ARTICLES

HOLOCENE ENDEMIC AND ANTHROPOCHOROUS WILD MAMMALS OF THE MEDITERRANEAN ISLANDS

Marco MASSETI*

Summary

In the Quaternary period, the mammalian fauna found on Mediterranean islands differed considerably from contemporary continental wildlife. The insular assemblages were characterized by species, which evolved in a rather peculiar way, of which significant examples can be found on the Balearics, Corsica, Sardinia, the Tuscan archipelago, Sicily, Malta, Crete, several Aegean islands, and Cyprus.

Apart from certain native taxa being identified from a few islands like Sicily, Crete and (perhaps) Cyprus, the almost complete absence of endemic species from the actual mammal fauna on the Mediterranean islands is quite surprising. Today the existing populations of non-flying, terrestrial mammals, are almost exclusively dominated by continental taxa whose appearance on the islands seems to be directly related to human intervention. Thus, the exploitation of natural resources on Mediterranean islands was a long-lasting process, beginning before the Neolithic period and lasting until historical times. Islands often represented natural enclosures where allochthonous species had been kept and bred since prehistory in a free-ranging state, while man exerted his control on the animal numbers through hunting being justified as occasionally demanded.

Key Words

Mediterranean islands, Holocene, Endemic and anthropochorous mammals.

Résumé

Mammifères sauvages endémiques et antropochores des îles méditerranéennes à l’Holocène.

Au Pléistocène, les mammifères des îles de la Méditerranée différaient considérablement de leurs contemporains du continent. Les ensembles faunistiques insulaires étaient caractérisés par la présence d’espèces ayant subi une évolution particulière : les îles Baléares, la Corse, la Sardaigne, l’Archipel Toscan, la Sicile, Malte, la Crète, les îles Égéennes et Chypre en offrent des exemples particulièrement illustratifs.

Il est assez surprenant de constater que toutes ces espèces endémiques autochtones sont absentes de la faune actuelle des îles méditerranéennes, à l’exception de quelques très rares taxons limités à la Sicile, à la Crète et peut-être à Chypre. À présent, ces peuplements de mammifères terrestres non volants sont largement dominés par des taxons continentaux, dont l’apparition sur les îles semble résulter directement de l’intervention humaine. Il apparaît donc que l’exploitation des ressources naturelles des îles méditerranéennes, initiée durant les phases pré-néolithiques et poursuivie jusqu’aux périodes historiques, s’est déroulée sur la longue durée. Les îles constituent souvent des territoires naturels à l’intérieur desquels les espèces allochtones sont préservées.

Mots clés

Îles médiiterranéennes, Holocène, Mammifères endémiques et antropochores.

* Istituto di Antropologia dell’Università di Firenze, via del Proconsolo 12, 50122 Firenze, Italia.
Introduction
According to paleontological evidence, several of the late Pleistocene mammalian faunas of the Mediterranean islands differed considerably from contemporary continental faunas (Azzaroli, 1971, 1977; Sondaar, 1971, 1977). The insular mammalian assemblages were characterized by a very low taxonomic diversity. 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 insectivores and rodents. These modifications are generally supposed to be above all a consequence of a genetic isolation from continental populations, a quantitative and qualitative reduction in food supply, an alteration of intraspecific competition, the lack of large carnivores, and concerning the micromammals, also endothermic adaptations. Among the fossil Mediterranean island faunas, examples from Balearics, Corsica and Sardinia, the Tuscan archipelago, Sicily, Malta, Crete, several Aegean islands, and Cyprus are significant. Each of these mammalian compositions, even though they were represented by few taxa, were repeated monotonously on most of the islands. They displayed peculiar endemic elements which differed extremely from one island to the other (Masseti, 1993). However, if we look at the present non-flying terrestrial mammals of these islands, we can hardly find any of the endemic elements that characterized the Pleistocene faunal structures. Although with few exceptions - constituted mainly by certain edemic taxa, such as few micromammals still reported from Sicily, Crete and, perhaps, Cyprus -, the island faunas display virtually the same species composition. It can be stressed that neither the repertoire of the modern species in Pleistocene deposits is traced, nor, all things considered, does it seem likely that they have reached the islands by swimming, jumping onto floating logs or other so-called sweepstake routes (Groves, 1989).

