

Prehistoric and Historic Artificial Dispersal of Lagomorphs on the Mediterranean Islands

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Introduction

The current Mediterranean fauna is a result of the interactions of diverse factors, primarily the multiple biogeographical origin of the species, Quaternary climatic changes (which produced a repeated turnover of biota) and Late Pleistocene-Holocene human-induced habitat modifications, including hunting and Holocene introductions of a variety of allochthonous continental taxa (Masseti 1998, 2002). Apart from sporadic cases, the complete absence of endemic species from the extant mammalian fauna of the Mediterranean islands is quite surprising. In the majority of the cases, in fact, the existing populations of non-flying terrestrial mammals display undoubtedly a homogeneous composition of elements, predominantly revealing a continental origin (Alcover 1980; Sanders and Reumer 1984; Vigne 1992, 1993; Blondel and Vigne 1993; Masseti 1993, 1998). To assess the range of the original insular distribution of the different species in the Mediterranean region, earlier chronologies prior to the Neolithisation should be considered, after which improved human seafaring skills and the established commercial networks between countries enabled the artificial exportation even of wild animals, together with those already involved in the process of domestication (Masseti 1998; Lorenzini et al. 2002). Recent archaeological investigation indicates that the first transfers of allochthonous faunal elements were carried out subsequent to early Neolithic times, as documented by the discovery of the Pre-Pottery Neolithic site of Shillourokambos on the island of Cyprus (end of the 9th–8th millennium B.C.) (Guilaine et al. 1996, 2000; Cucchi et al. 2002; Vigne et al. 2003). It seems that from these times on, man began to bring with him the animals he needed as economic supplies for the colonisation of new geographical areas. One of the faunal categories much exploited in this sense is represented by the Lagomorph family, originally represented among the Late Quaternary endemic faunal horizons of the Mediterranean islands only by one species, the ochotonid *Prolagus sardus* (Sardinian pika) (Wagner 1829), native and exclusive of the Upper Pleistocene-Holocene of Corsica and Sardinia. In the light of

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archaeozoological evidence, this endemic lagomorph survived on the two islands up to very recent times, probably coinciding with the Iron Age (Delussu 2000; Wilkens and Delussu 2003), or even up to Roman times (cf. Vigne and Valladas 1996; Vigne 1997). According to the Greek historian Polybius (3rd–2nd century B.C.), the island of Corsica of his time was not characterized by the occurrence of any species of hare, but was instead inhabited by this Sardinian pika, locally called the *kyniklos*. Polybius observed that “. . . when seen from a distance [it] looks like a small hare, but when captured it differs much from a hare both in appearance and taste. It lives for the most part under the ground” (*The Histories*, XII: 3.8–4.6 in Paton 1925). However, evidence shows that the extant lagomorphs of the Mediterranean islands exhibit an apparently undifferentiated continental origin. The occurrence of these continental forms on all the islands seems to be linked essentially to the introduction by man during the Holocene.

In the present work, we reviewed the earliest recorded introductions of the Apennine hare, *Lepus corsicanus* (De Winton, 1898), the European hare, *Lepus europaeus* (Pallas, 1778), the Iberian hare, *Lepus granatensis* (Rosenhauer, 1856), the Sardinian hare, *Lepus* (“*capensis*”) *mediterraneus* (Wagner, 1841), the Mountain hare *Lepus timidus* (Linnaeus, 1758), the European rabbit, *Oryctolagus cuniculus* (Linnaeus 1758), and the Nearctic Eastern cottontail, *Sylvilagus floridanus* (Allen 1890) onto the Mediterranean islands in the light of recent archaeological investigations. Moreover, we updated their extant insular distribution considering the fact that they have been the object of artificial translocations also carried out in very recent times.

Materials and Methods

Data on lagomorph distribution were gathered from: i) literature; ii) field observations (sightings and dead specimens) carried out on the Tuscan Archipelago (Italy), Sardinia, circum-Sicilian and Maltese Archipelagos, Ionian and Aegean Islands, Crete and Cyprus within the last 10 years; iii) museum collections (Natural History Museum, London; Muséum National d’Histoire Naturelle, Paris; Zoological Museum, University of Florence; Natural History Museum, Crete; Natural History Museum, Vienna; Research Institute and Natural History Museum Senckenberg, Frankfurt am Main; Alexander König Zoological Museum, Bonn; Zoological Museum, University of Patras; Zoological Museum, University of Athens and The Bavarian State Collection of Zoology, Munich). The area of each island where lagomorphs are present today has been recorded.

