguing questions that are still far from being answered.

Apart from the few aforementioned exceptions, this fauna displays virtually the same species composition, being almost exclusively characterised by continental taxa whose appearance on the islands has been almost essentially influenced by man.

The Holocene anthropical redefinition of the ecological equilibrium

Previous authors classified many of the modern mammals as subspecific geographic forms, almost entirely on the basis of arbitrary criteria and the examination of scattered materials (Masseti 2002d). Based on the data given in the literature, the various subspecies are distinguished by the coat patterns and by the size of body and skull. As is consequently understandable, this led to a multiplication of forms which now, however, demand better taxonomic and genetic definition. Throughout most of the 19th and the 20th centuries, it was common practice amongst scientific explorers to bring home an excessive number of subspecies from their explorations of the Mediterranean islands. This is the light in which we must consider the taxonomic treatment, on the part of the international scientific community, of the lagomorphs, the mustelids and the wild goats of the Balearic, Tyrrhenian and Aegean islands, as well as the Tyrrhenian and Cypriot mouflons, or the wild boars and the deer of Corsica and Sardinia (cf. Masseti 2007b). For instance, the Cretan marten, *Martes foina bunites* Bate 1906, was described as a geographic subspecies presumably dispersed on Karpathos, Crete and several other Aegean islands (Werner 1928, De Beaux 1929, Ondrias 1965, Corbet 1978, Douma-Petridou 1984, Masseti 1995a, 2002c), which was mainly distinguished by a smaller size and by a lighter and more yellowish coat colour than those of the nominal form *M. foina* Erxleben 1777 (Bate 1905b, Trouessart

1910, Miller 1912, Steesma and Reese 1996). The main phenotypic pattern was, however, indicated in the throat patch which was greatly reduced, despite being apparently absent in one of the seven skins examined by Bate (1905b). Studies on this aspect conducted by Niethammer and Niethammer (1967) and Ragni et al. (1999), however, failed to record the existence of such a characteristic in the current populations of Crete, suggesting that it should probably be attributed to the appalling conditions of conservation of the exemplars on which Bate (1905b) based his taxonomic description. In reality, all the Cretan martens examined by Niethammer and Niethammer (1967) and Ragni et al. (1999) displayed a pure white or greyish throat bib divided by a dark stripe into narrow irregular sections on left and right (Figure 19). In this regard, the Cretan beech marten falls within the phenotypic patterns of the Near-Eastern model, characterised by an irregular horseshoe-shaped throat mark which is displayed, for example, by the beech martens of the Levant (Syria and Palestine) (cf. Harrison and Bates 1991). It is, however, surprising that the Cretan marten is still described by MacDonald and Barrett (1993) as being characterised by "...a small greyish throat patch". Furthermore, Corbet and Ovenden (1980) have provided a pictorial description of the same taxon, with a small round patch in the middle of the throat, which is scarcely discernible and a far cry from the real throat patches of either the Near Eastern or the European beech martens.

Together with the Cretan marten, all the other populations described above are the result of ancient introductions performed by man since prehistoric times, and continued possibly without interruption throughout historical chronologies (Masseti 1998). As a consequence of this, they can be defined as populations of anthropochorous origin.

What appears evident is that, starting from the Early Holocene, there began a human colonisation of the Mediterranean islands that entailed the massive introduction of continental fauna species, accompanied by the gradual disappearance of the endemic elements. This effectively took place in a diachronic and differentiated form



Figure 19 It was at length believed that the Cretan marten, *Martes foina bunites* Bate 1906, was characterised by the extreme reduction, if not the complete absence, of the throat patch (Bate 1905b, Corbet and Ovenden 1980, MacDonald and Barrett 1993). Chania, Crete, June 1994 (photo: Marco Masseti).

in relation to the various species and the different insular complexes. The Neolithic settlement of the islands cannot be explained as the result of a merely casual maritime dispersal of the hunter-gatherers, but appears much more plausibly a movement of intentional and planned colonisation (Perlès 2001). The Neolithic settlement of islands, such as Crete and Cyprus, support this hypothesis. In both cases, the colonisation was accompanied by the transfer of the continental ecological appurtenances, also comprising domestic animals, the wild progenitors of which did not exist on the islands (Broodbank and Strasser 1991, Masseti 1998, Vigne and Buitenhuis 1999, Willcox 2001). Therefore, it is not simply a question of the transfer of breeding knowledge, but also of the physical transportation of the animals themselves. The human group and the related domestic animals that were moved by sea had to be sufficiently important and balanced to establish a vital population of men and beasts so that the agrarian way of life could be reproduced in a new territory. This ecological and cultural transplantation could not have been the result of casual maritime prospecting, but only the outcome of an expedition, or a series of expeditions, planned and prepared with a specific objective: the colonisation of an island.

Man brought with him the animals he needed as economic supplies for the colonisation of the new geographical areas, promoting their diffusion by eliminating ecological barriers and by augmenting the anthropogenic environment suitable for these species (Masseti 1998, Cucchi and Vigne 2006). Together with sheep, goats, pigs, cattle and dogs, a variety of wild species were also brought onto the Mediterranean islands, including shrews, hedgehogs, hares, mice, spiny mice, dormice, foxes, weasels, martens, badgers, cats and red and fallow deer. It should be emphasised, however, that in many cases such species have not been yielded by any of the Pleistocene deposits of the islands. It is not immediately apparent why man should have wanted to introduce all these animals, and the phenomenon can only be explained considering each case individually. Regarding this, Meiri et al. (2004) observed that carnivores found on modern-day islands could possibly be "...not colonizers, but insular relics from a time when a mainland-island connection existed". This is, however, not true in many cases, since there is sufficient evidence for the anthropochorous introduction of these animals (Masseti 2002b, 2003b). The evidence, in fact, suggests that continental carnivores were imported voluntarily by man, otherwise they would not have been able to pass unobserved on board the small boats employed to reach the islands (Vigne 1988b, 1995, Masseti 1995a). Synanthropic species, such as shrews and mice, on the contrary, may well have been transported involuntarily by man, hidden within foodstuffs (Masseti 1998). Furthermore, ethnozoological enquiry documents that hedgehogs (Vigne 1988b) and dormice (Carpaneto and Cristaldi 1994, Colonnelli et al. 2000) were utilised as food, medicine or for other purposes from prehistoric times onwards. Through the introduction of continental mammals, the endemic faunal elements were gradually replaced (cf. Vigne 1992), generating changes in the original ecosystem that can be observed throughout the Mediterranean basin.