Today the terrestrial non-flying mammalian wild fauna of most of the Mediterranean islands displays an unquestionably homogeneous composition of elements. Its structure is balanced by the presence of carnivores. It mainly consists of species that are more or less common to the present fauna of all the Mediterranean islands, and shows a generic continental origin (Alcover, 1980; Sanders and Reumer, 1984; Blondel and Vigne, 1993; Masseti, 1993) influenced by the faunistic composition of the nearest mainland.

Three out of eight Mediterranean islands studied here are still reputed to be inhabited by endemic mammalian species (37.5%) (tab. 1). This corresponds to 10.25% of the total of all the species occurring on the eight islands. The percentage decreases, however, up to 5.12% if one considers the representatives of the genus Acomys from Crete and Cyprus as subspecific forms.

Endemic and non-endemic insular mammals
Regarding Corsica and Sardinia, Azzaroli, as early as 1962, noted the inconsistency of the island fauna structures between Late Pleistocene and Holocene, observing that the arrival of the species occurring at present on the two islands has been most probably related mainly to the appearance of man. Baccetti (1964) expressed a similar opinion about the origin of the modern Sardinian mammals. On the basis of the lack of fossil evidence for sheep and goats on the islands, Payne (1968) and Poplin (1979) suggested that the mouflons and wild goats, still occurring on some Mediterranean islands, are ancient feral animals descending from captive specimens taken there since early Neolithic times. Although there is some evidence recorded from Sicily (Ambrosetti, 1968), Cyprus (Simmons, 1988, 1991; Swiny, 1988), Corsica (Vigne and Desse-Berset, 1995), and perhaps Sardinia (Sondaar et al., 1984, 1986) of pre-Neolithic human colonization which possibly (Vigne, 1996) overlaps with the existence of endemic mammals, it was especially from Early Neolithic periods onwards that most of the Mediterranean island faunas began to show evidence of human exploitation, enhancing a gradual extinction of the endemic species (Vigne, 1987; Vigne and Valladas, 1996). A certain amount of the Pleistocene species persisted beyond the end of the Pleistocene to become extinct during the Holocene. As far as is known today, the data available for the Mediterranean islands point to faunal extinction being the result of the human activities of land clearance and the introduction of allochthonous animals. Since the 1970s, many zooarchaeological studies have been carried out on the poor and unbalanced island faunas. Especially due to the research by Alcover (1980) and Alcover et al. (1981) on the Balearics, Vigne (1987, 1988a, 1988b, 1990, 1992) on Corsica and Sardinia (Vigne and Alcover, 1985), and Davis (1984, 1987, 1989, 1993) on Cyprus, a reconstruction of their ancient variations became possible. In fact, it is above all on the islands that the impact of extraneous elements on the unspoilt ecological system can be identified and its chronology specified with sufficient precision, due to the evidence it left and the relative rapidity of the consequences it produced (cf. Elton, 1958; Azzaroli, 1977; Watson et al., 1977; Davis, 1984). Archaeological evidences hint to the appearance of allochthonous species extraneous to the Pleistocene fauna, such as the hare, the fox, the cat, the boar, the deer, the ox, the sheep, the goat, and several micromammals in Neolithic periods. All these mammals can be considered to be imported by man, except those

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>Mallorca (1)</th>
<th>Menorca (2)</th>
<th>Corsica (3)</th>
<th>Sardinia (4)</th>
<th>Sicily (5)</th>
<th>Crete (6)</th>
<th>Rhodes (7)</th>
<th>Cyprus (8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erinaceus europaeus</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Erinaceus concolor</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Atelerix algirus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Hemiechinus auritus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Crocidura russula</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Crocidura suaveolens</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Crocidura zimmermanni</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Suncus etruscus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Lepus granatensis</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Lepus corsicanus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Lepus capensis</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Lepus europaeus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Oryctolagus cuniculus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Hystrix cristata</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Myoxus glis</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Eliomys quercinus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Muscardinus avellanarius</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Microtus savii</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Rattus rattus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Rattus norvegicus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Apodemus mystacinus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Apodemus sylvaticus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Mus domesticus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Mus spretus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Acomys minous</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Acomys nesiotes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Vulpes vulpes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>o</td>
<td></td>
</tr>
<tr>
<td>Mustela nivalis</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Martes foina</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Martes martes</td>
<td>n</td>
<td>n</td>
<td></td>
<td>?</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Meles meles</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Genetta genetta</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Sus scrofa</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Dama dama</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Cervus elaphus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Oris aegagrus</td>
<td>n</td>
<td>n</td>
<td></td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>39</td>
<td>12</td>
<td>11</td>
<td>16</td>
<td>19</td>
<td>18</td>
<td>17</td>
<td>12</td>
</tr>
</tbody>
</table>