Islands for Hares

Apennine hare, *L. corsicanus* De Winton, 1898. Endemic to the south-central Italian Peninsula and Sicily (Palacios 1996; Riga et al. 2003), this taxon was described by De Winton in 1898 on the basis of the examination of some

specimens obtained from Corsica. This fact has given rise to the unproven assumption that this hare was native to Corsica. Hares, however, never figured among the fossil horizons of the large Mediterranean island, where *L. corsicanus* has been possibly introduced shortly before the 16th century A.D. as documented by historical evidence (Vigne 1988a, 1990, 1992, 1999; Fig. 1). The Greek historian Polybius, for example, did not mention the occurrence of any type of hares among the Corsican mammalian fauna of his time (*The Histories*, XII: 3.8–4.6 in Paton 1925). The Apennine hare could have been originally present in the south-central Italian Peninsula and Sicily as an endemic relict population divergent from the hares dispersed in northern Italy, and possibly of a more ancient origin. In fact, these territories harbour several taxa of mammals that differ substantially from their northern counterparts, i.e., the Roman mole, the Apennine chamois, the red fox along with the snow vole, and the Italian roe deer (Fрати et al. 1998; Lorenzini et al. 2002). Recent morphometric (Palacios 1996; Lo Valvo et al. 1997; Riga et al. 2001, 2003) and genetic (Pierpaoli et al. 1999, 2003) analyses have confirmed the taxonomic validity of *L. corsicanus*, attesting at the same time its present occurrence in south-central Italy, on Corsica and Sicily (Angelici and Luiselli 2001).

The European hare, *L. europaeus* Pallas, 1778. The European hare is a continental faunistic element characteristic of the Palaearctic Biogeographical Region (cf. Corbet 1978). There is no fully convincing evidence for the importation of this hare on any islands before the Early Bronze Age (Masseti 2003a; Fig. 1). In the light of recent archaeozoological evidence, in fact, the earliest relevant documentation appears to come from the eastern Mediterranean basin from the islands of Crete (Reese 1995; Jarman 1996) and Amorgos (Trantalidou 2000). The existence of the lagomorph in insular environments has been documented by classical authors, such as Homer (*Odyssey*, IX, 116–124) and others. Xenophon (5th century B.C.), in his *Kinegeticon*

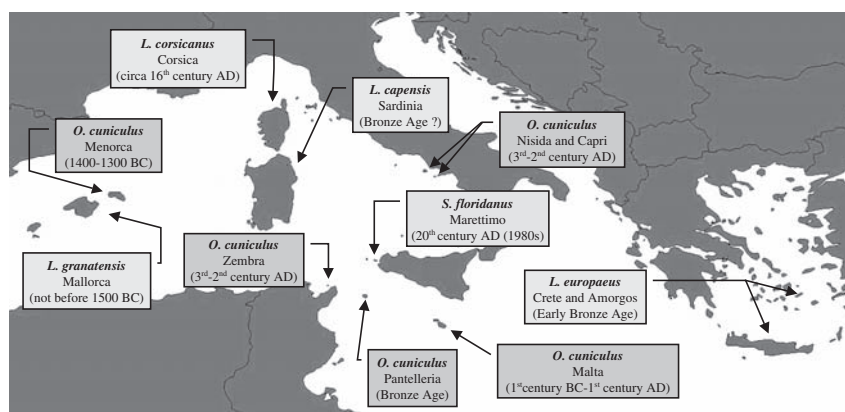


Fig. 1 Earliest recorded introductions of hares, European rabbit, and Eastern cottontail onto the Mediterranean islands

(24–26), observed that hares were particularly abundant on islands because predators such as foxes and eagles occur less frequently than on the mainland. The ancient practice of releasing hares on islands, considering the latter as natural enclosures, was maintained up to historical times in the *leporaria* of the Roman period (Varro, *De re rustica*, III, 12, 1; Bodson 1978) and the Middle Ages (Masetti 2003a). The European hare presently occurs on about 50 islands from the Central Mediterranean basin to Cyprus (cf. Averianov et al. 2003). Most of these islands (93%) are localized in the eastern basin and 71% are larger than 50 km². In the second half of the 20th century, the introduction of the species on Sardinia and Sicily has failed (Lo Valvo et al. 1997). The European hare has become extinct recently on at least five Greek islands: Sifnos (western Aegean Islands), Delos (Cycladic Archipelago), Paximada (Dionysades Islands), Astypalaia (Dodecanese), and Lemnos (north-eastern Aegean Islands). On the other Aegean islands, populations of European hare of ancient and/or modern introductions are today reported from several islands, such as Milos, Naxos, Amorgos, Crete, Karpathos, Rhodes, Ikaria, Samos, and others (Masetti 2003a).