In any case, to assess the range of the primeval distribution of the species, earlier chronologies prior to the Neolithisation of the Near-East and the Mediterranean should be considered. After this, the aforementioned improvement in human seafaring skills and the trade networks set up between the various countries enabled the artificial exportation of faunistic species of kinegetic interest, together with those already involved in the process of domestication (Masseti 1998, Lorenzini et al. 2002). Archaeozoological investigation records that the process of domestication of mammals, such as the wild boar, the Asiatic mouflon and the wild goat, was already established in the Near East from the Middle Pre-Pottery Neolithic B (MPPNB) (Peters et al. 1999, cf. Schmidt 1999). Thus, evidence of human cultural control over these mammals can be hypothesised, since they could have been imported onto the islands from mainland areas, even located very far afield.

As far as is presently known, the first transfers of allochthonous mammals to Mediterranean islands have been documented from Cyprus and are chronologically referred to the colonisation of this island that, as we have already seen, has been dated around the end of the 9th–8th millennium BC (Guilaine et al. 1996, 2000, Peltenburg et al. 2000, Guilaine and Le Brun 2003). However, for the first certain evidence of the importation of exotic ungulates towards more western territories we have to wait until later dates. This could, for example, be the case of the appearance of *Capra aegagrus* on the archipelago of the northern Sporades (Aegean Sea, Greece). Unknown in the oldest Mesolithic levels of the island of Youra, the remains of wild goats can be regarded as evidence of one of the most ancient human introductions in the Mediterranean area beyond the natural distribution of the species, which was completely extraneous to the fossiliferous horizons of the north-western Aegean region (Masseti 2002b). In fact, the date of Cal BC 6410–Cal BC 6220 (7th millennium BC) was obtained for the oldest *C. aegagrus* remains from the cave of Cyclops, through the radio-carbon analysis performed at the Beta Analytic Laboratory of Miami (Miami, FL, USA) (Masseti 2002b). The examination of data reported from the archaeological sites of the circum-Mediterranean area, yielding the first documentation of the appearance of Near Eastern caprines, reveals that the westward artificial diffusion of sheep and goats in the Mediterranean region seems to be quite independent of the cultural context in which they appeared for the first time: Pre-Pottery and Aceramic Neolithic, respectively, in the eastern Mediterranean and in the Aegean region, and Early Neolithic characterised by the production of impressed ware in the central and western Mediterranean (Masseti 1997, 1998, 2002b). In Sardinia, amongst the first immigrants around the end of the 7th–6th millennium BC are the fox, *Vulpes vulpes* L. 1758, the wild boar, *Sus scrofa* L. 1758, the wild goat, the Asiatic mouflon, and the red deer, *Cervus elaphus* L. 1758 (Masseti and Vianello 1991, Vigne 1992). The specific absence from the Pleistocene faunal horizons of osteological finds attributable to all these species means that they cannot be considered as endemic to Corsica and Sardinia, as has instead been hypothesised by Zachos and Hartl (2006) for *Cervus elaphus corsicanus* Erxleben 1777.

Characters of the extant insular mammals: generalist colonisers of pre-deserts

As already observed, the majority of the non-volant mammals which occur today on the Mediterranean islands can be considered as having been imported by man, except in the cases of the islands that were joined to the nearest land masses during the Late Pleistocene (Masseti 1998). With a few exceptions, the extant fauna reveals a distinctly homogeneous composition of elements, being no longer characterised by any of the endemic taxa previously reported (Masseti 2002b). Its structure is balanced by the presence of carnivores, essentially made up of continental species. In any case, the extant mammalian composition of the Mediterranean islands consists almost essentially of species that are more or less common to the present fauna of the rest of the Mediterranean region, and shows a generic continental origin influenced by the faunal composition of the nearest mainland (Alcover 1980, Sanders and Reumer 1984, Blondel and Vigne 1993, Masseti and Mazza 1996, Masseti 1993b, 1998, 2002b, 2006). Today, the most common insular carnivore is, for example, the aforementioned stone marten (Masseti 1995a), a species regarded as a follower of human cultures, which probably entered Europe from the continental Near East only at the end of the Pleistocene or in the early Holocene (Kurtén 1968, Anderson 1970, Sala 1992, Masseti 1995a, Yalden 1999).

The non-flying terrestrial mammals which today inhabit the Mediterranean islands are mainly represented by generalist species, animals which are able to thrive in a wide variety of environmental conditions and can exploit a range of different resources. When environmental conditions change, generalists are better able to adapt, while specialists tend to fall victim to local extinction much more easily (Townsend et al. 2003). Since these are almost exclusively species of continental origin, they are also those that manage to react better to the conditioning imposed by human cultural control and even to the effects of domestication. It is scarcely surprising that ungulates, such as the wild boar, the Asiatic mouflon, and the red deer, which were imported as tamed and/or semi-domestic livestock onto the islands since Neolithic times, occasionally escaped from their guardians' control, giving origin to the free-ranging population, the descendants of which persist up to the present time. Back in the wild, they maintained the morphological patterns of their Near-Eastern ancestors. In fact, as observed by Ryder (1983), the recognition of the origin of domestication is complicated by the fact that the first domestic animals did not differ greatly from their wild counterparts.