which reached those islands that were joined to the nearest land-masses during the Late Pleistocene. Through this introduction of continental terrestrial mammals, the autochthonous faunal elements, represented mainly by endemic forms, were gradually replaced. As far as is known today, less than one-fourth of the mammalian species found in the continental Mediterranean region have been described as endemic to the area (Cheylan, 1990), including very peculiar elements, such as Macaca sylvanus L., 1758, and Oryctolagus cuniculus (L., 1758). The number of the endemisms drastically decreases if we consider the composition of the extant mammalian fauna on islands. Recent genetic and morphometric analyses show that only a few endemic micromammals still survive on the Mediterranean islands, and that these can be referred to a few species of shrews and, perhaps, of spiny mice.
The Sicilian white-toothed shrew (fig. 1)

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 Crocidura sicula Miller, 1912 (Vogel et al., 1989). This taxon is a Sicilian-Maltese endemic, distributed on Sicily, Levanzo, Favignana, Marettimo, Ustica and Gozo, and it is considered being extinct on Malta and Lampedusa (Vogel et al., 1990; Sarà, 1995, 1996). Much evidence convincingly indicate that this is a probable survivor from the Pleistocene, but perhaps not related to the endemic 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). Further investigations are however needed to define better the phylogenetic relations between these two Sicilian shrews. Recently, C. sicula has been identified as a conspecific form of C. canariensis (Hutterer et al., 1987), endemic to the Canary islands (Sarà, 1995).

The Cretan white-toothed shrew

Crocidura zimmermanni Wettstein (1953) has been recognized by Reumer (1986) as a relic of the Early and Middle Pleistocene group of European Crocidura species, and of the Pleistocene Mediterranean fauna. Fossils of this species have probably been present since the Early Pleistocene. Crocidura has been found in association with those endemic mammals that lived on Crete during the Pleistocene. It regressed after the man-made introduction of those species which characterize the current fauna (Reumer and Payne, 1986). Today this shrew is not known anywhere outside of Crete (Reumer, 1996) and it is therefore considered endemic to this island (Vogel et al., 1990; Reumer, 1996).

It can be assumed that these two shrews are the last remnants of a vanished world. As observed by Reumer (1986, 1996) for the Cretan shrew, both of them are relics in two senses: firstly, they are the direct descendants of the Pleistocene group of Crocidura species that have disappeared from Europe and have been replaced by the present living species; secondly, they are the only known survivors of the wealth of endemic species that were found in most of the Mediterranean islands during the Pleistocene.

Spiny mice on Mediterranean islands

The Cretan spiny mouse, Acomys minous (Bate, 1906) (fig. 2), and the Cypriot spiny mouse, Acomys nesiotes (Bate, 1903) have also been described by some authors as endemic to the islands (Dieterlein, 1963; Matthey, 1963; Spitzenberger, 1979; Macholán et al., 1995). But against

Fig. 1: The small island of Ustica, off the north-western Sicilian shores, is inhabited by a melanistic population of the Sicilian white-toothed shrew, Crocidura sicula (Photograph by M. Sarà).
their supposed endemity, however, there is the lack of any Pleistocene fossil of the genus recorded so far from the islands. Genetic analyses demonstrate the vicinity of the Cretan and of the Cypriot spiny mice to the *A. cahirinus-dimitiadus* group, distributed in Sinai, the Near East, and southwestern Asia (Macholán et al., 1995). Except for *A. russatus* Wagner, 1840, which occurs from Egypt to eastern Arabia, the members of this group are the only spiny mouse taxa distributed outside the African continent. The assumption of an occasional importation on Crete and Cyprus of *Acomys* carried out by man from the nearest mainland has been also recently strengthened by the results of cytochrome b (non coding region of mtDNA) analyses. These suggest that the two island spiny mice possibly belong to the species *A. cahirinus* (Desmarest, 1819) *sensu stricto* (Barome et al., 1998). In fact, the low divergence between the sequences from *Acomys* from Cairo, Crete, Cyprus and Turkey suggests that the colonization of the islands is likely to be recent, and this could be explained as a dispersion due to humans (Barome et al., 1998). It is also convenient to note that in the Mediterranean region the spiny mouse has been found within human settlements, where it is as a rule sympatric with *Mus musculus* L., 1758, and *Rattus rattus* (L., 1758), often behaving as a true commensal with man (Tchernov, 1991). In the Levant, according to Tchernov (1984, 1991), the abrupt increase in the frequency of *Acomys cahirinus* since the Natufian culture layers may be explained as a rapid adaptation of the species to commensal life around human settlements.