Throughout most of the 19th and 20th centuries, however, there was a widespread practice among scientific explorers to bring home an excessive number of subspecies from their explorations of the Mediterranean islands. These authors often classified many of the insular populations as geographic forms, almost entirely on the basis of arbitrary criteria and the examination of scattered materials. Based on the data given in literature, the various subspecies of the insular hares are distinguished by the coat patterns and by the size of the body and skull. Therefore it is logical that this led to a multiplication of forms which now, however, demand better taxonomic and genetic definition. In this respect, we should therefore consider the extant taxonomic treatment on the part of the international scientific community of the lagomorphs of the Eastern Mediterranean islands, such as *L. e. creticus* Barrett-Hamilton, 1903, from Cephalonia (Miller 1912), Crete (Bate 1906 and 1913), and several small islets off Crete, including Gavdos and the Dionysades Islands (Niethammer 1992), *L. e. ghigii* (De Beaux, 1927), from Astypalaia (De Beaux 1927 and 1929), *L. e. carpathous* (De Beaux, 1929), from Karpathos (De Beaux 1929), *L. e. rhodius* (Festa, 1914), from Rhodes (De Beaux 1929; von Wettstein 1942), and *L. e. cyprius* (Barrett-Hamilton, 1903), from Cyprus (Ellerman and Morrison-Scott 1952).

Iberian hare, *L. granatensis* Rosenhauer, 1856. Endemic to the Iberian Peninsula (Palacios 1983), the Iberian hare is distributed throughout most of the territories of Portugal and Spain and also occurring at present on the Balearic island of Mallorca (Alcover 1988; Garcia-Perea and Gisbert 1999; Alves and Niethammer 2003). It was also formerly dispersed on Ibiza, where it is now extinct (Garcia-Perea and Gisbert 1999). Archaeological evidence documents the appearance of hares on the Balearics not before the Talayot culture (Alcover 1988), which flourished on these islands from 1500 B.C. to 500 B.C. (cf. Pericot Garcia 1972; Fig. 1). The earliest remains of the hare have

been provided by the excavation of the site of S'Illot, on Mallorca (Uerpmann 1971). In very recent times, the Iberian hare was also introduced onto Corsica, where there is however no evidence that the species established a population (Garcia-Perea and Gisbert 1999).

Sardinian hare, *L. ("capensis") mediterraneus* Wagner, 1841. In the light of recent genetic and morphometric research, the hare dispersed presently on Sardinia belongs to the subspecies *L. ("capensis") mediterraneus* (Trocchi et al. 2003). Thus, the geographical origin of this insular population might be to refer to the southern continental shores of the Mediterranean basin, from where hares might have been introduced onto Sardinia in ancient times. In fact, there is data that show that Sardinian hares are closely related to hares in northern Africa (Pierpaoli et al. 1999; Alves et al. 2003). There is, however, no archaeozoological evidence of the importation of hares on the large Mediterranean island prior to the Bronze Age (Fig. 1). In fact, the discovery of a tibia of a hare at the site of Sierra Nedda (Sorso, Sassari) attests the occurrence of the lagomorph on the island for the first time (Wilkens 2000). Unfortunately, this piece comes from a level which is disturbed by the presence of black-figure pottery and hence its dating to the Bronze Age is not certain (cf. Rovina 1986), even though the appearance of the hare on Sardinia is of a period that is quite early (Wilkens and Delussu 2003).

Mountain hare, *L. timidus* L., 1758. This taxon is characteristic of the northern Palaearctic Region (Sulkava 1999). At lower European latitudes, the natural distribution of this hare comprises only the Alpine mountain arch. The species seems to have been also reported from Pleistocene insular fossil deposits, such as Grotta dei Colombi, on the island of Palmaria (La Spezia, north-western Italy) (Regalia 1893; Cigna 1967). The appearance of the same taxon among the fossil fauna provided by the excavation of the Grotta di Reale (Porto Azzurro) on the island of Elba (Del Campana 1910; Malatesta 1950–1951) is to be referred to a Late Middle or Late Pleistocene chronology (cf. Rustioni and Mazza 1993). No evidence is, however, available for the occurrence of mountain hares on Mediterranean islands in historical times, although during the 19th and the 20th centuries the taxon *L. timidus* was often erroneously recorded from several islands of the Tuscan Archipelago (Lanza 1970), such as Pianosa (Zuccagni-Orlandini 1842), and Elba (Branchi 1839; Damiani 1923). These two latter islands are today characterised only by the occurrence of *L. europaeus*, introduced in the 20th century (De Marinis et al. 1996; Masseti 2003b).