There are even phytophages of small and medium size that can survive in the most hostile of insular habitats, comparable in terms of both environmental and trophic characteristics to veritable pre-deserts. These are wild goats, hares and rabbits (Masseti 2003a, Masseti and De Marinis 2008). The islands of Youra, Antimilos, Crete and Montecristo are still inhabited today by populations of wild goats that feature the morphological patterns of *Capra aegagrus* (Erhard 1858, Reichenow 1888, von Lorenz-Liburnau 1899, Toschi 1953, Zimmermann 1953,

De Beaux 1955, von Wettstein 1955, Couturier 1959, Schultze-Westrum 1963, Kahmann 1959, Masseti 1981, Groves 1989, Ciani and Masseti 1991, Masseti 1997, Ciani et al. 1999) (Figure 20). Other historical populations of wild goats of the Mediterranean islands, such as Samothrace (Greece), Tavolara (Italy) and La Galite (Tunisia), became extinct in the course of this century (Ciani et al. 1999, Masseti 2009b). Apart from Crete, all these populations survive in territories characterised by very low trophic conditions, and without any artificial food supply. And yet, if we consider some of the biogeographical parameters of the islands, such as area and altitude, as indirect indices of habitat heterogeneity (*iihh*) (Table 3), we note that wild goat populations can still prosper in small rocky islands with a mean altitude of less than 600 (571) m above sea level, and a mean surface area of less than 10 km² (9 km²) (Masseti 2003a) (Figure 21). Survival in such peculiar insular environments may also be rendered possible by the integration into the diet of mineral salts, which are assumed both by licking the deposits that form on the foreshore and by consuming the excreta of birds. For example, we can cite the case of the wild goats of Montecristo which occasionally feed on the excreta of yellow-legged gulls, *Larus michahellis michahellis* Naumann 1840. Several years ago, it was possible to document this feeding behaviour directly on the small island of the northern Tyrrhenian Sea, where the wild goats are in the habit of licking the excreta deposited by the gulls on the rocks that they use as roosts (Masseti 2009b).

Hares can survive on even smaller islands than wild goats, with an area of 3–3.5 km², as shown by the populations that still inhabit the islets of Ghiannissada and Dragonada (Dhionysiades archipelago), and Gavdos, Chrissi and Koufonissi, respectively, off the north-eastern and the southern coasts of Crete (Masseti 2003a, cf. Masseti and De Marinis 2008). Rabbits too can now be found on many Mediterranean islands of even much smaller dimensions (Masseti and De Marinis 2008). They can, however, damage vegetation, accelerate soil denudation and erosion, and may ultimately be responsible for the decline or extinction of various species of reptiles and birds (e.g., Martin 2002, Courchamp et al. 2003, Chapuis et al. 2004, Genovesi 2005). Consequently, in view of the



Figure 20 Pictorial representation of the Cretan wild goat or *agrimi*, *Capra aegagrus cretica* Schinz 1838, from the 16th century Ulisse Aldrovandi Fond of the University of Bologna.

Table 3 Former and present occurrence of populations of *Capra aegagrus* (Erxleben 1777) on some of the Mediterranean islands without artificial food supply (from Masseti 2003a and 2009b).

Island	Subspecies	Altitude (m)	Area (km ²)	Notes
Montecristo (Italy)	<i>Capra aegagrus pictus</i>	645	10.39	
Tavolara (Italy)	<i>Capra aegagrus</i>	555	6	Extinct
La Galite (Tunisia)	<i>Capra aegagrus</i>	400	10	Extinct
Samothrace (Greece)	<i>Capra aegagrus pictus</i>	1840	178	Extinct
Youra (Greece)	<i>Capra aegagrus dorcas</i>	570	11	
Antimilos (Greece)	<i>Capra aegagrus pictus</i>	686	8	

vulnerability of the insular ecosystems, it can often be advisable to seriously consider their eradication, as in the case of Columbrete Grande (Castellón, Spain) (Masseti and De Marinis 2008). Occasionally, wild boars too are able to survive on small islands, such as the populations that inhabit Caprera, Maddalena, Spargi, Asinara and Marittimo, in the Italian seas. On the other side of the Mediterranean basin, the occurrence of the same species has been reported on the small Turkish islets of Cleopatra (Sehir Adalari), Değirmen Bükü, on the Seven Islands (Yediadalar) in the Gulf of Gökova, on the island of Yildiz in the gulf of Marmaris, the island of Domuz in the gulf of Fethiye, the island of Gemile opposite Olüdeniz and the island of Geykova, all located very close to the south-western coast of Anatolia (Masseti 2007c).

Together with the stone marten, the weasel, *Mustela nivalis* (L. 1766) and the pine marten, *Martes martes* (L. 1758) also figure amongst the extant carnivores most widespread on the Mediterranean islands (Masseti 1995a, De Marinis and Masseti 2003). All these mustelids can be regarded as generalist predators, since they are able to vary their diets according to local and seasonal food availability (cf. De Marinis and Masseti 1995, De Marinis 1996, De Marinis et al. 2004). These are carnivores that humans have accepted as neighbours, but are also those best at avoiding contact with man (Ragni et al. 1999, Masseti 1995a, 2002b). In several islands, *Martes foina* can, for example, be found behaving as a

full commensal of man in urban areas (Masseti 2002c). At Amorgos, in the eastern Cyclades (Aegean Sea, Greece), it was even possible to surprise this mustelid while it was rummaging amongst the rubbish containers in the very centre of Chora, the capital of the island. In continental conditions, the pine marten is considered mainly as a vole predator, but it is, in reality, an opportunistic carnivore with a generalised diet, which appears to be capable of exploiting feeding resources in relation to their local availability (Clevenger 1993, De Marinis and Masseti 1995). On the island of Elba, in the northern Tyrrhenian Sea, for example, this mustelid even becomes a rat hunter, in view of the availability of this species of prey (De Marinis and Masseti 1996, De Marinis et al. 2004). In the more particular case of the weasel, its favourite continental prey is voles of the genus *Microtus* (Sheffield and King 1994). On the Mediterranean islands, however, these rodents are very rare and the carnivore changes its feeding ecology from specialised microtine hunter to murid hunter (De Marinis 1996, De Marinis and Masseti 2003).