**On the areas of provenance of the allochthonous mammals of Cyprus**

Interdisciplinary research, based on zoological, archaeological, paleontological, zoo-archaeological, biogeographical, paleoethnological, ethnological and ethnozooological evidence, provide important clues as to where a species was originally distributed. Thus, in some cases it is possible to ascertain the probable area of the original continental distribution of the allochthonous species occurring today on the Mediterranean islands. One striking example is the introduction of the modern white-toothed shrew, *C. suaveolens praecypria* (Reumer and Oberli, 1988) to Cyprus which...
Table 2: Distribution-types of the non-flying terrestrial wild mammals reported from Cyprus since Neolithic times (data from: Storrs and O’Brien, 1930; King, 1952; Harrison, 1964; Atallah, 1978; Spitzengerber, 1978, 1979; Lehmann and Nobis, 1979; Nobis and Lehmann, 1979; Davis, 1984, 1989; Harrison and Bates, 1991; Held, 1993; Hadjisterkotis and Masala, 1995; Macholán et al., 1995). * This includes all the species common to the boreal Euroasiatic region, the Mediterranean region and the Saharo-Sindian region.

<table>
<thead>
<tr>
<th>Endemic species</th>
<th>Palaeartic pluriregional species*</th>
<th>Irano-Turanian and Indo-Asiatic species</th>
<th>Human commensal species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemiechinus auritus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crocidura suaveolens</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suncus etruscus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Felis silvestris</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mustela nivalis</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vulpes vulpes</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sus scrofa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dama dama mesopotamica</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervus elaphus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ovis gmelini</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capra aegagrus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepus europaeus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mus domesticus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rattus ratti</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rattus norvegicus</td>
<td>u</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acomys nesiotes**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td>16</td>
<td>8</td>
<td>4</td>
</tr>
</tbody>
</table>

**Recent genetic analyses indicate the vicinity of the Cypriot A. nesiotes to the A. cahirinus-dimitiadus group, distributed in Sinai, the Near East, and southwestern Asia (Macholán et al., 1995).

took place long before the arrival of the species on Crete. The origin of the extant Cypriot shrew might not lie in Anatolia, but elsewhere in the Eastern Mediterranean region (Reumer and Oberli, 1988). This ancient Levantine origin of the Cypriot shrew reinforces the hypothesis made by King (1952), Zeuner (1958) and Ducos (1965), and followed by Davis (1984), about the Near-Eastern origin of another mammalian species, the Mesopotamian fallow deer, Dama dama mesopotamica (Brooke, 1875), documented since the Pre-Pottery Neolithic (Guilaine et al., 1996) and Aceramic Neolithic (Davis, 1984) throughout the Chalcolithic and Bronze Age contexts of the island (Croft, 1991). The lack of any archaeological evidence on Cyprus for the origin of its Neolithic human settlers (cf. Le Brun, 1989) allows their origin to be referred to the closest area of the “natural” Early Holocene distribution of the Mesopotamian fallow deer, which is reported to be confined to the Levant and Mesopotamia, excluding Anatolia (Uerpman, 1981).