Islands for Rabbits and Cottontails

European rabbit, *O. cuniculus* (Linnaeus, 1758). This species is regarded as a post-glacial endemism of the Iberian Peninsula (Rogers et al. 1994; Callou 2003; Kaetzke et al. 2003). Thus, the spread of this taxon is the most

important migration in Western Europe from an ancestral area restricted to these territories. This spread resulted from exchanges between human societies from the prehistory until the early Middle Ages (Callou 2004; Fig. 1). The earliest recorded introductions of rabbits onto the Mediterranean islands date back to the second half of the 2nd millennium B.C. (1400–1300 B.C.) when this lagomorph was apparently imported to Menorca, in the Balearic Archipelago, by ancient settlers from the Iberian Peninsula (Sanders and Reumer 1984). In the Central Mediterranean basin the subfossil evidence for the introduction of the species dates to no earlier than the 3rd-2nd century A.D., since remains of rabbits have been provided by the archaeological exploration of the islands of Nisida and Capri, in the Gulf of Naples (Italy), and Zembra in Tunisia (Barrett-Hamilton 1912; Vigne 1988b; Albarella 1992; Flux and Fullagar 1992; Flux 1994; Callou 2003; Kaetzke et al. 2003). Recent archaeozoological evidence, however, suggests an earlier importation of the lagomorph, comprised between the 1st century B.C. and the 1st century A.D., in the case, for example, of the sanctuary of Juno at Tas Silg on Malta (J. De Grossi Mazzorin, personal communication) or, at least, to the Bronze Age for the site of Mursia on the island of Pantelleria, in the Sicilian Channel (Italy) (Wilkens 1987). Rabbits were probably not imported onto the Eastern Mediterranean islands before the end of the Classical period and/or the beginning of the Middle Ages. This can be also observed in the lack of toponyms in the Eastern Mediterranean basin. Among the other elements supporting the theory of a recent historical introduction of the rabbit onto the latter territories, we can consider the fact that Turkish people still refer to the species as the *ada tavscan* (“hare of the islands”). In the course of the present study it was possible to report the occurrence of the European rabbit from at least 150 islands, localized in the whole Mediterranean basin. Almost half of the islands (53%) are smaller than 5 km². The species is also present on islets as small as 0.02 km² (i.e., Isola delle Femmine, northern Sicily), therefore it is really a successful colonizer of the Mediterranean islands. In very recent times, the rabbit became extinct on a few islands of the western Mediterranean: i.e., Frioul, France; Mezzomare and Lavezzi, Corsica. On the two latter islands, it disappeared in 1977 due to the spread of myxomatosis (Flux and Fullagar 1992; Vigne et al. 1994). To preserve the insular biological diversity, the species has been subject of several attempts of eradication in the course of the last decade. The only case of eradication carried out in the Mediterranean basin concerned the archipelago of Columbretes, Spain (Jimenez 1994). A total of 175 individuals was eradicated from the island of Columbrete Grande (14 ha), where their former occurrence drastically changed the climax community *Chamaeropo humilis-Rhamnetum lycioidis*. It was possible to report the coexistence of the European hare and the European rabbit from several Greek islands, such as Aegina (Saronic Gulf), Gadaironisi, Theodoru, and Koufonisi (circum-Cretan islands), Paros, Andros, Milos, Leros and Tinos (Cyclades), Kos (Dodecanese), Lesbos and

Fourni (north-eastern Aegean Islands). Among these islands, only Theodorou and Gadaironisi, off the northern and the southern shores of Crete, respectively, are smaller than 5 km².

Eastern cottontail, *S. floridanus* (J.A. Allen, 1890). This is a native species to the Nearctic Region, where its natural distribution occurs over broad geographic provinces from Canada to north-western South America (Chapman et al. 1980; Chapman and Ceballos 1990). Eastern cottontails have been widely transplanted beyond the territories of their natural distribution in North America and Europe. In the Old World, the species has been introduced to France, where it is now extinct, and as well as to Italy (Lapini 1999). In Italy, the earliest evidence of the occurrence of the lagomorph dates back to 1966 (Doria 1991; Spagnesi 2002; Andreotti et al. 2001), and populations of cottontail are today dispersed in Piedmont, Friuli-Venezia Giulia and Tuscany (Lever 1985; Lapini 1999; Spagnesi 2002; Masseti 2003b). The only known attempt for the introduction of the species onto Mediterranean islands seems to have been performed on Marettimo, in the Egadi Archipelago (north-western Sicily) during the 1980s, but there is no evidence that these animals originated any local population (Zava 1992; Fig. 1).