As far as is presently known, voles have been reported from only three Mediterranean islands inhabited by weasels: the Savi's pine vole, *Microtus savii* De Selys-Longchamps 1838, on Sicily (Amori 1993), the Thomas's pine vole, *M. thomasi* Barrett-Hamilton 1903 (Ondrias 1966, Thanou et al. 2006), and the common vole, *M. arvalis* Pallas 1778, on Euboea (Cheylan 1988), the latter being

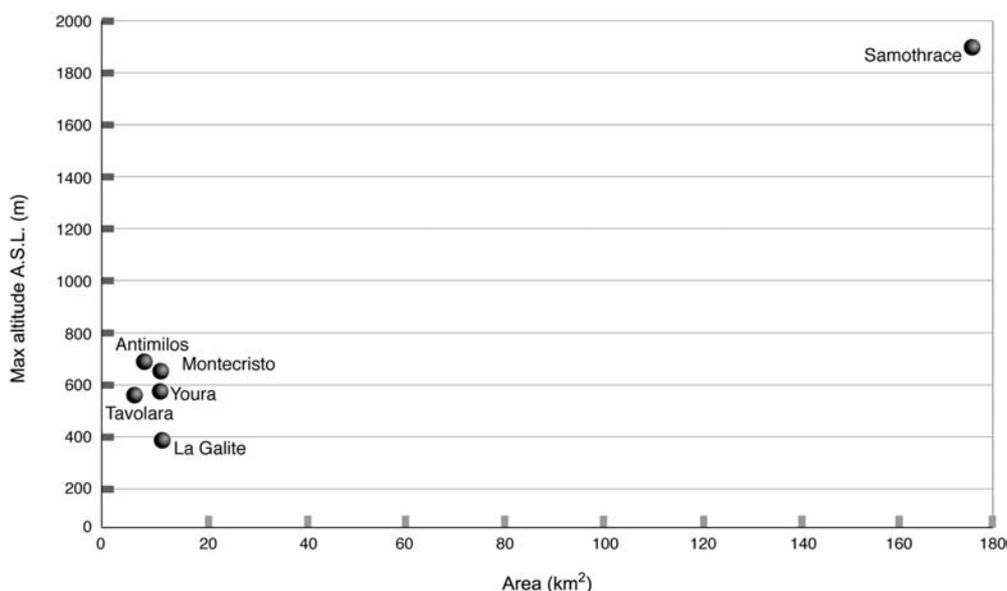


Figure 21 Former and present occurrence of populations of wild goats, referred to the phenotypes of *Capra aegagrus*, on Mediterranean islands <200 km², without artificial food supply (from Masseti 2003a).

also reported from Lesbos (Pieper 1981, Niethammer 1989). The Guenther's vole, *Microtus guentheri* Danford and Alston 1880, is known at present only on Lesbos (Pieper 1981, Niethammer 1989, Kryštufek 1999a), while a subfossil form of the same species, characterised by very large size, has been documented amongst the Holocene fauna of the island of Chios (Eastern Aegean Sea) (Besenecker et al. 1972, Kock 1974). Snow voles, *Chionomys nivalis* Martins 1842, have been found only in Euboea, where they have been reported from Mount Dirphys, at an altitude of 1700 m above sea level (Ondrias 1965, 1966). Cheylan (1988) also reported from Euboea the occurrence of the common pine vole, *Microtus subterraneus* de Sélvs-Longchamos 1836, whereas Niethammer and Krapp (1978) and Kryštufek (1999b) observed that this species is absent from the entire Mediterranean coast and islands.

Widespread in the continental areas and islands of more northerly Europe, voles are effectively considerably less diffuse in the Mediterranean insular ambits (cf. Corbet and Harris 1991, Corbet 1978, Mitchell-Jones et al. 1999), even if, as we have seen, the biogeography of Corsica, Sardinia and Malta was at length characterised by the presence of several endemic representatives of this taxonomic group. Beyond those just mentioned, very few other Mediterranean islands are known to be presently inhabited by voles. These are essentially Krk, in the Quarnero Gulf (Croatia), from where Tvrtković et al. (1985) dubiously recorded the presence of the bank vole, *Myodes glareolus* Schreber 1780, and the common vole, and Elba from where the Savi's pine vole was reported only once by Vesmanis and Hutterer (1980) and has never since been found in any of the subsequent studies conducted on the island (Contoli et al. 1988, Agnelli 1996, De Marinis and Masseti 1996, Nappi 2001). The Guenther's vole is also dispersed in Cyrenaica (north-eastern Libya), which can be regarded as an ecological island, being the only territory of the entire African continent where a representative of the Microtinae family occurs (Schlitter 1989). Since being reported in the faunistic associations of the island of Levanzo (Egades) in cultural contexts attributed to the late Upper Palaeolithic (Cassoli and Tagliacozzo 1982), the Eurasian water vole, *Arvicola amphibius* (L. 1758), appears to have survived in Sicily through the Neolithic chronologies (Grotta del Cavallo, Castellammare del Golfo, Trapani; Contrada Stretto di Partanna, Trapani) (Burgio et al. 2002, 2005, Cimò et al. 2005) up to relatively recent times (Casamento and Sarà 1995). The only modern record of its presence on the large Mediterranean island registered around the end of the 1950s by Pasa (1959) has been seriously questioned by Casamento and Sarà (1995), who were not able to confirm this vole as belonging to the present Sicilian fauna. Off the more northerly Tyrrhenian coast, some remains of the species – recently retrieved in Bronze Age archaeological contexts of the small islet of Vivara, in the Flegrean archipelago (Gulf of Naples) (Nappi and Carannante 2003, Carannante et al. 2005) – raise further interesting questions about the appearance of this vole in these territories. The present paucity of voles in the Mediterranean islands may even be related to the particular xerothermic conditions of these regions. In Israel, for

instance, evidence of the occurrence of the Eurasian water vole was found only in barn owls' pellets on the banks of the lake of Hula before this was drained during the early 1950s (Dor 1947), and it would appear to have been extirpated as a consequence of this event (Dimentman et al. 1992, Mendelssohn and Yom-Tov 1999) (Figure 22).

Based on the information provided by Pasa (1959), we could hypothesise that in Sicily too the presence of the species was documented only for chronologies prior to the definitive drainage of the wetlands of the surroundings of Agrigento. Moreover, regarding the assumption that Eurasian water voles were part of the Holocene fauna of Sicily, up to 1872 Doderlein (1872) claimed to have sighted numerous populations of this rodent in the marshes in the southern part of the island. The progressive desiccation of terrain in the Holocene as opposed to the Pleistocene might favour the survival of only those voles of more aquatic characteristics, such as precisely *Arvicola amphibius*. Instead in northern Europe, in more favourable conditions of humidity, this vole loses its more markedly aquatic capacities, expressing populations of a completely terrestrial nature. Furthermore, chrono-geographical data and molecular phylogenetic studies could sustain the possibility that the Italian water vole represents a taxon distinct from the other central and western populations grouped within *A. amphibius* (cf. Masini et al. 2007).