Apart from the white-toothed shrew, the present-day mammalian fauna of Cyprus includes another species characteristic of the Levantine region, the long-eared hedgehog (Hemiechinus auritus Gmelin, 1778), the only species of hedgehog occurring on the island (Spitzengerber, 1978), and which is not recorded from Anatolia (Harrison and Bates, 1991) (tab. 2). The extant Cypriot mammalian fauna also comprises another species of eastern origin, the Asiatic mouflon (Ovis gmelini Blyth, 1841), also introduced by man to the island since the Pre-Pottery Neolithic (Guilaine et al., 1996). The origin of C. suaveolens and D. d. mesopotamica seems to be the Eastern Mediterranean region, and probably the Levant area, whence they must have been imported since prehistorical times by the ancient human settlers of Cyprus. On the basis of current evidence, the present non-flying terrestrial mammalian fauna of Cyprus seems to have more elements in common with the extant fauna of the Levant than with that of southern Anatolia.

The prehistorical artificial diffusion of wild goats and mouflons in the Mediterranean region

Free-ranging populations of wild sheep and goats now inhabit several of the Mediterranean islands (fig. 3). They featured more or less the same morphological patterns, respectively, of the Asiatic mouflon and the bezoar goat (Capra aegagrus Erxleben, 1777) (Zimmermann, 1952; Toschi, 1953; De Beaux, 1955; Couturier, 1959; Kahmann, 1965; Payne, 1968; Poplin, 1979; Clutton-Brock, 1981; Masseti, 1981; Poplin and Vigne, 1983; Davis,
on the Mediterranean islands escaped from their guardians' control, giving origin to the free-ranging population, the descendants of which persist until today. 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 made difficult by the fact that the first domestic animals did not differ considerably from their wild counterparts. Analyses of the available osteological materials suggest a low level of morphological difference between the extant caprines of the Mediterranean islands and their prehistorical relatives. In fact, if any difference occurs, it seems to be limited more to the effects of domestication, such as the modification of the morphology of the horn cores (Boessneck, 1962; Vigne, 1988b) and of the size, than to other patterns. As observed by Davis (1984, 1989), the modern Cypriot mouflon is slightly smaller than its supposed ancestor - the Neolithic sheep - which may be due to island dwarfing. Paleontological data confirm that, on islands, dwarfism can develop in just a few millennia (Azzaroli, 1977). Still regarding Cyprus, however, throughout the periods of occupation of Khirokitia and Cape Andreas-Kastron, none of the three species - goat, fallow deer and boar - underwent any remarkable change in size (Davis, 1989), whereas it has been registered a small size increase in sheep (Davis, 1994). Measurements of fallow deer bones found in Vrysi (Legge, 1982) indicate that fallow deer did not change in size at least until the Ceramic Neolithic. The measurements of the cranial capacities of different insular population of extant wild
sheep and goats indicate that they are somewhat lower, on average, than those of their wild continental counterparts (Groves, 1989).

The possibility of studying the areas of provenance of the exotic elements is very complicated, partly because there might have existed special forms of "contamination" through the mediation of the coastal areas of the mainland. 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 oriented artificial diffusion of sheep and goats in the Mediterranean region seems to be quite independent from the cultural context in which it appears for the first time: Pre-Pottery and Aceramic Neolithic respectively in the eastern Mediterranean and in the Aegean region (8th-7th millennia BC), and Early Neolithic characterized by the production of impressed ware in the central and western Mediterranean, with a sort of Mesolithic enclave in southern France and in the Pyrenees (6th millennium BC) (Masseti, 1997b). To a certain extent, this diffusion also seems to contrast with the diffusionist model of the Neolithic colonization of Southern Europe (Ammerman and Cavalli-Sforza, 1984), due to the fact that proceeding toward the west, the evidence of the first introduction of sheep and goat is not accompanied by the contemporary diffusion of cultural elements of eastern origin, but it appears at times associated with different cultural stages and facies, characterized by the absence or the production of ceramics. For example, the Early Mediterranean Neolithic culture, associated with the appearance of tamed caprines and with the production of Cardial ware in the Western Mediterranean region, has been recognized as a locally developed cultural stage and not as a culture of Near Eastern origin (cf. Fagan, 1989).