Concluding Remarks

Together with the species already involved in the process of domestication, a variety of wild species were also brought onto the Mediterranean islands since Neolithic times, including shrews, hedgehogs, mice, spiny mice, dormice, foxes, weasels, martens, badgers, cats, deer and, last but not least, hares and rabbits. It is not immediately apparent why man should have wanted to introduce all these animals. This phenomenon can only be explained by considering each case individually (Masetti 1998). The evidence suggests, for example, that not all of the supposedly tamed and/or semi-domestic herbivores that were imported onto the islands may have been exploited in the same way, some of them being destined to breed in conditions of captivity and others in a free-ranging state while others still could have returned to the wild after their introduction, being subsequently hunted by man as fully established wild game (Masetti 1998). In fact, the appropriation to hunting (“*kynegitisation*”) might be a component of Neolithisation, just as is animal domestication (Vigne 1993). While some species were suitable for breeding, others were suitable for hunting. This is one way of simplifying management problems, considering the islands as natural enclosures and allowing the wild animal populations to derive their food supply directly from the carrying capacity of the natural environment (Masetti 1998). This was apparently the only way to exploit the natural resources of territories that could not be cultivated and were

generally unattractive economically (Masetti and Zava 2002a, 2002b). Some of the species more adaptable to the specific environmental conditions of even small and barren islands, such as hares, and later rabbits, were brought by sailors and released on islands so that they could breed and provide a source of fresh meat that would be readily available for the passengers of ships (Masetti 2003a). In fact, hares can survive on islands that do not exceed a surface area of 3–3.5 km². Rabbits can survive on even smaller islands than hares, as small as 0.02 km². For centuries, if not for millennia, several of the Mediterranean islands were better known for their richness in certain zoological species, most useful as a source for meat than for their faunal repertoire in general (Masetti 2002), and this is still reflected even now in the names of many of them, especially some of the smaller ones, such as Conejera (Spain), Isola dei Conigli (Italy), Conigliera (Tunisia), Levrera (Croatia), and others. Apart from the former introductions of hares and rabbits documented by the modern scientific research, during the last 4,000–3,500 years, this phenomenon could have taken place on a large number of other islands in the whole Mediterranean basin. Thus, the data reported in this work on the extant insular distribution of hares and rabbits may be still far from conclusive, especially in regard to their present occurrence on the islands of the Adriatic gulf, Ionian Sea, and the Aegean Sea. The invasion of Mediterranean islands by exotic taxa is currently viewed as one of the most important causes of the loss of biodiversity (Gippoliti and Amori 2002; Courchamp et al. 2003). Rabbits, for example, can damage vegetation, accelerate soil denudation and erosion, and can be ultimately responsible for the decline or extinction of several reptile and bird species (e.g., Courchamp et al. 2003; Chapuis et al. 2004; Genovesi 2005). Therefore, in regard to the vulnerability of the ecosystems of the Mediterranean islands, it would be advisable, from both a scientific and a cultural point of view, to seriously consider the eradication of the alien species of very recent invasion, as it was in the case of the rabbits of Columbrete Grande. But this leaves the question of how to treat the allochthonous populations of certified ancient anthropochorous origin that represent invaluable historic documents. The study and observation of these populations enable us to acquire fundamental information about the progress of man through the millennia of his process of civilisation; they therefore deserve to be protected, considering them in terms of a veritable “cultural heritage” (Masetti 2002).

Acknowledgements: We would like to express our appreciation and gratitude to the following friends and colleagues for their suggestions and assistance as we were preparing this chapter: Umberto Albarella, Department of Archaeology, University of Sheffield; Cécile Callou and Jean-Denis Vigne, Muséum National d’Histoire Naturelle, Paris; Jacopo De Grossi Mazzorin, Dipartimento di Beni Culturali, University of Lecce; Piero Genovesi e Valter Trocchi, Istituto Nazionale per la Fauna Selvatica, Ozzano dell’Emilia (Bologna); Barbara Wilkens, Dipartimento di Storia, University of Sassari.

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