Invasive alien species

As observed by Cucchi et al. (2005) and Cucchi and Vigne (2006), the success of island colonisation by small commensal mammals depends on the magnitude of the migrant flow and the availability of an ecological niche for the new migrants. Since very ancient times, migrant flow has been supported by the maritime traffic which enabled micromammals to reach territories they would have been unable to access independently. The availability of a favourable ecological niche depends on the intensity of human settlement and the presence of autochthonous rodents representing potential competitors and acting as an ecological barrier. Today, invasive rodents occur on over 80% of the world's major islands and continue to be introduced (Atkinson 1985, Pitman et al. 2005).

Amongst rodents, the generalist species currently most widespread on the Mediterranean islands are those commensal to man: apart from the aforementioned spiny mouse, these consist essentially of the house mouse, and both the brown rat, *Rattus norvegicus* Berkenhout 1769 and the black rat or ship rat (Masseti 2002b). Rats and house mice are most likely responsible for the greatest number of extinctions and ecosystem changes on islands (Townsend et al. 2006). Because they are omnivorous, their feeding habits affect plants, invertebrates, reptiles, mammals and birds (Atkinson 1985, Cuthbert and Hilton 2004, Townsend et al. 2006, Howald et al. 2007). More specifically, rats are efficient predators of eggs, large insects, large reptiles, tortoises, birds and plants. They compete for food sources with herbivores and also cause

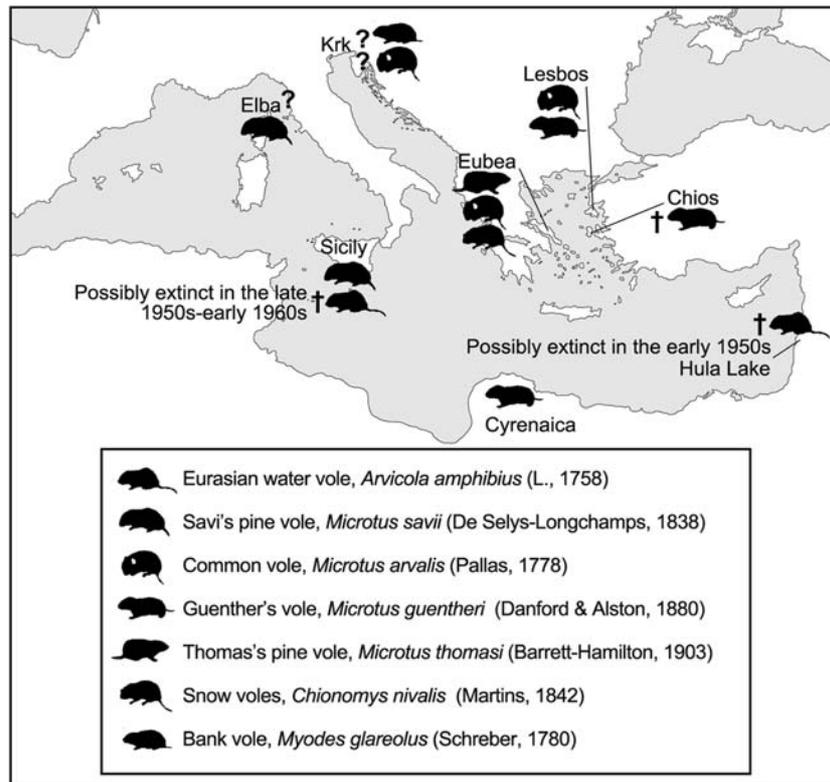


Figure 22 Present distribution of the representatives of the taxonomic group of Arvicolinae on the Mediterranean islands. The occurrence of the Guenther's vole, *Microtus guentheri* Danford and Alston 1880, in continental North Africa (Cyrenaica, Libya) and the location of the Hula Lake (Israel) are also indicated.

agricultural damage. Moreover, rats are the vectors of leptospirosis, a disease that can be deadly to humans and animals if not treated quickly (cf. Pascal et al. 2006).

The black rat is the most successful island colonist (Martin et al. 2000). Today, it is found on all continents of the earth. Although the species is believed to be native to the Middle East, it has been introduced to all continents through human overseas travel (cf. Masseti 2002b). It is widespread in forests and woodlands as well as being able to live in and around buildings. It feeds on and damages almost any edible item. It is very agile and often frequents tree tops, searching for food and nesting there in bunches of leaves and twigs. Ship rats are frequently associated with catastrophic declines in bird populations on islands (cf. Benchley 1999, Long 2003, De Marchi et al. 2006, Harris et al. 2007). Subject of an artificial diffusion beyond its homeland that is relatively recent in chronological terms and a consequence of human activity (Vigne 1992, Masseti 1995b, Pascal et al. 2006), the black rat is regarded as the most widespread invasive taxon of the alien species that continue to thrive on Mediterranean islands. Amongst the 292 Mediterranean islands examined in a recent review by Ruffino et al. (2009), comprising records of rat presence or absence, 201 (69%) were rat-infested, with the smallest rat-infested islet being 0.021 ha. The rodents were found on 36% of islands of <0.5 ha and on 99% of islands of >30 ha. *Rattus rattus* is the most common non-volant mammalian species in the Central Mediterranean archipelagos, including the islands of Hyères (Granjon and Cheylan 1990, Libois et al. 1996), the Quarnero islands

(Tvrtković et al. 1985), the Tuscan archipelago (De Marinis et al. 1996), the Egades (Krapp 1970), the Pelagian islands (Masseti and Zava 2002b), and the archipelagos of La Galite (Vesmanis 1972) and Malta (Lanfranco 1969, Schembri 1993). In the Italian seas alone, out of a total of 150 islands of a surface area ranging between 0.04 and 22,000 ha censused for rat presence/absence, the black rat was recorded in 83% of islands (Paolo Sposimo 2008, personal communication). Predation upon insular vertebrates by the black rat is considered a profoundly limiting factor for local biodiversity (cf. Orueta 2002). This rodent is in fact regarded as probably the single most dangerous and detrimental alien species currently affecting the insular ecosystems of the whole world (cf. Lowe et al. 2000), which explains various recent eradication campaigns (Orueta 2002, Genovesi 2002, 2005). Techniques for eradicating rodents from islands were developed over two decades ago (Howald et al. 2007). Since that time there has been a significant development and application of this conservation tool. Although worldwide 332 successful rodent eradications have been undertaken, not many have been carried out so far in the Mediterranean basin, one of the first being performed successfully in the Spanish archipelago of Chafarinas, off the Mediterranean coast of Morocco (Orueta 2002).