The earliest known Ovis fossils from Sardinia are reported from Corbeddu Cave and have been referred to the 6th millennium BC (Sanges, 1987; Masseti and Vianello, 1991). This date coincides with the advent of the Early Neolithic culture of the Mediterranean region (6th millennium BC) on the island and the appearance of other continental mammals, perhaps including the red deer (Cervus elaphus L., 1758) and the fox (Vulpes vulpes L., 1758). According to Hartl et al. (1995), recent analyses of the mtDNA of several European red deer populations have demonstrated the similarity between the extant Sardinian deer and the deer of southern Bulgaria, possibly representing C. e. maral (Gray, 1850) (see Groves and Grubb, 1987). In addition, recent genetic evidence seems also to support the hypothesis that the extant Sardinian foxes are more related to eastern Europe populations than others (Frati et al., 1997). These findings, together with the discovery of more ancient osteological remains of red deer, mouflon and fox in the same archaeological contexts on Sardinia, may also suggest a common origin (Hartl et al., 1995; Frati et al., 1997, 1998). Thus it can be assumed that, around the 6th millennium BC, in certain parts of the Mediterranean, some kind of contact had already been established between the Near Eastern prehistoric cultures bearing tamed ungulates and, perhaps, foxes, and representatives of the Early Mediterranean Neolithic culture, producer of the Impressed ware. One could also suggest that it was definitely not a Neolithic colonization from the Near East that invested the central Mediterranean and imported eastern artiodactyls, since that culture was characterized as early as the 6th millennium by ceramics that were completely different from the Impressed ware.

It now appears sufficiently credible that up to the early Holocene, the Mediterranean sea increasingly represented less a barrier than a bridge (Uerpmann, 1979; Lewthwaite, 1987; Binder, 1989; Guilaine, 1994; Orliac, 1997), promoting and multiplying in a relatively short time the circulation of ideas, of merchandise, of faunal elements, and of human groups, which spread into new and different environments, and over time, in various ways, became grafted onto the autochthonous substratum.

Aspects of early husbandry in the Mediterranean islands

Man brought with him the animals he needed as economic supplies for the colonization of the new geographical areas. 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, red and fallow deer. It is necessary again to argue that these 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. This phenomenon can only be explained considering each case individually. The evidence 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, 1988a, 1995; Masseti, 1995). Synanthropic species, such as shrews and mice, in contrast, could well have been transported involuntarily by man, hidden within foodstuffs. Furthermore, ethnozoological enquiry documents that hedgehogs (Vigne, 1988a) and dormice (Carpaneto and Cristaldi,
1994) were utilized as food, medicine or for other purposes from prehistorical times onwards. With respect to the exploitation of the imported animals, human behaviour might have differed as the circumstances suggested, moving from the basis either of the colonists’ economic needs or of the biological patterns of the different species exploited. As noted above, several of the Near Eastern large herbivores were of great economic importance in prehistory. Their biological patterns must have had some influence on related human behaviour. Not all of the tamed and/or semi-domestic ungulates that were imported into the islands might 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 and were subsequently hunted by man as fully established wild game. As early as 1976, Jarman summarized the prehistoric relationships between man and ungulates in six main patterns, basing his classification on human economic behaviour rather than on morphological and zoological criteria as follows: random predation, controlled predation, herd following, loose herding, close herding, and factory farming (Jarman, 1976). Regarding human behaviour towards ungulates imported on islands, however, Jarman’s first pattern of exploitation - random predation - was not fully appropriate, because it totally deviates aspects of “husbandry”, in the sense of an effective long-term economic strategy which favours the continued existence of both partners in the relationship. There is sufficient archaeological evidence from the Mediterranean islands for the other types of “husbandry” classified by Jarman (1976), such as factory farming, loose and close herding, and even controlled predation. According to Croft (1991), for example, the range of animals exploited during the Chalcolithic period on Cyprus shows continuity from the preceding Aceramic and Ceramic Neolithic periods. Caprines and pigs, both domesticated at the same time on the nearby mainland, were most probably kept in herds, but free-ranging populations may also have been hunted. As already noted, the Neolithic fauna of Cyprus also includes the Mesopotamian fallow deer, but it is unlikely that this species, also of great economic importance in Early Prehistoric Cyprus, was ever fully domesticated (Croft, 1991). Fallow deer seem to have made a relatively important contribution to man’s subsistence, and was possibly an animal that was released and hunted rather than a full domestic element. The prehistoric introduction of the other extant representative of the genus Dama, the European or common fallow deer, D. d. dama L., 1758, on islands such as Ayios Petros (Kyra-Panagya, Northern Sporades), Saligios (between Paros and Antiparos, Cyclades), Rhodes (Dodecanese), and Crete, in sufficient number to act as a breeding stock for the substantial population for which there is archaeological evidence (Masseti, in press) clearly argues for a high degree of control over the animals and for their sophisticated management (Jarman, 1982). Often the examination of the osteological elements provided by a prehistorical site, such as caves occasionally inhabited by man, seems to indicate that the animals were not slaughtered inside but outside the cave. Only certain parts of the carcass, mainly legs and limbs, were carried inside. The rarity of certain species in the excavation levels does not necessarily reflect a rarity of the animal themselves, because the larger pieces of meat may have been eaten outside the cave (Sampson, 1987). The bones of cattle, pig, sheep and goat provided by the Neolithic levels of Kalypthes Cave on Rhodes (Dodecanese archipelago, Greece), for example, derived from nearly all parts of the skeleton; variations in the representation of different parts of the skeleton could be purely the product of differences in the fragmentation, the survival, the recovery and the recognition of each anatomical element. It is likely, therefore, that these animals - which supposedly were kept in conditions of loose or close herding management - were killed and consumed in the vicinity of the cave (Halstead, 1987; Halstead and Jones, 1987). Among the deer material, in contrast, the best represented parts of the skeleton are the proximal humerus and proximal and distal femur. In this case it seems likely that particular joints of meat were selectively brought to the site probably from further afield (Halstead, 1987; Halstead and Jones, 1987), maybe from those areas of the island where the deer herds were previously released and then maintained in conditions of controlled predation.