The invasion of ecosystems by exotic taxa is currently viewed as one of the most important causes of the loss of biodiversity (Elton 1958, Hengeveld 1989, Shine et al. 2000, Pascal et al. 2006). Invasive alien species are recognised as one of the major causes of habitat destruction on a global scale, and islands are particularly vulnerable

in view of the high proportion of endemic species and the specific biogeographical situation linked to their isolation (Lowe et al. 2000, Clout 2002, Genovesi 2002, 2005, Gippoliti and Amori 2002, Masseti 2002d,e, Wittenberg 2002, Courchamp et al. 2003, Pascal et al. 2006). The most significant cases of biodiversity loss are effectively to be found on the islands, where we have seen indigenous species have often evolved in the absence of strong trophic competition, parasitism or predation (Masseti 2002d,e). As a result, the introduced species also thrive in the optimal insular ecosystems that affect their plant food, competitors or animal prey. It is above all on islands that the biological records offer univocal evidence of the appearance of allochthonous species and anthropogenic introductions. The fact is that on the islands the impact of extraneous elements on the unspoilt ecological system can be identified and its chronology specified with considerable precision, as a result of the evidence left and the relative rapidity of the consequences produced (Masseti and Vianello 1991).

Invasive mammals have caused the majority of the insular extinctions over the past thousand years (Atkinson 1989, Groombridge 1992, Howald et al. 2007). To alleviate the impact of such invasions for the sake of conservation, eradication of the alien species appears to be crucial (Genovesi 2005).

A weighty legacy

As pithily expressed by de Planhol (2004) in his book "Le paysage animal. L'homme et la grande faune: une zoogéographie historique": "...man, a superior predator, was destined to devastate and destroy. And he did." However, expounding an analysis rich in quantitative clarifications, the author goes on to argue that this phase is by now over and behind us: "For at least the last fifty years, humanity has shifted from the destruction stage to that of protection, even of resurrection, already recording brilliant successes, the number of which is bound to increase." Nevertheless, the legacy of the global redefinition of the original ecological equilibrium of the Mediterranean islands raises not inconsiderable problems of conservation and management. First of all, in the vast majority of cases, it is impossible to reconstruct the natural ecosystems of the past which have been irretrievably destroyed, lost thousands of years ago (Masseti 2002b,d).

In view of the vulnerability of the insular ecosystems, it is also critically important to prevent further introductions. From both a scientific and a cultural point of view, it would be advisable to seriously take into consideration the eradication of the alien species of very recent invasion, such as, e.g., *Myocastor coypus* Molina 1782, in Sicily and/or *Mustela vison* Schreber 1777, in Sardinia. But this results in the question of how to treat the allochthonous populations of certified ancient anthropochorous origin (Masseti 2002b, 2002d, 2007d). Each of such cases has to be considered individually. If, in fact, the eradication of rats, rabbits and feral goats imported in recent historical times is in many cases fundamental for the recovery of island ecosystems, several of the other

anthropochorous taxa represent invaluable historic documents, images which remain fixed in time and history. For instance, this would be the case of the martens of Elba (Figure 23), the genets of the Balearics, the red deer of Sardinia and Corsica, the moufflons of Cyprus and of the largest Tyrrhenian islands, the wild goats of Montecristo or Antimilos, and many other extant insular populations of mammals (Table 4; Figure 24).

Unlike the case of artistic monuments, however, here we are dealing with living organisms which interact with environments originally extraneous to their natural distribution, but which they have inhabited since ancient times. Their protection and their study can provide an opportunity for testing a range of different evolutionary theories. While the importance of these anthropochorous populations is not comparable, from a biological point of view, to that of veritable wild populations in their natural habitat, their elevated validity as environmental entities lies in their representing singular historical and cultural documents (Masseti 2002b). The exclusion of known anthropochorous taxa from conservation lists, followed by implementation of ulterior protective legislation, has been proposed as a necessary measure to maintain the uniqueness and richness of Mediterranean biodiversity (Gippoliti and Amori 2004, 2006). Nevertheless, an excessively philological and "purist" approach to the compilation of the conservation documents may even prove to be detrimental, as we have seen that the primeval ecosystems of the Mediterranean islands were irretrievably lost thousands of years ago. In the more specific case of the endemic mammals, they are practically entirely extinct.

Nor should we overlook the fact that many of these anthropochorous populations, which have inhabited the islands since immemorial time, constitute some of the few available points of reference for an understanding of the biological and ecological characteristics of their wild continental ancestors, by now long extinct. Consequently they deserve to be protected and considered in terms of a veritable "cultural heritage". Just as human artefacts and sites of archaeological and historical interest are subject to conservation strategies, we must thus also protect the populations of animals of ancient anthropo-



Figure 23 The extant occurrence of the pine marten, *Martes martes* L. 1758, on the island of Elba (Tuscan archipelago, Northern Tyrrhenian Sea, Italy) is assumed to be of ancient anthropochorous origin (photo: Marco Masseti).

Table 4 Some of the oldest populations of ungulates of anthropochorous origin still occurring on the Mediterranean islands (also see Figure 24).

Taxon	Island	Notes	References
<i>Sus scrofa meridionalis</i>	Corsica	Introduced in early Neolithic times	Vigne 1988a, 1999, Albarella et al. 2007
<i>Sus scrofa meridionalis</i>	Sardinia	Introduced in early Neolithic times	Sanges 1987, Masseti and Vianello 1991
<i>Cervus elaphus corsicanus</i>	Sardinia	Introduced in early Neolithic times	Sanges 1987, Masseti and Vianello 1991
<i>Dama dama dama</i>	Rhodes	Introduced in Neolithic times	Halstead and Jones 1987, Trantalidou 2002
<i>Capra aegagrus cretica</i>	Crete	Introduced in Neolithic times	von Lorenz-Liburnau 1899, Schultze-Westrum 1963, Sfougaris 1994, 1995, Jarman 1996
<i>Capra aegagrus pictus</i>	Antimilos	Possibly introduced in Neolithic times	von Lorenz-Liburnau 1899, Schultze-Westrum 1963, Sfougaris 1994, 1995
<i>Capra aegagrus pictus</i>	Montecristo	Possibly introduced in Neolithic times	Masetti and Vianello 1991, Masseti 1993b
<i>Capra aegagrus dorcas</i>	Youra	Introduced in ancient times	von Lorenz-Liburnau 1899, Reichenow 1888, Schultze-Westrum 1963, Sfougaris 1994, 1995
<i>Capra aegagrus cf. dorcas</i>	Mallorca	Introduced in pre-Hispanic times	Seguí et al. 2002, Seguí and Payeras 2002, Masseti 2009b
<i>Ovis orientalis ophion</i>	Cyprus	Introduced in early Neolithic times	Guilaine et al. 1996, Peltenburg et al. 2000, Guilaine and Le Brun 2003
<i>Ovis orientalis musimon</i>	Corsica	Introduced in early Neolithic times	Vigne 1984, 1988a
<i>Ovis orientalis musimon</i>	Sardinia	Introduced in early Neolithic times	Sanges 1987, Masseti and Vianello 1991

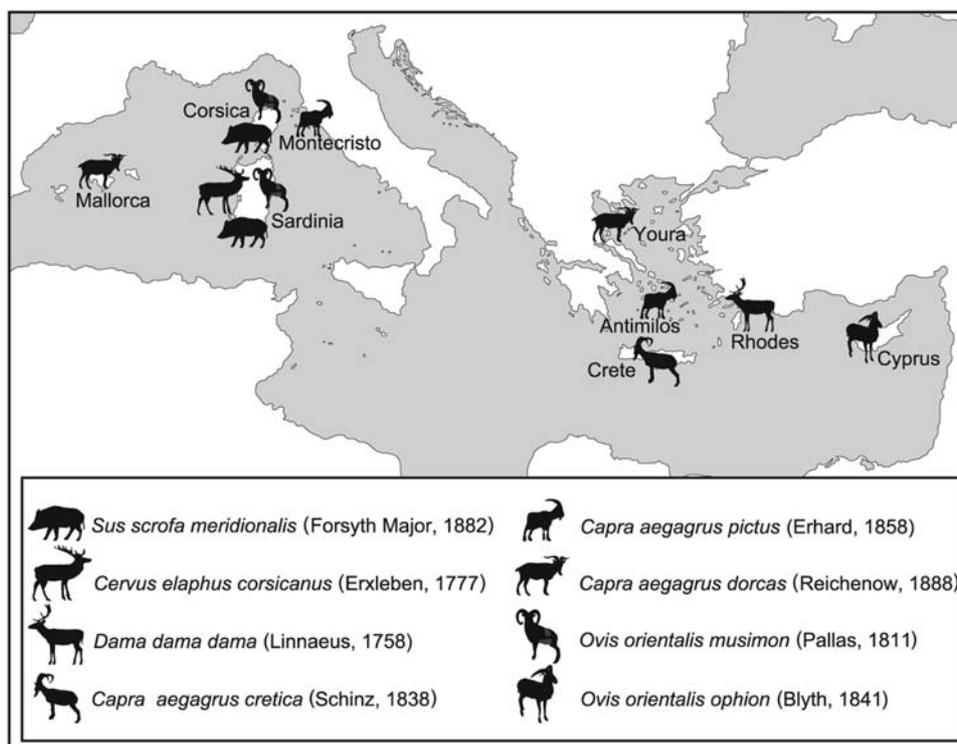


Figure 24 Some of the most ancient populations of ungulates of anthropochorous origin still dispersed on the Mediterranean islands.

chorous origin, acknowledging their importance as a common heritage of humanity, the study and observation of which enable us to acquire fundamental information about the progress of man through the millennia of his process of civilisation. These populations should therefore be assigned the significance of cultural heritage, through the application of zoological methods of research, attributing fundamental importance to the results of genetic analyses, always assessed through a critical examination of the information derived from biogeographical and historical research (Masetti 2002b). Today, unfortunately, we can still observe a widespread tendency towards an uncritical acceptance of the results

yielded by genetic analyses, without these being measured against other information originating from other disciplinary ambits, as should be the case. There are in fact genetic studies that are quite impeccable in terms of laboratory protocol, but less immediately comprehensible not only from a biological and biogeographical point of view, but also in terms of history and archaeozoology. In several cases, such studies can engender a degree of perplexity. Interpretations that are overly conditioned by the consideration of the genetic data alone can at times risk appearing simplistic or naive, since it is clear that other disciplines have already amply explored scenarios that are decidedly more plausible. Essentially, this can be

avoided by keeping under control the self-referencing aspect that often characterises certain genetic studies. In any case, modern research is beginning to reveal that the adoption of a multidisciplinary approach provides the opportunity to advance intriguing hypotheses which may prove particularly important in terms of the study, conservation and management of the extant Mediterranean insular fauna (cf. Hajji et al. 2007, Masseti et al. 2008). Another, and in no way secondary, aspect is the evaluation of the anthropozoological and zooethnographical importance of the ancient anthropochorous populations of the Mediterranean islands.