In addition to Cyprus and Rhodes, the practice of keeping wild mammals as hunting game is also documented from other territories of the Eastern Mediterranean region, from prehistory up to protohistorical and early historical times. In Minoan Crete, for example, the local wild goat was regarded as a true game animal as it is shown by several artistic representations (Masseti, 1997a). In prehistorical and early historical Mediterranean cultures, iconographical sources furnish valid information that supports the paleontological and zooarchaeological data, and this also counts for the Minoan art. In case of a naturalistic representation, an artistic production might easily become an important source of paleo faunistic and paleoenvironmental evidence. In this regard, a sanctuary stone vase (rython: Middle Minoan II-Late Minoan I. about 1650-
1500 BC, Herakleion Museum) from the Minoan palace of Zakros, in eastern Crete, shows an interesting decorative motif: a peak sanctuary, on the roof of which a group of four wild goats is resting, probably ruminating (cf. Platon, 1971). The rendering of the morphological patterns of the artiodactyls is so accurate that they can be referred without doubt to the Cretan wild goat or agrimi, which presently survives in the White Mountains range (Lefka Ori; Masseti, 1997a). This Near Eastern continental species was introduced to Crete by man in early Neolithic times (Jarman and Jarman, 1968; Jarman, 1996), generating free-ranging populations that still persisted into Minoan periods (Masseti, 1997a, b). Osteological material recorded from the archaeological site of Festos document, however, the occurrence of two distinct forms of goat at least since the Terminal Neolithic (about 3,000 BC) on Crete (Wilkens, 1996). One of these is identical to the present agrimi, and was often represented pursued by dogs among the rocky landscapes of the island. The other one is characterized by morphological characters of a domestic race. According to Vigne (1993), the appropriation to hunting (kinegetisation) might be a component of neolithisation, just as is animal domestication: while some species were appropriate to breeding, others were appropriate to hunting.

Islands as natural enclosures. Concluding remarks

In the light of all this, it cannot be excluded that deer, as well as part of the caprines and the boars imported to the islands, could have been kept and bred since prehistory in a free-ranging state, while man exerted his control on the animal number through hunting being justified as occasionally demanded (fig. 4). This particular relationship between man and ungulates is not so far removed from husbandry patterns still adopted on many islands of the Mediterranean, where domestic sheep and goats are kept in free-ranging conditions. These animals belong to a number of owners who capture them as need arises. This is one way of simplifying management problems, considering the islands as natural enclosures and allowing the livestock to derive its food supply directly from the carrying capacity of the environment. In many of the Aegean islands the custom of keeping livestock in free-ranging