The Rhodian deer. Concluding remarks

The latest techniques for investigating population genetics have shown that the fallow deer, *Dama dama dama* (L. 1758), which still survive on the island of Rhodes (Dodecanese, Greece) are very special, being of ancient lineage and distinct even from the relic populations sampled in Anatolia, the supposed source of the Rhodian stock introduced in Neolithic times (Masseti et al. 1996, 2002, 2006, 2008). According to archaeological evidence, it is possible to report the occurrence of fallow deer on Rhodes since at least the 6th millennium BC (Halstead and Jones 1987, Yannouli and Trantalidou 1999, Trantalidou 2002). On the contrary, it was at length believed that the animal was introduced onto the island from Asia Minor by the Knights of Saint John of Jerusalem, who conquered Rhodes at the beginning of the 14th century. The genetic data clearly show that the split between this Rhodian population and its probable source, which is to be found elsewhere in ancient Anatolia, occurred long before the establishment of the former (Masseti et al. 2008) (Figure 25).

Today, fallow deer are very rare in Turkey, and the only known surviving population is that preserved within the enclosed area of Düzlerçami (Termessos National Park, Antalya, Turkey), where it is currently dwindling dramatically, with only 25–30 animals surviving (Masseti 2007d). Considering the Anatolian population as the source for all the populations founded by humans since prehistoric times, Masseti et al. (2008) suggest the structuring of this population in genetically differentiated subpopulations. From one of these subpopulations, some animals were plausibly captured and artificially moved to Rhodes. Considering the current level of genetic diversity recorded, it is likely that a good number of animals were used to establish the Rhodian population. Otherwise, we would have expected a major reduction in genetic diversity typical of a bottleneck due to a founder event. In addition, if current archaeozoological records are correct and fallow deer arrived on Rhodes approximately 7–8 kya, this time span comprises too few generations for the accumulation of the current genetic variability starting from a situation of virtually no variation, as predictable in the case of a strong founder event. The example of the fallow deer of Rhodes illustrates that the human-driven foundation of animal populations does not necessarily result in erosion and/or depletion of the original genetic variability of the species involved (Poplin 1979, Poplin and

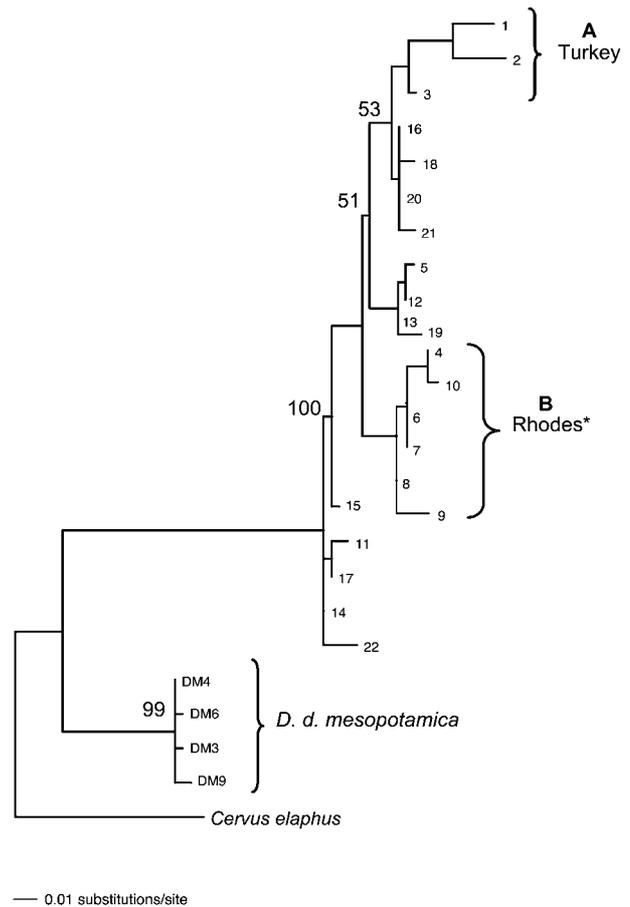


Figure 25 The latest techniques for investigating population genetics have shown that the fallow deer, *Dama dama dama* (L. 1758), which still survive on the island of Rhodes (Dodecanese, Greece) are very special, being of ancient lineage and distinct even from the relic populations sampled in Anatolia, the supposed source of the Rhodian stock introduced since prehistoric times. In the picture, the maximum-likelihood tree shows the different mtDNA haplotypes of the Rhodian cervid, the Turkish fallow deer and the Persian fallow deer, *D. dama mesopotamica* Brooke 1875, rooted with a sequence of red deer, *Cervus elaphus* L. 1758. Only bootstrap values (based on 1000 pseudo-replicates) and Bayesian posterior probability values above 50 are reported above each node (from top to bottom, ML, MP bootstrap and BI probability, respectively). Rhodes* denotes the cluster of haplotypes from Rhodian individuals carrying the 80 bp insertion (from Masseti et al. 2008).

Vigne 1983, Ryder 1983, Hemmer 1990, Masseti 2002b, Bruford et al. 2003, Zeder et al. 2006), and demonstrates that it is possible for some unique enclaves with a significant portion of the original genetic diversity to be created and maintained by chance (Masseti et al. 2008). It can be argued that this extraordinary process would be more likely with species selected for domestication, and additionally for hunting (Masseti 1998, 2002b). To this end, all the available evidence appears to confirm that fallow deer were employed as game animals in the majority of the geographical areas where they were artificially introduced outside their natural distribution (Masseti 1998). On Rhodes too, this species was imported in order to be hunted (Masseti 1998, 1999, 2002b, Trantalidou 2002). Instead, it is unlikely that fallow deer were ever fully domesticated (Croft 1991, Masseti 1998). The

probable foundation of the Rhodian population by humans in Neolithic times has resulted in the chance preservation of a significant portion of the mitochondrial genetic variability of the species up to the present time (Masseti et al. 2008). The current challenge is how to use this specific knowledge to manage and conserve this anthropochorous population. Its survival represents not only the first documented instance of 'ad hoc conservation', but is also significant in historical, archaeological and ecological terms. For these reasons too, its importance has to be considered on a par with that of a human artefact, as the dynamic testimony of ancient intervention which is still available for our evaluation and our appreciation, with all the consequences that such an estimate brings with it.

Similar to many other Mediterranean island anthropochorous mammal populations of ancient introduction, however, the Rhodian deer has never been recognised as an endemic subspecies or ecotype, nor has it appeared in the international conservation lists.

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