![Fig. 4: Several islets of the Aegean sea, such as Theodorou, Dia and Ayii Pantes facing the northern coast of Crete, are still employed as natural enclosures for the breeding of the Cretan wild goat, C. aegaros cretica SCHINZ, 1838 (Photograph by M. Masseti).](image)
conditions is still used not only in regard to domestic caprines, but also to other types of ungulates, for instance the horses of the island of Skyros, in the Northern Sporades (fig. 5). These small-sized horses possibly originated from very ancient introductions. They still graze and breed on the rocky plateaus of the island. As far as known today, they have been scantily employed as mounts due to their small size, that does not exceed the height of one meter at the withers. Until the 1960s, however, many of them were caught at harvesting time to be employed in threshing, and were then released again in the wild for the rest of the year (Coulentianou, 1981). According to Digard (1990), there is a category of domestic animals that are in a permanent condition of instable equilibrium between the domestic condition and the wild state, representing the relic of a very ancient breeding still adopted in several economically marginal areas of the world. To conclude, one may not overestimate the importance of the islands inhabited by free-ranging populations of herbivores, which represented living depositories of animal proteins available at any time along the marine routes of Antiquity since prehistorical periods. Indeed, some of the species, such as the hare and the goat, most adaptable to peculiar environmental conditions even of small islands were brought by sailors and left loose on islands so that they could breed and provide a store of fresh meat that would be readily available for the passengers of ships. As noted above, archaeological evidence of seafaring capability do exist since the pre-Neolithic period (Cherry, 1981, 1990, 1992; Vigne and Desse-Berset, 1995), and of the introduction of caprines on islands since the Pre-Pottery Neolithic (Jarman and Jarman, 1968; Davis, 1984; Halstead and Jones, 1987; Trantalidou, 1990, 1996; Guilaine et al., 1996), and of lago-morphs since probably the Bronze Age (Jarman, 1996), even underlined by reports of classical authors, such as Homer (Odyssey, IX, 116-124) and others. Xenophon, in his Kinegeticon (24-26), observed that hares were particularly abundant on islands due to the lack of predators that occurred conspicuously on the mainland. This practice 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. For the same reasons,
rabbits are now found on several Mediterranean islands, in northern Europe and in many other parts of the world (Clutton-Brock, 1981; Flux and Fullagar, 1992; Flux, 1994; Callou, 1995).

This might be seen in contrast with the fact that for centuries these islands were better known for their richness in certain animals, most useful as a source for meat than for their faunal repertoire in general. This is reflected even in the names of several Mediterranean islands, especially some of the smaller ones, such as Conejera, Isola dei Conigli, Levrera, Cabrera, Caprara, Caprera, Capraia, Capri, Egadi islands, and Polyaigos.

Acknowledgements
This research was made possible by the financial support of the EEC Human Capital and Mobility Project CHRX-CT94-0597. I would like to express my appreciation and gratitude to the following friends and colleagues for their suggestions and assistance as I was preparing this paper: A. Azzaroli, P.-O. Barome, J. Clutton-Brock, F. Fanfani, P. Halstead, A. Legakis, F. Masini, P. Mazza, C. Peretto, D. S. Reese, M. Sanges, M. Sarà, S. Swiny, A. Trichas, B. Wilkens. Special thanks are due to S. J. M. Davis and J.-D. Vigne for the critical reading of the manuscript and for their suggestions.

Bibliography


ANTHROPOZOLOGICA, 1998 N° 28

DE BEAUX O., 1955.– Posizione sistematica degli stammecchi e capre selvatiche viventi (Capra Linneo, 1758) e loro distribuzione geografica. Atti dell’Accademia Ligure di Scienze e Lettere, 12: 1-110.


ELTON C., 1958.– The ecology of invasions by animals and plants. London: Chapman and Hall.


KOTSAKIS T., 1986.– Crocidura esui n. sp. (Soricidae, Insectivora) du Pléistocène de Spinagallo (Sicilie orientale, Italie). Geologica Romana, 23: 51-64.


MILLER G. S., 1912.– Catalogue of the mammals of Western Europe. London: British Museum (Natural History), 1020 p.


VIGNE J.-D., 1988a.– Apports de la biogéographie insulaire à la connaissance de la place de mammifères sauvages dans les sociétés néolithiques méditerranéennes. Anthropozoologica, 8: 31-52.


